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THE UNIVERSITY OF ALBERTA

THE PHYLOGENETIC RELATIONSHIPS OF THE SALMONIFORM FISHES BASED ON THE SUSPENSORIUM AND ITS MUSCLES

by

Robert Ross Garry Williams

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE PHYLOGENETIC RELATIONSHIPS OF THE SALMONIFORM FISHES BASED ON THE SUSPENSORIUM AND ITS MUSCLES submitted by Robert Ross Garry Williams in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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Date Sept. 24, 1987

ABSTRACT

The order Salmoniformes has been important for phylogenetic research because it has been considered the basal group from which the higher teleosts (the Neoteleostei) evolved. However, there is currently no stable hypothesis of its interrelationships, and its relationship to other major teleostean lineages is uncertain. My study of the suspensorium and its muscles has provided new insight into this problem. The suspensorium is a functional unit of the fish skull, composed of eight bones, that forms the dorsolateral wall of the oral cavity, and is directly involved in feeding and respiration.

Phylogenetic analysis suggests that the order is divisible into two main holophyletic groups; the esocoids + salmonids, and the osmeroids + galaxioids + argentinoids. Because the osmeroids + galaxioids + argentinoids, together, form the primitive sister group of the neoteleosts (that is, they are more closely related genealogically to them than to the other salmoniforms), the order Salmoniformes, at least as traditionally defined, is paraphyletic. The osmeroids + galaxioids + argentinoids are united with the neoteleosts because they share an open, bony, lateral sensory canal on the preoperculum. The osmeroids + galaxioids + argentinoids are united because they share specialized teeth on the mesopterygoid. Since I found no evidence suggesting how the osmeroids, galaxioids, and argentinoids are related among one another, they form an unresolved trichotomy. The osmeroids include the osmerids, *Plecoglossus*, and the salangids + sundasalangids. The galaxioids include the retropinnids, prototroctids, galaxiids, and aplochitonids. *Lepidogalaxias salamandroides*, the tiny southwestern Australian endemic that some workers considered to be an esocoid, also belongs with the galaxioids, as originally proposed. The argentinoids include the argentinids, bathylagids, and opisthoproctids in one holophyletic group, and the alepocephalids and platytroctids in another.

The other major holophyletic group within the "traditional" Salmoniformes, the esocoids (the esocids + umbrids) + salmonids, is tentatively united because most species share a hyomandibular with a unique anteroventral wing, and an *adductor mandibulae* that

inserts directly onto the lower jaw and has no ligamentous connection with the maxilla. Partly on the basis of evidence from other sources, the Ostariophysi form part of an unresolved trichotomy along with the [illegible] + salmonids, and the (osmeroids + galaxioids + argentinoids) + neoteleosts.

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I express my heartfelt thanks to my parents for their unfailing support throughout all my endeavors, and for teaching me the value of an advanced education. Finally, I sincerely thank my wife, Kristine, and daughter Leah, for their endless patience, moral support, and encouragement throughout this study.

I dedicate this dissertation to the cherished memory of my father-in-law, The Honorable Mr. Justice Lorne P. Ferg.

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LIST OF ABBREVIATIONS USED IN FIGURES

Aa	angulo-articular
a	anterior
AAP	*adductor arcus palatini*
AAP.a	anterior end
AH	*adductor hyomandibulae*
AM	*adductor mandibulae*
AM.m, AM.md, AM.mv, A1, A2, A2α, A2β, A2.dm, A2.p, Aw, Aw.P	subdivisions of the *adductor mandibulae*
AM.m	medial subdivision
AM.md	medial subdivision, dorsal section
AM.mv	medial subdivision, ventral section
A1	dorsolateral subdivision
A2	lateral section that originates from the lateral surface of the suspensorium and inserts onto the lower jaw and sometimes the upper jaw at the same time
A2α	dorsal subdivision of section A2
A2β	ventral subdivision of section A2
A2.dm	dorsomedial subdivision of section A2
A2.pa	partial dorsolateral subdivision of section A2
Aw	subdivision filling the Meckelian fossa
Aw.p	posterior end of section Aw
AO.	*adductor operculi*
Bb	basibranchial

Bh		basihyal
Ct		ligamentous sheath of connective tissue
D		dentary
des		dorsal edge of skull
DO		*dilatator operculi*
E.lo		lamina orbitonasalis of ethmoid cartilage
E.pr		lateral prenasal process of ethmoid cartilage
Ec		ectopterygoid
	Ec.a	anterior arm
	Ec.p	posteroventral arm
	Ec.pr	ethmoid process
Ep		epaxial muscles
Fo		foramen
Fr		frontal
Hsc		hyomandibular-symplectic cartilage
Hm		hyomandibular
	Hm.af	anterior flange
	Hm.al	anterior lamina
	Hm.ap	anteroposterior ridge
	Hm.aw	anteroventral wing
	Hm.dv	dorsoventral ridge
	Hm.f	foramen for hyomandibular branch of facial nerve
	Hm.fl	lateral foramen for hyomandibular branch of facial nerve
	Hm.fm	medial foramen for hyomandibular branch of facial nerve
	Hm.h	head
	Hm.ls	lateral strut
	Hm.op	opercular arm
	Hm.pd	posterodorsal lamina

	Hm.pr	process onto which the dorsal subdivision of the LAP inserts
	Hm.pv	posteroventral lamina
	Hm.v	ventral arm
l		lateral
L		ligament (=tendon)
	L.A2	ligament connecting section A2 of the AM with the angulo-articular bone of the lower jaw
	L.a, L[illegible]d	ligaments connecting the AM with the lower jaw and/or maxilla in *Bathylagus pacificus* (see text)
	L.cm	coronoid-maxilla ligament
	L.m	new ligament that extends from the maxilla to the mandible in the Aplochitonidae
	L.mm	maxilla-mandibular ligament
	L.smx	supramaxillary ligament
	L.w, L.x, L.y, L.z	sections of the maxilla-mandibular ligament
	L.yr	remnant of section Y of the maxilla-mandibular ligament
LAP		*levator arcus palatini*
	LAP.a	anterior section
	LAP.d	dorsal subdivision
	LAP.p	posterior section
	LAP.v	ventral subdivision
Le		lateral ethmoid
LJ		lower jaw
LO		*levator operculi*
	LO.p	posterior subdivision
m		medial
md.V		mandibular branch of trigeminal nerve

Me		mesethmoid
Med		medial
mm		millimetre(s)
Ms		mesopterygoid (= endopterygoid)
	Ms.a	anterior end of mesopterygoid
	Ms.t	mesopterygoidal teeth
Mt		metapterygoid
	Mt.d	dorsolaterally directed flange
	Mt.e	endochondral wedge
	Mt.l	lateral ridge
	Mt.m	medial ridge
	Mt.p	posterior dermal lamina
	Mt.pd	posterodorsal lamina
	Mt.w	posteroventral wing
Mx		maxilla
Op		operculum
Pa		parietal
Par		parasphenoid
Pl		palatine
	Pl.a	autopalatine
	Pl.ac	anterior cartilage
	Pl.d	dermopalatine
	Pl.t	palatine teeth
Pl-ec		fused palatine and ectopterygoid
Pmx		premaxilla
Po		preoperculum
	Po.al	anterior lamina
	Po.af	anterior flange

	Po.ax	auxiliary canal(s)
	Po.d	dorsal limb
	Po.v	ventral limb
Pq		palatoquadrate cartilage
	Pq.a	anterior end
	Pq.p	posterior end
Pr		proethmoid
Pre		preethmoid
Pro		prootic
Pt		pterotic
	Pt.p	posterodorsal spine
Pts		pterosphenoid
Ptt		posttemporal
Q		quadrate
	Q.b	body
	Q.c	condyle
	Q.n	notch
	Q.j	quadratojugal arm
Se		supraethmoid
Smx		supramaxilla(e)
	Smx.a	anterior supramaxilla
	Smx.p	posterior supramaxilla
Sp		sphenotic
	Sp.s	sphenotic spine
Sy		symplectic
	Sy.l	lamina
t.AM		tendon or tendinous aponeurosis of the *adductor mandibulae* that extends to the coronomeckelian bone of the lower jaw

Vo		vomer
	Vo.t	vomerine teeth

I. INTRODUCTION

A. THE PROBLEM

The salmoniform fishes have traditionally been important to phylogenetic research because they are considered by most workers to be the basal group from which the higher teleosts (the Neoteleostei) evolved. However, ever since Greenwood *et al.*'s (1966) classic monograph entitled *Phyletic Studies of Teleostean Fishes with a Provisional Classification of Living Forms*, membership in the order, and the interrelationships of its species, have been a matter of great debate, and remain as one of the most controversial subjects in ichthyological systematics today. The frustration of recent workers who have studied these fishes is nicely summarized by Fink (1984b, p. 206) who stated that "It is always frustrating when one sets out to solve a particular problem and then comes to the end of the allotted time without a resolution.... I have not been able to unravel the interrelationships among the major basal euteleostean clades [which includes the salmoniforms]. Clearly more work is needed, especially with character suites which have been traditionally neglected." The goal of my thesis was to study the anatomy of one of these neglected character complexes, the suspensorium, with a view to using this information to better define the relationships of the salmoniforms (as defined by Rosen 1974 and Nelson 1984).

The modern controversy began in 1966 when Greenwood *et al.* created the superorder Protacanthopterygii, of which the order Salmoniformes is a member, from a variety of fishes that were once scattered widely among the lower teleosts (see Regan 1913; Berg 1940; Gosline 1960). They considered the Protacanthopterygii to be the basal group of higher teleost evolution from which the largest group of teleosts, the Acanthomorpha, evolved (the Acanthomorpha = the Paracanthopterygii + Acanthopterygii, with sixty percent of all living species according to Nelson 1984). The Protacanthopterygii consisted of four orders (the Salmoniformes, Cetomimiformes, Ctenothrissiformes, and Gonorynchiformes), the largest and most diverse being the Salmoniformes with eight suborders (the Salmonioidei, Argentinoidei, Galaxioidei, Esocoidei, Stomiatoidei, Alepocephaloidei, Bathylaconoidei, and Myctophoidei) and thirty-seven families. They noted (p. 369) that "the Salmoniformes as a group contains, in mosaic occurrence, all the necessary basic specializations to have provided the evolutionary raw materials for all the more advanced groups, including the Ctenothrissiformes, of this superorder [i.e., the Protacanthopterygii]. Such, in fact, is the substance of our reasons for the establishment of both the Salmoniformes and the Protacanthopterygii." They considered the Salmonidae (the whitefishes, graylings, trouts, charrs, and salmons) in particular, to be (p. 350) the "morphotype that may have given rise to the major radiations of Division III [i.e., the other protacanthopterygians and the advanced teleosts]."

Studies since have markedly reduced the membership of the Protacanthopterygii. Rosen and Greenwood (1970) placed the Gonorynchiformes in the Ostariophysi. The order Ctenothrissiformes, a fossil group, was placed in the Neoteleostei (the higher teleosts) by Rosen (1973) as the sister group of the Acanthomorpha. The extant family Macristiidae was formerly placed in the Ctenothrissiformes, but Rosen (1971) presented evidence that its two "species" may be larval aulopiforms, and Sulak (1977) concurred. The Cetomimiformes were dismembered by Rosen and Patterson (1969) and Rosen (1973), and its members distributed among the neoteleosts: the Giganturoidei were placed in the Aulopiformes as the family Giganturidae, and the others were distributed among the Beryciformes and Lampriformes (refer to Nelson, 1984, for details concerning their exact placement). With the removal of the aforementioned three orders the taxon Protocanthopterygii contains only the order Salmoniformes, and as such, its use is abandoned in favour of the ordinal name.

Greenwood *et al.*'s order Salmoniformes was also reduced in size. The Stomiatoidei were assigned their own order, the Stomiiformes, and placed within the Neoteleostei as the primitive sister group of the other neoteleosts (see Rosen 1973; Fink and Weitzman 1982; Fink 1984b). Rosen and Patterson (1969) removed the Myctophoidei from the Salmoniformes and placed them in their own order, the Myctophiformes. In 1973 Rosen divided Rosen and Patterson's Myctophiformes into the Aulopiformes and the Myctophiformes. Rosen considered the new Myctophiformes to be the sister group of the Acanthomorpha (including the † Ctenothrissiformes), and the Aulopiformes to be the sister group of the Myctophiformes + Acanthomorpha (Rosen, 1985, more recently doubted the holophyly of both orders; however, their placement as neoteleosts remains unchanged). These views of teleostean relationships are summarized in Figure 1.

With the removal of the stomiatoids and myctophoids the composition of the Salmoniformes has remained the same except for the addition of two newly discovered families, the Lepidogalaxiidae (e.g., see Mees 1961; Frankenberg 1969; Rosen 1973, 1974) and the Sundasalangidae (see Roberts 1981; 1984). However, there is no stable hypothesis of salmoniform interrelationships, and there is considerable doubt as to whether or not the order forms a holophyletic group (a group of species that share a common ancestor not shared with any other species). Patterson (1970, p.282) first alluded to this problem when he stated that "there is almost no evidence that the remaining protacanthopterygian group, the Salmoniformes [at this time Patterson's Salmoniformes also included the stomiatoids] is monophyletic (absence of ectopterygoid teeth seems the only advanced character common to all salmoniforms). Despite recent detailed anatomical work on four of the eight salmoniform suborders (osmeroids and stomiatoids, Weitzman 1967a,b; alepocephaloids, Gosline 1969; galaxioids, McDowall 1969), there is still no coherent picture of relationships among these groups." Even after the stomiatoids were removed by Rosen in 1973 there was still a question of the holophyly of the remaining salmoniforms. In Rosen's 1974 paper he considered the Salmoniformes to be holophyletic but noted (p. 310) that "The present evidence for regarding esocoids as members of the Salmoniformes is slight ... The following scheme, then, recognizes the uncertainty of esocoid relationships and ... includes them as the primitive sister group of other salmoniforms." Fink and Weitzman (1982) and Fink (1984b) concluded that the Salmoniformes as defined by Rosen (1974) are not holophyletic and removed the esocoids from the group, suggesting that they are the sister group of all other euteleosts (that is, the Ostariophysi + the remaining salmoniforms + the ~~Neoteleostei~~). Fink (1984b, p. 202) goes as far as stating that "today I would recognize it [the order Salmoniformes] as coextensive with the Salmonidae. Previously included taxa are now scattered, primarily as unresolved lineages at or near the base of the Euteleostei." Rosen (1985) also concluded, using other lines of evidence, that the Salmoniformes are not holophyletic and distributes the members of the group widely among the primitive euteleosts. His scheme is unusual in that he places the Clupeomorpha, esocoids, and the euteleosts (minus the esocoids) as part of an unresolved trichotomy.

Besides the question of the holophyly of the Salmoniformes there is no agreement as to the interrelationships of most of its members, and consequently, the subordinal, familial, and generic arrangements vary considerably from worker to worker. The only major current point of agreement concerns Greenwood and Rosen's (1971) Argentinoidei. They combined Greenwood *et al.*'s Argentinoidei, Alepocephaloidei, and Bathylaconoidei into a single holophyletic group, the Argentinoidei, with two superfamilies, the Argentinoidea (= Argentinoidei of Greenwood *et al.*) and the Alepocephaloidea (= Alepocephaloidei and Bathylaconoidei of Greenwood *et al.*). Most workers (e.g., Rosen 1973, 1974, 1985; Fink and Weitzman 1982; Fink 1984b; Nelson 1984) accept this hypothesis; however, there is no agreement as to the relationship of the Argentinoidei to the other salmoniforms.

Most consider the Esocoidae and Umbridae to be each other's closest relatives and place them in the suborder Esocoidei. However, their relationship to the other salmoniforms is unclear. The current view (as was previously mentioned) is that the esocoids are relatively distantly related to the other salmoniforms (see Nelson 1970a; Rosen 1974, 1985; Fink and Weitzman 1982; Lauder and Liem 1983; Fink 1984b; Nelson 1984), a view that as Nelson (1984) noted, was expressed in Berg's (1940) early classification. Parenti (1986), however, recently proposed that the esocoids belong in a group that also includes the osmeroids (*sensu* Fink and Weitzman 1982) and neoteleosts (see later).

The relationships of the remaining salmoniforms are also uncertain. Greenwood *et al.* (1966) placed these fishes in two suborders; the Salmonoidei, containing the Salmonidae, Plecoglossidae, and Osmeridae; and the Galaxioidei, containing the Salangidae, Retropinnidae, Galaxiidae, and Aplochitonidae. Weitzman (1967a) removed the family Osmeridae from the

Salmonoidei and placed it in its own suborder, the Osmeroidei, which he considered to be closely related to the Galaxioidei. He questioned Greenwood *et al.*'s placement of the Salangidae with the galaxioids, suggesting that perhaps the salangids should be considered a separate group with probable affinities with either the osmeroids or galaxioids.

McDowall (1969) studied the Galaxioidei of Greenwood *et al.* He removed *Prototroctes* from the Aplochitonidae and placed it in its own monotypic family, the Prototroctidae, considering it to be closely related to the Retropinnidae. This change has been accepted by subsequent workers; however, some prefer to place *Prototroctes* in the Retropinnidae, either in a separate monotypic subfamily, the Prototroctinae (Nelson 1984) or as part of an unresolved trichotomy along with *Retropinna* and *Stokellia* (Fink 1984b). McDowall also placed the Salangidae and the Plecoglossidae (which Greenwood *et al.* 1966, and Weitzman 1967a placed in the Salmonoidei) in the Osmeroidei along with the Osmeridae, and concluded that the suborder Galaxioidei was composed of the southern hemispheric families Galaxiidae, Aplochitonidae, Retropinnidae, and Prototroctidae. He also stated that the Aplochitonidae (minus *Prototroctes*) was closely related to the Galaxiidae, a view that has been upheld by subsequent workers (e.g., Nelson 1972; Rosen 1974; Fink 1984b). Nelson's (1972) study of the cephalic sensory canals, pores, and pitlines in esocoids and galaxioids supports McDowall's conclusions regarding the galaxioids; however, his classification is different: he places McDowall's four galaxioid families into a single family, the Galaxiidae, with two subfamilies, the Retropinninae (McDowall's Retropinnidae and Prototroctidae) and the Galaxiinae (McDowall's Galaxiidae and Aplochitonidae).

In 1974 Rosen presented a strictly cladistic classification of the Salmoniformes. In his favoured hypothesis, based on hyobranchial anatomy, he divided the order into three suborders, the Esocoidei, Argentinoidei (*sensu* Greenwood and Rosen 1971), and Salmonoidei (refer to Fig. 2A). The Esocoidei (Esocidae + Umbridae + Lepidogalaxiidae) formed the primitive sister group of the Argentinoidei + Salmonoidei. The Salmonoidei in turn had two superfamilies: the Salmonoidea with the Galaxiidae (with subfamilies Aplochitoninae and Galaxiinae) and Salmonidae, and the Osmeroidea with four families of uncertain relationship to one another, the Osmeridae, Plecoglossidae, Retropinnidae (including McDowall's Prototroctidae), and Salangidae. This classification is of interest biogeographically, and unlike that of previous ones, in that it considered each of the southern hemispheric families (Rosen's Lepidogalaxiidae, Galaxiidae, and Retropinnidae) to be more closely related cladistically to a group from the northern hemisphere (with the esocoids, salmonids, and osmeroids, respectively), than to one another. Patterson (1970) first alluded to this possibility when he suggested that the Retropinnidae (*sensu* Rosen 1974) be tentatively placed in the Osmeroidei (Osmeridae + Plecoglossidae + Salangidae) based on the structure of the caudal skeleton.

Fink and Weitzman (1982) questioned Rosen's hypothesis and provided an alternate. They placed the Osmeridae, Plecoglossidae, Salangidae, Retropinnidae (including *Prototroctes*), and Galaxiidae (the Galaxiidae and Aplochitonidae of McDowall 1969) in a single holophyletic group, the Osmeroidei, based on their sharing specialized teeth on the mesopterygoid, a specialized "tongue bite" mechanism, and the absence of basisphenoid and orbitosphenoid bones. However, they considered these five families to be of uncertain relationship to one another. The Osmeroidei in turn were considered to form the sister group of the Argentinoidei (*sensu* Greenwood and Rosen 1971); however, no evidence was given to support this placement. Why the argentinoids were placed with the osmeroids is unclear, since Fink himself later states (1984b, p. 202) that "Fink and Weitzman (1982) were unable to provide evidence bearing on relationships of these fishes [the Argentinoidei], even though their cladogram ... showed them as the sister group of the osmeroids." On Fink and Weitzman's cladogram of euteleostean relationships the Ostariophysi, Argentinoidei + Osmeroidei, Salmonidae, and Neoteleostei form an unresolved polychotomy, with the Esocae (= Esocoidei) forming their primitive sister group (refer to Fig. 2B). They questioned Rosen's placement of *Lepidogalaxias* in the Esocoidei but did not provide an alternate hypothesis. In the text they suggest that the Salmonidae may form the sister group of the Neoteleostei on the basis of their sharing two characters: both the basioccipital and exoccipital articulate with the first vertebra (versus, according to them, only the basioccipital in the primitive character state), and the salmonids possess cartilaginous nodules between the ethmoid and premaxillae that they consider to be homologous with the rostral cartilage of neoteleosts (also see Lauder and Liem 1983). In a more recent paper, Fink (1984b) presents (his fig. 108) a similar arrangement except that the Ostariophysi, Argentinoidei, Osmeroidei, and Salmonidae + *Lepidogalaxias* + Neoteleostei form an unresolved polychotomy, with the Esocoidei as their sister group (refer to Fig. 2C). *Lepidogalaxias* is linked with the neoteleosts on the basis of their sharing a *retractor dorsalis* muscle (absent in the Salmonidae) and an occipital condyle composed of the basioccipital and exoccipital bones (as in the Salmonidae). However, because the Salmonidae lack a *retractor dorsalis* muscle and *Lepidogalaxias* lacks even an incipient rostral cartilage, Fink considered neither to be neoteleosts. Fink reflects this ambiguity by placing the Salmonidae, *Lepidogalaxias*, and the Neoteleostei as an unresolved trichotomy, a move that I believe (and Fink concurs) is far from satisfactory because of the number of assumptions that are required to support it.

Fink (1984b) also presented two hypotheses concerning the interrelationships of the Osmeroidei (*sensu* Fink and Weitzman 1982), which he diagnosed as holophyletic based on several new characters in addition to those Fink and Weitzman (1982) discussed earlier (e.g., the loss or appearance late in ontogeny of the articular bone, the presence of a foramen in the posterior plate of the pelvic bone). In one hypothesis (p. 203) "all characters are given equal weight and paedomorphic traits are considered homologous," whereas the other "considers the paedomorphic reductive traits of salangids and galaxiids as non-homologous." Both are the same except that in the latter the Salangidae form the sister group of *Plecoglossus* + the Osmeridae, whereas in the former they form the sister group of the Galaxiidae (*sensu* Rosen 1974). Excluding the Salangidae, Fink divided the Osmeroidei into two major holophyletic groups: one made up of the southern hemispheric families Retropinnidae and Galaxiidae (both families *sensu* Rosen 1974), and the other made up of *Plecoglossus* + the Osmeridae from the Northern Hemisphere. The three retropinnid genera (*Retropinna, Stokellia,* and *Prototroctes*) formed an unresolved trichotomy, as did the Galaxiidae (subfamily Galaxiinae of Rosen 1974) *Lovettia*, and *Aplochiton* (the latter two taxa were placed in the subfamily Aplochitoninae of the family Galaxiidae by Rosen 1974). He also questioned the status of the

Osmeridae as a holophyletic group, stating (p. 203) that "it seems quite possible that *Plecoglossus* could be more closely related to some 'osmerids' than to others, and this would render the family paraphyletic." However, Fink considers his hypothesis of osmeroid relationships to be only tentative, stating (p. 203) that "The data used in this analysis were chosen partly because they have been used traditionally in osmeroid systematics but I have little confidence in some of them; as a result this analysis represents a preliminary sketch of a more detailed study."

In a 1985 paper Rosen carefully examined the anatomy of the neurocranial joint with the first vertebra, and the rostral cartilage, in the Euteleostei. This study was apparently stimulated by Fink and Weitzman's (1982) and Fink's (1984b) recent papers in which they used these characters to unite the Neoteleostei, and to link the Salmonidae to them as their sister group. By using his new data, along with other anatomical features gleaned from the literature, he reassessed the interrelationships of the Euteleostei and came to a number of interesting conclusions regarding the salmoniforms. On Rosen's cladogram (refer to Fig. 2D) the clupeomorphs, esocoids, and euteleosts (minus the esocoids) form an unresolved trichotomy. In the latter group the Argentinoidei, Ostariophysi, and Salmonidae + Osmeroidei (*sensu* Fink 1984b) + Neoteleostei form an unresolved trichotomy. In turn, the salmonids are the sister group of the Osmeroidei + Neoteleostei and the Osmeroidei are the primitive sister group of the Neoteleostei. His reasons for rejecting Fink and Weitzman's (1982) and Fink's (1984b) hypothesis that the Salmonidae are the sister group of the Neoteleostei are summarized (p. 51) in the following statement: "According to evidence presented here, the significance of the paired cartilages [the homologues of the rostral cartilage according to Fink and Weitzman] and tripartite occipital condyles found in some salmonids is ambiguous because of the uneven distribution of the characters, the lack of a good theory of relationships among the taxa, the occurrence of both features in some osmeroids, and a parsimony argument that favors osmeroids as a neoteleost sister group." He lists three synapomorphies uniting the osmeroids with the neoteleosts: acellular endoskeletal bone, a toothed alveolar process on the premaxilla which lies under the maxilla, and a caudal skeleton in which the neural spine on the second preural centrum is shorter than the one on the third preural centrum, and bladelike. In turn, he unites the salmonids with the osmeroids + neoteleosts on the basis of their sharing paired stegural outgrowths of the first uroneural and an endoskeleton that is at least partly made up of acellular bone. Unlike Fink (1984b), Rosen did not include *Lepidogalaxias* on his cladogram and simply states that its position is controversial. Rosen also believes that the holophyly of both the Salmonidae and Osmeroidei should be reevaluated.

Most recently, Parenti (1986) studied bone-type in the Euteleostei and hypothesized that because the Esocae (= Esocoidei), Osmeroidei (*sensu* Fink and Weitzman 1982), and Neoteleostei possess acellular bone (the presumed derived character state, in contrast to cellular bone) they form a holophyletic group.

From this account of the recent taxonomic history of the order Salmoniformes it is obvious that much work remains to be done before there will be a stable of hypothesis of salmoniform relationships. The following questions remain unanswered: is the order holophyletic, or is it paraphyletic as suggested by recent workers? What is the relationship of the Salmoniformes to other teleosts? What are the interfamilial relationships? Are some of the families paraphyletic (e.g., the Osmeridae and Salmonidae) as suggested by recent workers? What are the phylogenetic relationships of the two most problematic taxa, the Salangidae and *Lepidogalaxias*? What are the intergeneric relationships of each family? Most of these questions remain unanswered and there is presently almost as much uncertainty regarding the relationships of the Salmoniformes as there was at the time of Greenwood *et al.*'s (1966) monograph. Lauder and Liem (1983, p. 136) understated the problem, and the challenge, when they succinctly stated in their recent monograph entitled *The Evolution and Interrelationships of the Actinopterygian Fishes* that "the relationships of these 'lower' euteleostean fishes are in need of a comprehensive analysis."

The answers to these questions also have important biogeographic implications since aside from the Argentinoidei (which are pandemic, entirely marine, and bathypelagic) the salmoniforms are amphitropical, and both panboreal and panaustral in distribution (some salangids, the Sundasalangidae, and the galaxiid *Nesogalaxias* have a tropical distribution). Both continental drift and dispersal models have been proposed to account for the unusual distribution of these fishes (e.g., see Rosen 1974, 1978; McDowall 1980); however, the relative importance of these two dispersal mechanisms in the distribution of the salmoniforms is unresolved at present, and awaits new information, in particular a better understanding of salmoniform interrelationships.

Earlier studies of salmoniform relationships are of a general anatomical nature, and it is often difficult to be sure what character states are used to unite specific groups, and which are primitive and derived (e.g., Gosline 1960, 1969; Greenwood *et al.* 1966; Weitzman 1967a; McDowall 1969). More recent workers, however, have utilized specific character complexes to elucidate relationships. In addition, most attempt to present their data in a way that is more amenable to analysis and criticism by other workers, and have been more careful to outline what character states (derived) they have used to unite species. For example, Nelson (1970a) presented a classification of the salmoniforms based on gill-arch structure and in 1972 presented hypotheses of both esocoid and galaxioid (*sensu* McDowall 1969) interrelationships based on the anatomy of the cephalic sensory canals, pores, and pitlines. Rosen's (1974) preferred hypothesis of salmoniform interrelationships was based on hyobranchial anatomy and his alternate hypothesis was based on the anatomy of the caudal skeleton. Fink and Weitzman (1982) reviewed Rosen's data and presented a different hypothesis that used characters from the chondrocranium and suspensorium. Most recently, Rosen (1985) carefully studied the occipital region and rostral cartilage in teleosts and used these data, along with others from the literature, to formulate a new hypothesis of euteleostean relationships (which includes the salmoniforms). In other groups, studies of single character complexes have involved elements of the hyoid arch and opercular series (McAllister 1968), the gill arches (Nelson 1967a, 1968, 1969), and the anterior vertebrae (Rosen and Greenwood 1970). No one, however, has studied the suspensorium and the muscles associated with it, in detail, with a view to using it to elucidate salmoniform relationships, or to study the relationships of any other major teleost assemblage for that matter.

The primary objectives of my study were to test the hypothesis that the order Salmoniformes (*sensu* Rosen 1974; Nelson 1984) forms a holophyletic group, and to elucidate salmoniform interfamilial relationships. When possible I tested the holophyly of the families in the order, in particular those whose holophyly has been questioned recently (the Salmonidae and Osmeridae). Because all the genera belonging to the Osmeridae and Umbridae were available to me I present a scheme of their intergeneric relationships. I was also interested in determining the phylogenetic position of the neotenic salangoids (*sensu* Roberts 1984) and the enigmatic Australian species, *Lepidogalaxias salamandroides*, which Rosen (1974) considered to be related to the esocids and umbrids of the Northern Hem[illegible]here. This work also provides badly needed anatomical information on the bones and muscles of the suspensorium. This new information should serve as a starting point for future studies concerning the suspensorium and its biomechanics. Adaptive advances, especially those involving the feeding mechanisms of the higher teleosts, have involved the bones and muscles of the suspensorium and presumably have been partly responsible for the great evolutionary success of these fishes. These structural and functional advances are first seen in the salmoniforms and make this group particularly important in the study of teleost evolution.

B. THE SUSPENSORIUM

Bones

The teleost skull is subdivided into seven functional, or mechanical units (see Liem 1967a, 1967b, 1970; Gans 1969; Dutta 1975): the neurocranium and sensory capsules, the suspensory apparatus (or suspensorium), the opercular apparatus (the operculum, suboperculum, and interoperculum), the jaw apparatus (the mandible, maxillary, and premaxillary), the hyoid apparatus (the two hyoid bars including the branchiostegals, and two unpaired elements, the basihyal and urohyal), the pectoral girdle, and the branchial basket (the gill-bearing elements). There does not appear to be agreement as to exactly what a functional unit is. However, in essence it is a series of more than one bony element (and associated cartilage and ligaments) that form an independent mechanical entity, and move in unison to perform a specific function (or functions). Each functional unit is coupled to other functional units via joints, muscles, tendons, ligaments, and/or connective tissue.

The suspensorium is a mechanical unit that surrounds the ventral half of the eye, forms the dorsolateral wall of the oral cavity, and is directly involved in feeding and respiration (e.g., see Liem 1967a, 1967b, 1970; Gosline 1971; Dutta 1975; Harder 1975). It lies medial to the circumorbitals, except for the preoperculum. It is approximately triangular, with each of its angles represented by a joint: the palatocranial joint anteriorly, the quadratomandibular joint ventrally, and the craniohyomandibular joint posteriorly. The palatocranial joint connects the palatine to the anterior end of the neurocranium via usually two articular surfaces: a cartilaginous knob at the anterior end of the palatine abuts the lateral prenasal process of the ethmoid cartilage and the maxilla, and the palatoquadrate cartilage at the posterior end of the palatine extends posterodorsally to abut the lamina orbitonasalis of the ethmoid cartilage. The quadratomandibular joint is a synovial saddle joint that serves to suspend the lower jaw from the suspensorium; the saddle-shaped articular surface on the condyle of the quadrate rests on a similarly shaped facet on the posterodorsal end of the lower jaw (usually on the angulo-articular in teleosts, but see Nelson 1973). The craniohyomandibular joint is a synovial hinge-joint that connects the hyomandibular to the posterolateral surface of the neurocranium; a long and narrow cartilage on the dorsal edge of the head of the hyomandibular rests in a cartilage-lined facet on the skull (usually on the sphenotic, pterotic, and prootic bones). Well-developed ligaments serve to stabilize the palatocranial and quadratomandibular joints but appear to be lacking from the craniohyomandibular joint. The latter joint is stabilized by sheets of connective tissue that extend between the medial surface of the hyomandibular and the neurocranium.

In addition to the three main joints, the suspensorium articulates with the opercular apparatus via a synovial ball-and-socket joint; a round cartilaginous knob on the end of the opercular arm of the hyomandibular rests in a rounded socket on the anterodorsal corner of the operculum. The opercular apparatus is also connected to the posterior edge of the preoperculum (the posteriormost bone of the suspensorium) via connective tissue. Finally, the suspensorium aids in suspending the hyoid apparatus and the branchial basket. The small interhyal bone of the hyoid arch articulates with the cartilage connecting the posterior end of the symplectic with the ventral end of the ventral arm of the hyomandibular. The hyoid arch in turn articulates with the anteroventral end of the branchial basket. Because of this connection, a lateral movement of the suspensorium results not only in an expansion of the oral cavity, but also in a corresponding expansion of the branchial chamber. A medial movement of the suspensorium results in a compression of both chambers.

The suspensorium is composed of eight bones (from anterior to posterior): the palatine, ectopterygoid, mesopterygoid (= endopterygoid), quadrate, metapterygoid, symplectic, hyomandibular, and preoperculum (see Fig. 3). The palatine consists of a cylindrical autopalatine that is endochondral in origin, and a flattened tooth-bearing dermopalatine that is dermal in origin. The dermopalatine is usually imperceptibly fused to the ventral surface of the autopalatine. The ectopterygoid is a thin, splint-like bone that is dermal in origin. The mesopterygoid is a relatively thin and long dermal bone that may bear teeth on its ventral surface. Its medial edge is connected to the parasphenoid of the neurocranium by a sheet of connective tissue. The quadrate is a triangular endochondral bone that consists of a fan-shaped body, an anteroventral condyle that articulates with the lower jaw, and a posterodorsally extending quadratojugal arm. The metapterygoid is a triangular endochondral bone that lies at the junction of the mesopterygoid, quadrate, symplectic, and hyomandibular. It can have a dermal, laminar component. The symplectic is a small, relatively straight, tubular endochondral bone that bridges the gap between the hyomandibular and quadrate. It rests on the dorsomedial surface of the quadratojugal arm of the quadrate. The hyomandibular is a relatively robust endochondral bone that consists of a dorsal, triangular head, a posteriorly projecting opercular arm, and a ventrally projecting ventral arm. It also usually has a dermal lamina that extends along its anterior edge. The preoperculum is a flat dermal bone that has a bony sensory canal running along its anterolateral surface. It has traditionally been considered to be part of the opercular series;

however, Liem (1967a, 1967b, 1970) and Dutta (1975) have shown that the preoperculum is functionally part of the suspensorium, because as Liem (1970, p. 30) states "it serves as the origin of the adductor mandibulae muscles and its motions correspond to those of the suspensory apparatus and are independent of those of the opercular, interopercular, and subopercular. Inclusion of the preopercular in the opercular series (e.g., Patterson, 1964) is, therefore, based on purely morphological reasons, without functional justification." The palatoquadrate cartilage extends along the lateral surface of the suspensorium from the posterior end of the autopalatine to the metapterygoid. It is found between the palatine, ectopterygoid, mesopterygoid, quadrate and metapterygoid bones, and usually overlaps the former three to various degrees. It may also overlap parts of the symplectic and hyomandibular, but is not, strictly speaking, associated with them. Liem (1967a) claims that the presence of this cartilage between the bones of the suspensorium permits a limited amount of internal movement within the unit.

Ontogenetically the suspensorium is made up of the upper part of the first two visceral arches plus dermal elements (see Gosline 1971; Harder 1975; Jollie 1975; Hildebrand 1982). The upper part of the first visceral (or mandibular) arch is the palatoquadrate (the lower half is the mandible), the upper part of the second visceral (or hyoid) arch is the hyomandibular, or more correctly, the hyosymplecticum (the lower half is the hyoid bar consisting of the interhyal, epihyal, ceratohyal, and hypohyals). The palatoquadrate and hyosymplecticum are independent entitles during early development and only later do they unite into a single mechanical unit. The palatoquadrate develops into three endochondral bones; the autopalatine, quadrate, and metapterygoid; the hyosmplecticum into two, the hyomandibular and symplectic. Three dermal elements; the dermopalatine, ectopterygoid, and mesopterygoid develop in association with the palatoquadrate but are not derived from it. The preoperculum is also a dermal bone, but unlike the other bones of the suspensorium it develops in association with the opercular series rather than the first two visceral arches (see Verraes 1977).

There is limited information concerning the ontogeny of the suspensorium in the salmoniforms, and what is available concerns almost entirely the Salmonidae and Esocidae (see Saunderson 1935; Verraes 1974, 1977; Jollie 1975, 1984). Unfortunately current information contributes little to my understanding of the relationships of this order and is primarily of descriptive interest (e.g., the order of appearance of bones of the skull in *Esox*, see Jollie 1975).

Muscles

The muscles associated with the suspensorium are the muscles of the cheek, and include the *adductor mandibulae*, *levator arcus palatini* (LAP), *dilatator operculi* (DO), *adductor arcus palatini* (AAP), *adductor hyomandibulae* (AH), *levator operculi* (LO), and *adductor operculi* (AO). The *adductor mandibulae*, LAP, and DO are derivatives of the *constrictor dorsalis* of the mandibular arch, and are innervated by branches of the trigeminal nerve (see Winterbottom 1974a; Meijer 1975; Liem 1977). The AAP, AH, LO and AO are derivatives of the *constrictor dorsalis* of the hyoid arch, and are innervated by the hyomandibular branch of the facial nerve. The LO and AO do not actually insert or originate on the suspensorium; however, since they are derived from the same muscle segment, are innervated by the same nerve, and are adjacent to those that do (the AAP and AH), I consider them to be muscles of the suspensorium. The *adductor mandibulae*, LAP, DO and LO are superficial and visible when the cheek is viewed laterally (see Fig. 4).

The *adductor mandibulae* is the largest muscle and occupies most of the ventrolateral region of the cheek. It originates from the posterolateral surface of the suspensorium (usually from the preoperculum, hyomandibular, metapterygoid, symplectic, and quadrate) and inserts onto the lower jaw, ~~and~~ in some species, onto the upper jaw. It is primarily responsible for closing the mouth. Innervation is by the mandibular branch of the trigeminal nerve (see Winterbottom 1974a; Freihofer 1978; Lauder and Liem 1980).

Primitively in the Teleostei the *adductor mandibulae* has two subdivisions. Section A2 is the largest and is visible externally. It originates on the lateral surface of the suspensorium and inserts onto the lower jaw, either via a tendinous aponeurosis (usually) or directly. It also inserts onto the upper jaw (the maxilla) via a tendinous connection with the maxilla-mandibular ligament (= *ligamentum primordium*). In primitive teleosts this ligament extends from the posterolateral surface of the lower jaw to the anterior end of the maxilla. Section Aw (= *intramandibularis*) of the *adductor mandibulae* is smaller than section A2 and is usually not visible externally. It inserts in and fills the Meckelian fossa on the medial surface of the mandible and usually originates from the tendinous aponeurosis onto which section A2 inserts.

In more derived Teleosts the *adductor mandibulae* may be further subdivided. Winterbottom (1974a, p. 232) notes that "The number and nature of the subdivisions is very variable; there may be anything from a single moiety (e.g. in some siluriforms) to the ten sections distinguishable in certain monacanthins (Tetraodontiformes)." These subdivisions appear to be ultimately derived from the external subdivision, section A2. For example, section A2 may be divided into A2α (dorsal) and A2β (ventral) subdivisions; there may be a separate A3 section that lies medial to section A2 and is not visible externally; and there may be a separate A1 subdivision that lies dorsolateral to section A2 and inserts independently onto the maxilla via its own tendon (section A1 may also be subdivided into A1α and A1β subdivisions, see Winterbottom 1974a). In addition to the above changes, the maxilla-mandibular ligament may be changed in numerous ways: it may be completely lost so that the *adductor mandibulae* inserts only onto the lower jaw, it may subdivide, or else parts of it may be lost (e.g., its connection with the *adductor mandibulae* may be lost, as in most salmonids). In most teleosts (e.g., the Ostariophysi and the Neoteleostei) changes of the *adductor mandibulae* and its associated ligaments appear to be related to improvements in the feeding mechanism, in particular, the ability to protrude the jaw (e.g., see Rosen 1973; Motta 1984). In the Teleostei the *adductor mandibulae* is the most variable and, phylogenetically speaking, the most interesting muscle of the suspensorium. Apparently this is also the case in more primitive Actinopterygians such as *Lepisosteus, Polypterus*, and *Amia*, since Lauder (1980a, p. 314) noted that "The major variations in cranial myology occur in the adductor mandibulae complex, whereas all other jaw musculature is constant in position."

The LAP muscle is usually conical, with a dorsally-directed apex, and occupies the area at the posterior end of the orbit between the skull and the suspensorium. Its ventrolateral surface is usually covered by the *adductor mandibulae*. It usually originates from a spine on the sphenotic and inserts onto the mid-lateral surface of the hyomandibular and either the dorsomedial or dorsolateral surface of the metapterygoid. It functions to abduct the suspensorium. Innervation is by the maxillo-mandibular branch of the trigeminal nerve (see Winterbottom 1974a); however, apparently in some species the LAP (and DO) is secondarily innervated by a branch of the facial nerve (see Meijer 1975). It is occasionally subdivided.

The DO usually lies posteromedial to the LAP and connects the postorbital region of the skull and the suspensorium to the operculum. It usually originates from the dorsolateral surface of the hyomandibular and the lateral surfaces of the sphenotic and pterotic, and narrows posteroventrally to an insertion on the anterodorsal corner of the operculum. It abducts the operculum. The innervation is as described for the LAP. It is occasionally subdivided.

The LO lies immediately posterior to the DO and passes from the posterolateral surface of the skull (usually originating on the pterotic) to the operculum (usually inserting on its dorsomedial surface). Occasionally it has a posterior subdivision that extends between the operculum and the dorsal part of the pectoral girdle (e.g., *Esox*). The contraction of the LO serves to rotate the operculum anterodorsally, a motion that is the first step in a unique *levator operculi* - opercular series - mandible coupling mechanism that contributes to the lowering of the jaw in all halecostome fishes (see Lauder 1979, 1980a; Lauder and Liem 1980, 1983). The Halecostomi (*sensu* Lauder and Liem 1983) include all fishes with an interopercular bone.

The AO is a small conical muscle that lies between the AAP (the AH if it is present) and the LO and is not usually visible externally. It adducts the operculum. It originates from the posterolateral surface of the skull (usually from the pterotic ventral to the origin of the LO) and inserts onto the medial surface of the anterodorsal part of the operculum (usually anterior to the insertion of the LO).

The AAP is a rectangular muscle that originates from the ventrolateral surface of the skull at the rear of the orbit (usually from the parasphenoid and prootic) and inserts onto the medial surface of the suspensorium (primarily onto the hyomandibular and metapterygoid). It adducts the suspensorium. In more derived teleosts the AAP is expanded anteriorly so that it lines the floor of the orbit between the skull and the suspensorium, and is visible externally.

A separate AH muscle that adducts the hyomandibular is not present in all teleosts. When present it lies between the AAP and LO. Winterbottom (1974a) claims that it is derived either from the posterior region of the AAP or from the anterior part of the AO. It usually originates from the prootic and/or pterotic and inserts onto the medial surface of the posterodorsal region of the hyomandibular. It has evolved independently in a number of separate lineages.

C. ORDER SALMONIFORMES

In the present study I consider the order Salmoniformes to contain the fishes included in Rosen's (1974) and Nelson's (1984) classifications of the group. The specific composition of the order has remained essentially the same since Rosen removed the stomiatoids and myctophoids in 1973 and placed them among the higher teleosts.

The order Salmoniformes as defined herein contains about ninety genera and more than three hundred species distributed among seventeen families: the Esocidae, Umbridae, Salmonidae, Osmeridae, Plecoglossidae, Salangidae, Sundasalangidae, Retropinnidae, Prototroctidae, Lepidogalaxiidae, Galaxiidae, Aplochitonidae, Alepocephalidae, Platytroctidae, Argentinidae, Bathylagidae, and Opisthoproctidae. This familial arrangement follows that of Nelson (1984) with two exceptions: he places the Retropinnidae and Prototroctidae as subfamilies (the Retropinninae and Prototroctinae, respectively) within the family Retropinnidae, and the Galaxiidae and Aplochitonidae as subfamilies (the Galaxiinae and Aplochitoninae, respectively) within the family Galaxiidae. However, McDowall (1971b, 1976a, 1979, 1980) and Berra (1981) give each of these four taxa family status, and I followed this lead.

All salmoniforms except the Argentinoidei (*sensu* Greenwood and Rosen 1971) and some osmerids (see McAllister 1963) live permanently in fresh water or are anadromous. Except for the Argentinoidei they have an amphitropical (panboreal and panaustral) distribution. A few species (some salangids, the two sundasalangid species, and the galaxiid *Nesogalaxias*) are found in the tropics. Four of the seventeen families are restricted to the northern part of the Northern Hemisphere (the Esocidae, Umbridae, Salmonidae, and Osmeridae), three are found only in the Orient (the Plecoglossidae, Salangidae, and Sundasalangidae), and five are restricted to the southern part of the Southern Hemisphere (the Lepidogalaxiidae, Retropinnidae, Prototroctidae, Galaxiidae, and Aplochitonidae). The five argentinoid families (the Alepocephalidae, Platytroctidae, Argentinidae, Bathylagidae, and Opisthoproctidae) are entirely marine (most are deep-sea) and have a pandemic distribution.

Esocidae

The esocids, or pikes, are large predaceous fishes (some may reach two metres in length and weigh fifty kilograms) that are restricted to the fresh waters of the northern part of the Northern Hemisphere (see Berra 1981). They are important sport fish, and partly because of this there is an extensive literature dealing with their biology. The family has one genus, *Esox*, with five extant species. One species, *E. lucius* (the northern pike) has a circumpolar distribution, one is endemic in the Amur River region of Siberia (*E. reicherti*), and three species are restricted to eastern North America (*E. masquinongy, E. niger*; and *E. americanus*).

Compared to other salmoniforms the esocids have a good fossil record and numerous fossil species have been described (see Nelson 1972; Sytchevskaya 1976; Wilson 1980, 1984 for details). The oldest-known fossil esocid (in fact, the oldest known species that can definitely be assigned to an extant salmoniform family), *E. tiemani*, comes from Palaeocene formations of Alberta, Canada, and is about sixty million years old (see Wilson 1980, 1984). This species is similar morphologically to the extant *E. lucius*, more so than the numerous younger fossil species from Eurasia (the oldest of which is Oligocene).

Umbridae

The umbrids, or mudminnows, are small fishes (with a maximum length of about eighteen centimetres) that are the closest relatives of the pikes, and like them, are restricted to the fresh waters of the Northern Hemisphere (see Berra 1981; Wilson and Veilleux 1982). The family contains three extant genera with five (possibly six) species, and has an intriguing disjunct distribution in Europe, Siberia, and North America. The genus *Dallia* has one species, *D. pectoralis*, that is found in Alaska and easternmost Siberia, and according to Chereshnev and Balushkin (1980), a second, *D. admirabilis*, that is restricted to the Amguema River basin of easternmost Siberia. The genus *Novumbra* (with one extant species, *N. hubbsi*) has a very limited distribution in western North America; it is endemic to the Chehalis River and adjacent localities on the Olympic Peninsula of Washington State (see Hagen *et al.* 1972). The genus *Umbra* has three species: *U. krameri* in the Danube and Dniester River basins of eastern Europe; and two allopatric species in eastern North America, *U. pygmaea* along the Atlantic coast of the United States, and *U. limi* in the Great Lakes region and the Upper Mississippi Valley.

The fossil record of the Umbridae is better than most salmoniforms, and extends at least to the Oligocene, and possibly the Eocene and Palaeocene if the problematic esocoids *Boltyshia* and *Palaeoesox* are included in the family (see Cavender 1969; Nelson 1972; Sytchevskaya 1976). Cavender (1969) concluded that the Eocene genus *Palaeosox* was more closely related to the Umbridae than to the Esocidae, and Nelson (1972) included it *incertae sedis* within the Umbridae. Sytchevskaya (1976) placed it (along with the newly discovered *Boltyshia*) in its own family, the Palaeoesocidae, within the Esocoidei, but considered it more closely related to the mudminnows than to the pikes. A similar problem of placement occurs with many other esocoid fossils. The oldest fossil that can definitely be assigned to the Umbridae is *Novumbra oregonensis* from the Oligocene of Oregon, which differs little from its extant sister species *N. hubbsi* (see Cavender 1969). The extinct genus *Proumbra* from the Oligocene of Siberia is also almost certainly an umbrid (see Cavender 1969; Nelson 1972; Sytchevskaya 1976).

Salmonidae

The family Salmonidae contains the trouts, charrs, salmons, graylings, and whitefishes. It has a circumpolar distribution in the cool and cold waters of the northern part of the Northern Hemisphere, and includes both freshwater and anadromous species (see Berra 1981; Nelson 1984). Some species (e.g., *Salmo gairdneri*) have been introduced to other parts of the world because of their importance as sport fish, so that presently salmonids are found on all continents except Antarctica (see MacCrimmon 1971). Their maximum size ranges from about one fifth of a kilogram in *Coregonus kiyi* to one hundred and five kilograms in *Hucho hucho* (see Holčík 1982). Because the family includes some of the world's most important sport and commercial species there is an extensive literature dealing with the lower level taxonomy and fisheries management and biology of the group.

The Salmonidae is usually divided into three subfamilies: the Coregoninae (the whitefishes), the Thymallinae (the graylings), and the Salmoninae (the trouts, charrs, and salmons) (see Norden 1961; Kendall and Behnke 1984; Nelson 1984). According to Nelson (1984) there are ten genera with about sixty species. The Coregoninae consist of three genera: *Prosopium*, with six species; *Coregonus*, with twenty-five species placed in two subgenera; and *Stenodus*, with one species. *Stenodus* is anadromous and found in arctic Asia and arctic North America. *Coregonus* is circumpolar and usually found in fresh water (it is occasionally anadromous). One species of the freshwater genus *Prosopium* is found in North America and Siberia, the remaining five are endemic to North America (see Norden 1961; Behnke 1972). The subfamily Thymallinae contains only the genus *Thymallus* with four freshwater species (two in Mongolia, one in Europe, and one that is widespread across northern Asia and North America) (see Norden 1961). *Thymallus* reaches a maximum size of about two kilograms (see Holčík 1982). The Salmoninae are classified in six genera and about thirty species according to

Nelson (1984): *Brachymystax, Hucho, Salmothymus, Salvelinus, Salmo*, and *Oncorhynchus*. Some workers would also include *Cristivomer* and *Parasalmo* but exclude *Salmothymus* (see Vladykov 1963; Qa[illegible]i 1964; Kendall and Behnke 1984). *Brachymystax* contains one species found in fresh waters from northern Asia to Korea. *Hucho* has four species; three are freshwater and are found in the Danube River basin of Europe, and in northern Asia as far south as Korea; the fourth (*H. perryi*) is diadromous and is found in northern Japan, Sakhalin Island, and the adjacent areas on the mainland of Asia (see Vladykov 1963; Holčík 1982). *Salmothymus* has three freshwater species that are endemic to a small area in southern Yugoslavia. *Salvelinus* (the charrs), with eight or nine freshwater and anadromous species, is holarctic in distribution and has the most northerly distribution of any fish found in fresh water (see Behnke 1980). *Salmo* (the trouts), with about ten freshwater and anadromous species, occurs in Europe, eastern and western North America, and eastern Asia (see Vladykov 1963). *Oncorhynchus* (the Pacific salmon), with six or seven species, is anadromous, and is found in the coastal areas of the North Pacific from Japan to California, plus the adjacent parts of the Arctic Ocean.

The fossil record of the Salmonidae is not as good as that of the esocoids, but is better than that of the remaining salmoniforms (see LaRivers 1964; Cavender and Miller 1972; Kimmel 1975; Smith 1975; Wilson 1974, 1977). Apart from otolith and scale specimens, the oldest known salmonid is *Eosalmo driftwoodensis* from freshwater Eocene deposits of British Columbia, Canada (see Wilson 1974, 1977). Although Wilson (1977) placed *Eosalmo* in the subfamily Salmoninae he noted (p. 1) that it "is morphologically intermediate between Recent Thymallinae and Salmoninae." Other salmonid fossils include the giant salmonine, *Smilodonichthys rastrosus*, estimated to be nearly two metres long, from freshwater Pliocene deposits of California and Oregon. Cavender and Miller (1972) consider it to be closely related to the extant genus *Oncorhynchus*. The salmonine genera *Rhabdofario* and *Paleolox* have been described from freshwater Miocene-Pliocene deposits of eastern Idaho, as have various specimens that are assigned to the extant genus *Oncorhynchus* (see Kimmel 1975; Smith 1975). The Miocene of Europe has also yielded *Protothymallus* (see Wilson 1977), and

Salmo cyniclope was described by LaRivers (1964) from the Miocene of Nevada. The oldest known coregonine is the extinct species *Prosopium prolixus* from the Pliocene of eastern Idaho (see Smith 1975). According to Smith this species may be the largest, most predaceous, known coregonine, and is definitely the largest, most predaceous, known *Prosopium*.

Osmeridae

The Osmeridae, or smelts are relatively small (most species are less than twenty centimetres according to Nelson 1984), silvery, predaceous fishes that are commercially important (see McAllister 1963, 1966; Berra 1981; Nelson 1984). They are a circumpolar family found in the cold and temperate coastal waters of the Northern Hemisphere. The southern extent of their range is northern Japan and Korea in Asia, France in Europe, and California in North America. Most species spend their lives in the waters of the continental shelf, with some entering fresh water to spawn (andromous species), and some spawning in the ocean along beaches (e.g., *Mallotus*). Only a few species are restricted to fresh water (e.g., *Hypomesus olidus*). The presence of smelt in the Great Lakes of North America is the result of their introduction by man (see McAllister 1963).

In his 1963 revision of the Osmeridae, McAllister divided the family into two subfamilies with six genera and ten species: the Hypomesinae, containing *Hypomesus* (three species) and *Mallotus* (one species); and the Osmerinae, containing *Osmerus* (one species), *Allosmerus* (one species), *Spirinchus* (three species), and *Thaleichthys* (one species). Currently there is controversy concerning the number of species contained in the genera *Hypomesus* and *Osmerus* (see Lee *et al.* 1980). The genus *Hypomesus* has completely marine, anadromous, and freshwater forms that are found in the North Pacific and the adjacent parts of the Arctic Ocean and their drainages (see McAllister 1963). *Mallotus* is completely marine with a circumpolar distribution in the North Pacific, North Atlantic, and Arctic Oceans. *Osmerus* can be anadromous or landlocked, and has a circumpolar distribution in the North Pacific, North Atlantic, and Arctic Oceans, and their drainages (it is most common in the North Atlantic region). *Osmerus* readily adapts to a completely freshwater existence and natural freshwater populations are common, particularly in eastern North America. *Allosmerus* is completely marine and confined to the west coast of the United States. *Spirinchus* is anadromous and found in the North Pacific and its drainages. *Thaleichthys* is anadromous and restricted to the west coast of North America.

The fossil record of the Osmeridae is poor. The oldest osmerids are specimens of the genus *Mallotus* from the Pleistocene and post-Pleistocene of Canada, Greenland, Iceland, Norway, and Yugoslavia that are similar to living *Mallotus* (pers. obs.; McAllister 1963, 1966). According to McAllister (1966), Stinton (1963) described a new species, *Hypomesus glaber*, from otoliths in Miocene deposits of Victoria, Australia. However, considering the lack of corroborating evidence, and the biogeographic significance of such a find, I find Stinton's claim to be doubtful, as does Nolf (1985, p. 120) in his important monograph on fish otoliths. Patterson (1970) described two salmoniforms (*sensu* Greenwood *et al.* 1966) from the marine Upper Cretaceous of Lebanon (*Humbertia* and *Gaudryella*) that he considered similar to the Osmeroidei and Stomiatoidei (*sensu* Greenwood *et al.* 1966), especially the hypomesine osmerids (i.e., *Hypomesus* and *Mallotus*). However, he concluded (p. 207) that "these relationships are not sufficiently close to place either genus in one of these suborders, and they are left as Salmoniformes *incertae sedis*."

Plecoglossidae

The Plecoglossidae contains only one species that is endemic to the Orient, *Plecoglossus altivelis* (see Chapman 1941a; Berra 1981; Nelson 1984; Komada 1985; Howes and Sanford 1987). The ayu fish is distributed along the Pacific coast of northern China, Japan, Korea, and in mainland China south to (and including) Taiwan. This relatively small fish (its maximum length is about thirty centimetres) is usually anadromous but is also found in lakes. It has highly specialized dentition on its upper and lower jaws consisting of a series of movable, small, comb-like teeth that are seated on a fold of skin on the maxilla and mandible and that apparently serve to strain phytoplankton from the water (see Chapman 1941a; Komada 1985; Howes and Sanford 1987). Although it superficially resembles a salmonine, its closest affinities appear to be with the Osmeridae. *Plecoglossus* lacks a fossil record.

Salangidae

Salangids (the noodlefishes or icefishes) are relatively small, slender, soft-bodied, neotenic fishes that are transparent or translucent, and are endemic to the Orient (see Roberts 1981, 1984). They reach a maximum length of about sixteen centimetres. They can be anadromous or freshwater, and inhabit the sea coasts, rivers and lakes of eastern Asia, from southeastern Siberia (the Sakhalin Island, Amur River area) in the north (including Japan), to northern Vietnam in the south. According to Roberts (1984), the greatest concentrations of genera and species are in China and Korea. All are apparently predators, with the largest species feeding mainly on fishes. They are highly unusual in that their skeleton (including the suspensorium) is largely cartilaginous. Roberts (1984) created the superfamily Salangoidea to include the Salangidae + Sundasalangidae and noted (p. 203) that it "apparently differs from all other Pisces in having a suspensorium in which the cartilaginous palatine and pterygoid (of the mandibular arch) and quadrate and hyomandibular (of the hyomandibular arch) are fused into a single element, the hyopalatine."

The Salangidae were divided by Roberts (1984) into three subfamilies containing four genera and eleven species. The Protosalanginae are monotypic with only *Protosalanx chinensis*; the Salanginae have one genus, *Salanx*, with four species; and the Salangichthyinae have two genera, *Neosalanx*, with four species, and *Salangichthys* with two species. Only *Salanx reevesi* and *Neosalanx brevirostris* are found as far south as Vietnam. The Salangidae lack a fossil record.

Sundasalangidae

The sundasalangids (or Sundaland noodlefishes) are closely related to, but even more specialized than the salangids. The family was erected by Roberts in 1981, and contains only one genus, *Sundasalanx*, with two species, *S. microps* and *S. praecox*. However, Fink (1984b) does not accept the creation of this family because he believes (p. 204) it "would probably render the Salangidae paraphyletic" and "because it artificially breaks up a group all of whose members share a unique evolutionary history."

According to Roberts (1984) *Sundasalanx* is the only truly tropical genus in the order Salmoniformes. It is known only from fresh water, and so far, has been collected in only a few disjunct localities in Southeast Asia: the Kapuas River in western Borneo, the southernmost part of Thailand (the Isthmus of Kra), and the Mekong River and its tributaries in eastern Thailand. They are unusually small fishes, with a maximum size of less than twenty-five millimetres. In fact, *S. praecox* is thought to be the smallest adult salmoniform, and among the smallest of all adult vertebrates, with both sexes being sexually ripe at a standard length of only fifteen millimetres (see Roberts 1981). The Sundasalangidae have no fossil record.

Retropinnidae

The retropinnids, or Southern Hemisphere smelts, are small, silvery, shoaling fishes that superficially resemble the osmerids of the Northern Hemisphere, hence their common name (see McDowall 1978, 1979; Berra 1981; Nelson 1984). They have a maximum length of about fifteen centimetres, but are usually less than ten centimetres long. The family is found in the coastal seas, lowland rivers, and inland rivers and lakes of southeastern Australia, Tasmania, New Zealand, and the Chatham Islands. There are only two genera: *Retropinna*, with three species (*R. retropinna*, *R. semoni*, and *R. tasmanica*), and *Stokellia* with one species (*S. anisodon*). *R. retropinna* occurs as diadromous, brackish-lake, and freshwater-lake populations and is found around the entire coastline of New Zealand (it is sympatric with *Stokellia* along the eastern coast of South Island). The diadromous populations are thought to spawn in or just above estuaries (see McDowall 1979). *R. semoni* is a freshwater species that is present in the lakes and slow-flowing rivers of southeastern Australia (Queensland, New South Wales, Victoria and South Australia). It apparently lacks anadromous stocks. *R. tasmanica* is primarily anadromous (one landlocked population has been described) and is restricted to Tasmania. *S. anisodon* is anadromous and endemic to the eastern and southern coasts of South Island, New Zealand. The family has no fossil record.

Prototroctidae

The prototroctids, or Southern Hemisphere graylings, are relatively small (to about thirty centimetres in length) fishes that superficially resemble some salmonids, but are closely related to the Retropinnidae (see McDowall 1974, 1976a, 1978; Bell *et al.* 1980; Berra 1981). The family consists of one genus, *Prototroctes*, with two species, *P. maraena* (the Australian grayling) and *P. oxyrhynchus* (the New Zealand grayling). *P. oxyrhynchus*, which has not been collected since the mid-1920's and is probably extint, was once widely distributed in the rivers and streams of New Zealand (mostly near the sea), but was never recorded from the Chatham Islands. *P. maraena* is rare and is found in clear, gravel-bottomed coastal rivers in southeastern Australia, from about the latitude of Sydney southward along the coasts of New South Wales, Victoria, and Tasmania. The adults live and spawn in fresh water; however, the juveniles are apparently swept downstream into brackish water (see Berra 1981). Both species have highly specialized dentition and an alimentary canal that is longer than that of other salmoniforms (see McDowall 1974; Berra 1981). The dentition consists of numerous blunt, comb-like teeth on the long premaxilla that oppose a unique horny shelf (with teeth around its medial edge) on the lower jaw. According to Berra, Southern Hemisphere graylings are omnivorous and feed on algae, cladocerans, and insects. The specialized dentition in *Prototroctes* is unlike that found in *Plecoglossus* and is almost certainly an example of convergence (see Chapman 1941a; McDowall 1974; Komada 1985; Howes and Sanford 1987). The Prototroctidae have no fossil record.

Lepidogalaxiidae

The Lepidogalaxiidae contain one species of uncertain relationship, *Lepidogalaxias salamandroides* (see Mees 1961; Frankenberg 1969; McDowall 1969; Rosen 1974; Lake 1978; Allen 1982; Christensen 1982; McDowall and Pusey 1983; Merrick and Schmida 1984; Roberts 1984; Berra and Allen 1986). It is commonly called the scaled galaxiid (because it resembles the galaxiids, but unlike them, has scales) or the salamander fish. This tiny fish (it has a maximum length of almost seven centimetres) has a number of unusual features that include (to name a few) the ability to bend its neck either sideways and/or downwards when searching for food, the ability to survive periods of drought by burrowing in mud or under damp leaves, and a highly modified anal fin in the adult male that is unlike that found in any other teleost.

Lepidogalaxias is present only in fresh water and is endemic to a small area about two hundred and fifty kilometres from east to west, and thirty to sixty kilometres north to south, in the southwestern corner of western Australia (see Christensen 1982; McDowall and Pusey 1983, fig. 6). It is most commonly found in shallow streams and pools in a region of acidic, peaty flats. Three species of galaxiids, *Galaxias occidentalis, Galaxiella nigrostriata,* and *Galaxiella munda*, occur within its range. Interestingly, the latter two species are about the same size as *Lepidogalaxias*, and *Galaxiella nigrostriata* occurs sympatrically with it in small pools that dry up intermittently (Dr. T.M. Berra, pers. comm.; also see Berra and Allen 1986). *Galaxiella munda* has been collected at the type locality of *Lepidogalaxias* (see McDowall and Frankenberg 1981).

Since its description by Mees in 1961 its relationships have been controversial. Mees placed it in the Galaxiidae, but suggested that perhaps it should occupy a separate subfamily. Scott (1966) questioned its inclusion in the Galaxiidae and noted (p. 251) that "a new family is perhaps called for." Similarly, McDowall (1969, p. 796) stated that "From discussions with Donn E. Rosen, P. Humphrey Greenwood, and R. Frankenberg, it is agreed that the odd little species *Lepidogalaxias salamandroides* is not a galaxiid." Frankenberg (1969) noted that it shared morphological similarities with the esocoids (the pikes and mudminnows) of the Northern Hemisphere but concluded (p. 125) that "While the possibility of esocoid relationships for *Lepidogalaxias* must still be allowed, it is considered that the evidence as a whole favours a galaxioid relationship." He placed it in its own family, the Lepidogalaxiidae, and proposed (p. 125) that "the suborder Galaxioidei (of Greenwood, 1966) should be divided into two superfamilies, one to contain *Lepidogalaxias* (Lepidogalaxioidea), and the other the rest of the galaxioid families (Galaxioidea)." In a 1972 paper, Nelson (1972, p. 38) noted that "The relationships of *Lepidogalaxias* remain obscure.... [It] may be the sister group of all other galaxiines (Frankenberg, MS), but sensory canal and pore data are inconclusive. Further comparative study is called for." In a radical departure, Rosen (1974) presented evidence suggesting that *Lepidogalaxias* was an esocoid, and placed it in the Esocoidei as a separate superfamily (the Lepidogalaxioidea) along with the Esocoidea (the Esocidae + Umbridae). Fink and Weitzman (1982) were dubious of Rosen's hypothesis and noted (p. 80) that "Of the eleven characters Rosen (1974) used to place *Lepidogalaxias* in the Esocae [= Esocoidei], only four appear to be appropriate for inference of relationship between those groups ... In view of the reductive nature of all of these characters and the very small size and benthic 'habits' of *Lepidogalaxias*, and in view of the importance of the biogeographic hypothesis suggested by this hypothesis of relationships, it appears to us that a further search for characters is warranted." In a 1984 study of the salangoids, Roberts examined *Lepidogalaxias* and wrote (p. 216), "My observations suggest that *Lepidogalaxias* is indeed related to Galaxiidae ... but I doubt that it represents the 'primitive sister group of galaxiids or galaxioids'; it is more likely to be a highly specialized galaxiid or galaxioid derivative." Nelson (1984) placed it in its own suborder, the Lepidogalaxioidei, within the order Salmoniformes (along with the Esocoidei, Argentinoidei, and Salmonoidei). Finally, Fink (1984b, p. 205) stated that "I remain unconvinced by Rosen's (1974) hypothesis that the genus belongs with the esocoids," and using new characters, places it, along with the Salmonidae, as the sister group of the Neoteleostei (i.e., the three groups form an unresolved trichotomy). Fink, however, does not have much confidence in this placement, stating (p. 205) that "more work remains to be done before we can be really confident in the phylogenetic placement of this intriguing fish."

Galaxiidae

The family Galaxiidae is the most speciose, and has the widest distribution, of the five salmoniform families endemic to the Southern Hemisphere (see McDowall 1968, 1970, 1971a, 1973, 1978, 1984; Berra 1981; McDowall and Frankenberg 1981). It is comprised of relatively small, scaleless, and elongate fishes that are often benthic and cryptic in habit. According to McDowall (1978) most species are between four and fifteen centimetres long, although several reach about twenty-five and one is nearly sixty centimetres (*Galaxias argenteus* of New Zealand). Most are confined to fresh water, but several species are diadromous and have larval, post-larval and juvenile stages that occur in the sea. Diadromy is represented in at least six species, and it is McDowall's (1984) view that it is the primitive character state for the family. Numerous landlocked populations of diadromous species occur. All galaxiids are thought to spawn in fresh water, except for *Galaxias maculatus*, which spawns in tidal, estuarine waters. The larvae of this species are apparently washed out to sea and have been found as far as seven hundred kilometres from shore (see Nelson 1984).

The Galaxiidae are confined largely to the Southern Temperate zone and have an intriguing distribution. Species occur (from west to east) in southwestern Australia, southeastern Australia, Tasmania, Lord Howe Island, New Caledonia (the most northerly point of the group's distribution at latitude 22°S), New Zealand, Aukland and Campbell Island (both south of New Zealand), the Chatham Islands (east of New Zealand), southern Chile (south of latitude 33°S) and Argentina, Tierra del Fuego (the most southerly point of the group's distribution at about latitude 55°S), the Falkland Islands, and the southwestern corner of South Africa.

The Galaxiidae have six genera with thirty-seven species: *Galaxias*, with twenty-four species; *Galaxiella* with three species; *Paragalaxias* with four species; *Nesogalaxias* with one species; *Neochanna*, with three species; and *Brachygalaxias*, with two species (see McDowall 1970, 1971a, 1973, 1984; McDowall and Frankenberg 1981). *Galaxiella* is restricted to southwestern Australia (*G. nigrostriata* and *G. munda*) and southeastern Australia and Tasmania (*G. pusilla*). *G. pusilla* is apparently the only species in the family in which sexual dimorphism has been described (see McDowall and Frankenberg 1981). *Paragalaxias* is endemic to Tasmania. *Nesogalaxias* is found only in two mountain lakes in New Caledonia (see McDowall 1968). *Neochanna* (the mudfish) is endemic to New Zealand, and is unusual in that it aestivates in the mud during periods of drought (see McDowall 1970, 1978). *Brachygalaxias* is found only in central Chile (see McDowall 1971a). *Galaxias* is present in all the areas mentioned except New Caledonia. Most of its species are endemic to one area (e.g., *G. olidus* is found only in southeastern Australia, excluding Tasmania). However, five species that are diadromous have a wider distribution. *G. truttaceus* is found in southwestern Australia, southeastern Australia, and Tasmania; *G. brevipinnis* is found in southeastern Australia, Tasmania, New Zealand, and the Chatham, Auckland, and Campbell Islands; and *G. argenteus* and *G. fasciatus* are both present in New Zealand and the Chatham Islands. *G. maculatus* has the most widespread distribution of all galaxiids, and occurs in southwestern Australia, southeastern Australia, Tasmania, Lord Howe Island, New Zealand, the Chatham Islands, South America, and the Falkland Islands. The unique distribution of this species has raised interesting biogeographic questions, and both continental drift and dispersal mechanisms have been proposed to account for it (see Nelson 1984 for a review of this controversy).

Species abundance is greatest in Australia and Tasmania (with twenty species, eighteen of which are endemics) and decreases eastward to New Zealand (thirteen species, eleven endemics), South America (five species, four endemics), and South Africa (one endemic species). The most speciose area is southeastern Australia and Tasmania (Tasmania has eleven endemic species).

Although there are considerable data available concerning the ecology and population biology of the galaxiids, the intergeneric relationships of the six genera are unknown, and very little information is available concerning interspecific relationships (the only studies are based on overall similarity, see McDowall 1984).

The fossil record of the Galaxiidae is poor, and of no help in phylogenetic reconstruction. McDowall (1976b) described some galaxiid fossils from the Pliocene of New Zealand and concluded (p. 21) that "About all that can be said is that there existed in New Zealand Rivers, in Pliocene times, species of *Galaxias* no different from those now present in similar waters."

Aplochitonidae

The family Aplochitonidae has a trans-Pacific range with species in Tasmania and southern South America (see Blackburn 1950; McDowall 1969, 1971b, 1984). It contains two rather dissimilar genera, *Aplochiton* with two (perhaps three) species, and *Lovettia* with one species. *Aplochiton* is a relatively small, elongate, scaleless fish that, unlike the galaxiids, has an adipose fin and an anteriorly placed dorsal fin. It reaches a maximum standard length of about twenty-four centimetres. Its two species (*A. zebratus* and *A. taeniatus*) are similar morphologically, and are found in fresh water lakes and streams in southern Chile (south of latitude 39°S), the adjacent part of southwestern Argentina, Tierra del Fuego, and the Falkland Islands. It spawns in fresh water. According to McDowall (1984) some movement to sea occurs.

Lovettia sealii (the Tasmanian whitebait) is similar externally to *Aplochiton* but is much smaller (reaching a maximum standard length of only seven centimetres), rather weakly ossified, and the adults are distinctly sexually dimorphic. It is found only along the north and southeast coasts of Tasmania. Mature adults migrate from the sea to spawn in fresh water and the larvae drift downstream to the sea. Because the differences between *Lovettia* and *Aplochiton* are rather pronounced, and because they are widely separated geographically, there is some doubt as to whether or not *Lovettia* and *Aplochiton* are sister taxa (i.e., the Aplochitonidae may not be holophyletic). Fink (1984b) expressed this uncertainty by placing *Lovettia, Aplochiton* and the Galaxiidae as an unresolved trichotomy (also see McDowall 1971b, 1984; Berra 1981). The Aplochitonidae have no fossil record.

Alepocephalidae

The Alepocephalidae (the smooth-heads or slickheads) are a family of small to medium-sized (to about one metre standard length), marine, deep-sea fishes that often have large eyes and are usually darkly coloured (see Marshall 1966; Nielsen and Larsen 1968; Gosline 1969; Greenwood and Rosen 1971; Iwamoto *et al.* 1976; Markle 1976; Markle and Quéro 1984; Nelson 1984). They are deep-water benthic to pelagic and inhabit a depth range from one hundred to nearly six thousand metres, but are most commonly found below one thousand metres (see Markle 1976). They have been collected in most parts of the Pacific, Atlantic, and Indian Oceans, and appear to be most common along the continental slope and along submarine ridges.

In the most extensive study of the group to date, Markle (1976) places about sixty species in the family, distributed among twenty-four genera. The status of the Alepocephalidae as a holophyletic group is uncertain, since according to him, there is no derived character state uniting them. He divides the family into five "generic groups" (which represent grades of development and do not necessarily imply phylogenetic relationship) that he established "as a starting point for further work": the "Aulastomatomorpha group" with six genera (*Asquamiceps, Aulastomatomorpha, Conocara, Einara, Ericara,* and *Leptoderma*), the "*Bathyprion* group" with three genera (*Bathyprion, Mirognathus*, and *Rinoctes*), the "genus A group" with five genera (*Anomalopterichthys, Rouleina, Xenodermichthys, Photostylus*, and genus A), the "*Bathylaco* group" with four genera (*Bajacalifornia, Bathylaco, Herwigia,* and *Narcetes*), and the "*Alepocephalus* group" with six genera (*Alepocephalus, Bathytroctes, Nomoctes, Talismania, Brunichthys*, and *Bellocia*). The membership of each group is uncertain, as are the interrelationships. He tentatively places the genus *Leptochilichthys* (with two species) in its own monotypic family, the Leptochilichthyidae. In my study I follow Markle except that I include *Leptochilichthys* within the Alepocephalidae.

Other workers classify the alepocephalids differently. Marshall (1966) considered Markle's assemblage to be made up of three families: the Bathyprionidae (with only *Bathyprion*), the Leptochilichthyidae (with only *Leptochilichthys*), and the Alepocephalidae. Nielsen and Larsen (1968) and Nielsen (1972) recognized these three families plus the Bathylaconidae (with two genera, *Bathylaco* and *Herwigia*). Greenwood and Rosen (1971) recognized the Alepocephalidae (which included the Bathylaconidae and Leptochilichthyidae) and tentatively recognized the Bathyprionidae. Iwamoto *et al.* (1976) concurred with Greenwood and Rosen's placement of the bathylaconids within the Alepocephalidae. Finally, Nelson (1984) divided the family Alepocephalidae into four subfamilies: the Alepocephalinae (with about twenty-two genera), the Bathyprioninae (with *Bathyprion*), the Bathylaconinae (with *Bathylaco* and *Herwigia*), and the Leptochilichthyinae (with *Leptochilichthys*).

The only fossil alepocephalid is *Carpathichthys polonicus* from marine Oligocene deposits of Poland (see Jerzmańska 1979). Most bones of the suspensorium are relatively well preserved (the ectopterygoid, mesopterygoid, quadrate, metapterygoid, preoperculum, and hyomandibular) and closely resemble those of modern alepocephalids judging from Jerzmańska's descriptions and figures. Jerzmańska (p. 67) claims that the "Recent genus *Rouleina* Jordan displays the highest degree of resemblance to *Carpathichthys*."

Platytroctidae

The Platytroctidae (= Searsiidae or Searsidae) is a family of relatively small (most are less than twenty-five centimetres standard length), marine, deep-sea fishes that resemble, and are closely related to the Alepocephalidae (see Parr 1951, 1960; Marshall 1966; Nielsen and Larsen 1968; Gosline 1969; Greenwood and Rosen 1971; Markle 1976; Matsui and Rosenblatt 1979, 1987; Nelson 1984; Quéro *et al.* 1984). They are primarily mesopelagic and bathypelagic, and have been collected at depths of between one hundred and three thousand metres (they are most common below about five hundred metres). They are found in most parts of the Pacific, Atlantic, and Indian Oceans, and like the alepocephalids, appear most commonly along the continental slope and along submarine ridges.

Platytroctids are readily distinguished from alepocephalids by their possession of a unique structure called the shoulder or post-cleithral organ (for other differences see Matsui and Rosenblatt 1987). This organ is a large, round, black sac that lies directly medial to the dorsal part of the cleithrum, and opens to the exterior through a posteriorly-directed tube that is visible externally dorsal to the pectoral fins. It is apparently concerned with the secretion of a luminous material (see Parr 1960; Herring 1972; Matsui and Rosenblatt 1987).

In the first revision of the group, Parr (1960) recognized twelve genera with seventeen species: *Mirorictus* with one species, *Platytroctes* with one species, *Platytroctegen* with one species, *Sagamichthys* with one species, *Persparsia* with two species, *Searsia* with one species, *Holtbyrnia* with four species, *Maulisia* with one species, *Mentodus* with two species, *Normichthys* with one species, *Pellisolus* with one species, and *Barbantus* with one species. At this time the group was named either the Searsiidae or Searsidae. Since then, numerous other species have been discovered and described (e.g., see Matsui and Rosenblatt 1979). Matsui and Rosenblatt (1987) prepared a second revision of the family and changed the familial name to Platytroctidae because it has priority over Searsiidae. They recognize thirty-seven species in thirteen genera, including: *Persparsia* (one species), *Paraholtbyrnia* (one species), *Holtbyrnia (eight species), Sagamichthys* (three species), *Searsia* (one species), *Mirorictus* (one species), *Tragularius* (four species), *Pellisolus* (three species), *Maulisia* (five species), *Normichthys* (two species), *Searsioides* (two species), *Platytroctes* (two species), and *Barbantus*, (four species). They synonymize *Platytroctegen* with *Platytroctes*, and *Mentodus* with *Holtbyrnia*. Some of the taxa previously placed in *Mentodus* are placed in a new genus, *Tragularius*. The genera *Paraholtbyrnia* and *Searsioides* were erected by Krefft in 1967, and Sazonov in 1977, respectively (see Matsui and Rosenblatt 1987). No fossil platytroctids are known.

Argentinidae

The Argentinidae are a marine family of moderately small (most reach a maximum length of less than twenty-five centimetres), elongate, silvery fishes that usually have large eyes and small mouths (see Chapman 1942a; Cohen 1958a, 1964, 1970, 1984a; Cohen and Atsaides 1969; Parin and Shcherbachev 1982; Ahlstrom *et al.* 1984). They are commonly called argentines or herring smelts. The family contains two genera with twenty-one species: *Argentina* with twelve species (see Cohen 1958a; Cohen and Atsaides 1969), and *Glossanodon* with nine species (see Cohen 1958a, 1970; Cohen and Atsaides 1969; Parin and Shcherbachev 1982). The species are notably similar ecologically and morphologically according to Cohen (1958a), and are considered to be closely related to the bathylagids and opisthoproctids by most workers. Argentines, at least as adults, are usually found near the bottom, and are restricted to the deeper parts of the continental shelf and the edges of the continental slope. They have been collected from near the surface to about nine hundred metres, but are most common between one and four hundred metres (see Cohen 1958a; Cohen and Atsaides 1969). Their distribution is worldwide, and includes the shallower parts of the Pacific, Atlantic, and Indian Oceans.

The only fossil argentinid is *Glossanodon musceli* from marine Oligocene deposits of Poland and Romania (see Jerzmańska 1967; Kotlarczyk and Jerzmańska 1976). According to Jerzmańska this extinct species is very similar to extant species of the genus *Glossanodon*. Fossil species referred to the genus *Argentina* have been described from otoliths found in Tertiary deposits of various parts of Europe (see Cohen 1958a).

◆

Bathylagidae

The Bathylagidae (the deep-sea smelts) are small (to about twenty-five centimetres in length) marine, deep-sea fishes that can be black to silvery, and have large eyes that are on the end of stalks in many larvae, but not in adults (see Beebe 1933; Chapman 1943, 1948a; Bertelsen 1958; Cohen 1964, 1984b; Greenwood and Rosen 1971; Hart 1973; Ahlstrom *et al.* 1984; Nelson 1984). There is some disagreement as to what genera and species to include in this family (e.g., see Cohen 1964, 1984b; Greenwood and Rosen 1971; Ahlstrom *et al.* 1984). For the purpose of my study I consider the Bathylagidae to contain four genera: *Bathylagus* (which includes the genus *Leuroglossus* of Borodulina 1968 and Peden 1981), with about twenty-seven species (see Cohen 1964; Nelson 1984); *Microstoma*, with one or two species (see Cohen 1964; Ahlstrom *et al.* 1984); *Nansenia*, with thirteen species (see Ahlstrom *et al.* 1984); and *Xenophthalmichthys*, with one or two species (see Bertelsen 1958; Cohen 1964; Ahlstrom *et al.* 1984). I follow the opinion of most workers, who believe that the latter three genera are each others' closest relatives (e.g., Bertelsen 1958; Cohen 1964; Ahlstrom *et al.* 1984). The classification of these three genera is however a matter of current debate, with Cohen (1964, 1984b) placing them as a subfamily (the Microstomatinae) within the Argentinidae; Bertelsen (1958) and Ahlstrom *et al.* (1984) placing them in a separate family (the Microstomidae or Microstomatidae, respectively) that is most closely related to the Bathylagidae (= *Bathylagus*); and Greenwood and Rosen (1971) placing them in the subfar [illegible] hylaginae (along with *Bathylagus*) within the family Bathylagidae (which also includes [illegible] Opistoproctinae). Because most workers consider them to be more closely related to the genus *Bathylagus* than to the Argentinidae, I placed them in the Bathylagidae, along with *Bathylagus*, for the purpose of my analysis.

As defined herein, the Bathylagidae have a worldwide distribution that includes the Pacific, Atlantic and Indian Oceans. They are oceanic, mesopelagic to bathypelagic fishes that have been collected from the surface to about three thousand metres, with ~~most~~ collections being made between about five hundred and fifteen hundred metres (see Cohen 1964, 1984b). Some species are thought to carry on rather extensive daily vertical migrations. They are rather similar ecologically and morphologically. No fossil bathylagids are known.

Opisthoproctidae

The Opisthoproctidae (the spookfishes or barreleyes) are highly specialized, bizarrely-shaped, relatively small (to about twenty-five centimetres in length), marine deep-sea fishes (see Trewavas 1933; Chapman 1942b; Cohen 1964, 1984c; Greenwood and Rosen 1971; Ahlstrom *et al.* 1984; Nelson 1984). They have small mouths, are silvery to dark, and have large, tubular, telescopic eyes (except *Bathylychnops*) that are directed anteriorly, dorsally or dorsolaterally. They range in shape from being long and narrow, as in *Dolichopteryx*, to short and truncated, as in *Opisthoproctus*.

The family has a worldwide distribution that includes most parts of the Pacific, Atlantic, and Indian Oceans. They are mesopelagic and have been collected at depths of about fifty to nearly three thousand metres, but are most common between about two hundred and one thousand metres.

The family contains six genera with at least twelve species: *Bathylychnops*, with one or more species; *Dolichopteryx*, with six or more species; *Macropinna*, with one species; *Opisthoproctus*, with two species; *Rhynchohyalus*, with one species; and *Winteria*, with one species (see Cohen 1964, 1984c; Ahlstrom *et al.* 1984). In the past these genera were often placed in separate families (the Macropinnidae, Dolichopterygidae, Opisthoproctidae, and the Winteriidae); however, the current consensus is that they constitute a distinct holophyletic group, and are usually placed in a single family, the Opisthoproctidae (although Greenwood and Rosen, 1971, placed them within the family Bathylagidae as a separate subfamily, the Opisthoproctinae). The interrelationships of the genera are uncertain, although Cohen (1964) placed them in two main groups based essentially on their length: the elongate *Bathylychnops - Dolichopteryx* group, the short-bodied *Opisthoproctus - Macropinna - Winteria* group, and the intermediate genus, *Rhynchohyalus*. However, the genera appear relatively similar osteologically and myologically (pers. obs.). No fossil opisthoproctids are known.

II. MATERIALS AND METHODS

A. BONES

Most specimens examined were cleared and stained for cartilage and bone using a modification of Taylor and Van Dyke's (1985) method: staining for cartilage using alcian blue 8 GX, followed by clearing with trypsin, followed by staining using alizarin red S. Some specimens examined were stained only for bone (these were not stained by the author). All cleared and stained specimens were stored in pure glycerin to which a few crystals of thymol were added. Specimens were dissected and examined using a Wild M7A stereomicroscope. The suspensorium was first examined *in situ* after removing the bones that obscure its lateral surface (primarily the circumorbitals and parts of the premaxilla and maxilla). To observe the medial surface the suspensorium was usually removed from the skull. In selected cases pencil drawings of the suspensorium were prepared with the aid of the aforementioned microscope equipped with a camera lucida attachment. To show its attachment to the skull the lateral aspect of the suspensorium was drawn while the unit was *in situ* (the lower jaw, opercular series, circumorbitals, and parts of the maxilla and premaxilla obscuring the lateral surface were removed, and therefore were not included on this drawing). To draw the medial aspect the suspensorium was first removed from the skull. In some cases both lateral and medial views were drawn after the suspensorium was removed from the skull. After the pencil drawings were completed they were inked. On these drawings bone is indicated by stippling, while clear areas on and around bones that are bordered by lines indicate cartilage. Cartilaginous areas are readily distinguishable from areas of bone by studying both lateral and medial drawings of the suspensorium.

Radiographs of some specimens were taken as stereophoto pairs using a "Torrex 150 Radiographic - Fluoroscopic System" X-ray machine. Radiographs were taken only if permission to clear and stain a specimen was not granted, or if an important species was represented by only one or two specimens.

Dry skeletons were examined when available.

In some cases whole specimens preserved in alcohol were examined externally for selected characters (e.g., the preoperculum) by removing the skin covering the bone.

Osteological nomenclature usually follows Norden (1961) and Harder (1975), whose work in turn was based on the terminology of earlier workers. Commonly used synonyms are mentioned in the text where they first occur. Specialized terminology referring to parts of each bone of the suspensorium are shown on Figure 3. Abbreviations used in the figures appear in the key on pages xxiii-xxviii .

B. MUSCLES

Specimens were dissected under a Wild M7A stereomicroscope. Depending on the institution, they were preserved in either isopropyl or ethyl alcohol (fifty-five and seventy per cent, respectively). To observe the external muscles of the suspensorium it was necessary to remove the eye, the circumorbital bones, and any skin and/or connective tissue obscuring their view. To observe all the muscles medial to the suspensorium the skull was first inclined at an angle such that the suspensorium to be examined could be viewed ventromedially. The interhyal (of the hyoid arch) was then disconnected from the hyomandibular - symplectic cartilage (of the suspensorium), allowing the hyoid arch and branchial basket to be moved to the side so that the suspensorium could be clearly seen. Any skin and/or connective tissue covering the muscles inserting on the medial surface of the suspensorium and operculum was then removed. In some cases these muscles were viewed laterally by destructively removing the dorsal part of the suspensorium (usually the dorsal part of the head of the hyomandibular) and/or operculum.

For selected specimens the external muscles of the suspensorium were drawn in lateral view with the aid of the aforementioned microscope equipped with a camera lucida attachment. These pencil drawings were then inked. On these drawings muscles are indicated by closely spaced lines (usually curving) that run parallel to one another, while ligaments and tendons are shown as short, closely spaced dashes (e.g., see Fig. 4). Generally, only outlines of bones are shown, although in some cases bone is stippled for clarity.

The nomenclature of the muscles follows Winterbottom's (1974a) descriptive synonymy of teleostean muscles. The term tendon is often synonymized with ligament, primarily because I could not readily distinguish between the two in many cases. Abbreviations used in the figures appear in the key on pages xxiii-xxviii .

C. MATERIAL EXAMINED

Specimens from all the major salmoniform groups were examined except for the recently described Sundasalangidae. However, the suspensorium of the sundasalangids was adequately described by Roberts (1981, 1984), and closely resembles that of the related salangids, of which numerous specimens were available. An effort was made to examine as many species belonging to the salmoniform assemblages as possible. At a minimum, about half of the genera belonging to a specific family were examined (e.g., eleven of twenty-five alepocephalid genera were studied). In some cases all the genera belonging to a family were studied (e.g., the six genera belonging to the Osmeridae). When studying a species, specimens of varying size were examined, when available, to check for osteological or myological changes during ontogeny. Ontogenetic changes were noted in the description of these species; however, for the most part descriptions are based on specimens of similar size to facilitate comparison. Specimens from the major non-salmoniform teleostean lineages were examined and compared to the salmoniforms. Fossil material was also studied. Published descriptions of species filled gaps in the data when specimens were not available.

The specimens examined are deposited in the following collections: The Australian Museum, Sydney (AMS); California Academy of Sciences, San Francisco (CAS, CAS-SU denotes that the specimen was formerly deposited at Stanford University); National Museum of Natural Sciences, National Museums of Canada, Ottawa (NMC); Scripps Institution of Oceanography, San Diego (SIO); Royal Ontario Museum, Toronto (ROM); The University of

Alberta Museum of Zoology, Edmonton (UAMZ); The University of Alberta [illegible]te Paleontology Collections, Edmonton (UAVP); The University of British Columbia Institute of Fisheries, Vancouver (UBCIF); United States National Museum of Natural History (Smithsonian Institution), Washington D.C. (USNM); Western Australian Museum, Perth (WAM).

Specimens less than eighteen centimetres were measured with Helios needle-pointed dial calipers, those between eighteen and twenty nine centimetres were measured with KAR venier calipers, and specimens longer than twenty-nine centimetres were measured with the aid of outside calipers and a Westcott stainless steel ruler. The standard length of each specimen was measured. If only the skull was available for study the head length was taken using Helios needle-pointed dial calipers. For a few specimens both standard and head length were measured. The standard length is defined as the straight line distance from the most anterior end of the snout or upper lip, in normal resting position, to the caudal base. The caudal base is defined as the posterior end of the hypural plate complex at the midpoint of the depth of the fish. The head length is defined as the straight line distance from the most anterior end of the snout or upper lip, in normal resting position, to the most distant point of the operculum, excluding the opercular membrane. Fossil specimens were measured in the same way except that in some cases the lengths are approximate since parts of the skeleton were often disarticulated. Fossil specimens were measured to the nearest millimetre while all others were measured to the nearest tenth of a millimetre.

The following is a list of the material examined. The teleostean classification follows Nelson (1984) except that the prototroctids and aplochitonids are each given familial status and the Searsiidae are called the Platytroctidae in accordance with Matsui and Rosenblatt's recent revision of the group. The names of all extinct fossil taxa are preceded by a dagger (†). Catalogue abbreviations are listed on pages 41-42 . In the following list (*) denotes that a specimen is figured in the thesis; (P) denotes that a specimen was examined for the character state of the bony, lateral sensory canal of the preoperculum, in addition to being dissected for the muscles of the suspensorium (all cleared and stained specimens were examined for this feature); (M) denotes that a specimen is a male, (F) that it is a female; cleared and stained, unless noted, indicates that a specimen was cleared and stained for both cartilage and bone; S.L. denotes the standard length in millimetres; whole preserved specimen indicates a specimen that was preserved in either isopropyl or ethyl alcohol and examined for a specific character; the written number in parentheses adjacent to a catalogue number indicates the number of specimens of that catalogue number that were examined. The Salmoniformes are listed first, followed by the other Teleostei. Supraspecific taxa (order, family, and subfamily) are listed roughly phylogenetically while species within them are listed alphabetically.

SALMONIFORMES

Esocidae

Esox lucius. Cleared and stained: UAMZ 123 (two), standard length (S.L.) 15.0 and 14.4 mm; UAMZ 870, S.L. 34.9 mm; UAMZ 1704 (three), S.L. 27.5, 22.5 and 17.0 mm; UAMZ 3215 (two), S.L. 163.2 and 120.2 (*) mm; UAMZ 3278, S.L. 128.8 mm; UAMZ 3347, S.L. 57.5 mm; UAMZ 3398, S.L. 96.0 mm; UAMZ 3617, S.L. 89.0 mm; UAMZ 5199, S.L. 104.5 mm. Dry skeletons: UAMZ 4877 (disarticulated bones of skull, bones similar in size to UAMZ 4878); UAMZ 4878 (skull only, head length 161 mm). Muscle dissections: UAMZ 1247, S.L. 313.0 mm; UAMZ 2246, S.L. 180.8; UAMZ 3278 (five), S.L. 139.9, 125.0, 122.6, 114.4 and 103.0 (*) mm.

Esox masquinongy. Cleared and stained: UAMZ 3884 (two), S.L. 98.1 and 87.6 mm. Muscle dissections: UAMZ 3885 (two), S.L. 114.3 and 95.8 mm.

†*Esox tiemani*. Fossils: UAVP 15002 (holotype), S.L. 288 mm, head length 87 mm; UAVP 15005 (paratype, skull only), head length 40 mm.

Umbridae

Dallia pectoralis. Cleared and stained: UAMZ 3737 (two), S.L. 123.0 and 110.6 (*) mm; UAMZ 3738 (five), S.L. 23.4, 22.6, 19.6, 19.2 and 18.6 mm (stained for bone only); UAMZ 3739, S.L. 75.3 mm (stained for bone only); UAMZ 3741, S.L. 44.2 mm. Muscle dissections: UAMZ 3737 (three), S.L. 122.2, 115.8 (*) and 109.3 mm.

Novumbra hubbsi. Cleared and stained: UAMZ 3712 (six), S.L. 36.4, 31.5, 29.3, 23.9, 22.6 and 18.3 mm (stained for bone only); UAMZ 3718 (two), S.L. 53.7 (*) and 52.8 mm; UAMZ 3749 (five), S.L. 53.8, 53.0, 50.2, 49.1 and 48.3 mm (stained for bone only). Muscle dissections: UAMZ 3716 (three), S.L. 49.4 (*), 45.5 and 43.6 mm; UAMZ 3718 (two), S.L. 53.7 and 48.2 mm.

†*Novumbra oregonensis*. Fossil: UAVP 13404 (plaster cast), S.L. 85 mm.

Umbra krameri. Cleared and stained: UAMZ 3727, S.L. 62.4 mm; UAMZ 3745, S.L. 39.9 mm (stained for bone only); UAMZ 3898, S.L. 63.0 mm. Muscle dissections: UAMZ 3727 (two), S.L. 63.3 (*) and 44.6 mm.

Umbra limi. Cleared and stained: UAMZ 3721 (two), S.L. 74.5 and 41.2 mm (stained for bone only); UAMZ 3725 (three), S.L. 82.0, 74.0 (*) and 67.8 mm. Muscle dissections: UAMZ 3725 (two), S.L. 77.9 and 68.0 mm; UAMZ 3752 (two) S.L. 76.3 and 67.4 (*) mm.

Umbra pygmaea. Cleared and stained: UAMZ 3730 (four), S.L. 35.2, 30.3, 25.9 and 25.6 mm (stained for bone only); UAMZ 3731, S.L. 83.9 mm (stained for bone only); UAMZ 3734, S.L. 77.5 mm (stained for bone only), UAMZ 3750, S.L. 77.0 mm (stained for bone only). Muscle dissection: UAMZ 3735, S.L. 37.7 mm.

Salmonidae

Brachymystax coregonoides. Radiographed: USNM 076713, S.L. 235.2 mm.

Brachymystax lenok. Muscle dissection: USNM 102350, S.L. 140.0 (*) mm.

Coregonus artedii. Cleared and stained: UAMZ 3604 (two), S.L. 129.4 and 129.2 (*) mm; UAMZ 3607, S.L. 141.3 mm. Muscle dissection: UAMZ 3604 (four), S.L. 141.3 (*), 140.6, 136.2 and 127.4 mm.

Coregonus clupeaformis. Cleared and stained: UAMZ 1551, S.L. 130.0 mm; UAMZ 3774, S.L. 52.9 mm; UAMZ 3778, S.L. 30.7 mm. Muscle dissection: UAMZ 1551, S.L. 125.0 mm; UAMZ 3545, S.L. 389.0 mm.

†*Eosalmo driftwoodensis*. Fossils: UAVP 13409 (rubber peel), head length 51 mm; UAVP 13410 (rubber peel), head length 50-70 mm; UAVP 13411 (rubber peel), head length 50-70 mm; UAVP 13482, S.L. 379 mm.

Oncorhynchus kisutch. Cleared and stained: UAMZ 3149, S.L. 56.4 mm.

Oncorhynchus nerka. Cleared and stained: UAMZ 2063 (two), S.L. 126.9 and 122.1 mm. Muscle dissection: UAMZ 2063 (three), S.L. 133.3, 131.0 and 129.4 mm.

Prosopium cylindraceum. Muscle dissection: UAMZ 3393, S.L. 375.0 mm.

Prosopium williamsoni. Cleared and stained: UAMZ 518, S.L. 32.1 mm; UAMZ 2828 (two), S.L. 98.1 and 29.5 mm; UAMZ 3320, S.L. 143.2 mm; UAMZ 3400, S.L. 77.4 mm; UAMZ 3369 (two), S.L. 151.5 (*) and 130.5 mm. Muscle dissection: UAMZ 3369, S.L. 133.1 (*) mm; UAMZ 3923 (three), S.L. 146.7, 145.6 and 80.3 mm.

Salmo gairdneri. Cleared and stained: UAMZ 2213 (two), S.L. 21.2 and 7.12 mm.

Salmo trutta. Cleared and stained: UAMZ 2066, S.L. 127.5 mm; UAMZ 74 (two), S.L. 85.7 and 72.1 mm. Dry skeleton: UAMZ 6324 (skull only, head length 96.9 mm). Muscle dissection: UAMZ 74, S.L. 116.1 mm.

Salvelinus alpinus. Dry skeleton: UAMZ 7934 (disarticulated bones of skull, no length data).

Salvelinus fontinalis. Cleared and stained: UAMZ 3349 (three), S.L. 140.3, 93.0 and 76.0 (*) mm. Muscle dissections: UAMZ 84 (two), S.L. 215.0 and 206.4 mm; UAMZ 2067 (four), S.L. 148.5, 125.8, 87.1 and 81.5 (*) mm; UAMZ 3349 (two), S.L. 153.9 and 113.8 mm; UAMZ 5207 (two), S.L. 125.7 and 116.2 mm.

Salvelinus namaycush. Cleared and stained: UAMZ 6323, S.L. 118.8 mm.

Stenodus leucichthys. Cleared and stained: UBCIF BC63-748 (head preserved, right suspensorium removed and cleared and stained, head length 116.0 mm). Dry skeletons: UAMZ 4430 (disarticulated bones of skull, bones larger than UBCIF BC63-748); UAMZ 4810 (disarticulated bones of skull, bones similar in size to UAMZ 4430). Muscle dissections: UAMZ 3392, S.L. 364.0 mm (head length 76.3 mm); UBCIF BC63-748 (head preserved, muscles of left suspensorium dissected, head length 116.0 mm).

Thymallus arcticus. Cleared and stained: UAMZ 3421, S.L. 110.0 mm; UAMZ 3425, S.L. 95.2 (*) mm; UAMZ 3449, S.L. 67.2 mm. Muscle dissections: UAMZ 3421 (two), S.L. 117.7 (*) and 103.8 mm; UAMZ 3439, S.L. 150.9 mm; UAMZ 4326, S.L. 116.2 mm; UAMZ 4981 (two), S.L. 177.5 and 144.6 mm.

Osmeridae

Allosmerus elongatus. Cleared and stained: UBCIF BC75-9, S.L. 91.7 mm. Muscle dissections: UBCIF BC75-9 (two), S.L. 97.4 and 93.9 mm.

Hypomesus olidus. Cleared and stained: UAMZ 3516, S.L. 73.1 mm.

Hypomesus pretiosus. Cleared and stained: UAMZ 874 (two), S.L. 128.3 and 118.0 (*) mm; UAMZ 3185 (two), S.L. 48.6 and 46.6 mm; UAMZ 3515 (three), S.L. 129.8, 125.2 and 84.0 mm. Muscle dissections: UAMZ 3515 (five), S.L. 136.2, 135.4 (*), 133.1, 131.7 and 122.0 mm.

Mallotus villosus. Cleared and stained: NMC 62-0124, S.L. 136.0 (*) mm. Muscle dissection: NMC 62-0124, S.L. 127.0 mm. Whole preserved specimens, examined for character state of the mesopterygoid: UAMZ 5114, S.L. 49.4 mm; UAMZ 5635, S.L. 59.6 mm. Fossils: UAVP 1869, S.L. 120 mm; UAVP 22866, S.L. 110 mm.

Osmerus mordax. Cleared and stained: UAMZ 3514, S.L. 169.7 mm; UAMZ 3623, S.L. 151.0 mm. Muscle dissection: UAMZ 3514, S.L. 166.3 mm.

Spirinchus starksi. Cleared and stained: NMC 81-0486, S.L. 110.9 mm. Muscle dissection: NMC 81-0486, S.L. 111.4 mm.

Spirinchus thaleichthys. Cleared and stained: UAMZ 748, S.L. 85.0 mm; UAMZ 2776 (two), S.L. 117.5 (*) and 76.4 mm; UAMZ 3939 (two), S.L. 74.6 and 69.4 mm. Muscle dissection: UAMZ 1484, S.L. 89.4 mm; UAMZ 1960, S.L. 78.7 mm; UAMZ 3939, S.L. 66.7 mm.

Thaleichthys pacificus. Cleared and stained: UAMZ 2317 (two), S.L. 121.8 (*) and 120.1 mm. Muscle dissection: UAMZ 2317, S.L. 107.0 mm.

Plecoglossidae

Plecoglossus altivelis. Cleared and stained: UAMZ 3505 (two), S.L. 160.6 (*) and 144.1 mm; UAMZ 5668, S.L. 55.5 mm; UAMZ 5669, S.L. 77.9 mm. Muscle dissections: UAMZ 3505 (two), S.L. 163.6 and 159.8 (*) mm.

Salangidae

Salangichthys ishikawae. Cleared and stained: CAS-SU 6780, S.L. 70.4 (*) mm. Muscle dissection: CAS-SU 6780, S.L. 68.1 (*) mm.

Salangichthys microdon. Cleared and stained: CAS-SU 68878, S.L. 47.3 (*) mm. Muscle dissection: CAS-SU 68878, S.L. 55.9 (*) mm.

Salanx cuvieri. Muscle dissection: CAS-SU 32454, S.L. 57.4 mm.

Salanx prognathus. Cleared and stained: CAS 51439, S.L. 111.7 (*) mm. Muscle dissections: CAS-SU 33990, S.L. 97.2 mm; CAS 51439, S.L. 110.0 (*) mm.

Retropinnidae

Retropinna retropinna. Cleared and stained: UAMZ 4606 (two), S.L. 76.1 and 71.5 (*) mm. Muscle dissections: UAMZ 4606 (three), S.L. 77.0 (*), 74.6 and 67.4 mm.

Prototroctidae

Prototroctes maraena. Cleared and stained: UAMZ 6325, S.L. 117.0 (*) mm; AMS I. 20704-001, S.L. 68.8 mm. Muscle dissections: UAMZ 6325, S.L. 122.1 (*) mm; AMS I. 20704-001, S.L. 63.0 mm.

Lepidogalaxiidae

Lepidogalaxias salamandroides. Cleared and stained: WAM P. 7578-81 (M), S.L. 34.6 (*) mm. Radiographed: WAM P. 7578-81 (M), S.L. 34.6 (*) mm; WAM P. 8124-31 (F), S.L. 39.7 (*) mm. Muscle dissections: WAM P. 7578-81 (M), S.L. 34.6 mm; WAM P. 8124-31 (F), S.L. 39.7 (*) mm.

Galaxiidae

Brachygalaxias bullocki. Cleared and stained: CAS 51438, S.L. 27.0 mm. Muscle dissection: CAS 51438, S.L. 23.8 mm.

Galaxias brevipinnis. Cleared and stained: UAMZ 4608, S.L. 93.0 mm. Muscle dissection: UAMZ 4608, S.L. 88.0 mm.

Galaxias fasciatus. Muscle dissections: UAMZ 5122 (two), S.L. 100.2 and 95.2 (*) mm.

Galaxias maculatus. Cleared and stained: UAMZ 4609 (two), S.L. 117.9 (*) and 101.1 mm. Muscle dissections: UAMZ 4609 (three), S.L. 92.6 (*), 89.0 and 86.1 mm.

Galaxias paucispondylus. Cleared and stained: UAMZ 4610, S.L. 56.2 mm. Muscle dissection: UAMZ 4610, S.L. 62.2 mm.

Neochanna apoda. Cleared and stained: UAMZ 4607, S.L. 122.2 mm. Muscle dissection: UAMZ 4607, S.L. 126.2 mm.

Aplochitonidae

Aplochiton taeniatus. Cleared and stained: NMC 76-0393, S.L. 110.5 (*) mm. Muscle dissection: NMC 76-0393, S.L. 104.1 (*) mm.

Lovettia sealii. Cleared and stained: AMS IB. 2484-6 (two), S.L. 43.1 (F) and 41.8 (M) mm. Muscle dissections: AMS IB. 2484-6 (two), S.L. 46.4 (F) and 41.9 (F) mm.

Argentinidae

Argentina silus. Cleared and stained: UAMZ 1397, S.L. 142.7 (•) mm. Muscle dissections: UAMZ 1397 (two), S.L. 175.1 and 170.4 (•) mm.

Bathylagidae

Bathylagus pacificus. Cleared and stained: UAMZ 866, S.L. 141.0 (•) mm. Muscle dissections: UAMZ 866 (two), S.L. 150.0 and 129.2 (•) mm.

Opisthoproctidae

Dolichopteryx longipes. Cleared and stained: SIO H51-85, S.L. 127.2 (•) mm. Muscle dissection: SIO H51-85, S.L. 110.2 (•) mm.

Macropinna microstoma. Cleared and stained: NMC 66-0026, S.L. 103.0 (•) mm. Muscle dissection: NMC 66-0026, S.L. 103.0 mm.

Opisthoproctus soleatus. Cleared and stained: SIO (uncatalogued, stained for bone only), S.L. 53.4 mm. Muscle dissection: SIO 68-471, S.L. 73.2 mm.

Platytroctidae

Holtbyrnia latifrons. Cleared and stained: SIO 65-603, S.L. 73.1 mm. Muscle dissection: SIO 72-195, S.L. 63.3 (•) mm.

Mirorictus taningi. Cleared and stained: SIO 82-85, S.L. 101.4 (•) mm. Radiographed: SIO 70-95, S.L. 75.0 (•) mm; SIO 82-85, S.L. 101.4 (•) mm. Muscle dissection: SIO 70-95, S.L. 75.0 (•) mm.

Pellisolus facilis. Cleared and stained: SIO 60-235, S.L. 49.0 mm. Muscle dissection: SIO 60-235, S.L. 49.0 (•) mm.

Platytroctes apus. Cleared and stained: SIO 55-244 (left suspensorium of whole preserved specimen removed and cleared and stained), S.L. 141.1 (•) mm; SIO 55-246 (left suspensorium removed from whole preserved specimen and cleared and stained), S.L. 136.0 (•) mm. Radiographed: SIO 55-244, S.L. 141.1 (•) mm. Muscle dissection: SIO 55-244, S.L.

141.1 (*) mm; SIO 55-246, S.L. 136.0 mm.

Sagamichthys abei. Cleared and stained: NMC 65-406, S.L. 68.5 (*) mm. Muscle dissection: NMC 65-406, S.L. 68.5 mm.

Searsia koefoedi. Cleared and stained: SIO 77-38, S.L. 117.2 (*) mm. Radiographed: SIO 77-38, S.L. 117.2 (*) mm. Muscle dissection: SIO 77-38, S.L. 117.2 (*) mm.

Searsioides multispinus. Cleared and stained: SIO 61-32, S.L. 40.8 (*) mm. Muscle dissection: SIO 61-32, S.L. 54.0 mm.

Alepocephalidae

Alepocephalus bairdii. Cleared and stained: ROM 23044, S.L. 199.7 (*) mm.

Alepocephalus tenebrosus. Cleared and stained: SIO 82-50, S.L. 72.8 mm. Muscle dissection: SIO [illegible]2-50, S.L. 148.1 (*) mm

Bajacalifornia burragei. Cleared and stained: SIO 65-443 (left suspensorium removed from whole preserved specimen and cleared and stained), S.L. 128.1 mm. Muscle dissection: SIO 65-443, S.L. 135.1 mm.

Bathylaco nigricans. Cleared and stained: SIO 64-15 (right suspensorium removed from whole preserved specimen and cleared and stained), S.L. 84.4 (*) mm. Radiographed: USNM 206694, S.L. 227.8 mm; SIO 64-15, S.L. 84.4 (*) mm. Muscle dissection: SIO 64-15, S.L. 84.4 (*) mm.

Bathylaco sp.. Radiographed: USNM 200468, S.L. 56.2 mm. Muscle dissection: USNM 200468, S.L. 56.2 mm.

Bathytroctes microlepis. Cleared and stained: USNM 215497 (right suspensorium removed from whole preserved specimen and cleared and stained), S.L. 222.1 mm. Muscle dissection: UAMZ 215497, S.L. 222.1 mm.

Binghamichthys (=Talismania) aphos. Cleared and stained: SIO 72-144, S.L. 103.9 mm. Muscle dissection: SIO 72-144, S.L. 131.3 (*) mm.

Conocara mcdonaldi. Cleared and stained: USNM 263438 (left suspensorium removed from whole preserved specimen and cleared and stained), S.L. 269.1 mm. Muscle dissection:

USNM 263438, S.L. 175.2 (•) mm.

Leptoderma macrops. Cleared and stained: USNM 215604, S.L. 201.0 (•) mm. Muscle dissection: USNM 215604, S.L. 162.1 (•) mm.

Narcetes stomias. Cleared and stained: USNM 215509 (left suspensorium removed from whole preserved specimen and cleared and stained), S.L. 366.2 (•) mm. Muscle dissection: USNM 215509, S.L. 370.4 (•) mm.

Photostylus pycnopterus. Cleared and stained: USNM 215656, S.L. 75.8 (•) mm. Muscle dissection: USNM 215657, S.L. 96.1 mm; SIO 72-186, S.L. 95.6 (•) mm.

Rouleina maderensis. Cleared and stained: 215471 (left suspensorium removed from whole preserved specimen and cleared and stained), S.L. 218.1 (•) mm. Muscle dissection: USNM 215471, S.L. 237.4 mm.

Rouleina nudus. Muscle dissection: USNM 137736, S.L. 173.2 (•) mm.

Talismania antillarum. Cleared and stained: USNM 215556, S.L. 137.1 (•) mm. Muscle dissection: USNM 215556, S.L. 129.6 (•) mm.

Talismania bifurcata. Muscle dissection: SIO 69-489, S.L. 196.0 mm.

Xenodermichthys copei. Cleared and stained: USNM 215524, S.L. 151.6 (•) mm. Radiographed: USNM 215524 (nine), S.L. 150.9 (•), 148.1, 146.5, 143.6, 141.7, 139.7, 135.7, 134.6 and 133.1 mm. Muscle dissection: USNM 215524, S.L. 150.9 (•) mm.

OTHER TELEOSTEI

†Pholidophoriformes

†*Pholidophorus* sp.. Fossil: UAVP 1864, S.L. 121 mm.

Osteoglossiformes

†*Eohiodon rosei*. Fossil: UAVP 15958 (skull only), head length 31 mm.

Hiodon alosoides. Cleared and stained: UAMZ 3969, S.L. 100.0 (•) mm. Muscle dissections: UAMZ 117, S.L. 144.0 mm; UAMZ 3969, S.L. 118.6 mm; UAMZ 4044 (five), S.L. 83.4, 80.6, 74.0, 69.0 and 65.2 mm.

Osteoglossum bicirrhosum. Cleared~~ and stained~~: UAMZ 4642, S.L. 174.1 mm. Muscle dissection: UAMZ 6321, S.L. 216.0 mm.

Pantodon buchholzi. Muscle dissection: UAMZ 2273, S.L. 57.4 (P) mm.

†*Phareodus testis*. Fossils: UAVP 12712, S.L. 190 mm; UAVP 17657, S.L. 165 mm; UAVP 17658, S.L. 290 mm; UAVP 17659, S.L. 155 mm.

Xenomystus nigri. Cleared and stained: UAMZ 2272, S.L. 132.1 mm. Muscle dissection: UAMZ 2272, S.L. 118.2 mm.

Elopiformes

Elops affinis. Muscle dissection: UAMZ 6318, S.L. 204.4 mm.

Elops hawaiensis. Cleared and stained: UAMZ 6319, S.L. 81.5 mm.

Megalops cyprinoides. Cleared and stained: UAMZ 3528, S.L. 87.8 (*) mm. Muscle dissection: UAMZ 6320, S.L. 64.7 (*) mm.

†Ellimmichthyiformes

†*Diplomystus* sp.. Fossils: UAVP 22860, S.L. 94 mm; UAVP 22861, S.L. 68 mm; UAVP 22862, S.L. 78 mm; UAVP 22865, S.L. 98 mm.

Clupeiformes

<u>Chirocentridae</u>

Chirocentrus dorab. Cleared and stained: UAMZ 4523, S.L. 120.6 mm (stained for bone only). Muscle dissection: UAMZ 4522, S.L. 222.0 mm.

<u>Clupeidae</u>

Alosa pseudoharengus. Cleared and stained: UAMZ 6633 (two), S.L. 43.4 and 41.0 mm.

Alosa sapidissima. Cleared and stained: UAMZ 4510 (three), S.L. 71.0, 66.0 and 61.7 mm (stained for bone only). Muscle dissection: UAMZ 4510, S.L. 68.3 mm.

Anodontostoma chacunda. Muscle dissection: UAMZ 4061, S.L. 125.1 mm.

Clupea harengus. Cleared and stained: UAMZ 1483, S.L. 114.1 (*) mm; UAMZ 1956, S.L. 122.7 mm. Muscle dissections: UAMZ (1483), S.L. 120.0, 115.2, 105.5, 98.8 (*) mm.

Dorosoma petenense. Cleared and stained: UAMZ 4513, S.L. 68.7 mm.

Dussumieria hasselti. Cleared and stained: UAMZ 4498, S.L. 99.8 mm (stained for bone only). Muscle dissection: UAMZ 4499, S.L. 64.4 mm.

Etrumeus teres. Cleared and stained: UAMZ 4501, [illegible] (stained for bone only).

Harengula thrissina. Cleared and stained: UAMZ 4[illegible]1.2 mm (stained for bone only).

Hyperlophus sprattellides. Cleared and stained: UAMZ 4508, S.L. 62.4 mm (stained for bone only).

Ilisha furthii. Cleared and stained: UAMZ 4515, S.L. 116.1 mm (stained for bone only); CAS 27837, S.L. 106.7 mm (stained for bone only). Muscle dissection: UAMZ 4515, S.L. 92.0 mm.

Jenkinsia stolifera. Cleared and stained: UAMZ 4502 (three), S.L. 42.4, 36.7 and 33.2 mm (stained for bone only).

†*Knightia* sp.. Fossils: UAVP 17726 (skull only), head length 36 mm; UAVP 22856, S.L. 115 mm; UAVP 22857, S.L. 97 mm; UAVP 22868, S.L. 113 mm.

†*Knightia eocaena*. Fossil: UAVP 20303, S.L. 109 mm.

Nematalosa erebi. Cleared and stained: UAMZ 4514, S.L. 37.6 mm (stained for bone only).

Odontognathus compressus. Cleared and stained: UAMZ 4521, S.L. 133.6 mm (stained for bone only).

Odontognathus panamensis. Cleared and stained: UAMZ 4520, S.L. 121.4 mm (stained for bone only).

Engraulidae

Amentum devisi. Muscle dissection: UAMZ 3523, S.L. 80.6 (P) mm.

Anchoa mundeoloides. Muscle dissection: CAS 27827, S.L. 107.1 mm.

Anchoa panamensis. Cleared and stained: UAMZ 4533, S.L. 99.3 mm (stained for bone only).

Cetengraulis mysticetus. Cleared and stained: UAMZ 4530 (two), S.L. 113.8 and 110.5 mm (stained for bone only).

Engraulis sp.. Cleared and stained: UAMZ 2315, S.L. 115.4 mm (stained for bone only).

Thryssa (=Thrissocles) hamiltoni. Cleared and stained: UAMZ 4529, S.L. 112.5 mm. Muscle dissections: UAMZ 4529 (two), S.L. 118.7 and 117.8 mm.

Gonorynchiformes

Chanos chanos. Cleared and stained: UAMZ 3523, S.L. 91.8 (*) mm. Muscle dissections: UAMZ 6500, S.L. 295.0 mm (head length 70.6 mm); UAMZ 6501 (head preserved, head length 69.9 mm).

†*Notogoneus osculus*. Fossils: UAVP 15084, S.L. 470 mm; UAVP 17660, S.L. 236 mm; UAVP 17833, S.L. 450 mm.

Cypriniformes

Catostomus commersoni. Muscle dissection: UAMZ 5361 (three), S.L. 65.5, 62.8 and 54.8 mm.

Couesius plumbeus. Cleared and stained: UAMZ 2443 (two), S.L. 45.8 and 39.8 mm. Muscle dissection: UAMZ 3340, S.L. 76.3 mm.

Notropis blennius. Muscle dissection: UAMZ 3871, S.L. 73.2 mm.

Characiformes

Astyanax fasciatus. Muscle dissection: UAMZ 1164, S.L. 41.4 (P) mm.

Stomiiformes

Argyropelecus pacificus. Cleared and stained: UAMZ 4658, S.L. 44.5 mm. Muscle dissection: UAMZ 4658, S.L. 47.7 (P) mm.

Chauliodus macouni. Muscle dissection: UAMZ 872, S.L. 180.1 (P) mm.

Cyclothone pseudopallida. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 4665, S.L. 42.0 mm.

Diplophos taenia. Cleared and stained: SIO 68-52, S.L. 92.1 (*) mm. Muscle dissection: SIO 68-52-10, S.L. 85.8 (*) (P) mm.

Tactostoma macropus. Cleared and stained: UAMZ 1387, S.L. 239.3 mm. Muscle dissection: UAMZ 1387, S.L. 213.7 mm.

Vinciguerria nimbaria. Cleared and stained: UAMZ 6317 (two), S.L. 41.1 and 26.2 mm. Muscle dissections: UAMZ 6317 (two), S.L. 36.9 (*) and 30.0 mm.

Aulopiformes

Aulopus filamentosus. Muscle dissection: ROM 22028, S.L. 229.5 mm.

Chlorophthalmus agassizi. Cleared and stained: ROM 22028, S.L. 113.4 mm.

†*Nematonotus* sp.. Fossil: UAVP 13362, S.L. 89 mm.

Saurida tumbil. Cleared and stained: UAMZ 4046 (two), S.L. 155 (*) and 136 mm (stained for bone only).

Synodus foetens. Muscle dissection: UAMZ 1806, S.L. 139.5 mm.

Synodus saurus. Muscle dissection: UAMZ 5693, S.L. 77.1 mm.

Synodus synodus. Cleared and stained: UAMZ 1806, S.L. 146.6 mm.

Myctophiformes

Myctophum sp.. Cleared and stained: UAMZ 2689, S.L. 78.9 mm. Muscle dissection: UAMZ 2689, S.L. 76.3 (P) mm.

Protomyctophum thompsoni. Cleared and stained: UAMZ 1384, S.L. 44.4 mm. Muscle dissection: UAMZ 1384, S.L. 48.6 (P) mm.

Stenobrachius leucopsarus. Muscle dissection: UAMZ 1390, S.L. 110.0 (P) mm.

Symbolophorus sp.. Cleared and stained: UAMZ 2690, S.L. 46.8 mm. Muscle dissection: UAMZ 2690, S.L. 46.2 (P) mm.

Percopsiformes

Chologaster agassizi. Muscle dissection: UAMZ 1635, S.L. 57.0 (P) mm.

Percopsis omiscomaycus. Cleared and stained: UAMZ 3062, S.L. 74.4 mm. Muscle dissection: UAMZ 3062, S.L. 72.6 mm.

†*Tricophanes foliarum*. Fossil: UAVP 17741 (rubber peel), S.L. 38 mm.

Unidentified percopsid fossils: UAVP 21660 (skull only), head length 31 mm; UAVP 22869 (two), S.L. 144 and 137 mm; UAVP 22870, S.L. 33 mm.

Gadiformes

Lota lota. Dry skeleton: UAMZ 4813 (no length data). Muscle dissection: UAMZ 3216, S.L. 122.5 (P) mm.

Microgadus proximus. Muscle dissection: UAMZ 3939, S.L. 98.0 (P) mm.

Ophidiiformes

Ogilbia sp.. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 5692, S.L. 47.6 mm.

Batrachoidiformes

Porichthys notatus. Cleared and stained: UAMZ 6485 (two), S.L. 78.9 and 77.3 mm (stained for bone only).

Cyprinodontiformes

Cyprinodon nevadensis. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 3114, S.L. 38.8 mm.

Fundulus diaphanus. Cleared and stained: UAMZ 6629 (two), S.L. 61.0 and 35.8 mm.

Xiphophorus maculatus. Cleared and stained: UAMZ 6632, S.L. 39.4 mm.

Atheriniformes

Hypoatherina (=Allanetta) harringtonensis. Muscle dissection: UAMZ 2673, S.L. 57.1 (P) mm.

Melanotaenia (=Nematocentris) sp.. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 3526, S.L. 49.5 mm.

Menidia menidia. Cleared and stained: UAMZ 6631, S.L. 70.0 mm.

Thyrina crystallina. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 3589, S.L. 54.9 mm.

Beryciformes

Melamphaes lugubris. Muscle dissection: UAMZ 1388, S.L. 71.8 (P) and 60.1 (P) mm.

Plectrypops retrospinis. Cleared and stained: UAMZ 3639, S.L. 70.4 mm. Muscle dissection: UAMZ 3639, S.L. 86.7 (P) mm.

Photoblepharon palpebratus. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 4312, S.L. 70.8 mm.

Sargocentron (= Adioryx) coruscus. Muscle dissection: UAMZ 5074, S.L. 34.7 mm.

Gasterosteiformes

Gasterosteus aculeatus. Cleared and stained: UAMZ 5539 (six), S.L. 69.5, 67.1, 66.4, 64.7, 62.5 and 51.9 mm (stained for bone only).

Pungitius platygaster. Cleared and stained: UAMZ 4733 (four), S.L. 45.1, 44.3, 44.1 and 44.0 mm (stained for bone only).

Scorpaeniformes

Apistops caloundra. Muscle dissection: UAMZ 4058, S.L. 74.2 mm.

Chitonotus pugetensis. Cleared and stained: UAMZ 1972 (two), S.L. 110.5 and 90.8 mm (stained for bone only).

Cottus cognatus. Cleared and stained: UAMZ 1048 (three), S.L. 47.1, 45.6 and 42.2 mm (stained for bone only).

Liparis fucensis. Muscle dissection: UAMZ 3206, S.L. 47.4 (P) mm.

Malacocottus kincaidi. Cleared and stained: UAMZ 4497 (five), S.L. 52.6, 49.3, 43.9, 43.1 and 40.5 mm.

Sebastes ruberrimus. Dry skeleton: UAMZ 4817, S.L. 393 mm.

Perciformes

Caprodon schlegeli. Muscle dissection: UAMZ 920, S.L. 137.2 (P) mm.

Centropristis striata. Muscle dissection: UAMZ 1808, S.L. 132.1 (P) mm.

Chanda (=Ambassis) sp.. Muscle dissection: UAMZ 3526, S.L. 29.4 (P) mm.

Epinephelus adscensionis. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 3586, S.L. 55.7 mm.

Epinephelus sexfasciatus. Muscle dissection: UAMZ 4060, S.L. 67.6 (P) mm.

Etheostoma blennioides. Muscle dissection: UAMZ 2503, S.L. 45.9 (P) mm.

Gramma loreto. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 2672, S.L. 36.8 mm.

Hemichromis bimaculatus. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 4638, S.L. 45.2 mm.

Kuhlia sandvicensis. Whole preserved specimen, examined for character state of bony, lateral sensory canal of [illegible]um: UAMZ 928, S.L. 37.3 mm.

†*Mioplosus* sp.. Fo[illegible] UAVP 17828, S.L. 178 mm.

Morone americana. Cleared and stained: UAMZ 6630 (four), S.L. 55.2 (stained for bone only), 43.8, 36.8 and 28.8 mm.

Perca flavescens. Cleared and stained: UAMZ 1522 (two), S.L. 55[illegible]d 54.2 mm (stained for bone only). Muscle dissection: UAMZ 4344, S.L. 81.2 (P) mm.

Pomacentrus tripunctatus. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 3558, S.L. 66.4 mm.

Pomoxis nigromaculatus. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 4483, S.L. 127.9 mm.

†*Priscacara* sp.. Fossil: UAVP 22855, S.L. 104 mm.

†*Priscacara liops*. Fossils: UAVP 17726, S.L. 108 mm; UAVP 17831, S.L. 109 mm.

Rypticus saponaceus. Whole preserved specimen, exmained for character state of bony, lateral sensory canal of preoperculum: UAMZ 2603, S.L. 79.0 mm.

Stegastes (=Eupomacentrus) partitus. Whole preserved specimen, examined for character state of bony, lateral sensory canal of preoperculum: UAMZ 3640, S.L. 45.2 mm.

Stizostedion vitreum. Dry skeleton: UAMZ 4700, S.L. 562.0 mm.

D. PHYLOGENETIC RECONSTRUCTION

My approach to the study of salmoniform relationships is phylogenetic, *sensu* Hennig (1966). In this approach one attempts to reconstruct the phylogenetic, or genealogical relationships of a group of species hypothesized to be holophyletic. This assemblage (in my case, the order Salmoniformes) is termed the ingroup or the study group. Reconstructing the genealogical history of the study group involves the identification of holophyletic subgroups within the study group. I define a holophyletic group as a group of species that includes a single common ancestral species and all its descendants (the monophyletic group of Wiley 1981). Each holophyletic group (two or more species) is recognized by its joint possession of at least one derived (advanced or apomorphic) character state, presumed to have arisen in the common ancestor. In phylogenetic systematics, species are united only on the basis of their sharing one or more derived character states, since only shared derived character states (or synapomorphies) provide information about common ancestry (e.g., see Hennig 1966; Wiley 1981). Phylogenetic reconstruction therefore essentially involves a search for derived character states in the study group and uniting species into holophyletic groups on the basis of their sharing one or more of them. I define a character as a feature of an organism (e.g., a metapterygoid bone), and a character state as one of the alternate observed conditions of that character (e.g., a round metapterygoid). The primitive character state is the original character state, that arose earlier in time, and gave rise to the later, derived (advanced) character state.

In phylogenetic reconstruction there are several criteria for determining whether a given character state is primitive or derived. Methods for assessing the evolutionary polarity (the direction of evolutionary change) of a character include: the ontogenetic method, the stratigraphic method, and the outgroup comparison method, (e.g., refer to Hennig 1966; Hecht and Edwards 1977; Nelson 1978; Watrous and Wheeler 1981; Wiley 1981; Maddison *et al.* 1984). The ontogenetic criterion was the least useful method of polarizing data. In most cases the embryonic development of individual characters in a single species could not be studied because of a lack of specimens. The stratigraphic (paleontological) method was often critical in polarizing data at the higher taxonomic levels (e.g., the polarity of the bony, lateral sensory canal on the preoperculum within the Teleostei). However, because the fossil record of the salmoniforms is poor it was not very useful in clarifying their familial or generic relationships.

The primary criterion that I used to polarize data was the outgroup comparison method. In outgroup analysis one begins with an ingroup, or study group, hypothesized to be holophyletic on the basis of previous work, within which one wants to resolve the relationships of the taxa. In my case, the ingroup was the order Salmoniformes (species *sensu* Nelson 1984), hypothesized to be holophyletic by Rosen in 1973 and 1974. Once the data were polarized, species were united on the basis of their sharing derived character states. Competing hypotheses were then examined, and a preferred hypothesis was selected mainly on the basis of character weighting and the principle of parsimony or simplicity.

I will now briefly outline the methods that I used to reconstruct the phylogeny of the salmoniform fishes. First, I examined the suspensoria in members of the ingroup (the Salmoniformes) and outgroups for characters, and documented their character states. Because salmoniform interrelationships are poorly known I examined as many salmoniform species as possible. If members of a taxon (e.g., the Galaxiidae) were relatively similar morphologically, and there was strong previous evidence for holophyly, fewer specimens were examined than if a taxon (e.g., the Salmonidae) was morphologically diverse and of uncertain holophyly. Published descriptions of species were used when specimens were not available.

Once the characters and their states were documented, outgroup analysis was used to determine whether a given character state was primitive or derived. That is, the direction of evolutionary change (the polarity) of each character, from a primitive or ancestral state to a derived state, was estimated. Watrous and Wheeler (1981, p. 5) summarized outgroup analysis in its simplest form with the following rule: "For a given character with 2 or more states within a group [the ingroup], the state occurring in related groups [the outgroups] is assumed to be the plesiomorphic [= primitive or ancestral] state." I define the outgroup as the sister group of the ingroup, and sister groups as two taxa that share an ancestor unique only to them. The reason for selecting the character state in the outgroup as primitive is largely a parsimony argument in which fewer assumptions (of reversals and parallelisms) are required if the state in the outgroup is primitive, than if the state in the outgroup is derived (e.g., see Hecht and Edwards 1977; Watrous and Wheeler 1981; Maddison *et al*. 1984).

There may be a number of outgroups. The first or immediate outgroup is the sister group of the ingroup, the second outgroup is the sister group of the ingroup plus the first outgroup, the third outgroup is the sister group of the ingroup, plus the first and second outgroups, and so on. On the basis of previous studies (e.g., see Lauder and Liem 1983) I assumed that each of the outgroups of the Salmoniformes was holophyletic, and that the relationships of the outgroups to one another and to the ingroup were known. For example, if the Salmoniformes are holophyletic, its first outgroup, based on Patterson and Rosen's 1977 hypothesis of teleostean relationships, would be the higher teleosts (the Neoteleostei), followed by the Ostariophysi, the Clupeomorpha, Elopomorpha, and the Osteoglossomorpha (refer to Fig. 1). Before analysis, I hypothesized that the order Salmoniformes was holophyletic. However, since my analysis suggested that the Salmoniformes were not holophyletic, the outgroups for further analysis proved to be somewhat different. For example, the Neoteleostei were the first outgroup of only a subgroup within the Salmoniformes (the osmeroids + galaxioids + argentinoids) because the latter assemblage shared a derived character state with the neoteleosts, but not with the remaining salmoniforms (the esocoids and salmonids).

If I had some doubt as to the polarity of a character (that is, if the character states varied among the outgroups and the ancestral state could not be reliably estimated) it was not used in phylogenetic reconstruction. In practice, most characters used were those in which all the outgroups had the same character state (i.e., primitive) and the polarity could be reliably estimated (i.e., in essence, the outgroups were treated as a single group). In some cases an outgroup possessed a character state different from the others, and it could be argued that this state was probably an autapomorphy (a derived character state in a single lineage). In that case the character state common to the remaining outgroups was selected as primitive.

Once the polarity of each character was estimated the derived character states were used to unite species into holophyletic groups. If a derived character state was shared by two or more species then I considered this as evidence that these species formed a holophyletic group.

As an example of my method of phylogenetic reconstruction, consider the following. Within the order Salmoniformes the species belonging to the Retropinnidae and Prototroctidae possessed palatine and ectopterygoid bones that were fused together. Because the other salmoniforms (with one exception) and all the outgroups had a separate palatine and ectopterygoid, I considered that the character state "fused palatine and ectopterygoid" was derived. The joint possession of a "fused palatine and ectopterygoid" by the Retropinnidae and Prototroctidae was therefore evidence that these two taxa formed a holophyletic group. A similar approach was used to unite other taxa. The end result was that in some cases there were several hypotheses of relationships, each supported by a unique set of shared derived character states. For example, within the Umbridae (containing three genera) there was evidence for two hypotheses: *Dallia* and *Umbra* were sister-taxa or *Dallia* and *Novumbra* were sister taxa.

Since there is only one true phylogeny, if there is more than one hypothesis of the relationships of the same groups of species, only one is correct. The others are examples of parallelism, or the independant development of similar character states in different, but closely related lineages. The identification of parallelism is therefore critical when one is presented with several competing hypotheses. In an attempt to identify parallelisms I weighted the synapomorphies supporting each hypothesis. I gave the most weight to complex character states. I define a complex character state as one that can be subdivided into several parts, all of which appear to function together as a unit. Less weight was given to a simple character state; that is, one that cannot easily be subdivided. Reduction and loss character states were given the least weight because they are most prone to parallelism and therefore the least reliable indicators of phylogeny. Characters were used only if the character states were readily distinguishable.

The logic in giving complex character states the most weight is basically a parsimony argument. Complex character states are theoretically less likely to have evolved more than once (i.e., are less likely to exhibit parallelism). Also, even if a structure develops in parallel to it, the parallel character state will not be exactly like the original, and therefore will be more readily identifiable as an example of parallelism.

Character weighting was most useful when there were several hypotheses that were each supported by a more or less equal number of shared derived character states. By assessing the weight of each hypothesis I was at least able to suggest a preferred hypothesis. If there were several hypotheses supported by synapomorphies of equal weight, then the preferred hypothesis was the one with the most synapomorphies supporting it. In a case where one hypothesis was supported by a complex character state and its alternate was supported by several simple character states, the hypothesis supported by the single, complex synapomorphy might be selected as most likely if it could be shown that the character states supporting the alternate exhibited a relatively high degree of parallelism. In cases where a preferred hypothesis could not be selected all were considered equally likely, pending further investigation.

III. DESCRIPTIONS OF THE SUSPENSORIUM

This section is comprised of descriptions of the bones of the suspensorium, beginning with the families belonging to the order Salmoniformes (part A), followed by a less detailed description of those in the other Teleostei (part B). The salmoniform families are described in the following order: Esocidae, Umbridae, Salmonidae, Osmeridae, Plecoglossidae, Salangidae + Sundasalangidae, Retropinnidae, Prototroctidae, Lepidogalaxiidae, Aplochitonidae, Galaxiidae, Argentinidae, Bathylagidae, Opisthoproctidae, Alepocephalidae, and Platytroctidae. Following a brief introductory statement concerning the shape and osteological diversity of the suspensorium in each family, one representative species is described in detail (in the case of the Salmonidae and Osmeridae, which are divided into subfamilies, one species was selected to represent each subfamily). The bones in the representative species are described in the following order (from anterior to posterior): palatine, ectopterygoid, mesopterygoid, quadrate, symplectic, metapterygoid, hyomandibular, and preoperculum. After each bone is described, differences between it and those found in the other species belonging to the family are noted and discussed.

A. ORDER SALMONIFORMES

FAMILY ESOCIDAE

The suspensorium in the Esocidae is greatly elongated anteroposteriorly and has a number of unusual features that appear to be related to the piscivorous feeding habits of these fish. It differs only slightly (mainly in proportions) among the five extant species of *Esox* and the numerous fossil species (pers. obs.; also see Cavender *et al.* 1970; Jollie 1975; Sytchevskaya 1976; Wilson 1980, 1984; Fink 1981). The following description is of *Esox lucius*.

Palatine

The palatine is a long, dorsoventrally flattened bone that bears numerous large, sharply pointed teeth that face the inside of the mouth (Fig. 5).

The autopalatine is fused ventrally with the dermopalatine. It begins just anterior to the posterior end of the dermopalatine and extends to its anterior end. The posterior end of the autopalatine is truncated but not expanded. Its anterior end is slightly raised and expanded mediolaterally into lateral and medial rami. The short lateral ramus is directed anterolaterally, is round in cross section and is capped by a spherical cartilaginous knob. This cartilage is slightly concave where it contacts a facet on the anteromedial surface of the maxilla. The medial ramus is larger than the lateral one and projects anteromedially. It consists of dorsal and ventral lips that are joined posteriorly to form a socket lined with cartilage. This socket encloses the lateral prenasal process of the ethmoid cartilage: the ventral lip lies ventral to the cartilage-covered preethmoid bone; the dorsal lip lies dorsal to the lateral prenasal process, closely approaching, but not contacting, the proethmoid bone.

The entire ventral surface of the dermopalatine is covered with large, sharply pointed, posteromedially directed teeth. The teeth are smallest posteriorly and laterally, and increase in size both anteriorly and medially. The largest are found on the anteromedial area of the bone beneath the medial ramus. The palatine teeth in all esocids are depressible: they are free to move posteromedially but cannot move forward. This is the result of a unique mode of tooth attachment in which the teeth sit on a pedestal that is truncated posteromedially. Because there is no collagenous connection between the anterior tooth border and the pedestal, but a large posterior collagen area where the pedestal is truncated, the tooth is hinged with a posterior axis of rotation, and cannot be moved forward beyond a point where it is seated flush with the surface of the attachment base (see Cavender *et al.* 1970 and Fink 1981 for details). In addition to the aforementioned teeth, adult *Esox masquinongy* possess one or two greatly enlarged "canine" teeth in the inner marginal row near the anteromedial corner of the palatine (see Cavender *et al.* 1970). They are ankylosed to the bone (i.e., are non-depressible), and are much larger and straighter than the depressible teeth.

Ectopterygoid

The ectopterygoid is unusually large and robust with distinctive anterior and posteroventral arms. The posteroventral arm is laminar and overlaps the anteromedial surface of the body of the quadrate. The posterolateral surface of this arm is slightly concave for the reception of the body of the quadrate. The anterior arm has a complex shape. Posteriorly it has a bony prominence (hereafter called the ethmoid process) that extends dorsally to the lamina orbitonasalis of the ethmoid cartilage. Its anterior end is projected into a socket that encloses the posterior end of the autopalatine, forming a joint. The lateral part of this socket narrows to a point anteriorly and overlaps the dorsal surface of the posterior end of the autopa[illegible] Fig. 5). The medial part of the socket is formed by a wide do[illegible] flange on the medial side of the anterior arm (refer to Fig. 5). This [illegible] from just below the base of the ethmoid process to the anteroventral [illegible]. The anterior end of the flange overlies the dorsal surface of the [illegible]palatine and underlies the posterior end of the autopalatine at the [illegible]quadrate cartilage extends posteriorly from the posterior end of the autopalatine, along the dorsal part of the anterior arm of the ectopterygoid in a trough formed by the medial flange and the main part of the anterior arm, dorsally to the lamina orbitonasalis (adjacent to the medial surface of the ethmoid process of the ectopterygoid), and then posteroventrally to the mesopterygoid.

The ectopterygoid in the other esocids, both extant and extinct, is similar to that in *Esoc lucius*.

Mesopterygoid

The mesopterygoid is a small, moderately long, narrow, toothless bone, only slightly visible when the suspensorium is viewed laterally, that forms a brace between the anterior and posterior halves of the suspensorium. It is much smaller relative to the rest of the suspensorium than in most other salmoniforms. It narrows slightly toward each end: its posterior end fits into a facet on the medial surface of the anterodorsal corner of the metapterygoid, and its anterior end overlaps the medial surface of the ectopterygoid (at the junction of its two arms). It is bent dorsomedially near its mid-point.

The mesopterygoid in other esocids, both extant and extinct, is similar to that in *E. lucius*.

Quadrate

The quadrate has several unusual features. The anterior part of the body [illegible] farther dorsally than the posterior part and firmly braces the posteroventral arm of the ectopterygoid and the mesopterygoid. The anteromedial edge of the body is slightly indented for the reception of the ectopterygoid. The mid-dorsal section of the body is thinner than the rest so that the body is effectively divided into anterior and posterior sections. Both sides of the body and condyle are sculptured with a series of small ridges and thickenings. The condyle is relatively small and projects anteroventrally. The lateral face of the condyle bears a small bony prominence from which a ligament extends to the posterodorsal corner of the angulo-articular bone of the lower jaw. According to Sytchevskaya (1976, p. 104) "Contemporary pike species differ from fossil species in having a narrower and transversely elongated articular facet of the quadrate." The quadratojugal arm is spatulate, with a slightly expanded, rounded, posterior end that does not extend much beyond the posterior end of the body. It is deeply grooved ventrally for the reception of the anterodorsal edge of the ventral limb of the preoperculum (to which it is tightly bound). A relatively high dorsally projecting flange extends along the length of the dorsal edge of the quadratojugal arm. Its medial surface is tightly bound to the anterolateral surface of the symplectic. The quadrate notch (the area between the quadratojugal arm and the posterior edge of the body) is deep but very narrow due to the aforementioned flange on the quadratjugal arm.

The mesopterygoid in other esocids, both extant and extinct, is similar to that in *E. lucius*.

Symplectic

The symplectic is relatively large and slightly bent, with a narrow ventral lamina and a wide, well-developed dorsal lamina. The thin dorsal lamina widens posteriorly, overlapping the medial surfaces of the body of the quadrate and the anteroventral corner of the metapterygoid, respectively. The medial surface is flattened whereas the lateral surface is slightly concave and has a narrow, dorsally projecting flange that extends along the anterior half of the bone. The anterior two-thirds of the bone rests tightly in a groove on the dorsomedial side of the quadratojugal arm of the quadrate. The anterior end is capped with a large, bulbous cartilage that closely approaches the condyle of the quadrate. The symplectic is similar in other esocids, both extant and extinct.

Metapterygoid

The metapterygoid is large and roughly triangular, with a posterodorsally directed apex. The lateral surface is concave, and forms a deep, cup-like depression that serves as the area of origin for part of the *adductor mandibulae* muscle. Most of the bone is endochondral in origin. The anterior part is entirely endochondral except for a narrow dermal wedge overlapping the posteroventral corner of the mesopterygoid. This wedge divides the anterior endochondral section into two parts: a large ventral fan and a small section (with a cartilaginous knob at its anterior end) at the anterodorsal corner that overlaps the posterodorsal corner of the mesopterygoid. The posterior end of the metapterygoid extends posterodorsally to overlap the entire lateral surface of the anteroventral wing of the hyomandibular. This posterior section, which is continuous with the ventral one, widens posteriorly into a large bulbous cartilaginous knob that overlies the posterodorsalmost end of the wing. At the posteroventral corner of the posterior extension is a triangular dermal lamina that overlaps the anterior end of the anteroventral wing of the hyomandibular. A dermal flange that projects dorsolaterally extends anteriorly from the anterodorsal corner of the posterior cartilaginous knob along the lateral side nearly to the anterodorsal corner of the bone. The metapterygoid is similar in other esocids, both extant and extinct.

Hyomandibular

The hyomandibular is relatively long and robust with well-defined processes. The articular surface of the head is capped with cartilage and fits in a relatively shallow facet on the skull. The posterior half rests along the posteroventral surface of the pterotic (contacting both the autopterotic and dermopterotic) and the anterior half sits in a large area of cartilage between the sphenotic, prootic, and pterotic. The anteromedial corner rests in a prominent groove on the mid-dorsal edge of the prootic. The anterolateral corner is separated from the sphenotic by a wide band of cartilage; however, in larger specimens the cartilaginous area between the prootic, pterotic, and sphenotic is smaller and the hyomandibular is closer to the sphenotic. The head of the hyomandibular is convex dorsally, with both the anterior and posterior edges forming sharp angles with the main body of the bone. A small posterodorsal lamina is present; however, the posteroventral lamina is either absent or very small. The posteroventrally inclined opercular arm is long and narrow and is capped posteriorly with a cartilaginous knob that fits in a facet on the anterodorsal corner of the operculum. The ventral arm is similar in shape to the opercular arm but is longer. There is a small anterior lamina. A long, wide, dermal, anteroventral wing extends along the entire anterior edge of the ventral arm. It overlaps the metapterygoid as in the Umbridae, but unlike them is blunt anteriorly, reaches only the ventral end of the ventral arm, and does not contact the symplectic.

A robust, unique lateral strut extends from the ventral apex of the head to the posterodorsal corner of the ventral arm. It is wide mediolaterally but relatively short dorsoventrally, and projects laterally at a right angle to the main axis of the bone. Its lateral edge actually curves slightly anteromedially, as in most umbrids. Because of the inclination of the lateral strut a relatively deep concavity is formed by its anterior face and the part of the hyomandibular directly anterior to it. This area serves as part of the area of origin of the *adductor mandibulae*, and part of the area of insertion of the *levator arcus palatini*. The dorsal edge of the strut is straight and continuous with a ridge on the head, while the ventromedial side is deeply indented. Its posterolateral surface is grooved for the reception of the anterodorsal edge of the dorsal limb of the preoperculum, which it firmly abuts. A large elliptical opening is formed between the posterior edge of the ventral arm, the ventral edge of the lateral strut, and the anteroventral edge of the dorsal limb of the preoperculum through which the posterior part of the *adductor mandibulae* passes (to originate on the medial surface of the dorsal limb of the preoperculum and the ventral surface of the opercular arm of the hyomandibular).

The medial foramen for the hyomandibular branch of the facial nerve is large and located at the intersection of the anteroventral corner of the head and the anterior lamina. The lateral foramen is smaller and located near the posterodorsal corner of the lateral strut at the intersection of the anteroventral corner of the opercular arm and ventral arm.

The hyomandibular in other esocids, both extinct and extant, is similar to that in *E. lucius*. There are minor differences in the proportions of the parts and in ornamentation.

Preoperculum

The preoperculum in *Esox lucius* is relatively small but robust, with indistinct dorsal and ventral limbs that form an obtuse angle with each other. There is a slight constriction where the ventral and dorsal limbs intersect. The anterodorsal edge of the ventral limb and the anterodorsal edge of the dorsal limb are tightly braced against the quadratojugal arm of the quadrate and the lateral strut of the hyomandibular, respectively. A unique anteromedial flange, possibly homologous with the anterior lamina described in the other salmoniforms, extends anteriorly from the intersection of the two limbs along the dorsomedial edge of the ventral limb. Its posterior end is convex laterally and firmly abuts the cartilaginous joint between the symplectic and hyomandibular. The area between the lateral face of the flange and the dorsal edge of the ventral limb forms a concavity that serves as an area of origin for part of the *adductor mandibulae*. A bone-enclosed lateral sensory canal runs along the entire length of the preoperculum and gives off six pores: one at each end of the bone, two at the ends of short auxiliary canals that lead off of the main canal on the ventral limb, and two along the main canal on the dorsal limb.

Differences with other esocids concern mainly the relative size of the limbs and the degree of bend at their intersection. For example, in the fossil species *E. tiemani*, the bone is stouter than in recent *Esox*, with more of a central bend (pers. obs.; also see Wilson 1984).

FAMILY UMBRIDAE

The suspensorium in the Umbridae is much shorter anteroposteriorly than in the Esocidae. However, as in the esocids the individual bones are unusually robust, overlap one another to a greater extent than in most salmoniforms, and there is a relatively small amount of cartilage between them. The suspensorium as a whole is unusually solid and sturdy.

Although similar in many respects, the suspensorium in the three genera exhibits considerable osteological diversity (see Figs. 6&9). In *Dallia* the suspensorium is longer (anteroposteriorly) and shallower (dorsoventrally) than the other genera, whereas in *Umbra* it is shorter and deeper than in the other two. The suspensoria in the three species of *Umbra* are similar to one another.

Because my evidence suggests that *Novumbra* is the most primitive genus I will describe it in detail and then compare it to *Dallia* and *Umbra*.

Palatine

The palatine in *Novumbra* is a moderately short, stout, tooth-bearing bone that curves anteromedially towards the tip of the snout (Fig. 6).

The autopalatine is fused ventrally with the dermopalatine. It has a posterior expansion that is truncated posteriorly. The palatoquadrate cartilage emanates from the posterior end of the posterior expansion, extending posteriorly to overlap the mesopterygoid and ectopterygoid, and posterodorsally to contact the lamina orbitonasalis of the ethmoid cartilage. The anterior end of the autopalatine is unusual because it is only slightly expanded. Extending around the anterior end of the autopalatine (but apparently not part of it), in a U-shaped ring, is a relatively wide dermal flange that projects anterodorsally as a lip (see Fig.

6). Ventral to this dorsal lip is a thinner and smaller ventral lip that extends from the anteroventral end of the autopalatine. The two lips are joined posteriorly where they meet the autopalatine, and form a "glove-like" socket that encloses a small cartilaginous knob that is continuous with the cartilaginous core of the autopalatine. This cartilage appears to be homologous with the larger cartilaginous expansion found on the anterior end of the autopalatine in most teleosts. The socket and its cartilage rest snugly at the intersection of the anterior end of the maxilla, the dorsal articular process of the premaxilla, the anteromedial edge of the proethmoid bone, and the lateral prenasal process of the ethmoid cartilage, forming a joint. Perhaps significantly, the features at the anterior end of the autopalatine (and the joint that it forms with the skull) in *Novumbra* are reminiscent of the character state found in the Esocidae, and may be primitive for the Esocoidei.

The dermopalatine is the thickened, somewhat spongy section that underlies the autopalatine, and bears teeth on its ventral surface. Its posterior end extends posterior to the autopalatine and overlaps the ectopterygoid. Its anterior end is expanded mediolaterally beneath the anterior end of the autopalatine and extends anterior to it, curving anteromedially to underly the ventral surface of the lateral prenasal process of the ethmoid cartilage. Its anterior end abuts the anterolateral corner of the vomer and the medial edge of the premaxilla, both of which bear teeth on their ventral surface that are similar in size to those on the palatine. Because of this arrangement there is a more-or-less continuous biting surface on the anteroventral surface of the snout involving teeth on the palatine, premaxilla, and vomer (the maxilla is toothless).

Almost all of the ventral surface of the dermopalatine is covered with moderately large, sharply pointed, posteromedially directed teeth that are all about the same size. There is a lateral row of about twelve to fifteen teeth along the entire length of the bone, and a medial row of less than half that number on the expanded anterior section. The palatine in the extinct species, *N. oregonensis* (from freshwater Oligocene deposits of Oregon), appears similar to that in *N. hubbsi* (pers. obs.; also see Cavender 1969).

The palatine in *Dallia* is a long, robust, tooth-bearing bone that nearly reaches the quadrate (see Figs. 7, 8). It appears to be fused with the ectopterygoid.

The autopalatine is a small, dorsoventrally flattened tube with no distinctive anterior or posterior processes. Its posteroventral surface is fused ventrally with the autopalatine. Its anterior third to half extends anterior to the dermopalatine and forms the anteriormost part of the palatine. Its anterior end is capped with a small, round cartilaginous knob that rests at the intersection of the anterior end of the maxilla, the dorsal articular process of the premaxilla, the anterolateral edge of the proethmoid bone, and the lateral prenasal process of the ethmoid cartilage, forming a joint.

The dermopalatine is unusually large and robust and makes up most of the palatine. Its posterior end lies close to the anterodorsal corner of the body of the quadrate, with which it is connected by a short but strong ligament. Its lateral side is thickened dorsoventrally, has a spongy appearance, and bears a single row of about twenty to twenty-five large, posteromedially directed functional teeth that are firmly ankylosed to the bone, and decrease slightly in size posteriorly. The smaller specimens that I examined had about fifteen functional teeth. The teeth extend along most of the lateral edge of the dermopalatine. About level with the posterior end of the autopalatine, the dermopalatine and its teeth begin to curve anteromedially, cross the ventral surface of the autopalatine, and extend medial to its anteromedial edge (see Fig. 8). The anterior tip of the dermopalatine approaches, but does not contact, the anterolateral corner of the vomer (which also bears teeth) and forms a U-shaped biting surface, as in *Novumbra*. However, the premaxilla and its teeth are separated from the vomerine and palatine dentition by a wide space.

Extending along the dorsal surface of almost the entire dermopalatine posterior to the autopalatine is a distinct trough that is open dorsally. This trough is flanked laterally by a flange that projects dorsally, and medially by an even wider flange that projects dorsomedially. Both flanges are continuous anteriorly with the posterior edge of the autopalatine and narrow posteriorly (see Figs. 7, 8). The palatoquadrate cartilage emanates from the posterior end of the autopalatine, extends posterodorsally to contact the lamina orbitonasalis of the ethmoid cartilage, and then extends posteriorly along the trough on the dorsal surface of the dermopalatine to the mesopterygoid and quadrate.

The palatine in *Umbra limi* is moderately long and narrow, bears teeth, and tapers to a point posteriorly (see Fig. 9). Its overall shape is more similar to *Dallia* than to *Novumbra*.

Like *Dallia*, the autopalatine in *U. limi* is relatively small, dorsoventrally flattened, and lacks distinct anterior and posterior dorsoventral expansions. It is shaped essentially like a dorsoventrally flattened cone (versus a flattened tube in *Dallia*) that is broad and fan-shaped at its anterior end but narrow and flat at its posterior end. Like *Dallia*, it is fused ventrally to the anterodorsal surface of the dermopalatine and extends anterior to it so that the autopalatine forms the anteriormost part of the bone. The anterior end is capped with a moderately wide, dorsoventrally flattened cartilage at the intersection of the same bones as in the other genera. Its anterolateral and anterior surfaces are slightly concave where they abut the anteromedial end of the maxilla. The anteromedial surface is also slightly concave, and abuts the lateral surface of the lateral prenasal process of the ethmoid cartilage.

The dermopalatine is moderately large and robust, and tapers to a point posteriorly. Its posterior end is flattened and underlies the anterior ends of the ectopterygoid and mesopterygoid, and the bulb-shaped anterior end of the palatoquadrate cartilage. Almost all of the ventral surface of the dermopalatine is covered with moderately large, sharply pointed, posteromedially directed teeth that decrease slightly in size posteriorly (like *Dallia*). In *U. limi* there are two distinct rows of functional teeth: the lateral row has about fifteen, the medial about twelve. The teeth extend along most of the lateral edge of the palatine, and as in *Dallia*, begin to curve anteromedially about level with the autopalatine, reaching its anteromedial edge. In the specimens of *U. krameri* that I examined, the dermopalatine was narrower and less robust than in *U. limi*, less curved anteromedially, and had only a single row of about twelve teeth. The character state in *U. pygmaea* appears to be intermediate between those in the other two species in regards to the size and shape of the dermopalatine and the number of teeth, although the tooth rows are also indistinct.

In *Umbra* the gap between the teeth on the anterior end of the palatine and those on the premaxilla and vomer is wider than in *Dallia*.

Ectopterygoid

The ectopterygoid in *Novumbra* is moderately large, laminar, and has distinctive anterior and posteroventral arms (see Fig. 6). In its overall shape and the way it overlaps the surrounding bones, it is more similar to the ectopterygoid in *Esox* (i.e., primitive) than it is to the other umbrids. The posteroventral arm overlaps the entire anteromedial edge of the body of the quadrate while the anterior end of the anterior arm overlaps the posterolateral surface of the palatine. The dorsal part of the anterior arm is expanded dorsally towards the lateral ethmoid bone in a way that is vaguely reminiscent of the well-developed ethmoid process found in *Esox*. Cavender (1969, p. 9) stated that in the extinct species *N. oregonensis*, "There is a slight suggestion of a dorsal prominence [= ethmoid process] above the bend in the ectopterygoid," noting that such a process is absent in *N. hubbsi* and all the other esocoids except for *Esox* (where it is well-developed). This suggests that an ethmoid process may have been present in the common ancestor of the Esocoidei, and is either lost (*Dallia* and *Umbra*) or in the process of being lost (*Novumbra*) in the Umbridae.

The ectopterygoid in *Dallia* appears to be fused with the palatine (see Figs. 7, 8). The small, toothless lamellar section of the "palatine" that is adjacent to the quadrate probably represents the ectopterygoid since it occupies the same position, and has the same features as a typical ectopterygoid. In the small specimens that I examined (less than five centimetres) this section was relatively larger, and extended farther anteriorly than in the larger ones.

The ectopterygoid in *Umbra limi* is moderately small, nearly straight, short anteroposteriorly, and lacks anterior and posterior expansions (see Fig. 9). Its posterior end is narrow and lies adjacent to the anterodorsal corner of the body of the quadrate, with which it is connected by a ligament. Sometimes the two bones contact one another, in which case the ligament appears to be absent or poorly developed. It overlaps the anterolateral edge of the mesopterygoid. The anterior end lies dorsal to, but does not contact the posterodorsal end of the dermopalatine. However, a ligament extends from the posterior end of the dermopalatine to the anteroventral edge of the ectopterygoid, firmly uniting the two bones.

The anterior part of the palatoquadrate cartilage lies on the mesopterygoid medial to [illegible] ectopterygoid. Its anterior end is expanded into a condyle that rests on the anterodorsal [illegible]d of the mesopterygoid. This condyle extends anterodorsally to abut the posteroventral surface of the lamina orbitonasalis of the ethmoid cartilage, forming a joint. A tough, broad ligament extends from the posterior surface of the condyle to the posterior surface of the lateral ethmoid bone (this ligament is not drawn on Fig. 9). In the other esocoids (and most teleosts) the expanded anterior part of the palatoquadrate cartilage abuts the entire ventral surface of the lamina orbitonasalis, and at its anteriormost end is continuous with the expanded posterior end of the autopalatine.

The ectopterygoid in *U. pygmaea* is shorter, narrower, and straighter (i.e., more splint-like) than the other species. In *U. krameri* it is similar to *U. limi* but is straighter and slightly smaller.

Mesopterygoid

The mesopterygoid in *Novumbra* is moderately small, thin, nearly oval, and lacks teeth (see Fig. 6). Its dorsal surface is slightly concave and slopes dorsomedially towards the parasphenoid, from which it is separated by a moderately wide band of connective tissue. The anteroventral corner of the bone projects anteriorly and overlaps the medial surface of the anterior arm of the ectopterygoid. The posteroventral end projects posteriorly and fits into a shallow facet on the medial surface on the anterodorsal corner of the metapterygoid. It is widest centrally where it overlaps the dorsomedial surface of the body of the quadrate. The mesopterygoid in the extinct species *N. oregonensis* is similar to that in *N. hubbsi* (see Cavender 1969).

The mesopterygoid in *Dallia* is similar to that in *Novumbra* except that it is thicker and more robust, does not overlap the ectopterygoid, and is more oval, lacking the distinct anteroventral and posteroventral projections found in *Novumbra* (see Fig. 7).

The mesopterygoid in *Umbra limi* is larger and more lamellar than in *Novumbra* and *Dallia*, and has a different shape: it is elongated anteroposteriorly, tapers to a point anteriorly, and is broad posteriorly (see Fig. 9). Its broad posterior end is somewhat truncated and overlaps much of the anteromedial edge of the correspondingly wide metapterygoid. Unlike the other genera there is no facet on the metapterygoid for the reception of the mesopterygoid. The mesopterygoid is not fused to the quadrate and metapterygoid as claimed by Dineen and Stokely (1954). The mesopterygoid is similar in the other two species of *Umbra*.

Quadrate

The quadrate in *Novumbra* is moderately large and moderately robust (see Fig. 6). The body is distinctly fan-shaped with steeply sloping anterior and posterior edges. The ventral apex of the body is narrowly constricted where it meets the condyle and quadratojugal arm, unlike the other esocoids in which the connection is relatively broad. It also appears constricted in the fossil species *N. oregonensis* (see Cavender 1969, fig. 1). In one of the two specimens of *N. hubbsi* that I cleared and stained for cartilage and bone (UAMZ 3718, 53.7 mm SL, see Fig. 6) the mid-dorsal section of the body was thin and laminar, and was flanked by anterior and posterior endochondral wedges, as in *Esox lucius*. The condyle in *Novumbra* is large relative to the rest of the bone and has a broad articular facet. The lateral surface of the condyle has an unusually large prominence from which a ligament extends to the lower jaw. The quadratojugal arm is long, narrow, and tapers posteriorly. This is unlike *N. oregonensis* and *Esox*, in which it is relatively short and spatulate (see figs. in Cavender 1969 and Fig. 5, respectively). The quadrate notch is deep and moderately narrow. There is virtually no [illegible] on the quadrate, unlike the other esocoids.

The quadrate in *Dallia* is larger and more robust than in the other genera (see Fig. 7). The condyle, in particular, is greatly enlarged and lacks a distinct prominence on its lateral surface for the attachment of the ligament to the lower jaw. The quadrate notch is shallower than in *Novumbra* and *Umbra*.

The quadrate in *Umbra limi* rather closely resembles that in *Dallia* except that it is smaller relative to the rest of the suspensorium and the condyle is not as well-developed (see Fig. 9). The quadratojugal arm is also shorter. The quadrate is similar in *U. pygmaea* and *U. krameri*. The condyle in *U. pygmaea* is larger than in *U. limi* and *U. krameri*.

Symplectic

The symplectic in *Novumbra* is moderately long and wide with a slight central bend (see Fig. 6). It is relatively wide posteriorly and narrows towards its anterior end where it is capped with a small cartilaginous knob. There are moderately wide dorsal and ventral laminae that extend along the length of the bone and overlap the surrounding bones rather extensively.

The symplectic in *Dallia* is more robust and straighter than in the other genera. Although it lacks well-developed laminae (they are present, but are narrow and thick) it still closely abuts the surrounding bones as in the other esocoids (see Fig. 7). It is oval in cross section (versus somewhat flattened in the other esocoids) and has a peculiar spongy texture in large specimens.

The symplectic in *Umbra* is similar to that in *Novumbra* except that it has more of a central bend and has wider (but otherwise similar) laminae.

The central bend in *U. limi* is more pronounced than in the other species (see Fig. 9). The laminae in *U. limi* are also wider and the area of overlap with the surrounding bones is greater. The dorsal lamina in particular is unusually wide and broadly overlaps the medioventral surface of the metapterygoid and the medial surface of the posterior corner of the body of the quadrate. On the lateral surface of the anterior two thirds of the bone is a moderately wide, dorsally projecting flange. This flange is poorly developed in *U. krameri* and *U. pygmaea*. In *U. krameri* the laminae are narrower and overlap less of the surrounding bones than in *U. limi* and *U. pygmaea*. The shape of the symplectic is diagnostic of each species of *Umbra*.

Metapterygoid

The metapterygoid in *Novumbra* is a relatively small, mediolaterally flattened, roughly triangular bone that is primarily endochondral in origin (see Fig. 6). The endochondral portion is axe-shaped, with a posterodorsally directed apex. The dermal section is thin, moderately narrow, and extends around the posterior edge of the endochondral part. Its posterior edge is crenulated. The posteroventral end of the bone is closely applied to the lateral surface of the anterior half of the anteroventral wing of the hyomandibular.

The metapterygoid in *Dallia* is similar to that in *Novumbra*, but is slightly smaller, more distinctly axe-shaped, and has just a trace of a dermal lamina around its posterior edge (see Fig. 7).

The metapterygoid in *Umbra* is unlike that in the other two genera, and differs from the metapterygoid in the other salmoniforms that I examined. The shape of the metapterygoid is diagnostic of each species. In *U. limi* it is moderately large and consists of two plates that are joined to each other (see Fig. 9). It is not fused with the symplectic, quadrate (which it does not even contact), mesopterygoid, and hydomandibular, as claimed by Dineen and Stokely (1954). The ventral plate is endochondral in origin, moderately thick, inclined roughly vertically, and semicircular with a rounded ventral edge. It overlaps the lateral surfaces of the mesopterygoid (posteroventral corner), symplectic (dorsal lamina), and hyomandibular (the anterior half of the anteroventral wing). There is a thin, triangular dermal section at the posteroventral corner of the ventral plate. This section is also present in *U. pygmaea*, but is absent in *U. krameri*, where the entire ventral plate is endochondral. In all three species the posterodorsal corner of the ventral plate is moderately expanded (less so in *U. krameri*) and curves laterally so that there is a small space between it and the anteroventral wing of the hyomandibular. The anteroventral corner of the *levator arcus palatini* inserts in this space. The area of origin of the *adductor mandibulae* includes the entire lateral surface of the ventral plate.

The dorsal plate is smaller than the ventral plate, nearly triangular, and projects dorsomedially from the dorsal edge of the ventral plate (it has the same inclination as the mesopterygoid). It narrows towards the posteromedial corner of the mesopterygoid. It is essentially a thin dermal lamina that is slightly concave on its dorsal surface. Its posterior edge is separated from the hyomandibular by a relatively wide gap. Its anterior edge is straight and overlaps the dorsal surface of the posteromedial edge of the mesopterygoid in *U. limi* and *U. krameri*; however, in *U. pygmaea* it is crenulated and interdigitates with the similarly shaped posteromedial edge of the mesopterygoid. Reinforcing the dorsal plate is a narrow endochondral wedge that extends medially from the ventral plate, through the middle of the dorsal plate, to its medial corner, where it is capped with a small cartilaginous knob that nearly abuts the posteromedial corner of the mesopterygoid. This wedge is largest in *U. krameri*. Part of the *adductor arcus palatini* muscle inserts on the dorsal surface of the dorsal plate, its lateralmost fibres inserting along an anteroposterior ridge formed at the intersection of the two plates (and continuous with a similarly oriented ridge on the mesopterygoid).

Hyomandibular

The hyomandibular in *Novumbra* is a robust bone that is longer dorsoventrally than it is wide anteroposteriorly (see Fig. 6). The posterior two thirds of the cartilaginous head rests in a moderately shallow groove on the anteroventral surface of the pterotic, while the anterior third rests in cartilage between the sphenotic, pterotic, and prootic. The anteromedial corner sits in a prominent groove on the mid-dorsal edge of the prootic, while the anterolateral corner abuts the posteroventral edge of the sphenotic.

The opercular arm is moderately long, but smaller and shorter relative to the rest of the hyomandibular than in the other esocoids. Distinct posterodorsal and posteroventral laminae are present. There is a moderately wide anterior lamina that is concave laterally, and extends from the anterodorsal corner of the head to the middle of the ventral arm. The ventral arm is longer than the opercular arm (unlike the other umbrids) and expanded ventrally.

Like the other esocoids, the hyomandibular has an anteroventral wing. In *Novumbra* it extends along the anteroventral edge of the ventral arm and then projects far anteroventrally to broadly overlap, and brace, the metapterygoid and symplectic. It is large and robust, and tapers to a point anteriorly. Its anteroventral end separates into lateral and medial flanges that project slightly ventrolaterally and ventromedially, respectively, and enclose the posterodorsal edge of the symplectic between them.

A robust and distinct lateral strut extends ventrally from the ventral apex of the head to the middle of the ventral arm. It is wide mediolaterally and projects laterally at a right angle to the main axis of the bone. Its lateral edge curves distinctly anteromedially. Because of the inclination of the lateral strut, a deep, cup-like concavity is formed by its anterior face and the lateral face of the anterior lamina. This area serves as part of the area of origin of the *adductor mandibulae*, and part of the area of insertion of the *levator arcus palatini*. The dorsal edge of the lateral strut is indented ventrally along its medial side (as is the case in *Dallia*).

The canal for the hyomandibular branch of the facial nerve is moderately long and inclined posteroventrally from its medial to lateral foramina. The medial foramen is moderately large and located at the ventral apex of the head. The lateral foramen is the same size as the medial one and located posterior to the lateral strut, about a third of the way ventrally from its dorsomedial corner, near the beginning of the opercular arm.

The hyomandibular in *Dallia* is robust and has a number of unusual features (see Fig. 7). Unlike the other esocoids, it is broader anteroposteriorly than it is dorsoventrally (excluding the anteroventral wing). The opercular arm is longer and the ventral arm shorter than in the other esocoids. The club-shaped opercular arm is greatly enlarged and nearly twice the length of the poorly developed ventral arm. Unlike *Novumbra* there is no posteroventral lamina.

The cartilaginous dorsal edge of the head and the corresponding facet on the skull are wider than in the other esocoids and elliptical in outline (versus relatively long and narrow). The facet is also deeper. Unlike *Novumbra*, but like the other esocoids, only about half the head rests on the pterotic. Unlike the other esocoids there is no distinct groove on the mid-dorsal edge of the prootic in which the anteromedial corner of the head rests. *Dallia* resembles *Esox* in that the head articulates with both the autopterotic (the endochondral part of the pterotic) and the dermopterotic, versus only the autopterotic in the other esocoids.

The anterior edge of the hyomandibular (excluding the anteroventral wing) is unusually wide, and forms a groove that extends ventrally from near the anterodorsal corner of the head to the beginning of the anteroventral wing. The groove is bordered laterally by the moderately narrow anterior lamina, and medially by a similarly shaped and positioned lamina on the medial side. This groove serves as a part of the insertion of the unique dorsomedial subdivision of the *adductor mandibulae*.

The anteroventral wing is similar to that in *Novumbra* but is larger relative to the rest of the bone and broader mediolaterally.

The lateral strut is robust, moderately wide, and extends from the ventral apex of the head to near the posteroventral corner of the ventral arm. Its dorsal edge is indented ventrally along its medial side, as in *Novumbra*. Unlike the other esocoids the strut is inclined slightly posterolaterally, more so in larger specimens. In large specimens the anterior face of the strut and the area anterior to it are interlaced with a network of raised lattice-like ribs that give it a spongy appearance. Because of this, larger specimens lack the deep, cup-like concavity found in this area in the other esocoids. However, in the smaller specimens that I examined (less than forty-five millimetres) this lattice network was absent and the aforementioned area was concave, but less so than in the other esocoids.

The canal for the hyomandibular branch of the facial nerve is similar to that in *Novumbra*. When the nerve exits from the lateral foramen it courses ventrally, posterior to the strut, before passing anteroventrally through the notch on its medioventral edge, and then running anterior to the hyomandibular. This is basically the same as in the other esocoids; however, in *Dallia* a short branch of this nerve passes anteriorly through the middle of the lateral strut, via a small foramen (labelled as the lateral foramen of the hyomandibular branch of the facial nerve by Wilson and Veilleux 1982, fig. 7B), before the main nerve runs anterior to the hyomandibular. This side branch appears to innervate the unusually large *levator arcus palatini*.

The hyomandibular is relatively similar in the three species of *Umbra*. In *U. limi* it is moderately robust and slightly longer dorsoventrally than it is wide anteroposteriorly (see Fig. 9). The articulation of the head of the hyomandibular with the skull is similar to that described for *Novumbra* except that only about half the head rests on the pterotic. The head is broader and larger relative to the rest of the bone than in the other genera. The opercular arm is slightly shorter than the ventral arm, but is wider and expanded more at its end. The ventral arm is relatively narrow and only slightly expanded ventrally. In *U. pygmaea* these two arms are about the same length but the opercular arm is visibly larger. The opercular arm in *U. krameri* is slightly smaller than in *U. limi*. There is a small posteroventral lamina in *U. limi*; however, in *U. krameri* and *U. pygmaea* it is absent, as in *Dallia*. All three species have a well-developed posterodorsal lamina. A wide anterior lamina that is concave laterally extends along most of the anterior edge of the bone.

An anteroventral wing is present, but it is much smaller than in the other esocoids, and has a different shape (see Fig. 9). It overlaps the same bones as in *Dallia* and *Novumbra* but the area of overlap is smaller. In some specimens of *U. limi* and *U. krameri* the anteroventral end was separated into narrow lateral and medial flanges that slightly overlap the symplectic, as in *Dallia* and *Novumbra*. The wing is largest in *U. pygmaea*.

The lateral strut is quite similar to that described for *Novumbra* but is not quite as wide, and is slightly longer dorsoventrally, nearly reaching the posteroventral corner of the ventral arm. The dorsal edge of the strut is straight in *U. limi* and *U. krameri* but indented ventrally along its medial side in larger specimens of *U. pygmaea*.

The canal for the hyomandibular branch of the facial nerve is similar to that in the other genera except that the lateral foramen is closer to the dorsal edge of the lateral strut.

Preoperculum

The preoperculum in *Novumbra* is moderately large and robust with dorsal and ventral limbs of about equal size that meet at about a right angle (see Fig. 6). There is no suprapreoperculum. The dorsal half of the anterior edge of the dorsal limb fits tightly in a well-developed groove on the posterolateral surface of the lateral strut of the hyomandibular. The anterodorsal edge of the ventral limb fits in a groove on the ventral surface of the quadratojugal arm of the quadrate. The anterior lamina is large and slightly convex laterally. A bone-enclosed lateral sensory can runs along the entire length of the preoperculum and gives off five pores: one at each end of the bone, two at the ends of short auxiliary canals that lead off of the main canal on the ventral limb, and one along the main canal on the dorsal limb. The preoperculum in the extinct species *N. oregonensis* has a similar shape (see Cavender 1969)

The preoperculum in *Dallia* is more robust than in *Novumbra* and is broader, especially at the intersection of the two limbs (see Fig. 7). The ventral limb is slightly longer than the dorsal limb and the two meet at an angle slightly greater than ninety degrees. The entire anterior edge of the dorsal limb fits tightly into a well-developed groove on the posterolateral surface of the lateral strut of the hyomandibular. The anterior lamina is relatively small. The bone-enclosed lateral sensory canal gives off four pores: one at each end of the bone, and two at the ends of long auxiliary canals that lead off of the main canal (one at the intersection of the two limbs and one on the ventral limb). There is a lattice-like network of sculpture between the canals and on the anterior lamina. A feature unique to *Dallia* is a dorsomedially projecting flange on the dorsomedial side of the dorsal limb that lies just ventral to the ventromedial side of the opercular arm of the hyomandibular (see Fig. 7). The space between this flange and the dorsomedial surface of the dorsal limb of the preoperculum forms a groove into which the opercular arm might come to rest if the hyomandibular (but not the preoperculum) were displaced ventrally.

The preoperculum in *Umbra* closely resembles that in *Dallia* except that the dorsal limb is slightly longer and narrower than the ventral limb, the limbs meet at about a right angle, and only the middle part of the anterior edge of the dorsal limb rests against the lateral strut of the hyomandibular (see Fig. 9). The lateral sensory canal gives off four pores, as in *Dallia*, but the auxiliary canals are shorter and are located farther posteriorly. The preoperculum in *U. pygmaea* is larger than in the other two species and most closely resembles that in *Dallia*.

FAMILY SALMONIDAE

The family Salmonidae is usually divided into three subfamilies: the Coregoninae, the Thymallinae, and the Salmoninae. The suspensorium in the Salmonidae exhibits considerable osteological diversity, especially anteriorly (see Figs. 10-13), much of which appears to be related to the variable feeding habits of these fishes (most Coregonines are planktivorous whereas most salmonines are piscivorous). The Coregoninae (hypothesized by most workers to be the most primitive group) are described first, followed by the Thymallinae, and the Salmoninae, respectively.

Subfamily Coregoninae

The suspensoria in the three coregonine genera (*Coregonus*, *Prosopium*, and *Stenodus*) are similar, with the palatine and hyomandibular showing the most variability. The suspensorium in *Coregonus* and *Prosopium* is more delicately constructed than in the other salmonids; however, in *Stenodus* it is moderately robust, a feature apparently related to the piscivorous feeding habits of the latter genus.

Coregonus artedii is described in detail and then compared to the other coregonines (see Figs. 10, 11).

Palatine

The palatine in *Coregonus artedii* is moderately long, narrow, delicate, and bears a few teeth (see Fig. 10). The autopalatine (the endochondral part of the palatine) is small and forms the anterodorsalmost part of the bone. It is short anteroposteriorly, cylindrical in cross-section, and fused ventrally with the dermopalatine. Its anterodorsal end is turned upwards, is slightly expanded dorsally, and bears a cartilaginous knob on its dorsal surface that is dorsal to the rest of the palatine. The anterodorsal surface of this cartilage rests in a facet on the anteromedial side of the maxilla while the medial surface contacts the lateral prenasal process of the ethmoid cartilage. The dermopalatine is long, thin, extends posterior to the autopalatine, and bears a few tiny, delicate teeth on its ventral surface. Its posterior end is splint-like and overlaps, but is not fused with the anterior end of the ectopterygoid.

The palatine in *Coregonus clupeaformis* is similar to that in *C. artedii* except that the anterior end of the autopalatine is expanded more, is not turned upwards as distinctly (it is expanded anteriorly as well as dorsally) and the anterior cartilaginous knob is larger, does not extend as far dorsally, and does not contact the maxilla at all. The dermopalatine also has fewer teeth than in *C. artedii*. The palatine in *Stenodus* is similar to that of *C. clupeaformis* except that much of the ventral surface of the dermopalatine is covered by tiny, denticle-like teeth. According to Norden (1961, p. 720), "Weak small teeth are borne on the palatine during the young stages of all coregonines ... but they are lost as juveniles, except in *Stenodus leucichthys* and *Coregonus sardinella*." In *Prosopium* the palatine is toothless and weakly developed. The autopalatine is small with only a tiny dorsally directed anterior expansion (and cartilaginous knob) that is widely separated from the maxilla (see Fig. 11).

Ectopterygoid

The ectopterygoid in *Coregonus artedii* is moderately long and narrow with a moderate central bend and a posterior expansion that overlaps the anteromedial surface of the body of the quadrate (see Fig. 10). A narrow flange runs along most of its lateral surface.

The ectopterygoid in *C. clupeaformis* and *Stenodus* is similar to that in *C. artedii* but is slightly shorter and more robust. In *Prosopium* it is shorter and wider than the other species (see Fig. 11).

Mesopterygoid

The mesopterygoid in *Coregonus artedii* is a relatively thin, moderately long but narrow toothless bone that tapers to a point anteriorly (see Fig. 10). Its anterolateral edge runs adjacent to and sometimes contacts the medial edge of the ectopterygoid and palatine. One specimen (UAMZ 3604, 129.4 mm SL) had numerous tiny, loosely attached teeth scattered randomly over the posteroventral surface of the bone. No other coregonine or salmonid that I examined had teeth on the mesopterygoid.

The mesopterygoid in the other coregonines is similar to that in *C. artedii*; however, in *Prosopium* it is smaller and does not extend as far anteriorly (see Fig. 11).

Quadrate

The quadrate in *Coregonus artedii* is moderately delicate with few distinctive features (see Fig. 10). The quadratojugal arm is moderately long and narrow and is slightly separated from the anterior edge of the ventral limb of the preoperculum (to which it is bound by connective tissue). There is a distinct quadrate notch.

In *Stenodus* the quadrate is more robust and has a larger condyle than the other coregonines.

Symplectic

The symplectic in *Coregonus artedii* is relatively straight with a moderately wide posterodorsal lamina that overlaps the metapterygoid (see Fig. 10). A similar symplectic is found in the other coregonines except that in *C. clupeaformis* the dorsal lamina is narrower and in *Prosopium* it is absent altogether (see Fig. 11).

Metapterygoid

The metapterygoid in *Coregonus artedii* is a moderately robust, semicircular bone (see Fig. 10). It consists of a large, dorsoventrally inclined ventral section that is slightly concave laterally, and a much smaller anterodorsal section that projects dorsomedially from the anterodorsal margin of the ventral plate to overlap the posterodorsal surface of the mesopterygoid. The entire bone is endochondral in origin. The metapterygoid is similar in the other coregonines except that in *Prosopium* there is a narrow dermal flange along the posterodorsal edge of the ventral endochondral plate (see Fig. 11).

Hyomandibular

The hyomandibular in *Coregonus artedii* is a moderately robust bone that is longer dorsoventrally than it is wide anteroposteriorly (see Fig. 10). The articular surface of the head is capped with cartilage and fits in a shallow facet on the skull: the posterior half rests on the pterotic (it contacts only the autopterotic) and the anterior half rests in cartilage between the pterotic, prootic, and sphenotic. Its anterolateral corner contacts the posteroventral corner of the sphenotic and the anteromedial corner fits in a groove on the mid-dorsal edge of the prootic. The opercular arm is short and capped posteriorly with a cartilaginous knob that rests in a facet on the anterodorsal corner of the operculum. Both posterodorsal and posteroventral laminae are present. A long, moderately wide, posterolaterally inclined lateral strut extends from the ventral apex of the head to the posteroventral corner of the ventral arm. Its concave anterior surface, along with the concave lateral face of the anterior lamina, forms a large area for muscle origin and insertion. The anterior lamina is broad but thin, and extends along most of the anterior edge of the hyomandibular. Near its middle it projects anteroventrally as a strut that abuts the posteromedial edge of the metapterygoid. There is a ridge on the medial surface of the anterior lamina that extends anteroventrally to the tip of the aforementioned strut. The anterior end of the *adductor arcus palatini* inserts along and dorsal to this ridge. The ventral arm is moderately long and widens slightly ventrally. The anterolateral side of the ventral arm is excavated from just dorsal to its anteroventral corner nearly to its dorsal end. Extending along the anteroventral edge of the ventral arm, and continuous with the ventral end of the anterior lamina, is a thin and relatively small anteroventral wing that extends anteroventrally to overlap the medial surface of the mesopterygoid. The medial foramen for the hyomandibular branch of the facial nerve is moderately large and located at the ventral apex of the head. The lateral foramen is about the same size as the medial one and is found at the posterodorsal corner of the lateral strut, at the intersection of the anteroventral corner of the opercular arm and the ventral arm. The surface of the head and opercular arm have a moderate amount of sculpture.

The hyomandibular in *C. clupeaformis* is similar to that in *C. artedii* except that the strut extending from the anterior lamina to the metapterygoid is not as well-developed. The hyomandibular in *Prosopium* (see Fig. 11) differs from that in *C. artedii* in the following ways: it is not as robust, has less sculpturing, has a shorter opercular arm and a larger anteroventral wing and anterior lamina, and the anterior lamina lacks a distinct anterior strut (although it does extend anteroventrally to overlap the metapterygoid). The hyomandibular in *Stenodus* is more robust, shorter dorsoventrally (the ventral arm is shorter), and broader anteroposteriorly (the opercular arm is longer and the head is broader) than in the other genera. The lateral strut is also more robust and has a unique shape: it extends dorsoventrally along the ventral arm as in the other genera, but unlike them curves sharply anterodorsally about level with the opercular arm so that the dorsal part of the strut is nearly parallel with the posterodorsal edge of the head. Because of its shape and inclination the anterior face of the strut is more concave than in the other coregonines.

Preoperculum

The preoperculum in *Coregonus artedii* is relatively thin and flat with distinct dorsal and ventral limbs that meet at about a right angle (see Fig. 10). The dorsal limb is about one and a half times the length of the ventral limb. Both limbs are tapered. The middle of the anterior edge of the dorsal limb is braced against most of the posterolateral edge of the lateral strut of the hyomandibular. The anterior lamina is moderately large and slightly convex laterally. A bone-enclosed lateral sensory canal runs along the entire length of the preoperculum and gives off seven or eight pores: one at each end of the bone, four at the ends of moderately long auxiliary canals that lead off of the main canal on the ventral limb, and one or two along the main canal on the dorsal limb. There is no suprapreoperculum.

In *Prosopium* the preoperculum is narrower than in the other coregonines (see Fig. 11) whereas in *Stenodus* it is slightly broader. In *Prosopium* the lateral sensory canal gives off eight or nine pores: one at each end of the bone, four or five at the ends of moderately long, narrow auxiliary canals that lead off of the main canal on the ventral limb, and two along the main canal on the dorsal limb. In *Stenodus* the lateral sensory canal has eight pores (four are at the ends of auxiliary canals on the ventral limb).

Subfamily Thymallinae

The suspensorium in *Thymallus* is moderately robust and moderately long anteroposteriorly (see Fig. 12). It is intermediate to the Coregoninae and Salmoninae in numerous ways, but overall it more closely resembles the suspensorium in the Salmoninae. The following is a description of *Thymallus arcticus*.

Palatine

The palatine in *Thymallus arcticus* is intermediate between that in the coregonines and salmonines (see Fig. 12). Its overall shape is similar to that in *Coregonus artedii*; however, the bone is larger, more robust, and the teeth are larger and more numerous. The autopalatine is also shorter anteroposteriorly than in the coregonines. The anterodorsal end of the autopalatine is also expanded more and has a larger and uniquely shaped cartilaginous knob on its dorsal surface. This cartilage extends dorsally from the autopalatine and then expands laterally as a "hook" that projects laterally to overlie a facet on the anterodorsal surface of the maxilla. This palatine hook is found in the salmonines as well; however, in *Thymallus* it is longer and narrower. The dorsomedial side of the anterior palatine cartilage is only slightly expanded medially and is concave where it abuts the lateral prenasal process of the ethmoid cartilage. The dermopalatine is similar to that in *C. artedii* but is larger, more robust, and has about twelve moderately small, pointed, posteromedially directed teeth in an irregular row along its ventrolateral surface.

Ectopterygoid

The ectopterygoid is a small, splint-like bone with only a trace of a central bend (see Fig. 12). Unlike the coregonines, the posterior end is not expanded and overlaps only a small part of the body of the quadrate.

Mesopterygoid

The mesopterygoid is toothless and is similar in shape to that in *Coregonus artedii*, but is smaller (see Fig. 12).

Quadrate

The quadrate is basically the same as in the Coregoninae.

Symplectic

The symplectic is similar to that in the Coregoninae (see Fig. 12). As in *Prosopium* it lacks dorsal and ventral laminae.

Metapterygoid

The metapterygoid is similar to that in the coregonines except that the anterodorsal corner curves gently dorsomedially to overlap the mesopterygoid rather than projecting sharply dorsomedially as a distinct plate-like section (see Fig. 12 and compare to Figs. 10,11). In addition, in *Thymallus* there is a prominent, thin, dermal lamina that extends posterodorsally from the posterodorsal end of the endochondral section to overlie the ventrolateral part of the anterior lamina of the hyomandibular. Because this posterodorsal lamina projects slightly laterally there is a space formed between its medial surface and the lateral surface of the anterior lamina. The anteroventralmost part of the *levator arcus palatini* inserts in this space, with the lateralmost fibres inserting on the entire medial surface of the posterodorsal lamina of the metapterygoid. Part of the *adductor mandibulae* originates on the lateral surface of the posterodorsal lamina. An endochondral wedge radiates posterodorsally from the mid-dorsal edge of the ventral endochondral section through the posteroventral part of the posterodorsal lamina. The posterior end of this wedge is capped with a cartilaginous knob that abuts the anteroventral edge of the ventral arm of the hyomandibular.

Hyomandibular

Although the hyomandibular in *Thymallus* is basically similar to that in *C. artedii* there are several relatively minor differences (see Fig. 12). The area of cartilage between the pterotic, prootic, and sphenotic bones is larger than in the coregonines so that only the posterior third of the dorsal edge of the head of the hyomandibular rests on the pterotic. The lateral strut is also less developed (it is straighter, shorter, and narrower) and extends only to the middle of the posterior side of the ventral arm. It is inclined more posterolaterally than in the coregonines and lacks a distinct concavity on its anterior face. The anterior lamina is also smaller and lacks a distinct ridge on its medial surface. The lateral foramen for the hyomandibular branch of the facial nerve is more ventrally located than in the coregonines (near the middle of the posterior side of the lateral strut, ventral to the intersection of the anteroventral corner of the opercular arm and the ventral arm). *Thymallus* also lacks an anteroventral wing and the anterolateral side of the ventral arm is not excavated.

Preoperculum

The preoperculum is similar to that in the Coregoninae except that the limbs meet at a slightly obtuse angle (see Fig. 12). The bone-enclosed lateral sensory canal gives off eight pores: one at each end of the bone, four at the ends of moderately long auxiliary canals that lead off of the main canal on the ventral limb, and two along the main canal on the dorsal limb.

Subfamily Salmoninae

The suspensoria in the salmonines closely resemble one another, with major differences being proportional rather than structural. The salmonine suspensorium is more robust than in the other salmonids and has large, well-developed teeth on the palatine. Overall it is more similar to *Thymallus* than to the coregonines.

Salvelinus fontinalis is described in detail and then compared to the other salmonines (see Fig. 13).

Palatine

The palatine in *Salvelinus fontinalis* has the same general shape as in *Thymallus* but is larger, more robust, and has large well-developed teeth on its ventral surface (see Fig. 13). The autopalatine is similar to that described for *Thymallus* but is smaller and shorter (anteroposteriorly) relative to the rest of the bone, and has a "boat-like" shape when viewed laterally, with both anterior and posterior ends turning upwards. In larger specimens the entire dorsal surface of the autopalatine is made up of a lattice-like network of longitudinal and transverse ridges. The cartilage on the anterodorsal end of the autopalatine is similar to that in *Thymallus* except that it is larger, and the lateral palatine "hook" that overlies the anterodorsal surface of the maxilla is shorter (but wider). The palatoquadrate cartilage that projects from the posterior end of the autopalatine is different from that in the Coregoninae and Thymallinae: it is deeper dorsoventrally and extends dorsally to articulate with the lamina orbitonasalis of the ethmoid cartilage as soon as it exits from the posterior end of the autopalatine, rather than farther posteriorly. This articulation is dorsal to the posterior end of the autopalatine (and dorsal to the anterior end of the palatine) rather than distinctly posterior ~~to~~ the autopalatine (and dorsal to the posterior end of the palatine), as in the Coregoninae and Thymallinae (compare Fig. 13 with Figs. 10-12). The dermopalatine is most similar to that in the Thymallinae. However, it is larger, more robust, and curves anteromedially so that its anterior tip lies distinctly anteromedial to the anterior tip of the autopalatine. The posterior end tapers to a point that overlaps the medial surface of the anterior tip of the ectopterygoid. An irregular row of about twelve to fifteen large, robust, posteromedially directed teeth are found along the lateral surface of the dermopalatine from the anterior tip nearly to the posterior end. The teeth are largest beneath the autopalatine and decrease slightly in size towards each end. A relatively wide, thin skirt of bone extends around the entire ventrolateral side of the dermopalatine, obscuring the dorsal part of the teeth when the bone is viewed laterally. This skirt is more prominent in larger specimens. The palatine and vomerine teeth are separated by a narrow gap, but form a virtually continuous semicircular biting surface around the anterior margin of the palate.

The palatine in other salmonines differs in no significant way from that in *S. fontinalis*. Differences concern mainly the size of the bone relative to the rest of the suspensorium and the size and proportions of the various parts. In some salmonines the gap between the palatine and vomerine teeth is wider than in *S. fontinalis* (e.g., *Oncorhynchus*), however in others, such as *Hucho* and *Brachymystax*, there is no gap and the teeth form a continuous biting surface (pers. obs.; also see Norden 1961). The palatine in extinct salmonines is similar to that in extant species (see Cavender and Miller 1972; Kimmel 1975; Smith 1975; Wilson 1974, 1977). The most intriguing, as well as the oldest salmonine (and salmonid) is *Eosalmo driftwoodensis* from freshwater Eocene deposits of British Columbia (see Wilson 1974, 1977). According to Wilson this species may be an ancestral salmonine and is intermediate in several characters between the Salmoninae and Thymallinae. Its palatine, however, is more similar in relative size and proportions to that in *Thymallus* than to the salmonines (pers. obs.; also see fig. 7 in Wilson 1977).

Ectopterygoid

The ectopterygoid in *Salvelinus fontinalis* (see Fig. 13) and the other salmonines is basically as described for *Thymallus*. Unlike *Thymallus*, in all salmonines the anterior end of the ectopterygoid closely overlaps the posterior end of the dermopalatine so that the two bones appear continuous. No salmonine had what could be called a distinct posterior expansion of the ectopterygoid; however, in *Oncorhynchus* the bone had a slight central bend and overlapped more of the body of the quadrate than in the other salmonines examined. The extinct salmonine *Smilodonichthys rastrosus* is unusual in that although the ectopterygoid is relatively short and narrow it is sharply bent centrally (the two arms are about the same length). Its posteroventral arm overlaps the entire anteromedial edge of the body of the quadrate but does not appear to be expanded (see Cavender and Miller 1972).

Mesopterygoid

The mesopterygoid in *Salvelinus fontinalis* lacks teeth and is shorter, broader, and more robust than in the Coregoninae and Thymallinae (see Fig. 13). Unlike the latter two groups the posterior end is wide, distinctly truncated, and overlaps the medial surface of the anterodorsal part of the body of the quadrate (in addition to the metapterygoid). A similar mesopterygoid was found in the other salmonines examined, including *Brachymystax*, which is hypothesized by Norden (1961) to be the most primitive genus. According to Cavender and Miller (1972) the mesopterygoid covers the entire dorsal part of the medial surface of the body of the quadrate in the extinct species *Smilodonichythys rastrosus*. The mesopterygoid is not clearly visible in *Eosalmo driftwoodensis* and other extinct salmonines (see Smith 1975; Kimmel 1975; Wilson, 1974, 1977).

Quadrate

The quadrate in *Salvelinus fontinalis* is more robust and has more sculpture on its surface than in *Thymallus* and the coregonines (see Fig. 13). The quadratojugal arm is also shorter anteroposteriorly.

The quadrate in other salmonines is similar in most respects to that in *S. fontinalis*. Minor differences concern the curvature of the dorsal edge of the body, the shape and length of the quadratojugal arm, and the depth of the quadrate notch. The quadrate in most fossil salmonines is similar to that in extant species (see Smith 1975; Kimmel 1975; Wilson 1974, 1977); however, in *Smilodonichthys rastrosus* it is unusually robust and wide and appears to lack a quadrate notch (see Cavender and Miller 1972).

The position of the quadrate (and hence the articulation with the lower jaw) in the salmonines is unlike that in the other salmonids. It is located farther posteriorly (relative to the other bones of the suspensorium) than is usual, with its posterior end ventral to the anterior edge of the hyomandibular, and ventral to the metapterygoid, rather than anterior to the hyomandibular, and anteroventral to the metapterygoid (compare Fig. 13 with Figs. 10-12; also see figures in Norden 1961; Shaposhnikova 1968; Cavender 1970). A similar character state is found in the extinct salmonines *Smilodonichthys* (see Cavender and Miller 1972) and *Oncorhynchus salax* (see Smith 1975). However, in *Eosalmo driftwoodensis* the position of the quadrate is similar to that in *Thymallus* (pers. obs.).

Symplectic

The symplectic in *Salvelinus fontinalis* and other salmonines, both extinct and extant, is basically similar to that described for *Thymallus*.

Metapterygoid

The metapterygoid in *Salvelinus fontinalis* is similar to that described for *Thymallus* but is larger, more robust, and lies dorsal, rather than posterodorsal to the quadrate (see Fig. 13 and compare to Fig. 12). Unlike *Thymallus*, the anterodorsal corner of the bone (and the adjacent posterodorsal end of the palatoquadrate cartilage) does not curve noticeably dorsomedially (i.e., the anterodorsal edge of the bone is straight and extends anteroposteriorly rather than curving anteromedially). More of the metapterygoid overlaps the mesopterygoid than in *Thymallus* and the coregonines. The endochondral wedge that radiates from the endochondral section through the posterodorsal lamina is smaller than in *Thymallus* and was absent in the largest specimen of *S. fontinalis* that I examined (UAMZ 3349, 140.3 mm SL).

The metapterygoid in the other salmonines is similar to that in *S. fontinalis* (also see Shaposhnikova 1968; Cavender 1970). The major differences concern the relative size of the posterodorsal dermal lamina and the size of the endochondral wedge that radiates through it (the wedge was reduced in larger specimens, as in *S. fontinalis*, but was not absent in any other species that I cleared and stained). The metapterygoid in *Salmo trutta* was unlike the other salmonines examined because its anterodorsalmost corner curved slightly anteromedially and the posterodorsal corner of the adjacent palatoquadrate cartilage projected medially to the posteromedial corner of the mesopterygoid as a distinct finger-like extension (as in *Thymallus*).

The metapterygoid in most fossil salmonine specimens is not visible (including those of *Eosalmo* that I examined); however, when visible (as in *Smilodonichthys rastrosus* and *Oncorhynchus salax*; see Cavender and Miller 1972 and Smith 1975, respectively) it resembles that in extant salmonines.

Hyomandibular

The hyomandibular in *Salvelinus fontinalis* is slightly more robust, wider anteroposteriorly and shorter dorsoventrally than in *Thymallus* and all the coregonines except for *Stenodus* (see Fig. 13). The articulation of the head of the hyomandibular with the skull is similar to that in *Thymallus* except that the posterior half of the head rests on the pterotic rather than only the posterior third. The lateral strut is different than in *Thymallus* and the coregonines because it is more lamina-like than strut-like: it is thinner, wider anteroposteriorly, and is inclined farther posteriorly and only slightly laterally so that its entire anterior face, together with the rest of the lateral face of the hyomandibular, forms an unusually large, flat area for muscle origin and insertion. Because of its size and inclination its posterior end covers the anterolateral surface of the opercular arm. The anterior lamina is similar to that in the Thymallinae except that it is larger. The hyomandibular lacks an anteroventral wing. The largest specimen (UAMZ 3349, 140.3 mm SL) had a small excavation on the anterolateral surface of the ventral end of the ventral arm as in the Coregoninae (but it did not extend along the entire anterior edge of the ventral arm as in that subfamily).

The hyomandibular in other salmonines is basically similar to that in *Salvelinus fontinalis*; differences concern mainly proportions and the amount of sculpture. However, the lateral strut has two forms in the salmonines: the broad, laminar form described for *S. fontinalis* and a form in which the strut is more robust (pers. obs.; also see Shaposhnikova 1968; Cavender 1978, 1980; Gorshkov *et al.* 1979). The laminar form is found in *Hucho*, *Salvelinus fontinalis*, *S. confluentus*, *S. namaycush*, *S. pluvius*, *Salmo gairdneri*, and *Salmo trutta*. Associated with this type of strut is a broad anterior lamina. The robust form is similar to that in *Thymallus* and the coregonines. It is found in *Brachymystax*, most *Oncorhynchus*, *Salvelinus alpinus*, and *Salvelinus malma*. This type is thicker and more strut-like, shorter dorsoventrally (it does not extend as far dorsally) and narrower anteroposteriorly (it does not overlap much of the opercular arm), and is directed more laterally. Generally speaking, the anterior lamina is also smaller. A small anteroventral wing of the hyomandibular that overlaps the medial surface of the posteroventral corner of the metapterygoid, similar to that in the Coregoninae but smaller, is found in *Oncorhynchus nerka* (pers. obs.), and *Salvelinus confluentus* (see Cavender 1980, fig. 9).

The hyomandibular in the extinct salmonines is not always well-preserved, however, it appears basically similar to that in extant species (see Cavender and Miller 1972; Smith 1975; Kimmel 1975; Wilson 1977). The hyomandibular in *Eosalmo driftwoodensis* is similar to that in *Thymallus* but has a broader anterior lamina and a slightly more robust lateral strut (pers. obs.). It is impossible to tell with certainty whether or not any of the fossil species possesses an anteroventral wing on the hyomandibular.

Preoperculum

The preoperculum in *Salvelinus fontinalis* is smaller than in *Thymallus* and the coregonines, with dorsal and ventral limbs that meet at an obtuse angle (see Fig. 13). The ventral limb is distinctly abbreviated anteriorly so that the dorsal limb is at least twice as long as the ventral limb. As in all extant salmonines, there is a suprapreoperculum dorsal to the dorsal tip of the dorsal limb. The dorsal part of the dorsal limb overlaps the lateral edge of the lateral strut of the hyomandibular rather than abutting its posterolateral surface as in most salmonids (including most salmonines with the robust, but not laminar type of lateral strut). The bone-enclosed lateral sensory canal gives off only six pores: one at each end of the bone, three at the ends of moderately long auxiliary canals that lead off of the main canal on the ventral limb, and one along the main canal on the dorsal limb.

The preoperculum in other salmonines is basically similar to that described for *S. fontinalis*. The differences concern primarily the relative size of the bone, the angle formed by the intersection of the two limbs, the degree of abbreviation of the anterior end of the ventral limb, and the number of lateral sensory pores (pers. obs.; also see Shaposhnikova 1968; Cavender 1970; Gorshkov *et al.* 1979). The size of the preoperculum is quite variable in the salmonines. It is relatively broad with an expanded posterior margin in *Oncorhynchus*, whereas in *Salvelinus namaycush* it is even smaller than in *S. fontinalis* with barely a trace of a ventral limb (pers. obs.). Most salmonines examined had six (*Salvelinus fontinalis*, *S. namaycush*) or seven (*Salmo gairdneri*, *S. trutta*, and *Oncorhynchus nerka*) sensory pores on the preoperculum. However *Salmothymus ohridanus* apparently has eight (see Cavender 1970, fig. 3) and *Brachymystax* has eight or nine (pers. obs.). The preoperculum in the latter genus is also more similar in shape to that in *Thymallus* than to the other salmonines; it lacks a distinctly abbreviated ventral limb, and has dorsal and ventral limbs that meet at only a slightly obtuse angle.

The preoperculum in most extinct species is similar to that in extant salmonines (see Cavender and Miller 1972, 1982; Smith 1975; Wilson 1974, 1977). In *Smilodonichthys rastrosus* it is broader and more robust than in most salmonines, most closely resembling that in the extant genus *Oncorhynchus* (see Cavender and Miller 1972). The preoperculum in *Eosalmo driftwoodensis* is more similar to that in *Thymallus* than to the other salmonines, and has seven to nine sensory pores (pers. obs.; also see Wilson 1974, 1977). According to Wilson (1974, p. 208) "A suprapreopercular has not been seen" in *Eosalmo*.

FAMILY OSMERIDAE

In his 1963 revision McAllister divided the Osmeridae into two subfamilies with six genera and ten species: the Hypomesinae, containing *Hypomesus* (three species) and *Mallotus* (one species); and the Osmerinae containing *Osmerus* (one species), *Allosmerus* (one species), *Spirinchus* (three species), and *Thaleichthys* (one species). The overall shape of the suspensorium in the Osmeridae more or less corresponds to this grouping: in the Hypomesinae it is moderately long and narrow anteroposteriorly (see Figs. 14, 15) whereas in the Osmerinae it is shorter anteroposteriorly but deeper dorsoventrally (see Figs. 16, 17). Because my evidence suggests that hypomesines are more primitive than the osmerines, the Hypomesinae will be described first, followed by the Osmerinae.

Subfamily Hypomesinae

The suspensorium in *Mallotus* (see Fig. 14) is longer anteroposteriorly and has fewer and smaller teeth than in *Hypomesus* (see Fig. 15). Although the overall shape of the suspensorium in the two genera is similar the individual bones show considerable variability. *Hypomesus pretiosus* is described in detail and then compared to *Mallotus villosus*. *Hypomesus olidus* was also examined but differed in no significant way from *H. pretiosus*.

Palatine

The palatine in *Hypomesus pretiosus* is a moderately small, moderately robust tooth-bearing bone (see Fig. 15). When *in situ*, and viewed dorsally, it is inclined only slightly anteromedially. The autopalatine, which makes up most of the bone, is cylindrical in cross-section and is moderately expanded at its anterior and posterior ends. The anterior end of the anterior expansion is capped with a round, cartilaginous knob that extends anterodorsally. This cartilage is slightly expanded anterolaterally and anteromedially. The anterolateral expansion contacts a small cartilage covered knob on the anteromedial side of the maxilla. The edge of the anteromedial expansion is slightly concave where it receives the lateral prenasal process of the ethmoid cartilage. Emanating posteriorly from the posterior expansion is the palatoquadrate cartilage. This cartilage expands slightly dorsally, where it is concave and receives the lamina orbitonasalis of the ethmoid cartilage. It overlies the anterodorsal surface of the mesopterygoid before extending posteriorly. The dermopalatine is a tiny, flat tooth-bearing element that is applied closely to, but not fused with, the central part of the anteroventral surface of the autopalatine. It extends slightly anterior to the autopalatine. It has up to six small, pointed, posteriorly directed teeth on its ventral surface.

The palatine in *Mallotus* is similar to that in *Hypomesus* but is distinctly longer anteroposteriorly (see Fig. 14). The anterior expansion and its cartilage are flattened dorsoventrally and expanded mediolaterally. The dermopalatine, also longer than in *Hypomesus*, is fused to the autopalatine, and has up to ten small teeth extending in one row along its ventral surface.

Ectopterygoid

The ectopterygoid in *Hypomesus pretiosus* is long and moderately narrow with distinct anterior and posteroventral arms that meet at nearly a right angle (see Fig. 15). The posteroventral arm is expanded and overlaps the anteromedial surface of the body of the quadrate, extending nearly to the condyle. The part of the ectopterygoid that overlaps the quadrate is slightly concave laterally. At the intersection of the two arms is a posterodorsally directed finger-like extension that extends towards the anteriormost corner of the metapterygoid. This process was better developed in some specimens than in others. It was present in *H. olidus*. The anterior arm is about three times as long as the posteroventral arm. In one specimen of *H. pretiosus* (UAMZ 3515, 125.2 mm SL) the posteroventral edge of the anterior arm of both ectopterygoids possessed two adjacent, small, anteroventrally directed teeth. The anterior end of the ectopterygoid overlaps the posteroventral surface of the autopalatine. The posterior end of the dermopalatine in turn overlaps the anteriormost end of the ectopterygoid. A relatively narrow, dorsolaterally projecting flange extends along most of the lateral surface of the bone.

The ectopterygoid in *Mallotus* resembles that in *Hypomesus* but is longer anteroposteriorly (see Fig. 14). The posterodorsal extension at the intersection of the two arms is also larger and slightly overlaps the medial surface of the anteriormost corner of the metapterygoid.

Mesopterygoid

The mesopterygoid in *Hypomesus pretiosus* is a moderately robust, moderately long, relatively narrow bone that has numerous large teeth on its ventral surface (see Fig. 15). Its dorsal surface is concave and slopes dorsomedially towards the parasphenoid, from which it is separated by a moderately wide band of connective tissue. It is widest posteriorly where it overlaps the anteromedial surface of the metapterygoid and narrows anteriorly to a point that overlaps the posteromedial surface of the autopalatine. Its lateral edge is separated from the ectopterygoid by a narrow band of cartilage; however, slight overlap occurs in some specimens. The palatoquadrate cartilage that covers its anterodorsal surface is relatively narrow mediolaterally.

The medioventral surface of the mesopterygoid bears a series of large, pointed teeth that curve ventrolaterally. The teeth extend along nearly the entire anteroposterior length of the bone and increase in number posteriorly (anteriorly they form a single row). The medialmost teeth (especially those at the posterior end of the bone) are the largest and are arranged in irregular rows that run anteroposteriorly. The teeth lateral to these are smaller, and more randomly distributed. The part of the mesopterygoid that bears the teeth is thickened, especially posteriorly where there are several rows of teeth. The posteriormost teeth rest on a unique, expanded, raised, bony platform that projects posterior to the main part of the mesopterygoid. This "platform" underlies, and extends posterior to the anterodorsal corner of the metapterygoid. The ventrolaterally directed teeth on the mesopterygoid oppose a large number of similar, but dorsomedially directed teeth on both the basihyal and basibranchials, forming a specialized bite mechanism. There were from twenty to fifty functional teeth on each mesopterygoid in the seven specimens that I cleared and stained. The number of teeth on each mesopterygoid was about the same in an individual.

The mesopterygoid in *Mallotus* is less robust than in *Hypomesus*, has a different shape, and smaller and fewer teeth (see Fig. 14). Posteriorly the bone is moderately wide and roughly oval in shape; however, anteriorly it narrows abruptly and becomes a long finger-like extension whose anteriormost end overlaps the posteromedial surface of the autopalatine. The most notable difference concerns the dentition: in *Mallotus* the teeth are small (although still directed ventrolaterally), fewer in number (about twelve in a single row), and located more centrally than in *Hypomesus*. The part of the mesopterygoid that bears the teeth is not thickened, and there is no posteriorly extending, thickened tooth-bearing platform extending posteriorly. The mesopterygoidal dentition opposes a small number of similar, dorsomedially directed teeth on the posterior end of the basibranchials.

Quadrate

The quadrate in *Hypomesus pretiosus* has few distinctive features other than a relatively small condyle and a moderately long quadratojugal arm (see Fig. 15).

The quadrate in *Mallotus* is more delicate than that in *Hypomesus pretiosus*, has a smaller condyle, a shorter quadratojugal arm, a wider quadrate notch, and some sculpture on the medial surface of the body consisting of a few ridges radiating from the condyle (see Fig. 14).

Symplectic

The symplectic in *Hypomesus pretiosus* is slightly bent centrally with a moderately wide dorsal lamina (see Fig. 15). My specimen of *H. olidus* lacked a dorsal lamina.

The symplectic in *Mallotus* is more similar in shape to that found in adult *Plecoglossus altivelis* than it is to the other five osmerid genera (see Fig. 14 and compare to Figs. 18). Like *Plecoglossus* it has a distinct central bend and a V-shaped lamina on its anterodorsal edge that overlaps the anterior end of the quadrate notch. The quadrate notch in both genera is also wide and has a similar shape.

Metapterygoid

The metapterygoid in *Hypomesus pretiosus* is moderately large and robust with a complex shape (see Fig. 15). It lies posterodorsal to the body of the quadrate and firmly abuts the anterior part of the hyomandibular. The metapterygoid is made up of an anterior section that is endochondral in origin and a posterior laminar section that is dermal in origin. The endochondral part consists of a large dorsoventrally inclined ventral plate that curves dorsomedially at its anterodorsal corner to overlap the posterior end of the mesopterygoid. The palatoquadrate cartilage extends around its entire anterior edge. The posterior end of the tooth-bearing platform on the ventral surface of the posteromedial corner of the mesopterygoid extends posterior to the anterodorsal corner of the endochondral part.

The posterior part of the metapterygoid is triangular, dermal in origin, and projects posterodorsally as a large, complex lamina that broadly overlaps the hyomandibular. Laterally it overlaps most of the anterolateral surface of the ventral arm of the hyomandibular. Its narrow posterior end underlies the ventral edge of the lateral strut and closely approaches the anterior edge of the dorsal limb of the preoperculum. The posterior dermal lamina of the metapterygoid is notched at its ventralmost corner where it intersects the endochondral part (adjacent to the anteroventral corner of the ventral arm of the hyomandibular). There is a narrow, but distinct ridge on the lateral surface of the metapterygoid that extends from near its centre diagonally to the posterodorsal corner, bisecting the dermal lamina. The anterior part of the *levator arcus palatini* inserts along this lateral ridge and on the lateral concave surface of the dermal lamina dorsal to it. Part of the *adductor mandibulae* originates on the lateral surfaces of the dermal lamina and endochondral part of the metapterygoid ventral to the ridge.

On the medial surface of the metapterygoid there is a relatively wide, moderately sharp, ventromedially projecting ridge that ~~curves~~ posteroventrally from the anterodorsal corner towards the posteroventral corner of the bone (at the intersection of the laminar and endochondral sections). The anterior part of the *adductor arcus palatini* inserts along this medial ridge and on the medial surface of the dermal lamina dorsal to it. The posterior end of the medial ridge is expanded into a laminar wing (hereafter called the posteroventral wing of the metapterygoid) that projects posteroventrally to overlap the medial surface of the anteroventral corner of the ventral arm of the hyomandibular.

The metapterygoid in *Mallotus* (see Fig. 14) is similar to that described for *Hypomesus* but is larger, squarish when viewed laterally (versus roughly triangular in *Hypomesus*), and is located only slightly posterodorsal to the body of the quadrate (its anterior edge is located slightly posterior to the anterodorsal corner of the body of the quadrate) versus distinctly posterodorsal to the body of the quadrate in *Hypomesus*. The endochondral section is larger than the posterior laminar section. It overlaps the ectopterygoid as well as the mesopterygoid and is separated from the quadrate by a narrow band of cartilage (versus a relatively wide band in *Hypomesus*). The posterior edge of its posteroventral corner is distinctly flattened and abuts the anteroventral corner of the ventral arm of the hyomandibular. The posterior dermal lamina is smaller than in *Hypomesus*, overlaps less of the hyomandibular, and has a less distinct lateral ridge. The lamina does not extend to the anterodorsal corner of the endochondral section, unlike the other osmerids. The medial ridge is sharper than in *Hypomesus* and is relatively narrow. The posteroventral wing on the medial side of the metapterygoid has a straight posterior edge and is longer dorsoventrally than in *Hypomesus*.

McAllister (1963) diagnosed the Hypomesinae (*Hypomesus* and *Mallotus*) and Osmerinae (the other osmerids) partly on the basis of characters of the metapterygoid. He claimed (p. 26) that in the Hypomesinae the dorsal edge of the metapterygoid has a "deeply rounded notch" and that the metapterygoid has a "broad dorsal vane extending up over [the] articular head of [the] hyomandibular," whereas in the Osmerinae (p. 7) the dorsal edge of the metapterygoid is "almost straight" and the metapterygoid is "without [a] dorsal vane over [the] hyomandibular head." Upon closer examination it appears that both these features are essentially useless in defining the two subfamilies (refer to Figs. 14-17). Only *Mallotus* has what might be called a distinct notch along the dorsal edge of the metapterygoid, and it is not rounded (see Fig. 14). A small "rounded notch" was found along the posterior edge of the bone in some specimens of *Hypomesus*; however, this was not the case in all of them (e.g., see Fig. 15). In addition, it might be argued that *Thaleichthys* (see Fig. 16) and various other osmerines (e.g., *Osmerus*) have such a notch. Therefore the "rounded notch" at best might define the genus *Mallotus*. I would also argue that all osmerids have a similar "dorsal vane" (see Figs. 14-17) and that it overlaps the hyomandibular in all of them. McAllister claimed that the osmerines lacked a "dorsal vane." Furthermore, in most specimens of *Hypomesus* the dorsal edge of the metapterygoid is "almost straight," not just the osmerines (and only debatably in some of them) as claimed by McAllister. In conclusion, the characters of the metapterygoid listed by McAllister to diagnose the Hypomesinae and Osmerinae define neither group and should not be used.

Hyomandibular

The hyomandibular in *Hypomesus pretiosus* is a moderately robust bone that is relatively long dorsoventrally (see Fig. 15). The articular surface of the head is capped with cartilage and fits in a moderately shallow facet on the skull. The posterior half rests along the posteroventral surface of the pterotic while the anterior half rests in cartilage between the sphenotic, prootic, and pterotic. The anteromedial corner abuts the mid-dorsal edge of the prootic while the anterolateral corner abuts the posteroventral edge of the sphenotic.

The opercular arm is moderately long and is capped posteriorly with a cartilaginous knob that rests in a facet on the anterodorsal corner of the operculum. Distinct posterodorsal and posteroventral laminae are present (the posteroventral lamina on the specimen shown on Fig. 15 is abbreviated ventrally; however, in the other specimens of *Hypomesus* examined it extended ventrally to about the middle of the ventral arm). A moderately wide, flat anterior lamina is present. In some specimens it is abbreviated ventrally (see Fig. 15) while in others it extends ventrally to about the middle of the ventral arm. The ventral arm is relatively long and narrow. A moderately robust, posterolaterally inclined lateral strut extends from the ventral apex of the head to the middle of the ventral arm. The strut is slightly truncated at its ventral end where it abuts the posterior corner of the metapterygoid. The posteriormost part of the *levator arcus palatini* inserts on the anterior face of the lateral strut.

The canal for the hyomandibular branch of the facial nerve is moderately long and inclined posteroventrally from the medial to the lateral foramina. The medial foramen is moderately large and located at the ventral apex of the head. The lateral foramen is moderately small and located at the posterodorsal corner of the lateral strut, at the intersection of the anteroventral corner of the opercular arm and the ventral arm. The hyomandibular lacks sculpture.

The hyomandibular in *Mallotus* has several unique features (see Fig. 14). The head is smaller, relative to the rest of the bone, than in *Hypomesus*. The anterior lamina is much narrower, especially its dorsal half; however, its ventral half is expanded where the metapterygoid overlaps it. Well-developed posterodorsal and posteroventral laminae are present. The opercular arm is shorter and smaller than in the other osmerids. The ventral arm, however, is expanded and distinctly larger and wider than in the other osmerids. The lateral strut is similar to that in *Hypomesus* but is longer dorsoventrally. The canal for the hyomandibular branch of the facial nerve is narrower, and the medial foramen smaller, than in *Hypomesus*. On the medial surface there is a distinct, but rather weakly-developed dorsoventral ridge that extends from the ventral apex of the head to the ventral end of the ventral arm (see Fig. 14). A trace of such a ridge is debatably present in *Hypomesus* (see Fig. 15).

Preoperculum

The preoperculum in *Hypomesus pretiosus* is a relatively thin, flat bone with distinct dorsal and ventral limbs that meet at about a right angle (see Fig. 15). The dorsal limb is slightly longer than the ventral limb. Both dorsal and ventral limbs taper toward their ends. There is no suprapreoperculum (as in the other osmerids). The anterior lamina is moderately large and slightly convex laterally. The anterior edge of the dorsal end of the dorsal limb abuts the posterolateral edge of the lateral strut of the hyomandibular, to which it is attached by connective tissue.

Unlike the esocoids and salmonids, *Hypomesus* has an open, bony, lateral sensory canal on the preoperculum (refer to Fig. 15). The canal is completely open posterior to a moderately wide flange that runs along the entire length of the anterolateral surface of the preoperculum. The anterior edge of this anterior flange is continuous with the anterolateral surface of the preoperculum. It projects posterolaterally on the dorsal limb and ventrolaterally on the ventral limb, and is slightly convex laterally. A distinct posterior facing groove (the open, bony, lateral sensory canal) is formed between the medial surface of the flange and the lateral surface of the preoperculum.

The preoperculum in *Mallotus* is similar to that in *Hypomesus pretiosus* except that the ventral limb is shorter than the dorsal limb and the anterior flange is narrower (see Fig. 14).

Subfamily Osmerinae

The suspensorium in *Osmerus, Allosmerus, Spirinchus*, and *Thaleichthys* is shorter anteroposteriorly and deeper dorsoventrally than in the Hypomesinae (see Figs. 16, 17 and compare to Figs. 14, 15). My evidence suggests that the Osmerinae (but not the Hypomesinae) is holophyletic. Because the suspensorium in *Thaleichthys* appears to be more derived than the other osmerines, and is morphologically most unlike the primitive osmerid state found in *Hypomesus*, it is described in detail and then compared to the other osmerines and to the hypomesines. *Thaleichthys* contains only one species, *T. pacificus*.

Palatine

The palatine in *Thaleicthys pacificus* is distinct from that in the Hypomesinae with regard to its shape and proportions (see Fig. 16 and compare to Figs. 14, 15). It is more robust, deeper dorsoventrally, wider mediolaterally, and has larger teeth than the

Hypomesinae. The anterior and posterior ends of the autopalatine are greatly expanded into large condyles that are joined centrally by a relatively short, narrow, isthmus of bone (i.e., the autopalatine is distinctly constricted centrally). The anterior end of the anterior condyle bears a similarly shaped cartilage that is slightly flattened dorsoventrally. The articulation with the maxilla and lamina orbitonasalis of the ethmoid cartilage is similar to that in the Hypomesinae and the other osmerines. The palatoquadrate cartilage that extends from the posterior condyle is also unusually large and is expanded mediolaterally (versus smaller and relatively narrow mediolaterally in the hypomesines). It projects posterodorsally to the lamina orbitonasalis of the ethmoid cartilage and posteriorly to overlap the anterodorsal surface of the mesopterygoid. The dermopalatine is larger than in the Hypomesinae. It is moderately long and narrow, fused to the ventral surface of the autopalatine, and extends posterior to it as a splint that overlaps the anteroventral end of the ectopterygoid. On its ventral surface there is a single row of about ten equally spaced, moderately large, pointed teeth that all curve posteroventrally and are about the same size.

The palatine in *Allosmerus, Osmerus,* and *Spirinchus* (see Fig. 17) is similar to that described for *Thaleichthys*: it is robust, relatively short anteroposteriorly, has greatly expanded anterior and posterior ends, and has well-developed teeth on the ventral surface of a relatively large dermopalatine. The major differences concern the relative size of the palatine, the degree of expansion of the ends, and the size, shape, and number of teeth. The palatine in *Osmerus* is more robust and has larger teeth than in the other osmerids. There are five or six (seven to ten according to Rembiszewski 1964) large, fang-like teeth in a single row on the anteroventral surface of the dermopalatine ventral to the autopalatine. The teeth were all about the same size; however, in one of the two specimens examined the anteriormost tooth on one palatine was notably larger than the other teeth, agreeing with McAllister's (1963) observation that the palatine teeth in *Osmerus* are enlarged anteriorly. The palatine in *Allosmerus* is slightly smaller than in the other osmerines but has the same basic shape (with four or five teeth on its ventral surface). In *Spirinchus* the palatine is stout (see Fig. 17) and had five to nine teeth on its ventral surface in the two species that I examined. The teeth in *S.*

starksi were smaller and more numerous than in *S. thaleichthys* (five or six versus eight or nine, respectively). *S. starksi* is also unusual because the anteroventral end of the autopalatine extends upwards as a lip of bone that covers the ventral part of the anterior facing surface of the anterior cartilaginous knob. The palatoquadrate cartilage at the posterior end of the posterior condyle is also slightly smaller and narrower mediolaterally in *Osmerus*, *Allosmerus*, and *Spirinchus* than in *Thaleichthys*.

Ectopterygoid

The ectopterygoid in *Thaleichthys pacificus* is shorter anteroposteriorly than in the hypomesines (see Fig. 16). The bone is expanded at the intersection of the two arms where it overlaps the medial surface of the anteroventral corner of the metapterygoid. The anterior arm is distinctly shorter than in the hypomesines. The anterior end of the anterior arm does not contact the autopalatine but overlaps the end of the dermopalatine.

The ectopterygoid in other osmerines is similar in most respects to that described for *Thaleichthys pacificus* (see Fig. 17). However, in *Osmerus* it is more robust and has less of a central bend and a smaller posterior expansion than the other osmerids.

Mesopterygoid

The mesopterygoid in *Thaleichthys pacificus* is a relatively small (smaller than in the other osmerids) and delicate bone that is roughly oval in shape (see Fig. 16). The dorsal surface is only slightly concave and is inclined dorsomedially towards the parasphenoid. The rounded anterior edge is widely separated from the posterior end of the palatine. The wide palatoquadrate cartilage spans the distinct gap between the palatine and mesopterygoid, overlapping the anterodorsal surface of the latter. The aforementioned cartilage also spans the distinct gap between the mesopterygoid and ectopterygoid.

The ventral surface of the mesopterygoid has a single row of moderately small, pointed teeth extending along the entire medial side of the bone. Sometimes there are a few teeth lateral to the main row at the posterior end of the bone. The teeth are all the same size and directed ventrolaterally, and unlike *Hypomesus* and *Mallotus*, curve slightly anteriorly. They oppose dorsomedially directed teeth of similar size and shape on the posterior two thirds of the basibranchial plate. In one specimen (UAMZ 2317, 121.8 mm SL) there were nine teeth on each mesopterygoid, whereas in another (UAMZ 2317, 120.1 mm SL) there were fourteen on each bone. The part of the mesopterygoid bearing the teeth is only slightly thickened. However, the posterior end of the tooth-bearing section is thicker than the rest of the bone and projects posteriorly to underlie the anterodorsal corner of the metapterygoid, but unlike *Hypomesus* it does not form an expanded, raised platform.

Contrary to my observations, Chapman (1941b, p. 287) noted that "Mesopterygoid dentition [is] absent in adults." According to Scott and Crossman (1973), specimens of *Thaleichthys pacificus* reach sexual maturity at three years of age when they are from 104-144 millimetres long fork length. The specimens that I examined (120 and 122 millimetres long standard length) were probably adults. It may be that Chapman examined fish that were captured near or during the spawning season, since both McAllister (1963) and Scott and Crossman (1973) noted that teeth (including mesopterygoidal teeth) tend to be lost in spawners, particularly males.

The mesopterygoid in *Spirinchus* has basically the same shape and bears the same spatial relation to the surrounding bones as in *Thaleichthys* (see Fig. 17 and compare to Fig. 16; also see fig. 2 in Weitzman 1967a). It differs, however, in that it is larger, more robust, has larger (but about the same number of) teeth, and more closely approaches the autopalatine. The number of teeth on each mesopterygoid ranged from eight to seventeen in the six specimens that I stained and cleared, with ten to twelve being most common. Occasionally, there were a few teeth lateral to the main row at the posterior end of the bone (invariably these teeth were smaller). The mesopterygoidal teeth oppose dorsomedially directed teeth of similar size and shape along the entire length of the basibranchial plate (versus opposing less of the plate in *Thaleichthys*).

The mesopterygoid in *Osmerus* and *Allosmerus* is longer anteroposteriorly than in *Spirinchus* and *Thaleichthys*, and like *Hypomesus* and *Mallotus*, narrows anteriorly to a point that overlaps the posteromedial surface of the autopalatine. The anterior few teeth in one specimen of *Osmerus* were larger than the others (unlike the other osmerids examined). The teeth in both genera oppose dorsomedially directed teeth of similar size and shape along the entire length of the basibranchial plate and the posterior part of the basihyal. In *Allosmerus* there is a single row of about twenty moderately large, pointed teeth along the length of the bone. The central part of the tooth row is located closer to the middle of the bone than in the other osmerines. In *Osmerus* there were from eleven to fifteen large (larger than in *Allosmerus*), pointed teeth in a single irregular row along the entire medial edge of the bone. Chapman (1941b, p. 281) reported that the mesopterygoid had "a row of eleven or twelve teeth, with many tiny teeth interspersed between, running along [the] mesial edge of [the] bone to end posteriorly in a circular pad of many teeth." My specimens did not have any teeth lateral to the main row and there was no "circular pad of many teeth" at the posterior end of the bone. The "tiny teeth" that Chapman refers to may be replacement teeth with unossified bases, which were relatively numerous in my specimens. The number and distribution of teeth appear to be slightly variable within the genus *Osmerus* (*sensu* McAllister 1963) since Rembiszewski (1964) noted that in *O. eperlanus* (my specimens and those of Chapman were *O. mordax*) there were about thirty-five teeth on each bone that were arranged in three or four rows on the posterior part.

Quadrate

The quadrate in *Thaleichthys pacificus* is similar to that described for *Hypomesus pretiosus* but is more delicate and has some sculpture on the medial surface of the body consisting of a few ridges radiating from the condyle. The condyle is unusually small and delicate, and in this respect resembles that in *Mallotus* more than the other osmerids.

The quadrate is more robust in the other osmerines and is moderately variable. In *Spirinchus* both sides are sculptured and the quadratojugal arm is relatively short and spatulate (see Fig. 17). It is similar in *Allosmerus* but has less sculpture. The quadrate in *Osmerus* is more robust, and the condyle larger and more rounded than in the other osmerids.

Symplectic

The symplectic in the *Thaleichthys pacificus* and the other osmerines is similar to that described for *Hypomesus*.

Metapterygoid

The metapterygoid in *Thaleichthys pacificus* is unusually large, moderately robust, and squarish when viewed laterally (see Fig. 16). It has the same basic features as in the Hypomesinae. As in the other osmerines, it lies directly dorsal to the body of the quadrate. Its anterior edge is located anterior to the anterodorsal corner of the body of the quadrate. The endochondral section is as described for *Mallotus*. The posterior dermal lamina is relatively large and overlaps the dorsolateral surface of the ventral arm of the hyomandibular, including the "lateral strut" (it is more like a dorsoventral flange than a strut in *Thaleichthys*). The lateral ridge is distinctly longer, wider, and sharper than in *Hypomesus* and *Mallotus*, a feature shared with the other osmerines. It extends diagonally across the entire lateral surface of the bone, bisecting the endochondral part as well as the posterior lamina. The medial ridge is also longer, wider, and sharper than in the hypomesines. The relationship of the cheek muscles to both ridges is as in the Hypomesinae. The posteroventral wing on the medial side is less distinctive than in the other osmerids, and overlaps less of the ventral arm of the hyomandibular.

The metapterygoid in the other osmerines is similar to that described for *Thaleichthys* (see Fig. 17). Minor differences concern the relative size of the bone (it is larger and more robust in *Osmerus* than in the other osmerids), the amount of overlap with the mesopterygoid (it overlaps more of the mesopterygoid in *Osmerus*, *Allosmerus*, and *Spirinchus* than in *Thaleichthys*), the shape of the posteroventral wing on the medial side, and the relative size of the lateral and medial ridges. Unlike *Thaleichthys*, the pointed posterior end of the metapterygoid in the other osmerines underlies the ventral edge of the well-developed lateral strut of the hyomandibular (see Fig. 17). In *Spirinchus starksi* and in smaller specimens of *S. thaleichthys* there is a finger-like endochondral projection (continuous anteriorly with the endochondral part) that extends posterodorsally through the posterior lamina, bisecting it, and reaching its posterior tip, where it is capped by a small cartilaginous knob that underlies the lateral strut of the hyomandibular. A similar, but smaller, endochondral projection is found in *Mallotus*; however, in this genus it does not reach the posterior end of the posterior lamina and there is no posterior cartilaginous knob.

Hyomandibular

The hyomandibular in *Thaleichthys pacificus* is a moderately delicate bone with reduced laminae and long and slender arms (see Fig. 16). The articular surface of the relatively small head is capped with an unusually large cartilage. Its articulation with the skull is similar to that described for *Hypomesus* except that there is more cartilage between the sphenotic, prootic, and pterotic.

The opercular arm is very long and narrow. There is a small posterodorsal lamina but no posteroventral lamina. A tiny, narrow anterior lamina is found at the intersection of the head and ventral arm. The ventral arm is relatively long and narrow. A true lateral strut is not present. However, its homologue appears to be a long, narrow flange that extends dorsoventrally from the posterodorsal corner of the head to about the middle of the ventral arm. Its ventral half is covered by the metapterygoid. Shorter flanges on the opercular arm and on the anterior part of the head join the "lateral strut" near its middle. Corresponding to the "lateral strut", on the medial side is an even wider dorsoventral flange that extends from the posterodorsal corner of the head to the ventral end of the ventral arm. The anterior face of this flange serves as part of the area of insertion for the posterior part of the *adductor arcus palatini*. A shorter, anteroposteriorly running flange on the medial surface of the opercular arm joins the upper end of the medial dorsoventral flange. The *adductor hyomandibulae* inserts along and dorsal to this flange. There is no real canal for the hyomandibular branch of the facial nerve, simply a large hole at the ventral apex of the head through which the nerve passes (all osmerines have this feature). The nerve courses posteroventrally after it passes laterally through the foramen, crosses the "lateral strut," and then runs ventrally posterior to the strut along the posterior edge of the ventral arm.

The hyomandibular in the other osmerines is similar to that in *Thaleichthys* but is more robust and not as narrow and elongated (see *Spirinchus*, Fig. 17). The cartilage on the dorsal edge of the head is smaller than in *Thaleichthys*. A posterodorsal lamina of variable size is always present (it is widest in *Osmerus*). A small posteroventral lamina is found in *Spirinchus* and *Allosmerus*. The length of the opercular arm varies from genus to genus, but is relatively long and narrow in all of them. The anterior lamina is always reduced, but was slightly larger in *Spirinchus starksi*. The overall shape of the bone in *Allosmerus* is quite similar to that in *Spirinchus*. The hyomandibular in *Osmerus* is more robust and has a head that is distinctly broader than in the other osmerines (its opercular arm is about as long as in *Thaleichthys*). A medial dorsoventral flange is present in *Osmerus, Allosmerus*, and *Spirinchus* but is narrower and shorter than in *Thaleichthys*.

Osmerus, Allosmerus, and *Spirinchus* differ from the other osmerids because they share a unique, arm-like lateral strut (see Fig. 17). The strut has been reduced at its dorsal and ventral ends so that it consists almost entirely of a central expansion found at the intersection of the ventral arm and the anteroventral corner of the opercular arm. This expansion extends posteriorly (*Spirinchus*) or posterodorsally (*Osmerus* and *Allosmerus*) as a robust arm-like projection that reaches, or nearly reaches, the anterior edge of the dorsal limb of the preoperculum. The arm in *Osmerus* is more robust and longer than in *Allosmerus* and *Spirinchus* (the shortest) and expands posteriorly. As in *Thaleichthys* there is no canal for the hyomandibular branch of the facial nerve, simply a large hole at the ventral apex of the head through which the nerve passes. The foramen is slightly anterodorsal to the dorsal edge of the lateral strut.

Preoperculum

The preoperculum in *Thaleichthys pacificus* (see Fig. 16) is similar to that described for *Hypomesus pretiosus* but is thinner and more delicate (more so than in any other osmerid). The anterior flange is also reduced and narrower than in the other osmerids. The ventral limb is abbreviated anteriorly so that the dorsal limb is longer than the ventral limb (it is about one and three quarter times the length of the ventral limb). The anterior edge of the dorsal limb is widely separated from the "lateral strut" and the ventral arm of the hyomandibular. The dorsal end of the dorsal limb, however, is firmly attached to the posteriormost tip of the metapterygoid and the opercular arm of the hyomandibular via tough connective tissue.

The preoperculum in the other osmerines is similar to that in *Thaleichthys* except that it is more robust; the anterior flange is wider, and the anterior edge of the dorsal end of the dorsal limb is adjacent to the posterior edge of the lateral strut of the hyomandibular (see Fig. 17 of *Spirinchus*). The gap between the anterior edge of the dorsal limb and the ventral arm of the hyomandibular was wider in *Osmerus, Allosmerus*, and *Thaleichthys* than in *Spirinchus*. Chapman (1941b, p. 288) claimed that in *Spirinchus* there was "No opening between [the] hyomandibular and preopercle." However, this was not the case in my specimens, and judging from Weitzman's figures (1967a, figs. 2 and 3), was not the case in his either.

FAMILY PLECOGLOSSIDAE

The Plecoglossidae contains only one species, *Plecoglossus altivelis*. The anterior part of the skull in the adult has numerous unique specializations related to its habit of feeding on algae. The dentition on its upper and lower jaws consists of a series of small, comb-like teeth that are seated on a fold of skin on the maxilla and mandible (pers. obs.; also see Chapman 1941a; Komada 1985; Howes and Sanford 1987). Concomitant with these teeth are numerous specialized features of the gut, the bones of the upper and lower jaws, the anterior end of the snout, and some of the bones of the suspensorium. The rest of the skeleton, however, is relatively primitive. Juveniles do not possess many of these features and are similar osteologically to the osmerids (pers. obs.), and like most of them feed primarily on zooplankton (see Chapman 1941a; McAllister 1963; Howes and Sanford 1987). During, ontogeny the fish changes its behaviour (ascends a river after living in the sea, and begins feeding on plankton) and undergoes the aforementioned anatomical changes.

The description that follows is of the adult; however, because of the osteological changes that occur during ontogeny it is compared to the juvenile when differences occur. Two large specimens (160.6 and 144.1 mm SL) and two relatively small specimens (77.9 and 55.5 mm SL) were cleared and stained. The smallest specimen was almost certainly a juvenile and was relatively similar to the osmerids, whereas the second smallest specimen had nearly completed its metamorphosis, and was similar to the adults in most respects.

The suspensorium in the adult (see Fig. 18) is robust and is unusually deep dorsoventrally compared to its length. However, the suspensorium in the juvenile (55.5 mm SL) is more similar proportionally to that in *Hypomesus* (Osmeridae).

Palatine

The palatine in adult *Plecoglossus altivelis* is unique among the salmoniforms (see Fig. 18). It is small relative to the rest of the suspensorium, is relatively long and wide, and is compressed dorsoventrally. The bone is edentulous and lacks a dermopalatine. When *in situ* the palatine (= autopalatine) is inclined only slightly anteromedially. The flattened anterior end curves anteroventrally and is expanded mediolaterally into rather poorly defined lateral and medial rami. Its end is capped with a similarly snaped, dorsoventrally flattened cartilage that is also expanded anterolaterally and anteromedially. The lateral ramus and its cartilage contacts a distinctive, cartilage-covered facet on a small condyle found on the dorsomedial surface of the anterior end of the maxilla. The medial ramus abuts a shallow concavity on the lateral prenasal process of the ethmoid cartilage. The ethmoid cartilage is unusually small in the adult. Chapman (1941a, p. 439) claimed that "The palatine ends anteriorly in two cartilage-capped condyles, one of which is terminal and articulates with the ... process of the premaxillary and the other ... which is lateral and articulates with the maxillary." The anterior end of the palatine in my specimens lacked two separate condyles and contacted only the maxilla. Chapman erroneously considered the anteriormost end of the maxilla to be part of the premaxilla (also see Howes and Sanford 1987).

The posteriormost end of the palatine is dorsoventrally flattened and expanded mediolaterally, like the anterior end. The palatoquadrate cartilage emanates posteriorly from it, expands slightly dorsally to abut the posteroventral surface of the lamina orbitonasalis of the ethmoid cartilage (overlapping the anterodorsal surface of the mesopterygoid), and then narrows posteriorly. Anterior to the posterior expansion of the palatine, on the posterodorsal surface of the palatine, is a unique dorsally projecting condyle that bears a knob of cartilage on its dorsal surface. This cartilaginous knob articulates with the anteroventral surface of the lamina orbitonasalis of the ethmoid cartilage. No other teleost that I examined possessed a similar condyle on the posterodorsal surface of the palatine.

The palatine in the smallest specimen that I examined (55.5 mm SL) differed from the adult in several important ways. Like the adult, the bone was flattened dorsoventrally, with mediolateral expansions at both ends; however, unlike it the autopalatine was more tube-like, was expanded posteriorly both dorsoventrally and mediolaterally, and lacked the unique posterodorsal condyle. In addition, there was a dermopalatine, extending along and fused to the entire ventral surface of the autopalatine, that possessed four moderately long, posteroventrally curved teeth. The vomer also bore several similar teeth at this stage, and the mandible had a single row of sharp teeth. A relatively long and narrow supramaxilla was also present. The palatine in the second largest specimen (77.9 mm SL) had the shape of the one in the adult except that the posterodorsal condyle was in the process of forming, but was not yet a separate entity because the section of the palatine posterior to it had not yet ossified. A reduced dermopalatine, bearing a single tooth on one palatine, was still present at this stage. The vomer and mandible lacked teeth. There was only a thread-like vestige of the supramaxilla. The unique, comb-like teeth on the maxilla and mandible are completely formed at this stage.

Ectopterygoid

The ectopterygoid in *Plecoglossus* is moderately long and narrow with distinct anterior and posteroventral arms that meet at nearly a right angle (see Fig. 18). The posteroventral arm is expanded and overlaps the anteromedial surface of the body of the quadrate. The part of the ectopterygoid that overlaps the quadrate is slightly concave laterally. The anterior arm in the adult is about two to two-and-a-half times as long as the posteroventral arm; however, in the juvenile (55.5 mm SL) it was longer (about three times as long). The narrow tip of the anterior arm closely approaches or slightly overlaps the posteroventral corner of the palatine. Along the lateral surface of the anterior arm runs a wide flange that projects laterally from the bone. This lateral flange lies dorsal to the broad ligament that extends anteriorly from the *adductor mandibulae* to the maxilla. The osmerids, and numerous other salmoniforms, have a lateral flange on the ectopterygoid; however, in these fish the flange is narrower, longer anteroposteriorly, and invariably projects dorsally or dorsolaterally. The flange in smaller specimens of *Plecoglossus* is narrower than in the adults, but still projects laterally.

Mesopterygoid

The mesopterygoid in adult *Plecoglossus* is a moderately robust bone that is relatively small compared with the more posterior bones of the suspensorium (see Fig. 18). It is shorter anteroposteriorly than in the osmerid *Hypomesus*, and is somewhat truncated at its posterior and anterior ends. Its dorsal surface is moderately concave and slopes dorsomedially toward the parasphenoid, from which it is separated by a moderately wide band of connective tissue. It is widest posteriorly where it overlaps the anteromedial surface of the metapterygoid. The anterior end does not quite reach the posterior end of the palatine. Its lateral edge slightly overlaps the ectopterygoid. The palatoquadrate cartilage that covers its anterodorsal surface is relatively narrow mediolaterally.

The medioventral surface of the mesopterygoid bears a series of relatively small, pointed teeth that curve ventrolaterally. The teeth extend along the posterior two-thirds of the bone and oppose a relatively small number of similar but dorsomedially directed teeth on the basibranchials and the posterior end of the basihyal. The basihyal tooth-plate and its dentition were greatly reduced in the two largest specimens examined (the tooth-plate was a small triangular wedge at the posteriormost end of the basihyal). The basibranchial tooth-plate was not reduced; however, its dentition was, and was essentially restricted to the edges of the plate (a few denticles were centrally located). The teeth on the mesopterygoid are all about the same size. In the two largest specimens there were about fifteen to twenty on each mesopterygoid. They form a single row; however, at the posteriormost end of the bone there are usually a few teeth lateral to the main row (this was not the case in the mesopterygoid illustrated on Fig. 18). As in *Hypomesus*, the posteriormost teeth rest on an expanded, thickened, bony platform; however, it is smaller and projects only slightly posterior to the main part of the mesopterygoid.

The dentition on the mesopterygoid in small specimens of *Plecoglossus* is more similar to that in the osmerid *Hypomesus* than to larger, adult specimens of *Plecoglossus*. In the two smallest specimens that I examined (77.9 and 55.5 mm SL) there were from twenty-five to thirty-five functional teeth on each mesopterygoid. Unlike adults, they extended along nearly the entire anteroposterior length of the bone. Along the medial side of the bone was a single irregular row that ran anteroposteriorly. Posteriorly there were numerous teeth lateral to this medial row that were arranged in another irregular anteroposterior row (or two). Teeth were most numerous at the posteriormost end of the bone, where they were clumped together, as in *Hypomesus*. As in the adult, the posteriormost teeth rest on an expanded, thickened, bony platform. However, the platform closely resembles that in *Hypomesus*: it is relatively large, robust, and projects posterior to the main part of the mesopterygoid as a distinct lip that underlies and extends posterior to the anterodorsal corner of the metapterygoid. This platform forms the posteriormost corner of the bone (as in *Hypomesus*), unlike the adult in which the pointed posteroventral corner of the mesopterygoid does. The teeth are slightly larger than in the adult (but smaller than in *Hypomesus*) and are all about the same size (the posteriormost teeth are slightly larger than the others). The bite is similar to that described for adult *Plecoglossus* except that the teeth on the basihyal and basibranchials are more numerous, and the basihyal tooth-plate is larger (it covers the entire basihyal) and is entirely covered with teeth.

Quadrate

The quadrate in adult *Plecoglossus* has several unique features (see Fig. 18). The body is relatively small with a straight dorsal edge (rather than curved, as is usual). The lateral part of the condyle is greatly expanded. When viewed laterally it consists of a wide, thick, ventrolaterally projecting flange with rounded edges that forms the anteroventral end of the bone. The medial side of the condyle is relatively small and not expanded. The facet is pear-shaped with the lateral part forming the expanded section. The quadratojugal arm is relatively short and pointed posteriorly. The quadrate notch is relatively short but wide.

The quadrate in the second smallest specimen (77.9 mm SL) was like that in the adults except that the lateral part of the condyle was not quite as large. However, the quadrate in the juvenile (55.5 mm SL) was different and closely resembled that in *Hypomesus*, except that the lateral part of the condyle was slightly enlarged relative to the medial one.

Symplectic

The symplectic in *Plecoglossus* is relatively small, thin mediolaterally, and distinctly bent centrally (see Fig. 18). The entire bone fits tightly in a groove on the dorsomedial surface of the quadratojugal arm of the quadrate. The posterior end is noticeably wider than the anterior part and is separated from the ventral end of the ventral arm of the hyomandibular by a wide area [illegible] cartilage. The posterior edge of the symplectic is crescent-shaped. The anterior end is slightly expanded and capped by a cartilaginous knob. The anterior end of this cartilage fits in a notch at the posterior end of the quadrate condyle. There is a small V-shaped lamina on the mid-dorsal edge of the symplectic that overlaps the anterior end of the quadrate notch.

The symplectic in the second smallest specimen (77.9 mm SL) was like that in the adults except there was less of a central bend, just a trace of a V-shaped lamina on its mid-dorsal edge, and the anterior cartilaginous knob did not fit into a notch. The juvenile (55.5 mm SL) was the same except that there was less of a posterior expansion.

Metapterygoid

The metapterygoid in adult *Plecoglossus* is a large, robust bone with a complex shape (see Fig. 18). It shares several important similarities with the osmerids (refer to Figs. 14-17). As in *Mallotus* it is located only slightly posterodorsal to the body of the quadrate (its anterior edge is located slightly posterior to the anterodorsal corner of the body of the quadrate). It firmly abuts the anterior part of the hyomandibular. As the osmerids, it is made up of an anterior section that is endochondral in origin and a large posterior laminar section that is dermal in origin.

In the adult the endochondral part is smaller than the dermal section. It consists of a dorsoventrally inclined plate that curves slightly dorsomedially at its anterodorsal corner to overlap the dorsolateral surface of the posterior end of the mesopterygoid. Its anterodorsal corner is capped anteriorly with a small cartilaginous knob that is a remnant of the posteromedial corner of the palatoquadrate cartilage. Its posteroventral corner lies adjacent to the anteroventral corner of the ventral arm of the hyomandibular.

The posterior dermal section (labelled Mt.p on Fig. 18) consists of a dorsal lamina and a posterior cup-like wing. The dorsal lamina is relatively large, moderately thin, and triangular with a dorsally directed apex. Its entire posterior edge runs adjacent to most of the anterior edge of the anterior lamina of the hyomandibular. Its anteroventral corner is formed into a flattened, finger-like projection that overlaps the lateral surface of the posteromedial corner of the mesopterygoid. This flattened projection is continuous with the ridge on the medial side of the metapterygoid, and is present, but in a much reduced form, in some osmerids (it is most distinct in *Hypomesus*). The dorsomedial subdivision of section A2 of the *adductor mandibulae* originates on the slightly concave lateral surface of the dorsal lamina.

The posterior wing is rounded, distinctly concave laterally, and broadly overlaps the ventrolateral surface of the ventral arm of the hyomandibular. Its posterodorsal corner abuts the ventral end of the lateral strut of the hyomandibular. As in the Osmeridae, it is notched at its ventralmost corner where it intersects the endochondral section. The entire dorsal edge of the posterior wing is thickened and curls laterally to form a robust ridge. This lateral ridge is homologous with the diagonally extending ridge on the lateral surface of the metapterygoid found in the Osmeridae (refer to Figs. 14-17). The anterior part of the *levator arcus palatini* inserts along this ridge and on the posterior edge of the dorsal lamina dorsal to it (as in the Osmeridae, except that in the osmerids the entire dorsal lamina serves as an area of insertion). Part of section A2 of the *adductor mandibulae* (not the dorsomedial subdivision) originates on the concave lateral surface of the posterior wing ventral to the ridge and on the endochondral section anterior to it.

As in the Osmeridae, there is a relatively wide ridge on the medial surface that curves posteroventrally from the anterodorsal corner toward the posteroventral corner of the bone (at the intersection of the dermal and endochondral sections). The medial ridge projects ventromedially and is slightly rounded dorsally in a way that is reminiscent of *Hypomesus* (the ridge in the other osmerids is sharper). As in the osmerids, the anterior part of the *adductor arcus palatini* inserts along this ridge and on the entire dermal lamina dorsal to it. As in the osmerids, there is a distinctive posteroventral wing at the posterior end of the medial ridge that overlaps the medial surface of the anteroventral corner of the ventral arm of the hyomandibular.

The metapterygoid in the second smallest specimen (77.9 mm SL) was similar to that in the adult except that the lateral ridge was not as well-developed. The metapterygoid in the juvenile (55.5 mm SL) was smaller than the other specimens mainly because the posterior dermal section was less developed at this stage, particularly the dorsal lamina. [illegible] dorsal lamina did not extend as far dorsally as in the others and was separated from the anterior edge of the anterior lamina of the hyomandibular by a relatively wide space. The posterior wing was proportionally about the same size as in the adult. The lateral ridge was present but poorly developed. The medial side was as in the others except that the posteroventral wing did not quite overlap the ventral arm of the hyomandibular. Unlike the other specimens, but as some osmerids, there was a moderately wide, finger-like endochondral projection (continuous anteriorly with the endochondral part) that extended posterodorsally through the posterior dermal section, bisecting it, and reaching its posterior tip adjacent to the ventral end of the lateral strut of the hyomandibular.

Hyomandibular

The hyomandibular in adult *Plecoglossus* is long, moderately wide, and robust (see Fig. 18). The cartilaginous condyle on the dorsal edge of the head is long and narrow and forms a straight and tight joint with the skull. Its posterior half sits in a moderately deep groove on the posteroventral surface of the pterotic. This groove is bordered by relatively high ridges that serve to stabilize the joint. The anterior half rests in cartilage betwen the pterotic, sphenotic, and prootic; most of its anterolateral side closely abuts the posteroventral edge of the sphenotic while most of its anteromedial side sits along the posterodorsal edge of the prootic.

The opercular arm is greatly reduced and represented by only a small, cartilage-capped protuberance on the posterodorsal edge of the bone. Posterodorsal and posteroventral laminae are absent. A moderately wide, flat anterior lamina extends along most of the anterior edge of the bone. The ventral arm is relatively long and wide with a broad ventral expansion. A robust, posterolaterally inclined, lateral strut extends from the beginning of the opercular arm to the ventral end of the ventral arm. Its moderately concave anterior face ~~serves~~ as the insertion area for the posteriormost part of the *levator arcus palatini*.

The canal for the hyomandibular branch of the facial nerve is relatively long and narrow and inclined posteroventrally from the medial to the lateral foramina. The medial foramen is relatively small and located at the ventral apex of the head. The lateral foramen is slightly larger and located at the posterodorsal corner of the lateral strut, at the intersection of the anteroventral corner of the opercular arm and the ventral arm. The hyomandibular lacks sculpture.

The hyomandibular in the second smallest specimen (77.9 mm SL) was like that in the adult but was less robust and had more of an opercular arm. Only the posterior third of the cartilaginous condyle on the dorsal edge of the head rested on the pterotic (the area of cartilage between the sphenotic, prootic, and pterotic was larger). The hyomandibular in the juvenile (55.5 mm SL) was superficially similar to that in *Hypomesus*. It was less robust than the other specimens of *Plecoglossus*, had a narrower anterior lamina, a moderately short but distinct opercular arm, small posterodorsal and posteroventral laminae, and a larger medial foramen for the hyomandibular branch of the facial nerve. Its lateral strut was also less robust, inclined more posterolaterally, and did not extend as far ventrally (its ventral end was located slightly ventral to the middle of the ventral arm, like in *Mallotus*). Almost the entire cartilaginous condyle on the dorsal edge of the head rested in cartilage between the sphenotic, prootic, and pterotic bones.

Preoperculum

The preoperculum in adult *Plecoglossus* is a thick bone with distinct dorsal and ventral limbs that meet at about a right angle (see Fig. 18). The dorsal limb is about twice as long as the ventral limb. The ventral limb is abbreviated anteriorly while the dorsal limb tapers dorsally, reaching only the opercular arm of the hyomandibular. The anterior edge of the dorsal end of the dorsal limb abuts the posterolateral edge of the lateral strut of the hyomandibular, to which it is attached by connective tissue.

Unlike the osmerids there is a suprapreoperculum that extends between the dorsal tip of the dorsal limb and the posterior end of the temporal sensory canal on the pterotic. Klyukanov (1975, fig. 5) illustrated a suprapreoperculum in the same position. Chapman did not mention or illustrate a suprapreoperculum in his 1941 paper. However, he did illustrate (his fig. 6) the preoperculum as reaching the posterodorsal corner of the hyomandibular, whereas in Klyukanov's figure and in my specimens it reached only the opercular arm. This suggests that Chapman may have overlooked the suprapreoperculum and considered it to be the dorsal tip of the preoperculum.

The sensory canal on both the suprapreoperculum and the pterotic runs in an open, bony trough (the suprapreoperculum is not shown on Fig. 18; however, the open temporal sensory canal is visible). Although the osmerids lack a suprapreoperculum the temporal sensory canal is open as in *Plecoglossus* (compare Fig. 18 with Figs. 15-17). The only other salmoniforms to have a suprapreoperculum are the salmonines (Salmonidae). These differed from *Plecoglossus* in that the sensory canal on both the suprapreoperculum and pterotic was enclosed in a bony tube and opened to the exterior via pores.

Unlike the osmerids, *Plecoglossus* has a bone-enclosed lateral sensory canal that runs along the entire length of the preoperculum and gives off eight pores (refer to Fig. 18): one at each end of the bone, three on the ventral limb that are separated from one another by pillars of bone, and three relatively wide foramina along the main canal on the dorsal limb. The foramina on the ventral limb occur almost directly along the main canal and with one exception, there were no true auxiliary canals. In one adult (UAMZ 3505, 144.1 mm SL) the two posterior pores on the ventral limb opened at the end of short auxiliary canals. Chapman (1941a, fig. 6) illustrated seven pores in his specimen, four on the ventral limb, three on the dorsal limb.

A typical anterior lamina is absent in adults. Instead, the entire area anterior to the posterior edge of the sensory canal at the intersection of the two limbs is thickened and convex laterally. As a result, the anterior edge of the bone is rounded and broad at the intersection of the two limbs.

The preoperculum in the second smallest specimen (77.9 mm SL) was like that in the adults except that the bone was less robust and the ventral limb was slightly longer. The anterior edge of the bone was less thickened than in the adult and a moderately narrow anterior lamina was present along the anterior edge of the ventral end of the dorsal limb. In the juvenile (55.5 mm SL) the ventral limb was not abbreviated anteriorly and was longer than in the other specimens (the dorsal limb was only about one and a quarter to one and a third times longer than the ventral one). At the intersection of the two limbs was a thin anterior lamina that was convex laterally. The lateral sensory canal was enclosed in bone, but less so than in the other specimens. The canal on the entire dorsal half of the dorsal limb was open posterior to a flange that extended to the dorsal tip of the preoperculum. Because of this there were only six foramina along the canal, four on the ventral limb and two on the dorsal limb.

FAMILIES SALANGIDAE + SUNDASALANGIDAE

Roberts (1984) divided the family Salangidae into three subfamilies containing four genera and eleven species. The Protosalanginae are monotypic with only *Protosalanx chinensis*; the Salanginae have one genus, *Salanx*, with four species; and the Salangichthyinae have two genera, *Neosalanx*, with four species, and *Salangichthys*, with two species. The family Sundasalangidae has one genus, *Sundasalanx*, with two species (see Roberts 1981, 1984). Roberts (1984) placed these two families into their own superfamily, the Salangoidea, primarily because they share a suspensorium unlike that in any other Pisces.

The suspensorium in the Salangidae and Sundasalangidae is unique because the dorsal part of the mandibular arch (the palatoquadrate) and the dorsal part of the hyoid arch (the hyosymplectic) are united into a single continuous cartilaginous element that Roberts (1984) calls the hyopalatine (the palatohyomandibuloquadrate in his 1981 paper). In other fishes (including other salmoniforms) in which early development of these arches has been observed, the cartilaginous palatoquadrate and hyosymplectic are always separate (pers. obs.; also see Roberts 1984). The hyopalatine is divided into anterior and posterior sections in the sundasalangid *Sundasalanx microps*; however, according to Roberts (1984) the division is more anterior (the palatine is separated from the fused hyomandibular-quadrate section) than the primitive character state found in the young of other fishes (where the division is between the palatoquadrate and the hyosymplectic).

According to Roberts (1984) the suspensorium in the Sundasalangidae and some Salanginae and Salangichthyinae is entirely cartilaginous. However, in other Salanginae and

Salangichthyinae, and in *Protosalanx*, there are some dermal and endochondral ossifications that correspond to all the bones of the suspensorium except the symplectic. *Protosalanx* has the most extensive ossification and is considered by Roberts (1984) to be the most primitive salangoid. Its suspensorium is elongated anteroposteriorly, has a long ossified dermopalatine bearing numerous large teeth, and has ossifications corresponding to the mesopterygoid, metapterygoid, quadrate, and hyomandibular (see fig. 9 in Roberts 1984).

In the following account the suspensorium of the salangid *Salangichthys ishikawae* is described in detail (see Fig. 19) and then compared to two other salangids that I cleared and stained, *Salanx prognathus* (see Fig. 20) and *Salangichthys microdon* (see Fig. 21). Information concerning the suspensorium in other salangids was obtained from Fang (1934), Wakiya and Takahasi (1937), and Roberts (1981, 1984). I did not examine any sundasalangids; however, detailed descriptions of the suspensorium in this group are found in Roberts (1981, 1984).

The suspensorium in *Salangichthys ishikawae*, as in other salangids, is united into a continuous cartilaginous element (the hyopalatine) and is notably longer anteroposteriorly than it is deep dorsoventrally (see Fig. 19). It has ossifications corresponding to the palatine, mesopterygoid, quadrate, metapterygoid, hyomandibular, and preoperculum. The suspensorium in *S. ishikawae* appears to be relatively primitive since it exhibits more ossification than many other salangids (see Figs. 20, 21 for example).

The cartilaginous section corresponding to the palatine is long anteroposteriorly and relatively flat dorsoventrally with an anterolateral expansion that contacts the maxilla and a slight anteromedial expansion that abuts the lateral prenasal process of the ethmoid cartilage. Extending anterodorsally to the lamina orbitonasalis (of the ethmoid cartilage) from the posterior end of the "palatine" is a uniquely shaped cartilaginous knob that differs from that found in other salmoniforms examined. A long, thin, tooth-bearing, ossified dermopalatine is present that bears a few small, posteroventrally directed teeth on its anteroventral surface (five on the left bone, three on the right). The dermopalatine expands anteriorly to underlie the lateral prenasal process. An ossified ectopterygoid is absent.

A moderately large, thin, edentulous, ossified mesopterygoid is present that distinctly overlaps the medial surface of the anterodorsal corner of the quadrate and closely approaches the posterior end of the dermopalatine.

There is an ossified quadrate with a small body but a well-developed condyle and quadratojugal arm.

A small, saddle-shaped ossification that corresponds to the metapterygoid rests on cartilage posterior to the mesopterygoid.

A separate, ossified symplectic is absent, as is apparently the case in all other salangoids (see Roberts 1984). However, the symplectic may be represented by a raised, anteroposteriorly-directed thickening on the lateral surface of the hyopalatine posterodorsal to the adjacent quadratojugal arm of the quadrate.

The large area between the quadrate and the posterior articulation of the suspensorium with the skull (that corresponds to the hyomandibular-symplectic) is almost entirely cartilaginous. There is a rounded, thin, ossified plate on the medial and lateral surfaces of the middle of what would normally correspond to the head of the hyomandibular. The hyomandibular branch of the facial nerve passes through the mid-anterior part of this ossification. A small, rounded, and partly ossified lateral strut is located anteroventral to the lateral foramen of this nerve. The lateral surface of the hyopalatine between the lateral strut and the body of the quadrate is distinctly concave and serves as an area of muscle origin.

The preoperculum in *S. ishikawae* is a broad, flat, thin bone that is completely ossified. As is the case in all Salangidae (less so in *Protosalanx*), the dorsal limb is distinctly shorter than the ventral limb and does not extend to the opercular arm of the "hyomandibular." The bony, lateral sensory canal is open along the entire length of the preoperculum, but unlike other salmoniforms with this character state, there is no flange along the anterolateral surface of the bone. A flange is also absent in *Salanx prognathus* (see Fig. 20); however, in *Salangichthys microdon* a trace of a flange is present (see Fig. 21).

The suspensorium in the other salangids is basically similar to that described for *Salangichthys ishikawae*. The most notable differences concern the amount of ossification and its distribution (see Figs. 19-21 and figs. 9-12 in Roberts 1984).

The size of the dermopalatine and the size and number of teeth on its ventral surface, in particular, are variable in the Salangidae. The most primitive character state, according to Roberts (1984), is probably that found in *Protosalanx* in which the dermopalatine is long anteroposteriorly, robust, and has two rows of numerous, large, conical teeth along most of its length. Wakiya and Takahasi (1937, p.273) noted that in *Protosalanx* there were about ten teeth in the outer row and about eighteen in the inner row, and that "a few anterior teeth in [the] inner series [were] much enlarged and recurved." In other salangids the dermopalatine is smaller and the teeth (when present) are much smaller, fewer in number, and in a single row (e.g., see Figs. 19-21). The most derived state occurs in the genus *Neosalanx* in which the dermopalatine is realtively small and lacks teeth (see Roberts 1984).

A separate, ossified ectopterygoid is probably absent in all salangids, although Roberts (1984) suggests that the "palatal toothplate" (= my dermopalatine) may be an ectopterygoid. However, this does not seem likely because of its anterior location and because it bears teeth (the ectopterygoid in all other salmoniforms is edentulous).

A mesopterygoid is apparently present in most salangids (see Roberts); however, its size is variable. It is absent in *Salangichthys microdon* (see Fig. 21) and tiny in *Salanx prognathus* (see Fig. 20).

The quadrate appears to be ossified (but to varying degrees) in most salangids.

Most salangids lack an ossified metapterygoid (see Figs. 20, 21 and Roberts 1984). However, a distinct and large metapterygoid is present in *Protosalanx* (see Roberts 1984, fig. 9). Unlike the Osmeridae and Plecoglossidae it appears to lack sculpture and a posteroventral wing.

Most other salangids (except *Protosalanx*) appear to lack hyomandibular ossifications.

The suspensorium in the Sundasalangidae is similar to that described for the Salangidae but is even more derived: it is entirely cartilaginous (even lacking a dermopalatine), edentulous, and lacks a preoperculum (see Roberts 1981, 1984).

FAMILY RETROPINNIDAE

The family Retropinnidae contains only *Retropinna* (with three species) and *Stokellia* (with one species). The four species "are very similar to each other" according to McDowall (1979, p. 112). The description that follows is of *Retropinna retropinna*. Its suspensorium is moderately delicate, moderately long, bears numerous teeth, and lacks sculpture (see Fig. 22).

Palatine-ectopterygoid

The palatine and ectopterygoid are fused to each other in *Retropinna retropinna* (see Fig. 22). When viewed laterally this bone is long anteroposteriorly and dorsoventrally flattened anteriorly. The area posterior to the posteriormost tooth is part of the original ectopterygoid. Immediately posterior to this tooth the bone is slightly constricted. The area posterior to this constriction is relatively straight and inclined at a slightly different angle than the anterior part. The posteriormost end is slightly expanded. It overlaps the medial surface of the anterodorsal corner of the quadrate as in a typical ectopterygoid. The posterior section is also edentulous as is the ectopterygoid of the other salmoniforms. Finally, the posterior section is flattened and blade-like as in a typical ectopterygoid. The area anterior to the central constriction, which includes the teeth, widens gradually mediolaterally in an anterior direction. The sides of this part curve dorsomedially and dorsolaterally so that a trough is formed along the entire dorsal surface of the palatine. The lateral side of the trough extends posteriorly nearly to the middle of the ectopterygoid section. The autopalatine is small and only slightly expanded at each end. It is relatively short anteroposteriorly and flattened dorsoventrally, resting on (and apparently fused with) the anterodorsal surface of the dermopalatine trough. A small, egg-shaped, anteriorly projecting cartilage sits at the anterior end of the autopalatine. The anterolateral corner of this cartilage barely touches a tiny facet on the anteromedial side of the maxilla. The anteromedial side is slightly concave where it receives the lateral prenasal process of the ethmoid cartilage. The palatoquadrate cartilage emanates from the posterior end of the autopalatine, expanding posteromedially to fill the dermopalatine trough and cover the anterodorsal surface of the mesopterygoid. Unlike the Osmeridae and most other salmoniforms, this part of the palatoquadrate cartilage is flat and does not extend dorsally to meet the lamina orbitonasalis of the ethmoid cartilage. The lamina orbitonasalis of the ethmoid cartilage projects ventrally to meet the dorsal surface of the palatoquadrate cartilage, resting in a shallow concavity on the dorsal surface of the latter. The palatoquadrate cartilage narrows posteriorly, running along the dorsolateral surface of the posterior end of the fused palatine-ectopterygoid and the dorsolateral edge of the mesopterygoid before reaching the quadrate.

The dermopalatine consists of the trough mentioned previously and its teeth. The anterior end of the dermopalatine does not extend anterior to the autopalatine. The dermopalatine teeth are moderately robust, pointed, and directed posteroventrally. There are up to fifteen teeth in a row along the ventrolateral surface of the dermopalatine, extending from below the middle of the autopalatine to about the middle of the fused bone. A few teeth are usually found medial to the main row. The dermopalatine teeth together with the large vomerine teeth form a nearly continuous U-shaped biting surface around the anterior end of the snout that lies inside of the premaxillae and maxillae dentition.

Mesopterygoid

The mesopterygoid in *Retropinna retropinna* is a moderately long but wide bone that has numerous large teeth on its ventral surface (see Fig. 22). It is widest posteriorly, tapering abruptly to a point at its anterior end. Its dorsal surface is concave and slopes dorsomedially toward the parasphenoid, from which it is separated by a relatively wide band of connective tissue. The posteroventral corner overlies the mid-dorsal part of the medial surface of the body of the quadrate. The lateral edge of the mesopterygoid overlaps parts of the palatine-ectopterygoid. Its anterior end overlaps the dorsomedial surface of the dermopalatine but does not approach the autopalatine.

As in the Osmeridae and Plecoglossidae the medioventral surface bears a series of large, pointed teeth that curve ventrolaterally. The teeth extend along nearly the entire anteroposterior length of the bone. Unlike *Hypomesus*, the teeth do not noticeably increase in number posteriorly, and they do not form a single row anteriorly. In the two specimens that I cleared and stained there were from thirty to forty functional teeth on each mesopterygoid. The medialmost teeth form an irregular row of about fifteen to twenty teeth. There are an equal number of equally spaced teeth lateral to the medialmost row that are more randomly distributed and form one or two irregular rows. McDowall (1969, p. 801) noted that in *R. osmeroides* (synonymized with *R. retropinna* by McDowall 1972) the "mesopterygoids are large, with a band of teeth two to five wide on the mesial half." The medial row of teeth and the teeth at the posteriormost end are larger than the more lateral ones. There are a relatively large number of small replacement teeth scattered loosely among the functional teeth. The area bearing the teeth is slightly thickened (less so than in *Hypomesus*) relative to the rest of the mesopterygoid. The posterior end of the tooth-bearing area is thickest and forms a slightly raised platform (as in *Hypomesus* but smaller) that extends slightly posterior to the main part of the bone. As in *Hypomesus*, this "platform" underlies (but projects only slightly posterior to) the anterodorsal corner of the metapterygoid. The teeth on the mesopterygoid oppose a series of dorsomedially directed teeth of similar size and shape on the posterior half of the basihyal and on the basibranchials.

Quadrate

The quadrate in *Retropinna retropinna* has few distinctive features (see Fig. 22). The body is shorter dorsoventrally, with less steeply sloping sides than in *Hypomesus*. Its posterodorsal corner is separated from the metapterygoid by a wide band of cartilage. The condyle is larger than in *Hypomesus*. The quadratojugal arm is relatively long and does not taper noticeably posteriorly.

Symplectic

The symplectic in *Retropinna retropinna* is different from that in *Hypomesus* (see Fig. 22). It is a moderately short but wide bone with a distinct central bend. There is only a trace of dorsal lamina. The posterior end is broad and separated from the correspondingly wide ventral end of the ventral arm of the hyomandibular by a broad area of cartilage. Most of the bone rests in a groove on the dorsomedial surface of the quadratojugal arm of the quadrate. The anterior end of the bone is capped by an unusually large cartilaginous knob that extends nearly to the quadrate condyle.

Metapterygoid

The metapterygoid in *Retropinna retropinna* is moderately large, nearly oval, and lies posterodorsal to the quadrate (see Fig. 22). The entire bone is endochondral in origin except for a very narrow dermal lamina that extends along the dorsal edge. The posterior end is inclined more or less dorsoventrally and is slightly concave laterally. The anterior end of the metapterygoid is slightly convex laterally and curves dorsomedially to overlap the posterodorsal surface of the mesopterygoid. The palatoquadrate cartilage extends around most of the ventral edge of the bone. The cartilage at the anterodorsal corner is expanded anteriorly into a knob. The posterior end of the metapterygoid and the palatoquadrate cartilage extending around it overlap about the ventral two thirds of the anterolateral surface of the hyomandibular, including most of the anterior lamina. The palatoquadrate cartilage at the posterodorsal corner of the metapterygoid is expanded and extends posteriorly to the anteroventral corner of the opercular arm of the hyomandibular, abutting the middle of the anterior face of the posterodorsally curved lateral strut, and covering the ventral half of the lateral foramen for the hyomandibular branch of the facial nerve. Unlike the Osmeridae and Plecoglossidae there is no ridge on the medial surface of the metapterygoid; however, the part along which the *adductor arcus palatini* inserts is slightly rounded. In one specimen (UAMZ 4606, 76.1 mm SL) there was a tiny crescentic flange on the medial surface adjacent to the posterior edge of the laminar part of the mesopterygoid.

Hyomandibular

The hyomandibular in *Retropinna retropinna* is a stout bone that is moderately short and wide; the width is about two thirds the length (see Fig. 22). The cartilaginous condyle on the dorsal edge of the head rests entirely in the large area of cartilage that lies between the pterotic, sphenotic, and prootic. The posteriormost end of the condyle abuts a notch at the anteroventral corner of the pterotic, unlike most salmoniforms in which the posterior end sits along a groove on the surface of the pterotic. The anterolateral and anteromedial corners of the condyle are separated from the ventral edge of the sphenotic and the dorsal edge of the prootic, respectively, by cartilage.

The head of the hyomandibular is broad dorsally and narrows only slightly ventrally, unlike the osmerids in which the ventral apex is narrow. The opercular arm is moderately long and broad. It is capped posteriorly with a cartilaginous knob that rests in a facet on the anterodorsal corner of the operculum. Distinct posterodorsal and posteroventral laminae are present. A moderately wide anterior lamina that is slightly concave laterally extends along the entire anterior edge of the hyomandibular. The ventral arm is relatively short and broad. The lateral strut is relatively small and has an unusual shape. It begins anteriorly near the posterodorsal edge of the ventral arm and curves in an arc (the arc is convex dorsally) that extends posterodorsally to the middle of the opercular arm. The strut in the smaller specimen (UAMZ 4606, 71.5 mm SL, see Fig. 22) was smaller than in the larger one (UAMZ 4606, 76.1 mm SL). McDowall (1969, p. 801) claimed that in *R. osmeroides* (which he synonymized with *R. retropinna* in 1972) the "hyomandibular ... has no lateral spur [= strut] at the level of its articulation with the opercular." The canal for the hyomandibular branch of the facial nerve is moderately long and is inclined posteroventrally from the medial to the lateral foramina. The medial foramen is large and located at the anteroventral corner of the head. The lateral foramen is about the same size and located at the middle of the bone at the intersection of the apex of the head and the dorsalmost part of the ventral arm. It lies anterior to the middle of the lateral strut and is partly covered by the large cartilage at the posterodorsal corner of the metapterygoid. When the nerve exits from the lateral foramen it courses ventrally medial to the expanded cartilage that covers it and then runs ventrally along the lateral surface of the ventral arm before extending anteriorly.

Preoperculum

The preoperculum in *Retropinna retropinna* is a relatively thin, broad, flat bone with dorsal and ventral limbs that meet at about a right angle (see Fig. 22). The ventral limb is longer than the dorsal limb and tapers anteriorly to a point. The dorsal limb is abbreviated dorsally, extending only to the posteroventral corner of the opercular arm of the hyomandibular. There is no suprapreoperculum. The anterior lamina is wide, thin, slightly convex laterally, and extends along virtually the entire anterior edge of the dorsal limb. The middle of the lamina overlaps the posteroventral corners of the symplectic and ventral arm of the hyomandibular, as well as the posterolateral surface of the hyomandibular-symplectic cartilage. The dorsal limb of the preoperculum is separated from the lateral strut and the ventral arm of the hyomandibular by a moderately wide gap. There is an open, bony, lateral sensory canal on the preoperculum like that described for the osmerid *Hypomesus*. McDowall (1969, p. 801) claimed that "The preopercular ... has a partially enclosed laterosensory canal." However, the canal appears completely open judging from his figure 3A.

FAMILY PROTOTROCTIDAE

The family Prototroctidae contains only one genus, *Prototroctes*, with two species, *P. maraena* and *P. oxyrhynchus* (now thought to be extinct). Both species are very similar to one another anatomically (see McDowall 1974, 1976a). The description that follows is of *Prototroctes maraena*.

The suspensorium in *Prototroctes* is similar to that in *Retropinna* but is more robust (see Fig. 23 and compare it to Fig. 22).

Palatine—ectopterygoid

The palatine and ectopterygoid are fused to each other in *Prototroctes*, [illegible] in *Retropinna* (see Fig. 23 and compare to Fig. 22). This agrees with McDowall (1969), but not with Gosline (1960), who claimed that the two elements were separate in *Prototroctes* (but fused in *Retropinna*). This fused bone is similar to that described for *Retropinna*; however, there are several differences. In *Prototroctes* the bone is straighter than in *Retropinna*. The area posterior to the teeth, probably part of the original ectopterygoid, is not bent relative to the anterior section. There is no constriction immediately posterior to the posteriormost tooth as in *Retropinna*. The posteriormost part of the bone is not expanded where it overlaps the quadrate and has a blunt or fimbriated end. The anterior tooth-bearing portion is formed into a trough similar to that in *Retropinna*; however, in *Prototroctes* the lateral side of the trough begins posterior to the posteroventral corner of the autopalatine and is lower than in *Retropinna*.

The dermopalatine consists of the aforementioned trough and its teeth. The teeth are smaller than in *Retropinna*, begin near the anteriormost end of the dermopalatine (ventral to the autopalatine), and extend posteriorly along its ventrolateral surface in two irregular rows of about ten to fifteen teeth each(the posteriormost teeth are in a single row). In the larger specimen (UAMZ 6325, 117.0 mm SL) there were about 30 functional teeth on each palatine whereas in the smaller one (AMS I.20704-001, 68.8 mm SL) there were about twenty. The teeth in the smaller specimen were more delicate and did not extend as far posteriorly as in the larger one.

The autopalatine is even smaller than in *Retropinna* and has an unusual shape. It is short, triangular, and sits at the anteriormost end of the dermopalatine trough. It is apparently not fused with the dermopalatine and extends anterior to it, unlike *Retropinna*. The autopalatine has no anterior expansion and is widely separated from the maxilla (which also lacks an articular facet on its anteromedial side). The palatoquadrate cartilage emanates from the expanded posterior end of the autopalatine. It first expands slighty posterodorsally (its medial side abutting the lateral prenasal process of the ethmoid cartilage) and then flattens (as in *Retropinna*) as it extends posteriorly to fill the [illegible]atine trough and cover the anterodorsal surface of the mesopterygoid. Its contact with the lateral prenasal process of the ethmoid cartilage is as in *Retropinna*.

Mesopterygoid

The mesopterygoid in *Prototroctes* is as described for *Retropinna* but has a rather blunt anterior end that is notched (see Fig. 23). The medioventral surface bears a series of large, pointed, ventrolaterally directed teeth; however, *Prototroctes* has more teeth than *Retropinna* and they cover more of the medial side of the bone. The larger specimen (117.0 mm SL) had about eighty functional teeth whereas the smaller one (68.8 mm SL) had about half that number. As in *Retropinna* the medial row of teeth and those at the posteriormost end are largest, with tooth size decreasing laterally. The medialmost teeth form an irregular row (or two) of about fifteen to twenty teeth that run anteroposteriorly from near the anterior end to the posteromedial corner of the mesopterygoid. The more central, smaller teeth appear to be randomly distributed. The tooth-bearing area is thicker, and the posteriorly extending tooth-bearing platform larger and more robust than in *Retropinna*. The basihyal and basibranchial tooth-plates in *Prototroctes* are also wider than in *Retropinna*, and in the larger specimen possessed more teeth.

Quadrate

The quadrate in *Prototroctes* is similar to that in *Retropinna* but has a smaller body, a larger and more robust condyle, and a shallower quadrate notch (see Fig. 23).

Symplectic

The symplectic in *Prototroctes* is very similar to that described for *Retropinna* (see Fig. 23). The symplectic in the smaller specimen (68.8 mm SL) was slightly different than in the larger one (117.0 mm SL): it was bent more centrally, the anterior tip of the bony part was posterior to the body of the quadrate, and the anterior cartilaginous knob was longer.

Metapterygoid

The metapterygoid in *Prototroctes* is similar to that described for *Retropinna* (see Fig. 23). The dorsal dermal lamina in the larger specimen of *Prototroctes* (117.0 mm SL) was wider than in the smaller specimen (68.8 mm SL) and in *Retropinna*. The expansion of the palatoquadrate cartilage at the posterodorsal corner of the metapterygoid is also larger than in *Retropinna* and extends farther posteriorly, reaching the middle of the opercular arm of the hyomandibular and nearly abutting the anterodorsal edge of the dorsal limb of the preoperculum. This cartilage also overlaps the entire middle part of the anterior face of the posterodorsally inclined lateral strut of the hyomandibular, and covers virtually the entire lateral foramen for the hyomandibular branch of the facial nerve. The medial side is like in *Retropinna*.

Hyomandibular

The hyomandibular in *Prototroctes* is similar to that in *Retropinna* but is slightly more robust (see Fig. 23). The articulation with the skull in the smaller specimen (68.8 mm SL) was like in *Retropinna*; however, in the larger one (117.0 mm SL) the posteriormost end of the condyle rested on a short groove on the anteroventral corner of the pterotic rather than abutting a notch at the anteroventral corner of the bone and resting in cartilage. The opercular arm in *Prototroctes* is slightly smaller than in *Retropinna*. The lateral strut is similar in shape to the one in *Retropinna* but is longer and wider. It begins anteriorly near the posterior edge of the middle of the ventral arm and curves in an arc (the arc is convex dorsally) that extends posterodorsally to the posteroventral corner of the opercular arm. The strut in both specimens was equally well-developed. McDowall (1969, p. 812) claimed that "there is no spur [= lateral strut] on the hyomandibular" in *Prototroctes*. The canal for the hyomandibular branch of the facial nerve is longer than in *Retropinna*. Its medial foramen is located slightly farther anteriorly and its lateral foramen is located slightly farther ventrally than in *Retropinna*.

Preoperculum

The preoperculum in *Prototroctes* is similar to that in *Retropinna* but has a narrower dorsal limb and a narrower gap between its anterior edge and the ventral arm of the hyomandibular (see Fig. 23). The dorsal tip of the dorsal limb also overlaps the posterodorsal corner of the lateral strut of the hyomandibular and nearly abuts the posterior edge of the expansion of the palatoquadrate cartilage at the posterodorsal corner of the metapterygoid.

FAMILY LEPIDOGALAXIIDAE

The Lepidogalaxiidae contains only one species, *Lepidogalaxias salamandroides*. Its suspensorium is moderately long, moderately robust, lacks sculpture, and shares a number of similarities with both the Aplochitonidae and Galaxiidae (see Fig. 24, and compare to Figs. 25, 26).

Palatine

The palatine in *L. salamandroides* is a moderately long and narrow bone that is expanded anteriorly where it contacts the skull (see Fig. 24). Unlike the Galaxiidae and Aplochitonidae, it consists of both an autopalatine and a tooth-bearing dermopalatine. When *in situ*, and viewed dorsally, it is straight and is inclined slightly anteromedially towards the end of the skull.

The splint-like dermopalatine forms the entire ventral surface of the bone and tapers posteriorly. It is flattened dorsoventrally and moderately wide mediolaterally. Its entire mid-ventral surface bears a single row of moderate-sized, closely spaced, sharply-pointed teeth that are directed ventrally, and decrease slightly in size posteriorly. Each palatine had eight functional teeth, plus there were several tiny replacement teeth. In Frankenberg's (1969) specimens each palatine possessed six to twelve teeth. In the specimen illustrated by Roberts (1984) there were nine teeth on the palatine. The ventral surface of the vomer had four teeth, and together with those on the palatines form a nearly continuous, U-shaped biting surface.

The autopalatine is the relatively small, triangular, cartilage-capped expansion that forms the anterodorsal end of the palatine. It is imperceptibly fused with the anterodorsal surface of the dermopalatine. There is no posterior expansion of the autopalatine, unlike most other teleosts; however, the anterodorsal end is expanded and extends anterodorsally towards the lateral ethmoid bone. It is capped by a cartilage that is located dorsal to most of the palatine. The cartilage has an unusual shape. When it emerges from the bone it extends anterodorsally for a short distance, then extends laterally as a moderately long, finger-like hook that contacts the anteromedial surface of the maxilla. This lateral cartilaginous hook is reminiscent of that found in *Thymallus* (Salmonidae). There is no medial extension of the palatine cartilage; however, its dorsomedial surface is concave where it abuts the posteroventral surface of the lateral ethmoid.

In no other salmoniform does the lateral ethmoid bone lie dorsal to the anterior end of the palatine and contact the cartilage at the anterior end of the palatine. In the other salmoniforms the anterior palatine cartilage is anterior to the lateral ethmoid and contacts the maxilla and the lateral prenasal process of the ethmoid cartilage. The lateral ethmoid invariably lies posterior to the autopalatine.

The shape and position of the anterior part of the palatoquadrate cartilage is unusual in *Lepidogalaxias*. From the anterodorsal corner of the body of the quadrate it extends anteriorly as a narrow strip along the lateral surface of the ectopterygoid, barely reaching the posterior tip of the palatine. In most other salmoniforms this cartilage emerges from the posterior end of the autopalatine and expands posteriorly, contacting the lamina orbitonasalis of the ethmoid cartilage (but not the lateral ethmoid directly), and overlapping the anterodorsal surface of the mesopterygoid before narrowing posteriorly along the lateral surface of the ectopterygoid to the quadrate (compare Fig. 24 with Fig. 25).

Ectopterygoid

The ectopterygoid is straight, short anteroposteriorly, with no posterior expansion. It overlaps the medial surfaces of the quadrate (the anterodorsal corner of the body) and mesopterygoid (the anteroventral edge). The anterior end is adjacent to the posterior end of the dermopalatine and is connected to it by tough connective tissue.

Mesopterygoid

The mesopterygoid is a moderately small and delicate bone that is nearly elliptical. It is widest posteriorly where it overlaps the medial surfaces of the quadrate (the anterodorsal part of the body) and metapterygoid (the anteroventral surface) and narrows slightly anteriorly. Its dorsal surface (excluding the section overlapping the quadrate, which is inclined dorsoventrally) is only slightly concave and slopes dorsomedially toward the parasphenoid, from which it is separated by a moderately wide band of connective tissue.

The mesopterygoid lacked teeth in both of my specimens, an observation confirmed by Rosen (1974), McDowall and Pusey (1983), and Roberts (1984). This is in contrast to Mees's (1961) original description in which he claimed that such teeth were present. However, McDowall and Pusey examined the holotype and paratypes (plus numerous other specimens) and concluded that Mees had mistaken the prominent palatine teeth for mesopterygoidal teeth.

Quadrate

The quadrate is a moderately large, moderately robust bone that is longer anteroposteriorly than it is dorsoventrally. Its shape, especially that of the condyle and quadratojugal arm, is reminiscent of that in the galaxiids. The condyle is unusually large, and its broad, elliptical shaped articular facet faces anteroventrally. The quadratojugal arm is long, tapers posteriorly, and is grooved ventrally for the reception of the anterodorsal edge of the ventral limb of the preoperculum. The quadrate notch is moderately deep and wide.

Symplectic

The symplectic is moderately long and wide with a slight central bend. It is larger relative to the other bones of the suspensorium than is usually the case. There are moderately wide (and thick) dorsal and ventral laminae running along most of the length of the bone.

The symplectic narrows slightly towards its anterior end, where it is capped with a cartilaginous knob that rests in a small concavity on the medial surface of the quadrate (at the intersection of the quadratojugal arm and body). The posterior end is separated from the ventral end of the ventral arm of the hyomandibular by an unusually narrow band of cartilage, so narrow in fact that the posterodorsal corner of the symplectic nearly contacts the ventral arm of the hyomandibular. In most salmoniforms this cartilage is relatively wide and the ends of the two bones are distinctly separated.

Metapterygoid

The metapterygoid is a relatively small, flattened, triangular bone that is entirely endochondral in origin. Its broad ventral end is continuous with the palatoquadrate cartilage, and its narrow dorsal end is capped by a tiny cartilaginous knob. It rests on the dorsal surface of the posteromedial part of the mesopterygoid, and like that bone, is inclined dorsomedially towards the parasphenoid. Although it is widely separated from the hyomandibular, the gap between the two bones is spanned by connective tissue. A finger-like extension of the palatoquadrate cartilage extends posteriorly from the posterior corners of the metapterygoid and quadrate (body) in a way reminiscent of that in the aplochitonid, *Lovettia*. Overall, the metapterygoid is very similar to that in the Aplochitonidae (especially to *Lovettia*, in which it also occupies the same position).

Hyomandibular

The hyomandibular is a moderately large and robust bone that is, relative to most other teleosts, very broad anteroposteriorly but short dorsoventrally (the width is slightly longer than the length). When viewed medially, the hyomandibular is nearly square, a feature unique to *Lepidogalaxias* among the teleosts that I examined. The overall shape of the bone and the proportions of the various parts are distinctly similar to those of the Galaxiidae (compare Fig. 24 with Fig. 26).

The cartilaginous condyle on the dorsal edge of the head is thinner than in most teleosts, and forms a straight and tight joint with the skull. The entire condyle rests on bone because there is virtually no cartilage separating the sphenotic, pterotic, and prootic. In most teleosts the latter three bones are separated by cartilage, and the anterior part of the hyomandibular condyle rests along it. In *Lepidogalaxias* the posterior half of the condyle rests along a moderately shallow groove on the anteroventral surface of the pterotic. The posterior corner of the condyle abuts a ventrolaterally projecting process at the posterior end of this groove. The anterior half of the condyle sits in a bony groove formed ventrally by the dorsolateral edge of the prootic and dorsally by the ventrolateral edge of the sphenotic. The anterolateral corner abuts a small ventral extension of the sphenotic and the anteromedial corner sits in a depression on the anterodorsal edge of the prootic. The entire facet in which the condyle sits appears to be lined with cartilage.

The head of the hyomandibular is very broad anteroposteriorly, short dorsoventrally, and narrows only slightly ventrally. The opercular arm is large and expanded posteriorly. It is continuous both anteriorly and dorsally with the head. A small posterodorsal lamina (dermal) extends between the posterior edge of the head and the posterodorsal edge of the opercular arm. A very large, dermal, posteroventral lamina is present (larger by far than in any other salmoniforms) that fills the entire area between the posterior edge of the ventral arm and the ventral edge of the opercular arm. The ventral arm is very short relative to the rest of the hyomandibular and expands ventrally. A moderately wide anterior lamina (dermal) extends along the entire anterior edge of the bone.

The lateral strut is moderately well-developed and has an unusual shape. It is relatively long dorsoventrally, but narrow mediolaterally, and lies perpendicular to the mid-ventral surface of the hyomandibular. It extends ventrally from the middle to the mid-ventral edge of the bone, and then projects ventrally as a finger-like extension that reaches the mid-anterior edge of the preoperculum. The posterior edge of the strut is grooved and abuts the anterior edge of the ventral half of the dorsal limb of the preoperculum. The narrow anterior facing surface of the strut is only slightly concave; part of the *levator arcus* *palatini* (LAP) inserts onto its dorsalmost surface (and onto the dorsal edge of the strut) and part of the *adductor mandibulae* originates on its ventral surface ventral to the insertion of the LAP.

The canal for the hyomandibular branch of the facial nerve is relatively long and wide and extends nearly ventrally from the medial to lateral foramina (versus posteroventrally in most teleosts). The medial foramen is moderately large, round, and located at the intersection of the head and the ventral arm. The lateral foramen is larger than the medial one, and is located on the mid-ventral edge of the hyomandibular, medioventral to the ventralmost edge of the lateral strut before it projects ventrally, and adjacent to the posteroventral corner of the ventral arm. It is only clearly visible when the bone is viewed ventrally.

Preoperculum

The preoperculum is moderately robust, with dorsal and ventral limbs of about equal length that meet at a slightly obtuse angle. There is virtually no anterior lamina. There is a wide gap between the "anterior lamina" and the hyomandibular-symplectic joint. A bone-enclosed lateral sensory canal runs the entire length of the anterolateral surface of the preoperculum and gives off three pores: one at each end of the bone and one that opens to the exterior at the end of a very short auxiliary canal at the intersection of the two limbs. In this respect, it differs from all other galaxioids in which the canal is open along the entire length of the preoperculum.

FAMILY APLOCHITONIDAE

The family Aplochitonidae contains only *Aplochiton* (with two, perhaps three species) and *Lovettia* (with one species). *Lovettia* is considerably smaller than *Aplochiton* and is weakly ossified. In the following, *Aplochiton taeniatus* is described in detail and then compared to *Lovettia sealii*.

The suspensorium in *Aplochiton* is long, moderately delicate, bears teeth and lacks sculpture (see Fig. 25). It is similar in *Lovettia* but is more delicate and weakly ossified (especially the hyomandibular, symplectic, metapterygoid, and palatine).

Palatine

The palatine in *Aplochiton taeniatus* is relatively small, lacks teeth (and a dermopalatine), and has an elongated cartilage at the anterior end of the autopalatine (see Fig. 25). The autopalatine is small and shaped like a long, narrow tube that is slightly constricted centrally. The anterior end is slightly expanded, rounded in cross-section, and is capped by a highly unusual cartilage that emanates anteriorly towards the premaxilla and maxilla. This anterior cartilage is almost as long as the autopalatine, elliptical in cross-section, and expanded mediolaterally (but flattened dorsoventrally) at its anterior end. Virtually the entire anterior end of the cartilage overlaps a large facet on the anteromedial side of the maxilla, as well as part of the dorsally projecting ascending process of the premaxilla. The lateral prenasal process of the ethmoid cartilage overlaps the entire dorsomedial surface of the anterior cartilage posterior to its anterior expansion, as well as the dorsal surface of the anteromedial corner of the autopalatine. The autopalatine has a short and narrow dorsomedially projecting flange on its dorsomedial side (at the posterior end of the anterior expansion). A moderately wide ligament extends from this flange to the ethmoid cartilage (at the posterior end of the lateral prenasal process). The posterior end of the autopalatine is expanded mediolaterally and is flatter dorsoventrally than the anterior expansion. Emanating from the posterior expansion is the palatoquadrate cartilage. The palatoquadrate cartilage is flattened dorsoventrally and expands posteromedially to cover the dorsolateral surface of the mesopterygoid posterior to the anterior end of the bone, unlike *Retropinna* and *Prototroctes* in which the entire anterodorsal end is overlain. As in *Retropinna* and *Prototroctes* the palatoquadrate cartilage does not extend dorsally to meet the lamina orbitonasalis of the ethmoid cartilage. As in the latter two genera, the lamina orbitonasalis is large, expanded far laterally, and overlies the dorsal surface of the palatoquadrate cartilage. The palatoquadrate cartilage is slightly concave where the lamina orbitonasalis overlaps it. The palatoquadrate cartilage narrows posteriorly, running along the dorsolateral edge of the mesopterygoid (an ectopterygoid is absent) before reaching the anterodorsal corner of the quadrate. The palatine in *Aplochiton zebra* is similar to that in *A. taeniatus* except that the anterior cartilage appears to be short and knob-like and only abuts the maxilla and lateral prenasal process of the maxilla (see Chapman 1944c; McDowall 1969).

The palatine in *Lovettia sealii* is poorly ossified. In my specimens the ossified central portion was not distinctly separate from the cartilage at the ends. Although the palatine lacks teeth and a dermopalatine, it differs from that in *Aplochiton* because the autopalatine is shorter anteroposteriorly, wider and more flattened posteriorly, and has a relatively small anterior cartilaginous knob that contacts only the maxilla and the lateral prenasal process of the ethmoid cartilage. In this respect it more closely resembles the palatine in the galaxiids. The palatoquadrate cartilage at the posterior end of the autopalatine also covers more of the anterior end of the mesopterygoid than in *Aplochiton*. The palatine in my specimens of *Lovettia* lacked the "lateral process similar to *Galaxias* [see my Fig. 26]" that McDowall (1969, p. 812) claimed was present. Chapman (1944c, p. 155) claimed that in *Aplochiton zebra* the palatine abuts "the vomer anteriorly." However, in *A. taeniatus* the two bones are separate.

Ectopterygoid

The ectopterygoid in *Aplochiton taeniatus* and *Lovettia* is absent. In its place is a prominent, relatively wide, tough ligament that extends from the posteroventral end of the lateral side of the autopalatine to the anterodorsal corner of the body of the quadrate. An ectopterygoid is absent in *A. zebra* according to Chapman (1944c) and McDowall (1969); however, they do not mention the ligament. McDowall (1969, p. 812) claimed that *Lovettia* had "a small, splint-like ectopterygoid" that lies between, but does not contact, the palatine or quadrate (see his fig. 3D). However, since parts of the ligament often take on a slightly red colour after the suspensorium is stained with alizarin red it is possible that McDowall was mistaken.

Mesopterygoid

The mesopterygoid in *Aplochiton taeniatus* is a long, moderately narrow, relatively thin, tooth-bearing bone (see Fig. 25). The dorsal surface is concave and slopes dorsomedially toward the parasphenoid, from which it is separated by a relatively wide band of connective tissue. The bone is widest at about its posterior third where it is separated from the body of the quadrate by a wide band of cartilage. It narrows towards its posteromedial corner, which projects posterior to the anterodorsal corner of the metapterytoid. The mesopterygoid is separated from the metapterygoid by a narrow band of cartilage. From its widest part the mesopterygoid tapers gradually anteriorly. Its anterior end is medial to, but does not contact, the autopalatine. A ligament extends from the anterior end of the mesopterygoid to the posterolateral corner of the vomer.

Along the anteromedial edge of the ventral surface of the mesopterygoid is a single row of eight large, sharply pointed, equally spaced functional teeth that are all about the same size. The area bearing the teeth is slightly thickened relative to the rest of the mesopterygoid. All the teeth curve distinctly anterolaterally and oppose a series of similarly shaped, but posterodorsally directed teeth on the basihyal (the teeth are found only along the edge of the basihyal; the basibranchial tooth-plate is edentulous). The posterior teeth on the basihyal are about the same size as those on the mesopterygoid; however, the anterior ones are much larger. This is unlike in the Osmeridae, Plecoglossidae, Retropinnidae, and Prototroctidae, in which the ventral teeth on the mesopterygoid are directed only laterally and oppose either the basibranchial and basihyal teeth or only the basibranchial teeth, but never only the basihyal teeth. The teeth on the basihyal and basibranchials in the latter four families are also more numerous, found on all parts of the basihyal and basibranchial tooth plates, and in most cases curve dorsomedially. Between most of the functional teeth in *A. taeniatus* are smaller replacement teeth. *A. zebra* also apparently has eight functional teeth that are similar to those in *A. taeniatus* (see Chapman 1944c).

The mesopterygoid in *Lovettia sealii* is similar in shape to that in *Aplochiton taeniatus* but is slightly shorter anteroposteriorly; its anterior tip barely reaches the posterior end of the autopalatine. *Lovettia* also has only four functional teeth on the mesopterygoid. However, they are larger relative to the rest of the suspensorium, and curved even more sharply anterolaterally, than in *Aplochiton*.

Quadrate

The quadrate in *Aplochiton taeniatus* is much longer anteroposteriorly than dorsoventrally (see Fig. 25). The body is small relative to the rest of the bone and separated from the mesopterygoid and metapterygoid by a [illegible] band of cartilage. The body is short dorsoventrally and extended posterodorsally so [illegible] angle formed by the posterior edge of the body is much shallower than the one formed by the anterior edge. The anteroventrally projecting condyle is moderately robust; its anterolateral edge curving somewhat posteroventrally. Perhaps this is what Chapman (1944c, p. 156) meant when he stated that in *A. zebra* "The ventral end of the quadrate condyle is somewhat produced and projects into the oral cavity almost like a large tooth." The facet of the condyle is broad and somewhat elliptical in shape with the lateral side expanded and distinctly larger than its medial side. The quadratojugal arm is very long (about twice as long as the body is wide), moderately wide, and tapers slightly posteriorly. The arm is grooved ventrally for the reception of the anterodorsal edge of the ventral limb of the preoperculum. The quadrate notch is moderately deep and moderately narrow. The quadrate in *A. zebra* appears similar to that in *A. taeniatus* (see Chapman 1944c).

The quadrate in *Lovettia* is similar to that in *Aplochiton* except that it is relatively poorly ossified, the body does not project posterodorsally (and therefore the anterior and posterior edges form about the same angle), and the condyle and its facet are smaller (the lateral side of the facet is not expanded).

Symplectic

The symplectic in *Aplochiton taeniatus* is moderately long and wide, with a distinct central bend (see Fig. 25). There is a narrow lamina along most of the dorsal edge and a short, narrow lamina along the mid-ventral edge. The posterior end is very broad and separated from the greatly expanded ventral end of the ventral arm of the hyomandibular by a broad expanse of cartilage. The symplectic narrows towards its anterior end, which is capped by a cartilaginous knob that extends nearly to the condyle of the quadrate. Most of the symplectic sits snugly in a groove on the dorsomedial surface of the quadratojugal arm of the quadrate. The symplectic in *A. zebra* is similar (see Chapman 1944c).

The symplectic in *Lovettia sealii* is more similar in shape to that in *Retropinna* than to that in *Aplochiton*. It is a moderately short but wide bone that has a slight central bend. It lacks dorsal and ventral lamina. The posterior end is only moderately expanded and is more widely separated from the ventral end of the ventral arm of the hyomandibular by cartilage than in *Aplochiton*. The symplectic narrows only slightly towards its anterior end, which ends posterior to the posterodorsal corner of the body of the quadrate. The anterior end is capped by a large cartilaginous knob that extends nearly to the condyle of the quadrate. As in *Aplochiton* and *Retropinna* most of the symplectic rests in a groove on the dorsomedial surface of the quadratojugal arm of the quadrate.

Metapterygoid

The metapterygoid in *Aplochiton taeniatus* is a small but thick bone with an unusual shape (see Fig. 25). Virtually the entire bone is endochondral in origin. Anteriorly it is separated from the mesopterygoid and quadrate by cartilage. The palatoquadrate cartilage extends around its entire anterior edge. The anterior part is triangular, with a rounded anterior edge and a posterodorsally directed apex. It is slightly convex laterally and curved slightly dorsomedially. Beginning at the apex of the triangular portion, the bone extends posteriorly as a moderately long narrow posterior tube-like section that is capped at its posterior end by a small cartilaginous knob. The posterior end of the "tube" and the cartilaginous knob overlap the lateral surfaces of part of the hyomandibular-symplectic cartilage and the anteroventral corner of the ventral arm of the hyomandibular. The only dermal portion is a narrow lamina that extends along the posteroventral edge, from the anteroventral corner of the triangular portion to near the middle of the posterior tube-like extension. The dorsal edge of the triangular portion extends posteroventrally onto the medial side of the posterior tube-like extension as a short, narrow ridge along which part of the *adductor arcus palatini* inserts. The metapterygoid in *Aplochiton zebra* is similar in shape to that in *A. taeniatus*; however, apparently it does not overlap the hyomandibular, extending only to the posterior end of the symplectic (see figures in Chapman 1944c and McDowall 1969).

The metapterygoid in the two specimens of *Lovettia sealii* that I cleared and stained, was weakly ossified and had an indistinct outline. It had the same shape as in *Aplochiton* (i.e., triangular) and was located at the posterior end of the palatoquadrate cartilage (which extended towards the hyomandibular as a finger-like extension, as in *Lepidogalaxias*). The metapterygoid was smaller than in *Aplochiton* and unlike it, slightly overlapped the posterodorsal surface of the mesopterygoid. The metapterygoid and the posterior end of the palatoquadrate cartilage were separated from both the symplectic and hyomandibular by a gap. A similar, apparently ossified metapterygoid was illustrated by McDowall (1969, fig. 3D).

Hyomandibular

The hyomandibular in *Aplochiton taeniatus* is a large, broad, and robust; the width is about two thirds the length (see Fig. 25). The cartilaginous condyle on the dorsal edge of the head forms a straight and tight joint with the skull. Its posterior quarter to third rests in a moderately shallow groove on the anteroventral surface of the pterotic. The anterior three quarters to two thirds rests entirely in a relatively large area of cartilage between the sphenotic, prootic, and pterotic. The anterolateral corner is separated from the posteroventral edge of the sphenotic by a moderately wide band of cartilage. The anteromedial corner approaches a rounded notch on the mid-dorsal edge of the prootic, but is separated from it by a narrow band of cartilage. The articulation with the skull appears similar in *A. zebra* (see Chapman 1944c; McDowall 1969).

The head of the hyomandibular is large, broad, and narrows only slightly ventrally. The opercular arm is long, broad, and robust and is capped posteriorly by a large cartilaginous knob that rests in a facet on the anterodorsal corner of the operculum. Distinct posterodorsal and posteroventral laminae are present. The anterior lamina is greatly reduced and is represented by a narrow band extending along the anterior edge of the hyomandibular from near the anterodorsal corner of the head to the dorsal third of the ventral arm. The ventral arm is moderately long and broad. It is constricted dorsally but enlarges ventrally so that its posterior end is greatly expanded. The lateral strut is moderately robust, moderately long and narrow, and curves in an arc that extends posterodorsally from the mid-dorsal surface of the ventral arm to near the middle of the posterior third of the opercular arm. The strut projects laterally (and slightly ventrally) from the body of the hyomandibular and its anterodorsally facing surface serves as part of the insertion area for the *levator arcus palatini*. The posterior corner of the lateral strut approaches, but does not contact, the anterior edge of the dorsalmost part of the dorsal limb of the preoperculum. This differs from the condition in *Aplochiton zebra* in which the strut apparently abuts the dorsal limb (see McDowall 1969). The canal for the hyomandibular branch of the facial nerve is moderately short, narrow, and is inclined slightly posteroventrally from the medial to the lateral foramina. The medial foramen is small and located at the intersection of the anteroventral corner of the head and the anterior lamina. The lateral foramen is about the same size and located at the middle of the dorsalmost part of the ventral arm, directly anterior to the anteroventral corner of the lateral strut. When it exits from the lateral foramen the nerve runs ventrally along the lateral surface of the ventral arm before running anteriorly.

The hyomandibular in *Lovettia sealii* is weakly ossified, moderately large, and about as wide as it is long. The posterior end of the skull where the hyomandibular articulates is poorly ossified and the sphenotic, prootic, and pterotic bones are indistinct. Consequently, the head sits entirely in cartilage, but in the same position as in *Aplochiton*. McDowall (1969, fig. 2) illustrates a small sphenotic, prootic, and pterotic and an articulation area similar to that in *Aplochiton*. The head of the hyomandibular is similar in shape to that in *Aplochiton* but is even broader relative to the rest of the bone. The posterodorsal lamina appears to be incorporated into the head since the entire dorsal part of the opercular arm is continuous with the posterior end of the head. A posteroventral lamina, anterior lamina, and lateral strut are absent. The absence of a lateral strut was also noted by McDowall (1969). Although the ventral arm is broad, it is abbreviated ventrally so that the length is only slightly greater than the width. It is not constricted dorsally and only slightly expanded ventrally. The canal for the hyomandibular branch of the facial nerve is similar to that described for *Aplochiton* except that it is [illegible]amina are larger.

Preoperculum

The preoperculum in *Aplochiton taeniatus* is similar to that described for *Retropinna* and *Prototroctes* (see Fig. 25). It is moderately thin and flat and has dorsal and ventral limbs that meet at about a right angle (very slightly obtuse). The ventral limb is longer than the dorsal limb and tapers anteriorly. The dorsal limb (it is about three quarters the length of the ventral limb) tapers dorsally, extending to the posterodorsal corner of the opercular arm of the hyomandibular. The anterior lamina is moderately large and extends along the anterior edge of the preoperculum from the middle of the ventral limb to about a third of the way from the dorsal tip of the dorsal limb. The middle of the lamina overlaps the posterolateral surface of the hyomandibular-symplectic cartilage. The dorsal limb is separated from the ventral arm of the hyomandibular by a wide gap. As described for the Osmeridae, Retropinnidae, and Prototroctidae the bony, lateral sensory canal is open along the entire length of the preoperculum. There is no suprapreoperculum. A similar preoperculum is found in *A. zebra* (see Chapman 1944c; McDowall 1969).

The preoperculum in *Lovettia sealii* is weakly ossified and is very thin and delicate. It is narrower than in *Aplochiton* and the limbs meet at a slightly obtuse angle. The ventral limb is longer than the dorsal limb but does not extend as far anteriorly as in *Aplochiton*. The dorsal limb extends to the posteroventral corner of the opercular arm of the hyomandibular. Both limbs taper towards their ends. The anterior lamina is small, restricted to the intersection between the two limbs, and overlaps the posterolateral surface of the hyomandibular-symplectic cartilage. The dorsal limb is separated from the posterior edge of the ventral arm by a moderately wide gap. The bony, lateral sensory canal is open as in *Aplochiton*. There is no suprapreoperculum.

FAMILY GALAXIIDAE

The family Galaxiidae contains six genera with thirty-seven species: *Galaxias*, with twenty-four species; *Galaxiella*, with three species; *Paragalaxias* with four species; *Nesogalaxias* with one species; *Neochanna*, with three species; and *Brachygalaxias*, with two species (see McDowall 1968, 1969, 1970, 1971a, 1973, 1984; McDowall and Frankenberg 1981). Although the family is moderately speciose and exhibits considerable ecological diversity, it is relatively homogeneous osteologically. The suspensorium, in particular, varies little amongst its members, with the main differences being proportional rather than structural. Because of this I will describe the suspensorium in detail in only one species, the widely-distributed *Galaxias maculatus*, and then compare it to the other galaxiids that I cleared and stained (*Galaxias brevipinnis, G. paucispondylus, Brachygalaxias bullocki*, and *Neochanna apoda*), and to other galaxiids described in the literature.

The suspensorium in *G. maculatus* is moderately long, robust, bears teeth on the mesopterygoid, and lacks sculpture (see Fig. 26). It was similar in the other galaxiids examined except that in *Neochanna apoda* it was even more robust and lacked teeth on the mesopterygoid.

Palatine

The palatine in *Galaxias maculatus*, like in the Aplochitonidae, is relatively small and lacks both teeth and a dermopalatine (see Fig. 26). The autopalatine is moderately short anteroposteriorly, relatively wide mediolaterally, and flattened dorsoventrally. The anterior end is slightly expanded dorsoventrally, elliptical in cross-section, and is capped by a mode[illegible] cartilaginous knob that projects anteriorly. The anterolateral side and most of the an[illegible] end of this cartilage overlap a well-developed facet on the anteromedial side of the maxilla, while the posteromedial side is distinctly concave where it receives the lateral prenasal process of the ethmoid cartilage. In one specimen [illegible] 26) a short, splint-like spur extended posteriorly from the posterolateral corner [illegible] autopalatine towards the quadrate. A narrow, laterally projecting dermal flange extends along most of the lateral edge of the autopalatine. A corresponding, but wider medially projecting flange extends along the medial side. The posterior end of the autopalatine is expanded mediolaterally but flattened dorsoventrally. Emanating from the posterior end is the palatoquadrate cartilage. As in *Aplochiton*, the palatoquadrate cartilage is flattened dorsoventrally (but even more so), does not extend dorsally to meet the lamina orbitonasalis of the ethmoid cartilage, and expands posteromedially to cover the dorsolateral surface of the mesopterygoid posterior to the anterior end of the bone. The lamina orbitonasalis and the lateral ethmoid bone are unusually large and greatly expanded laterally, overlapping the dorsal surface of the anterior part of the mesopterygoid and the palatoquadrate cartilage, and projecting lateral to the lateral edge of the anterior part of the suspensorium. Unlike in *Aplochiton taeniatus*, there is no trace of a concavity on the dorsal surface of the palatoquadrate cartilage where the lamina orbitonasalis overlaps it. The ventral part of the distal end of the lamina orbitonasalis is rounded and rests in a concavity on the medial side of a large wing that forms the anterodorsal part of the lachrymal bone, forming a joint. A large cupped wing on the lachrymal was absent in the other galaxiids I examined, but is apparently present in *Nesogalaxias neocaledonicus* (see Frankenberg 1969; Rosen 1974). The wing is either reduced or absent in the other galaxiids (pers. obs.; also see Frankenberg 1969); however, in the ones I examined the lamina orbitonasalis still contacted the medial surface of the lachrymal. As in the Aplochitonidae, the palatoquadrate cartilage narrows posteriorly, running along the dorsolateral edge of the mesopterygoid (the ectopterygoid is absent) before reaching the anterodorsal corner of the quadrate.

The palatine is similar in the other galaxiids and is invariably toothless (pers. obs.; also see Frankenberg 1969; McDowall 1969; Rosen 1974; Andrews 1976). One of the most variable characters is the presence or absence of the posterolateral spur. In *Galaxias paucispondylus* the autopalatine lacked a posterolateral spur, the bone was short, not expanded at its ends, and lacked distinctive medial and lateral dermal laminae. McDowall (1969) noted the absence of a spur in this species; however, the other differences may be related to the relatively small size of my specimen (56 mm versus a commonly attained size of 80 to 85 mm according to McDowall 1970). The palatine in *Brachygalaxias bullocki* had the same shape as in *G. maculatus* but was entirely cartilaginous; again perhaps related to the small size of my specimen (27 mm; McDowall 1971a, found few longer than 50 mm). The palatine in *Neochanna apoda* was more robust than in the other galaxiids, with wide medial and lateral dermal laminae, a long posterolateral spur, and a smaller cartilaginous knob at the anterior end. The palatine in *G. brevipinnis* differed in no significant way from that in *G. maculatus* and had a posterolateral spur.

Ectopterygoid

As in *Aplochiton*, an ectopterygoid was absent in *Galaxias maculatus* and the other galaxiids. No galaxiid is reported to possess an ectopterygoid (see Frankenberg 1969; McDowall 1969). As in the Aplochitonidae, in its place there is a prominent, relatively wide, tough ligament that extends from the posteroventral end of the lateral side of the autopalatine (from the posterolateral spur if it is present) to the anterodorsal corner of the body of the quadrate (see Fig. 26).

Mesopterygoid

The mesopterygoid in *Galaxias maculatus* is a moderately large, moderately thick, tooth-bearing bone that is nearly elliptical (see Fig. 26). Unlike the Aplochitonidae, the dorsal surface is flat to slightly concave and slopes dorsomedially at a steeper angle toward the parasphenoid, from which it is separated by a moderately wide band of connective tissue. The bone is widest just posterior to its centre where it is separated from the body of the quadrate by a moderately wide band of cartilge. It narrows gradually to its posterior end, which is rounded and barely overlaps the medial surface of the anterodorsal corner of the metapterygoid. From its widest part the mesopterygoid narrows gradually anteriorly, its slightly rounded anterior end lying medial to the posteromedial corner of the autopalatine. A ligament extends from the anterior end of the mesopterygoid to the posterolateral corner of the vomer.

As in the Aplochitonidae, along the anteromedial edge of the ventral surface of the mesopterygoid there is a single row of seven or eight, large, pointed, equally spaced functional teeth that are all about the same size, and curve anterolaterally. Between most of these are smaller replacement teeth. The functional teeth are slightly shorter, not as pointed, and are directed less distinctly anterolaterally than those in the Aplochitonidae. The dentition on the basihyal and basibranchial tooth-plates, and the bite formed between the basihyal and mesopterygoidal teeth are as described for *Aplochiton*, except that the basihyal teeth are smaller.

The mesopterygoid is similar in the other galaxiids. Differences concern mainly the relative size and robustness of the bone and the dentition (pers. obs.; also see Frankenberg 1969; McDowall 1968, 1969, 1970, 1971a, 1973; McDowall and Frankenberg 1981; Rosen 1974; Andrews 1976). *Galaxias brevipinnis* is similar to *G. maculatus* except that there is a gap between the mid-lateral edge of the bone and the palatoquadrate cartilage. In *G. paucispondylus* the mesopterygoid was smaller than in the other galaxiids examined, and its posterior end was widely separated from the metapterygoid, extending posteriorly only to the middle of the body of the quadrate. In addition, the teeth on the mesopterygoid were fewer in number (four on one bone, six on the other) and weaker than in *G. maculatus*. In *Brachygalaxias bullocki* the mesopterygoid was even smaller than in *G. paucispondylus*, extending posteriorly only to the anterior edge of the quadrate. Only the anteromedial tooth-bearing corner was well ossified. Its ventral surface bore a single row of well-developed teeth (seven on one bone and eight on the other) similar to those in *G. maculatus*. The mesopterygoid in *Neochanna apoda* was larger (overlapping the medial surface of the anterodorsal part of the body of the quadrate as well as the metapterygoid) and more robust than the other galaxiids. It lacked teeth.

Almost all galaxiids possess teeth in a single row on the ventral surface of the anteromedial side of the mesopterygoid (see Frankenberg 1969; McDowall 1968, 1969, 1970, 1971a, 1973; McDowall and Frankenberg 1981; Andrews 1976). However, the degree of development, and number of teeth vary from species to species. Teeth are few in number and sometimes absent in *Galaxias cleaveri* (see Andrews 1976; McDowall and Frankenberg 1981). Mesopterygoidal teeth are also either absent or few in number in the genus *Neochanna*. According to McDowall (1970, p. 396) they are "poorly developed and few in number, or lacking" in *N. burrowsius*, lacking in *N. apoda*, and usually lacking in *N. diversus* (in one specimen that he examined there was a single tooth on each mesopterygoid).

Quadrate

The quadrate in *Galaxias maculatus* is moderately large and robust (see Fig. 26). As in the Aplochitonidae, it is longer anteroposteriorly than dorsoventrally. The body is is larger and more robust than in *Aplochiton*. The condyle is as in *Aplochiton* but larger. The quadratojugal arm is long, wide, and expanded posteriorly where it broadly overlaps the ventral limb of the preoperculum. The arm is deeply grooved ventrally for the reception of the anterodorsal edge of the ventral limb of the preoperculum. The quadrate in the smaller specimen of *Galaxias maculatus* examined (UAMZ 4609, 101.1 mm SL) was slightly less robust, had a slightly smaller body, and a slightly narrower quadratojugal arm than the larger one (UAMZ 4609, 117.9 mm SL, see Fig. 26).

The quadrate in the other galaxiids has the same basic shape as in *Galaxias maculatus*; however, there are a number of differences. In *G. brevipinnis* the condyle is very large relative to the rest of the bone, the body is small, the angles formed by the anterior and posterior edges are steep, and the quadratojugal arm is larger relative to the rest of the bone. The quadrate in *G. paucispondylus* resembles that in *G. maculatus* except that the condyle is larger relative to the rest of the bone. In *Brachygalaxias bullocki* the quadrate is as described for *G. maculatus* except that the body is smaller and separated from the mesopterygoid and metapterygoid by a wider band of cartilage. The quadrate in *Neochanna apoda* was larger and more robust than in the other galaxiids. The medial surface of the anterodorsal part of the body is widely overlapped by the mesopterygoid while the posterodorsal edge of the body is separated from the metapterygoid by only a narrow band of cartilage. Along the anteroventral edge of the body is a small anterodorsally projecting finger of bone that serves as part of the insertion area for the ligament that replaces the ectopterygoid. The condyle has the same shape as in *G. maculatus* but is much larger relative to the rest of the quadrate, and projects farther anteroventrally away from the body. The quadratojugal arm is relatively short (it is about as long as the quadrate is deep) but wide with a very deep ventral groove for the reception of the anterodorsal edge of the ventral limb of the preoperculum.

Symplectic

The symplectic in *Galaxias maculatus* is relatively large, moderately long and wide, and has a slight central bend (see Fig. 26). There are moderately wide dorsal and ventral laminae along most of the length of the bone. The laminae were narrower in the smaller specimen (UAMZ 4609, 101.1 mm SL). The posterior end is broad and separated from the expanded ventral end of the ventral arm of the hyomandibular by cartilage. The symplectic narrows abruptly to its anterior end, which is very narrow relative to the posterior end. It is capped by a small cartilaginous knob that rests in a small concavity near the posterior end of the condyle of the quadrate. The symplectic fits tightly in a groove on the dorsomedial side of the quadratojugal arm of the quadrate, filling the entire quadrate notch. The blunt anterodorsal edge abuts the posterior edge of the body of the quadrate (but not in the smaller specimen). The posterodorsal edge abuts the anteroventral edge of the metapterygoid; its posteriormost edge actually rests in a groove on the mid-ventral edge of the metapterygoid.

The symplectic in the other galaxiids examined differed little from that described for *Galaxias maculatus* (also see Frankenberg 1969). Differences concerned the size of the laminae and the relationship of the anterodorsal edge with the posterior edge of the body of the quadrate (for instance, in *G. brevipinnis* the edges were adjacent but did not contact one another). In the two smallest specimens (*G. paucispondylus* and *Brachygalaxias bullocki*) the anterior end was wider relative to the posterior end and had a larger cartilaginous knob than in the larger specimens.

Metapterygoid

The metapterygoid in *Galaxias maculatus* is a relatively small and robust bone that consists of an anterior endochondral section and a posterior dermal laminar section (see Fig. 26). The endochondral section is axe-shaped like in *Aplochiton* with a posterodorsally directed apex. The palatoquadrate cartilage extends around the entire anterior edge of the endochondral section. The laminar section is relatively large and extends posterodorsally from the apex of the endochondral section to contact the hyomandibular. In the larger specimen (see Fig. 26) a moderately narrow, short, laterally projecting ridge extended from the apex of the endochondral section posterodorsally to about the middle of the dermal lamina. Part of the *levator arcus palatini* inserts on the dorsal side of this ridge. In the smaller specimen the ridge was rounded and indistinct. The posterior edge of the dermal lamina is blunt and fits tightly against the anterior edge of the hyomandibular from the anteroventral corner of the ventral arm to about the middle of the anterior lamina. Thus the entire ventral edge of the metapterygoid is tightly braced against both the hyomandibular and symplectic (see symplectic section). A small notch on the posteroventral corner of the dermal lamina serves as the passageway for one of the cheek nerves. The posteroventral part of the dermal lamina overlaps the lateral surface of the anterodorsal part of the ventral arm of the hyomandibular and abuts the anteroventral corner of the lateral strut. In the larger specimen (~~see Fig.~~ 26) there was a moderately wide ventromedially directed flange on the medial side of the metapterygoid between the posterior tip of the mesopterygoid and the anteroventral corner of the hyomandibular. Part of the *adductor arcus palatini* inserts along and dorsal to this flange.

The metapterygoid in the other galaxiids is basically the same as in *Galaxias maculatus* (pers. obs.; also see Frankenberg 1969; McDowall 1969; Rosen 1974). In *Neochanna apoda* it is more robust, has a reduced dermal lamina, lacks lateral or medial ridges, and has a squarish shape. Its posterior edge closely abuts the posterodorsal edge of the symplectic and the anterior edge of the hyomandibular, but does not overlap the lateral surface of the hyomandibular or contact the lateral strut as in *Galaxias maculatus*. The metapterygoid in *Galaxias brevipinnis* is similar in size and shape to that in *Neochanna apoda* but differs in that the endochondral section is relatively small and the posterior dermal lamina is large and well-developed. Lateral and medial ridges are lacking. The posterior edge is thickened and closely abuts the posterodorsal edge of the symplectic and the wide anterior edge of the hyomandibular (from the anteroventral corner of the ventral arm to the middle of the anterior lamina). The posteriormost corner abuts the anteroventral corner of the lateral strut of the hyomandibular as in *G. maculatus*. The metapterygoid in *Brachygalaxias bullocki* is as described for *G. maculatus* except that the dermal lamina does not overlap the lateral surface of the hyomandibular or contact the lateral strut, there do not appear to be lateral or medial ridges, and the bone is widely separated ~~from the~~ posterior end of the mesopterygoid. In *Galaxias paucispondylus* the metapterygoid is small and shaped like the one in *Neochanna apoda*. It has a greatly reduced dermal lamina. It is widely separated from the posterior end of the mesopterygoid by a gap, and widely separated from the quadrate by an expanse of cartilage. Although it lies adjacent to the symplectic and hyomandibular, the metapterygoid does not contact either bone, unlike the other species examined. Frankenberg (1969, p. 23) stated that in the galaxiids the metapterygoid "usually braces the hyomandibular and symplectic," but noted that *Galaxiella pusilla* and *Galaxiella nigrostriata* were exceptions "in that the metapterygoid does not overlap the hyomandibular." Perhaps the character state in

Galaxias paucispondylus was related to the relatively small size of my specimen?

Hyomandibular

The hyomandibular in *Galaxias maculatus* is a large and robust bone that is broad anteroposteriorly but relatively short dorsoventrally; the width is about equal to the length (see Fig. 26). The cartilaginous condyle on the dorsal edge of the head forms a long, straight, and tight joint with the skull. This joint appears to be more stable than the one in *Aplochiton* since there is closer contact with the sphenotic, prootic, and pterotic bones. The posterior two thirds to half of the condyle rests in a moderately deep groove on the anteroventral surface of the pterotic. This groore is bordered medially, laterally, and posteriorly by a continuous, moderately high ridge (less distinct in the other galaxiids examined) that is widest posteriorly. The anterior part of the condyle rests in cartilage between the sphenotic, prootic,and pterotic bones. Almost the entire anterolateral side closely abuts the posteroventral edge of the sphenotic while the anteromedial side rests along the mid-dorsal edge of the prootic.

The head of the hyomandibular is very broad anteroposteriorly, short dorsoventrally, and narrows only slightly ventrally. The robust opercular arm is very long, wide, and expanded posteriorly. Distinct posterodorsal and posteroventral laminae are present. Unlike *Aplochiton*, the posteroventral lamina extends from the posteroventral corner of the opercular arm to the posteroventral corner of the ventral arm. The anterior lamina is moderately wide and extends along the anterior edge of the bone from the anterodorsal corner of the head to the middle of the ventral arm. The ventral arm is moderately short (it is about the same length as the opercular arm) and broad. The lateral strut is robust, relatively wide, and curves in an arc that extends posterodorsally from the dorsal end of the ventral arm to the middle of the beginning of the opercular arm. It projects distinctly laterally from the body of the hyomandibular and widens posteriorly into a shelf whose anterodorsally facing surface serves as part of the insertion area for the *levator arcus palatini*. The posterior end of the strut approaches, but does not contact the anterodorsal edge of the dorsal limb of the preoperculum. The canal for the hyomandibular branch of the facial nerve is moderately short, moderately wide, and inclined posteroventrally from the medial to lateral foramina. The medial foramen is moderately large, round, and located at the intersection of the anteroventral corner of the head and the anterior lamina. The lateral foramen is about the same size and, as in *Aplochiton*, is located at the middle of the dorsalmost part of the ventral arm, but unlike *Aplochiton*, is directly posterior to the ventral end of the lateral strut.

The hyomandibular in the other galaxiids is basically the same as in *Galaxias maculatus*. Minor differences concern shape, the degree of development of the lateral strut, whether or not the strut contacts the dorsal limb of the preoperculum, and the position of the lateral foramen for the hyomandibular branch of the facial nerve relative to the lateral strut (pers. obs.; also see Frankenberg 1969; McDowall 1969; Rosen 1974). For instance, in *Neochanna apoda* and *Galaxias brevipinnis* the hyomandibular is distinctly wider than in *G. maculatus*, with an even shorter ventral arm. The lateral strut in *N. apoda* is also shorter anteroposteriorly, but is wider and projects farther laterally, abutting the anterodorsal edge of the dorsal limb of the preoperculum. Because the anterior end of the strut is abbreviated, the lateral foramen for the hyomandibular branch of the facial nerve is located directly medioventral to the ventralmost edge of the lateral strut. However, in the other galaxiids I examined the lateral foramen had the same position relative to the lateral strut as in *G. maculatus*. Frankenberg (1969, p. 23) noted similar variation regarding the lateral strut and lateral foramen when he stated that the lateral strut "may extend anteroventrally so that the foramen opens posterior to it, or on the other hand, only the posterior part of the wing [= lateral strut] may be developed so that the foramen is entirely anterior to the wing." In *Galaxias paucispondylus* and *Brachygalaxias bullocki* the lateral strut was longer anteroposteriorly than in the other species examined, extending from the middle of the ventral end of the ventral arm to the middle of the opercular arm. McDowall (1969, p. 805) claimed that in *G. paucispondylus* "the spur [= lateral strut] which projects outwards from the hyomandibular is very weak." However, this was not the case in my specimen. The articulation of the dorsal edge of the head of the hyomandibular with the skull was similar to *G. maculatus* in the other specimens except that in the two smallest ones (*G. paucispondylus* and *Brachygalaxias bullocki*) there was slighty more cartilage between the prootic and pterotic and less overlap with the pterotic.

Preoperculum

The preoperculum in *Galaxias maculatus* is similar to that in *Aplochiton* but is broader and more robust (see Fig. 26). The dorsal and ventral limbs meet at about a right angle (slightly acute). The ventral limb is only slightly longer than the dorsal limb and tapers slightly to a rather blunt anterior end. The dorsal limb tapers slightly to a a rounded dorsal end that is adjacent to the posterodorsal corner of the head of the hyomandibular. The anterior lamina is moderately large and restricted mainly to the intersection of the two limbs (the lamina extends along less of the anterior edge of the preoperculum than in most other salmoniforms). As in *Aplochiton*, the dorsal limb is separated from the ventral arm of the hyomandibular by a wide gap. As described for the Osmeridae, Retropinnidae, Prototroctidae, and Aplochitonidae the bony, lateral sensory canal is open along the entire length of the preoperculum. There is no suprapreoperculum.

The preoperculum in the other galaxiids is similar to that described for *Galaxias maculatus*. The two limbs are about the same length in *Neochanna apoda*; however, in *Galaxias brevipinnis*, *G. paucispondylus*, *Brachygalaxias bullocki*, and apparently *Nesogalaxias neocaledonicus* (see Rosen 1974, see fig. 13A), the dorsal limb is shorter than the ventral limb and extends only to the dorsal edge of the opercular arm of the hyomandibular. The angle formed by the intersection of the two limbs is slightly acute in *G. brevipinnis*, nearly a right angle in *Neochanna apoda*, and slighty obtuse in *G. paucispondylus*, and *Brachygalaxias bullocki*. Frankenberg (1969, p. 20) noted that in the galaxiids he examined the preoperculum was "usually in the form of a right-angle with the arms about equal length," but that in some species the dorsal limb was shorter and the angle more obtuse. The anterior lamina had the same basic shape in the other galaxiids but the size varied from very large in *G. brevipinnis* to moderately small and not reaching the hyomandibular-symplectic cartilage in *G. paucispondylus*, *B. bullocki*, and *N. apoda*. The preoperculum in *Neochanna apoda* was more robust, broader, and had a wider anterior flange than the other galaxiids.

FAMILY ARGENTINIDAE

The family Argentinidae contains only *Argentina*, with twelve species, and *Glossanodon* with nine species. The species are relatively similar ecologically and morphologically (see Cohen 1958a, 1970; Cohen and Atsaides 1969; Parin and Shcherbachev 1982). The fossil argentinid, *Glossanodon musceli*, is very similar to extant species of the genus *Glossanodon* according to Jerzmańska (1967).

The description that follows is of *Argentina silus*. Its suspensorium is moderately robust and greatly elongated centrally where the very large eye rests (see Fig. 27).

Palatine

The palatine in *Argentina silus* is a relatively long, moderately robust, tooth-bearing bone that closely abuts the anterior end of the snout (see Fig. 27). The autopalatine and dermopalatine are imperceptibly fused to each other. The autopalatine is perceived to be the bony portion, with a cartilaginous core, that makes up the anterodorsal part of the palatine. It abuts the snout anteriorly and is continuous with the palatoquadrate cartilage posteriorly. The dermopalatine includes the tooth-bearing section ventral to the autopalatine, and the large dorsoventrally inclined posterior laminar extension that broadly overlaps the anterolateral surface of the ectopterygoid. The posterior end of the autopalatine is flattened mediolaterally but expanded dorsoventrally. The palatoquadrate cartilage emanates posteriorly from the posterior end of the autopalatine, expands dorsally and mediolaterally to contact the lamina orbitonasalis (of the ethmoid cartilage) and overlie both the anterodorsal surface of the mesopterygoid and the dorsolateral surface of the ectopterygoid, and then narrows posteriorly. The anterior part of the palatine is expanded mediolaterally but is relatively flat dorsoventrally, lacks a cartilage at its anterior end, and has a porous appearance. It is somewhat "claw-like", curving anteroventrally (and slightly medially at the same time) towards the anterior end of the snout, which it closely abuts. The dorsolateral surface of the anterior part is moderately concave, and rises dorsomedially to a sharp ridge whose d[illegible] edge projects slightly dorsolaterally. This ridge extends along the dorsomedial edge of the autopalatine, from near the anterior end to the beginning of the posterior dorsoventral expansion. The anteromedial side of the ridge is distinctly concave for the reception of the moderately small, bulb-like lateral prenasal process of the ethmoid cartilage that rests on the mid-lateral edge of the mesethmoid bone. The ethmoid cartilage narrows anteriorly from the lateral prenasal process and then expands medially to cover the dorsal surface of the anterolateral side of the vomer. The entire medial edge of the palatine anterior to its contact with the lateral prenasal process abuts the anterolateral edge of the vomer (and the cartilage on its surface). The two bones are also connected to one another by tough connective tissue. A tough ligament extends from the anterior tip of the palatine to the anterolateral corner of the vomer.

The ethmoid ossifications anterior to the lateral ethmoid bone are unusual, and deserve comment because they relate to the unique bite mechanism that involves the palatine and vomerine dentition. The anterior ethmoid bones are fused into a single, broad, shield-shaped bone (called the mesethmoid by most workers) that is closely applied to the dorsal surface of the head of the vomer. The vomer is large, with a moderately long and wide posterior shaft, and a wide and robust anterior head that, unlike most teleosts, extends distinctly anterior to the anterior edge of the mesethmoid. The blunt anterior edge of the mesethmoid abuts a similar, but posterior facing edge on the raised mid-dorsal part of the vomer (the edges are slightly separated by cartilage), firmly bracing the two bones. The anterior part of the ethmoid cartilage extends around the entire anterior edge of the mesethmoid, contacting the palatine and overlapping the vomer as described previously.

Extending along the anteroventral edge of the vomer is a single row of about twenty moderately small, sharply pointed, closely spaced, posteroventrally directed teeth. On the adjacent anteroventral surface of the lateral edge of the palatine is a band of about twenty posteromedially directed, closely spaced teeth that extend to the anterior tip of the bone. They are in a single row posteriorly but in two rows anteriorly. The teeth on the vomer and palatine are all about the same size and shape. In the specimens of *A. silus* that Cohen (1958a, p. 119) examined there were "about 25 teeth on each palatine and about 18 teeth on the head of the vomer", in a "band ... from 1 to 3 teeth wide." Because the palatine and vomerine teeth are closely spaced and the two bones closely abut one another, a continuous U-shaped biting surface is formed around the anteroventral edge of the snout (see Fig. 28). These teeth oppose a sharp ridge on the anterodorsal edge of the edentulous dentary, and form the primary bite of the anterior end of the snout since both the premaxillae and maxillae lack teeth. There are large, sharply pointed, posterodorsally directed teeth around the edge of the anterior end of the greatly elongated basihyal (the rest of the basihyal and the basibranchials are edentulous); however, these oppose the edentulous, posteroventral surface of the vomer and not the palatine-vomerine dentition.

The palatine, the anatomy of the anterior end of the snout, and the bite are similar in other species of the genus *Argentina* (see Chapman 1942a; Cohen 1958a, 1964; Cohen and Atsaides 1969). One of the main differences is apparently the number of teeth and tooth rows. For example, in *A. brucei* there are about seventy teeth on each palatine and fifty-five on each vomer in two to five rows, whereas *A. silus* represents the other extreme (see Cohen 1958a, 1964; Cohen and Atsaides 1969). Cohen (1958a) noted that teeth are present on the dentary in larvae, but not juveniles or adults of *A. silus* and *A. sialis*.

Judging from the literature, although the palatine and the anatomy of the anterior end of the snout in *Glossanodon* appear basically similar to *Argentina*, there are notable differences (see Cohen 1958a, 1964, 1970; Cohen and Atsaides 1969; Greenwood and Rosen 1971; Parin and Shcherbachev 1982). In *Glossanodon* the mesethmoid is narrower than in *Argentina*, but its relationship to the vomer is the same (see Greenwood and Rosen 1971, fig. 21). The teeth on the palatine and vomer are also smaller, fewer in number, more widely spaced, and generally found in less regular rows. The vomerine teeth are located farther posteriorly on the bone than in *Argentina*, and are easily distinguished from the palatine teeth because, according to Cohen (1958a, p. 143) "an area of unossified cartilage generally separates the two bones." The basihyal teeth (when present) are distinctly smaller than in *Argentina* and located only at the anterior edge of the wide basihyal. The primary bite in *Glossanodon*, however, appears to be the same as in *Argentina* in that the palatine-vomerine dentition opposes the dentary (dentary teeth are present in adults, except for *G. pygmaeus*), and the maxilla and premaxilla are toothless. *Glossanodon pygmaeus* is unlike the other members of the genus because, according to Cohen (1964, p. 21), "The tooth-bearing areas of [the] palatines [are] poorly ossified; [and] the anteriormost portion of the bone [is] a thin, tooth-bearing plate; [that is] present in the same body of cartilage as the main body of the ossified palatine but not connected to it by bone." Its vomer is also poorly ossified, especially at its anterior end.

Ectopterygoid

The ectopterygoid in *Argentina silus*, is a straight, nearly rectangular, moderately robust, laminar-like bone that is relatively short anteroposteriorly but wide dorsoventrally (see Fig. 27). It broadly overlaps the surrounding bones, tightly bracing the palatine with both the posterior part of the suspensorium and the lateral ethmoid bone. Unlike most salmoniforms there is a small posteriorly directed flange on the posterolateral surface that slightly overlaps the anterolateral surface of the body of the quadrate. Projecting dorsally (and slightly posteriorly) from the mid-lateral part of the main body of the ectopterygoid is a unique "pear-shaped" laminar extension that is slightly convex laterally. Its narrow dorsal tip overlaps the lateral surface of the posteroventral corner of the lamina orbitonasalis of the ethmoid cartilage. A strong ligament also extends from the dorsal tip of the extension to the ventral part of the lateral ethmoid bone, further bracing it to the ethmoid region of the skull. Except for its dorsal tip, its entire medial surface overlaps the palatoquadrate cartilage.

The ectopterygoid in *Argentina sphyraena* is similar to that described for *A. silus* except that, judging from Chapman's figure (1942a, fig. 3), the "pear-shaped" extension is wider and overlaps both the lateral surface of the quadrate and palatine. The ectopterygoid in the other argentinids is not mentioned in the literature.

Mesopterygoid

The mesopterygoid in *Argentina silus* is unusually large, lacks teeth, and broadly overlaps the surrounding bones (see Fig. 27). It is greatly elongated anteroposteriorly, broad mediolaterally, but at the same time moderately thin and pliable. The broad posterior end is concave on its dorsomedial surface and slopes dorsomedially toward the parasphenoid, from which it is separated by a moderately wide band of connective tissue. The posterolateral side of the bone is inclined dorsoventrally (slighty laterally) and is covered laterally by the part of the palatoquadrate cartilage that extends between the quadrate, symplectic, and metapterygoid. On the concave portion between the dorsal part of the body of the quadrate and the metapterygoid is an unusual, long, elliptical, grainy-looking area of heavier ossification. Chapman (1942a) noted a similar feature in *Argentina sphyraena*.

The mesopterygoid in *A. sphyraena* is similar to that described for *A. silus* but appears slightly shorter anteroposteriorly judging from Chapman's (1942a) figure. The mesopterygoid is apparently edentulous in all argentinids (see Cohen 1958a, 1964, 1970; Cohen and Atsaides 1969; Parin and Shcherbachev 1982).

Quadrate

The quadrate in *Argentina silus* is a moderately large, moderately robust bone that is firmly braced against the surrounding bones (see Fig. 27). The body is shaped almost like a semicircle, with a broad, rounded dorsal edge, and anterior and posterior edges that are nearly level with the horizontal. The anterior edge is crenulated where it overlaps the ectopterygoid. The body is broadly attached to the condyle and the anterior end of the quadratojugal arm. The condyle is of a moderate size with an elliptical facet that is expanded laterally. The condyle is turned upwards so that the articular surface faces anteriorly, contacting the posteriorly facing facet on the angulo-articular bone of the lower jaw, and forming a relatively tight joint. When the mouth is in the normal position (at least in specimens preserved in alcohol or cleared and stained), a straight line, parallel with the horizontal, can be drawn anteriorly from the posterior end of the ventral limb of the preoperculum, along the dorsal edge of the limb (and along the lower arm of the symplectic and the quadratojugal arm of the quadrate, which are closely attached and parallel to the limb), through the condyle of the quadrate and along Meckel's cartilage nearly to the anterior end of the lower jaw.

The quadratojugal arm is moderately long, moderately wide when viewed dorsally (but narrow when viewed laterally), and tapers posteriorly to a point. The arm is grooved ventrally for the reception of the wide, rounded, anterodorsal edge of the ventral limb of the preoperculum. The quadrate notch is shallow but moderately wide. The quadrate has a small amount of sculpture on the condyle and on the ventral part of the body.

The quadrate in *Argentina sphyraena* is similar to that described for *A. silus* (see Chapman 1942a). The bone in the extinct species *Glossanodon muscell* is similar but apparently has a broader body, a shorter quadratojugal arm and lacks a quadrate notch (see Jerzmańska [illegible]).

Symplectic

The symplectic in *Argentina silus* is a long and narrow bone with a distinct central bend (see Fig. [illegible]). The anterior half is aligned horizontally with the ventral limb of the preoperculum while the posterior half is aligned anteroventrally with the ventral arm of the hyomandibular. The posterior end is only slightly wider than the anterior end, and is only about half the width of the ventral end of the ventral arm of the hyomandibular. The anterior half of the symplectic rests securely in a shallow groove on the dorsal surface of the quadratojugal arm of the quadrate. The anterior end is capped by a cartilaginous knob that rests securely in a concavity at the anterior end of the quadrate notch. The anterior end of the symplectic (excluding the cartilaginous knob) barely reaches the posterodorsal corner of the body of the quadrate and is a long distance from the condyle. At the angle formed by the intersection of the two halves of the symplectic is a moderately wide dorsal lamina and a trace of a ventral lamina.

The symplectic in *Argentina sphyraena* is similar to that described for *A. silus* (see Chapman 1942a). The bone in the extinct species *Glossanodon muscell* is also typical of the family according to Jerzmańska (1967).

Metapterygoid

The metapterygoid in *Argentina silus* is a very small, relatively thin and flat, triangular bone that bridges the gap between the mesopterygoid and the hyomandibular (see Fig. 27). It is entirely endochondral in origin except for dermal laminae that extend along the medial and lateral edges. The shape is reminiscent of the metapterygoid in *Aplochiton*. The wide anterior end overlaps the middle of the posterodorsal edge of the mesopterygoid and the lateral surface of both the posterodorsal corner of the symplectic and the anterodorsal surface of the hyomandibular-symplectic cartilage. The palatoquadrate cartilage emanates anteriorly from the anterior edge of the metapterygoid. The narrow posterior end overlaps the lateral surface of the anteroventral corner of the ventral arm of the hyomandibular. Its posterior tip is capped by a tiny cartilaginous knob.

The metapterygoid in *Argentina sphyraena* is similar to that described for *A. silus* (see Chapman 1942a). The metapterygoid in the other argentinids is not mentioned in the literature.

Hyomandibular

The hyomandibular in *Argentina silus* is a moderately robust bone that is relatively long and narrow; the width is about half the length (see Fig. 27). It is unusual in that the ventral part (represented by the ventral arm, lateral strut and anterior lamina) is bent sharply anteroventrally relative to the dorsal part (compare to Fig. 15 for contrast). The cartilaginous condyle on the dorsal edge of the head is moderately long and narrow and forms a straight and tight joint with the skull. Its posterior half rests in a moderately deep groove on the anteroventral surface of the pterotic. This groove is bordered medially, laterally, and posteriorly by a continuous, moderately high ridge that is widest posteriorly. The anterior half of the condyle rests in cartilage between the sphenotic, prootic, and pterotic bones. The anterolateral corner abuts the posteroventral edge of the sphenotic while most of the anteromedial side rests along the mid-dorsal edge of the prootic.

Although the head is relatively broad anteroposteriorly, it is short dorsoventrally, and narrows only slightly ventrally. The opercular arm is moderately long, and is capped posteriorly by a cartilaginous knob that rests in a facet on the anterodorsal corner of the operculum. The anteroventrally inclined ventral arm is long, relatively narrow, and expanded slightly ventrally. There is a distinct posterodorsal lamina but virtually no posteroventral lamina. The anterior lamina is moderately wide and extends from the anterodorsal corner of the head to about the middle of the anterior edge of the ventral arm. A long, moderately wide posterolaterally inclined lateral strut extends from the intersection of the opercular arm and the head, to the middle of the ventral end of the ventral arm The canal for the hyomandibular branch of the facial nerve is moderately long, moderately wide, and inclined posteroventrally from the medial to the lateral foramina. The moderately large medial foramen is located at the intersection of the anterior lamina and the middle of the anterior edge of the head. The lateral foramen is smaller and located about the middle of the posterior side of the lateral strut, opposite, and slightly ventral to the posterior apex of the anterior lamina. Its location is unusual because it is located distinctly ventral to the opercular arm rather than at its anteroventral corner.

The hyomandibular in *Argentina sphyraena* is similar to that described for *A. silus* (see Chapman 1942a). The bone in the extinct species *Glossanodon musceli* is also apparently typical of the family according to Jerzmańska (1967).

Preoperculum

The preoperculum in *Argentina silus* is a relatively large and robust bone with dorsal and ventral limbs that meet at about a right angle (see Fig. 27). There is no suprapreoperculum. The ventral limb is longer than the dorsal limb. The dorsal limb is about three quarters the length of the ventral limb and tapers dorsally, extending to the posterodorsal corner of the head of the hyomandibular. The middle of the anterior edge of the dorsal limb closely abuts the posterolateral edge of the dorsal part of the lateral strut of the hyomandibular, to which it is attached by connective tissue. The anterior lamina is large and slightly convex laterally. It extends along the anterior edge of the preoperculum from the [illegible] of the ventral limb to the middle of the dorsal limb, overlapping the posteroventral [illegible] of the symplectic, the ventral part of the hyomandibular-symplectic cartilage, and the posteroventral corner of the ventral arm of the hyomandibular.

The bony, lateral sensory canal on the ventral limb is completely open ventral to a moderately wide, ventrolaterally projecting flange that extends anteroposteriorly along nearly the entire limb. Because the ventral limb medial to this flange projects ventromedially, an open, ventral facing trough extending the length of the bone is visible when the limb is viewed ventrally (the limb appears relatively narrow when viewed laterally because of this feature). The canal on the dorsal limb is enclosed in bone, but opens to the exterior via a pore at each end (the ventral pore opens into the posterior end of the trough on the ventral limb), and at the end of two wide, funnel-shaped auxiliary canals ~~that lead~~ off of the main canal.

The preoperculum in *Argentina sphyraena* is similar to that described for *A. silus* (see Chapman 1942a). The preoperculum in the extinct species *Glossanodon musceli* has the same basic shape as that of *A. silus* (see fig. 7 in Jerzmańska 1967). It may have had an open sensory canal since Jerzmańska (p. 201) states that "Préopercule grand ... portant au milieu les traces distinctes des canaux sensoriels, sous forme de deux sillons typiquement courbés," which translated means, "Preoperculum large, bearing distinct traces in the middle of sensory canals, in the form of two typically curved grooves."

FAMILY BATHYLAGIDAE

The Bathylagidae debatably contains the genera *Bathylagus, Nansenia, Microstoma,* and *Xenophthalmichthys*. Except for the former two genera (see Chapman 1943, 1948a), detailed osteological information is lacking.

The description that follows is of *Bathylagus pacificus*. Its suspensorium is moderately short but deep, moderately delicate, and bears teeth only on the palatine (see Fig. 29). The suspensorium in *Nansenia schmitti* is similar, but also resembles *Argentina* in several ways (see Chapman 1948a). Bertelsen (1958) described the postlarva of *Xenophthalmichthys* and noted that (p. 5) "In position and shape the opercular bones of the jaws and hyoid arch are very similar to those of *Nansenia schmitti* as described by Chapman (1948, p. 9 fig. 4)," but does not elaborate.

Palatine

The palatine in *Bathylagus pacificus* is a relatively short but deep, tooth-bearing bone that curves slightly anteroventrally at its anterior end (see F[illegible]9). The dermopalatine is easily distinguished from the autopalatine. It is a tiny, flat, spongy-looking, triangular structure that rests in a concavity on the medial side of the anteroventral corner of the autopalatine (refer to Fig. 29). Its medial side appears to be fused to the autopalatine. It bears a single row of six, small, rather blunt teeth on its ventral edge that are directed slightly anterolaterally. The autopalatine makes up the rest of the palatine. Although the autopalatine is flattened mediolaterally along its entire length (unlike *Argentina* in which the anterior end is expanded mediolaterally) it expands dorsoventrally from an anterior point to a broad, fan-like posterior end. There is a very tiny cartilage on the dorsal edge of the anterior tip. The palatoquadrate cartilage emanates posteriorly from the posterior end of the autopalatine, overlapping the anterodorsal surface of the mesopterygoid and the dorsolateral surface of the ectopterygoid before reaching the quadrate. Unlike *Argentina*, but like *Nansenia* (see Chapman 1948a), the cartilage extends posteriorly only to the posterodorsal corner of the body of the quadrate. The lamina orbitonasalis of the ethmoid cartilage lies dorsal to the [illegible] end of the palatine, abutting the palatoquadrate cartilage just as the latter exits [illegible] the posterodorsal corner of the palatine. This is unlike *Argentina* and the opisthoproctids in which this contact is distinctly posterior to the palatine (compare Figs. 29 with Figs. 27, 31). The posteroventral corner of the palatine rests securely in a trough on the anterodorsal end of the ectopterygoid (see ectopterygoid for details concerning this structure).

The palatine closely abuts the anterior end of the snout, as in *Argentina*, except that the connection is firmer and more extensive (compare Figs. 29, 30 with Figs. 27, 28). The entire dorsomedial side of the bone firmly abuts the ethmoid cartilage in *Bathylagus*, beginning posteriorly at the lamina orbitonasalis and extending anteriorly to the anterolateral corner of the ethmoid cartilage adjacent to the vomer (a distinct lateral prenasal process is lacking on the ethmoid cartilage, unlike *Argentina*). Because the ethmoid cartilage is sandwiched between the mesethmoid dorsally, and the vomer ventrally, and projects slightly lateral to the lateral edges of both bones, the palatine does not directly contact either the vomer or mesethmoid.

As in *Argentina*, the vomer projects anterior to the anterior edge of the mesethmoid. Extending along the entire thickened, spongy-looking, anteroventral edge of the vomer is a single row of seventeen teeth that are similar to those on the palatine, but project anteroventrally. Because the palatine and vomerine teeth are closely spaced and the two bones closely abut one another, a continuous U-shaped biting surface is formed around the anteroventral edge of the snout (see Fig. 30), as in *Argentina*. These teeth oppose a series of tiny, sharply pointed, triangular teeth on the anterodorsal edge of the dentary, and form the primary bite of the anterior end of the snout, since like *Argentina*, both premaxillae and maxillae lack teeth. The basihyal and basibranchials are edentulous. A short, but tough ligament extends from the anterior tip of the palatine to the anterolateral corner of the vomer, filling the narrow gap between the palatine and vomerine teeth. Some of Chapman's (1943) observations regarding the palatine and its relationship to the vomer in *B. pacificus* differ from mine, mainly I believe because he did not refer to cleared and stained specimens, and mistook the dermopalatine for the anterolateral part of the vomer (which it lies adjacent to and closely resembles). Although he claimed that the vomerine teeth (p. 148) "are set in sockets in bone," this was not the case in my specimen.

The palatine in *Nansenia schmitti*, including its relationship to the anterior end of the snout, is similar to *B. pacificus* (see Chapman 1948a). Although detailed information is lacking for the other bathylagids, the palatine and vomer are apparently basically the same, with primary differences concerning the number of teeth and their shape (e.g., see Beebe 1933; Bertelsen 1958; Cohen 1958b, 1964; Borodulina 1968).

Ectopterygoid

The ectopterygoid in *Bathylagus pacificus* is straight, short anteroposteriorly, and roughly elliptical (see Fig. 29). Although it is separated from the mesopterygoid by a relatively wide band of cartilage, it firmly braces the palatine with the quadrate. Dorsally, it is split into lateral and a medial flanges, forming a trough that encloses the anterior end of the body of the quadrate and the posteroventral end of the palatine. The lateral surface bears a lattice-like network of moderately wide ridges that extend anteroposteriorly.

The ectopterygoid in *Nansenia* is larger than in *Bathylagus*, nearly filling the gap between the quadrate and palatine (see Chapman 1948a, fig. 4). Although it overlaps the lateral surface of the latter two bones, it is unclear from Chapman whether or not their medial surface is overlapped as well. The ectopterygoid resembles the one in *Argentina* in that it also sends a dorsal projection toward the lateral ethmoid. The ectopterygoid in the other bathylagids is not described in the literature.

Mesopterygoid

The mesopterygoid in *Bathylagus pacificus* is moderately large, thin, roughly pear-shaped, and lacks teeth (see Fig. 29). It broadly overlaps the dorsomedial surface of the body of the quadrate and slightly overlaps the posteromedial surface of the palatine. It is inclined less sharply towards the parasphenoid than in *Argentina* and most other salmoniforms (i.e., its dorsal surface faces more laterally than is usually the case).

The mesopterygoid in *Nansenia schmitti* is similar to that in *B. pacificus* (see Chapman 1948a).

Quadrate

The quadrate in *Bathylagus pacificus* is similar to that described for *Argentina silus* except that the body is more semicircular with a very broad, rounded dorsal edge, and anterior and posterior edges that are virtually level with the horizontal (see Fig. 29). The quadratojugal arm is also shorter anteroposteriorly (but wider mediolaterally) and a quadrate notch is absent.

The quadrate in *Nansenia schmitti* is similar to that in *B. pacificus* except that the quadratojugal arm is longer (see Chapman 1948a).

Symplectic

The symplectic in *Bathylagus pacificus* is shorter and has more of a central bend than in *Argentina silus* (see Fig. 29). The anterior end and its cartilaginous knob barely overlap the quadratojugal arm of the quadrate, and are posterior to the posterior edge of the body of the quadrate. There is a gap between the dorsal edge of the symplectic and the mesopterygoid, but the two are joined by connective tissue.

The symplectic in *Nansenia schmitti* is more similar to that in *Argentina silus* than to *B. pacificus* (see Chapman 1948a): it is long and narrow, is bent to the same degree, and its anterior end (excluding the cartilaginous knob) just barely reaches the posterodorsal corner of the body of the quadrate. Unlike *Argentina* and *Bathylagus*, it appears to lack a dorsal lamina (see fig. 4 in Chapman). Like *Bathylagus*, its dorsal edge apparently does not contact either the mesopterygoid or metapterygoid.

Metapterygoid

The metapterygoid in *Bathylagus pacificus* is very tiny and thin (see Fig. 29). It slightly overlaps the posterior end of the mesopterygoid. The triangular endochondral portion is widest anteriorly where it is capped by a small cartilaginous knob. In some of Chapman's (1943) specimens a metapterygoid was absent; however, when present it was tiny and did not overlap any of the surrounding bones.

The metapterygoid in *Nansenia schmitti* is similar in size and shape to that in *Argentina silus* except that the posterior end is even narrower and does not overlap the ventral arm of the hyomandibular (see Chapman 1948a).

Hyomandibular

The hyomandibular in *Bathylagus pacificus* is similar to that described for *Argentina silus* except that the ventral part is not bent sharply anteroventrally relative to the dorsal part, the anterior lamina is smaller, and the dorsal end of the lateral strut is expanded and curves anterolaterally, providing a larger area for muscle insertion and origin (see Fig. 29). The canal for the hyomandibular branch of the facial nerve in *B. pacificus* is narrower than in *A. silus*, the lateral foramen is more dorsally located, and the medial foramen is located more ventrally and obscured by a dorsoventrally running flange that projects anteromedially.

The hyomandibular in *Nansenia schmitti* resembles that in *B. pacificus* (including apparently the unusual shaped lateral strut), but is like *Argentina silus* in that the ventral part is bent sharply anteroventrally relative to the dorsal part (see Chapman 1948a).

Preoperculum

The preoperculum in *Bathylagus pacificus* is smaller than in *Argentina silus* and has limbs of equal length (see Fig. 29). The ventral limb is only slightly trough-like when viewed ventrally. As in *A. silus*, the bony, lateral sensory canal on the ventral limb is completely open ventral to a moderately wide flange. The dorsal limb is also enclosed in bone, but opens to the exterior via foramina of varying sizes that open directly along the posterior edge of the closed canal. There are no auxiliary canals.

The preoperculum in *Nansenia schmitti* is broader and more laminar than either *Bathylagus* or *Argentina* (see Chapman 1948a). In this respect it resembles the opisthoproctids. The ventral limb is longer than the dorsal limb, and bears a sensory canal that is open along its entire length, as in the latter two genera. The canal on the dorsal limb is enclosed in bone, and opens to the exterior via a pore at the dorsal end, and via a pore at each end of two moderately long auxiliary canals that lead off of the main canal at its ventral end. The preoperculum in *Xenophthalmichthys* evidently lacks auxiliary canals, but judging from Bertelsen's drawing (1958, fig. 5) no more can be stated with certainty.

FAMILY OPISTHOPROCTIDAE

The Opisthoproctidae contains six genera with at least twelve species: *Bathylychnops*, with one or more species; *Dolichopteryx*, with six or more species; *Macropinna*, with one species; *Opisthoproctu*. with two species; *Winteria*, with one species; and *Rhynchohyalus*, with one species. The former two genera are long-bodied, the next three are short-bodied, and *Rhynchohyalus* is intermediate (see Cohen 1964). This difference appears to be reflected in the proportions of the suspensorium (pers. obs.). Otherwise, the species are relatively similar osteologically.

In the account that follows, *Macropinna microstoma* (a short-bodied form) is described in detail and compared to *Dolichopteryx longipes* (a long-bodied form) and *Opisthoproctus soleatus* (a short-bodied form). Detailed information is lacking for the other opisthoproctids. The suspensorium in *M. microstoma* (see Fig. 31) and *O. soleatus* is moderately short anteroposteriorly but deep dorsoventrally, whereas in *D. longipes* (see Fig. 32) it is very long anteroposteriorly but relatively short dorsoventrally (reminiscent of *Argentina* in this respect). It is moderately delicate in all three species and lacks sculpture. In the opisthoproctids most of the anteromedial side of the suspensorium closely abuts the snout (including the palatine, the anterior half of the palatoquadrate cartilage, and in some species, the mesopterygoid) rather than just the palatine as in the argentinids and bathylagids.

Palatine

The palatine in *Macropinna microstoma* is a small, tooth-bearing bone with a shape similar to that in *Bathylagus pacificus* (see Fig. 31). As in the argentinids and bathylagids, the anterior end is not expanded dorsoventrally, lacks a cartilage, and curves anteroventrally.

It is flattened mediolaterally along its entire length, as in *B. pacificus*, but is even thinner. The autopalatine and dermopalatine are imperceptibly fused to one another.

As in *B. pacificus*, the entire dorsomedial side of the palatine closely abuts the anterolateral side of the snout (see Figs. 31 and compare to Fig. 29). However, in *M. microstoma* and the other opisthoproctids the connection is even more secure. The palatine contacts the snout in the same way as in *B. pacificus* except that it directly contacts the vomer and mesethmoid (mainly via flanges), as well as abutting the lateral edge of the ethmoid cartilage (as in *B. pacificus*, a lateral prenasal process is lacking). Unlike *B. pacificus*, the anterior tip of the palatine actually meshes with the anterolateral edge of the vomer, further stabilizing the connection.

The ventral surface of the anterolateral side of the palatine bears a series of about thirty small, sharply pointed, closely spaced, posteromedially directed teeth that are arranged in about three irregular rows (see Fig. 33). In the specimen of *M. microstoma* that Chapman (1942b) examined there were (p. 281) "twelve teeth ... in a patch ... arranged irregularly in a double row." The vomer projects anterior to the anterior edge of the mesethmoid as in the Argentinidae and Bathylagidae. Extending along the entire anteroventral edge of the vomer are a large number of teeth, similar to those on the palatine, that curve posteroventrally. There were at least forty teeth in the anterior row and perhaps an equal number distributed irregularly posterior to it (Chapman noted that there were forty teeth in one irregular row in his specimen). Because the anterior tip of the palatine and the anterolateral corner of the vomer overlap, and teeth extend to their edges, a continuous U-shaped biting surface extends around the entire anteroventral edge of the snout, as in the Argentinidae and Bathylagidae (see Fig. 33). However, unlike the latter two groups, the vomer, palatine, and their teeth are virtually indistinguishable where the two bones join. The teeth oppose a sharp ridge, bearing a few very tiny teeth, on the anterodorsal edge of the dentary, forming the primary bite of the anterior end of the snout. The premaxillae, maxillae, basihyal, and basibranchials lack teeth in all opisthoproctids (see Cohen 1964). Premaxillae are absent in *M. microstoma*.

The anterior part of the palatoquadrate cartilage in the opisthoproctids has a unique relationship with the anterior end of the snout that is unlike that in the Argentinidae and Bathylagidae. The lamina orbitonasalis of the ethmoid cartilage is located more posterior, relative to the other bones of the suspensorium, than in the latter two families. In *M. microstoma* and *Opisthoproctus soleatus* its contact with the palatoquadrate cartilage is level with the posterior end of the body of the quadrate. In *Dolichopteryx longipes* it was posterior to the body, and level with the middle of the quadratojugal arm. In *M. microstoma* the entire dorsomedial edge of the palatoquadrate cartilage anterior to its contact with the lamina orbitonasalis, underlies and closely abuts the ventrolateral edge of the ethmoid cartilage, further stabilizing the anterior end of the suspensorium with the snout (see Fig. 31). This feature was also found in *D. longipes* and *O. soleatus*; however, in these two species the medial edge of the mesopterygoid underlies the lateral side of the broad anterior end of the parasphenoid as well (the parasphenoid is relatively narrow anteriorly in *M. microstoma*, hence no overlap with the mesopterygoid).

The palatine and its relationship to the anterior end of the snout in *O. soleatus* and *D. longipes* is basically the same as in *M. microstoma*. Primary differences concern the number and size of the teeth on the vomer and palatine, and the degree of overlap of the palatine with the surrounding bones. The palatine in *O. soleatus* is even smaller than in *M. microstoma*, has fewer and smaller teeth (about three in a single row on each bone). The palatine in *D. longipes* was larger and more robust than in the other two species, and was more firmly attached to the vomer. It was impossible to separate the two bones without breaking them, mainly because the area on the palatines and vomer bearing the teeth is fused into a single, continuous tooth-plate (see Fig. 32). The teeth are also longer, more sharply pointed, and more numerous. Extending posteroventrally from the posteroventral corner of the palatine is a dorsoventrally inclined laminar wing (reminiscent of the one in *Argentina*) that overlaps the anterolateral surface of the ectopterygoid. Information for the other species is limited to the number and distribution of teeth on the vomer and palatines (e.g., see Cohen 1964).

Ectopterygoid

The ectopterygoid in *M. microstoma* is a relatively small, straight, elliptical bone that braces the palatine with the quadrate (see Fig. 31). It overlaps the medial surfaces of the quadrate (the anterior end of the body) and palatine (the posteroventral corner). It is separated from the mesopterygoid by a wide band of cartilage.

The ectopterygoid in *O. soleatus* is similar to that in *M. microstoma*. The ectopterygoid in *D. longipies* is larger than in the other two species and more broadly attached to the palatine and quadrate (see Fig. 32). Projecting dorsally from the mid-lateral surface of the main part of the ectopterygoid is an oval extension that overlaps the lateral surfaces of the palatine and quadrate. It is reminiscent of the structure in *Argentina* (see Fig. 27) but unlike it, is located anterior to the lateral ethmoid.

Mesopterygoid

The mesopterygoid in *M. microstoma* is moderately small and thin, roughly oval, lacks teeth, and extends anteriorly only to the middle of the body of the quadrate, whose dorsomedial surface it overlaps (see Fig. 31). Its dorsal surface is flat to slightly convex, and like *Bathylagus pacificus*, faces more laterally than is usually the case.

The mesopterygoid in *O, soleatus* is similar to that in *M. microstoma*. In *D. longipes* it is longer anteroposteriorly and its posterodorsal surface is slightly concave adjacent to the metapterygoid (see Fig. 32).

Quadrate

The quadrate in *M. microstoma* is similar to that described for *B. pacificus* but has a smaller condyle and a different shaped quadratojugal arm (see Fig. 31).

The quadrate in *O. soleatus* is similar to that in *M. microstoma*. In *D. longlpes* the condyle is smaller, and the quadratojugal arm longer and narrower than in the other two species (see Fig. 32).

Symplectic

The symplectic in *M. microstoma* is moderately long, has a moderate central bend, and has a relatively wide dorsal lamina (see Fig. 31). The anterior end and its cartilaginous knob are posterior to the body of the quadrate.

The symplectic in *O. soleatus* is similar to the one in *M. microstoma* but has a sharp central bend (the two halves meet at about a sixty degree angle). Partly because of this, the posterior tip of the symplectic is distinctly anterior to the ventral tip of the ventral arm of the hyomandibular, yet both lie on about the same horizontal plane. The ends of the bones are joined by a long, sinuous hyomandibular-symplectic cartilage (when straightened, it is nearly as long as the symplectic) that extends anteroposteriorly (also see fig. 7 in Trewavas 1933). The symplectic in *D. longipes* is straight, longer and narrower than in the other species, and lacks a dorsal lamina (see Fig. 32). Its posterior half is completely covered laterally by the anterior lamina of the preoperculum. The anterior tip of the bony part of the symplectic does not reach the posterior edge of the body of the quadrate. However, the cartilaginous knob at its end is long and rests in a groove between the body and the quadratojugal arm.

Metapterygoid

The metapterygoid in *M. microstoma* is absent (also see Chapman 1942b). The palatoquadrate cartilage narrows posteriorly to the area normally occupied by a metapterygoid (see Fig. 31).

In the specimen of *O. soleatus* examined the right side possessed a metapterygoid similar in size and shape to that in *B. pacificus* but it rested entirely on the mid-dorsal surface of the posterior end of the mesopterygoid. Trewavas (1933) does not report a metapterygoid in this species but Parr (1937) apparently does according to Chapman (1942b). In *D. longipes* there is a small, thin metapterygoid that narrows posteriorly (see Fig. 32). It rests on the dorsal surface of the posterolateral corner of the mesopterygoid and is overlapped along its ventrolateral edge by the anterior lamina of the preoperculum. It abuts the posterodorsal edge of the symplectic but does not contact the hyomandibular nor the hyomandibular-symplectic cartilage. The palatoquadrate cartilage emanates anteriorly from its anterior edge.

Hyomandibular

The hyomandibular in *M. microstoma* is a moderately robust bone that is relatively long dorsoventrally, but narrow anteroposteriorly (see Fig. 31). The head is small relative to the rest of the bone. The anterior two thirds of its cartilaginous condyle rests in cartilage between the sphenotic, prootic, and pterotic, rather than just the anterior half like in *Argentina silus* and *Bathylagus pacificus*. The opercular arm is short and blunt. There are narrow posterodorsal and posteroventral laminae. The narrow anterior lamina extends ventrally only to the dorsal end of the anterior edge of the long and narrow ventral arm. A moderately long, moderately wide, posterolaterally inclined lateral strut extends from near the anterodorsal corner of the head to the middle of the ventral arm. The canal for the hyomandibular branch of the facial nerve is relatively short and narrow. The medial foramen is more ventrally located than in *A. silus* and *B. pacificus*; it is at the intersection of the ventral part of the anterior lamina and the dorsal end of the ventral arm (see Fig. 31). The lateral foramen is located posterior to the lateral strut; it is about one half to two-thirds of the way down from the strut's dorsal tip. Like in *A. silus* the lateral foramen is distinctly ventral to the opercular arm. The hyomandibular illustrated for *M. microstoma* by Chapman (1942b, fig. 1) appears broader at its dorsal end than in my specimen.

The hyomandi[illegible]ar in *O. soleatus* is as described for *M. microstoma* but has a ventral arm that is excavated along its anterodorsal edge, and a much narrower lateral strut (it is more like a ridge). The hyomandibular in *D. longipes* is more robust and shorter dorsoventrally than the other two species (see Fig. 32). The head is relatively broad, but short dorsoventrally, and projects posterodorsally beyond the opercular arm. The ventral arm is shorter and broader than in the other species. The lateral strut is reduced; it is a small, short, posterolaterally inclined flange located at the dorsal end of the ventral arm. The elliptical lateral foramen is much larger than the medial one and is located along the entire dorsal half of the posterior side of the lateral strut.

Preoperculum

The preoperculum in *M. microstoma* is a very broad, moderately thin bone with dorsal and ventral limbs that meet at about a right angle (see Fig. 31). It was significantly larger than in the other salmoniforms examined. The ventral limb and the ventral part of the dorsal limb are greatly expanded (also see fig. 2 in Chapman 1942b). The ventral part of this expansion curves sharply ventromedially to meet (and overlap) its opposite near the ventral mid-line of the head, forming a shield that protects the ventral surface of the head. The anterior lamina is large and overlaps the symplectic and the ventral arm of the hyomandibular. Unlike the Argentinidae and Bathylagidae the entire bony, lateral sensory canal is open posterior to a narrow flange that runs along the entire length of the anterolateral surface of the preoperculum. A similar canal is found in *O. soleatus* and *D. longipes*.

The preopercula in *O. soleatus* and *D. longipes* are large, but are not expanded like in *M. microstoma*, and do not meet ventrally beneath the head. In *O. soleatus* the two limbs are about the same size, and the dorsal end of the dorsal limb covers the opercular arm and the posterior half of the head of the hyomandibular. In *D. longipes* the ventral limb is greatly elongated anteroposteriorly (see Fig. 32). The dorsal limb is half the length of the ventral one and its dorsal tip does not reach the opercular arm of the hyomandibular. The large anterior lamina broadly overlaps the surrounding bones. None of the three species examined had a suprapreoperculum.

FAMILY ALEPOCEPHALIDAE

The family Alepocephalidae contains twenty-five extant genera (if you synonymize *Binghamichthys* with *Talismania* as suggested by Markle 1976, and include *Leptochilichthys*) and about sixty species. There is one extinct species that is placed in its own genus, *Carpathichthys* (see Jerzmańska 1979).

In the account that follows, the suspensorium in *Talismania antillarum* is described in detail (see Fig. 34) and compared to the following species that were cleared and stained: *Alepocephalus bairdii* (see Fig. 35), *A. tenebrosus*, *Bathytroctes microlepis*, *Binghamichthys* (= *Talismania*) *aphos*, *Bajacalifornia burragei*, *Bathylaco nigricans* (see Fig. 36), *Narcetes stomias* (see Fig. 37), *Rouleina maderensis* (see Fig. 38), *Photostylus pycnopterus* (see Fig. 39), *Xenodermichthys copei* (see Fig. 40), *Leptoderma macrops* (see Fig. 41), and *Conocara mcdonaldi*. Reference was also made to the literature, especially Markle (1976).

As illustrated by the figures, the suspensorium in the Alepocephalidae shows considerable osteological diversity. The suspensorium in *Talismania antillarum* is perhaps intermediate; it is moderately robust, moderately long, and has a few relatively small teeth on the palatine (see Fig. 34). The extremes are best illustrated by *Narcetes* (see Fig. 37) and *Leptoderma* (see Fig. 41). The suspensorium in many alepocephalids is similar to the one in the platytroctids (compare Figs. 34, 40 to Figs. 42, 43). Except for the palatine and symplectic, the bones of the suspensorium in the fossil *Carpathichthys* are well-preserved. They resemble those in various extant alepocephalids (see Jerzmańska 1979).

Palatine

The palatine in *T. antillarum* is a relatively long and narrow (mediolaterally), tooth-bearing bone (see Fig. 34). When *in situ*, and viewed dorsally, it is relatively straight and inclined only slightly anteromedially.

The small, narrow, splint-like dermopalatine is fused to the anteroventral surface of the autopalatine. It extends anteromedially from the anterior end of the autopalatine to underly the ventrolateral surface of the lateral prenasal process of the ethmoid cartilage. On the anteroventral surface of its lateral side is a single row of nine small, pointed, closely spaced teeth that point posteroventrally. On the adjacent anterolateral edge of the vomer is a tiny tooth-plate (not fused to the vomer) that bears two teeth similar to those on the palatine. The size of the dermopalatine, and tooth number and size vary from species to species within the genus *Talismania* (see Grinols and Heyamoto 1965; Sulak 1975).

The autopalatine is relatively flat mediolaterally and is expanded at its anterior and posterior ends. The anterior expansion is capped by a round cartilaginous knob that extends anterodorsally. Its articulation with the ethmoid cartilage and maxilla is as described for *Sagamichthys abei* (Platytroctidae). The palatoquadrate cartilage emanates from the posterior expansion, extending posteriorly to the mesopterygoid, and posterodorsally to the lamina orbitonasalis of the ethmoid cartilage.

The palatine in the other alepocephalids is variable (refer to Figs. 35-41). Overall, it resembles the palatine in the platytroctids (especially) and osmerids more than it does the other salmoniforms. The main differences among genera concern proportions and the presence or absence of a dermopalatine and/or its dentition. Palatine teeth have been reported in sixteen of the twenty-five genera that I include in the Alepocephalidae (see Marshall 1966; Nielsen and Larsen 1968; Markle 1976). There is a trend within the family for loss of teeth on the dermopalatine, and ultimately, loss of the dermopalatine itself. In the alepocephalids that I examined, a tooth-bearing dermopalatine that was fused to the autopalatine was found only in *T. antillarum* (see Fig. 34), *Narcetes* (see Fig. 37), and *Bathylaco* (see Fig. 36). In *Narcetes* there were about fifteen teeth in two irregular rows. In *Bathylaco* there were twenty irregularly distributed teeth on each palatine in a large specimen (USNM 206694, 227.8 mm SL), and eleven (USNM 200468, 56.2 mm SL) and six (SIO 64-15, 84.4 mm SL, see Fig. 36) teeth in an irregular row on each palatine in two smaller specimens. In *Alepocephalus* (see Fig. 35; also see Gosline 1969) and *Conocora* the dermopalatine is long, bears numerous sharply pointed teeth, and is closely applied, but not fused to the autopalatine. In contrast, in *Photostylus* (see Fig. 39) a small flat, oval, toothless dermopalatine was closely applied, but not fused to, the anteroventral surface of the autopalatine. A vestige of a dermopalatine (lacking teeth) was present in *Leptoderma* (see Fig. 41). *Bathytroctes, Rouleina* (see Fig. 38), *Xenodermichthys* (see Fig. 40), and *Binghamichthys* lacked both teeth and a dermopalatine.

The autopalatine also shows considerable variation within the family, mainly in regards to proportions (length, size of anterior and posterior expansions). Its shape is similar to *T. antillarum* in *Alepocephalus* (see Fig. 35), *Conocara, Leptoderma* (see Fig. 41), and

Bajacalifornia. The autopalatine is relatively short with relatively large anterior and posterior expansions in *Bathytroctes*, *Rouleina* (see Fig. 38), *Narcetes* (see Fig. 37), *Xenodermichthys* (see Fig. 40), and *Binghamichthys*. The autopalatine in *Photostylus* is relatively short but is only slightly expanded at its ends (see Fig. 39). In *Bathylaco* the autopalatine was smaller and shorter than in the other species examined (see Fig. 36).

Ectopterygoid

The ectopterygoid in *T. antillarum* is a large, boomerang-shaped bone that is bent centrally and overlaps the quadrate, mesopterygoid, and palatine (see Fig. 34). A moderately wide, dorsolaterally projecting flange extends along its dorsolateral surface between the quadrate and palatine (the posterior end of the palatine rests in the groove formed between the flange and the dorsolateral surface of the anterior end of the ectopterygoid).

The relative size and shape of the ectopterygoid in the Alepocephalidae is moderately variable (see Figs. 35-41). Nielsen and Larsen (1968) reported teeth on the "pterygoid" in four of the eleven specimens of *Bathylaco* that he examined. However, none of the alepocephalids (including *Bathylaco*) that I or Markle (1976) examined had teeth on the ectopterygoid.

The ectopterygoid in the extinct species *Carpathichthys polonicus* is basically the same as in extant alepocephalids such as *T. antillarum* (see Jerzmańska 1979).

Mesopterygoid

The mesopterygoid in *T. antillarum* is moderately thin, nearly elliptical, and lacks teeth (see Fig. 34).

The mesopterygoid in the other alepocephalids is similar to that in *T. antillarum*, differing only in relative size and shape (see Figs. 35-41). The mesopterygoid lacked teeth in all the specimens that I examined. None of the large number of alepocephalids that Markle (1976) studied had teeth on the mesopterygoid, including *Xenodermichthys copei*, in which Weitzman (1967a) reported them. None of the ten specimens of *X. copei* that I examined had mesopterygoidal teeth. The mesopterygoid in the extinct species *Carpathichthys polonicus* (see Jerzmańska 1979) also lacks teeth, and is roughly the same size and shape as in the extant alepocephalid *Rouleina* (see Fig. 38).

Basihyal and basibranchial teeth were absent in all the alepocephalids that I examined. With the exception of *Rinoctes nasutus*, no alepocephalid regularly has basihyal and/or basibranchial teeth (see Markle 1976; Markle and Merrett 1980). The basibranchial tooth-plate in *R. nasutus* has one median row of recurved teeth. *Bajacalifornia calcarata* sometimes has a single row of teeth along the midline of the basihyal. Because teeth are almost always absent on the basihyal, basibranchial, and mesopterygoid, the primary bite in the alepocephalids is between teeth on the dentary of the lower jaw and teeth on the premaxilla, maxilla, palatine, and vomer. However, the bones of the upper jaw that actually participate in the bite are variable since teeth may be present on only some of them, depending on the species (also see Markle 1976).

Quadrate

The quadrate in *T. antillarum* has a relatively large body, a narrow quadratojugal arm that tapers posteriorly, and a relatively small condyle with an oval facet that faces anteroventrally (see Fig. 34).

The quadrate in *Bajacalifornia*, *Xenodermichthys* (see Fig. 40), *Photostylus* (see Fig. 39), *Narcetes* (see Fig. 37), *Rouleina* (see Fig. 38), *Bathytroctes*, *Binghamichthys*, *Bathylaco* (see Fig. 36), and the fossil *Carpathichthys* (see Jerzmańska 1979, fig. 1) is similar to that in *T. antillarum* except that in the latter six genera the quadratojugal arm does not extend posterior to the body (as was also the case in the seven platytroctids examined). In contrast, the quadrate in *Alepocephalus*, *Leptoderma*, and *Conocara* has a relatively small body that is short dorsoventrally, a moderately large condyle, and a moderately long quadratojugal arm that extends posterior to the body (see Figs. 35, 41).

Symplectic

The symplectic in *T. antillarum* is long, narrow, and straight. Its anterior end is capped by a cartilaginous knob that fits in a notch at the posterior end of the quadrate condyle (see Fig. 34).

The quadrate in the other alepocephalids examined (and *Aulastomatomorpha*, see Lloyd 1906) is similar to that in *T. antillarum* (see Figs. 35-41). In *Conocara* there is a [illegible]tely wide dorsal lamina that overlaps the medioventral surface of the metapterygoid (there is a narrow dorsal lamina in *Leptoderma* but it does not overlap the metapterygoid). The anterior end of the symplectic in *Leptoderma* extends only to the posterior corner of the body of the quadrate (see Fig. 41). The symplectic in *Bathylaco* is short with a wide posterior end that narrows abruptly anteriorly (see Fig. 36).

Metapterygoid

The metapterygoid in *T. antillarum* is moderately large, robust, and lies posterodorsal to the quadrate (see Fig. 34). Except for a medial ridge (see later), the entire bone is endochondral in origin. It consists of a large, vertically inclined, ventral section that is slightly concave laterally, and a smaller anterodorsal section that projects dorsomedially to overlap the posterodorsal surface of the mesopterygoid. The palatoquadrate cartilage extends ventrally around its edge from the anterodorsal to posterodorsal corner. The cartilage at the posterior end of the metapterygoid abuts the posterodorsal edge of the symplectic and slightly overlaps the lateral surface of the anteroventral end of the hyomandibular. On the medial surface of the metapterygoid is a well-developed, sharp, dorsomedially projecting, dermal ridge that extends posteroventrally from near the anterodorsal corner to the posterior edge of the bone. The anterior part of the *levator arcus palatini* inserts along, and dorsal to, this ridge.

Although the metapterygoid varies somewhat in shape, size, and amount of overlap with the surrounding bones, it is basically as described for *T. antillarum* in the other alepocephalids (see Figs. 35-41; also Lloyd 1906 and Markle 1976). A medial dermal ridge of some form or another was present in all the specimens I examined. In the fossil

Carpathichthys the metapterygoid is rounded as in *Alepocephalus* (see Fig. 35 and Jerzmańska 1979). The metapterygoid in *Leptoderma* is smaller than the others and has a diffrent shape (see Fig. 41). The palatoquadrate cartilage does not extend in a continuous band around its edge. A medial ridge is present but reduced. None of the *levator arcus palatini* (LAP) inserts onto the metapterygoid in *Leptoderma*. The metapterygoid in *Conocara* is similar to *Leptoderma* but larger, with a better developed medial ridge. The LAP inserts onto the medial surface of the posterodorsal corner of the metapterygoid but not onto the medial ridge. The size, shape, and position of the metapterygoid in *Aulastomatomorpha* is similar to *Leptoderma* judging from Lloyd's (1906) figure.

Hyomandibular

The hyomandibular in *T. antillarum* is a moderately delicate bone that is relatively long and narrow (see Fig. 34). The posterior two-thirds of the cartilaginous condyle on the dorsal edge of the head rests in a moderately deep groove (bordered by a ridge) on the anteroventral surface of the pterotic, while the anterior third rests in cartilage between the sphenotic, prootic, and pterotic (abutting the edges of the former two bones).

The opercular arm is long, narrow, and capped posteriorly by a small cartilaginous knob. Distinct posterodorsal and posteroventral laminae are lacking. The anterior lamina is moderately narrow and extends along most of the anterior edge of the bone. The ventral arm is long, narrow, and only slightly expanded ventrally. A long and wide posterolaterally inclined lateral strut extends from near the posterodorsal corner of the head to the posteroventral corner of the ventral arm.

The dorsal part of the lateral strut is reinforced by a relatively wide rib that radiates diagonally from near the anterodorsal corner of the head to the strut's posterodorsal edge. Part of the *levator arcus palatini* inserts along this rib. Smaller ribs intersect the larger one and the dorsal part of the lateral strut at various points. On the medial surface of the hyomandibular are two moderately narrow ridges: one that runs dorsoventrally from the posterodorsal corner of the head to the middle of the ventral arm, and another that is inclined roughly anteroposteriorly and curves posteriorly from the anterodorsal corner of the head to join the other ridge at the beginning of the opercular arm. The *adductor arcus palatini* inserts along, and dorsal to the anteroposterior ridge.

The canal for the hyomandibular branch of the facial nerve is short and moderately narrow. The medial foramen is located at the ventral apex of the head, directly ventral to the anteroposterior ridge. The lateral foramen is about the same size and located posterior to the dorsal part of the lateral strut, slightly posteroventral to the medial foramen.

Although basically the same as in *T. antillarum*, the hyomandibular in the other alepocephalids shows considerable variation in regards to relative size, shape, and robustness (see Figs. 35-41; also Lloyd 1906 and Markle 1976). The hyomandibular in *Binghamichthys, Bajacalifornia, Bathytroctes, Rouleina* (see Fig. 38), and *Xenodermichthys* (see Fig. 40) is similar to that in *T. antillarum* (see Fig. 34). The most obvious difference concerns the size and shape of the anterior lamina. The hyomandibular in the aforementioned six genera is more similar to the one in the platytroctids than to that in the other alepocephalids. The hyomandibular in *Photostylus* is moderately short dorsoventrally, the anterior surface of the lateral strut faces anteromedially (rather than anterolaterally), and there are large posteroventral, posterodorsal, and anterior laminae (see Fig. 39). In *Bathylaco* the bone is extremely oblique, has a poorly-developed lateral strut, and a centrally located, posteroventrally inclined opercular arm that is continuous ventrally with the ventral arm (see Fig. 36). The hyomandibular in *Narcetes* (it is slightly oblique) and *Alepocephalus* is a moderately short (dorsoventrally) but wide (anteroposteriorly) bone with a large anterior lamina and an unusually well-developed lateral strut (see Figs. 37 and 35, respectively). In *Bathyprion* the hyomandibular is oblique, as in *Bathylaco*. However, unlike the other genera, the opercular arm in *Bathyprion* emanates from the lower third of the posterior side of the hyomandibular (see Markle 1976, fig. 9B). In *Leptoderma* the opercular arm is very long and located near the posterodorsal corner of the head (see Fig. 41). The lateral strut is reminiscent of that in the Galaxiidae and Aplochitonidae in that it is inclined posterolaterally and curves posterodorsally from the middle of the ventral arm to near the end of the opercular arm. Unlike the other genera, in *Leptoderma* there are no dorsoventral or anteroposterior medial ridges. Instead, a single, well-developed posterolaterally inclined medial ridge curves from the ventral corner of the anterior lamina to the middle of the posterior end of the opercular arm. The hyomandibular in *Conocara* is similar to the one in *Leptoderma* except that the opercular arm is more ventrally located, the lateral strut sends a branch to the posterodorsal corner of the head as well as to the opercular arm, and there is a narrow dorsoventral ridge on the medial side in addition to the curving ridge described for *Leptoderma*. The latter ridge is narrower in *Conocara* than in *Leptoderma*. The shape of the hyomandibular in *Aulastomatomorpha* is similar to that in *Leptoderma* and *Conocara* judging from Lloyd's (1906) figure. Although Markle (1976, p. 95) claimed that *Leptoderma* and *Conocara* had "a relatively indistinct opercular process [= opercular arm] on the hyomandibular," this was certainly not the case in my specimens. Perhaps the presence of a wide posterodorsal lamina in both genera, and the proximity of the opercular arm to the posterodorsal corner of the head, might give one the impression that the opercular arm is short? The hyomandibular in the fossil genus *Carpathichthys* (see Jerzmańska 1979) is well-preserved, and most closely resembles the one in *Narcetes* (see Fig. 37) among the genera illustrated (see Jerzmańska 1979).

Preoperculum

The preoperculum in *T. antillarum* is moderately large with dorsal and ventral limbs that meet at a slightly obtuse angle (see Fig. 34). The dorsal limb is slightly longer than the ventral limb. There is no suprapreoperculum. The anterior lamina is narrow and bordered posteriorly by a laterally projecting ridge that extends along the most of the anterolateral edge of the bone. The anterior lamina extends about half way along the anterior edge of the dorsal and ventral limbs. The lateral surface of the preoperculum has sculpturing that is reminiscent of that in *Sagamichthys abei* and the other platytroctids.

The bony, lateral sensory canal is open along most of the length of the preoperculum. The anterior flange that borders the open canal is wide along the ventral limb but narrows dorsally on the dorsal limb. The canal is closed at the dorsal end of the dorsal limb and partly closed at the intersection of the two limbs. At the intersection of the limbs, bridges of bone extend between the anterior flange and the lateral surface of the preoperculum in an irregular pattern, creating a partially closed canal. There are no auxiliary canals leading off of the main canal.

The preopercula in *Binghamichthys, Bathytroctes, Narcetes* (see Fig. 37), *Bajacalifornia, Alepocephalus* (see Fig. 35), *Rouleina* (see Fig. 38), *Xenodermichthys* (see Fig. 40), and *Photostylus* (see Fig. 39) are basically similar to that decribed for *T. antillarum* (see Fig. 34). The main differences between these genera concerns overall shape (e.g., the dorsal limb is very broad dorsally in *Bajacalifornia*), relative size of the anterior lamina (greatly reduced in *Xenodermichthys* and *Photostylus*), and the form of the bony, lateral, sensory canal (see later). The ventral limb in *Photostylus* is unusual in that it is inclined sharply anteroventrally relative to the dorsal limb (see Fig. 39). The preoperculum in *Bathylaco* (see Fig. 36) is small relative to the rest of the suspensorium, straight (it lacks dorsal and ventral limbs), closely applied to the posterior edge of the hyomandibular and symplectic, and inclined sharply anterodorsally (along with the hyomandibular and symplectic). In *Leptoderma* (see Fig. 41) and *Conocara* the preoperculum is long and narrow, the ventral limb is longer than the dorsal, and the anterior lamina is split into medial and lateral sections, between which originates part of the *adductor mandibulae*. The posterior edge of the preoperculum forms an arc in *Conocara*. The preoperculum in *Aulastomatomorpha* is similar to that in *Leptoderma* and *Conocara* judging from the figure in Lloyd (1906).

The character state of the bony, lateral sensory canal in the Alepocephalidae is variable (refer to Figs. 34-41). It is completely open in *Rouleina* (posterior to a moderately wide anterior flange), *Bathylaco* (relatively narrow anterior flange), *Xenodermichthys* (trace of an anterior flange), and *Photostylus* (no anterior flange). The canal in *Alepocephalus* (see Fig. 35), *Binghamichthys, Bathytroctes, Narcetes* (see Fig. 37), *Leptoderma* (see Fig. 41), *Conocara*, and *Aulastomatomorpha* (see Lloyd 1906) is partly closed with the location, number, and size of the foramina varying from genus to genus. Some species, such as

Narcetes and *Alepocephalus* (see Figs. 37 and 35, respectively), had several funnel-shaped auxiliary canals leading off a main canal that is closed at the interesection of the two limbs. The canal in *Leptoderma* (see Fig. 41), *Conocara*, and *Aulastomatomorpha* (see figure in Lloyd 1906) is open along most of the length of the bone; however, the posterior edge of the anterior flange has a scalloped appearance, and attaches to the lateral surface of the bone at several points. The canal in *Bajacalifornia* is reminiscent of that in the platytroctid *Sagamichthys abei* except that the ventral part of the canal is partly closed in the former.

The preoperculum in the fossil genus *Carpathichthys* is most similar in shape to the one in *Alepocephalus* (see Fig. 35) among the species illustrated, but is even broader and has a smooth posterior edge (see Jerzmańska 1979). It appears to have a very narrow anterior lamina and a bony, lateral sensory canal that is open along the entire length of the bone (posterior to a moderately wide anterior flange).

FAMILY PLATYTROCTIDAE

The family Platytroctidae (= Searsiidae) contains thirteen genera and thirty-seven species according to a recent revision by Matsui and Rosenblatt (1987). No fossil platytroctids are known.

In the account that follows, the suspensorium in *Sagamichthys abei* is described in detail (see Fig. 42) and compared to the following species that were cleared and stained: *Holtbyrnia latifrons*, *Searsia koefoedi* (see Fig. 43), *Searsioides multispinus* (see Fig. 44), *Platytroctes apus* (see Fig. 45), *Mirorictus taningi* (see Fig. 46), and *Pellisolus facilis* Reference was also made to the literature.

The suspensorium in *Sagamichthys abei* is moderately long, moderately robust, and has one tooth on the palatine and one of the mesopterygoid (see Fig. 42). Except for *Platytroctes*, it has the same basic shape in the other platytroctids (see Figs. 43-46). The suspensorium in *Holtbyrnia* is very similar to that in *Sagamichthys*, adding credibility to Matsui and Rosenblatt's (1987) hypothesis that the two genera are sister taxa. The platytroctids share a number of similarities with the alepocephalids (compare Figs. 42-46 with Figs. 34-41).

Palatine

The palatine in *Sagamichthys abei* is a moderately short and stout tooth-bearing bone (see Fig. 42). When *in situ*, and viewed dorsally, it is relatively straight and does not curve perceptibly anteromedially.

The dermopalatine is a small, thin, oval plate that is closely applied, but not fused with the anteroventral surface of the autopalatine. It bears a single, small tooth that points posteroventrally. The vomer has one tooth at its anterior end. In the large specimen that Parr (1960) examined (210 mm SL, versus 68.5 mm SL for mine) there were two teeth on the vomer and a group of about five on each palatine.

The autopalatine is expanded dorsoventrally at its anterior and posterior ends but is relatively flat mediolaterally. The anterior expansion is capped by a round cartilaginous knob that extends anterodorsally. The anterolateral side of this cartilage abuts a small cartilage covered knob on the anteromedial side of the maxilla while the anteromedial side closely abuts the ventrolateral surface of the lamina orbitonasalis of the ethmoid cartilage. The palatoquadrate cartilage emanates from the posterior expansion of the autopalatine, extending posterodorsally to abut the lamina orbitonasalis of the ethmoid cartilage and posteriorly to overly the anterodorsal surface of the mesopterygoid.

The palatine in the other platytroctids is similar in shape to that described for *S. abei* except that in *Searsia* (see Fig. 43) and *Mirorictus* (see Fig. 46) it is wider mediolaterally. In *Mirorictus* (see Fig. 46) and *Platytroctes* (see Fig. 45) the cartilaginous knob at the anterior end is smaller, and in *Mirorictus* is divided into a lateral and a medial part by a strip of bone that bisects the cartilage. The palatine in *Holtbyrnia* was most similar to the one in *S. abei*, but differed in that it had two teeth on the left palatine (one on the right) and the dermopalatine plate was imperceptibly fused to the autopalatine. Palatine teeth and a dermopalatine were absent in *Searsia* (see Fig. 43), *Pellisolus*, *Platytroctes* (see Fig. 45), and

Mirorictus (see Fig. 46). A vestige of a dermopalatine that lacked teeth was present in my specimen of *Searsioides multispinus* (see Fig. 44); however, teeth were noted in some specimens by Matsui and Rosenblatt (1979). Matsui and Rosenblatt (1987) report that among the thirteen genera of platytroctids, palatine teeth are absent in four (*Searsia*, *Mirorictus*, *Platytroctes*, and *Normichthys*). When present they are invariably small, few in number (usually one or two, up to five in one specimen of *S. abei* examined by Parr 1960), and closely spaced if there are more than one (also see Parr 1960; Krefft 1970, 1980; Matsui and Rosenblatt 1979).

Ectopterygoid

The ectopterygoid in *S. abei* is similar to the one described for the alepocephalid *Talismania antillarum* except that it is narrower (see Fig. 42).

The ectopterygoid in the other platytroctids is similar to that in *S. abei* except that in *Mirorictus* the posteroventral arm is shorter (see Figs. 43-46). According to Matsui and Rosenblatt (1987) teeth are variably present on the ectopterygoid in larger specimens of *Holtbyrnia* and *Sagamichthys* (they were absent in my specimens). However, when present they are not numerous, since Krefft (1980) recorded only four on the right ectopterygoid in the holotype of *H. anomala*.

Mesopterygoid

The mesopterygoid in *S. abei* is a moderately large, moderately thin, elliptical, tooth-bearing bone (see Fig. 42). The dorsal surface is concave and slopes dorsomedially toward the parasphenoid, from which it is separated by a moderately wide band of connective tissue. The anterior end overlaps the palatine and ectopterygoid, whereas the posterior end overlaps the medial surface of the anterodorsal corner of the metapterygoid. The posteromedial extension that overlaps the metapterygoid is slightly thickened, and bears a single, small, pointed tooth that curves ventrolaterally. This tooth opposes a single row of five dorsally-directed teeth of similar size and shape on the middle of the basibranchial tooth-plate (the basihyal tooth-plate has seven similar teeth distributed irregularly at its anterior end).

Although the shape of the mesopterygoid is similar to *S. abei* in the other platytroctids, the size is somewhat variable (see Figs. 43-46). It was smallest in *Mirorictus* (see Fig. 46) and *Searsia* (see Fig. 43), and largest in *Platytroctes* (see Fig. 45). It did not overlap the palatine in *Mirorictus*, *Searsioides*, *Holtbyrnia*, and *Platytroctes* (the palatine was not ossified in my specimen of *Pellisolus*).

The major difference between species concerns the number, size, and location of the teeth on the mesopterygoid. Of the seven platytroctids I examined, only *Mirorictus* lacked teeth on the mesopterygoid (they are sometimes present according to Matsui and Rosenblatt, 1987). Among the species with teeth, *Pellisolus facilis* possessed one small feeble tooth on the ventral surface of the anteromedial part of the right mesopterygoid (the other mesopterygoid was edentulous). Matsui and Rosenblatt (1987) claimed that the mesoptergoid was edentulous in *P. facilis*. *Holtbyrnia* had one small ventrolaterally directed tooth on the anteromedial part of the right mesopterygoid and three similar teeth on the left one, two at the anteromedial end and one at the posteromedial end of the bone. In a specimen of *Holtbyrnia* sp. that Krefft (1980) examined there were thirteen teeth on the left mesopterygoid and sixteen on the right one. *Platytroctes apus* (see Fig. 45) possessed seven moderately small, ventrolaterally directed teeth in a single row on the left mesopterygoid, and five on the right one. These are borne on a slightly thickened area and oppose a single irregular row of about twelve similar dorsally directed teeth on the basibranchial tooth-plate. Matsui and Rosenblatt (1987, p. 14) noted that in *P. apus* "there is usually one row of teeth [on the mesopterygoid], but in one individual the mesopterygoid was covered by a patch of teeth." *Searsia* (see Fig. 43) had seven moderate-sized, ventrolaterally directed teeth in one row along the anteromedial side of the posterior two-thirds of the left mesopterygoid, and six on the right mesopterygoid. These teeth are borne on a thickened area, and oppose three closely spaced teeth on the middle of the basibranchial tooth-plate. *Searsioides* (see Fig. 44) had eighteen, small, ventrolaterally directed teeth in two irregular rows along the entire anteromedial side of the left mesopterygoid, and sixteen on the right mesopterygoid. They oppose about six similarly sized teeth in a single row on the basibranchials. Matsui and Rosenblatt (1979, p. 72) noted that *Searsioides multispinus* had "One or two uneven rows of up to 15 mesopterygoid teeth on a side."

In their recent revision of the family, Matsui and Rosenblatt (1987, p. 14) state that "Most platytroctids have one or two longitudinal rows of teeth on part of, or the entire length of, the mesopterygoid." They found teeth on the mesopterygoid in twelve of the thirteen genera that they include in the family (they were absent only in *Barbantus*). Although mesopterygoidal teeth are present in *Maulisia*, Matsui and Rosenblatt (1979, p. 63) noted in their generic description that they are "present in smaller individuals but lacking in larger ones."

Quadrate

The quadrate in *Sagamichthys abei* has a relatively large body and a moderately large condyle with an oval facet that faces anteroventrally (see Fig. 42). The quadratojugal arm is short and does not extend posterior to the posterodorsal corner of the body.

The quadrate in *Holtbyrnia, Searsia* (see Fig. 43), *Mirorictus* (see Fig. 46), *Pellisolus* and *Searsioides* (see Fig. 44) is similar to that in *S. abei*. However, in *Platytroctes* the body is larger and longer dorsoventrally than the others, the condyle is smaller, and the quadratojugal arm is reduced to a narrow, sharp, splint (see Fig. 45).

Symplectic

The symplectic in *Sagamichthys abei* is a moderately long bone with a slight central bend and no distinctive laminae (see Fig. 42).

The symplectic in the other platytroctids is similar to that in *S. abei* except that in *Mirorictus*, *Platytroctes*, and *Searsioides* it is perfectly straight (see Figs. 46, 45, and 44, respectively).

Metapterygoid

Aside from a slight difference in shape, the metapterygoid in *Sagamichthys abei* is identical to the one described for the alepocephalid *Talismania antillarum* (see Fig. 42 and compare to Fig. 34).

The metapterygoid in *Holtbyrnia, Searsia* (see Fig. 43), *Searsioides* (see Fig. 44), and *Pellisolus* is similar to that in *S. abei*. In *Mirorictus* it is crescent-shaped (see Fig. 46). The metapterygoid in *Platytroctes* has the same features as the other platytroctids but has an unusual shape (see Fig. 45).

Hyomandibular

The hyomandibular in *Sagamichthys abei* is moderately short dorsoventrally but wide anteroposteriorly (see Fig. 42). The posterior half of the cartilaginous condyle on the dorsal edge of the head rests in a shallow groove on the pterotic (bordered by just a trace of a ridge), while the anterior half rests in the large area of cartilage between the sphenotic, pterotic, and prootic.

The opercular arm is long, narrow, and curves slightly posteroventrally. There is a small posteroventral lamina but no posterodorsal lamina. The anterior lamina is relatively narrow and extends along the entire anterior edge of the hyomandibular. The ventral arm is short relative to the rest of the hyomandibular. A moderately narrow posterolaterally inclined lateral strut extends dorsoventrally from near the posterodorsal corner of the head to the posteroventral corner of the ventral arm. It closely abuts the anterior edge of the dorsal limb of the preoperculum. The anterior face of the strut is only slightly concave. The dorsal part of the strut is reinforced by a series of ribs that radiate diagonally across the lateral surface of the head to the strut's posterodorsal edge. On the medial surface of the hyomandibular there are two ridges similar to the ones in the alepocephalid *Talismania antillarum*: a moderately wide ridge that runs dorsoventrally from the posterodorsal corner of the head nearly to the ventral end of the ventral arm, and a slightly narrower ridge that runs anteroposteriorly from the anterior lamina to join the dorsoventral ridge at the beginning of the opercular arm. The *adductor arcus palatini* inserts along, and dorsal to the anteroposterior ridge.

The canal for the hyomandibular branch of the facial nerve is moderately short. The medial foramen is at the ventral apex of the head immediately dorsal to the anteroposterior ridge. The lateral foramen is about the same size, and located posterior to the dorsal part of the lateral strut at the intersection of the anteroventral corner of the opercular arm and the ventral arm.

The hyomandibular in the other platytroctids is basically similar to that in *S. abei*. The only difference between *Holtbyrnia* and *S. abei* is that the former has a wider lateral strut and a slightly longer and narrower ventral arm. The proportions are similar in *Pellisolus*; however, the lateral strut is even wider and the anteroventral ridge on the medial surface radiates diagonally across the head to join a very wide dorsoventral ridge. The hyomandibular in the other platytroctids was longer and narrower (see Figs. 43-46). The anterior lamina is greatly reduced or absent in *Platytroctes, Mirorictus*, and *Searsioides*. In *Platytroctes* there is only one ridge on the medial side; however, it is relatively wide, reinforced by a lattice-like network of ribs, and curves in an arc (convex dorsally) that extends posterodrosally from the anterior edge of the upper part of the ventral arm to the posterior edge of the opercular arm. The medial ridges in *Mirorictus* were less distinct than in the other platytroctids.

Preoperculum

The preoperculum in *S. abei* is moderately large with dorsal and ventral limbs that meet at a slightly obtuse-angle (see Fig. 42). The ventral limb is abbreviated anteriorly (the dorsal limb is almost twice as long as the ventral limb). The anterior lamina is indistinct. There is no suprapreoperculum. The anterolateral surface has an unusual pattern of sculpture that consists of numerous ridges, flanges, and thickenings.

The bony, lateral sensory canal is open along the entire length of the preoperculum. The moderately narrow anterior flange that borders the canal is unusual in that it is interrupted along parts of the dorsal limb. Also, there are several short flanges of bone posterior, and parallel to, the anterior flange that may represent posterior remnants of what was once the posterior part of a closed bony tube.

The preoperculum in *Searsia* (see Fig. 43) and *Holtbyrnia* is similar to that in *S. abei* except that the ventral limb is slightly longer in the former two. In *Mirorictus* the limbs are indistinct and the bone expands anteriorly (see Fig. 46). In *Searsioides* (see Fig. 44), *Pellisolus*, and *Platytroctes* (see Fig. 45) the limbs meet at a moderately obtuse angle. *Platytroctes* was the only taxon with a distinct anterior lamina.

The bony, lateral sensory canal was completely open posterior to an anterior flange (of varying width) in *Holtbyrnia, Searsia* (see Fig. 43), *Searsioides* (see Fig. 44), *Pellisolus*, and *Mirorictus* (see Fig. 46). The flange in *Searsioides* was virtually absent. In *Holtbyrnia* the posterior edge of the anterior flange narrowly joins the lateral surface of the preoperculum at a few points. The canal in *Platytroctes* is partly closed at the intersection of the two limbs and along the middle of the dorsal limb (see Fig. 45).

B. OTHER TELEOSTEI

In this section I will briefly outline the salient features of the suspensorium in the other teleosts (including extinct species), particularly with a view to comparing them to character states in the Salmoniformes that were useful in phylogenetic reconstruction. The primitive outgroups of the Salmoniformes will be discussed first, followed by the higher teleosts (Neoteleostei). For ease of discussion, the reader is referred to Figure 1 depicting the relationships of the major extant teleostean lineages.

PRIMITIVE TELEOSTS: EXTINCT BASAL TELEOSTS, OSTEOGLOSSOMORPHA, ELOPOMORPHA, CLUPEOMORPHA, OSTARIOPHYSI

Extinct basal teleosts

This includes the primitive fossil teleosts, of often uncertain relationship, that are hypothesized to be near the ancestry of the extant teleosts. These extinct species have been assigned at various times to the following orders, which are not necessarily holophyletic: the Ichthyodectiformes, Leptolepidiformes, Pholidophoriformes, Aspidorhynchiformes, and Pachycormiformes (see Patterson and Rosen 1977; Lauder and Liem 1983; Nelson 1984). The suspensorium in many of these species is often poorly preserved; however, a number of general statements can be made concerning the suspensorium in these fossil forms. Information concerning character states was found in : Sainte-Seine 1949; Schaeffer and Rosen 1961; Griffith and Patterson 1963; Bardack 1965; Nybelin 1966, 1974; Wenz 1967; Cavender 1970; Waldman 1971; Patterson 1973; Patterson and Rosen 1977; Arratia 1981; Schaeffer and Patterson 1984.

Generally, the inclination of the posterior part of the suspensorium is nearly vertical or only slightly oblique, and there is considerable overlap among the individual bones.

The palatine is often not visible, or else is poorly preserved. However, it appears to have both endochondral (the autopalatine) and dermal (the dermopalatine) components that are fused to each another, is expanded at one or both ends, and articulates anteriorly with the maxilla and the anterolateral end of the snout. Teeth may or may not be present on its ventral surface (the presence of teeth appears to be primitive since they are found in most members of the primitive outgroups of the Teleostei).

The ectopterygoid is relatively large, overlaps the palatine, mesopterygoid, and quadrate, and has distinct anterior and posteroventral (the shorter, but broader one) arms that are inclined at an angle to each another. Its surface often bears numerous small teeth.

The mesopterygoid is elongated anteroposteriorly, concave dorsally, and tapers anteriorly. Its posterior end invariably overlaps the metapterygoid. Small teeth are often present on its ventral surface.

The quadrate has a fan-shaped body, a condyle that articulates with the lower jaw, and a quadratojugal arm. This process is continuous anteriorly with the condyle and body, and projects posterodorsally as an arm that overlaps the dorsal edge of the ventral limb of the preoperculum.

There is a separate, moderately small, and relatively straight symplectic that extends between the hyomandibular and quadrate. Its anterior part rests on the dorsomedial surface of the quadratojugal arm of the quadrate.

The metapterygoid is moderately large, roughly semicircular in shape, and overlaps the anterior part of the hyomandibular. It is probably almost entirely endochondral in origin. It consists of a vertically inclined ventral section and a smaller anterodorsal section that curves dorsomedially towards the parasphenoid (overlapping the mesopterygoid).

The hyomandibular is longer dorsoventrally than it is an[illegible]posteriorly. The articular facet on the dorsal edge of the head is single and fits in a distinct groove on the sphenotic, pterotic, and prootic. The ventral arm is notably longer than the moderately short opercular arm. There are posterodorsal and posteroventral lamina. A moderately wide anterior lamina extends along most of the anterior edge of the bone. Although it is difficult to tell in many specimens, many hyomandibulars appear to have a dorsoventrally inclined lateral strut (or at least a ridge) that abuts the dorsal limb of the preoperculum. The canal for the hyomandibular branch of the facial nerve is relatively long and courses posteroventrally through the bone from the medial to lateral foramina. The medial foramen is located at the intersection of the head and anterior lamina and the lateral foramen is located on the ventral arm posterior to the lateral strut. Many of the more primitive species have what most workers call a preopercular process. This finger-like projection extends posterodorsally from the posteroventral end of the ventral arm of the hyomandibular to the preoperculum (e.g., see Patterson and Rosen 1977). It is absent in extant teleosts.

The preoperculum is well-developed and has dorsal and ventral limbs that meet at about a right angle. The dorsal limb is invariably longer than the ventral limb. There is a moderately narrow anterior lamina. All have a bone-enclosed lateral sensory canal on the preoperculum that opens to the exterior via a pore at each end of the bone and via pores at the end of numerous, long auxiliary canals that lead off of the main canal (there were nineteen auxiliary canals in one specimen of *Pholidophorus bechei* examined by Nybelin 1966).

There is considerable variation within the Osteoglossomorpha. For figures and/or descriptions of the suspensorium in this assemblage (including fossils) refer to: Ridewood 1904a, 1905a; Roellig 1967; Gaudant 1968; Greenwood 1970, 1973; Wilson 1974; Kershaw 1970, 1976; Taverne 1977, 1978. The following statements do not apply to the highly specialized mormyrids (*sensu* Lauder and Liem 1983).

Generally speaking, the suspensorium in the osteoglossoids is much more robust, and the bones overlap one another to a greater extent than in the notopteroids.

The palatine and ectopterygoid are fused in most osteoglossomorphs. The two bones form a relatively straight line. Fusion does not occur in *Heterotis* and the Hiodontidae (see Fig. 47); however, the two bones closely overlap one another. In most species the ventral surface of the palatine and ectopterygoid are covered with numerous well-developed teeth. However, according to Gaudant (1968) and Greenwood (1970) there are no teeth on the ectopterygoid (apparently it is not fused with the palatine) in the oldest known fossil osteoglossomorph, the Jurassic genus *Lycoptera* (the primitive sister group of the Hiodontidae). The palatine in the osteoglossomorphs is also unusual in that it appears to lack a distinct autopalatine: there is no distinct bony, tube-like expansion, with a cartilaginous core, that forms the anterodorsal end of the bone. Instead, the anterior end of the palatoquadrate cartilage simply rests on the dorsal surface of the dermopalatine. An autopalatine has not been described in *Lycoptera* (see Gaudant 1968; Greenwood 1970).

The mesopterygoid usually bears teeth on its ventral surface. The size, number, and distribution of these teeth are variable.

The primitive character state of the quadrate, symplectic, metapterygoid, and preoperculum in the Osteoglossomorpha may be similar to that in *Hiodon* (see Fig. 47) since in *Hiodon* these bones resemble those in *Lycoptera* and the outgroups of the Osteoglossomorpha. However, the hyomandibular in *Hiodon* is somewhat atypical of the other osteoglossomorphs: it has a large foramen on its head, a greatly enlarged opercular arm, and articulates with the intercalar as well as the sphenotic, pterotic, and prootic. The primitive

Lycoptera, which most closely resemble the character states in the primitive outgroups.

Elopomorpha

For figures and descriptions of the suspensorium in the more primitive elopomorphs refer to: Ridewood 1904b; Vrba 1968; Forey 1973a; Taverne 1974; Greenwood 1977. The primitive character state is probably similar to that found in *Elops* and *Megalops* (see Fig. 48). The features are essentially like those described for the extinct basal teleosts, and overall appear to resemble them more closely than do most osteoglossomorphs.

In *Megalops* and *Elops* the palatine and ectopterygoid are separate, but closely overlap, and bear numerous tiny, denticle-like teeth on their ventral surfaces. There is a large dermopalatine; however, the autopalatine consists only of a small cup-shaped concavity on the anterodorsal end of the dermopalatine in which rests the anterior end of the palatoquadrate cartilage (i.e., it does not consist of a bony tube). Forey (1973a) noted that in the genus *Tarpon* (the sister genus of *Megalops*) the autopalatine may ossify in large individuals. In the fossil genera *Davichthys* and *Osmeroides* (both from the Upper Cretaceous) the autopalatine is ossified and expanded anteriorly into a condyle (see Forey 1973a).

Most of the ventral surface of the mesopterygoid is covered with a large number of tiny, denticle-like teeth.

The bone-enclosed lateral sensory canal on the preoperculum is unusual, and unlike the outgroups of the elopomorphs, in that it lacks distinct auxiliary canals. Instead the canal opens to the exterior via pores that open directly along the posterior side of the closed canal.

The suspensorium in the Albulidae is essentially like that in *Megalops* and *Elops*, but is longer anteroposteriorly and has a number of derived features (see Ridewood 1904b and Forey 1973a, and other parts of this thesis). The suspensorium in the highly specialized Notacanthiformes and Anguilliformes (*sensu* Nelson 1984) was not investigated in detail, but also has numerous specializations (see Greenwood 1977).

Clupeomorpha

For figures and descriptions of the suspensorium in extant and extinct clupeomorphs refer to: Ridewood 1905b; Phillips 1942; Chapman 1944a, 1944b, 1948b; Kirchhoff 1958; Bardack 1965; Greenwood 1968; Nelson 1970b; Forey 1973b, 1975; Grande 1982a, 1982b, 1985; Grande and Nelson 1985. The suspensorium in this group shows considerable variation, particularly in regards to: its inclination; the presence or absence of teeth on the palatine, ectopterygoid, and mesopterygoid; the shape of the hyomandibular; and the character state of the bony, lateral sensory canal on the preoperculum. Aside from the total absence of teeth on the bones and a nearly completely open, bony, lateral sensory canal on the preoperculum, the suspensorium in the genus *Clupea* is rather typical of that found in extant clupeoids (see Fig. 49). In all clupeomorphs except the engrauloids (*sensu* Grande and Nelson 1985) the inclination of the posterior part of the suspensorium is nearly vertical. In the engrauloids it is distinctly oblique (especially the hyomandibular), a feature that Grande and Nelson consider to be an autapomorphy of that group.

In clupeomorphs the autopalatine is prominent (and is usually expanded at each end) whereas the tooth-bearing dermopalatine is reduced and often absent (as in *Clupea*, see Fig. 49). Small teeth are often present on the ventral surface of the palatine. This is probably the primitive character state since they are found in *Denticeps*, the primitive sister group of all extant clupeomorphs (see Greenwood 1968; Forey 1973b), and the extinct genus *Ornategulum*, thought by Forey (1973b) to be the primitive sister group of all clupeomorphs, and in most of the outgroups of the Clupeomorpha.

The ectopterygoid in the clupeomorphs is similar to that in the primitive elopomorphs except that it rarely possesses teeth. Small teeth are present in the engrauloids and a few clupeoids; however, most lack them, including the fossil genera *Orneteguium, Erichalcis, Diplomystus*, and the extant genus *Denticeps*. This suggests that the absence of ectopterygoid teeth might be primitive for the group.

The quadrate, symplectic, metapterygoid, and mesopterygoid in the clupeomorphs is basically similar to that in *Clupea* (see Fig. 49). The metapterygoid is almost entirely endochondral in origin, like the primitive outgroups. The ventral surface of the mesopterygoid bears small teeth in many taxa, including *Ornategulum* and *Denticeps* (see Forey 1973b and Greenwood 1968, respectively). In the extinct genera *Diplomystus* (pers. obs.), *Ellimmichthys*, and *Armigatus* the teeth are enlarged, curve ventrolaterally, and are restricted to the medial side of the bone. However, I believe that the primitive character state in the Clupeomorpha is for there to be numerous small teeth on the mesopterygoid, as in the primitive elopomorphs (see pages 323-333 for details).

The primitive character state of the hyomandibular in the clupeomorphs is probably similar to that found in all the aforementioned extinct species, which have a hyomandibular that is similar to that described for the extinct basal teleosts. The hyomandibular in all the extant species, except for *Denticeps*, has a unique feature that appears to be an autapomorphy of all extant clupeomorphs, excluding *Denticeps*. On the anterolateral surface of the hyomandibular, adjacent to the posterior edge of the anterior lamina, is a flange that extends dorsoventrally and projects anterolaterally (labelled Hm.af on Fig. 49). The anterodorsal corner of this anterior flange (Forey 1975, p. 171, calls it "a special anterodorsal process of the hyomandibular") extends anterodorsally towards the spine on the sphenotic. This process (labelled Hm.pr on Fig. 49) serves as the point of insertion for a unique dorsal subdivision of the *levator arcus palatini* (also absent in *Denticeps*) that originates broadly along and ventral to a curved ridge on the frontal. Because this ridge is also apparently absent in *Denticeps* and the primitive fossil relatives of the extant clupeomorphs, the dorsal subdivision of the muscle was also probably absent in the ancestor of the clupeomorpha (also see Forey 1975). Whether the flange on the hyomandibular is in fact a modified lateral strut is uncertain, but, it may not be since a relatively small, but distinct, ridge-like lateral strut is found posterior to the flange (labelled Hm.ls on Fig. 49). However, suggesting the contrary is the observation that the lateral foramen for the hyomandibular branch of the facial nerve is located posterior to the dorsal end of the anterior flange, but anterodorsal to the "lateral strut".

The primitive character state of the preoperculum in the Clupeomorpha appears to be similar to that described for the extinct basal teleosts, since a similar state is found in the primitive fossil clupeomorphs: there is a bone-enclosed lateral sensory canal with auxiliary canals, the dorsal limb is longer than the ventral one, the two limbs meet at right angles to each another, and there is a moderately narrow anterior lamina. Although the preoperculum is basically the same in many extant clupeomorphs, many others are significantly different. In *Denticeps* the canal is only partly enclosed in bone and has a highly unusual shape (see Greenwood 1968). In the engrauloids (*sensu* Grande and Nelson 1985) there is virtually no ventral limb, the bone is inclined distinctly anterodorsally (as is the rest of the posterior end of the suspensorium), and the bony, lateral sensory canal is invariably open along most of its length. The preoperculum in the other extant clupeomorphs is similar to the primitive character state except that the bony lateral sensory canal exhibits a wide variety of character states, ranging from a bone-enclosed canal with auxiliary canals (but fewer than in the extinct species), such as in *Dussumeria* (pers. obs.), to a canal that is almost completely open, as in *Clupea* (see Fig. 49).

Ostariophysi

For figures and descriptions of the suspensorium in extant and extinct ostariophysans refer to: Weitzman 1954, 1962, 1964; Alexander 1964; Ballintijn 1969; Gosline 1973; Roberts 1966, 1969, 1971, 1973; Howes 1976, 1979, 1980; Chardon and De la Hoz 1977; Vari 1979; Fink and Fink 1981; Weitzman and Fink 1983; Patterson 1984a, 1984b; Gayet 1985, 1986. As could be expected in such a diverse group, the suspensorium exhibits considerable variability. However, the primitive charcter state may be similar to that found in the primitive gonorynchiform, *Chanos* (see Fig. 50), which Fink and Fink (1981) consider to be the sister group of all other gonorynchiforms, with the gonorynchiforms in turn the sister group of all other extant ostariophysans (the Otophysi; i.e., the Cypriniformes + Characiformes + Siluriformes).

In *Chanos* the palatine lacks a dermal component (the dermopalatine and its teeth) and the autopalatine is expanded slightly at each end (see Fig. 50). Since most other ostariophysans share this derived character state Fink and Fink (1981) consider it to be a synapomorphy uniting the group. This character state is also found in the well-preserved fossil genus *Chanoides* (see Patterson 1984a). The palatines in the cypriniforms, siluroids, and gymnotoids have a number of unique features that Fink and Fink (1981, p. 316-319) consider to be autapomorphies of each group.

The shape and size of the ectopterygoid in the Ostariophysi is variable. It is greatly reduced posteriorly in the siluroids, absent in the gymnotoids, and does not overlap the palatine anteriorly in the cypriniforms (permitting mobility of the palatine relative to the rest of the suspensorium according to Fink and Fink 1981). However, in *Chanos* the ectopterygoid is similar to that in the clupeomorphs, except that it has a unique posterior extension that reaches the metapterygoid (this extension appears to be an autapomorphy of the genus). In the fossil *Chanoides* the bone appears to lack this extension and is distinctly like that in the clupeomorphs (see Patterson 1984a). This is probably the primitive character state for the Ostariophysi. The ectopterygoid in most ostariophysans lacks teeth (including *Chanos* and *Chanoides*); however, they are found in some characiforms (particularly in the more specialized genera, see Weitzman 1964; Roberts 1969).

The mesopterygoid in *Chanos* is similar to that in the primitive outgroups of the Ostariophysi except that it lacks teeth. Most other ostariophysans lack teeth on the mesopterygoid, including the fossils *Chanoides* (see Patterson 1984a) and *Judeichthys* (see Gayet 1985). However, some characiforms have small conical teeth scattered on the ventral surface of the bone (see Weitzman 1964). The gonorynchiform, *Gonorynchus*, has specialized mesopterygoidal teeth ; however, they are absent in the other gonorynchiforms (see Patterson 1984b and Gayet 1985), and they are unlike those present in most other teleosts. This suggests that this character state is probably an autapomorphy of the genus. The mesopterygoid in the cypriniforms, siluroids, and gymnotoids is derived in a number of ways over that in the other ostariophysans (see Fink and Fink 1981, p. 319-320).

The quadrate, symplectic, and metapterygoid in *Chanos* and *Chanoides* (see Patterson 1984a) are basically like those in the primitive outgroups of the ostariophysi and probably represent the primitive character state for the assemblage. However, in *Chanos* (and apparently other extant gonorynchiforms; see Fink and Fink 1981, character 29, p. 320) the area between the condyle of the quadrate and the hyomandibular is elongated anteroposteriorly to a greater degree than in most other ostariophysans and other primitive teleosts (they consider this to be an autapomorphy of the order). Another autapomorphy of *Chanos* is that the anterior end of the symplectic is widely separated from the body of the quadrate and does not rest along a groove on the quadratojugal arm. In most other ostariophysans (including the fossil *Chanoides*) the character state is similar to that in the primitive outgroups (see Figs. 47-49). In the siluroids a symplectic and quadratojugal arm of the quadrate are absent (see Fink and Fink 1981, character 33, p. 321). The metapterytoids in the Cypriniformes, Characiformes, and Siluriformes share a number of derived features that are not found in *Chanos* and most primitive teleosts (see Fink and Fink 1981, characters 30-32, pages 320-321, for details).

The hyomandibular in *Chanos* and most other primitive ostariophysans is basically like that described for the extinct basal teleosts except that there is no preopercular process.

The primitive character state of the preoperculum in the Ostariophysi appears to be similar to that found in *Chanos* (see Fig. 50) and *Chanoides* (see Patterson 1984a, fig. 2). The preoperculum in *Chanoides*, in particular, is very similar to that described for the extinct basal teleosts. In *Chanos* the ventral limb is longer than the dorsal limb whereas in *Chanoides* and most other primitive ostariophysans the opposite is true. The preoperculum in the suluroids is unusual in that there is virtually no ventral limb (an autapomorphy of the group according to Fink and Fink 1981, character 34, p. 321). Most Ostariophysi, including *Chanos* and the fossils *Chanoides*, *Judeichthys*, *Ramallichthys*, and *Lusitanichthys* have a bone-enclosed lateral sensory canal on the preoperculum. The primitive character state appears to be for there to be a relatively large number of auxiliary canals leading off of the main canal, as in the latter five genera.

HIGHER TELEOSTS: STOMIIFORMES, AULOPIFORMES, MYCTOPHIFORMES, PARACANTHOPTERYGII, ACANTHOPTERYGII

Stomiiformes

Because the Stomiiformes are considered to be the primitive sister group of the other neoteleosts (see Fink and Weitzman 1982) the suspensorium in the more primitive members of this group may approximate that found in the common ancestor of the Neoteleostei. The genus *Diplophos* is hypothesized by Fink (1984a) to be the sister group of the rest of the order. The suspensorium in *Diplophos* is basically similar to that found in other primitive stomiiforms (see Fig. 51 and refer to figures and descriptions in Gregory 1933; Beebe and Crane 1939; Günther and Deckert 1953, 1955; Tchernavin 1953; Grey 1964; Weitzman 1967a, 1967b, 1974; Baird 1971; Fink and Weitzman 1982; Fink 1985).

In the more primitive stomiiforms such as *Diplophos* the inclination of the posterior part of the suspensorium is nearly vertical or only slightly oblique; however, in many of the more specialized lineages it is distinctly oblique.

The palatine in *Diplophos* is expanded at both ends, consists of an autopalatine and a tooth-bearing dermopalatine, and overlaps the ectopterygoid and mesopterygoid. Virtually all stomiiforms have a relatively small number of moderately small, sharp teeth (usually in a single row) on the ventrolateral surface of the bone.

The ectopterygoid in *Diplophos* is very large, broadly overlaps the surrounding bones, consists of two arms that are inclined at an angle to each another, and lacks teeth. It is similar in most primitive stomiiforms except that its size varies. I found no record of any stomiiform bearing teeth on the ectopterygoid. In many of the specialized lineages the ectopterygoid is reduced in size and represented by a long and narrow splint.

The mesopterygoid in all the primitive stomiiforms is basically like that in *Diplophos* (see Fig. 51). Its ventral surface may or may not bear tiny, randomly distributed, denticle-like teeth (a small patch of such teeth is visible on the anteroventral surface of the bone in Fig. 51). The number and distribution of these teeth apparently vary from species to species. They have been recorded in the following relatively primitive genera: *Diplophos, Triplophos, Polymetme, Pollichthys, Gonostoma, Yarella, Cyclothone, Margrethia, Maurolicus,* and *Bonapartia*. In specialized stomiiforms teeth are invariably absent, and the mesopterygoid is reduced in size and sometimes lost (e.g., see Weitzman 1967b and Fink 1985). *Gonostoma bathyphilum* is unusual according to Grey (1964, p. 182) because the mesopterygoid (what she calls the pterygoid) has "a patch of rather small teeth, and a few much enlarged ones posteriorly." However, the fact that no other species of *Gonostoma*, or any other stomiiform, has similar enlarged teeth on the mesopterygoid, suggests that this character state is an autapomorphy of *G. bathyphilum*.

The quadrate in *Diplophos* is elongated dorsoventrally and lacks a quadratojugal arm and a quadrate notch. The symplectic is small and straight and its anterior part rests along a groove on the posteromedial surface of the quadrate. The two bones are essentially the same in all stomiiforms except that in the specialized species they are inclined anterodorsally along with the rest of the posterior end of the suspensorium. Sometimes the quadrate has a short quadratojugal arm and a shallow quadrate notch (e.g., *Argyropelecus*, pers. obs.).

The metapterygoid in *Diplophos* is a large, squarish bone that lies dorsal to the quadrate and is almost entirely endochondral in origin. On the lateral surface of the posterodorsal corner there is a moderately wide dorsolaterally directed flange (its ventral half appears to be endochondral in origin) whose posterior edge abuts the lateral strut of the hyomandibular. The area medial to the flange is part of the main body of the bone and is not a medial ridge (compare lateral and medial views in Fig. 51). No stomiiforms appear to possess a dermal, medial ridge like that found in some salmoniforms (see Figs. 16, 34, 42 and compare to *Diplophos*, Fig. 51). The metapterygoid in the other stomiiforms appears basically similar to that in *Diplophos*, although there is a moderate amount of variation in regards to relative size and shape. Unfortunately, it is difficult to tell from most of the drawings in the literature whether or not a flange is present on the lateral surface of the bone, as is the case in *Diplophos* (it was present in *Vinciguerria* and *Argyropelecus*, but absent in *Tactostoma* among the other stomiiforms that I examined).

The hyomandibular in *Diplophos* is a long (dorsoventrally), relatively narrow (anteroposteriorly), and moderately delicate bone. It has a moderately wide anterior lamina, a relatively small head, and long and narrow opercular and ventral arms. The well-developed posterolaterally inclined lateral strut extends along most of the posterior edge of the bone. The canal for the hyomandibular branch of the facial nerve is relatively long and courses posteroventrally through the bone from the medial to lateral foramina. The medial foramen is located on the head while the lateral foramen is located posterior to the upper third of the lateral strut at the intersection of the ventral and opercular arms. The nerve does not pass through the small foramen on the mid-lateral surface of the head shown in Fig. 51. The hyomandibular in the other stomiiforms is basically the same as that in *Diplophos* (the length of the ventral arm and the size and shape of the opercular arm appear to be the most variable elements). In many of the more specialized species it is inclined sharply anterodorsally.

In *Diplophos* the preoperculum is relatively small, with a moderately narrow anterior lamina, and an abbreviated ventral limb that extends anteroventrally from its intersection with the dorsal limb. The shape of the preoperculum is similar in the other primitive stomiiforms. In many of the specialized stomiiforms the preoperculum is virtually straight, very narrow, and inclined sharply anterodorsally (see figs. in Weitzman 1967b and Fink 1985). In *Diplophos taenia* the bony, lateral sensory canal is completely open along the entire length of the preoperculum posterior to an anterior flange (see Fig. 51). This canal is completely, or mostly, open in almost all primitive stomiiforms, and it appears that this character state is primitive for the order.

The fossil record of the Stomiiformes is relatively poor and extends only to the Oligocene with certainty (see Crane 1966; Jerzmańska 1968; Weitzman 1974). Although it is difficult to be sure of the character states of the suspensorium from descriptions and illustrations in the aforementioned papers, overall it appears to be basically the same as the extant species.

Aulopiformes

For figures and descriptions of the suspensorium in extant and extinct aulopiforms refer to: Regan 1911; Parr 1929; Günther and Deckert 1960; Walters 1961; Goody 1969a; Sulak 1977; Johnson 1982. The suspensorium in this large assemblage exhibits considerable variability. In many of the specialized lineages (the alepisauroids in particular) its shape and inclination closely parallels that in the specialized stomiiforms. The primitive character state may be similar to that found in the genera *Aulopus* (which most workers consider to be the most primitive aulopiform, see Goody 1969a; Rosen and Patterson 1969; Rosen 1973; Sulak 1977) and *Chlorophthalmus* (which also has a generalized, relatively primitive suspensorium). In these generalized aulopiforms the posterior part of the suspensorium is nearly vertical. The separate bones are surprisingly similar to those described for the primitive teleosts. The palatine has dermal and endochondral components, is expanded at both ends (although the anterior end is somewhat modified), and the ventral surface bears teeth. The ectopterygoid is moderately large, angled, and bears numerous tiny teeth in *Aulopus*, but none in *Chlorophthalmus*. In *Aulopus* the ventral surface of the mesopterygoid bears numerous tiny, denticle-like teeth that are similar to those described for the stomiiforms; however, in *Chlorophthalmus* the bone is edentulous. Unlike most stomiiforms the quadrate has a quadratojugal arm (but a shallow quadrate notch). The metapterygoid in *Aulopus* is moderately large, is similar in shape to that in *Diplophos*, but lacks the dorsolaterally directed flange. In *Chlorophthalmus* the bone is smaller and shaped like a half circle. The other bones are similar to the primitive character state for the Teleostei except that in *Aulopus* there are two cartilaginous condyles on the dorsal edge of the head of the hyomandibular that contact the skull (versus one in *Chlorophthalmus*).

Most of the other aulopiforms bear teeth on the palatine (they are often very large); however, the presence of teeth on the ectopterygoid and mesopterygoid exhibits a mosaic distribution. The mesopterygoidal teeth are similar to those in *Aulopus*. However, in the genera *Saurida* and *Harpadon* they are enlarged and superficially resemble those found in some salmoniforms.

Myctophiformes

For figures and descriptions of the suspensorium in extant and extinct Myctophiformes (Myctophidae + Neoscopelidae) refer to Regan 1911; Paxton 1972; Kusaka and Thuc 1972; Nafpaktitis 1977; Nafpaktitis *et al.* 1977. Paxton in particular presents a detailed account of the bones of the suspensorium in the Myctophidae.

The suspensorium in the Myctophidae is similar to that found in the primitive stomiiforms described previously. The dermopalatine usually extends rather far posteriorly as a splint that overlaps the ectopterygoid, and much of its ventral surface bears teeth, that are large and fang-like in some species. The ectopterygoid occasionally bears tiny, widely separated teeth. The quadrate, symplectic, mesopterygoid, metapterygoid, hyomandibular, and preoperculum are essentially as described for *Diplophos*. However, unlike most stomiiforms the head of the hyomandibular has two condyles on its dorsal edge that articulate with the cranium (the anterior one rests on the sphenotic and the posterior one on the pterotic). The ventral surface of the mesopterygoid bears teeth that are similar to those in the stomiiforms (about three quarters of the ventral surface is covered in most myctophids according to Paxton 1972). The metapterygoid has a dorsolaterally directed flange on the posterolateral surface that is similar to that in *Diplophos*. The shape and size of this flange (Paxton calls it a posterolateral strut) varies but it is invariably present (pers. obs., also see Paxton 1972, p. 17). In *Protomyctophum* it narrows anteriorly into a ridge that nearly reaches the anteroventral corner of the bone in a way that is reminiscent of the lateral ridge found in some osmerids (pers. obs.). In some myctophids (e.g., *Protomyctophum*) the area medial to the flange projects far dorsomedially as a dermal lamina. As in the stomiiforms there is no medial ridge on the metapterygoid.

Limited data are available for the Neoscopelidae. However, all three genera bear small teeth on the palatine, the ectopterygoid bears teeth in *Neoscopelus*, and the mesopterygoid bears teeth in *Neoscopelus* and *Solivomer* (see Nafpaktitis 1977). Their size and distribution are similar to those in the Myctophidae.

The suspensorium in the extinct Upper Cretaceous myctophiform, *Sardinioides*, appears similar to that in extant species except that the condyle on the dorsal edge of the head of the hyomandibular is single (see Goody 1969a). Goody noted a resemblance with the extant aulopiform *Aulopus*, and I concur judging from his description and figure.

Acanthomorpha (Paracanthopterygii + Acanthopterygii)

The suspensorium in this very large assemblage shows great diversity, as could be expected in a group that comprises over sixty percent of all living teleosts. I examined only a small percentage of this group; however, there is considerable information in the literature concerning the character states of the suspensorium in both extinct and extant acanthomorphs, including (to name a few): Gregory 1933; Blair and Brown 1961; Rosen 1962, 1964; Patterson 1964, 1967a; Kim and Kim 1965; Gosline 1966; Mujib 1967; Osse 1969; Rosen and Patterson 1969; Smith 1971; Rognes 1973; Anker 1974; Greenwood 1976; Zehren 1979; Parenti 1981, 1984; Arratia 1982; Bowne 1985. The primitive character state of the suspensorium in this assemblage is probably similar to that in the closely related Upper Cretaceous fossils *Aulolepis* and *Ctenothrissa* (see Patterson 1964; Rosen 1973), which Rosen considers to form the primitive sister group of the Paracanthopterygii + Acanthopterygii; similar to that in the primitive beryciforms, which are considered to form the basal group of acanthopterygian evolution and are the first to appear in the fossil record (see Patterson 1964, 1967a; Zehren 1979); and similar to that in the extinct Upper Cretaceous genus *Sphenocephalus*, which may be ancestral to the most primitive paracanthopterygian lineage, the percopsiforms (see Rosen and Patterson 1969; Nelson 1984). The suspensorium in the aforementioned fishes is basically similar: the posterior part is vertically inclined and the bones are robust and rather closely overlap one another. The palatine consists of both an autopalatine and dermopalatine, is expanded at both ends, and its ventral surface bears numerous tiny teeth. There is a distinct process on the anterodorsal end of the bone (most workers call it the maxillary process) that extends anterolaterally to contact the maxilla (the anterior tip of this process is capped with cartilage). This unique process is found in many acanthomorphs and most likely is related in some way to jaw protrusibility. The other bones of the suspensorium are essentially like those described for the aulopiform *Aulopus*. However, unlike *Aulopus*, the cartilaginous facet on the dorsal edge of the head of the hyomandibular is single, and the bony lateral sensory canal on the preoperculum is completely open posterior to a well-developed anterior flange. Both the ectopterygoid and mesopterygoid have numerous tiny teeth on their ventral surfaces, similar to those described for *Aulopus*. Among other acanthomorphs, the presence of teeth on the palatine, ectopterygoid, and mesopterygoid shows an uneven distribution; however, the primitive character state appears to be for tiny teeth to be present on all three bones.

IV. DESCRIPTIONS OF THE MUSCLES OF THE SUSPENSORIUM

This section is comprised of descriptions of the muscles associated with the suspensorium, beginning with the families belonging to the order Salmoniformes (part A), and followed by a less detailed description of these muscles in the other Teleostei (part B). The salmoniform families are described in the following order: Esocidae, Umbridae, Salmonidae, Osmeridae, Plecoglossidae, Salangidae, Sundasalangidae, Retropinnidae, Prototroctidae, Lepidogalaxiidae, Galaxiidae, Aplochitonidae, Alepocephalidae, Platytroctidae, Argentinidae, Bathylagidae, and Opisthoproctidae. One species was selected to represent each salmoniform family (e.g., *Esox lucius* for the Esocidae), and its muscles are described in detail, in the following order: *adductor mandibulae, levator arcus palatini, dilatator operculi, levator operculi, adductor operculi, adductor arcus palatini*, and *adductor hyomandibulae* (when present). At the end of the description of each muscle, differences between it and that found in other species belonging to the family are noted and discussed.

A. ORDER SALMONIFORMES

FAMILY ESOCIDAE

Adductor mandibulae

The *adductor mandibulae* in *Esox lucius* is large, thick, covers most of the *levator arcus palatini*, and has more subdivisions than in the other salmoniforms examined (distinct sections Aw, A2α, A2β, and A3; see Fig. 52). The ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal end of the *adductor mandibulae* at the division of sections A2 and Aw before running lateral to section Aw and then medial to the lower jaw.

Section A2 has two subdivisions, A2α and A2β, and occupies the entire lateral surface of the cheek posterior to section Aw. Subdivision A2α is relatively thin and flat and lies lateral to the dorsal part of subdivision A2β. It originates from the pterotic (the lateral edge of the temporal sensory canal) and sphenotic (the posterolateral edge of the spine). Subdivision A2β is thicker and larger than subdivision A2α and originates from the lateral surfaces of the quadrate (the posterodorsal part of the body and the quadratojugal arm), and most of the symplectic and hyomandibular (most of the ventral arm and most of the anterior face of the lateral strut, and the ventral surface of most of the opercular arm). The origin also includes the lateral surface of the anterior lamina of the preoperculum and most of the medial surface of the dorsal limb (dorsal to the anterior lamina and ventral to the opercular arm of the hyomandibular).

There is a moderately thin and flat A3 section (not visible externally) that is distinctly separate from, and medial to, section A2 (unlike subdivisions A2α and A2β in which their anteromedial fibres appear to be continuous). It originates from the lateral surfaces of the quadrate (the anterodorsal part of the body), metapterygoid (the entire surface), mesopterygoid (between the quadrate and metapterygoid), symplectic (posterodorsal edge), and hyomandibular (the anterior edge of the ventral arm and the medialmost part of the anterior face of the lateral strut).

Sections A2 and A3 insert anteriorly onto a very broad, tough tendinous aponeurosis that overlaps parts of the quadrate, metapterygoid, and hyomandibular before passing medial to the lower jaw. This aponeurosis is composed of essentially two parts: a relatively narrow ventral tendon, and a much broader dorsal aponeurosis that lies dorsolateral to the ventral tendon and with which it is continuous posteriorly (lateral to the quadrate-metapterygoid junction). The entire aponeurosis bifurcates posterior to the lower jaw, as in *Novumbra* (Umbridae). The ventral tendon narrows anteriorly and attaches to the coronomeckelian bone of the lower jaw. Section A3 of the *adductor mandibulae* inserts onto the posterolateral and posteromedial surfaces the ventral tendon. The dorsal aponeurosis extends into the Meckelian fossa of the lower jaw (attaching broadly along Meckel's cartilage and the angulo-articular and dentary bones). Section A2 inserts onto the posterolateral and posteromedial surfaces of the dorsal aponeurosis (posterior to section Aw) and anterolaterally onto the posterior surface of section Aw (onto an anteroventrally running sheet of fascia, reminiscent of that in the

Umbridae, that is continuous medially with the dorsal aponeurosis).

Section Aw is roughly triangular, unusually large, and inserts directly onto the lower jaw. Its posterior end is bulbous and visible externally, as in *Novumbra*. It originates from the anterolateral surface of the dorsal aponeurosis and from the anterior end of section A2 (from the same fascia onto which section A2 inserts). It inserts in (and fills) the Meckelian fossa (which includes Meckel's cartilage, and the angulo-articular and dentary bones) on the medial face of the lower jaw and along the posterior edge of the mandible via connective tissue.

The *adductor mandibulae* inserts only onto the lower jaw and lacks a direct ligamentous connection with the maxilla. A broad, tough, strap-like maxilla-mandibular ligament extends from the lateral surface of the angulo-articular bone (the posteroventral corner) to the anterior end of the maxilla (the dorsolateral edge). Although there is a single supramaxilla there is no supramaxillary ligament extending from it to the lower jaw. A unique, relatively narrow, tough ligament (hereafter called the coronoid-maxilla ligament), that is separate from the maxilla-mandibular ligament, extends from the lateral surface of the coronid process (dentary) to the middle of the maxilla (the dorsomedial edge). A similar ligament was found in all other esocoids that I examined. Eaton (1935) described and illustrated (but did not name) this ligament in the umbrid *Umbra*, but its presence in the Esocidae and the other umbrids has never been mentioned in the literature.

My interpretation of the *adductor mandibulae* in *E. lucius* is similar to that of other workers (see Vetter 1878; Kampf 1961; Winterbottom 1974a). The major difference concerns the naming of the various sections, and in this regard I basically follow Winterbottom's interpretation.

The *adductor mandibulae* and the other muscles of the suspensorium in *E. masquinongy* are similar to those in *E. lucius* (pers. obs.).

Levator arcus palatini

The *levator arcus palatini* (LAP) is a large, broad, roughly rectangular muscle that is almost entirely covered laterally by the *adductor mandibulae* (see Fig. 52). It originates broadly from the skull and appears to have two subdivisions. The somewhat flattened dorsomedial subdivision lines the posterodorsal part of the orbit, originating from the ventrolateral surface of the frontal at the back of the orbit and the lateral surfaces of the pterosphenoid, sphenotic (ventralmost part of the body) and prootic (part of the anterodorsal corner). Its fibres run posteroventrally and converge onto a tendinous sheath that inserts onto the lateral surface of the anterodorsal corner of the head of the hyomandibular. This subdivision has not been mentioned previously in the literature.

The main part of the muscle is thick and rectangular, and originates from the sphenotic (from the lateral surface of the body and the lateral edge and ventral surface of the spine), pterotic (the anterolateral surface of the temporal sensory canal medial to the origin of the *adductor mandibulae*), and from the large area of cartilage between the pterotic and sphenotic. It inserts on the medial surface of the metapterygoid (from the posterior half of the dorsal flange, lateral to the *adductor arcus palatini*) and on the lateral surface of the hyomandibular (the anterior lamina, anterior edge of the head, and the dorsalmost part of the anterior face of the lateral strut).

Dilatator operculi

The *dilatator operculi* (DO) is a large, thick, roughly conical muscle that originates from the lateral surfaces of the hyomandibular (most of the head and part of the opercular arm) and pterotic (the posterolateral surface of the temporal sensory canal dorsal to the hyomandibular-skull joint), and from the cartilage between the pterotic and sphenotic (see Fig. 52). It inserts onto the articular process of the operculum. Its anterior fibres are difficult to separate from the posterior fibres of the LAP.

Levator operculi

The *levator operculi* (LO) has two subdivisions (see Fig. 52). The small posterior subdivision is a thin, narrow slip that originates from the ventral end of the post-temporal bone of the pectoral girdle and inserts onto the dorsomedial surface of the posterodorsal corner of the operculum. The broad, flat, fan-shaped anterior section (the LO of most teleosts) originates from the lateral surface of the posterodorsal corner of the pterotic (which includes a poorly defined spine) and expands ventrally to insert onto the operculum. It inserts along the lateral ridge (that extends posteriorly and slightly ventrally from the articular process across about two-thirds the width of the bone) and on the lateral surface of the operculum posterodorsal to it, as well as on the dorsal edge and posteromedial surface of the bone (also see Wilson 1984).

The LO in *E. masquinongy* is similar to that in *E. lucius* except that the posterior subdivision is absent.

Adductor operculi

The *adductor operculi* is a moderately flattened, conical to cylindrical muscle that is completely covered by the anterior part of the *levator operculi* (LO). It originates from the lateral surface of the pterotic (the posteroventral corner) and a small part of the exoccipital adjacent to it. The origin is medioventral to that of the LO. It inserts along a small ridge on the medial surface of the anterodorsal corner of the operculum slightly ventral to the insertion of the anterior part of the LO and lying medial to it (this small medial ridge is not part of the lateral opercular ridge onto which part of the LO inserts).

Adductor arcus palatini

The *adductor arcus palatini* (AAP) is a moderately long (anteroposteriorly) and thick rectangular muscle whose anterior end is visible externally (see Fig. 52). It originates from the lateral surfaces of the parasphenoid (the posterior part, anterior to, and including the ascending wings), prootic (the dorsal surface), and pterotic (the anteroventral corner). It inserts on the mesopterygoid (the posterodorsal surface adjacent to the metapterytoid), and on the medial surfaces of the metapterygoid (the anterior half of the dorsal flange and along the ventral edge of the posterior half of the flange medioventral to the insertion of part of the LAP), and hyomandibular (the anterodorsal edge of the anteroventral wing and the medial surfaces of the anterior lamina and head).

Closely associated with the posterior end of the AAP, but distinctly separate from it, is a moderately wide, slightly flattened cylindrical *adductor hyomandibulae*. It originates from the mid-ventral surface of the pterotic and inserts on the dorsomedial surface of the opercular arm of the hyomandibular. A similar muscle is present in *E. masquinongy*. Kampf (1961) illustrates a separate *adductor hyomandibulae* in *E. lucius* that inserts onto the opercular arm (7B on his fig. 41) and another that inserts onto the head only (7A on his fig. 41) in addition to the AAP. However, I found no separate AH inserting only onto the head and interpret the muscle that he labels 7A as the posterior part of the AAP.

FAMILY UMBRIDAE

Adductor mandibulae

Novumbra hubbsi. The *adductor mandibulae* in *Novumbra hubbsi* is a moderately large and thick muscle that is relatively short anteroposteriorly (see Fig. 53). The posterodorsal corner covers the lateral surface of the ventral half of the *levator arcus palatini*. It is divided into a posterior A2 section and an anterior Aw section. As in the Esocidae, the posterior end of section Aw extends posterior to the posterodorsal corner of the lower jaw and is visible externally. The ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal end of the *adductor mandibulae* at the division of sections A2 and Aw before running lateral to section Aw and then medial to the lower jaw.

Section A2 is undivided and originates from the lateral surface of the anterior lamina and the anterolateral edge of the dorsal limb of the preoperculum, and from the lateral surfaces of the hyomandibular (the lateral edge of the anterior face of the lateral strut, the ventral end of the ventral arm, and the anteroventral wing), metapterygoid (the entire lateral surface), symplectic (most of the lateral surface), and quadrate (the posterodorsal end of the body and the posterior end of the quadratojugal arm). The anterior fibres insert onto the lateral surface of the posteroventral part of a moderately wide, tough, tendinous aponeurosis that overlies the body of the quadrate and part of the metapterygoid (the anteriormost fibres appear to insert on the posterior side of a sheet of fascia on the aponeurosis that runs anteroventrally from its posterodorsal corner).

The aponeurosis bifurcates at the posterior edge of the lower jaw and extends along its medial surface. The relatively narrow ventral tendon runs steeply anteroventrally and attaches to the coronomeckelian bone and the posterodorsal edge of Meckel's cartilage. Muscle fibres from the anteroventral end of section A2 insert along the posterior end of this tendon. These fibres might represent part of an A3 section (as in the Esocidae) since they occupy the same position and its fibres run in a different direction than those lateral to them. The wider dorsal tendon broadens anteriorly and attaches onto the anterodorsal end of Meckel's cartilage and the anterior end of the angulo-articular and dentary bones.

Section Aw is roughly triangular, large, and inserts directly onto the lower jaw. As in the Esocidae, its posterior end is bulbous, extends posterior to the lower jaw so that it is visible externally (it lies lateral to the dorsal part of the body of the quadrate at this point), and abuts the anterior end of section A2. It originates from the lateral surface of the tendinous aponeurosis and from the dorsal tendon after the aponeurosis bifurcates (none of its fibres originate on the ventral tendon). As in the Esocidae, the posteriormost fibres originate from the anterior side of a sheet of fascia on the aponeurosis (onto which the anterior fibres of section A2 insert). Section Aw inserts in (and fills) the Meckelian fossa (which includes Meckel's cartilage, and the angulo-articular and dentary bones) on the medial surface of the lower jaw. Unlike *Esox*, fibres do not appear to insert directly along the posterior edge of the mandible via connective tissue.

As in the Esocidae, the *adductor mandibulae* inserts only onto the lower jaw and lacks a direct ligamentous connection with the maxilla. There is a single, small supramaxilla but no supramaxillary ligament extending from it to the lower jaw. A maxilla-mandibular ligament is absent (unlike the Esocidae); however, like the Esocidae, a well-developed coronoid-maxilla ligament is present. It is moderately short anteroposteriorly, flattened, and extends from the lateral surface of the coronoid process (the posteriormost end of the upper arm of the dentary) to the dorsomedial surface of the posterior third of the maxilla.

<u>Umbra</u> <u>limi</u>. In this description, and the one of *Dallia* that follows, the *adductor mandibulae* is as described for *Novumbra* unless noted.

The *adductor mandibulae* in *Umbra limi* is thicker, and larger (it covers more of the cheek) than in *Novumbra* (see Fig. 54). The posterodorsal corner covers the lateral surface of the ventral two-thirds of the *levator arcus palatini*. The origin is essentially as in *Novumbra* except that it originates from the entire lateral surface of the vertical, semicircular plate of the metapterygoid (ventral to the ridge separating the ventral plate from the dorsal plate) and from almost the entire lateral surface of the preoperculum (anterior to the posterior edge but not covering the sensory pores). In *U. pygmaea* and *U. krameri* (see Fig. 55) the muscle is slightly smaller than in *U. limi* and covers less of the preoperculum.

The ventral fibres of section A2 run anterodorsally and the dorsal fibres run anteroventrally, converging onto the sides (ventral and dorsal, respectively) of a ridge of tissue that runs anteroposteriorly along the lateral surface of the tendinous aponeurosis that extends to the lower jaw. The insertion also includes the lateral surface of the tendinous aponeurosis adjacent to the ridge. A well-developed tendon (it is continuous posteromedially with the aponeurosis) extends anteriorly from the anterolateral end of section A2 to the lateral surface of the lower jaw (the posterodorsal corner of the angulo-articular). This lateral tendon (labelled L.A2 on Fig. 54) is also present in *U. pygmaea* but is absent in *U. krameri* (see Fig. 55) and the other esocoids. Therefore, only in *U. limi* and *U. pygmaea* does section A2 insert onto both medial and lateral surfaces of the mandible.

The ramus mandibularis of the trigeminal nerve occupies the same relative position as in the other esocoids before running medial to the lower jaw. However, unlike them the nerve in *U. limi* (and *U. pygmaea*) passes medial to the lateral tendon and the anterolateral fibres of section A2 that converge onto it.

Section Aw is smaller than in *Novumbra* (the Meckelian fossa is also correspondingly smaller). Its posterior end is also less bulbous and is only slightly visible externally. Section

Aw originates from the lateral surface of the tendinous aponeurosis (as in *Novumbra*), but unlike *Novumbra*, there is no sheet of fascia from which the posteriormost fibres originate. Winterbottom (1974a, p. 235) believed that "In *Umbra* it [section Aw] arises from [illegible] dorsal surface of the main mass of A2A3 [my A2]." However, although section A2 (his A2A3) and Aw are adjacent, they are not continuous, but arise independently from the tendinous aponeurosis.

The coronoid-maxilla ligament in *U. limi* originates from the lateral surface of the posteriormost end of the upper arm of the dentary, as in *Novumbra*, but also on the adjacent posterodorsal corner of the angulo-articular. It inserts on the dorsomedial surface of the middle of the maxilla (like *Esox*, but unlike *Dallia* and *Novumbra* in which the insertion is farther posteriorly). Eaton (1935, p. 162) appears to have been the first to describe this ligament in *Umbra*, stating that "*Umbra* has a ... long ligament to the coronoid part of the mandible ... this never seems to have been attached to the articular region or to the adductor mandibulae."

Other than where noted above, the *adductor mandibulae* in the other two species of *Umbra* is similar to that in *U. limi*.

Dallia pectoralis. The *adductor mandibulae* in *Dallia pectoralis* is an unusually bulbous muscle that is larger and thicker than in the other umbrids. It covers almost the entire posterior region of the cheek from the edge of the skull roof to the ventral edge of the preoperculum (see Fig. 56).

As in the other two genera, the *adductor mandibulae* has an A2 and an Aw section. However, unlike them, the part posterior to the lower jaw is divided into two sections. The part that covers most of the cheek is section A2. There is also a smaller subdivision (labelled A2.dm? on Fig. 56) that lies slightly dorsomedial to section A2 and is visible only when the eye is removed, and the head is viewed slightly dorsolaterally. This subdivision originates medial to the *levator arcus palatini* and inserts (along with A2) on the medial surface of the lower jaw. This part might be interpreted either as a dorsomedial subdivision of A2, or as a posterior expansion of Aw.

Section A2 (excluding the "subdivision") originates from the same areas as in *Novumbra* and *Umbra* but differs in that it includes the ventrolateral edge of most of the temporal sensory canal on the pterotic (originating via a broad tendon), less of the metapterygoid (only the anteroventral corner), and none of the ventral arm and anteroventral wing of the hyomandibular. As in *U. limi*, but not *U. pygmaea*, *U. krameri*, *Novumbra*, and the Esocidae, the origin includes almost the entire lateral surface of the preoperculum anterior to its posterior edge. Unlike the condition in the other esocoids, the muscle actually covers the dorsal pore on the dorsal limb (however it opens to the exterior via a canal made of connective tissue that traverses the muscle to the exterior).

Also as in *Umbra*, the ventrolateral fibres and the dorsolateral fibres converge onto the sides (ventral and dorsal, respectively) of an anteroposteriorly extending ridge of tissue on the tendinous aponeurosis that extends to the lower jaw. As in *Umbra* (and probably *Novumbra*) there is no A3 subdivision. The tendinous aponeurosis on which A2 inserts is wider than in *Umbra* and *Novumbra* and unlike them does not bifurcate anteriorly. It narrows anteriorly and attaches to the coronomeckelian bone, but is unusual in that it then continues anteriorly (as a narrow ligament) along the dorsal edge of Meckel's cartilage to near the anterior end of the angulo-articular bone. A similar but thinner ligament extends from the coronomeckelian bone anteriorly in *Umbra limi*, but was absent in *Esox* and *Novumbra*.

The subdivision that lies dorsomedial to section A2 is unique to *Dallia*, and unlike that found in any other salmoniform (see Fig. 56). It is as thick (dorsoventrally) as it is wide (mediolaterally), bulbous, and extends posteriorly medial to the *levator arcus palatini*. Its posterior end is expanded and originates from a moderately wide groove extending along the entire anterior edge of the hyomandibular (from the anterodorsal corner of the head to the anteroventral corner of the ventral arm), and from the lateral surfaces of the anteroventral wing of the hyomandibular, metapterygoid (posterolateral surface), symplectic (from a concavity on the posterodorsal corner), and tendinous aponeurosis (adjacent to, but not continuous with section A2). It inserts anteriorly (mainly posterior to the lower jaw) onto a well-developed tendon that extends anteroventrally to attach to the medial surface of the angulo-articular bone and the anterior end of the ligament that extended anteriorly from the coronomeckelian bone. This tendon is not continuous, other than at its anterior end, with the tendinous aponeurosis onto which section A2 inserts. Muscle fibres extend between the tendon and the ventral tendinous aponeurosis for their entire length, and are continuous posteriorly with those of the dorsomedial subdivision. The anteriormost fibres insert in the small Meckelian fossa (it is smaller than in the other two genera) and appear to represent section Aw.

It is difficult to tell if the muscle section dorsomedial to section A2 was derived from it, and is therefore a subdivision of section A2, or whether it represents a posterior expansion of section Aw. Normally, section Aw is restricted to the Meckelian fossa and does not extend far posteriorly (although *Esox* and *Novumbra* appear to be exceptions to the rule). Although subdivisions of section A2 usually originate far posteriorly on the suspensorium and pass medial to the *levator arcus palatini*, I know of no example in which section Aw does this (also see Winterbottom 1974a). However, some evidence suggests that this section may be a posterior expansion of section Aw. First, by definition, section Aw inserts in and fills the Meckelian fossa (see Winterbottom 1974a), as does the anterior end of the subdivision in *Dallia*. The fibres filling the fossa are continuous with those of the dorsomedial subdivision and share a similar insertion and origin (but are separate from those of section A2). Thus, functionally and partly topographically this subdivision represents part of section Aw Also, the ramus mandibularis of the trigeminal nerve has the same relation to the subdivision as it does to section Aw in the other esocoids: it lies lateral to the anterodorsal end of the *adductor mandibulae* at the division of section A2 and the subdivision (Aw?) before running medial to the lower jaw. This is distinctly unlike salmoniforms in which a true dorsomedial subdivision of section A2 has been identified (the Galaxiidae and *Plecoglossus*, refer to Figs. 71, 63). In these the nerve rests anterior to the dorsomedial subdivision and section A2 (compare to Fig. 56 of *Dallia*), and then passes laterally to divide the subdivision and section A2 from section Aw (which is distinct and entirely medial to the lower jaw in the galaxiids, but absent in

Plecoglossus) before running lateral to section Aw medial to the lower jaw.

Unlike the other umbrids and the Esocidae, the coronoid-maxilla ligament in *Dallia* originates only from the lateral surface of the posterodorsal corner of the angulo-articular bone (versus the dentary in *Esox* and *Novumbra*, and both the dentary and angulo-articular in *Umbra*). As in *Novumbra*, it inserts on the dorsomedial surface of the posterior third of the maxilla.

Levator arcus palatini

The *levator arcus palatini* (LAP) in *Novumbra hubbsi* is a moderate-sized muscle with a conical shape (see Fig. 53). It originates from the sphenotic (from the spine and the area ventral to it) and inserts onto the lateral surface of the hyomandibular (from the anterior edge of the head, the anterior lamina, the anterior face of the lateral strut, the anterior half of the ventral arm, and the posterior half of the anteroventral wing). Like *Dallia*, but unlike *Umbra* and the Esocidae, there is no insertion on the metapterygoid.

The LAP in *Umbra limi* (see Fig. 54) is larger than in *Novumbra*, and roughly pear-shaped (the part medial to the *adductor mandibulae* is expanded and rather bulbous). The area of origin is also broader (the spine on the sphenotic is larger) and the insertion differs in that it includes the metapterygoid (the dorsomedial edge of the rounded endochondral expansion on the posterodorsal corner of the ventral plate). The LAP in the other two species of *Umbra* is similar to *U. limi* (see Fig. 55).

The LAP in *Dallia pectoralis* (see Fig. 56) is larger, with a broader area of origin and insertion than in *Umbra* and *Novumbra* (it is roughly rectangular in shape and rather bulbous), and has two subdivisions. Its ventral two-thirds is covered by the *adductor mandibulae*, as in *Umbra*. The anterior subdivision is larger than the posterior one. It originates from the sphenotic (from the very large spine and the area ventral to it) and the ventrolateral edge of the anterior end of the temporal sensory canal on the pterotic. It inserts onto a broad, thin aponeurosis, which in turn inserts ventrally along the hyomandibular (the anterolateral edge, from the anterodorsal corner of the head to the anteroventral corner of the ventral arm, but not the anteroventral wing), preoperculum (the lateral edge of the dorsal part of the anterior lamina), and the symplectic (the ventral edge of the concavity on the posterodorsal end). This aponeurosis lies immediately lateral to the origin of the dorsomedial "subdivision" of the *adductor mandibulae*.

The posterior subdivision is thinner than the anterior one and is conical. Its dorsolateral and anterolateral surface are covered by the anterior subdivision. It originates (via a tendinous aponeurosis) from the posterior end of the spine on the sphenotic (medial to the posterodorsal corner of the anterior subdivision). Its fibres run posteroventrally, at an angle to those of the anterior subdivision, and insert onto the lateral surface of the hyomandibular (on the anterior half of the head, the ventral arm, and the entire anterior face of the lateral strut). The medialmost fibres appear to be continuous with those of the anterior subdivision.

Dilatator operculi

The *dilatator operculi* (DO) in *Novumbra hubbsi* is moderately large, roughly conical, with a posteroventrally directed apex (see Fig. 53). The lateral surface of its anterodorsal corner is overlapped slightly by the *levator arcus palatini*. It originates from the lateral surfaces of the sphenotic (posteroventral corner), pterotic (along and ventral to the ventrolateral edge of the temporal sensory canal), and hyomandibular (most of the head and opercular arm); and inserts onto the articular process of the operculum.

The DO in *Umbra limi* is similar to the one in *Novumbra*.

The DO in *Dallia* is longer and narrower than in the other genera, with a well-developed tendon connecting it to the articular process of the operculum.

Levator operculi

The *levator operculi* (LO) in *Novumbra hubbsi* is flattened, broad, and fan-shaped (see Fig. 53). It originates from the lateral surface of the posterodorsal corner of the pterotic (posteroventral to the posteriormost temporal sensory pore). The LO expands ventrally to insert on the dorsal quarter of the medial surface of the operculum. Its anteroventralmost fibres insert along and dorsal to a poorly-developed ridge that extends posterodorsally from the articular process towards the posterodorsal corner of the bone.

The LO in *Umbra limi* is larger than in *Novumbra* and *Dallia* (only its dorsal third is visible externally, compared with its dorsal two thirds in *Novumbra*, and most of the LO in *Dallia*). It inserts broadly onto the dorsal third of the medial surface of the operculum; its ventralmost fibres inserting along, and dorsal to, a moderately well-developed ridge that extends posteriorly from the articular process to nearly the posterior edge of the bone.

The LO in *Dallia* is smaller than in the other genera, elliptical, and almost completely visible externally. It also has a broader area of origin from the pterotic and a smaller area of insertion on the operculum. It inserts narrowly on the medial surface of most of the dorsal edge (posterodorsal to the articular process). There is no medial ridge on the operculum.

Adductor operculi

The *adductor operculi* (AO) in *Novumbra hubbsi* is a moderately flattened, conical to cylindrical muscle that is almost completely covered laterally by the anterior part of the LO. It originates from the lateral surface of the pterotic (the posteroventral corner) and a small part of the exoccipital adjacent to it. The origin is medioventral to that of the LO. It inserts along the anterior part of a ridge on the medial surface of the operculum (slightly ventral to the insertion of the anterior part of the LO, and lying medial to it).

The AO in *Umbra limi* is similar to *Novumbra* but is thinner.

The AO in *Dallia* is smaller than in the other genera. It is relatively long, narrow, and thin (i.e., strap-like) and has a narrower insertion on the operculum (it does not insert onto a ridge, since it is absent).

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *Novumbra hubbsi* is a moderately long (anteroposteriorly) and thick, rectangular muscle whose anterior end is visible externally (see Fig. 53). It originates from the lateral surfaces of the parasphenoid (the posterior half, including the ascending wings), prootic (dorsal surface), pterotic (ventral surface), and exoccipital (anterodorsal surface). It inserts on the mesopterygoid (the posterior third of the dorsal surface, its lateral edge inserting along an anteroposteriorly oriented ridge that is continuous with the dorsal edge of the metapterygoid), metapterygoid (mainly the dorsomedial edge but some fibres insert along the dorsolateral surface), and the medial surface of the hyomandibular (the dorsomedial edge of the anteroventral wing, the anterodorsal part of the ventral arm, the anterior lamina, the head, and the dorsal part of the opercular arm).

A partially separate (incipient?) *adductor hyomandibulae* (AH) may be present; however, it is difficult to be sure because the muscles (the AAP and AO) are close to one another in this area. The posteriormost fibres of the AAP run at a slightly different angle than the more anterior ones, and have the same origin (the posteroventral surface of the pterotic and the adjacent part of the exoccipital) and insertion (the dorsomedial surface of the opercular arm of the hyomandibular) as is usually the case when a separate *adductor hyomandibulae* exists.

The AAP in *Umbra limi* is similar to that in *Novumbra* except that the area of insertion on the mesopterygoid is more extensive, and the insertion includes the entire dorsal surface of the dermal dorsal plate of the metapterygoid but not the medial surface. There does not appear to be an incipient *adductor hyomandibulae*, although the fibres that insert onto the hyomandibular run at a slightly different angle than the more anterior ones.

The AAP in *Dallia* is similar to that in the other genera except that it is thicker and only partly visible externally (the expanded *adductor mandibulae* obscures it). A separate, thick, and relatively short *adductor hyomandibulae* (AH) is present. The AH originates on the lateral surface of the pterotic (the posteroventral part) and inserts onto the dorsomedial surface of the opercular arm of the hyomandibular.

FAMILY SALMONIDAE

Subfamily Coregoninae

Adductor mandibulae

The *adductor mandibulae* in *Coregonus artedii* is a relatively small, thin, triangular muscle that is divided into a posterior A2 section and an anterior Aw section (see Fig. 57). The posterodorsal corner covers the lateral surface of the ventral half to third of the *levator arcus palatini*. The ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal end of the *adductor mandibulae* at the division of sections A2 and Aw before running lateral to section Aw and then medial to the lower jaw.

Section A2 is undivided and originates from the lateral surfaces of the hyomandibular (the ventral end of the ventral arm and the lateral edge of the anterior face of the lateral strut), metapterygoid (the entire surface of the vertically inclined semicircular plate), symplectic (most), quadrate (the posterodorsal end of the body and the posterior end of the quadratojugal arm), and part of the anterior edge of the preoperculum.

The fibres of section A2 converge anteriorly onto the lateral surface of a moderately long, wide, and tough tendinous aponeurosis that is slightly thickened and folded centrally. This aponeurosis bifurcates at the posterior edge of the mandible and continues along its medial surface. The ventral tendon runs anteroventrally and attaches to the coronomeckelian bone and the posterodorsal edge of Meckel's cartilage. The dorsal tendon runs anteroventrally (but less steeply than the ventral one), narrowing anteriorly to a point that lies in the Aw muscle mass and attaches near the anterior end of the angulo-articular bone. Unlike the esocoids, the dorsal tendon is narrower than the ventral one.

Section Aw is relatively small, roughly triangular, and fills the Meckelian fossa on the medial side of the lower jaw. A small part of its posterior end is visible externally. It originates from the lateral surface of the tendinous aponeurosis adjacent to the insertion of section A2, from the dorsal tendon after the aponeurosis bifurcates, and from the anterior part of the ventral tendon. Within the Meckelian fossa the fibres originating from the dorsal part of the dorsal tendon run anterodorsally whereas those originating from the ventral half and those originating from the anterior border of the ventral tendon run anteroventrally. The insertion of section Aw in the Meckelian fossa includes Meckel's cartilage, and the angulo-articular and dentary bones.

As in the Esocoidei, the *adductor mandibulae* inserts only onto the lower jaw and lacks a direct ligamentous connection with the maxilla. A moderately wide, strap-like maxilla-mandibular ligament extends from the lateral surface of the angulo-articular bone (the posteroventral corner) of the lower jaw to a knob on the dorsolateral edge of the anterior end of the maxilla. There is a single supramaxilla but no supramaxillary ligament extending from it to the lower jaw.

The *adductor mandibulae* in *Coregonus clupeaformis* is very similar to that in *C. artedii*. However, in the other two coregonine genera, *Prosopium* and *Stenodus*, there are several differences, the most important of which is that the *adductor mandibulae* has a direct ligamentous connection with the maxilla and the lateral surface of the lower jaw, that is, a complete maxilla-mandibular ligament is present as in primitive teleosts.

In *Prosopium williamsoni* (see Fig. 58) and *P. cylindraceum* the *adductor mandibulae* is larger than in *Coregonus* and is expanded anteriorly to the posterior edge of the mandible. Its anterodorsal end extends anteriorly to insert onto the coronoid process (the angulo-articular) of the lower jaw via a tendinous sheath of connective tissue. This tendinous sheath in turn continues anteriorly as a tough ligament (called section L.z on Fig. 58) that is continuous anteriorly with the part of the maxilla-mandibular ligament that extends from the lateral surface of the angulo-articular bone to a knob on the dorsolateral surface of the maxilla.

The ramus mandibularis of the trigeminal nerve in *Prosopium* passes lateral to the anterodorsal end of the *adductor mandibulae* as in the other coregonines; however, unlike them it crosses the muscle farther posteriorly and actually enters the muscle mass through which it runs anteriorly to the lower jaw (see Fig. 58). Although the path of this nerve usually divides sections A2 and Aw, it is difficult to tell if the fibres anterior to where the nerve crosses the muscle are part of section A2 or Aw because the fibres are more or less continuous in this area. A distinct Aw section is present medial to the lower jaw, but it is difficult to tell where it ends posteriorly.

The *adductor mandibulae* in *Stenodus* is slightly larger than in the other two genera (refer to Fig. 100). The posterior end of section Aw is visible externally, and originates from a pocket-like area formed by a folding of the anterodorsal part of the lateral surface of the tendinous aponeurosis. As in *Prosopium*, section A2 is connected ligamentously to the maxilla and the lateral surface of the lower jaw via a ligament (section L.z on Fig. 100) that extends anteriorly from the anterodorsal corner of the muscle to the maxilla-mandibular ligament. However, unlike *Prosopium* the *adductor mandibulae* does not insert onto the coronoid process of the lower jaw, and section L.z is reduced. Section L.z joins the maxilla-mandibular ligament farther posteriorly than in *Prosopium*.

Levator arcus palatini

The *levator arcus palatini* (LAP) in *Coregonus artedii* is a moderately large, conical muscle. It originates from the sphenotic (from its broad spine and the area ventral to it) and expands ventrally to insert mainly onto the lateral surface of the hyomandibular (the anterior edge of the head, the anterior lamina, most of the anterior face of the lateral strut, most of the anterior surface of the ventral arm, and the dorsal surface of the anteroventral wing medial to the metapterygoid). The anteroventralmost fibes insert onto the dorsomedial edge of the posterior half to two-thirds of the vertically inclined semicircular plate of the metapterygoid.

The LAP in *Coregonus clupeaformis* and *Prosopium williamsoni* is similar to that in *C. artedii*. However, in *Stenodus* it is broader anteroposteriorly with a wider origin on the skull than the other salmonids (the LAP is about as wide as it is deep dorsoventrally). Associated with this well-developed LAP is a hyomandibular that is more robust than in the other coregonines (especially the lateral strut).

Dilatator operculi

The *dilatator operculi* in *Coregonus artedii* is a moderate-sized, conical muscle with a posteroventrally directed apex. The lateral surface of the anterodorsal side is overlapped slightly by the *levator arcus palatini*. It originates from the lateral surfaces of the sphenotic (the posteroventral side), pterotic (the anteroventral side ventral to the ventrolateral edge of the anterior part of the temporal sensory canal), and hyomandibular (most of the head and perhaps some of the dorsal part of the opercular arm). It inserts onto the articular process of the operculum.

The *dilatator operculi* in *C. clupeaformis*, *Propopium williamsoni*, and *Stenodus leucichthys* is similar to that described for *C. artedii*.

Levator operculi

The *levator operculi* in *Coregonus artedii* is a flattened, moderately broad, roughly fan-shaped muscle that is only partly visible externally (see Fig. 57). It originates from the lateral surface of the posterodorsal spine of the pterotic, ventral to the posteriormost temporal sensory pore. From the rather broad origin the muscle expands ventrally to insert onto the dorsal third to quarter of the medial surface of the operculum. No part of the muscle inserts onto the short, but relatively wide, medial ridge emanating posteroventrally from the articular process.

The *levator operculi* in *C. clupeaformis*, *Propopium williamsoni*, and *Stenodus leucichthys* is similar to that described for *C. artedii*. However, in *P. williamsoni* very little of the muscle is visible externally (see Fig. 58).

Adductor operculi

The *adductor operculi* (AO) in *Coregonus artedii* is a moderately flattened, conical to cylindrical muscle that is not visible externally. It originates from the lateral surface of the posteroventral part of the pterotic and the anterodorsal corner of the exoccipital adjacent to it. It inserts along a short ridge on the medial side of the operculum that runs posteroventrally from the articular process.

The *adductor operculi* in *P. williamsoni* and *S. leucichthys* is similar to that described for *C. artedii.*

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *Coregonus artedii* is a moderately thick, roughly rectangular muscle that is only slightly visible externally. It originates from the lateral surfaces of the parasphenoid (the ascending wing), prootic (the anterior and dorsal surface), pterotic (ventral surface), and exoccipital (anter dorsal surface). It inserts exclusively on the medial surface of the hyomandibular, including the dorsal part of the opercular arm, the head, and the anterior lamina along and dorsal to a ridge that extends anteroventrally to its anterior tip.

The AAP in *Prosopium williamsoni* and *Stenodus leucichthys* is as described for *C. artedii* except that in the former two species the muscle also inserts onto the metapterygoid (along the posteromedial edge of the dorsomedially inclined anterodorsal section) as well as the hyomandibular. All coregonines that I examined lacked a separate *adductor hyomandibulae.*

Subfamily Thymallinae

Adductor mandibulae

The *adductor mandibulae* in *Thymallus arcticus* (see Fig. 59) is similar to that described for the coregonines except that the tendinous aponeurosis and dorsal and ventral tendons are thicker, and the origin from the metapterygoid includes the entire lateral surface of the posterodorsal lamina (unique to *Thymallus* and the salmonines) that overlaps the anterior lamina of the hyomandibular. As in *Coregonus artedii* the *adductor mandibulae* inserts only onto the lower jaw and lacks a direct ligamentous connection with the maxilla. The maxilla-mandibular ligament is as described for *C. artedii.* There is one supramaxilla and no supramaxillary ligament.

Levator arcus palatini

The *levator arcus palatini* is similar to that in the coregonines except that the insertion includes the entire medial surface of the posterodorsal lamina of the metapterygoid.

Dilatator operculi

The *dilatator operculi* is as described for *C. artedii.*

Levator operculi

The *levator operculi* is similar to that described for the coregonines.

Adductor operculi

The *adductor operculi* is similar to that in the coregonines except that its origin does not include the exoccipital.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) is similar to that in the coregonines except that it does not originate from the exoccipital and the anterior area of insertion is slightly different: its insertion begins anteriorly at the anterodorsal corner of the metapterygoid, runs posteriorly along its dorsomedial edge (but not onto the posterodorsal lamina), and then extends onto the hyomandibular, inserting along the anteromedial edge of the ventral two-thirds to three-quarters of the anterior lamina before extending posteriorly across its medial surface.

Unlike the Coregoninae, there is a moderately wide *adductor hyomandibulae* that is adjacent to the posterior end of the *adductor arcus palatini*. It originates from the lateral surface of the posteroventral part of the pterotic and inserts onto the dorsomedial surface of the opercular arm of the hyomandibular.

Subfamily Salmoninae

Adductor mandibulae

The *adductor mandibulae* in *Salvelinus fontinalis* is larger (covering more of the cheek) and more bulbous than in the coregonines and *Thymallus* (see Fig. 60). Unlike them, the origin includes most of the anterior edge of the preoperculum and more of the lateral surface of the hyomandibular, including the entire ventral arm and most of the anterior face of the lateral strut (which is occupied mainly by the *levator arcus palatini* in the other two subfamilies). As in *Thymallus*, the origin on the metapterygoid is from almost its entire lateral surface, including the entire surface of the posterodorsal lamina that overlaps the anterior lamina of the hyomandibular. The posterodorsal corner of section A2 covers the lateral surface of the ventral two-thirds of the *levator arcus palatini*.

As in the coregonines and *Thymallus* the fibres of section A2 converge anteriorly onto a tendinous aponeurosis; however, unlike them, the aponeurosis is distinctly larger, tougher, has a more complex shape, and is located closer to the lower jaw. At the posteroventral end of the aponeurosis is a narrow tendon that extends posterodorsally to the metapterygoid. The posteromedial fibres of section A2 insert partly onto this tendon. A similar tendon was described in *S. fontinalis* by Lauder and Liem (1980). The rest of the fibres of section A2 insert onto the wider anterior part of the tendinous aponeurosis (before it bifurcates anteriorly), the more lateral fibres inserting into a pocket-like area (almost the width of the aponeurosis) that faces posterolaterally and is formed by a folding of its lateral surface. The aponeurosis bifurcates anteriorly; however, its ventral section is distinctly shorter and wider posteriorly than in *Thymallus* and the coregonines. Section Aw is larger than in the latter two taxa and located entirely medial to the lower jaw.

As in *Coregonus* and *Thymallus* the *adductor mandibulae* inserts only onto the lower jaw and lacks a direct ligamentous connection with the maxilla. The maxilla-mandibular ligament is also similar but is slightly narrower. There is one supramaxilla and no supramaxillary ligament.

The *adductor mandibulae* in the other salmonine genera dissected (*Salmo, Oncorhynchus*, and *Brachymystax*) is similar to that in *S. fontinalis*. It is slightly smaller in *Oncorhynchus* and smaller still in *Brachymystax* (see Fig. 61). The *adductor mandibulae* in *Brachymystax* is somewhat intermediate in size and shape between the other salmonines on one hand, and the coregonines and *Thymallus* on the other.

Levator arcus palatini

The *levator arcus palatini* (LAP) in *S. fontinalis* inserts onto less of the lateral surface of the hyomandibular than in the coregonines and *Thymallus* (only the anterior half of the head and the anterior lamina). The LAP does not insert on the lateral strut. The insertion on the metapterygoid is as described for *Thymallus* but covers even more of its medial surface.

The LAP in the other salmonines examined is as described for *S. fontinalis* except that in *Brachymystax* the origin on the skull is broader and the insertion on the lateral surface of the hyomandibular includes the dorsal part of the anterior face of the lateral strut. In *Salmo trutta* the origin on the skull is as broad as in *Brachymystax*.

Dilatator operculi

The *dilatator operculi* in *S. fontinalis* and the other salmonines is similar to that in the Coregoninae and Thymallinae. I found no fibres originating on the frontal bone in *S. fontinalis* as claimed by Lauder and Liem (1980).

Levator operculi

The *levator operculi* in *S. fontinalis* and the other salmonines is similar to that in the Coregoninae and Thymallinae.

Adductor operculi

The *adductor operculi* in *S. fontinalis* and the other salmonines is similar to that in the Thymallinae and Coregoninae. Lauder and Liem (1980) claimed that in *S. fontinalis* fibres originate from both the pterotic and prootic; however, in my specimens only the former bone served as an area of origin.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *S. fontinalis* is similar to that described for *Thymallus arcticus* except that its anterior insertion includes the dorsal surface of the posteromedial corner of the mesopterygoid (medial to the anterior part of the metapterygoid). Lauder and Liem (1980) do not mention an insertion on the mesopterygoid in *S. fontinalis*; however, Greene and Greene (1913) noted that there is insertion on the mesopterygoid in *Oncorhynchus tshawytscha*. The insertion on the metapterygoid is as in *T. articus* except that it is ventral to the anterior fibres of the *levator arcus palatini* (which does not insert as far anteriorly, and therefore overlap with the AAP, in *T. arcticus* and the coregonines). The insertion on the hyomandibular is as in *T. arcticus* except that the muscle covers slightly more of the anteromedial edge and dorsomedial surface of the anterior lamina. Lauder and Liem (1980) claimed that the AAP in *S. fontinalis* originated only from the prootic but I found that the origin was more extensive (see *T. arcticus* section).

The AAP in the other salmonines examined is similar to that in *S. fontinalis*.

An *adductor hyomandibulae* similar to that described for *T. arcticus* was present in all the salmonines that I dissected (*S. fontinalis, Salmo trutta, Oncorhynchus nerka*, and *Brachymystax lenok*). Lauder and Liem claimed that it originated from the prootic in *S. fontinalis*, but in my specimens it originated only from the pterotic, as in *T. arcticus*.

FAMILY OSMERIDAE

Adductor mandibulae

The *adductor mandibulae* in *Hypomesus pretiosus* is a moderately thin, triangular muscle that is divided into a posterior A2 section and an anterior Aw section (see Fig. 62). The ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal end of the *adductor mandibulae* at the division of sections A2 and Aw before running lateral to section Aw and then medial to the lower jaw.

Section A2 is undivided and originates from the anterolateral edge of the preoperculum and the lateral surfaces of the hyomandibular (the ventral half of the ventral arm), metapterygoid (on the dorsoventrally inclined part ventral to the lateral ridge, refer to Fig. 15), symplectic, and quadrate (posterodorsal end of the body and the posterior end of the quadratojugal arm). The medial fibres insert on the lateral surface of a tendinous aponeurosis that overlies the quadrate and metapterygoid. This aponeurosis bifurcates when it passes medial to the lower jaw, the ventral tendon attaching to the coronomeckelian bone and the longer dorsal tendon attaching to Meckel's cartilage and the angulo-articular bone adjacent to the dentary. The Aw section of the *adductor mandibulae* is moderately large, oval to triangular, and fills the Meckelian fossa on the medial side of the lower jaw. It originates primarily from the dorsal tendon (anterior to section A2) and inserts onto the angulo-articular bone, the dorsal border of Meckel's cartilage, and parts of the dentary adjacent to the angulo-articular.

The dorsolateral fibres of section A2 converge onto a tough, flattened tendon (it is continuous with the dorsal part of the tendinous aponeurosis) that extends anteriorly to join the posterodorsal part of the maxilla-mandibular ligament. The maxilla-mandibular ligament extends anteriorly from the lateral surface of the posteroventral part of the angulo-articular bone to a knob on the dorsolateral surface of the anterior end of the maxilla. A relatively thin, flattened supramaxillary ligament extends posteriorly from the anterior tip of the supramaxilla to the angulo-articular bone adjacent to the posterior part of the maxilla-mandibular ligament.

The *adductor mandibulae* in the other osmerid genera dissected (*Osmerus, Allosmerus, Spirinchus, Thaleichthys*, and *Mallotus*) is very similar to that described for *H. pretiosus* (also see fig. 3 in Eaton 1935). Minor differences concern the relative size of the muscle (unusually large and bulbous in *Osmerus*), the point at which the tendon from section A2 joins the maxilla-mandibular ligament, and whether or not the posterior end of the supramaxillary ligament joins the maxilla-mandibular ligament. In *Hypomesus* section Aw is deeper dorsoventrally and shorter anteroposteriorly than in the other genera. This shape reflects a similarly shaped lower jaw that is unlike that in the other genera.

Levator arcus palatini

The *levator arcus palatini* (LAP) in *H. pretiosus* is a large, roughly conical muscle that originates from the lateral surface of the sphenotic (from the anterior and ventral part of the spine and from the anterolateral surface). It inserts mainly on the lateral surfaces of the hyomandibular (the anterior lamina, the dorsal part of the ventral arm, the anterior face of the lateral strut, and the anterior edge of the head), and metapterygoid (along and dorsal to the lateral ridge).

The LAP in the other genera is similar to that described for *H. pretiosus*. In genera with a larger metapterygoid and a reduced anterior lamina and lateral strut on the hyomandibular (*Osmerus, Allosmerus, Thaleichthys,* and *Spirinchus*), there is a larger area of insertion on the metapterygoid and a smaller area of insertion on the hyomandibular than in *Hypomesus* (and *Mallotus*).

Dilatator operculi

The *dilatator operculi* (DO) in *H. pretiosus* is a large, broadly conical muscle that originates from the lateral surfaces of the head of the hyomandibular, the sphenotic (from the posterior part of the spine and the posterior surface of the body), and the pterotic (from the anteroventral surface along and ventral to the lateral edge of the anterior part of the temporal sensory canal). It inserts broadly onto the articular process of the operculum.

The DO in the other genera is similar to that described for *H. pretiosus*.

Levator operculi

The *levator operculi* (LO) in *H. pretiosus* is a flattened, broad, roughly fan-shaped muscle that originates from the lateral surface of the posterodorsal spine of the pterotic. It expands ventrally to insert on most of the dorsal third of the medial surface of the operculum. Its anteroventralmost fibres insert along a short ridge that extends posteroventrally from the articular process.

The LO in the other genera is similar to that described for *H. pretiosus* but inserts on less of the operculum. In *Mallotus* the anterior part inserts on the dorsolateral surface of the operculum while the posterior half inserts on the dorsomedial surface.

Adductor operculi

The *adductor operculi* (AO) in *H. pretiosus* is a moderately flattened, conical to cylindrical muscle that is completely covered by the anterior part of the *levator operculi* (LO). It originates from the lateral surfaces of the pterotic and exoccipital medioventral to the origin of the LO and inserts on the medial surface of the anterodorsal corner of the operculum, along the ridge that extends posteroventrally from the articular process. The insertion is slightly ventral to the insertion of the anterior part of the LO, and lies medial to it.

The AO in the other genera differs in no significant way from that in *H. pretiosus*.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *H. pretiosus* is a thick, roughly rectangular muscle that is only slightly visible externally. It originates from the lateral surfaces of the prootic and the posteroventral part of the pterotic. It does not appear to originate on the parasphenoid. It inserts on the medial surfaces of the metapterygoid (along and dorsal to the medial ridge, refer to Fig. 15) and hyomandibular (on the anterior lamina, the head, and the opercular arm). There is no *adductor hyomandibulae*.

The AAP in the other osmerid genera is similar to that described for *H. pretiosus*. In *Spirinchus* and *Thaleichthys* its posterior end is subdivided so that there is a separate *adductor hyomandibulae* that originates on the lateral surface of the posteroventral part of the pterotic and inserts onto the dorsomedial surface of the opercular arm of the hyomandibular.

FAMILY PLECOGLOSSIDAE

Adductor mandibulae

The *adductor mandibulae* in *Plecoglossus altivelis* is a short, thick and rather bulbous muscle that has a dorsomedial subdivision and is ligamentously connected to the upper and lower jaws in an unusual way (Fig. 63). Its aberrant pattern is probably related to its highly specialized mode of feeding, and is associated with other major specializations of the jaws and the anterior part of the snout (see Chapman 1941[illegible]d Sanford 1987). The ramus mandibularis of the trigeminal nerve passes la[illegible]terodorsal end of section A2 before running medial to the lower jaw as in the O[illegible].

Section A2 originates from the mid-anterior edge of the preoperculum and the lateral surfaces of the hyomandibular (the ventralmost part of the ventral arm and the ventrolateral edge of the anterior face of the lateral strut), metapterygoid (most of the lateral surface), symplectic, and quadrate (the dorsal part of the body and the posterior end of the quadratojugal arm). The mid-medial fibres that originate primarily on the large, concave posterior wing of the metapterygoid that overlaps the hyomandibular may represent a partially separate A3 section. Section A2 has a dorsomedial subdivision, visible externally, that passes medial to the *levator arcus palatini* muscle. It originates mainly on the lateral surface of the large triangular dorsal lamina of the metapterygoid that lies adjacent to the anterior edge of the anterior lamina of the hyomandibular. Only the anteroventral fibres of this subdivision are continuous with those of the main muscle mass.

The medial fibres of the dorsomedial subdivision and the medial and ventrolateral fibres of the main muscle mass insert onto the lateral surface of a broad, tough tendinous aponeurosis that overlies the quadrate and metapterygoid. This aponeurosis narrows anteriorly into a tough, thick tendon that passes medial to the lower jaw and attaches to the coronomeckelian bone, virtually filling the greatly reduced Meckelian fossa. There is no Aw section.

The dorsolateral fibres of the main muscle mass (a partial dorsolateral subdivision), and those of the dorsomedial subdivision, converge anteriorly onto separate tendons (both are continuous with the dorsal part of the tendinous aponeurosis) that almost immediately join each other and then extend anteriorly as a single tendon that joins the posterodorsal part of the maxilla-mandibular ligament.

The maxilla-mandibular ligament is unusually broad and tough, being almost cord-like posteriorly. Its posterior end attaches directly to the shallow coronoid process of the lower jaw. The main point of attachment is the posterodorsal corner of the dentary with another section extending posteriorly onto the lateral surface of the adjacent part of the angulo-articular bone. Anteriorly the maxilla-mandibular ligament passes through an area of tough connective tissue that lies between the maxilla and the suspensorium. Unlike the condition in the other salmoniforms, its anterior end bifurcates, with the lateral branch attaching onto the anteromedial surface of the maxilla immediately posterior to its articulation with the palatine, and the medial branch attaching onto the anterolateral surface of the palatine. There is no supramaxilla and consequently no supramaxillary ligament. However, a single supramaxilla was present in the smallest specimen that I examined (55.5 mm SL) and there was a vestige in the next smallest (77.9 mm SL).

Levator arcus palatini

The *levator arcus palatini* is a moderately large, thick, conical muscle that originates from the lateral surface of the sphenotic (from the anterior and ventral part of the expanded spine and from the anterolateral surface of the body). It inserts mainly on the lateral surfaces of the hyomandibular (the anterior edge of the head, the anterior lamina, most of the anterior face of the lateral strut, and the dorsal part of the ventral arm), and metapterygoid (along the wide, curved, lateral ridge, and along the posterior edge of the dermal lamina dorsal to it).

Dilatator operculi

The *dilatator operculi* is a large, thick, conical muscle that originates from the lateral surfaces of the head of the hyomandibular and from the large concave area dorsal to it that includes the sphenotic (from the posterior part of the spine and the posterior surface of the body) and pterotic (from the anteroventral surface along and ventral to the lateral edge of the temporal sensory canal). It inserts broadly onto the articular process of the operculum.

Levator operculi

The *levator operculi* is a moderately flat, roughly fan-shaped muscle that originates primarily from the pterotic (from the lateral surface of posterodorsal spine and the lateral edge of the posteriormost part of the temporal sensory canal adjacent to it). Some fibres originate from the posterodorsal corner of the head of the hyomandibular. The muscle expands ventrally to insert onto most of the dorsal third of the medial surface of the operculum. Its ventralmost fibres insert along a ridge that extends posteroventrally from the articular process to about half way to the posterior edge.

Adductor operculi

The *adductor operculi* is a moderately flattened, conical muscle that is completely covered by the anterior part of the *levator operculi* (LO). Its origin and insertion are exactly as described for the Osmeridae.

Adductor arcus palatini

The *adductor arcus palatini* is a thick, roughly rectangular muscle that is not visible externally. It originates from the lateral surfaces of the prootic, pterotic (posteroventral surface), and parasphenoid (posterolateral surface). It inserts on the medial surfaces of the metapterygoid (along and dorsal to the medial ridge so that the dorsal dermal lamina is covered) and hyomandibular (the anterior lamina and head). There is no *adductor hyomandibulae*.

FAMILY SALANGIDAE

Adductor mandibulae

The *adductor mandibulae* in *Salangichthys ishikawae* is a relatively thin muscle that is elongated anteroposteriorally (see Fig. 64). It is divided into a posterior A2 section and an anterior Aw section. The ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal end of the *adductor mandibulae* at the division of sections A2 and Aw before running lateral to section Aw and then medial to the lower jaw. However, the nerve sits medial to the posterior end of the tendon extending from the muscle to the maxilla-mandibular ligament rather than crossing its lateral surface before running to the lower jaw as in the Osmeridae and Plecoglossidae.

Section A2 is undivided and originates from the anterolateral edge of the preoperculum and the lateral surface of the large concave cartilaginous area between the ossified body of the quadrate and the tiny ossified lateral strut. The origin also includes the anteroventral surface of the lateral strut and the dorsolateral surface of the ossified quadratojugal arm of the quadrate. The medial fibres insert onto the lateral surface of a tendinous aponeurosis before it bifurcates medial to the lower jaw. The ventral tendon attaches to the posterodorsal surface of the unusually large Meckel's cartilage (a coronomeckelian bone is absent) and the longer dorsal tendon attaches farther anteriorly.

The Aw section is long and narrow, filling the Meckelian fossa (of the same shape) on the dorsomedial part of the lower jaw. It originates primarily from the dorsal tendon (anterior to section A2) and inserts along the dorsal border of Meckel's cartilage and on the medial surfaces of the angulo-articular and dentary bones.

The ventrolateral fibres of section A2 converge onto a flattened tendon (it appears to be continuous dorsally with the tendinous aponeurosis) that extends anteriorly to join the posterodorsal part of the maxilla-mandibular ligament. The maxilla-mandibular ligament extends anteriorly from the lateral surface of the posteroventral part of the angulo-articular bone to a small protuberance on the anterodorsal end of the maxilla. A supramaxillary ligament extends from the anterior tip of the supramaxilla to the lateral surface of the angulo-articular but does not join the maxilla-mandibular ligament.

The *adductor mandibulae* in *Salanx cuvieri* is similar to that described for *Salangichthys ishikawae* except that a supramaxilla, and hence the supramaxillary ligament, is absent. All members of the genus *Salanx* lack a supramaxilla; however, one is present in all other salangids (see Roberts 1984). It was impossible to differentiate the course of the ramus mandibularis of the trigeminal nerve in my specimen of *Salanx cuvieri*.

The *adductor mandibulae* in *Salangichthys microdon* (see Fig. 65) is similar to *Salangichthys ishikawae* except that the tendon extending from the *adductor mandibulae* to the maxilla-mandibular ligament is longer, narrower, and joins the middle, rather than the posterior end of the maxilla-mandibular ligament. It was impossible to tell if a supramaxillary ligament was present. [illegible] *Salanx prognathus* (see Fig. 66) some anterolateral fibres of section A2 appear to insert directly onto the dorsal surface of the greatly enlarged Meckel's cartilage. There is no tendon extending from section A2 to the maxilla-mandibular ligament, so that the *adductor mandibulae* inserts only onto the lower jaw (otherwise the maxilla-mandibular ligament has the same position as in *Salangichthys ishikawae*). A unique ligament extends anteriorly from the dorsolateral surface of Meckel's cartilage (anterior to the insertion of section A2) to the posterior tip of the premaxilla.

Levator arcus palatini

The *levator arcus palatini* (LAP) in *Salangichthys ishikawae* is a large, bulbous muscle that originates broadly from an area of cartilage at the posterodorsal part of the orbit normally occupied by the sphenotic bone (see Fig. 64). The insertion is primarily on the lateral surface of the cartilaginous area anterior to the lateral strut, extending anteroventrally from the anterodorsal corner of the "hyomandibular" to the small ossified metapterygoid (including the anterodorsal surface of the lateral strut and the lateral surface of the metapterygoid).

The LAP in the other salangids examined is similar to that described for *S. ishikawae*.

Dilatator operculi

The *Dilatator operculi* (DO) in *Salangichthys ishikawae* is a moderately large, flat conical muscle that originates from the lateral surfaces of the "hyomandibular" dorsal and posterior to the lateral strut (including its posterior surface) and from the cartilaginous area of the skull normally occupied by the posterior part of the sphenotic and the anterior part of the pterotic. It inserts broadly onto the articular process of the operculum.

The DO in the other salangids examined is similar to that described for *S. ishikawae*.

Levator operculi

The *levator operculi* (LO) in *S. ishikawae* is a flat, thin, and broad muscle that originates from the cartilaginous posterolateral surface of the skull normally occupied by the pterotic bone. It inserts along most of the dorsomedial edge of the operculum (the operculum has no medial ridge).

The LO in the other salangids examined is similar to that described for *S. ishikawae*.

Adductor operculi

The *adductor operculi* (AO) in *S. ishikawae* is a moderately flattened, cylindrical muscle that is almost completely covered by the anterior part of the LO. It originates from the cartilaginous posterolateral surface of the skull medioventral to the origin of the anterior part of the LO and inserts onto the dorsomedial surface of the operculum anteroventral to the insertion of the anterior part of the LO.

The AO in the other salangids examined is similar to that described for *S. ishikawae*.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *S. ishikawae* is a moderately thick, rectangular muscle that is long anteroposteriorly. It is not visible externally. It originates from the cartilaginous lateral surface of the skull (primarily from the cartilaginous "prootic") ventral to the articulation of the "hyomandibular". It inserts broadly on the medial surface of the suspensorium, covering the metapterygoid and extending posteriorly to the posterior end of the "hyomandibular". Although it is difficult to tell, there may be a separate (or incipient) *adductor hyomandibulae* since the posteriormost fibres of the AAP run at a different angle, and are slightly [illegible] from those anterior to them.

The AAP in the other salangids examined is similar to that described for *S. ishikawae*; however, there appeared to be no trace of an *adductor hyomandibulae* in any of them.

FAMILY SUNDASALANGIDAE

I did not examine the muscles of the suspensorium in the Sundasalangidae nor have they been described in the literature. However, they may be generally similar to those in the Salangidae since these two families form a distinct clade based partly on their highly unusual suspensorium (also see Roberts 1981, 1984). All that can be said with certainty is that, because the sundasalangids lack a supramaxilla they undoubtedly lack a supramaxillary ligament.

FAMILY RETROPINNIDAE

Adductor mandibulae

The *adductor mandibulae* in *Retropinna retropinna* is a moderately thin, triangular muscle that is divided into a posterior A2 section and an anterior Aw section (see Fig. 67). The ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal end of the *adductor mandibulae* at the division of sections A2 and Aw before running lateral to section Aw and then medial to the lower jaw.

Section A2 is undivided and originates from the anterolateral edge of the preoperculum (including virtually all of the lateral surface of the large anterior lamina) and the lateral surfaces of the hyomandibular (the ventral arm, and the ventral surface of the anterior face of the small lateral strut adjacent to the cartilage at the posterodorsal corner of the metapterygoid), metapterygoid (on the dorsoventrally inclined part of the body ventral to the narrow posterodorsal dermal lamina), symplectic, and quadrate (posterodorsal end of the body and the posterior end of the quadratojugal arm). The medial fibres insert on the lateral surface of a tendinous aponeurosis that overlies the quadrate and metapterygoid. This aponeurosis bifurcates when it passes medial to the lower jaw, the ventral tendon attaching to the coronomeckelian bone and the longer dorsal tendon attaching farther anteriorly along and adjacent to Meckel's cartilage.

Section Aw is relatively long and narrow, filling the Meckelian fossa on the medial side of the lower jaw. It originates primarily from the dorsal tendon (anterior to section A2) and inserts onto the dorsal border of Meckel's cartilage and the angulo-articular and dentary bones.

The dorsolateral fibres of section A2 converge onto a tough, flattened tendon (it is continuous with the dorsal part of the tendinous aponeurosis) that extends anteriorly to join the posterodorsal part of the maxilla-mandibular ligament. The maxilla-mandibular ligament extends anteriorly from the lateral surface of the posteroventral part of the angulo-articular bone to the dorsal edge of the anterior end of the maxilla. There is no supramaxilla and consequently no supramaxillary ligament.

Levator arcus palatini

The *levator arcus palatini* (LAP) in *R. retropinna* is a moderately large, slightly bulbous, conical muscle that originates from the lateral surface of the sphenotic (from the spine, and from the anterolateral surface and the adjacent cartilage). It inserts onto the lateral surfaces of the hyomandibular (the anterior lamina, anterior edge of the head, and the dorsal surface of the anterior face of the lateral strut) and metapterygoid (on the narrow posterodorsal dermal lamina) and the dorsal portion of the cartilage at the posterodorsal end of the bone).

Dilatator operculi

The *dilatator operculi* (DO) in *R. retropinna* is a moderately large, broadly conical muscle that originates from the lateral surfaces of the head of the hyomandibular, the sphenotic (from the posterior surface), and the pterotic (from the anteroventral surface). It inserts broadly onto the articular process of the operculum.

Levator operculi

The *levator operculi* (LO) in *R. retropinna* is a flattened, moderately broad, roughly fan-shaped muscle that originates from the lateral surface of the posterodorsal spine of the pterotic. It expands ventrally to insert onto the dorsal third to quarter of the medial surface of the operculum.

Adductor operculi

The *adductor operculi* (AO) in *R. retropinna* is a moderately flattened, conical to cylindrical muscle that is completely covered by the anterior part of the *levator operculi* (LO). It originates from the lateral surfaces of the pterotic and exoccipital (and the cartilage between these two bones) medioventral to the origin of the LO. It inserts on the medial surface of the anterodorsal corner of the operculum, along a short ridge that extends posteroventrally from the articular process. The insertion is slightly ventral to the insertion of the anterior part of the LO, and lies medial to it.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *R. retropinna* is a moderately thick, roughly rectangular muscle that is not visible externally. It originates primarily from the lateral surfaces of the prootic and from the large area of cartilage between the prootic and pterotic. It inserts on the dorsomedial surface of the metapterygoid and on the medial surface of the hyomandibular (on the anterior lamina and the head).

Closely adjacent to, but separable from the posterior end of the AAP is a moderately wide *adductor hyomandibulae* that originates on the lateral surface of the posteroventral part of the pterotic and inserts along the dorsomedial edge of the opercular arm of the hyomandibular.

FAMILY PROTOTROCTIDAE

Adductor mandibulae

The *adductor mandibulae* in *Prototroctes maraena* (see Fig. 68) is similar to that described for *Retropinna retropinna*, but with the following differences. Unlike *Retropinna*, in *Prototroctes* the ramus mandibularis of the trigeminal nerve passes medial to the posterodorsal end of the *adductor mandibulae* before running medial to the lower jaw. It passes between the anterolateral surface of the tendinous aponeurosis and the anteromedial surface of section A2 before running medial to the lower jaw.

The area of origin and the insertion are the same as in *R. retropinna* except that there is a greater area of origin on the lateral strut (since the strut is larger and extends farther ventrally).

As in *Retropinna* the dorsolateral fibres of section A2 converge onto a tough, wide, flat tendon that is continuous with the dorsal part of the tendinous aponeurosis. However, unlike it the anterior end of this tendon almost directly joins the posterior end of the maxilla-mandibular ligament (compare Figs. 68 and 67). The posterior end of the maxilla-mandibular ligament is also broader than in *Retropinna* and attaches onto the lateral surface of the posterodorsal corner of the angulo-articular bone adjacent to the dentary rather than the posteroventral corner. Also unlike *Retropinna*, the anterior end of the maxilla-mandibular ligament attaches to a prominent finger-like extension that projects posteromedially from the anterodorsal edge of the maxilla (it is not visible on Fig. 68). There is no supramaxilla.

Levator arcus palatini

The *levator arcus palatini* in *P. maraena* is similar to that described for *R. retropinna* except that there is no insertion on the dorsal surface of the anterior face of the lateral strut (since this part is covered entirely by the large cartilage at the posterodorsal end of the metapterygoid).

Dilatator operculi

The *dilatator operculi* in *P. maraena* is similar to that described for *R. retropinna.*

Levator operculi

The *levator operculi* in *P. maraena* is similar to that described for *R. retropinna.*

Adductor operculi

The *adductor operculi* in *P. maraena* is similar to that described for *R. retropinna.*

Adductor arcus palatini

The *adductor arcus palatini* in *P. maraena* is similar to that described for *R. retropinna.* A similar *adductor hyomandibulae* is present.

FAMILY LEPIDOGALAXIIDAE

Adductor mandibulae

The *adductor mandibulae* in *Lepidogalaxias salamandroides* is a moderately thick, bulbous muscle that extends unusually far dorsally (see Fig. 69). The ramus mandibularis of the trigeminal nerve passes medial to the anterodorsal end of the *adductor mandibulae* before running medial to the lower jaw. It passes between the anterolateral surface of the tendinous aponeurosis and the anteromedial surface of section A2 before running medial to the lower

Section A2 extends dorsally onto the skull (dorsal to the spine on the sphenotic), overlapping (and partly originating from) the lateral surface of the *levator arcus palatini* (the ventral half to two-thirds) and part of the anterolateral surface of the *dilatator operculi* (dorsal to the preoperculum). The thicker and larger ventral part of the muscle originates from the preoperculum (the dorsal tip, the anterior edge and the anterolateral surface), and the lateral surfaces of the hyomandibular (the ventral part of the anterior facing surface of the lateral strut), symplectic (all except the posterodorsal corner), and quadrate (most of the body and quadratojugal arm). What might be interpreted as a partial (incipient?) dorsomedial subdivision, similar to that described for *Aplochiton taeniatus*, was found in the larger specimen (WAM P8124-31, 39.7 mm SL). However, unlike *Aplochiton*, it appears to originate from the symplectic and the *levator arcus palatini*.

The medial fibres of section A2 (including the "subdivision") insert onto a tough, moderately long, flat, narrow tendinous aponeurosis (not visible externally) that overlies the quadrate and extends anteriorly medial to the lower jaw to attach onto the coronomeckelian bone. The tendinous aponeurosis does not bifurcate anteriorly. An Aw section of the *adductor mandibulae* is absent.

The lateral fibres of section A2 insert ligamentously onto both the maxilla and lower jaw in a way that is similar to that in the Galaxiidae (especially) and Aplochitonidae. They converge anteriorly to fit into a tough ligamentous "glove" that is open posteriorly. The glove, in turn, inserts directly onto the medial and lateral surfaces of the coronoid process (dentary) of the lower jaw (refer to Fig. 69). There does not appear to be a short, separate ligament extending ventrally from this insertion to the angulo-articular bone (as there is in the Aplochitonidae and most Galaxiidae, labelled L.y on Figs. 70-72), and in this respect it resembles the galaxiid *Neochanna apoda*. Extending anteriorly from the anterodorsal part of the ligamentous glove is a tough, relatively short, flattened strap-like ligament that inserts directly onto the dorsal edge of the posterior third of the maxilla. As in the Galaxiidae, this ligament (and the ligamentous glove) is not continuous with the tendinous aponeurosis that extends to the coronomeckelian bone.

Like the Aplochitonidae and Galaxiidae there is no supramaxilla (and consequently no supramaxillary ligament). A short, tough ligament extends from the middle of the medial surface of the posterior end of the maxilla to the coronoid process (dentary) of the lower jaw (anterior to the insertion of the *adductor mandibulae*).

Levator arcus palatini

The *levator arcus palatini* (LAP) is a moderately large, moderately thick, barrel-shaped muscle with a shape reminiscent of that in the Galaxiidae (but flatter). About two thirds of its ventrolateral surface is covered by the *adductor mandibulae*. Its origin is unusual in that it includes the dorsolateral surface of the skull dorsal to the spine on the sphenotic. It originates from the lateral surfaces of the sphenotic (covering most of the spine and the entire area anterior and dorsal to it), pterosphenoid, possibly the prootic (anterodorsal corner) and pterotic (anterodorsal surface), and the lateral edges of the frontal and parietal. It inserts on the lateral surfaces of the hyomandibular (the anterior lamina, the entire ventral arm, and the dorsal part of the anterior facing surface of the lateral strut as well as the dorsal edge of the strut), symplectic (posterodorsal corner), and palatoquadrate cartilage (posterodorsal corner).

Dilatator operculi

The *dilatator operculi* (DO) is a moderately thin, fan-shaped muscle that has an origin and insertion similar to that described for *Galaxias maculatus*. However, unlike it the origin includes the entire lateral surface of the head and most of the lateral surface of the opercular arm of the hyomandibular.

Levator operculi

The *levator operculi* (LO) is similar in shape and origin to that in *G. maculatus* (see Fig. 69). However, unlike the galaxiids and aplochitonids the LO inserts only along the dorsal edge of the operculum (mostly along the dorsomedial edge but with the lateralmost fibres extending onto the dorsolateral surface). There is no distinct opercular ridge along which the muscle inserts, although the dorsal edge of the bone is somewhat thickened and rounded.

Adductor operculi

The *adductor operculi* (AO) is a moderately flattened, conical to cylindrical muscle that is broader anteroposteriorly than in the Galaxiidae and is partly visible externally. It originates mainly from the lateral surface of the pterotic (the posteroventral part medioventral to the origin of the LO) as in *G. maculatus*, but some fibres also originate on the lateral surface of the exoccipital adjacent to the pterotic. It inserts about half way along the dorsomedial edge of the operculum (beginning anteriorly at the posterior end of the articular process and extending posteriorly to insert slightly ventral to the insertion of the anterior part of the LO, and lying medial to it). There is no distinct opercular ridge along which the AO inserts.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) is a moderately long (anteroposteriorly), moderately thick, rectangular muscle whose anterior end is visible externally (see Fig. 69). It originates from the same area as described for *G. maculatus* but covers more of the lateral surface of the prootic and less of the pterotic. The insertion is very similar to that in *Lovettia sealii* and includes the hyomandibular (virtually the entire medial surface), the palatoquadrate cartilage (the entire dorsomedial edge posterior to the metapterygoid, the metapterygoid (the entire lateral surface) and the mesopterygoid (the posterodorsal surface adjacent to the metapterygoid to about level with the condyle of the quadrate). There is no *adductor hyomandibulae*.

FAMILY GALAXIIDAE

Adductor mandibulae

The *adductor mandibulae* in *Galaxias maculatus* is moderately thick, extends farther anteriorly than in most other salmoniforms, is ligamentously connected to the upper and lower jaws in an unusual way, and has a small dorsomedial subdivision (see Fig. 70). The ramus mandibularis of the trigeminal nerve passes medial to the anterodorsal end of the *adductor mandibulae* before running medial to the lower jaw. It passes between the [illegible]eral surface of the tendinous aponeurosis and the anteromedial surface of section A2 [illegible]ning medial to the lower jaw.

[illegible] A2 originates from the anterior edge and anterolateral surface of the [illegible] (including the entire anterior lamina) and the lateral surfaces of the [illegible] (the ventral arm, the lateral edge and posterior facing surface of the lateral [illegible] the anteroventral surface of the opercular arm medial to the preoperculum), metapterygoid (most of the lateral surface), symplectic, and quadrate (most of the body and quadratojugal arm). Section A2 has a small dorsomedial subdivision, slightly visible externally, that passes medial to the *levator arcus palatini*. It originates mainly from the dorsolateral surface of the anterior, triangular endochondral portion of the metapterygoid, and from the posterior dermal lamina medial to the rounded ridge onto which part of the *levator arcus palatini* inserts. The anteroventral fibres of the subdivision are continuous with those of the main muscle mass.

The medial (including the subdivision) and posterodorsal fibres of section A2 insert onto a tough, moderately narrow tendinous aponeurosis (that is visible externally when the *adductor mandibulae* is viewed dorsolaterally). This aponeurosis overlies the quadrate and metapterygoid and bifurcates when it passes medial to the lower jaw, the ventral tendon attaching to the coronomeckelian bone and the longer (but narrower) dorsal tendon attaching to Meckel's cartilage and the angulo-articular bone adjacent to the dentary. Section Aw of the *adductor mandibulae* is moderately small, elliptical when viewed medially, and fills the

Meckelian fossa on the dorsomedial side of the lower jaw. It originates primarily from the dorsal tendon (anterior to section A2) and inserts on the angulo-articular bone, the dorsal border of Meckel's cartilage, and parts of the dentary adjacent to the angulo-articular.

The ventrolateral fibres of section A2 converge anteriorly into a tough, moderately narrow, somewhat flattened strap-like ligament (it is not continuous with the tendinous aponeurosis) that extends anteriorly to insert onto the dorsolateral surface of the middle of the maxilla (on the posterior edge of a laterally projecting flange that runs along the lateral surface of the anterior part of the bone). The anterior end of section A2 that conver[illegible] this ligament is unusual in that it extends farther anteriorly than in most other salmoniforms and actually overlaps part of the posterolateral surface of the lower jaw (see Fig. 70). A unique ligamentous arrangement that attaches section A2 onto the posterior part of the lower jaw is revealed if the anterolateral fibres of section A2 are removed (see Fig. 70). A relatively short and narrow ligament (section L.y on Fig. 70) extends ventrally from the posteriormost end of the ligament connecting section A2 directly to the maxilla (section L.x on Fig. 70) to join the angulo-articular bone immediately dorsal to the joint with the quadrate. In addition, another separate, moderately long, narrow ligament (section L.w on Fig. 70) extends anteroventrally from the intersection of ligaments L.x and L.y to insert onto the coronoid process (the posterodorsal corner of the dentary) of the lower jaw.

There is no supramaxilla and consequently no supramaxillary ligament. A short, but tough ligament extends from the middle of the medial surface of the slightly expanded posterior end of the maxilla to the coronoid process (dentary) of the lower jaw.

The *adductor mandibulae* in the other galaxiids dissected (*Galaxias brevipinnis*, *G. fasciatus*, *G. paucispondylus*, *Brachygalaxias bullocki*, and *Neochanna apoda*) is basically similar to that in described for *G. maculatus*. However, there are several notable differences concerning the relative size of the muscle, its shape, and the length and the degree of development of the ligaments connecting section A2 to the upper and lower jaws.

The *adductor mandibulae* in *Brachygalaxias* is similar in shape and relative size to that *G. maculatus*. In *G. paucispondylus* it is elongated anteroposteriorly, roughly elliptical when viewed laterally, and does not extend as far posterodorsally as in the other species. In *G. fasciatus* (see Fig. 71), *G. brevipinnis*, and *Neochanna* (especially) the muscle is shorter anteroposteriorly, thicker, and more bulbous than in the other galaxiids. In *Neochanna* it is especially large, shaped like a sphere that is flattened slightly mediolaterally, and expanded onto the skull roof. It entirely covers the *levator arcus palatini* and *dilatator operculi*. Its origin includes about half the posterodorsal surface of the roof of the skull (including the frontal, parietal, dorsal surface of the sphenotic, anterolateral surface of the epaxial muscle mass, and the spine on the posterodorsal part of the pterotic next to the origin of the *levator operculi*) in addition to the normal sites of origin. All galaxiids examined had a dorsomedial subdivision of section A2 that was approximately the same size.

The ligament extending from section A2 to the maxilla (section L.x on Figs. 70, 71) is shorter, broader and inserts farther posteriorly on the maxilla in the other galaxiids than in *G. maculatus*. In *G. paucispondylus* and *Neochanna* ligament L.x is short, moderately broad, and inserts about a third of the way from the posterior end of the maxilla, whereas in *Brachygalaxias*, *G. brevipinnis*, and *G. fasciatus* (see Fig. 71) it is slightly longer and inserts slightly farther anteriorly. Only the latter two species have a distinct lateral flange on the maxilla onto which the ligament inserts (as in *G. maculatus*).

Like *G. maculatus*, in *G. paucispondylus*, *G. brevipinnis*, *G. fasciatus* (see Fig. 71), and *Brachygalaxias* a relatively short, narrow ligament (section L.y on Fig. 71) extends ventrally from the posteriormost end of ligament L.x to join the angulo-articular bone of the lower jaw next to the quadrate joint. Also like *G. maculatus*, all the other galaxiids have a separate ligament (section L.w on Fig. 71) that extends anteroventrally from the intersection of ligaments L.x and L.y to attach section A2 directly onto the coronoid process (invariably the posterodorsal corner of the dentary) of the lower jaw. The shape and size of this ligamentous connection, however, is quite variable. The ligament (L.w) in *G. paucispondylus* is similar to that in *G. maculatus* but is broader and shorter. In *Brachygalaxias*, *G. brevipinnis*, and *G. fasciatus* (see Fig. 71) it is shorter and broader than in *G. paucispondylus* and forms a tough ligamentous sheath that inserts broadly onto the coronoid process. In *Neochanna* this ligamentous sheath is even larger and extends ventrally onto the angulo-articular bone, as well as inserting onto the dentary. Unlike the other galaxiids, *Neochanna* lacks a distinct L.y ligament that joins the angulo-articular. However, a vestige of section L.y was present [illegible] the posteroventral corner of the ligamentous sheath on one side of each of the two specimens that I examined.

As in *G. maculatus*, all the other galaxiids have a ligament extending from the posteromedial surface of the maxilla to the coronoid process. Although distinguishable in *Neochanna*, this ligament is more difficult to locate because it is found in a large, broad sheet of tough connective tissue that also extends between the posteromedial surface of the maxilla and the dentary. In *G. paucispondylus* a ligament also extends from the posterior tip of the premaxilla to the middle of the posteromedial surface of the maxilla.

Levator arcus palatini

The *levator arcus palatini* (LAP) in *G. maculatus* is a large, thick, laterally bulbous, barrel-shaped muscle with an unusually broad area of origin on the skull (see Fig. 70). As in *Lepidogalaxias*, its origin includes the dorsolateral surface of the skull dorsal to the spine on the sphenotic. It originates from the lateral surfaces of the pterosphenoid, prootic (anterodorsal corner), sphenotic (covering most of the spine and the entire area anterior and dorsal to it), and the lateral edges of the frontal and parietal. It inserts on the lateral surfaces of the hyomandibular (the anterior lamina, the anterior edge of the head, and the entire anterior facing surface of the lateral strut) and metapterygoid (along the dorsal side of the rounded ridge on the posteroventral surface, and on the posteroventral corner adjacent to the lateral strut).

Except for slight proportional differences, the LAP is similar in *G. paucispondylus*, *G. brevipinnis*, and *G. fasciatus* (see Fig. 71). In *Brachygalaxias* the LAP is smaller, conical, not expanded dorsally, and originates only from an area of cartilage normally occupied by the sphenotic (most of the posterior part of the skull is cartilaginous). The LAP in *Neochanna* is entirely covered laterally by the greatly enlarged *adductor mandibulae* and has a very broad area of origin (primarily along the lateral edges of the frontal and pterosphenoid in the wide gap between the tiny eye and the sphenotic). From its origin the muscle narrows posteroventrally to insert on the same bones as in *G. maculatus*.

Dilatator operculi

The *dilatator operculi* (DO) in *G. maculatus* is a moderately large, broadly conical muscle that originates from the lateral surfaces of the hyomandibular (primarily from the head), the sphenotic (from the posterior part of the spine and the posteroventral surface), and the pterotic (from the anteroventral surface). It inserts broadly onto the articular process of the operculum.

The DO in the other species is similar to that in *G. maculatus*. However, in *N. apoda* it is unusually small relative to the other muscles and is entirely covered laterally by the *adductor mandibulae*.

Levator operculi

The *levator operculi* (LO) in *G. maculatus* is a moderately large, slightly bulbous, fan-shaped muscle that originates from the lateral surface of the posterodorsal spine of the pterotic. It expands ventrally to insert on most of the dorsal third of the medial surface of the operculum posterior to the articular process. Its anteriormost fibres insert along a short ridge that extends posteroventrally from the articular process.

The LO in *G. brevipinnis*, *G. paucispondylus*, *G. fasciatus*, and *Brachygalaxias* is similar to that in *G. maculatus* except that it inserts onto more of the operculum (the dorsal third to half). In *Neochanna* the LO is larger and thicker than in the other species. It overlaps about the dorsal two thirds of the medial surface of the operculum (posterior to the articular process) and the corresponding area on the lateral surface.

Adductor operculi

The *adductor operculi* (AO) in *G. maculatus* is a moderately flattened, conical to cylindrical muscle that is completely covered by the anterior part of the *levator operculi* (LO). It originates from the lateral surface of the posteroventral part of the pterotic (medioventral to the origin of the LO) and inserts along a ridge on the medial surface of the anterodorsal corner of the operculum slightly ventral to the insertion of the anterior part of the LO, and lying medial to it.

The AO in the other galaxiids examined is similar to that described for *G. maculatus*. In *Neochanna* it is unusually small relative to to the other muscles of the suspensorium.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *G. maculatus* is a long (anteroposteriorly), moderately thick, rectangular muscle whose anterior end is visible externally (see Fig. 70). It originates from the posterolateral surface of the parasphenoid and from the lateral surfaces of the prootic and pterotic (the ventral part). It inserts on the posterodorsal surface of the mesopterygoid (extending anteriorly to about level with the condyle of the quadrate) and the medial surfaces of the metapterygoid (along and dorsal to the medial flange) and hyomandibular (the anterior lamina, the head, and the opercular arm). There is no *adductor hyomandibulae*.

The AAP in the other galaxiids examined is similar to that described for *G. maculatus*. The other species (except for *G. fasciatus*, which was not checked) lacked a flange on the medial side of the metapterygoid onto which part of the AAP inserted. The other species also lacked an *adductor hyomandibulae* (*Brachygalaxias* was not checked). The anterior end of the AAP was visible externally in all species except for *Neochanna* (in which it occupied the same position as the others but was obscured by the *adductor mandibulae* and *levator arcus palatini*).

FAMILY APLOCHITONIDAE

Adductor mandibulae

The *adductor mandibulae* in *Aplochiton taeniatus* is a moderately thin muscle that is elongated anteroposteriorly (Fig. 72). The path of the ramus mandibularis of the trigeminal nerve is as described for the Galaxiidae and Lepidogalaxiidae.

Section A2 originates from the same area as described for *Galaxias maculatus*. It does not extend as far anteriorly as in the galaxiids, just barely overlapping the posterolateral surface of the lower jaw. There is a small, partial (incipient?) dorsomedial subdivision (not visible externally) whose dorsolateral fibres can be separated from those of the main muscle mass. Unlike *G. maculatus* this subdivision does not pass medial to the *levator arcus palatini* (although its medialmost fibres run posteromedially as do those of the galaxiid subdivision) and the ventral fibres are continuous with those of the main part of the muscle. It originates primarily from the lateral surfaces of the metapterygoid (ventral to a line drawn along the dorsal edge of the posterior tube-like extension) and symplectic (posterodorsal part)

The medial fibres of section A2 (including the subdivision) insert onto a tough, moderately narrow tendinous aponeurosis (not visible externally) that overlies the quadrate and metapterygoid and bifurcates when it passes medial to the lower jaw. The ventral tendon attaches to the coronomeckelian bone and the longer (but narrower) dorsal tendon attaches to Meckel's cartilage and the angulo-articular bone adjacent to the dentary. Section Aw of the *adductor mandibulae* is as described for *G. maculatus* but is larger.

The lateral fibres of section A2 converge anteriorly onto a long, tough, moderately wide, flattened, strap-like ligament (it is barely continuous at its posterodorsal corner with the tendinous aponeurosis) that extends anteriorly to insert onto a well-developed flange on the dorsolateral surface of the anterior end of the maxilla. As in *G. maculatus*, a relatively short, narrow ligament (section L.y on Fig. 72) extends ventrally from the posteriormost end of the aforementioned ligament (section L.x on Fig. 72) to the lateral surface of the angulo-articular bone immediately dorsal to the joint with the quadrate. Also like *G.*

maculatus, a ligament (section L.w on Fig. 72) extends anteroventrally from the intersection of ligaments L.x and L.y to insert onto the coronoid process (dentary) of the lower jaw. The ligament in *Aplochiton*, however, is thinner and less distinct than in *G. maculatus*.

Unlike [illegible] [illegible], *Aplochiton* has a unique ligament (L.m on Fig. 72), separate from the [illegible] mandibular ligament (but continuous with it at both ends, and possibly derived [illegible]) that extends from the ventral end of section L.y of the maxilla-mandibular ligament to the anterior end of section L.x where it inserts onto the maxilla. A similar ligament is present in the other aplochitonid genus, *Lovettia*.

As in the Galaxiidae and Lepidogalaxiidae there is no supramaxilla, and consequently no supramaxillary ligament. A short, tough ligament extends from the posteromedial surface of the maxilla to the coronoid process of the lower jaw.

The *adductor mandibulae* in *Lovettia sealii* is similar in most respects to that described for *Aplochiton*. There does not appear to be a partial dorsomedial subdivision of section A2; however, because of the small size of the specimens it is difficult to be sure. The ligamentous connections are similar to *Aplochiton* as are the general shape and proportions of the muscle. I am uncertain whether or not the posteriormost end of the ligament extending from the *adductor mandibulae* to the maxilla is connected to the tendinous aponeurosis. The course of the ramus mandibularis of the trigeminal nerve is as in *Aplochiton*. Although the hyomandibular lacks a lateral strut the origin of section A2 on that bone is essentially as in *Aplochiton*.

Levator arcus palatini

The *levator arcus palatini* (LAP) in *Aplochiton* is a moderately broad, roughly conical muscle that originates from the spine and the anterolateral surface of the sphenotic (see Fig. 72). It inserts on the lateral surface of the hyomandibular (the very narrow anterior lamina, the anterior edge of the head, the entire anterior face of the lateral strut, and the anterolateral surface of the ventral arm), and the dorsal edge of the posterior half of the posterior tube-like extension of the metapterygoid.

The LAP in *Lovettia* is similar to that described for *Aplochiton*. However, the origin is slightly different because the sphenotic is almost entirely cartilage (as is much of the posterior part of the skull). The insertion is on the lateral surfaces of the hyomandibular (the anterior edge of the head and the anterolateral surface of the ventral arm) and symplectic (posterodorsal corner). The hyomandibular has no lateral strut or anterior lamina.

Dilatator operculi

The *dilatator operculi* (DO) in *Aplochiton* is similar to that described for *G. maculatus* except that there is no origin on any part of the sphenotic spine and there is a large area of origin on the broad area of cartilage between the sphenotic and pterotic. The same is true of *Lovettia* except that the origin is almost entirely from cartilage (the sphenotic and pterotic are indistinct and only slightly ossified).

Levator operculi

The *levator operculi* (LO) in *Aplochiton* is a moderately small, flattened, fan-shaped muscle. Its origin and insertion are as in *G. maculatus* except that it inserts onto a smaller area of the operculum (the dorsal quarter or less).

The LO in *Lovettia* is as in *Aplochiton* (but the operculum is shorter dorsoventrally and the medial ridge onto which the anterior fibres of the LO insert is shorter and less distinct).

Adductor operculi

The *adductor operculi* in *Aplochiton* and *Lovettia* is similar to that in *G. maculatus*.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *Aplochiton* is a moderately long (anteroposteriorly), moderately thick, rectangular muscle whose anterior end is visible externally (see Fig. 72). It originates from the same area as in *G. maculatus*. The insertion is on the mesopterygoid (the posterodorsal surface adjacent to the metapterygoid), metapterygoid (the dorsomedial surface of the posterior tube-like extension and the adjacent dorsomedial edge of the anterior triangular section medial to the origin of the *adductor mandibulae*), and hyomandibular (as in *G. maculatus*). There is no *adductor hyomandibulae*.

The AAP in *Lovettia* is as described for *Aplochiton* except that it inserts on the entire lateral surface of the metapterygoid, which is only slightly ossified. It has no *adductor hyomandibulae*.

FAMILY ALEPOCEPHALIDAE

Adductor mandibulae

The *adductor mandibulae* in *Alepocephalus tenebrosus* is a moderately large and thick muscle that is divided into a posterior A2 section and an anterior Aw section (see Fig. 73). The ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal end of the *adductor mandibulae* at the division of sections A2 and Aw before running lateral to section Aw and then medial to the lower jaw.

Section A2 originates from the anterior edge of the preoperculum and the lateral surfaces of the hyomandibular (the entire ventral arm and most of the anterior face of the lateral strut), metapterygoid, symplectic, and quadrate (posterodorsal end of the body and the posterior end of the quadratojugal arm). The medial fibres insert onto the lateral surface of a tendinous aponeurosis that overlies the quadrate and part of the metapterygoid. The dorsolateral fibres converge onto a tough, flat ligament (it is continuous with the dorsal part of the tendinous aponeurosis) that extends anteriorly to insert onto the dorsolateral surface of the anterior part of the maxilla. The anteriormost dorsolateral fibres that join this ligament can be separated from the fibres medial to them, and represent a partial subdivision of section A2. Unlike in more primitive salmoniforms this ligament (section L.z-L.x on Fig. 103) does not send a posteroventral branch to the lateral surface of the angulo-articular bone (i.e., section L.y on Fig. 103 is absent and presumed lost).

The tendinous aponeurosis bifurcates when it passes medial to the lower jaw, the ventral tendon attaching to the coronomeckelian bone and the longer dorsal tendon attaching to Meckel's cartilage and the angulo-articular bone adjacent to the dentary. Section Aw of the *adductor mandibulae* is moderately large, roughly triangular to rectangular, and fills the Meckelian fossa on the medial side of the lower jaw. It originates primarily from the dorsal tendon anterior to section A2 and inserts on the angulo-articular bone, the dorsal border of Meckel's cartilage, and parts of the dentary adjacent to the angulo-articular.

The *adductor mandibulae* in the other alepocephalid genera examined (*Xenodermichthys, Rouleina, Bathytroctes, Talismania, Binghamichthys, Leptoderma, Conocara, Narcetes, Photostylus, Bajacalifornia,* and *Bathylaco*) is basically similar to that described for *A. tenebrosus*; however, there is still considerable variation within the family (see Figs. 74-81; also see Markle 1976, 1980; Markle and Merrett 1980). All possess the *adductor mandibulae* — maxilla ligament; however, its length and point of insertion on the maxilla vary from genus to genus. As in *Alepocephalus*, the insertion is on the dorsolateral surface of the anterior third to half of the maxilla in *Xenodermichthys, Rouleina* (see Fig. 74), *Narcetes* (see Fig. 75), *Bajacalifornia, Bathytroctes, Talismania* (see Fig. 76), *Binghamichthys* (see Fig. 77), and *Bathylaco* (see Fig. 78). However, in *Photostylus* (see Fig. 79) the insertion is on the dorsomedial surface of the anterior third whereas in *Conocara* (see Fig. 80) and *Leptoderma* (see Fig. 81) the ligament inserts onto a knob on the dorsolateral surface of the anterior condyle. In three genera (*Rouleina, Narcetes,* and *Xenodermichthys*) there is a thin and delicate ligamentous slip that extends ventrally from the posteriormost end of the main ligament to the posterolateral surface of the angulo-articular bone (labelled L.yr on Figs. 74, 75). This might represent a remnant of the well-developed ventral ligamentous branch (section L.y on Fig. 4) found in other salmoniforms (the Osmeridae for example). In *Bathylaco* and *Photostylus* there is an additional ligament extending anteriorly from the lateral surface of the angulo-articular bone to the maxilla (see Figs. 78, 79). Thin sheets of folded connective tissue were found in the same area in the other genera.

In *Leptoderma* (like *Alepocephalus*) the anterolateralmost fibres of section A2 that converge on the *adductor mandibulae* — maxilla ligament can be separated from the fibres medial to them and represent a partial subdivision (this is not visible on Fig. 81). In *Talismania* and *Binghamichthys* (which Markle 1976, synonymizes with *Talismania*) a lateral part of section A2 has totally subdivided so that there is a separate A1 section that inserts ligamentously onto the maxilla (section A2 now inserts only onto the lower jaw). In *T. bifurcata* and *B. aphos* (and apparently *T. oregoni* according to Markle 1976) section A1 covers the dorsal two-thirds of section A2 whereas in *T. antillarum* section A1 is smaller and covers only the middle third of section A2 (see Figs. 76, 77). In *Leptochilichthys* there is also a separate dorsolateral A1 subdivision that inser[illegible]amentously onto the dorsolateral surface of the middle of the maxilla (see Markle 1976). Section A2 in *Leptochilichthys* is also subdivided into sections A2α (ventrolateral) and A2β (the main part) that insert only onto the lower jaw.

Bathylaco has a small, narrow dorsolateral A1 subdivision that inserts, via a short but wide ligament, onto the dorsal edge of the middle of the maxilla (see Fig. 78). A narrow slip of muscle extends anterodorsally from the anteroventral corner of section A2 to join the anteroventral corner of the A1 subdivision where it attaches to the ligament that extends to the maxilla. The large A2 section inserts onto a broad tendinous aponeurosis that bifurcates and inserts onto the medial surface of the mandible as in the other alepocephalids. A short, narrow, but tough ligament extends anteriorly from the coronoid process of the lower jaw to the dorsomedial surface of the posterior end of the maxilla. Because it rests medial to the supramaxilla and maxilla when the mouth is closed it is not visible externally.

My description of the *adductor mandibulae* in *Bathylaco* differs notably from Markle's [illegible]76); however this may be related to the size of the specimens since the one I dissected was smaller (SIO 64-15, 84.4 mm SL) than the one he examined (268 mm). He does not mention the coronoid-maxilla ligament, the dorsolateral A1 subdivision (or the slip of muscle that joins its anterior end), or the ligament that connects the *adductor mandibulae* to the maxilla. Instead he claims that section A2 has two subdivisions: a broad dorsolateral A2α section that inserts directly onto the maxilla and a larger A2β section that inserts adjacent to it on the maxillary (as well as apparently extending to the lower jaw).

Markle's descriptions of some other alepocephalids also differ from my observations. For instance, on his figure 3A of *Conocara* a ligament extends from the middle of the dorsal edge of section A2 to the maxilla. However, in my specimen (see Fig. 80) this ligament extends anteriorly from the anterodorsal corner of section A2 ~~(as is typical)~~. Because the posterior end of section Aw is located posterior to the lower jaw, extends to the anterior tip of section A2, and is visible externally, Markle might have misidentified it as the anterior end of section A2, hence the unusual origin of the ligament on his figure. Another discrepancy concerns *Narcetes*. Markle (p. 8) claimed that section A2 "has both a tendinous insertion midway along the maxillary and a musculous insertion anteriad on the maxillary and also on the ventral surface of the lacrimal." Although in my specimen section A2 was connected to the maxilla via a tough ligament, there was no direct muscular connection with the maxilla or lacrimal as claimed by Markle (see Fig. 75).

Levator arcus palatini

The *levator arcus palatini* (LAP) in *A. tenebrosus* (see Fig. 73) is a moderately large, broadly conical muscle that originates from the lateral surface of the sphenotic (from the spine and its vicinity). It inserts on the lateral surface of the hyomandibular (the anterior lamina, the dorsal part of the ventral arm, the dorsal part of the anterior face of the lateral strut, and the anterior edge of the head); and on the dorsomedial surface of the posterior part of the metapterygoid (along and dorsal to the medial ridge; refer to Fig. 35). The fibres of the posterolateral part are slightly separable from those medial to them and insert along a ridge on the lateral surface of the hyomandibular that extends anterodorsally from the lateral strut to the anterodorsal corner of the head.

The LAP in *Asquamiceps* (see Markle 1980), *Xenodermichthys*, *Binghamichthys*, *Talismania*, *Conocara*, and *Bathylaco* is similar to that in *A. tenebrosus*. In *Talismania* and *Binghamichthys* the insertion on the medial surface of the metapterytoid is only on the posterodorsalmost corner of the bone (also see *adductor arcus palatini*). In *Rouleina*, *Bathytroctes*, *Narcetes*, *Leptoderma*, *Bajacalifornia*, and *Photostylus* the muscle is larger (especially *Narcetes*) and somewhat barrel-shaped with an expanded posterior section that originates on the anterolateral surface of the pterotic as well as the sphenotic. It appears similar in *Ericara*, *Einara*, *Bathyprion*, *Leptochilichthys*, and *Rinoctes* judging from figures and descriptions in Markle (1976) and Markle and Merrett (1980). Most species lacked a subdivision of the LAP; however, like *A. tenebrosus*, *Xenodermichthys copei* had what might be interpreted as a partial posterolateral subdivision. *Leptoderma* had a complete posterior subdivision of the LAP that was thin, roughly rectangular dorsoventrally, and slightly overlapped the posterolateral edge of the main anterior section of the muscle. The posterior subdivision originated broadly from the lateral surfaces of the anterior part of the pterotic and the posterior part of the sphenotic, and inserted onto the lateral surface of the hyomandibular. The LAP inserted only on the hyomandibular in *Leptoderma*.

Dilatator operculi

The *dilatator operculi* (DO) in *A. tenebrosus* is a moderately large, conical muscle that originates from the lateral surfaces of the head of the hyomandibular, the sphenotic (the posterior part of the spine and posterior part of the body), and the pterotic (the anterior part). It inserts, via a tendon, onto the articular process of the operculum.

The dilatator operculi in the other alepocephalids examined is similar to that described for *A. tenebrosus*. Main differences concern size and the degree to which the LAP overlaps the anterolateral surface of the muscle (the wider the part of the LAP posterior to the sphenotic spine, the more of the DO that is overlapped). However, the character in *Bathylaco* is unusual. In my specimen (84.4 mm SL) the muscle originated from the lateral surfaces of the pterotic and hyomandibular (the posterior part of the head) and the fibres ran parallel to one another posteriorly to insert broadly on the medial side of the anterior edge of the operculum (see Fig. 78). The operculum lacked an articular process; however, Markle (1976) noted one in a "small specimen" on which the DO inserted. Markle claimed (p. 10) that in the large

(268 mm SL) specimen he dissected "The DO no longer inserts on the opercle but rather on the medial face of the hyomandibular. The functional DO is the anterior subdivision of the levator operculi which is a parallel muscle arising from the pterotic and hyomandibular and inserting broadly on the anteroventral edge of the opercle thus eliminating the need for the dilatator spine [= articular process] which normally receives a point rather than a broad insertion. The posterior section of the LO is normally situated." His interpretation is most unusual, especially after the figure of his specimen (his fig. 2A) is examined. By definition his DO cannot be the DO, but might be more properly interpreted as a subdivision of the *adductor arcus palatini* or a separate *adductor hyomandibulae*. Because his "anterior subdivision of the levator operculi" is in exactly the same position as the DO in my specimen, and occupies the same position as the DO in other teleosts, it should be interpreted as such.

Levator operculi

The *levator operculi* (LO) in *A. tenebrosus* is a flattened, rather narrow, conical muscle that originates from the lateral surface of the posterodorsal spine of the pterotic (see Fig. 73). It inserts on the dorsomedial edge of the posterior half of the operculum along and dorsal to a narrow ridge that extends posteriorly from the articular process to the posterodorsal corner.

The LO in most of the other alepocephalids examined is similar to that described for *A. tenebrosus* with minor differences concerning size, shape, and points of origin and insertion. In *Leptoderma* and *Conocara* the muscle is small and narrow, and inserts along and slightly dorsal to a ridge on the dorsomedial edge of the middle of the operculum. In contrast, in *Narcetes* the muscle is large, broad, and square to rectangular. It inserts along most of the dorsomedial edge of the operculum and has a broad area of origin on the lateral surface of the epaxial muscle mass next to the pterotic, as well as on posterodorsal spine of the pterotic. The LO in *Rouleina* and *Bathylaco* also has an area of origin on the epaxial muscle mass, but it is narrower than in *Narcetes*. In *Narcetes* and *Rouleina* the posteriormost end of the LO is partly subdivided from the more anterior fibres, and sends a thin, narrow slip posterodorsally to the lateral surface of the supracleithrum of the pectoral girdle.

Adductor operculi

The *adductor operculi* (AO) in *Alepocephalus tenebrosus* is partly visible externally and lies adjacent to the anterior edge of the *levator operculi* (see Fig. 73). It originates from the lateral surfaces of the pterotic and exoccipital medioventral to the origin of the *levator operculi* and inserts along and dorsal to a ridge on the medial surface of the anterodorsal corner of the operculum anterior to the insertion of the *levator operculi.*

An AO basically similar to that described for *A. tenebrosus* was found in all other alepocephalids examined. Markle (1976) claimed that a separate AO was absent in *Narcetes* but this was not the case in my specimen.

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *A. tenebrosus* is a thick, rectangular muscle that is only slightly visible externally (see Fig. 73). It originates primarily from the lateral surfaces of the parasphenoid and prootic. It inserts only onto the medial surface of the hyomandibular (on the anterior lamina along and dorsal to a posterodorsally inclined ridge, and the ventral part of the head). The anterior part that inserts on the anterior lamina is partly subdivided from the posterior portion.

The AAP in *Xenodermichthys, Rouleina, Bathytroctes, Narcetes, Photostylus, Bajacalifornia, Conocara,* and *Bathylaco* is similar to that described for *A. tenebrosus*. In *Leptoderma* a tiny part of the anteroventral corner inserts on the medial surface of the posterodorsal corner of the metapterygoid. In *Talismania* and *Binghamichthys* the anteroventral part of the AAP inserts on the dorsomedial surface of the posterior part of the metapterygoid (along and dorsal to the medial ridge) and is visible externally. The insertion of the *levator arcus palatini* on the metapterygoid, in turn, includes only the posterodorsal corner of the medial surface (unlike the other alepocephalids it does not insert on the medial ridge).

Markle (1976) did not find an *adductor arcus palatini* in *Ericara salmonea* nor could he find an *adductor arcus palatini*, *adductor hyomandibulae* or *adductor operculi* in *Photostylus pycnopterus*. My specimen of *P. pycnopterus*, however, possessed the latter three muscles.

Adductor hyomandibulae

There is a separate, moderately wide *adductor hyomandibulae* (AH) in *A. tenebrosus* that lies adjacent to the AO and AAP, and is partly visible externally. It originates from the lateral surface of the posteroventral part of the pterotic and inserts onto the dorsomedial surface of the opercular arm of the hyomandibular.

A separate AH of varying sizes and shapes is found in most alepocephalids. One is found in *Rouleina*, *Xenodermichthys*, *Talismania*, *Binghamichthys*, *Narcetes* (but absent according to Markle 1976), *Photostylus*, *Bathylaco*, *Bajacalifornia*, and is apparently also present in *Asquamiceps*, *Einara*, *Ericara*, *Bathyprion*, and *Leptochilichthys* (see Markle 1976, 1980). Although Markle claimed that in *Bajacalifornia* the AO and AH form a single muscle mass distinctly separate from the AAP and LO, this was not the case in my specimen in which both a separate AO and a separate AH were present. I did not find an AH in *Bathytroctes*, *Leptoderma*, or *Conocara* (incipient?); however, Markle (1976) claimed that one was present in all three genera.

FAMILY PLATYTROCTIDAE

Adductor mandibulae

The *adductor mandibulae* in *Holtbyrnia latifrons* is a relatively short (anteroposteriorly) and thin muscle that is divided into three distinct sections: Aw and A2, which insert only onto the lower jaw, and section A1 which inserts only onto the upper jaw (see Fig. 82). The ramus mandibularis of the trigeminal nerve passes lateral to the anterior ends of sections A1 and A2 before running lateral to section Aw and then medial to the lower

The dorsolateral part of section A2 has completely subdivided to produce a separate, thin, flat, A1 section that overlaps the dorsolateral surface of section A2. Section A originates from the lateral strut of the hyomandibular (the lateral edge of the ventral two thirds of the anterior face) and the dorsal limb of the preoperculum (the mid-anterolateral edge). The fibres converge anteriorly onto a ligament that bifurcates almost immediately and extends anteriorly to the upper jaw. The shorter, and wider dorsal ligament attaches onto the mid-lateral surface of the anterior end of the anterior supramaxilla. The longer, narrower, ventral ligament attaches onto the dorsolateral surface of the anterior end of the maxilla. Lik[illegible] in the alepocephalids, this ligament (section L.z-L.x on Fig. 103) does not send a posteroventral branch to the lateral surface of the angulo-articular bone (i.e., section L.y on Fig. 103 is absent and presumed lost). There is no supramaxillary ligament.

Section A2 is moderately thin and flat and originates from the lateral surfaces of the quadrate (dorsal part of the body), symplectic (post half), metapterygoid (the posterior part), hyomandibular (the ventral arm and most of the anterior face of the lateral strut), and the anterolateral edge of the preoperculum (the ventral part of the dorsal limb). It inserts onto the lateral surface of a moderately wide tendinous aponeurosis that overlies parts of the quadrate and metapterygoid. This aponeurosis bifurcates when it passes medial to the lower jaw, the ventral tendon attaching to the posterodorsal edge of Meckel's cartilage (there does not appear to be a coronomeckelian bone) and the broader dorsal tendon attaching to the angulo-articular and dentary bones and perhaps Meckel's cartilage.

Section Aw is moderately large, flat, and triangular and fills the Meckelian fossa on the medial side of the lower jaw. It originates mainly from the aforementioned dorsal tendon (anterior to section A2) and inserts onto the medial surfaces of the angulo-articular and dentary bones and the dorsal border of Meckel's cartilage.

The *adductor mandibulae* in the other platytroctids examined (*Searsia koefoedi, Searsioides multispinus, Sagamichthys abei, Platytroctes apus, Pellisolus facilis*, and *Mirorictus taningi*) is basically similar to that in *H. latifrons*. The main differences concern the ligaments connecting it with the upper and lower jaws and the presence or absence of a distinct A1 section (see Figs. 83-86).

In *Searsiodes, Sagamichthys*, and *Platytroctes* (see Fig. 83) there is a completely separate dorsolateral A1 subdivision that inserts only onto the upper jaw, as in *Holtbyrnia*. In this respect they resemble the alepocephalids *Talismania, Binghamichthys, Bathylaco*, and *Leptochilichthys*. In *Searsia* section A1 is completely separate except for its posteriormost fibres, which are continuous with those of section A2 (see Fig. 84). In *Mirorictus* (see Fig. 85) and *Pellisolus* (see Fig. 86) there is no A1 subdivision, and section A2 inserts ligamentously onto both the upper and lower jaw, as in most alepocephalids.

The ligaments connecting the *adductor mandibulae* to the upper and lower jaws are also quite variable in the other platytroctids (see Figs. 83-86). For example, in *Searsia* (see Fig. 84), *Platytroctes* (see Fig. 83), and *Searsioides* there is a separate, narrow, thin ligament that extends from the lateral surface of the angulo-articular bone of the lower jaw to the anterior end of the maxilla. A well-developed maxilla-mandibular ligament was present only in *Mirorictus* (see Fig. 85). *Mirorictus* is also unlike the other platytroctids in that the *adductor mandibulae* is also connected to the lateral surface of the angulo-articular bone of the lower jaw via a narrow, thin, but distinct ligament that extends between the posterior end of the maxilla-mandibular ligament and the posterior end of the ligament that connects the *adductor mandibulae* directly to the maxilla. This character state is reminiscent of the primitive character state for the Teleostei in which there is a single ligament connecting the *adductor mandibulae* to the maxilla and the lateral surface of the lower jaw at the same time (e.g., the Osmeridae, see Fig. 62). *Searsia* is unusual in that the anterodorsal part of section A2 is directly connected to the coronoid process of the lower jaw via a broad tendon that is also continuous with the medial tendinous aponeurosis onto which most of section A2 inserts (see Fig. 84).

Levator arcus palatini

The *levator arcus palatini* (LAP) in *Holtbyrnia* is a relatively flat, barrel-shaped muscle that originates broadly from the spine and posterolateral surface of the sphenotic and from the cartilage betwen the sphenotic and pterotic (see Fig. 82). The insertion is as described for *Alepocephalus tenebrosus* (Alepocephalidae) except that there is no partial posterolateral subdivision that inserts along a ridge on the hyomandibular.

Except for *Mirorictus*, the LAP in the other platytroctids is as described for *H. latifrons*. In *Mirorictus* (see Fig. 85) the muscle is conical and originates narrowly from the sphenotic. The insertion on the hyomandibular is the same as the others, but it inserts only on the medial surface of the posterodorsal corner of the metapterygoid (not along the medial ridge, which is occupied by the *adductor arcus palatini*).

Dilatator operculi

The dilatator operculi (DO) in *Holtbyrnia* is similar to that described for *Alepocephalus tenebrosus* but is flatter and inserts more broadly onto the operculum (see Fig. 82).

The DO in the other platytroctids is basically similar to that in *Holtbyrnia*.

Levator operculi

The *levator operculi* (LO) in *Holtbyrnia* is a flattened, moderately wide, conical muscle that has basically the same origin and insertion as described for *Alepocephalus tenebrosus* except that the insertion onto the operculum is slightly broader.

The LO in the other platytroctids is basically similar to that in *Holtbyrnia* except that in *Mirorictus* it inserts along virtually the entire dorsal edge of the operculum posterior to the articular process, and it has a narrow posterior subdivision that originates from the post-temporal bone of the pectoral girdle (see Fig. 85).

Adductor operculi

The *adductor operculi* (AO) in *Holtbyrnia* is similar to that described for *Alepocephalus tenebrosus* but is much narrower. The origin is primarily from the pterotic and from the cartilage posterior to it (the exoccipital was not ossified in my specimen).

The AO in the other platytroctids is similar to that in *Holtbyrnia*. The AO in *Mirorictus* is difficult to distinguish from the LO, but appears to be a narrow strip of muscle (separable along its entire length from the LO) adjacent to the anteromedial surface of the LO (and sharing nearly the same origin).

Adductor arcus palatini

The *adductor arcus palatini* (AAP) in *Holtbyrnia* is similar to that described for *Alepocephalus tenebrosus* but originates only from the prootic and is only slightly visible externally.

The AAP in the other platytroctids examined is similar to that in *Holtbyrnia*. In *Platytroctes* the anteriormost fibres also originate from the posterolateral surface of the parasphenoid. In *Mirorictus* the anterior part also inserts onto the anterior edge of the ventral arm of the hyomandibular and onto the dorsomedial surface of the posterior part of the metapterygoid (along and dorsal to the medial ridge) medioventral to the insertion of the anterior end of the LAP. In this respect *Mirorictus* resembles some alepocephalids (*Talismania* and *Binghamichthys*).

Adductor hyomandibulae

Holtbyrnia has an *adductor hyomandibulae* (AH) similar to that described for *Alepocephalus tenebrosus*.

A separate AH, similar to that in *Holtbyrnia*, was found in *Searsia*, *Pellisolus*, and *Mirorictus*, but was absent in *Platytroctes*. An AH may be present in *Searsioides* because the posteriormost fibres of the AAP that insert onto the opercular arm of the hyomandibular are thicker and run in a different direction than the anterior ones. However, because of the relatively poor condition and small size of my specimen, it was difficult to be sure if this posterior section was a separate muscle. *Sagamichthys* was not checked for an AH.

FAMILY ARGENTINIDAE

Adductor mandibulae

The *adductor mandibulae* in *Argentina silus*, is moderately thick, narrow, and long (anteroposteriorly) with a shape closely contouring the ventral border of the very large eye (see Fig. 87). The ramus mandibularis of the trigeminal nerve passes medial to the anterodorsal end of the *adductor mandibulae* before running medial to the lower jaw. It passes between the anterolateral surface of the tendinous aponeurosis and the anteromedial surface of section A2 (just posterior to the intersection of sections A2 and Aw) before running medial to the lower jaw.

Section A2 originates from the anterolateral surface of the preoperculum (including the entire anterior lamina) and the lateral surfaces of the hyomandibular (most of the ventral arm, the ventralmost part of the anterior face of the lateral strut and its entire lateral edge), metapterygoid (the entire narrow posterior extension and the ventral half of the anterior triangular portion), symplectic (the entire surface), mesopterygoid (the posterior surface dorsal to the symplectic and between the posterodorsal corner of the body of the quadrate and the anteroventral corner of the metapterygoid), and quadrate (the posterodorsal corner of the body and the quadratojugal arm).

The fibres of section A2 are short and insert directly along the ventral surface of a tough, broad, tendinous aponeurosis that overlies most of the dorsal surface of the muscle anterior to the *levator arcus palatini* (refer to Fig. 87). The anteriormost fibres insert directly onto the posterior end of section Aw (actually onto a tough sheet of fascia separating the two sections), thus effectively connecting section A2 directly to the lower jaw. The anterolateralmost fibres converge onto a small short ligament that attaches directly to the posterior edge of the angulo-articular bone.

The tendinous aponeurosis extends medial to the lower jaw (it does not bifurcate) and attaches along the entire, very large coronomeckelian bone that forms the floor of most of the Meckelian fossa. Section Aw of the *adductor mandibulae* is large and inserts directly onto the lower jaw. Its posterior end is visible externally and originates directly from the anterior end of section A2 (actually from a tough sheet of fascia separating the two sections) and from the anterior surface of the tendinous aponeurosis. It inserts directly along the broad posterodorsal edge of the lower jaw (the angulo-articular and the posterodorsal corner of the dentary; i.e., the coronoid process) and fills the large Meckelian fossa (including the angulo-articular, dentary, and the anterior end of Meckel's cartilage).

The *adductor mandibulae* inserts only onto the lower jaw and lacks a direct ligamentous connection to the maxilla, unlike the Platytroctidae and Alepocephalidae. Greenwood and Rosen (1971) noted the same in *Argentina striata*. There is no supramaxilla (and therefore no supramaxillary ligament), nor is there a ligament extending from the posteromedial surface of the maxilla to the coronoid process of the lower jaw.

Levator arcus palatini

The *levator arcus palatini* in *A. silus* is a moderately large, barrel-shaped muscle with a broad origin from the lateral surfaces of the sphenotic (almost exclusively from the ventral surface of the large spine) and pterotic (from the wide lateral flange of the temporal sensory canal). It inserts on the lateral surface of the hyomandibular (the anterior edge of the head, the anterior lamina, most of the anterior face of the lateral strut, and the anterodorsal surface of the ventral arm) and the anterior edge of the dorsalmost part of the dorsal limb of the preoperculm.

Dilatator operculi

The *dilatator operculi* is a moderately large, conical muscle that originates from the lateral surfaces of the head of the hyomandibular, the sphenotic (the posterior surface), and the pterotic (the anteroventral surface). It inserts broadly onto the articular process of the operculum.

Levator operculi

The *levator operculi* is a moderately large, flattened muscle that is only partly visible externally. It originates from the lateral surface of the posterodorsal spine of the pterotic and expands posteroventrally to insert onto most of the dorsal third of the medial surface of the operculum (its anteriormost fibres insert along a short ridge that extends posteroventrally from the articular process).

Adductor operculi

The *adductor operculi* is a moderatey long and flattened cylindrical muscle that is not visible externally. Its ventral end is obscured by the *levator operculi* and operculum, and its dorsal end is covered by the hyomandibular. It originates from the lateral surface of the pterotic (the posteroventral part, medioventral to the origin of the *levator operculi*) and inserts along the ridge on the medial surface of the anterodorsal corner of the operculum slightly ventral to the insertion of the anterior part of the *levator operculi* (and lying medial to it).

Adductor arcus palatini

The *adductor arcus palatini* is a moderately long and thick rectangular muscle whose anterior two-thirds is visible externally (see Fig. 87). It originates from the lateral surfaces of the parasphenoid (posterior part), prootic (dorsal part), and pterotic (anteroventral part). It inserts onto the mesopterygoid (posterodorsal surface [illegible] to the metapterytoid), metapterygoid (along most of the dorsomedial edge), and hyomandibular (the anterior edge of the ventral arm and the medial surfaces of the anterior lamina and head). There is no *adductor hyomandibulae*.

FAMILY BATHYLAGIDAE

Adductor mandibulae

The *adductor mandibulae* in *Bathylagus pacificus* is reminiscent of that in *Argentina silus* but is shorter anteroposteriorly and has an unusual ligamentous arrangement anteriorly. Unlike *A. silus* and the other Argentinoidea, part of the anterior end of section A2 is ligamentously connected to the maxilla and the lateral surface of the lower jaw, although weakly (see Fig. 88). The course of the ramus mandibularis of the trigeminal nerve is as described for *A. silus*.

Section A2 originates from the lateral surfaces of the hyomandibular (all of the ventral arm, and the ventral half to two-thirds of both the anterior face of the lateral strut and anterior lamina) and perhaps the tiny metapterygoid (the ventral part of the lateral surface?), and from the same parts of the preoperculum, symplectic, mesopterygoid, and quadrate as in *A. silus*.

The fibres of section A2 insert primarily along the ventral surface of a tendinous aponeurosis similar to that described for *A. silus* (refer to Fig. 88). The anteroventral fibres converge onto an unusual thin ligament, with three parts, that extends in three different directions from a central axis. The short ventral section extends ventrally to attach to the angulo-articular bone immediately dorsal to its joint with the quadrate (L.a on Fig. 88). The wider middle section extends anteriorly to the middle of the medial surface of the maxilla (L.b on Fig. 88). The dorsal section is obscured by muscle fibres (and therefore not visible on Fig. 88) and extends anterodorsally to attach directly to the coronoid process (primarily the dentary) of the lower jaw. Some of the centrolateral fibres of the anterior end of section A2 appear to overlap those of section Aw and insert directly onto the coronoid process. A thin, rather delicate "ligament" (L.d on Fig. 88) extends from the anterodorsal part of section A2 (the posterodorsal part of section Aw?) ventrally to the angulo-articular (attaching just anterior to ligament L.a on Fig. 88), as well as anteriorly (ending in connective tissue between the maxilla and lower jaw). *B. pacificus* is apparently unlike *B. stilbius*, in which Greenwood and Rosen (1971) claimed that no part of the *adductor mandibulae* inserted onto the maxilla.

Most of section Aw appears to be posterior to the lower jaw (and visible externally) but is virtually inseparable from the anterodorsal fibres of section A2. It originates from the anterior and of section A2 (there is no fascia separating the two sections) and from the anterior part of the tendinous aponeurosis. Its insertion is as in *A. silus* except that the Meckelian fossa (and therefore the area of insertion in it) is much smaller and restricted to a small area posteroventral to the coronoid process.

There is no supramaxilla (and therefore no supramaxillary ligament), nor is there a ligament extending from the posteromedial surface of the maxilla to the coronoid process of the lower jaw.

Levator arcus palatini

The *levator arcus palatini* in *B. pacificus* is a moderate-sized, barrel-shaped muscle that is similar in shape and position to that in *A. silus* (see Fig. 88). It has a relatively broad origin from the skull that includes the lateral surfaces of the sphenotic (the spine and area adjacent to it) and pterotic (the middle, along a narrow ridge). It inserts on the lateral surface of the hyomandibular (the anterior edge of the head, the dorsal half to third of both the anterior lamina and anterior face of the lateral strut, and the posterior face of the expanded dorsalmost part of the lateral strut) and on the preoperculum (as described for *A. silus*).

Dilatator operculi

The *dilatator operculi* is a moderate-sized, conical muscle that originates from the same area as in *A. silus* but inserts narrowly onto the articular process of the operculum.

Levator operculi

The *levator operculi* is a relatively small, flattened, roughly conical muscle that has the same origin as *A. silus* but has a narrow insertion on the medial surface of only the posterodorsal corner of the operculum. It does not insert along a ridge.

Adductor operculi

The *adductor operculi* is similar in shape and origin to that in *A. silus* but is partly visible externally, and inserts onto the medial surface of the anterodorsal corner of the operculum anterior to the insertion of the *levator operculi*. It does not insert along a ridge.

Adductor arcus palatini

The *adductor arcus palatini* is a very broad, but relatively thin muscle that lines the floor of most of the orbit (see Fig. 88). Its origin and insertion are as in *A. silus* except that the origin includes most of the lateral edge of the parasphenoid and the insertion includes most of the dorsomedial surface of the mesopterygoid. It also appears to insert on the dorsolateral surface of the tiny metapterygoid. There is no *adductor hyomandibulae*.

FAMILY OPISTHOPROCTIDAE

Adductor mandibulae

The *adductor mandibulae* (termed the AM hereafter because it is undivided) in *Dolichopteryx longipes* is a long, roughly tube-shaped muscle that is located entirely posterior to the lower jaw (see Fig. 89). It inserts only onto the lower jaw and lacks a ligamentous connection with the maxilla. There is no supramaxilla (and therefore no supramaxillary ligament), nor is there a ligament extending from the posteromedial surface of the maxilla to the coronoid process of the lower jaw. A separate Aw section that inserts in and fills the Meckelian fossa is absent. However, because most of the anterolateral fibres of the Am are not continuous with the posterolateral fibres, and share a central myocomma, the anterolateral fibres may represent a partial anterolateral subdivision of the muscle that may be homologous with the Aw section found in most other teleosts. Unlike in *Argentina silus* and *Bathylagus pacificus*, the ramus mandibularis of the trigeminal nerve passes lateral to the anterior end of the *adductor mandibulae* before running medial to the lower jaw.

The AM originates from the preoperculum (the anterior edge of the ventral limb and the lateral surface of the anterior half of the anterior lamina), hyomandibular (the anteroventral corner of the ventral arm), symplectic (parts of the dorsolateral surface), metapterygoid (the entire lateral surface), and basically the same areas of the mesopterygoid and quadrate as in *A. silus* and *B. pacificus*.

The medial fibres insert onto a relatively thin tendinous aponeurosis (overlying the quadrate and mesopterygoid) that extends anteriorly medial to the lower jaw to attach to the the coronomeckelian bone. The tendinous aponeurosis does not bifurcate anteriorly.

The lateral fibres of the AM converge onto a relatively tough, wide, flattened tendon that extends anteriorly to insert directly onto the medial surface of the coronoid process of the lower jaw (onto the dorsalmost surface of the angulo-articular and the posterodorsal edge of the dentary). The Meckelian fossa (into which this ligament inserts) is similar in size and position to that in *B. pacificus*.

The AM in *Opisthoproctus soleatus* is essentially as described for *D. longipes* except that it is shorter (anteroposteriorly) and broader, and the ligament onto which the lateral fibres converge inserts only onto the angulo-articular bone. Greenwood and Rosen (1971) noted that the AM in *O. soleatus* did not insert onto the maxilla, confirming my observations. The AM in *Macropinna microstoma* is similar to that in *O. soleatus* (also see Chapman 1942b).

Levator arcus palatini

The *levator arcus palatini* (LAP) in *D. longipes* is a very small, poorly developed, narrow, conical muscle that originates from the spine of the sphenotic and inserts exclusively on the lateral surface of the hyomandibular (the anterior edge of the head, the anterior lamina, the anterior face of the small lateral strut, and the anterodorsal surface of the ventral arm).

The LAP in *O. soleatus* is similar to that described above. Although the LAP in my specimen of *M. microstoma* was damaged, the muscle appears similar to *O. soleatus* (also see Chapman 1942b).

Dilatator operculi

The *dilatator operculi* (DO) in *D. longipes* is a small, flat conical muscle that originates from the lateral surfaces of the hyomandibular (the middle of the head), the sphenotic (posterior surface), the cartilage between the sphenotic and pterotic, and the parietal (the lateralmost edge). It inserts onto the anterodorsal corner of the operculum.

The DO in *O. soleatus* is similar to that in *D. longipes* except there is a smaller area of origin on the hyomandibular and the insertion on the operculum is very broad.

Levator operculi

The *levator operculi* (LO) in *D. longipes* is a relatively small, flat, but broad muscle that originates from the lateral surface of the posterodorsal corner of the pterotic and the lateral edge of the parietal. The spine on the posterodorsal corner of the pterotic is poorly developed. The insertion is as in *B. pacificus* but even less of the dorsomedial surface of the operculum is covered and some fibres insert onto the dorsolateral edge of the bone.

The LO in *O. soleatus* is similar to that in *D. longipes* but it is not visible externally.

Adductor operculi

The *adductor operculi* (AO) is a moderately wide, relatively short (dorsoventrally), flattened cylindrical muscle that is not visible externally. The origin is as in *A. silus*. It inserts onto the medial edge of the anterodorsal corner of the operculum (its anterior end is slightly ~~anterior to~~ the anterior edge of the LO). It does not insert along a ridge.

The AO in *O. soleatus* is as in *D. longipes* but it is very long and narrow and inserts farther ventrally (along a ridge that emanates posteroventrally from the opercular facet).

Adductor arcus palatini

The *adductor arcus palatini* (AAP) is a moderately long, broad, but relatively thin muscle that lines the floor of the posterior half of the orbit (see Fig. 89). It originates primarily from the posterolateral surface of the parasphenoid (with some fibres arising from the lateral surface of the anterodorsal corner of the prootic). It inserts onto the mesopterygoid (the dorsomedial surface of the posterior half) and the hyomandibular (the anterior edge of the ventral arm and the medial surfaces of the anterior lamina and the anterior edge of the head). There is no *adductor hyomandibulae*.

The AAP in *O. soleatus* is as above except that it originates on more of the prootic and inserts on more of the hyomandibular. It has no *adductor hyomandibulae*.

The AAP in *M. microstoma* is similar to that in *D. longipes* (also see Chapman 1942b). According to Chapman it also lacks an *adductor hyomandibulae*.

B. OTHER TELEOSTEI

This section is not intended to be a detailed account of the muscles of the suspensorium in the major teleostean lineages. The reader is referred to the literature for more detailed descriptions. Instead, I will briefly outline the salient features of the muscles in the major groups, with a view to comparing them to the character states in the salmoniforms. The muscles described in the most detail are the ones that were useful in reconstructing the phylogeny of the salmoniforms, especially the *adductor mandibulae*. The primitive outgroups of the salmoniforms will be described first, followed by the higher teleosts (the Neoteleostei).

PRIMITIVE TELEOSTS: OSTEOGLOSSOMORPHA, ELOPOMORPHA, CLUPEOMORPHA, OSTARIOPHYSI

Adductor mandibulae

Osteoglossomorpha

The Osteoglossomorpha are considered to be the primitive sister group of all other extant teleosts (see Patterson and Rosen 1977; Lauder and Liem 1983). Within this assemblage there appear to be two main patterns of the *adductor mandibulae*: one in the Osteoglossoidei and another in the Notopteroidei (both *sensu* Lauder and Liem 1983).

The pattern in the Notopteroidei appears to represent the primitive character state. In this group there are only two subdivisions of the muscle: an external A2 section that lies lateral to the suspensorium, and an Aw section that lies medial to the lower jaw and is not visible externally. This arrangement appears to be primitive for the Teleostei as a whole (pers. obs.; also see Schaeffer and Rosen 1961; Winterbottom 1974a; Lauder 1980a, 1980b). In addition, section A2 is connected ligamentously to the anterior end of the maxilla, and to the lateral surface of the angulo-articular bone of the lower jaw at the same time, via the maxilla-mandibular ligament (called the *ligamentum primordium* by some workers). These character states were found in the three notopteroids that I dissected: *Notopterus* (Notopteridae), *Xenomystus* (Notopteridae) and *Hiodon* (Hiodontidae)

The *adductor mandibulae* in the Osteoglossoidei (with five genera) is derived over that in the Notopteroidei and most other lower teleosts (pers. obs.; also see Kershaw 1976). In all genera except *Heterotis*, the external (A2) section is subdivided to various degrees: a separate A1 subdivision that inserts directly along the maxilla is found in *Pantodon* (pers. obs.), *Osteoglossum* (pers. obs.), and *Scleropages*; in *Osteoglossum* (pers. obs.), *Scleropages*, and *Arapaima* there is a separate A3 subdivision that inserts onto the lower jaw along with section A2. Section Aw is apparently absent in all osteoglossoids except for *Scleropages formosus* and *Osteoglossum bicirrhosum* (see Kershaw 1976). Although Kershaw did not discuss the maxilla-mandibular ligament, I found that it was present in the two species that I dissected, but somewhat modified. In *Pantodon buchholzi* (UAMZ 2273, 57.4 mm SL) it extended from the lateral surface of the angulo-articular bone to the posteromedial surface of the maxilla, but was not connected to the *adductor mandibulae*. In *Osteoglossum bicirrhosum* (UAMZ 6321, 216.0 mm SL) the ligament extended from the angulo-articular bone to insert along the dorsal edge of the maxilla. The fibres of section A1 of the *adductor mandibulae* in *O. bicirrhosum* converge onto a short, tough ligament that joins the maxilla-mandibular ligament (and also the posterior end of the maxilla). Some lateral fibres of sections A2 and A3 also appear to insert along the posterior end of the maxilla-mandibular ligament via tough connective tissue.

In all the osteoglossomorphs that I examined, the ramus mandibularis of the trigeminal nerve passes lateral to the anterior end of section A2 before running medial to the lower jaw.

In summary, I conclude that the character states in the notopteroids are primitive for the Osteoglossomorpha and were present in the common ancestor of the Notopteroidei + Osteoglossoidei. Evidence for this is also suggested by the observation that the primitive members (as suggested by osteological characters from all parts of the skeleton) of the other primitive teleostean assemblages have an *adductor mandibulae* similar to that in the notopteroids, and share a general similarity in regard to the shape of the suspensorium. In addition, the shape of the suspensorium in the oldest fossil osteoglossomorph (*Lycoptera*, the primitive sister group of the Hiodontidae; see Greenwood 1970), and in the oldest known teleosts, the leptolepids (e.g., see Nybelin 1974), resembles that in the notopteroids that I examined, suggesting that the *adductor mandibulae* was possibly similar. In contrast, the *adductor mandibulae* and suspensoria in the osteoglossoids appear specialized relative to the other lower teleosts.

Elopomorpha

Most workers consider the Elopidae (= *Elops*) and Megalopidae (= *Megalops*) to be the most primitive elopomorphs, and to be anatomically among the most primitive of all teleosts. Greenwood (1977), in a study of the anatomy of the Elopomorpha (which included the muscles), hypothesized that the Elopiformes (Elopidae + Megalopidae) formed the primitive sister group of the Albuliformes + Anguilliformes.

The *adductor mandibulae* in *Elops* and *Megalops* (see Fig. 90) is similar to the primtive character state in the Osteoglossomorpha, as exemplified by *Notopterus*, *Xenomystus*, and *Hiodon* (see Fig. 90 and refer to Vrba 1968; Winterbottom 1974a; Greenwood 1977). However, unlike the Osteoglossomorpha two supramaxillae are present (the primitive character state for the Teleostei) and a supramaxillary ligament extends from the anterior tip of the posterior supramaxilla to join the posterior part of the maxilla-mandibular ligament (a supramaxillary ligament appears to be primitive for the Teleostei). In this respect, these elopomorphs are more primitive than the extant osteoglossomorphs since all of the latter lack supramaxillae. However, a supramaxillary ligament might have been present in the common ancestor of the osteoglossomorpha since a single supramaxillary is found in numerous fossils, including *Lycoptera* (see Taverne 1977, 1978).

Vrba (1968) claimed that in *Megalops cyprinoides* there was a separate A3 subdivision medial to section A2; however, this subdivision was absent in my specimen.

In *Elops* and the primitive albuliform *Albula* (see Greenwood 1977), the ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal surface of section A2 before running medial to the lower jaw. However, in *Megalops* it passes medial to section A2. The character state in *Megalops* appears to be an autapomorphy of this lineage because it was not found in any of the other lower teleosts that I examined.

I did not examine the *adductor mandibulae* in the Albuliformes + Anguilliformes assemblage. However, Greenwood (1977, p. 66) noted in regard to the anguilliforms (the eels) that "although highly specialized in some details, the anguilliform 'bauplan' is essentially that of a basic elopomorph such as *Elops*." The Albuliformes in contrast are derived over the pattern found in the other elopomorphs. They appear to be united on the basis of the maxilla-mandibular ligament having lost its connection with the *adductor mandibulae*, as in the Albulidae and Halosauridae, or else having completely lost the maxilla-mandibular ligament, as in the Notacanthidae (see Greenwood 1977). Although in most albuliforms the *adductor mandibulae* has a number of subdivisions, and often a complex set of ligaments connecting them to the upper and lower jaws, the primitive character state appears to be similar to that found in the albulid, *Pterothrissus*, which has only A2 and Aw sections. In *Albula* a supramaxillary ligament joins the single supramaxilla with the maxilla-mandibular ligament, but appears to be absent in the other albuliforms (as are supramaxillae) illustrated by Greenwood. Greenwood considered the Albulidae (*Albula* and *Pterothrissus*) to be the primitive sister group of the other two extant albuliform families.

Clupeomorpha

The clupeomorpha are a moderately large assemblage whose interrelationships are poorly known. The *adductor mandibulae* does not show much diversity and in most is essentially similar to that in the primitive elopomorphs. There is an external A2 section that lies lateral to the suspensorium and an Aw section that lies medial to the lower jaw (see Fig. 91). Section A2 is connected to the anterior end of the maxilla, and to the lateral surface of the angulo-articular bone of the lower jaw at the same time, via the maxilla-mandibular ligament. In addition, a supramaxillary ligament is present that joins the anterior tip of the posterior supramaxilla with the posterior part of the maxilla-mandibular ligament. In all the clupeomorphs that I dissected the ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal surface of section A2 before running medial to the lower jaw.

The *adductor mandibulae* in the Engraulidae is unlike that found in the other clupeomorphs. This difference is probably related to the unusual shape of the skull and suspensorium (it is oriented obliquely) in this family, and its pattern is almost certainly an autapomorphy because no other clupeomorphs have a similar one (nor do the fossil clupeomorphs have a similar skull and suspensorium). In the Engraulidae the fibres of section A2 are oriented dorsoventrally (rather than anteroposteriorly), extending ventrally or posteroventrally from a broad area of origin on the suspensorium and skull to insert narrowly onto the lower jaw. A maxilla-mandibular ligament (and possibly a supramaxillary ligament) appears to be present but is not connected with section A2. Two of the three species that I dissected (*Anchoa mundeoloides* and *Amentum devisi*) had a separate, thin A1 subdivision that rests lateral to the middle of the ventral half of section A2, and inserts, via a short (but wide) tendon, directly onto the anterior part of the maxilla.

In the genus *Denticeps*, believed to be the primitive sister group of all other extant clupeomorphs, there is apparently an A2 section that inserts onto the lower jaw, and a tendon that connects it to the maxilla (see Greenwood 1968). There does not appear to be an extension of this tendon to the lateral surface of the lower jaw; however, because of the sketchiness of Greenwood's figure of the cheek muscles, more specimens should be examined before its absence is confirmed or denied.

Ostariophysi

The pattern of the *adductor mandibulae* in the Ostariophysi is unique among the lower teleosts, and according to Fink and Fink (1981), is an autapomorphy of the group. In the Ostariophysi the *adductor mandibulae* has an A1 subdivision (it is not homologous with the A1 of higher teleosts according to Fink and Fink) that lies ventrolateral to section A2 (e.g., see figs. in Takahasi 1925; Kampf 1961; Alexander 1964; Ballintijn 1969; Winterbottom 1974a; Howes 1976, 1985; Vari 1979). Fink and Fink (p. 343) noted that "In primitive ostariophysans the ventral division [section A1] attaches directly to the maxilla (gonorynchiforms, cypriniforms, and primitive characiforms including most distichodontids) or to the ligamentum primordium (some characiforms)." The pattern in the more derived ostariophysans, the gymnotoids and siluroids, is apparently derived over that in the others. In the former group section A1 attaches only onto the lower jaw, whereas in the latter it is absent (see Fink and Fink 1981). Fink and Fink (p. 343) considered the character states found in some characiforms and in the siluriforms (the gymnotoids + siluroids) "to be secondary reductions from a primitive attachment to the maxilla."

In addition to the A1 subdivision, the *adductor mandibulae* invariably has an external A2 section (which may be subdivided) and an Aw section medial to the lower jaw. A separate maxilla-mandibular ligament is apparently found in some characiforms (see Alexander 1964; Howes 1976; Vari 1979) but is absent in most ostariophysans (but may be incorporated into the tendon connecting section A1 of the *adductor mandibulae* to the upper jaw). When a separate maxilla-mandibular ligament is present, the *adductor mandibulae* usually does not insert onto it; however, this is apparently not the case in the characiform *Pyrrhulina*, since Alexander (1964, p. 181) noted "that the portion of A1 which originates on the quadrate inserts on the articular-maxillary ligament [= the maxilla-mandibular ligament] instead of on the articular."

Except for a few characiforms, the Ostariophysi lack supramaxillae (and therefore a supramaxillary ligament). Fink and Fink consider the lack of supramaxillae to be an autapomorphy of the group. However, a supramaxillary ligament might have been present in the ancestor of the Ostariophysi since two supramaxillae are found in the extinct Cretaceous genus *Lusitanichthys* (see Gayet 1986), and one is found in the Eocene *Chanoides* (see Patterson 1984a). The supramaxilla in *Chanoides* has a shape very reminiscent of that in teleosts with a supramaxillary ligament; it is pear-shaped with a relatively long, narrow anterior extension. It is possible that a maxilla-mandibular ligament was also present: there is a groove on the lateral surface of the angulo-articular bone that might have served as an area of attachment for the posterior end of the ligament (similar to that found in extant teleosts with this ligament), and the anterior end of the maxilla has a number of processes that might have served as the attachment point for the ligament's anterior end. The shape of the skull and the suspensorium in *Chanoides* is also remarkably similar to that found in various extant clupeomorphs (compare my Fig. 49 with Patterson's figs. 2 and 5), suggesting that the *adductor mandibulae* and its ligaments may have been similar.

The ramus mandibularis of the trigeminal nerve passed lateral to the anterodorsal surface of section A2 of the *adductor mandibulae* in all the ostariophysans that I dissected. However, its position relative to section A1 was variable: in a gonorynchiform (*Chanos*) and a characiform (*Astyanax*) it was lateral to its anterior end, whereas in three cypriniforms (*Couesius, Notropis,* and *Catostomus*) it was medial to its anterior end before running medial to the lower jaw. The primitive character state may be similar to that in *Chanos* (laterally on both A1 and A2) since this genus is hypothesized to be the sister group of all other gonorynchiforms, which in turn form the sister-group of all other Ostariophysi.

Levator arcus palatini

The *levator arcus palatini* (LAP) occupies essentially the same position in all the teleosts: it originates from the lateral surface of the skull at the posterodorsal corner of the orbit, and inserts onto the lateral surface of the posterior part of the suspensorium (also see Winterbottom 1974a). The major differences concern the shape of the muscle (it is usually roughly conical, with a dorsally directed apex), its degree of development, whether or not it has any subdivisions (usually it is a single muscle mass), and its area of origin (it usually centres on the spine of the sphenotic) and insertion (usually on the hyomandibular and metapterygoid).

Osteoglossomorpha

For a detailed description of the LAP in the Osteoglossoidei refer to Kershaw (1976). In the Osteoglossoidei the LAP is large and well-developed, squarish to rectangular, is sometimes subdivided (e.g., *Scleropages*), and has a broad area of origin on the skull and a moderately broad area of insertion on the suspensorium. In the notopteroids that I examined (*Xenomystus* and *Hiodon*) the LAP is less well-developed. In *Xenomystus* it is barrel-shaped with a broad area of origin on the sphenotic and pterotic. The LAP in *Hiodon* is smaller than the other osteoglossomorphs, conical (with a dorsally directed apex), and has a narrow area of origin on the sphenotic (primarily from the spine and the area adjacent to it). In *Hiodon* the insertion includes only the hyomandibular, whereas in *Xenomystus* the insertion also includes the posterodorsal corner of the metapterygoid.

Elopomorpha

The LAP in *Elops* and *Megalops* (see Fig. 90) is partly subdivided (pers. obs.). The posterior section originates broadly from the lateral surface of the posterior part of the sphenotic as well as the pterotic, and inserts onto the hyomandibular and the dorsal tip of the preoperculum. The anterior section originates narrowly from the sphenotic spine and inserts broadly onto the hyomandibular and metapterygoid. Vrba (1968) illustrated the LAP in *Elops* and *Megalops*, and Winterbottom (1974a) illustrated it in *Elops*, but neither indicated that it was subdivided. The LAP in the Albuliformes shows considerable variation in regard to its shape, and is often subdivided (see Greenwood 1977).

Clupeomorpha

The LAP in *Denticeps*, the primitive sister group of all other extant clupeomorphs, is a moderate-sized conical muscle that originates narrowly from the spine on the sphenotic and broadens ventrally to insert onto the hyomandibular (see Greenwood 1968; Forey 1975). In all other extant clupeomorphs the LAP is divided into a ventral and dorsal subdivision (see Fig. 91), a character state considered to be an autapomorphy of the group by Lauder and Liem (1983). The ventral subdivision corresponds to the LAP in *Denticeps*. The dorsal subdivision originates broadly from a ridge on the frontal and narrows ventrally to insert onto a process (labelled Hm.pr on Fig. 49) at the anterodorsal corner of the anterior flange (labelled Hm.af on Fig. 49) of the hyomandibular. Forey (1975) considered the character state in *Denticeps* to be primitive for the Clupeomorpha, and I concur

Ostariophysi

The LAP in the Ostariophysi does not exhibit much variability (pers. obs.; also see Takahasi 1925; Kampf 1961; Alexander 1964; Ballintijn 1969; Winterbottom 1974a; Howes 1976, 1985). In many the character state is similar to that found in the primitive gonorynchiform *Chanos*: the muscle is moderately large, conical, originates on the sphenotic (the spine and vicinity), and expands ventrally to insert onto the lateral surface of the hyomandibular and the medial surface of the posterodorsal corner of the metapterygoid. In some species the insertion includes only the hyomandibular (see Takahasi 1925; Ballintijn 1969), in others a subdivision of the *adductor mandibulae* passes medial to the LAP (see Howes 1976).

Dilatator operculi

The dilatator operculi (DO) does not vary much in the Teleostei. In most it is roughly conical (with a posteroventrally directed apex), is usually partly covered laterally by the LAP, originates from the lateral surfaces of the sphenotic, pterotic, and hyomandibular, and inserts onto the articular process of the operculum. Differences usually concern the shape (it is strap-like in some), its degree of development, and the area of origin on the skull. In the osteoglossomorph *Heterotis* it is unusually large and inserts along most of the dorsolateral edge of the operculum (see Kershaw 1976). The character state in the primitive clupeomorph *Denticeps* is unlike that in any other lower teleost: the DO is either absent or represented by a small slip that extends from the sphenotic (posterior to the LAP) to the hyomandibular (see Greenwood 1968; Forey 1975).

Levator operculi

Like the DO, the levator operculi (LO) does not vary much in the teleosts. It is roughly fan-shaped, originates from the lateral surface of the skull (usually centring on the pterotic) and expands ventrally to insert onto the operculum (usually along the dorsomedial surface). However, there are often major differences in the degree of development and the area of insertion on the operculum, even in closely related species. Occasionally the LO has a posterior subdivision that extends between the posterodorsal corner of the operculum and pectoral girdle, such as in the osteoglossomorph *Xenomystus* (pers. obs.), the salmoniform *Esox* (pers. obs.), and the paracanthopterygian *Microgadus* (see Winterbottom 1974a, fig. 6A). Sometimes the LO is not separate from the *adductor operculi*, as in the elopomorph *Elops* (see Winterbottom 1974a) and the osteoglossomorph *Heterotis* (see Kershaw 1976).

Adductor operculi

The *adductor operculi* (AO) is similar in most teleosts: it is conical to cylindrical, is usually covered laterally by the LO, originates from the lateral surface of the skull medioventral to the origin of the LO (often centring on the pterotic), and inserts onto the medial surface of the anterodorsal corner of the operculum. Occasionally a distinct AO is not present, as in *Heterotis* and *Elops* (where it is continuous with the LO and *adductor arcus palatini* according to Winterbottom 1974a).

Adductor arcus palatini

The *adductor arcus palatini* (AAP) occupies essentially the same position in all teleosts: it originates from the ventrolateral surface of the skull and inserts onto the posteromedial surface of the suspensorium (also see Winterbottom 1974a). However, within the Teleostei the muscle varies considerably in regard to its relative size and areas of origin and insertion. These differences in size and position proved useful in my analysis of the phylogenetic relationships within the salmoniforms, and may prove useful in the analysis of other groups.

Primitively, the AAP is located posteriorly, originating from the prootic and the posterior end of the parasphenoid, and inserting onto the hyomandibular, and usually the metapterygoid (also see Winterbottom 1974a). In more derived teleosts the muscle is expanded farther anteriorly so that it lines the floor of the orbit between the skull and the suspensorium and is visible externally.

Osteoglossomorpha

The AAP is relatively short anteroposteriorly and is usually not visible externally, being restricted to the posterior part of the orbit (pers. obs.; also see Kershaw 1976). The origin is from the posterior end of the parasphenoid and usually the prootic. The insertion is variable, and may include the hyomandibular and operculum (*Osteoglossum* and *Scleropages*, see Kershaw 1976) or the hyomandibular, metapterygoid, and the posteriormost end of the mesopterygoid (*Xenomystus* and *Hiodon*, pers. obs.).

Elopomorpha

In *Elops* and *Megalops* the AAP is located unusually far posteriorly and is not visible externally (pers. obs.). The origin is primarily from the prootic and the insertion is mainly on the hyomandibular. In the Albuliformes the AAP is greatly reduced or absent (see Greenwood 1977). This appears to be an autapomorphy of this group.

Clupeomorpha

In the clupeomorphs that I dissected (*Clupea, Anchoa, Amentum, Thryssa*, and *Chirocentrus*) the AAP is relatively short antgroposteriorly, restricted to the posterior part of the orbit, and is slightly visible externally in some species. The origin is primarily from the prootic, but also from the posterior end of the parasphenoid. The insertion is on the hyomandibular in *Clupea* (extending anteriorly along a strut-like extension of the anterior lamina of the hyomandibular nearly to the mesopterygoid), and on the hyomandibular, metapterygoid, and the posteriormost part of the dorsal surface of the mesopterygoid in the engraulids (*Anchoa, Amentum, Thryssa*) and *Chirocentrus*. Greenwood (1968) claimed that an AAP was absent in the clupeoids that he examined (*Clupea* and two engraulids, *Coilia* and *Engraulis*).

The AAP in *Denticeps* is apparently larger than in the clupeomorphs that I studied, filling almost the posterior third of the orbit and appearing to insert onto the hyomandibular and metapterygoid, and possibly the mesopterygoid (see Greenwood 1968).

Ostariophysi

As could be expected in such a large group, the AAP shows considerable variability. In some species (e.g., the gonorynchiform *Chanos* and the cyprinid *Couesius*, pers. obs.; and the characids *Rhaphiodon* and *Hydrolycus*, see Howes 1976) it is restricted to the posterior part of the orbit and the insertion is almost exclusively on the hyomandibular and metapterygoid. In others the AAP is expanded anteriorly so that it lines most of the floor of the orbit, originating from most of the parasphenoid and inserting anteriorly along most of the dorsomedial surface of the mesopterygoid (e.g., the catostomid *Catostomus*, pers. obs.; and the characid *Cynodon*, see Howes 1976). The anteriormost fibres insert onto the palatine in some species (e.g., the characid *Hydrocyon*, see Kampf 1961; and in some cobitids, see Takahasi 1925).

Adductor hyomandibulae

A separate *adductor hyomandibulae* (AH) that lies between the AAP and AO (it separates from either the posterior region of the AAP or the anterior region of the AO) has evolved independently in a number of teleostean lineages and is present in some members of most major assemblages (also see Winterbottom 1974a,b). However, as a rule, it appears to be found less frequently in the lower teleosts (pers. obs.). When present in the Teleostei, it originates from the lateral surface of the skull (usually from the pterotic and/or prootic) and usually inserts onto the medial surface of the posterodorsal region of the hyomandibular.

Osteoglossomorpha

According to Kershaw (1976) an AH is present in *Pantodon* and *Heterotis* among the Osteoglossoidei. It is present in the notopteroid *Mormyrus* according to Winterbottom (1974a) but was absent in *Xenomystus* and *Hiodon* (both pers. obs.).

Elopomorpha

A separate AH was absent in *Elops* and *Megalops* (both pers. obs.) and is apparently absent in the Albuliformes (see Greenwood 1977).

A separate AH was absent in the clupeomorphs that I examined (*Clupea, Anchoa, Amentum*).

Ostariophysi

An AH is present in some ostariophysans. Takahasi (1925) examined various cyprinoids, cobitoids, and siluroids and found that it was present only in the latter group.

HIGHER TELEOSTS: STOMIIFORMES, AULOPIFORMES, MYCTOPHIFORMES, PARACANTHOPTERYGII, ACANTHOPTERYGII

Adductor mandibulae

Stomiiformes

The Stomiiformes were hypothesized by Fink and Weitzman (1982) to be the sister group of all other Neoteleostei. One of the derived character states that Fink and Weitzman (1982, p. 72) used to unite the Stomiiformes was the "Presence of a medial division of the adductor mandibulae muscle which is subdivided into two sections, a dorsal one inserting directly onto the maxilla, and a ventral one inserting onto the primordial ligament [= maxilla-mandibular ligament]." Both medial sections are present in *Diplophos*, which Fink and Weitzman hypothesized to be the sister group of the rest of the order (see Fig. 92). They also noted (p. 72) that "Among many more specialized stomiiforms, one or the other of these [sections] is emphasized, and the other is reduced or lost. In a few members of the group, such as *Gonostoma* and *Margrethia*, additional sections are present." For example, in *Vinciguerria* (see Fig. 93), a relatively generalized stomiiform, there is only a single medial subdivision of the *adductor mandibulae* that inserts directly along the posterior end of the maxilla-mandibular ligament. For other patterns refer to figures in Günther and Deckert 1953, 1955, and Rosen 1973. Fink and Weitzman hypothesized that the medial A1 subdivision found in the Stomiiformes is not homologous with the A1 subdivision found in other higher

A distinct maxilla-mandibular ligament extending from the anterior end of the maxilla to the lateral surface of the angulo-articular bone appears to be present in most Stomiiformes, including the more generalized and primitive members (pers. obs.; also see Günther and Deckert 1953, 1955). A supramaxillary ligament extends posteriorly from the anterior tip of the posterior supramaxilla to join the maxilla-mandibular ligament in relatively primitive genera such as *Diplophos*, *Vinciguerria*, and *Argyropelecus* (all pers. obs.), and *Cyclothone* (see Günther and Deckert 1953, fig. 8). However, unlike the primitive teleosts the *adductor mandibulae* usually inserts directly along the posterior part of the maxilla-mandibular ligament (see Figs. 92, 93 and compare to the primitive teleost shown in Fig. 91).

In all stomiiforms that I dissected the ramus mandibularis of the trigeminal nerve passes lateral to the anterodorsal surface of the *adductor mandibulae* (sections A1 and A2) before running medial to the lower jaw.

Aulopiformes

The Aulopiformes are hypothesized by Rosen (1973) to be the sister group of the Myctophiformes + Paracanthopterygii + Acanthopterygii. Most workers agree that the genus *Aulopus* (of the monotypic family Aulopodidae) is the most primitive aulopiform (see Goody 1969a; Rosen and Patterson 1969; Rosen 1973; Sulak 1977), and it is Rosen's hypothesis, based partly on jaw musculature, that the Aulopoidei is the primitive sister group of the other aulopiforms (the Alepisauroidei). To quote Rosen (1973, p. 436), "Aulopoids have a generalized type of muscular control of the maxilla involving separation of a large, dorsal, external bundle of the adductor mandibulae (the A1 component) that inserts on the maxilla-mandibular ligament." In the aulopoid that I examined (*Aulopus filamentosus*) there was a separate A1 subdivision of the *adductor mandibulae* that inserted directly along the maxilla-mandibular ligament, while section A2 inserted only onto the lower jaw. There was no distinct supramaxillary ligament. The ramus mandibularis of the trigeminal nerve passed medial to section A1, but lateral to section A2 before running medial to the lower jaw. In (presumably only the lateral fibres) inserting along the posteriormost end of the maxilla-mandibular ligament, but this was not the case in my specimen of *Aulopus filamentosus*.

The pattern of the *adductor mandibulae* in the Alepisauroidei is derived over that in the Aulopoidei (see fig. 3 in Günther and Deckert 1960 and figs. 38, 39, 59 to 64 in Rosen 1973). Rosen (p. 438) related the specializations in this group to "a reorientation in connection with enlargement of the gape and backward migration of the lower jaw articulation." In the synodontids *Saurida* and *Harpadon* section A1 is broad and sheet-like and appears to insert directly along the upper jaw (maxilla?). However, it is difficult to be sure from Rosen's figures (38 and 39) whether this is the case or whether the insertion is along the maxilla-mandibular ligament. This ligament is not shown in his figures, but it may be obscured by the very long upper jaw since Günther and Deckert (1960) showed its posteriormost end in their figure of *Harpadon*. I dissected the closely related genus *Synodus* and found there to be a distinct maxilla-mandibular ligament that extends from the lower jaw anteriorly along the dorsal edge of the maxilla. Section A1 inserts directly along the posterior part of this ligament (the ligament in turn is connected along most of the dorsal edge of the maxilla by connective tissue). The posteroventral corner of section A1 also appears to insert onto the low coronoid process of the lower jaw via tough connective tissue. The path of the ramus mandibularis of the trigeminal nerve was as in *Aulopus*.

The *adductor mandibulae* in the other alepisauroids exhibits a number of specializations. For example, in *Alepisaurus, Omosudis, Odontostomops,* and *Scopelarchoides* the muscle fibres are inclined dorsoventrally, rather than anteroposteriorly as in the primitive character state (see figs. 60, 61, 63 and 64 in Rosen 1973). A separate A3 subdivision (in addition to A1 and A2) is found in *Alepisaurus* and *Omosudis*. In *Sudis, Anotopterus, Odontostomops*, and *Scopelarchoides* (see figs. 59, 62, 63, and 64 in Rosen 1973) the *adductor mandibulae* is not subdivided externally (section A1 is lost?) and in the former three genera inserts only onto the lower jaw. In *Scopelarchoides* the *adductor mandibulae* inserts onto the connective tissue. In *Sudis* there is a distinct maxilla-mandibular ligament, but it is not connected to the *adductor mandibulae*, a character state convergent on that found in some salmoniforms (e.g., *Esox*).

Myctophiformes

The Myctophiformes are the sister group of the Paracanthopterygii + Acanthopterygii according to Rosen (1973) and Lauder and Liem (1983), and consist of only two families, the Myctophidae and Neoscopelidae. The character state in the neoscopelids is similar to that in *Aulopus*: there is an A1 subdivision that lies dorsolateral to section A2 and inserts directly along the posterior part of the well-developed maxilla-mandibular ligament (see plate 57 in Rosen and Patterson 1969 and fig. 3 in Winterbottom 1974a). Although there is a supramaxilla (see Paxton 1972), I do not know if there is a supramaxillary ligament.

The character state in the Myctophidae is similar to that in some stomiiforms: there is a medial subdivision of the *adductor mandibulae* that converges anteriorly onto a ligament that extends anteriorly to insert only onto the anterior end of the maxilla (pers. obs.; also see plate 55 in Rosen and Patterson 1969; fig. 40 in Rosen 1973; fig. 4 in Winterbottom 1974a). Unlike most stomiiforms, a maxilla-mandibular ligament was absent in my specimens, as were supramaxillae (and consequently, a supramaxillary ligament). Supramaxillae are absent in most myctophids, and when one is present, it is reduced (see Paxton 1972).

Fink and Weitzman (1982) consider the medial subdivision of the *adductor mandibulae* in the Myctophidae to be an autapomorphy of the family (i.e., it is not homologous with that in the Stomiiformes), and the A1 subdivision found in the Neoscopelidae to be primitive for the Myctophiformes.

Paracanthopterygii + Acanthopterygii

The pattern of the *adductor mandibulae* in this assemblage (the Acanthomorpha of Rosen 1973) exhibits considerable morphological diversity, as could be expected in a group that comprises over sixty percent of all living teleosts. I examined relatively few advanced teleosts; however, the literature dealing with the cheek muscles in this group is extensive. Information concerning the *adductor mandibulae* and other muscles of the suspensorium in the major assemblages can be found in (to name a few): Takahasi 1925; Eaton 1935; Schaeffer and Rosen 1961; Rosen 1962, 1964, 1973; Greenwood *et al.* 1966; Alexander 1967a, 1967b; Osse 1969; Rosen and Patterson 1969; Liem 1970; Anker 1974; Winterbottom 1974a, 1974b; Elshoud-Oldenhave and Osse 1976; Freihofer 1978; Stiassny 1981; Fink and Weitzman 1982; Motta 1984; Gosline 1986. Many of the specializations of the *adductor mandibulae* found in this assemblage appear to be related to advances in the feeding mechanism, in particular, jaw protrusion, which is a characteristic of many acanthomorphs.

Most of the character states found in the other neoteleosts, and more, are present in this assemblage. A maxilla-mandibular ligament is primitively found in the Acanthomorpha since it appears to be present, in some form, in most of its members. Subdivisions of the *adductor mandibulae* that insert onto the maxilla are almost always present (section, A1), and the part (section A2) inserting onto the lower jaw is frequently subdivided as well.

The primitive character state for the Acanthomorpha is probably similar to that in primitive acanthopterygians such as the Beryciformes (considered to be the basal group of acanthopterygian evolution, since they are structurally the most primitive acanthopterygians, and are the first acanthomorphs to appear in the fossil record) and Lampriformes. In these fish there is an external A1 subdivision that lies dorsolateral to section A2 and inserts directly along the maxilla-mandibular ligament (pers. obs., also see figures in Rosen 1973). One of the most primitive patterns may be that in *Plectrypops*, which Zehren (1979) considered to be part of the group that formed the primitive sister group of the other beryciforms (as taken from Keene and Tighe 1984). In *Plectrypops* (pers. obs.) there is a single, rather indistinct A1 subdivision (its fibres are difficult to separate from those of section A2) that lies dorsolateral to section A2. The fibres of both parts run anteroposteriorly and insert directly along the maxilla-mandibular ligament (pers. obs.). A supramaxillary ligament is absent. Overall, the muscle is notably similar to that in the primitive members of the outgroups of the

Acanthomorpha, the myctophiforms and aulopiforms (especially *Aulopus*). A similar pattern is also found in primitive lineages of the order Perciformes (the largest acanthopterygian order, and the one thought to have given rise to several other orders) such as the Percichthyidae (*Morone*, pers. obs.), Serranidae (see Stiassny 1981), and Percidae (*Perca*, pers. obs.; *Gymnocephalus*, see Elshoud-Oldenhave and Osse 1976). In contrast, in the Paracanthopterygii Rosen and Patterson (1969, p. 371) note that "When present ... A1 is invariably feeble and has a tendinous association with the maxillary-mandibular ligament (text fig. 6A, B). It is absent from all examined members of the group save gadids, merclúccids, and percopsids. The major superficial cheek muscle is A2, and in almost all the many species of paracanthopterygians examined, and more importantly in at least some members of each included family, it is divided into a distinct dorsal and ventral subdivision."

A medial subdivision of the *adductor mandibulae* that inserts onto the maxilla is often present in the Acanthomorpha. This section lies medial to section A2, and in some cases, medial to the *levator arcus palatini* as well (e.g., the beryciform, *Photoblepharon*, see Rosen 1973, fig. 33). Both Rosen (1973) and Winterbottom (1974a) considered it to have probably arisen through a subdivision of section A1, and called it section A1β. It is often found in conjunction with the external subdivision A1, in which case A1 is usually called A1α (see figs. 31, 32, 33 in Rosen 1973 and fig. 6 in Winterbottom 1974a).

A supramaxillary ligament was absent in the acanthomorphs that I examined.

The path of the ramus mandibularis of the trigeminal nerve was not indicated in most of the literature (but see Freihofer 1978; Stiassny 1981; Winterbottom 1974b). However, in all the acanthomorphs that I dissected, except for the beryciform *Melamphaes*, the nerve passed medial to the external A1 subdivision of the *adductor mandibulae* (when it was present), and then passed along the lateral surface or dorsolateral edge of section A2 before running medial to the lower jaw (similar to the character state in the aulopiform, *Aulopus*). In *Melamphaes*, the nerve passed lateral to both section A1β, A1α, and A2 before running medial to the lower jaw; however, this genus is a relatively derived beryciform since section A1 has two subdivisions (also see Keene and Tighe 1984).

In most tetraodontiforms there are two subdivisions of section A2: a dorsolateral A2α section and a ventromedial A2β section. According to Winterbottom (1974b), in some families the nerve lies medial to both sections while in others it separates the two divisions, passing medial to A2α (dorsal) and lateral to A2β (ventral).

The relation of the nerve to the medial (A1β) subdivision (when present) appears to be variable. In the percopsiforms *Percopsis* and *Chologaster* it passed lateral to A1β, whereas in the gadiforms *Microgadus* and *Lota* , it passed medial to it (all pers. obs.).

Levator arcus palatini

Stomiiformes

The LAP in all the stomiiforms that I dissected was essentially the same. It is moderately large and conical, is not subdivided, originates mainly from the sphenotic (centring on the spine), and expands ventrally to insert onto the hyomandibular (the lateral surfaces of the anterior edge of the head, the anterior lamina, the anterior face of the lateral strut, and the ventral arm) and metapterygoid. In *Diplophos* and *Vinciguerria* the insertion on the metapterygoid was on the medial surface of the triangular, dorsolaterally directed flange on the posterodorsal corner of the bone (labelled Mt.d on Fig. 51), and on the lateral surface of the dorsomedially inclined laminar expansion medial to it (part of the main body of the bone). However, in *Chauliodus, Tactostoma,* and *Argyropelecus* the insertion was only on the medial surface of the flange (the bone was not expanded medially to it). In *Argyropelecus* the ventralmost fibres insert along a shelf found at the intersection of the ventromedial edge of the flange and the main body of the bone. In none of the specimens was the insertion along a ridge on the medial surface of the metapterygoid (all pers. obs.). In *Cyclothone* the LAP has a number of subdivisions according to Günther and Deckert (1953), and appears to insert almost exclusively on the metapterygoid in a way reminiscent of that in *Diplophos* and *Vinciguerria*.

It is difficult to speculate as to what the primitive character state for the stomiiforms is; however, it may be similar to that in *Diplophos* since Fink and Weitzman (1982) hypothesized that this genus may be a sister group of the rest of the order.

Aulopiformes

The LAP in the primitive genus *Aulopus* is moderately large, conical, and originates mainly from the spine of the sphenotic (pers. obs.). It expands ventrally to insert onto the hyomandibular (the lateral surfaces of the anterior edge of the head, the anterior lamina, the anterior face of the lateral strut, and the ventral arm) and metapterygoid (the medial surface of the posterodorsal part). In *Synodus* the muscle is similar (pers. obs.), but broader, and the insertion on the metapterygoid extends nearly to the anterior edge of the bone (which has a narrow anterior extension). In the genus *Harpadon* the muscle apparently has two subdivisions: a large, conical anterior section that appears to insert on the lateral surfaces of the hyomandibular, metapterygoid, and mesopterygoid; and a much smaller, conical, posterior section that inserts onto the dorsal surface of the hyomandibular (see Günther and Deckert 1960, fig. 4). The LAP also appears to be subdivided in *Scopelosaurus* (see Rosen 1973, fig. 29).

Myctophiformes

The LAP in the two myctophids that I examined (*Myctophum* and *Protomyctophum*) was roughly conical, and unusually long dorsoventrally. The origin was mainly from the sphenotic (centring on the spine) but some fibres originated from the pterotic and the large circumorbitals. The insertion was similar to that described for the stomiiform *Diplophos* and *Vinciguerria*, as was the shape of the metapterygoid; however, fibres also inserted along the broad dorsal edge of the dorsal limb of the preoperculum. In addition, because the laminar expansion medial to the posterodorsal flange was larger in the myctophids, the area of insertion on the metapterygoid was proportionally larger than in the aforementioned stomiiforms.

Paracanthopterygii + Acanthopterygii

The LAP in this large assemblage is basically like that found in the other teleosts, and exhibits similar diversity.

Dilatator operculi, Levator operculi, and Adductor operculi

In the Neoteleostei, these three muscles are basically similar to, and exhibit the same diversity as in the lower teleosts.

Adductor arcus palatini

Stomiiformes

The AAP is moderately variable in the stomiiforms. In *Diplophos, Vinciguerria*, and *Argyropelecus* it is small and restricted to the posterior part of the orbit (pers. obs). It originates primarily from the prootic and inserts onto the medial surface of the hyomandibular. A similar character state is found in *Cyclothone*; however, in this genus the AAP has four subdivisions according to Günther and Deckert (1953). Although Günther and Deckert call this muscle the *adductor hyomandibulae*, Winterbottom (1974a, p. 239) synonymized it with the AAP, and I concur. In *Argyropelecus* the anteroventralmost fibres of the AAP insert onto a tendinous aponeurosis that extends between the hyomandibular and the anterodorsal corner of the metapterygoid, effectively inserting it onto the metapterygoid.

A more derived character state is found in the more specialized and derived stomiiforms. In *Chauliodus* and *Tactostoma* (both pers. obs.), and *Photostomias* (see Günther and Deckert 1955) the AAP is expanded anteriorly so that it lines the entire floor of the orbit, originating primarily along the parasphenoid, and inserting onto the hyomandibular, metapterygoid, and mesopterygoid (a mesopterygoid is absent in *Tactostoma*, pers. obs.; but apparently present in the other two genera, see Günther and Deckert 1955). The insertion in these genera appears to also include part of the ectopterygoid and/or palatine.

In none of the stomiiforms that I examined did the AAP insert along a ridge on the medial surface of the hyomandibular.

Aulopiformes

The AAP in *Aulopus* and *Synodus* is restricted to the posterior part of the orbit, originating from the prootic and parasphenoid, and inserting onto medial surfaces of the hyomandibular and metapterygoid, and the dorsal surface of the posteriormost end of the mesopterygoid (pers. obs.).

Myctophiformes

The AAP in the two myctophids that I examined (*Myctophum* and *Protomyctophum*) was restricted to the posterior part of ~~the~~ orbit, as in the aulopiforms, but extended slightly farther anteriorly. It originated from the prootic and parasphenoid and inserted onto the medial surface of the hyomandibular, the metapterygoid (the dorsal surface of the medial laminar expansion), and the mesopterygoid (the dorsal surface of the posterior end). The AAP in the neoscopelid, *Neoscopelus*, is restricted to the posterior part of the orbit, and partly visible externally, as in the myctophids (see Winterbottom 1974a, fig. 3).

Paracanthopterygii + Acanthopterygii

The AAP in most acanthomorphs is relatively large and extends farther anteriorly than in most other teleosts. The origin usually includes both the prootic and parasphenoid. In all the specimens that I dissected the muscle was visible externally and the insertion included at least part of the dorsal surface of the mesopterygoid, as well as the metapterygoid and hyomandibular. The AAP in the Paracanthopterygii is greatly enlarged and lines the entire floor of the orbit, inserting anteriorly along most of the dorsal surface of the mesopterygoid. This was the case in all the specimens that I examined (*Percopsis*, *Chologaster*, *Lota*, and *Microgadus*) and in the paracanthopterygians described and illustrated by Rosen (1962) and Rosen and Patterson (1969).

The pattern in the acanthopterygians is more variable, but overall the AAP is well-developed. Among the three beryciforms that I dissected the muscle was restricted to the posterior part of the orbit in two (*Plectrypops* and *Adioryx*) but filled most of the orbit floor in the other (*Melamphaes*). It is difficult to be sure what the primitive character state of the AAP in this basal acanthomorph group is since Rosen and Patterson (1969, p. 373) noted that "In about half of the berycoids the adductor arcus palatini is confined to the rear of the orbit; in the others it is large and fills the orbit floor."

In the Atherinomorpha there is similar variation (see Rosen 1962, 1964). Among the Cyprinodontiformes (*sensu* Nelson 1984) the cyprinodontoids and adrianichthyoids have a greatly developed AAP that fills the floor of the orbit whereas in the exocoetoids it is, according to Rosen (1964, p. 236) "rather small and confined to the posterior wall of the orbit." Among the Atheriniformes, the latter character state is present in the atherinoids (*Hypoatherina*, pers obs.; Rosen 1964), whereas the former is found in the phallostethoids (see Rosen 1964).

In the Percomorpha there is also a trend for the AAP to expand anteriorly along the floor of the orbit. In the percoids (the basal group of the Perciformes, the largest order in the Acanthopterygii) that I examined the muscle was found along the posterior third of the floor of the orbit in *Perca* (Percidae) and *Ambassis* (Centropomidae), the posterior two thirds in *Epinephelus* (Serranidae), and over three quarters in *Etheostoma* (Percidae), *Centropristis* (Serranidae), and *Apistops* (Scorpaenidae). Among the other percomorphs the AAP is large and fills the orbit floor in the Gasterosteidae (see Kampf 1961), the Nandidae (see Liem 1970), and most Tetraodontiformes (see Winterbottom 1974b), to name a few.

Adductor hyomandibulae

A separate *adductor hyomandibulae* (AH) has evolved independently in a number of higher teleosts, as it has in the lower teleosts.

Stomiiformes

Among the stomiiforms I dissected it appeared to be absent in *Diplophos*, *Vinciguerria*, and *Argyropelecus*. According to Günther and Deckert (1955) an AH is present in the specialized genus *Chauliodus*.

Aulopiformes

An AH is present in *Synodus* (pers. obs.) and *Harpadon* (see Günther and Deckert 1960).

Myctophiformes

An AH was absent in *Myctophum* (pers. obs.).

Paracanthopterygii + Acanthopterygii

An AH is widely distributed in this assemblage. It was present in the paracanthopterygians *Percopsis* (Percopsiformes) and *Microgadus* (Gadiformes) (both pers. obs.). It is present in numerous acanthopterygians, including *Perca* and *Gymnocephalus* (Perciformes), *Gasterosteus* (Gasterosteiformes), and various tetraodontiforms (see Osse 1969; Elshoud-Oldenhave and Osse 1976; Anker 1974; and Winterbottom 1974b, respectively).

V. DISCUSSION: SALMONIFORM RELATIONSHIPS

My preferred hypothesis of the phylogenetic relationships of the salmoniform fishes, based on shared derived character states of the bones and muscles of the suspensorium, is shown in Figure 94. My evidence suggests that the order is divisible into two main holophyletic groups: the esocoids + salmonids, and the osmeroids + galaxioids + argentinoids. Because the latter assemblage is the primitive sister group of the higher teleosts (that is, it is more closely related cladistically to them than to the other salmoniforms) the order Salmoniformes, as traditionally defined by Rosen (1974) and Nelson (1984), is not holophyletic, but paraphyletic. The other salmoniform group, the esocoids + salmonids, forms part of an unresolved trichotomy along with the Ostariophysi and the (osmeroid + galaxioid + argentinoid) + neoteleost assemblage because I have no evidence suggesting how these three groups are related to one another.

I tentatively accept other lines of evidence (see Lauder and Liem 1983; Fink 1984b) that the Euteleostei (the Ostariophysi + Salmoniformes + Neoteleostei) are holophyletic. However, it is evident that the Euteleostei are rather poorly defined and the synapomorphies uniting them (the presence of: an adipose fin, nuptial tubercles, and an anterior membranous outgrowth of the first uroneural that does not meet its opposite in the midline) need to be more closely investigated.

In the discussion that follows, the shared derived character states of the suspensorium that were used to unite the various salmoniform groups will be discussed first, followed by a similar section dealing with those of the muscles.

A. RELATIONSHIPS: BONES OF THE SUSPENSORIUM

ESOCOIDEI + SALMONIDAE

The Esocoidei (Esocidae + Umbridae) and Salmonidae are united because they share a hyomandibular with a unique wing of bone that extends anteroventrally from the anteroventral edge of [illegible] ventral arm to overlap the medial surface of the metapterygoid and sometimes part of the symplectic. This wing, hereafter called the anteroventral wing of the hyomandibular, is not part of the anterior lamina, although it extends from its ventral end (see Figs 5-7, 9-11).

All esocoids have an anteroventral wing. Although its shape varies it occupies the same relative position in all of them (see Figs. 5-7, 9). The coregonines, hypothesized to be the most primitive salmonids, all possess a relatively small anteroventral wing that closely resembles that in *Umbra* among the esocoids (compare Figs. 10, 11 with Fig. 9). The Thymallinae and most Salmoninae lack an anteroventral wing. However among the Salmoninae, *Oncorhynchus nerka* (pers. obs.) and *Salvelinus confluentus* (see Cavender 1980) have an anteroventral wing similar to that in the Coregoninae. No other salmoniforms or any of the other teleosts examined possessed an extension of the hyomandibular similar to that found in the Esocoidei and Salmonidae.

Esocoidei

The Esocidae and Umbridae share several derived character states of the bones. Both possess a well-developed and distinctive lateral strut on the hyomandibular that is different from that found in any other group (see Figs. 5-7, 9). In the Esocoidei (Ecocidae + Umbridae) the lateral strut is unusually robust and is nearly perpendicular to the main body of the hyomandibular. In *Novumbra* and *Umbra* the lateral edge of the strut actually curves anterolaterally so that there is a distinctive concavity between it and the anterior lamina. In contrast, the strut is virtually perpendicular in *Esox* and *Dallia*. In all esocoids the lateral strut is unusually robust and closely applied to the anterior edge of the dorsal limb of the preoperculum. The primitive character state for the lateral strut is similar to that in the Salmonidae, in which it is relatively long dorsoventrally, only moderately robust, and inclined posterolaterally (see Figs. 10-13).

Other relatively minor derived character states that unite the Esocoidei, but are shared with some other Salmoniformes, include the following:

1. The mesopterygoid distinctly overlaps the dorsomedial surface of the body of the quadrate (shared with most Salmoninae, some Salangidae, the Retropinnidae, the Prototroctidae, the Lepidogalaxiidae, *Neochanna* (Galaxiidae), a few Alepocephalidae (*Leptoderma* and *Conocara*), and the Argentinoidea.
2. The metapterygoid distinctly overlaps the symplectic (shared with most Galaxiidae, the Argentinidae, and some Opisthoproctidae).
3. The opercular arm of the hyomandibular is relatively long. However, relatively long opercular arms are found in numerous other Salmoniformes (most Osmeridae, the Galaxiidae, the Platytroctidae, and the Alepocephalidae, for example).
4. The bone-enclosed, lateral sensory canal on the preoperculum has a reduced number of pores (six or fewer). Among the other Salmoniformes with a completely bone-enclosed canal, the Salmonidae (the immediate outgroup of the Esocoidei) usually have seven or eight pores (a few Salmoninae have six), the Plecoglossidae eight, and the Lepidogalaxiidae three (the exception). The primitive character state is for a relatively large number of pores (pers. obs.; also see Fink and Fink 1981, and Patterson 1984a for the Ostariophysi; Forey 1973b, 1975, and Grande 1982a for the Clupeomorpha; Forey 1973a for the Elopomorpha; and Patterson 1967b for some other primitive teleosts).

The derived character states unique to the family Esocidae are numerous (for example, all species have a highly specialized palatine with unique teeth). Because these character states are autapomorphies (the family contains only one genus, *Esox*), and I examined only two of the five species of *Esox*, I will not discuss them here. The reader, however, is referred to the descriptive part of this thesis for a detailed description of *E. lucius*.

The Umbridae (*Novumbra* + *Dallia* + *Umbra*) are judged to be holophyletic on the basis of the following shared derived character states of the suspensorium:

1. The ectopterygoid is relatively straight, with no distinct posterior expansion (shared with the Salmoninae and Thymallinae, the Retropinnidae, the Prototroctidae, the Lepidogalaxiidae, and the Argentinoidea).
2. The sensory canal on the preoperculum has five or fewer pores. The Esocidae have six pores (*E. americanus* can occasionally have five according to Cavender 1969) and most Salmonidae have seven or eight.
3. The anteroventral wing of the hyomandibular extends farther ventrally than the ventral arm of the hyomandibular. This is unlike the immediate outgroup, the Esocidae, in which the anteroventral wing extends only slightly ventral to the ventral arm. The character state in the Umbridae may be the result of a shortening of the ventral arm of the hyomandibular since the arm is relatively longer in the Esocidae than the Umbridae.
4. Except for the contact with the anteroventral wing of the hyomandibular, the metapterygoid is relatively widely separated from the hyomandibular. The metapterygoid is also relatively widely separated from the hyomandibular in the Lepidogalaxiidae, *Lovettia* (Aplochitonidae), Bathylagidae (where the metapterygoid is greatly reduced), and the Opisthoproctidae (where the metapterygoid is usually absent).

My finding that both the Esocidae and Umbridae are holophyletic is consistent with the findings of recent workers (see Cavender 1969; Nelson 1972; Rosen 1974; Sytchevskaya 1976; Wilson and Veilleux 1982; Martin 1984). However, Malloy and Martin (1982, taken from Martin 1984, p. 142) apparently suggest that *Esox* and *Umbra* are closely related on the basis of "three ontogenetic characteristics" that they share. However, it is not clear whether these "characteristics" are primitive or derived, and whether or not other esocoids were examined.

Interrelationships of the Umbridae. The interrelationships of the three umbrid genera have been the subject of numerous disagreements. Cavender (1969) and Sytchevskaya (1976) concluded that *Novumbra* and *Dallia* are each other's closest relatives (and together form the sister group of the genus *Umbra*), whereas Nelson (1972) and Wilson and Veilleux (1982) concluded that *Dallia* and *Umbra* are each other's closest relatives (and together form the sister group of the genus *Novumbra*). Rosen (1974) presented evidence agreeing with both hypotheses. Reist (1987) criticized previous hypotheses, and proposed that *Umbra* and *Novumbra* are phenetically each other's closest relatives based on (p. 275) "shape data derived from the external body morphometry ... in which the effects of size were standardized."

My findings, using only the shared derived character states of the bones of the suspensorium, are equivocal. Of the three possible sets of relationships for the umbrid genera I found no reliable evidence supporting the hypothesis that *Novumbra* and *Umbra* are sister taxa. My evidence, however, supports both the hypothesis that *Dallia* and *Umbra* are sister taxa and the hypothesis that *Novumbra* and *Dallia* are sister taxa.

The derived character states supporting the hypothesis that *Dallia* and *Umbra* are sister taxa include the following:

1. The palatines are relatively similar (compare Figs. 7, 8 with Fig. 9). The autopalatine is small relative to the dermopalatine, flattened dorsoventrally, without distinct anterior and posterior dorsoventral expansions (as in *Esox*), and forms the anteriormost part of the palatine (the dermopalatine extends only part way along the ventral surface of the autopalatine). Also, the anterior end of the autopalatine and its cartilage are similar in size and shape.
2. The ectopterygoid is reduced in size (it is fused to the palatine in *Dallia*) and does not overlap the body of the quadrate (it is separated from the quadrate in *Dallia* and barely adjacent to it in *Umbra*). A short, but distinct ligament extends from the posterior tip of the ectopterygoid to the anterodorsal corner of the body of the quadrate in *Dallia* and a trace of a ligament is present in *Umbra*. Also, the ectopterygoid lacks the dorsal process that extends towards the lateral ethmoid bone found in *Esox* (distinct) and *Novumbra*

(less distinct).

3. The preoperculum is similar in shape and proportions (refer to Figs. 7, 9). Also, the auxiliary canals of the sensory canal are unusually long and the canal opens to the exterior via four pores. This is unlike the character state in the Esocidae and *Novumbra* where the auxiliary canals are relatively short and there are six (sometimes five) and five pores, respectively.
4. The hyomandibular is similar in shape: it is relatively wider anteroposteriorly and shorter dorsoventrally than is the case in *Novumbra* and the Esocidae.

The derived character states supporting the hypothesis that *Novumbra* and *Dallia* are sister taxa include the following:

1. The mesopterygoid is similar in shape (oval), size (small relative to the rest of the suspensorium), and occupies the same position relative to the surrounding bones (compare Figs. 6 and 7).
2. The metapterygoid is axe-shaped, small, and similar in position. Also, the bone is almost entirely endochondral in origin and lacks well-developed dermal laminae. This character state is unlike that in *Umbra* and the Esocidae in which the metapterygoid is larger, rectangular, and has distinctive dermal, laminar portions.
3. The anteroventral wing of the hyomandibular is large, long, relatively narrow, and tapers to a point. It extends far anteroventrally to broadly overlap both the symplectic and metapterygoid. This character state is unlike that in *Umbra* in which the anteroventral wing is much smaller, and *Esox* in which it is broader and extends only slightly ventral to the hyomandibular.

My evidence more or less equally supports the hypothesis that *Dallia* and *Umbra* are sister taxa and the hypothesis that *Novumbra* and *Dallia* are sister taxa, provided that each shared derived character state is given equal weight. Previous hypotheses of umbrid interrelationshps have not used many characters of the suspensorium. Cavender (1969) and Sytchevskaya (1976), who favour the latter hypothesis, do not mention any characters of the suspensorium in their analysis of relationships, and indeed it is difficult to be sure what character states they used to unite species. Nelson (1972), who favoured the former hypothesis, used synapomorphies of the cephalic sensory canals as evidence of relationship, one of which included the number of preopercular pores (which I also used). Wilson and Veilleux (1982), who agreed with Nelson, used synapomorphies from all parts of the skeleton to indicate relationship. However, of the thirteen synapomorphies that they used to support their preferred hypothesis (*Dallia* + *Umbra*) only one was from the suspensorium (a reduced ectopterygoid, which I also used). Of their four synapomorphies supporting *Novumbra* + *Dallia*, and three supporting *Novumbra* + *Umbra*, none were from the suspensorium.

Salmonidae

The Salmonidae share a single derived character state of the suspensorium. All have a distinctive autopalatine (the endochondral portion of the palatine) that is reduced in size, with an upturned anterodorsal end, and a cartilaginous cap that emerges from the anterodorsal end and is located dorsal to the rest of the palatine (see Figs. 10-13). In *Stenodus leucichthys* and *Coregonus clupeaformis* (but not *C. artedii*) the anterior end of the autopalatine is not turned upwards as noticeably as in the other species and the anterior cartilage does not extend as far dorsally. Nevertheless, the autopalatine in all the salmonids, including the aforementioned two species, has basically the same shape. Also, although the interrelationships of the Coregoninae have not been investigated in great detail, most workers agree that *Prosopium* is the sister group of the other coregonines (see Norden 1961; Dorofeyeva *et al.* 1980; Kendall and Behnke 1984). If this were the case, then the modified autopalatine found in *C. clupeaformis* and *Stenodus* might represent a secondary modification of the ancestral salmonid character state (found in all the other salmonids).

The only other salmoniform with an autopalatine that vaguely resembles that in the Salmonidae (in particular, the Thymallinae and Salmoninae) is *Lepidogalaxias*. However, because the autopalatine in the two groups differs in other significant ways, and other evidence suggests that *Lepidogalaxias* is a galaxioid, I conclude that this resemblance is most likely an example of parallelism.

Although I have found only one shared derived character state supporting the holophyly of the Salmonidae, the findings of other investigators agree with mine (see Kendall and Behnke 1984, for a survey of current hypotheses). Kendall and Behnke list five salmonid synapomorphies: a tetraploid karyotype (also see Allendorf and Thorgaard 1984), an axillary pelvic process, parr marks in juveniles, three postcleithra, and a toothless mesopterygoid. Of these five, only the first three appear to me to be synapomorphies. The presence of three postcleithra is apparently the primitive character state within the Teleostei (pers. obs.) and a toothless mesopterygoid is of dubious value because its polarity is uncertain at this level and because it is an absence character state. In conclusion, because the holophyly of the Salmonidae is supported by relatively few synapomorphies, and because there is little agreement as to the family's phylogenetic position (contrast my hypothesis with that of Rosen 1974, 1985 and Fink 1984b), additional evidence bearing on the holophyly of this family is highly desirable.

Interrelationships of the Salmonidae. The Salmonidae consist of three subfamilies (the Coregoninae, Thymallinae and Salmoninae) according to most recent authors (see Norden 1961; Cavender 1970; Behnke 1970; Kendall and Behnke 1984; Sanford 1987).

Assuming that each subfamily is holophyletic, there are three possible hypotheses concerning their relationship to one another: the Coregoninae and Salmoninae are sister taxa, the Coregoninae and Thymallinae are sister taxa, or that the Thymallinae and Salmoninae are sister taxa. I found no evidence supporting the former two hypotheses; however, the hypothesis that the Thymallinae and Salmoninae are sister taxa is supported by the following shared derived character states:

1. The autopalatine is short anteroposteriorly and small relative to the dermopalatine, with a cartilage at its anterior end that is similar in size and shape. This hook-like anterior cartilage is larger than in the Coregoninae and expanded laterally where it contacts the maxilla (compare Figs. 12, 13).

2. The ectopterygoid is splint-like, with only a slight bend and virtually no posterior expansion. In the Coregoninae the bone is more distinctly angled and has a distinct posterior expansion that more broadly overlaps the quadrate.
3. The metapterygoid is similar. It is triangular, with a large, ventral, endochondral section and a relatively large posterodorsal, dermal lamina that overlaps the anterior lamina of the hyomandibular. A triangular endochondral wedge that varies in size extends from the main endochondral section posteriorly through the posterodorsal lamina to the hyomandibular. Also, the metapterygoid is inclined more or less dorsoventrally (it does not curve distinctly dorsomedially at its anterodorsal end as it does in the Coregoninae and the other outgroups) and overlaps the mesopterygoid in the same way. The metapterygoid in the Coregoninae is similar to that found in the primitive teleosts (e.g., the gonorynchiform *Chanos*) and represents the primitive character state: it is somewhat semi-circular, lacks a distinct posterodorsal lamina, and curves dorsomedially at its anterodorsal end to overlap most of the posterodorsal end of the mesopterygoid.
4. The hyomandibular lacks an anteroventral wing (except for *Oncorhynchus nerka* and *Salvelinus confluentus*). This character state is derived if, as was previously argued, an anteroventral wing is a synapomorphy of the Esocoidei and Salmonidae.

The findings of other investigators are similar to mine. Fink (1984b) considers the loss of ossification of the supraethmoid to be a synapomorphy of the Thymallinae + Salmoninae whereas Kendall and Behnke (1984) unite them on the basis of the yolk sac (the yolk is large, with an extensive vitelline system, and has a uniform intense pigment) and certain larval characteristics (the larval stage is bypassed).

OSMEROIDS + GALAXIOIDS + ARGENTINOIDS

The osmeroids, galaxioids, and argentinoids (*sensu* Greenwood and Rosen 1971) constitute the second major salmoniform holophyletic group (see Fig. 94). They share a complex derived character state: the mesopterygoid possesses a series of relatively large, specialized teeth on its medioventral surface that curve laterally (anterolaterally in the Galaxiidae and Aplochitonidae) and oppose the basihyal and/or basibranchial dentition. Although their size and distribution may vary, they are found in all Osmeridae, Plecoglossidae, Retropinnidae, Prototroctidae, Galaxiidae (except one genus, *Neochanna*, of the six galaxiid genera), Aplochitonidae, and Platytroctidae (except the genus *Mirorictus*, of the seven genera examined) (refer to Figs. 14-18, 22, 23, 25, 26, 42-45). Teeth are absent in the Salangidae, Sundasalangidae, Lepidogalaxiidae, and four of the five argentinoid families (Alepocephalidae, Argentinidae, Bathylagidae, and Opisthoproctidae); however, for reasons I will outline later, I hypothesize that they have been secondarily lost in these lineages.

Fink and Weitzman (1982) originally proposed that specialized teeth on the mesopterygoid were a synapomorphy uniting the osmeroid and galaxioid fishes (excluding the Lepidogalaxiidae). They did not include the Argentinoidei within this assemblage, although they considered them to be its sister group. However, the reason they did this is uncertain and to quote Fink (1984b, page 202), "Fink and Weitzman (1982) were unable to provide evidence bearing on relationships of these fishes, even though their cladogram ... showed them as the sister group of the osmeroids [my osmeroids + galaxioids]."

In this assemblage the primitive character state for mesopterygoidal teeth is found in *Hypomesus* (Osmeridae), the Retropinnidae, and the Prototroctidae (see Figs. 15, 22, 23): there is a relatively large number of teeth on the medioventral surface that extend along nearly the entire anteroposterior length of the bone. The medialmost teeth are the largest and are arranged in somewhat irregular rows; the teeth lateral to these are smaller, and more randomly distributed. The ventrolaterally - directed, pointed, mesopterygoidal teeth oppose a large number of similar, dorsomedially - directed teeth on both the basihyal and basibranchials. There are a number of trends in the other salmoniforms with mesopterygoidal teeth, including: loss of teeth, in particular, those in the lateral rows; reduction in size or enlargement of the remaining teeth; restriction of teeth to certain parts of the bone; and change in inclination. Associated with the above changes are changes in the basihyal and basibranchial dentition. There are essentially three derived character states that could be derived from the ancestral state: one in *Mallotus* (Osmeridae) and adult *Plecoglossus* (Plecoglossidae) in which there is a single row of tiny teeth on the posterior half of the bone (see Figs. 14, 18); one in the other Osmeridae (*Osmerus*, *Allosmerus*, *Spirinchus*, and *Thaleichthys*) and some Platytroctidae where there is a single, medial row of relatively large teeth along the entire length of the bone (and sometimes a few smaller lateral teeth) (e.g., see Figs. 16, 17, 43); and another in the Galaxiidae and Aplochitonidae where there is a single, medial row of large, anterolaterally - directed teeth along the anterior half of the bone (see Figs. 25, 26). These patterns will be discussed later in greater detail.

Other primitive teleosts possess teeth on the mesopterygoid. However, with one exception (the extinct clupeomorph *Diplomystus* and its relatives), they are distinctly different in size, shape, and/or position from those in the osmeroid, galaxioid, and argentinoid assemblage. The primitive character state, that found in most teleosts with mesopterygoidal teeth, is for a relatively large number of ventrally - directed, tiny, denticle-like teeth that are randomly distributed over most of the ventral surface (for example, the elopomorph *Megalops*, Fig. 48) or are restricted to various parts of the ventral surface (for example, the osteoglossomorph *Hiodon*, Fig. 47). This character state is widely distributed in the Teleostei and is found in both extant and extinct members of most major lineages, for example, in the following genera:

Osteoglossomorpha: *Arapaima* (see Kershaw 1976), *Hiodon* (pers. obs.) and the fossil genus *Lycoptera* (Greenwood 1970).

Elopomorpha: *Elops, Megalops* (both pers. obs.), plus numerous extinct species (see Forey 1973a).

Clupeomorpha: *Denticeps* (Denticipitidae, see Greenwood 1968); many clupeoids, including the Dussumieriidae (pers. obs., also see Whitehead 1963); numerous Clupeidae (*Pellonula, Pellona, Pristigaster, Coilia;* see Ridewood 1905b, Moona 1963); most Engraulidae (pers. obs., also see Ridewood 1905b; Chapman 1944b, 1948b; Moona 1963); and the fossil clupeomorph *Ornategulum*, hypothesized by some to be the most primitive clupeomorph (see Forey 1973b, 1975; Lauder and Liem 1983).

Ostariophysi: Most lack teeth on the mesopterygoid; however, the characiform genus *Hoplerythrinus* (Erythrinidae) apparently possess teeth similar to the primitive character state (see Weitzman 1964).

Stomiiformes: Many genera, including relatively primitive ones such as *Diplophos, Triplophos, Photichthys, Polymetme, Gonostoma,* and *Cyclothone* (pers. obs., also see Weitzman 1967a, 1974; Fink and Weitzman 1982).

Aulopiformes: *Aulopus*, the only genus in the monotypic family Aulopodidae, considered to be the most primitive one of the order (see Sulak 1977; Nelson 1984), as well as numerous fossil Aulopiformes (see Goody 1969a).

Myctophiformes: All Myctophidae (pers. obs., also see Paxton 1972).

Paracanthopterygii: The two genera (*Aulolepis* and *Ctenothrissa*) in the extinct order Ctenothrissiformes (see Patterson 1964); *Aphredoderus*, the only genus in the family Aphredoderidae (Percopsiformes) (see Rosen 1962); and the fossil percopsiform *Sphenocephalus*, thought to be near the ancestry of the extant percopsiforms (see Rosen and Patterson 1969).

Acanthopterygii: Most members of the beryciform families Polymixiidae, Berycidae, and Monocentridae (pers. obs., also see Zehren 1979), and numerous fossil beryciforms (see Patterson 1964, 1967a).

Although the mesopterygoidal teeth in the aforementioned species do not resemble those found in the salmoniform families, a number of other teleosts have enlarged teeth on the mesopterygoid. In the ostariophysan *Gonorynchus* (Gonorynchidae, Gonorynchiformes) the posteroventral surface of the mesopterygoid has, according to Ridewood (1905c, p. 365) a "circular patch of stout bluntly conical teeth" that oppose a similar patch of teeth on the second basibranchial. Similarly shaped teeth are also found in the relatively derived elopomorph *Albula* (Albulidae) (see Ridewood 1904b; Forey 1973a; Shaklee and Tamaru 1981), and apparently in its sister genus *Pterothrissus* (see Forey 1973a). In *Albula* the teeth are in an elliptical patch on the mid-medioventral surface of the mesopterygoid and oppose (along with the similarly shaped parasphenoid teeth, which are absent in salmoniforms) a large patch of similar teeth on the basibranchials. However, I conclude that these teeth are convergent with those of the salmoniforms and are probably autapomorphies of their respective lineages because: they are different in shape and position from those in the salmoniforms; they are absent in the other ostariophysans and elopomorphs, respectively; and because the Ostariophysi and Elopomorpha are each well-defined holophyletic groups (see Lauder and Liem 1983).

Four extant osteoglossomorph genera also have enlarged teeth on the mesopterygoid: *Osteoglossum* (Osteoglossidae), *Scleropages* (Osteoglossidae), *Pantodon* (Osteoglossidae), and *Heterotis* (Arapaimidae) (pers. obs.; also see Ridewood 1905a; Kershaw 1970, 1976). Similar teeth are also found in the fossil osteoglossid *Brychaetus* (see Roellig 1967). As in the salmoniforms there is a series of relatively large, ventrolaterally curved, pointed teeth along most of the medioventral surface of the mesopterygoid that oppose the basihyal and basibranchial dentition. In this regard they are similar to the primitive character state within the salmoniforms, as represented by the Retropinnidae, Prototroctidae, and *Hypomesus* (Osmeridae). Unlike the salmoniforms, however, most of the rest of the ventral surface is covered by tiny denticle-like teeth similar to those found in most teleosts with mesopterygoidal teeth. In addition to the above morphological difference there is relatively good evidence that the Osteoglossomorpha are a holophyletic group and that they are phylogenetically distant from the salmoniforms (see Lauder and Liem, 1983, for a review of the evidence), suggesting that the similarity with the salmoniforms is convergent.

Among the euteleosts, the aulopiform genus *Saurida* (Synodontidae) and its sister genus *Harpadon* have enlarged mesopterygoidal teeth that superficially resemble those found in the salmoniforms (pers. obs.; also see Sulak 1977). However, these teeth are undoubtedly convergent with those in the salmoniforms and may represent a *Saurida* + *Harpadon* synapomorphy. First, there is considerable evidence that the Aulopiformes are relatively distant phylogenetically from the salmoniforms (see Rosen 1973; Sulak 1977; Nelson 1984). In addition, no other aulopiforms have similar teeth. Also, unlike the salmoniforms, the teeth in *Saurida* are restricted to a centrally located oval patch on the anteroventral surface of the bone and their inclination is different; instead of pointing laterally or anterolaterally (as in the salmoniforms) they point distinctly medially (see Fig. 95).

The only teleosts, to my knowledge, with mesopterygoidal teeth similar to those in the salmoniforms are found in the extinct clupeomorph genus *Diplomystus* (pers. obs.; also see figs. 8 and 9 in Zhang *et al.* 1985) and apparently in the other species belonging to the extinct family Ellimmichthyidae (see Grande 1982a). These teeth and their distribution are most similar to those in the osmerid *Hypomesus* (see Fig. 15) among the salmoniforms that I examined, and oppose similar teeth on the basihyal and basibranchial tooth-plates. However, because the other clupeomorphs lack such teeth, including the two most primitive genera (*Ornategulum* and *Erichalcis*, see Forey 1973b and 1975, respectively), their presence in the Ellimmichthyidae probably represents an autapomorphy of the family.

The teeth on the mesopterygoid are probably functionally important in that they form part of a specialized bite mechanism in which food is manipulated between them and the basihyal and/or basibranchial dentition. The primitive character state is when they oppose both the basihyal and basibranchial dentition. This is found in *Retropinna*, *Prototroctes*, *Plecoglossus*, and some osmerids (*Hypomesus*, *Osmerus*, and *Allosmerus*). There are two derived character states: one in which the mesopterygoidal teeth oppose only the basihyal teeth (Galaxiidae and Aplochitonidae), and another in which the mesopterygoidal teeth oppose only the basibranchial teeth (the osmerids *Mallotus*, *Spirinchus*, and *Thaleichthys*; and the platytroctids *Searsia koefoedi*, *Searsioides multispinus*, *Sagamichthys abei*, *Holtbyrnia latifrons*, and *Platytroctes apus*).

Fink and Weitzman (1982, p. 84) first suggested that "in osmeroids and galaxiids there is a specialized 'tongue bite' mechanism in which food is manipulated between the basihyal teeth and the mesopterygoidal teeth." However, as I noted, I disagree with the nature of this bite. A true "tongue bite" is found only in the Galaxiidae and Aplochitonidae among the salmoniforms with mesopterygoidal teeth and, as I pointed out, I consider this to be a derived character state and a synapomorphy uniting these two families.

The primary bite in salmoniforms and most other teleosts without mesopterygoidal teeth is between the bones at the edge of the upper jaw (the premaxillae, maxillae, vomer, and palatine) and the dentary (and sometimes the basihyal). This bite may involve teeth on all, or only some of the above bones. For example, in the Salmoninae there are large teeth on the premaxillae, maxillae, and palatine that oppose those on the dentary, and large vomerine teeth that oppose greatly enlarged teeth on the basihyal (the mesopterygoid and basibranchials are edentulous). In the Alepocephalidae examined (mesopterygoidal, basihyal, and basibranchial teeth are absent) the bite is between teeth on the premaxillae, maxillae (when teeth are present), palatine (when teeth are present), vomer (when teeth are present) and the dentary. The bite in the Esocoidei involves teeth on the palatine, vomer, and premaxillae (weakly developed in the Esocidae) opposing those on the dentary and basihyal (basihyal teeth are absent in *Dallia* and *Umbra*, see Wilson and Veilleux 1982).

As I mentioned before, of the five families in the Argentinoidei, only the Platytroctidae have teeth on the mesopterygoid. However, I hypothesize that mesopterygoidal teeth were present in the common ancestor of the Argentinoidei and that they have been secondarily lost in all argentinoids except the Platytroctidae. If this is the case, then the Argentinoidei belong in the osmeroid and galaxioid assemblage. The assumption is that the Argentinoidei are a holophyletic group. I accept Greenwood and Rosen's (1971) hypothesis that the Argentinoidei are holophyletic. Some evidence from the suspensorium, as well as evidence from the muscles of the suspensorium (that I will outline later), corroborates their hypothesis.

The size, number and position of the mesopterygoidal teeth varies in the various Platytroctids (see description of the family and the accompanying figures). However, they are similar in most respects to those in the osmeroids and galaxioids and I consider them to be homologues: they are relatively large, distributed along the medioventral surface, curve ventrolaterally, and as in some osmerids, oppose similar teeth on the basibranchials (when basibranchial teeth are present). The mesopterygoidal teeth in the Argentinoidei are more similar to those in the osmeroids and galaxioids than they are to those in the other teleosts with mesopterygoidal teeth.

There is a distinct trend within the Argentinoidei for reduction and/or loss of dentition. Within the three families belonging in the Argentinoidea, all genera lack teeth on the premaxillae, maxillae, mesopterygoid, and basibranchials, and all, except for the Agentinidae, lack teeth on the basihyal (pers. obs.; also see Trewavas 1933; Chapman 1942a, 1942b, 1943, 1948a; Bertelsen 1958; Cohen 1958a, 1964; Borodulina 1968; Nelson 1970a). The palatine and vomer are the only bones of the upper jaw with an extensive dentition, and this feature is a shared derived character state (that forms part of a specialized bite mechanism) of the Argentinoidea. The Alepocephaloidea (Alepocephalidae + Platytroctidae) have a more extensive dentition than the Argentinoidea but also exhibit a reduction and/or loss of teeth, particularly on the mesopterygoid, vomer, palatine, basihyal, and basibranchials (pers. obs., also see Parr 1960; Greenwood and Rosen 1971; Rosen 1974; Markle 1976; Matsui and Rosenblatt 1979; Markle and Merrett 1980). No alepocephalid has teeth on the mesopterygoid and of the twenty-four genera listed by Markle (1976) twelve lack vomerine teeth, eight lack palatine teeth, and twelve lack teeth on the maxillae. Virtually all alepocephalids lack basihyal and basibranchial dentition. However, *Bajacalifornia calcarata* has uniserial teeth along the basihyal, but no basibranchial teeth (see Markle 1976) and *Rinoctes nasutus*, which according to Markle and Merrett (1980) has the most extensive dentition in the Argentinoidei, has a single row of small, recurved teeth along the first three basibranchials (but no basihyal teeth). The Platytroctidae usually have teeth on the maxillae and premaxillae; however, the teeth on the palatine and vomer (when present) are usually small, relatively delicate, and reduced in number. The basihyal and basibranchials usually bear teeth but in all cases these are small, delicate, and few in number (pers. obs.; also see Greenwood and Rosen 1971; Rosen 1974; Markle 1976; and Matsui and Rosenblatt 1979).

Ontogenetic evidence also suggests that the common ancestor of the Argentinoidei had more extensive dentition, including mesopterygoidal teeth. In two platytroctid genera that Matsui and Rosenblatt (1979) examined, smaller, younger specimens had more extensive dentition. For example in the genus *Maulisia* they note (p. 63) that "A short outer tooth row

Similarly, teeth on the basihyal, palatines, and mesopterygoids [are] present in smaller individuals but [are] lacking in larger ones." They noted a similar pattern in the genus *Searsia*.

Within the galaxioids and osmeroids there is a trend for reduction and/or loss of dentition on the mesopterygoid and the opposing basihyal and basibranchials. The primitive character state, represented by the Retropinnidae, Prototroctidae, and *Hypomesus* (Osmeridae) is for there to be a large number of moderately large mesopterygoidal teeth, in several rows, that oppose a large number of teeth (of similar size) on the basihyals and basibranchials. In more derived osmerids (*Spirinchus* for example) and galaxioids (the Galaxiidae and Aplochitonidae) there are fewer (one row) but larger teeth on the mesopterygoid that oppose a reduced number of teeth on the basihyal and basibranchials, as in the Osmeridae, and larger but fewer basihyal teeth (the basibranchials are edentulous), as in the Galaxiidae and Aplochitonidae.

Also, within the Teleostei there is an overall trend for reduction of dentition on the gill arches (including the basihyal and basibranchials) and the bones of the upper jaw and suspensorium (see Nelson 1968, 1969). On a small scale, there is a distinct trend within the Clupeidae (Clupeiformes) for loss of teeth on the basihyal, basibranchials, mesopterygoid, and other bones (pers. obs.; also see Nelson 1967a, 1970b).

Overall it is more parsimonious to hypothesize that the common ancestor of the Argentinoidei had a more extensive dentition (including teeth on the mesopterygoid) than its descendents, and that they, together with the osmeroids and galaxioids represent a single holophyletic group. This argument is based on the following assumptions and evidence: that the Argentinoidei are holophyletic; that there is a trend for reduction and/or loss of dentition within the Argentinoidei; that there is a trend for reduction (and sometimes loss) and specialization of teeth on the mesopterygoid, basihyal, and basibranchials within groups that have well developed mesopterygoidal teeth; that the loss of a structure (i.e., mesopterygoidal teeth) is more likely than their gain; that the mesopterygoidal teeth in the Argentinoidei are homologous with those in the osmeroids and galaxioids; and lastly, that the occurrence of mesopterygoidal teeth (and teeth in general) in young specimens, and their absence in larger specimens of the same species of some platytroctids, suggests that the common ancestor had mesopterygoidal teeth. This hypothesis, requires an initial acquisition of mesopterygoidal teeth and then a number of independent losses (a minimum of four) within the various lineages that lack them (the Salangidae and Sundsalangidae, Lepidogalaxiidae, Alepocephalidae, and the Argentinoidea). If the teeth in the Platytroctidae are not homologous with those in the osmeroids and galaxioids then this character state would unite the osmeroids and galaxioids. This hypothesis requires that mesopterygoidal teeth be acquired independently twice (in the osmeroids and galaxioids, and in the Platytroctidae) and then be lost (reversed) in two independent lineages (the Salangidae + Sundasalangidae and the Lepidogalaxiidae). A third possibility is that mesopterygoidal teeth were acquired independently four times (Osmeridae + Plecogossidae, Retropinnidae + Prototroctidae, Galaxiidae + Aplochitonidae, and in the Platytroctidae).

Of the above three hypotheses I prefer the first (the osmeroids + galaxioids + Argentinoidei, together, form the sister group of the Neoteleostei) in which mesopterygoidal teeth are hypothesized to be present in the common ancestor of the osmeroids + galaxioids + Argentinoidei (i.e., to have been acquired only once), because I believe that loss of mesopterygoidal teeth is more likely to have occurred repeatedly than is the independent development of similar structures in independent lineages.

Two other lineages, the Salangidae + Sundasalangidae and the Lepidogalaxiidae, also lack teeth on the mesopterygoid, but are included with the osmeroids and galaxioids, respectively. For reasons that I will discuss later, I hypothesize that mesopterygoidal teeth were present in the ancestor of each of these lineages and have been secondarily lost.

In my preferred hypothesis, therefore, the osmeroids, galaxioids, and Argentinoidei are united on the basis of their sharing specialized teeth on the mesopterygoid that form part of a specialized bite mechanism. However, because I have no evidence suggesting how these three groups are related to one another they form an unresolved trichotomy (see Fig. 94).

I will now discuss each of these three major groups, and their constituent taxa, as defined by shared derived character states of the suspensorium.

Osmeroids

The Osmeridae and Plecoglossidae form a distinct assemblage because they share a similar metapterygoid, with a complex shape, that is unlike that found in the other salmoniforms and teleosts (compare Figs. 14-18):-

1. The posterior part is projected into a large dermal lamina (labelled Mt.p on Figs. 14-18) that overlaps the ventral arm and anterior lamina of the hyomandibular to varying degrees. Among the salmoniforms, the Salmoninae (Salmonidae) and Galaxiidae also have a dermal lamina. However, the lamina in the Salmoninae is unlike that in the Osmeridae and Plecoglossidae in that it overlaps only the anterior lamina of the hyomandibular (versus mainly the ventral arm), is divided by a small endochondral wedge, and is not crossed by a lateral ridge. The lamina in the Galaxiidae is more similar to that in the Osmeridae and Plecoglossidae; however, I have considerable evidence suggesting that the Galaxiidae are part of another holophyletic group (the galaxioids).
2. There is a ridge on the lateral surface that extends from near the centre of the bone diagonally to the posterodorsal corner. This lateral ridge (labelled Mt.l on Figs. 14-18) is moderately developed in *Hypomesus* and *Mallotus* but well-developed in the other four osmerid genera. In *Plecoglossus* it is more robust than in the osmerids and is curved. However, I consider it to be homologous because it occupies the same relative position and, as in the Osmeridae, its dorsal edge serves as an insertion area for part of the *levator arcus palatini*. Some galaxiids have a lateral ridge on the metapterygoid; however, most do not. Of the five species (in three genera) that I examined, only *Galaxias maculatus* had a lateral ridge, and of the two specimens that I examined, it was distinct in only one.
3. On the medial side there is a relatively wide and sharp ridge that extends posteroventrally from the anterodorsal corner towards the posteroventral corner. Part of the *adductor*

arcus palatini inserts dorsal to this medial ridge (labelled Mt.m on Figs. 14-18). The posterior end of the ridge is expanded into a laminar wing (hereafter called the posteroventral wing of the metapterygoid, labelled Mt.w on Figs. 14-18) that projects posteroventrally to overlap the medial surface of the anteroventral corner of the ventral arm of the hyomandibular. Other salmoniforms have a ridge on the medial side of the metapterygoid; however, in most cases it is not truly a ridge, but simply a rounded, raised section onto which part of the *adductor arcus palatini* inserts. A true ridge similar to that in the Osmeridae and Plecoglossidae was observed only in *Galaxias maculatus* (where it is more flange-like, runs in a different direction, and was found in only one of the two specimens examined; see Fig. 26) and in the Alepocephaloidea (Platytroctidae and Alepocephalidae) where it may be an alepocephaloid synapomorphy. Also, the ridge in the alepocephaloids is probably not homologous with that in the Osmeridae and Plecoglossidae since in most alepocephaloids (twelve of fourteen alepocephalid species and six of seven platytroctid species examined) the *adductor arcus palatini* inserts only onto the hyomandibular, and the medial metapterygoidal ridge is occupied by the *levator arcus palatini*. No other salmoniform examined possessed a posteroventral wing on the metapterygoid.

4. There is a relatively wide, round notch on the lateral side between the ventral end of the posterior dermal lamina and the posteroventral corner of the endochondral portion. A trace of a notch can be found in this area in some galaxiids (*Galaxias maculatus* and *Brachygalaxias*) while a moderately wide notch is found in *Thymallus* (Thymallinae) and a few salmonines.

The metapterygoid in the Osmeridae and Plecoglossidae may function partly as a buttress: its posterior edge is broad and closely abuts the anterior edge of the ventral arm of the hyomandibular. Little mediolateral movement of the posterior end of the metapterygoid seems possible since the posterior lamina overlaps the lateral side of the ventral arm of the hyomandibular and the posteroventral wing overlaps the medial side of the ventral arm. The posterior edge of the metapterygoid in the Galaxiidae similarly closely abuts the anterior edge of the hyomandibular, forming a relatively tight and immovable joint; however, the metapterygoid differs in several ways from that in the Osmeridae and Plecoglossidae and the similarity is considered to be convergent.

The function of the buttress-like metapterygoid may be related to the bite between the mesopterygoidal and basihyal - basibranchial teeth. Based on tooth orientation and the arrangement of the muscles of suspensorium, this bite probably involves primarily a mediolateral movement of the suspensorium, and the buttress might stabilize the suspensorium by restricting excessive mediolateral movement of the metapterygoid and its adjacent bones. The metapterygoid - to - hyomandibular joint in the Galaxiidae may serve a similar function since this family also has a bite between the mesopterygoidal and basihyal teeth. However, in none of the other salmoniforms with a similar bite does the metapterygoid and hyomandibular have a similar interlocking joint (i.e., the Retropinnidae, Prototroctidae, Aplochitonidae, and Platytroctidae).

Osmeridae + Plecoglossidae

The family Osmeridae consists of six genera (*Hypomesus, Mallotus, Osmerus, Allosmerus, Spirinchus*, and *Thaleichthys*) and ten species (see McAllister 1963). Although each genus is well defined, the relationships of the six genera to one another are uncertain, and a number of conflicting hypotheses exist. For example, Chapman (1941b) considered there to be two main groups: one consisting of *Hypomesus* and *Mallotus* and another consisting of *Osmerus, Allosmerus*, and *Thaleichthys* (which he considered to be the most primitive osmerid). He hypothesized that *Spirinchus* was intermediate between the two groups. McAllister (1963) divided the Osmeridae into two subfamilies: the Hypomesinae, consisting of *Hypomesus* and *Mallotus*, and the Osmerinae, consisting of *Allosmerus, Thaleichthys, Osmerus*, and *Spirinchus* (which he considered to be the most primitive osmerine, and possibly the most primitive osmerid). Using the same data, but phenetic techniques, McAllister (1966) reversed the positions of *Spirinchus* and *Thaleichthys* (so that *Thaleichthys* was now the most primitive osmerid). Patterson (1970), in a critique of

McAllister's work came to entirely different conclusions, stating that (p. 280) the "Hypomesinae are the plesiomorph sister-group of [the] Osmerinae, and that *Hypomesus* is the most primitive osmerid genus." Klyukanov (1975), using only partly original data, criticized Patterson's findings and noted (p. 16) that "The subfamily Thaleichthyinae [= *Thaleichthys*], with the greatest number of primitive structural features, is the most primitive among the osmerids."

Except for Patterson (1970), the former authors did not distinguish between primitive and derived character states in their analysis, and because of this, their results are suspect. Also, their choice of the Salmoninae (considered by most recent workers, and myself, to be the most derived salmonid subfamily) as their outgroup is doubtful. A different outgroup, such as the Coregoninae, would reverse the polarity of some key characters, and lead to the opposite conclusion (i.e., that *Spririnchus* and *Thaleichthys* are the most derived genera).

More[1] recently, Rosen (1974) and Fink (1984b) raised doubts as to whether or not the Osmeridae constitute a holophyletic group. Rosen (1974, p. 310) noted, in a critique of McAllister's (1963) work, that of the thirty-five traits he used to define the Osmeridae, "only six can be considered derived in relation to their condition in other teleosteans," and "Not one of these six characters is peculiar to osmerids." To quote Fink (1984b, p. 203) "no evidence has ever been presented that the family [Osmeridae] is a monophyletic group. Indeed, it seems quite possible that *Plecoglossus* could be more closely related to some 'osmerids' than to others, and this would render the family paraphyletic." In support to this suggestion, Howes and Sanford (1987, p. 133) studied "the development of the teeth, jaws, oral cavity ethmoid and suspensorial elements" in *Plecoglossus* and concluded that because it shares several derived character states "with certain genera of the family Osmeridae ... the Osmeridae is a paraphyletic assemblage."

As I documented previously, my evidence strongly suggests that the Osmeridae and Plecoglossidae, together, form a distinct holophyletic group. Since representatives of all six osmerid genera and the only known species of *Plecoglossus* were available to me, I tested the hypothesis, using the bones of the suspensorium, that the family Osmeridae is holophyletic.

Although my findings suggest that the Osmeridae are not holophyletic, this conclusion is far from certain. I found no convincing shared derived character state of the suspensorium uniting the Osmeridae. However, within the family there is one well-defined holophyletic group, consisting of *Osmerus, Allosmerus, Spirinchus,* and *Thaleichthys*. This assemblage corresponds to McAllister's (1963) Osmerinae. The shared derived character states uniting the above four genera are the following (refer to Figs. 16, 17):

1. The autopalatine is similar in shape. Overall, it is robust, relatively short anteroposteriorly, and with greatly expanded anterior and posterior (especially) ends. This character state is unlike that in *Hypomesus, Mallotus, Plecoglossus,* and the outgroups, in which the anterior and posterior ends of the autopalatine are either only moderately expanded or only slightly expanded.
2. The ridge on the lateral surface of the metapterygoid is well developed and distinctive. It is wide, directed either laterally or ventrolaterally, and extends from the anteroventral part of the endochondral portion to the posterodorsal corner of the dorsal lamina. This is unlike the unique character state in *Plecoglossus* (see Fig. 18) and unlike the character state in *Hypomesus* (see Fig. 15) and *Mallotus* (see Fig. 14) where the lateral ridge is only moderately developed, narrower, and shorter anteroposteriorly (extending only from the posterodorsal corner of the endochondral portion to the posterodorsal corner of the dorsal lamina).
3. The hyomandibular has a number of derived features, that when taken together, are indicative of relationship. The opercular arm is unusually long and narrow (a relatively similarly shaped opercular arm is found in the Esocidae, and many alepocephalids and platytroctids). The lateral strut is unique and unlike that in any other salmoniform: in *Osmerus, Allosmerus,* and *Spirinchus* it is reduced dorsally and ventrally and has an expanded middle section that extends posteriorly or posterodorsally as a brace that approaches the dorsal limb of the preoperculum. In *Thaleichthys* the strut is further reduced and consists only of a long, narrow, dorsoventrally aligned ridge. The four genera also lack a distinct canal for the hyomandibular branch of the facial nerve. Instead

there is a foramen at the base of the head through which the nerve passes (versus a distinct canal in other salmoniforms). Also, the "lateral" foramen for the canal is located at the dorsal edge of the lateral strut and is entirely visible externally. In most other salmoniforms and teleosts the lateral foramen is hidden by the lateral strut and is located posterior to its dorsal half (the primitive character state). All osmerines have a relatively well-developed ridge on the medial surface that runs dorsoventrally along the head and ventral arm (a somewhat similar, but weakly-developed ridge is found in *Hypomesus* and *Mallotus*, but is absent in *Plecoglossus*). A similar, well-developed medial ridge is found in many Alepocephalidae and Platytroctidae (e.g., see Figs. 34, 42).

Within the Osmerinae, *Spirinchus* and *Thaleichthys* form a holophyletic group on the basis of their sharing a similar mesopterygoid: it is reduced in size, roughly oval in shape, and separated from the autopalatine by a relatively wide band of cartilage. A similarly shaped mesopterygoid bearing the same relation to the autopalatine is found in numerous alepocephalids and platytroctids. The primitive character state, found in the other osmerids, *Plecoglossus*, and most other salmoniforms is for a relatively large, anteroposteriorly elongated mesopterygoid that closely approaches or overlaps the autopalatine.

The position of *Osmerus* and *Allosmerus* relative to the other osmerines is uncertain from my data; they form part of an unresolved trichotomy that includes *Osmerus*, *Allosmerus*, and *Spirinchus* + *Thaleichthys*

The interrelationships of *Hypomesus*, *Mallotus*, *Plecoglossus*, and the Osmerinae are uncertain. Some evidence suggests that *Mallotus* and *Plecoglossus* may be sister taxa, including: a symplectic that has a prominent central bend with a similar V-shaped dorsal lamina, and mesopterygoidal teeth that are small, delicate, and aligned in a single row along the posterior half of the medial side of the bone (compare Figs. 14 and 18). However, this hypothesis has little credibility since juvenile specimens of *Plecoglossus* have different character states that are similar to those found in the osmerid *Hypomesus* (i.e., primitive, with a relatively straight symplectic without laminae, and numerous relatively large mesopterygoidal teeth distributed along the entire medial side of the bone). Unlike

Plecoglossus, the suspensoria in adult and juvenile specimens of *Mallotus* (and *Hypomesus*) are relatively similar (pers. obs.). This ontogenetic evidence suggests that the character states found in adult *Plecoglossus* are probably autapomorphies of the lineage and are not indicative of relationship with *Mallotus*.

I found no derived character states linking *Plecoglossus* with *Hypomesus*. However, *Hypomesus* and *Mallotus* share an ectopterygoid with a finger-like extension at its bend that extends posterodorsally towards the metapterygoid (overlapping the metapterygoid in *Mallotus*, see Fig. 14). The extension in the specimen of *Hypomesus* figured (Fig. 15) was the least distinctive of all specimens that I examined.

My preferred hypothesis of the interrelationships of the six osmerid genera and *Plecoglossus* is shown in Fig. 96. In this scheme *Hypomesus*, *Plecoglossus*, *Mallotus*, and the Osmerinae [*Osmerus* + *Allosmerus* + (*Spirinchus* + *Thaleichthys*)] form an unresolved quadrachotomy because I have no reliable information suggesting how they are related to one another. The Osmerinae, as originally defined by McAllister (1963), are supported as being holophyletic. However, the evidence for placing *Hypomesus* and *Mallotus* in the Hypomesinae, as he proposed, is not convincing. Suggestions by McAllister (1963, 1966) and Klyukanov (1975) that *Spirinchus* and/or *Thaleichthys* are the most primitive osmerid genera are not supported; in fact, my evidence suggests the opposite: that they are the most derived genera and are sister genera. Perhaps significantly, if McAllister's (1963, 1966) and Klyukanov's (1975) evidence (which includes evidence from all parts of the skeleton) is examined critically, using only derived character states and more appropriate outgroups, the polarity of a number of character states is reversed in such a way that they now support my hypothesis that *Spirinchus* and *Thaleichthys* are sister taxa and the most derived osmerids. None of the aforementioned workers investigated the phylogenetic relationships of *Plecoglossus* to the osmerid genera, and only state that it is closely related to the Osmeridae (along with the Salangidae).

To sum up, although my evidence clearly suggests that *Plecoglossus* plus the Osmeridae form a holophyletic group, it may be that the Osmeridae, as defined by McAllister

(1963), are paraphyletic (i.e., some osmerids may be more closely related to *Plecoglossus* than they are to the other osmerids). The holophyly of the Osmeridae evidently requires further testing, and the relationship of the Osmeridae to *Plecoglossus* and the Salangidae + Sundasalangidae must be determined using other parts of the skeleton and different approaches. Until then I prefer to retain the families Osmeridae and Plecoglossidae (see Fig. 94).

Salangidae + Sundasalangidae

The Salangidae, and the recently described Sundasalangidae (see Roberts 1981), are unique and there is little doubt that the two families together constitute a holophyletic group (pers. obs.; also refer to Roberts 1981, 1984). Evidence from all parts of the skeleton, especially the suspensorium, supports this hypothesis. However, Fink (1984b, p. 204) does not accept the family Sundasalangidae because he believes that its recognition "would probably render the Salangidae paraphyletic." He does not doubt, however, that the Sundasalangidae and Salangidae, together, are holophyletic. Until more evidence bearing on the relationship of *Sundasalanx* (the family Sundasalangidae consists of only this genus) to the four salangid genera is forthcoming, I prefer to retain the family Sundasalangidae as defined by Roberts (1981).

Using my evidence, the Salangidae and Sundasalangidae constitute a holophyletic group on the basis of their sharing a complex character state: the suspensorium is unlike that found in any other salmoniforms (or any other Pisces according to Roberts 1984). It is united into a single, continuous, cartilaginous element that Roberts termed the hyopalatine (see Figs. 19-21). The hyopalatine represents a fusion of the dorsal portions of the mandibular and hyoid arches (the palatoquadrate and hyosymplectic, respectively). In *Sundasalanx praecox* the hyopalatine is divided into anterior and posterior sections. However, this character state is undoubtedly an autapomorphy since a united suspensorium is found in its sister species (*S. microps*) and all salangids. The character state in *S. praecox* could readily be derived from that in *S. microps* by simply loss of the narrow section of cartilage between the "palatine" and "quadrate" sections.

The suspensorium in the Sundasalangidae is entirely cartilaginous. However, most salangids have dermal and/or endochondral ossifications corresponding to some or most of the bones normally comprising the suspensorium. All appear to have ossifications corresponding to the preoperculum and dermopalatine, but none has a symplectic (pers. obs.; Roberts, 1984). However, in most cases these "bones" have poorly defined outlines, are often thin and weakly ossified, and lack sculpturing. Most of the endochondral ossifications are ossified only externally and retain a cartilaginous core (pers. obs.).

Although the Salangidae + Sundasalangidae are a distinct holophyletic group, the phylogenetic position of these strange neotenic fishes within the salmoniforms is still far from certain (see Gosline 1960; Weitzman 1967a; McDowall 1969; Rosen 1974; Fink 1984b; Roberts 1981, 1984). My evidence suggests only that they may belong in the osmeroid + galaxioid + argentinoid assemblage. Like the aforementioned group, the Salangidae + Sundasalangidae possess a preoperculum with an open, bony, lateral sensory canal (open posterior to a flange that runs along the lateral surface of the bone). However, in most salangids the flange is either very narrow or lost entirely (the Sundasalangidae lack a preoperculum). I discuss this derived character state of the preoperculum later; however, it is also shared with the higher teleosts (the Neoteleostei) and as such does not necessarily assign the salangids + sundasalangids to the osmeroid + galaxioid + argentinoid assemblage.

Evidence from other workers, using other parts of the skeleton, places the salangids + sundasalangids somewhere in the osmeroid + galaxioid + argentinoid group. Nelson (1970a) suggested (using evidence from the gill arches) that the Salangidae were related to the Argentinidae; however, most workers believe that they are either osmeroids or galaxioids (see Gosline 1960; Weitzman 1967a; McDowall 1969; Rosen 1974; Fink and Weitzman 1982; Fink 1984b).

Although the evidence, which I discuss below, is inconclusive, most suggests that the salangids + sundasalangids are probably osmeroids, but does not indicate whether or not they are more closely related to the Osmeridae or Plecoglossidae. I tentatively agree with this hypothesis, and rather than place them *incertae sedis* within the osmeroid + galaxioid + argentinoid group place them as part of an unresolved trichotomy along with the Osmeridae and Plecoglossidae (see Fig. 94). Although I presented suspensorial evidence linking the Osmeridae and Plecoglossidae, a valid comparison of these fishes with the salangids + sundasalangids is impossible because of the highly unusual suspensorium in the latter group.

The evidence for placing the salangids + sundasalangids with the Osmeridae and Plecoglossidae (versus with the galaxioids) is reviewed by Fink (1984b). Although he states (p. 204) that "What little evidence I have been able to find about the relationships of salangids [= salangids + sundasalangids] is equivocal," he appears to favour a relationship with the osmeroids as more likely, and I agree. His evidence for a galaxioid relationship (as the sister group of the Galaxiidae + Aplochitonidae) is supported entirely by reductive character states (ectopterygoid bone absent, extrascapular absent, coracoid-cleithrum process absent, posterior pubic symphysis absent, scales absent, vomerine teeth absent) that are also shared with the Galaxiidae and Aplochitonidae. The evidence for placement within the osmeroids is more convincing and consists primarily of what he calls (p. 204) "a complex caudal skeleton character" in which the caudal skeleton has a unique fusion pattern that is similar to, but derived over that found in the galaxioids, that in turn is derived over that in the Argentinoidei and other outgroups (for further discussion refer to Rosen 1974; Fink and Weitzman 1982; Fink 1984b).

Other evidence suggests that the salangids + sundasalangids are osmeroids, and corroborates my hypothesis that the Osmeridae and Plecoglossidae are closely related. The Osmeridae and Plecoglossidae are similar in that they have a unique egg, with what Fink (1984b) and Hearne (1984) call an "anchor membrane" that is adhesive and attaches it to the substrate (also see Takahashi 1978; Soin 1980). The egg in the salangids also attaches to the substrate, but via filaments instead of an adhesive disc. However, one salangid (*Salangichthys ishikawae*) that appears to be relatively primitive has an egg that lacks filaments and is very similar to the osmerid-plecoglossid egg (see Wakiya and Takahasi 1937; Takahashi 1978). This suggests that an egg with an anchor membrane was perhaps present in the common ancestor of the salangid + sundasalangid lineage and that filaments were evolved secondarily. In this case, the presence of an anchor membrane would be a synapomorphy uniting the osmerids + plecoglossids + salangids + sundasalangids, not just the osmerids and *Plecoglossus* as claimed by Fink (1984b, fig. 107).

Soin (1980) and Hearne (1984) noticed similarities between the larvae of the salangids + sundasalangids, osmerids, and *Plecoglossus* and speculated that this might be indicative of relationship. The larvae of *Plecoglossus* and the osmerids are especially similar to one another, perhaps indicating a sister-group relationship.

Another apparent synapomorphy uniting the salangids + sundasalangids, osmerids, and *Plecoglossus* is the presence of what Matsuoka and Iwai (1983) call an adipose fin cartilage that is located at the base of the adipose fin. This cartilage was absent in all the other salmoniforms they examined as well as in all the outgroups except for the Myctophidae and Neoscopelidae (where it is different, and considered to be convergent).

However, if the salangids + sundasalangids are considered to be osmeroids within the osmeroid + galaxioid + argentinoid assemblage, then the assumption must be made that their common ancestor had teeth on the mesopterygoid and that they have been secondarily lost. Most salangids, but no sundasalangids, have a mesopterygoid, but none have teeth on it (pers. obs.; Roberts 1981, 1984). The assumption that mesopterygoidal teeth have been secondarily lost is well founded since there is an obvious trend within the group for reduction of ossification and dentition (pers. obs.; also see Nelson 1970a; Roberts 1984). The fact that the most primitive salangid, *Protosalanx*, has the most ossification and the most complete dentition also suggests that the ancestor of the group was perhaps well ossified and conceivably had mesopterygoidal teeth. *Protosalanx* has well-toothed dentaries, maxillae, premaxillae, and palatines and is one of only two species with basihyal teeth (small and few in number). Basibranchial toothplates are absent in all salangids. The bite is between the teeth on the premaxillae, maxillae, and palatines and those on the dentary (there is no vomer in any salangid).

Galaxioids

The five galaxioid families (Retropinnidae, Prototroctidae, Lepidogalaxiidae, Galaxiidae, and Aplochitonidae) are united because they share the following derived character states:

1. The ectopterygoid is unique, exhibiting a number of character states that can ultimately be derived from the primitive state found in the outgroups. A morphoclinal series depicting the hypothetical pathways of evolutionary change of the ectopterygoid within the galaxioids is depicted in Fig. 97. [illegible] condition is present in the Osmeridae, Plecoglossidae, Alepocephalidae, Platytroctidae, [illegible]dae, Coregoninae (Salmonidae), and most lower and higher teleosts. P[illegible] the ectopterygoid is relatively long anteroposteriorly, overlaps both the palatine and quadrate, is angled centrally or posteriorly, and has a posterior expansion that overlaps the quadrate. The character states of the ectopterygoid in the five galaxioid families are derivable from the ancestral pattern by an initial straightening of the bone.

   A relatively straight ectopterygoid that is modified in various ways is a synapomorphy uniting the galaxioid families: it can be straight and shortened, with no distinct posterior expansion, as in the Lepidogalaxiidae; straight, with no distinct posterior expansion, and fused with the palatine as in the Retropinnidae and Prototroctidae; or lost entirely and replaced by a ligament as in the Galaxiidae and Aplochitonidae. Therefore, in addition to uniting the galaxioids, the character states of the ectopterygoid help to define three other holophyletic groups, each ultimately derivable from the hypothetical (straight) condition: the Retropinnidae + Prototroctidae (fusion with the palatine), the Lepidogalaxiidae + Galaxiidae + Aplochitonidae (shortening of a straight ectopterygoid), and the Galaxiidae + Aplochitonidae (replacement of the ectopterygoid by a ligament). Each of the above character states will be discussed in greater detail below.

The character state uniting the galaxioids (a relatively straight ectopterygoid) is also found in the Umbridae, some Salmonidae (the Thymallinae and Salmoninae) and the Argentinoidea. However, the ectopterygoid in most of the aforementioned groups differs in other ways from that in the galaxioids (especially the Argentinoidea) and each assemblage is defined as a holophyletic group on the basis of numerous other character states. I therefore conclude that this similarity is a result of convergence.

2. The position of the lateral foramen for the hyomandibular branch of the facial nerve relative to the lateral strut is unique (refer to Figs. 22-26). It is located either anterior to the middle of the lateral strut (Retropinnidae and Prototroctidae); or directly anterior (Aplochitonidae), directly posterior (most Galaxiidae), or directly ventral (Lepidogalaxiidae and the galaxiid *Neochanna*) to its ventralmost end. Primitively, the lateral foramen is located posterior to the dorsal half of the lateral strut (ranging, for example, from about the middle, as in *Esox*, to the dorsalmost corner, as in *Coregonus*). This primitive character state is present in all the other salmoniforms (and the other teleosts examined) except for four osmerid genera (*Osmerus, Allosmerus, Spirinchus,* and *Thaleichthys*). In these genera the lateral foramen is located at the dorsal edge of the strut and is entirely visible externally, a character state considered to be a synapomorphy uniting the four genera.
3. The autopalatine is relatively small (refer to Figs. 22-26). A relatively small autopalatine is also present in most Salmonidae and some Umbridae (*Dallia* and *Umbra*). Primitively, the autopalatine is moderately large with expanded ends (for example, see Figs. 34, 42).
4. The palatoquadrate cartilage at the posterior end of the autopalatine is relatively flattened and does not extend posterodorsally to meet the lamina orbitonasalis of the ethmoid cartilage. Instead, the lamina orbitonasalis rests on the dorsal surface of the flattened anterior surface of the palatoquadrate (see Figs. 22, 23, 25, 26). Primitively, the palatoquadrate cartilage is expanded at the posterior end of the autopalatine and extends dorsally to meet the lamina orbitonasalis (for example, see Figs. 13, 15, 34, 42).

In the Lepidogalaxiidae the anterior part of the palatoquadrate cartilage is greatly reduced (extending barely to the posterior tip of the dermopalatine), the autopalatine has cartilage only at its anterior end, and this cartilage directly contacts the lateral ethmoid bone (see Fig. 24). This unique character state is considered to be an autapomorphy of the Lepidogalaxiidae.

5. The ventral limb of the preoperculum is as long as, or longer than, the dorsal limb (refer to Figs. 22-26). This character state is shared with *Dallia* (Umbridae), the Salangidae, and the Argentinoidea (Argentinidae + Bathylagidae + Opisthoproctidae). Primitively, the dorsal limb is longer than the ventral limb.
6. The mesopterygoid overlaps the dorsomedial surface of the body of the quadrate. This character state is found in the Retropinnidae, Prototroctidae, Lepidogalaxiidae, and some Galaxiidae (*Neochanna*). The assumption is that overlap has been secondarily lost in the Aplochitonidae and most Galaxiidae. The mesopterygoid also overlaps the quadrate in most Salmoninae, some Salangidae, a few Alepocephalidae, and the Argentinoidea.

Within the Galaxioidea my data defines three holophyletic groups: The Retropinnidae + Prototroctidae, the Lepidogalaxiidae + Galaxiidae + Aplochitonidae, and the Galaxiidae + Aplochitonidae.

Retropinnidae + Prototroctidae

The shared derived character states of the suspensorium that unite the Retropinnidae and Prototroctidae include the following:

1. The ectopterygoid is straight, with no distinct posterior expansion, and fused with the palatine. Primitively, the two bones are separate but overlap at their ends. The derived character state could be derived directly from a straight ectopterygoid by fusion of the overlapping bones, as depicted in the morphoclinal series shown in Fig. 97. The only other salmoniform with a fused ectopterygoid and palatine is the umbrid *Dallia*. However, this is probably an example of convergence because the shape of the fused bone is different (more robust with larger and more numerous teeth) as is its position (its

posterior end does not overlap the quadrate). There is also considerable evidence from other parts of the anatomy suggesting that *Dallia* is an esocoid, not a galaxioid, and that *Retropinna* and *Prototroctes* belong in the galaxioid assemblage.

Most other workers agree that the ectopterygoid is fused with the palatine in the Retropinnidae and Prototroctidae, and that this character state is indicative of relationship between the two groups (see McDowall 1969; Patterson 1970). However, without explanation, Fink (1984b, p. 203) states that the presence of an "Ectopterygoid bone ... ventral to [the] autopalatine" is a derived character state uniting the two families (versus a primitive character state in which the "Ectopterygoid bone ... [is] posterior to [the] autopalatine"). I disagree with Fink's interpretation of this character, and believe that the tooth-bearing section that is ventral and posterior to the autopalatine is the dermopalatine, not the ectopterygoid.

2. The shape and position of the lateral foramen for the hyomandibular branch of the facial nerve relative to the lateral strut is unlike that found in any other salmoniform: it is relatively large, anterior to the middle of the lateral strut, and half covered by the large cartilage at the posterodorsal end of the metapterygoid (refer to Figs. 22, 23). In the other salmoniforms it is never covered by the palatoquadrate cartilage and is located either at the ventral end of the lateral strut (the other galaxioids), at the dorsal edge of the lateral strut (Osmerinae), or posterior to its dorsal half (all other salmoniforms).
3. The lateral strut of the hyomandibular begins near the middle of the ventral arm and curves in an arc (convex dorsally) that extends posterodorsally to the middle of the opercular arm (refer to Figs. 22, 23). Primitively, the lateral strut begins near the middle or bottom of the ventral arm and extends dorsally to about the apex of the head. It is sloped posterolaterally and is usually concave on its anterolateral surface (for example, see Figs. 34, 27, 18, 10).

The lateral strut in the Galaxiidae and Aplochitonidae is broadly similar to that in the Retropinnidae and Prototroctidae except that it is more robust and somewhat different in shape and position (refer to Figs. 25, 26). However, because the character-state in the former two families is more similar to that in the Retropinnidae and Prototroctidae than any other salmoniforms it is possible that it is a synapomorphy uniting the four families (that is, if it is more broadly defined). The lateral strut in *Lepidogalaxias* is unlike that in any other salmoniform, and is interpreted as an autapomorphy (see Fig. 24). I prefer, however, to interpret the lateral strut character in the more restricted sense because the three character states (the Retropinnidae + Prototroctidae, the Galaxiidae + Aplochitonidae, and *Lepidogalaxias*) are only broadly similar and are not easily derivable from one another.

4. The metapterygoid is similar in shape, relative size, and position (refer to Figs. 22, 23). It is moderately large, roughly oval, with a narrow dorsal (dermal) lamina, and lacks a distinctive medial ridge. The cartilage at its posterior corner is expanded and extends posterior [illegible] strut of the hyomandibular, covering most of the lateral foramen of the hyomandibular branch of the facial nerve. Some Platytroctidae and Alepocephalidae have a relatively large cartilage at the posterodorsal corner of the metapterygoid; however, in these the metapterygoid and its cartilage have a different shape, and the bone and cartilage only slightly (versus broadly) overlaps the hyomandibular.

5. The symplectic is similar in shape (refer to Figs. 22, 23): it has a prominent central bend, a broad posterior end, and an unusually large cartilaginous knob at its anterior end (less so in the larger specimen of *Prototroctes*). Primitively, there is only a slight central bend, the posterior end is narrower, and the cartilaginous knob is smaller. Among the other salmoniforms, the character state in *Mallotus*, *Plecoglossus*, and *Aplochiton* is most similar to that in *Retropinna* and *Prototroctes*; however, *Retropinna* and *Prototroctes* are more similar to each other than either is to any of the other aforementioned genera. Also, the cartilaginous knob at the anterior end is larger relative to the rest of the symplectic than in the other salmoniforms examined.

Lepidogalaxiidae + Galaxiidae + Aplochitonidae

The second major holophyletic group within the galaxioids, and the sister group of the Retropinnidae + Prototroctidae, is the Lepidogalaxiidae + Galaxiidae + Aplochitonidae. The latter three families are united on the basis of their sharing the following derived character states:

1. The ectopterygoid is straight and short anteroposteriorly, with no distinct posterior expansion, as in the Lepidogalaxiidae; or else lost entirely and replaced by a ligament, as in the Galaxiidae and Aplochitonidae. These character states could be derived directly from a straight ectopterygoid (the state in the hypothetical ancestral galaxioid) by initially shortening the bone (see Fig. 97). A straight and short ectopterygoid, with no distinct posterior expansion, is therefore hypothesized to have been present in the common ancestor of the Lepidogalaxiidae (where it is retained) + Galaxiidae + Aplochitonidae, and is a synapomorphy uniting the three families. The character state in the Galaxiidae + Aplochitonidae is directly derivable from this ancestral ectopterygoid (see Galaxiidae + Aplochitonidae section for details).

   Besides the Lepidogalaxiidae, a straight and relatively short ectopterygoid is also found in the Argentinoidea and in *Umbra* (Umbridae). The ectopterygoid in the Argentinoidea, however, differs significantly from that in all other salmoniforms and its character state is a synapomorphy uniting its families (see the Argentinoidei section later for details).

   Although the ectopterygoid in *Umbra* is superficially similar to that in *Lepidogalaxias*, upon closer examination there are enough significant differences between the two genera to suggest that this similarity is most likely due to convergence (compare Figs. 24 and 9). The ectopterygoid in *Umbra* differs from that in *Lepidogalaxias* in the following ways: it is relatively longer and narrower (it is splint-like in *U. pygmaea*), it is tapered at its posterior end (versus broad in *Lepidogalaxias*), its posterior end does not overlap the medial surface of the posterodorsal corner of the body of the quadrate (versus distinct overlap in *Lepidogalaxias*), it overlaps the lateral surface of the mesopterygoid (versus the medial surface in *Lepidogalaxias*), the anterior end distinctly overlaps the posterodorsal end of the palatine (versus barely, if at all, in *Lepidogalaxias*), and the anterior end of the palatoquadrate cartilage is expanded into a bulb-like condyle dorsal to the anterior end of the ectopterygoid (versus a narrow strip of cartilage that barely reaches the anterior end of the ectopterygoid in *Lepidogalaxias*).

2. [illegible] foramen for the hyomandibular branch of the facial nerve is located at the ve[illegible] of the lateral strut. It is located either directly anterior to (Aplochitonidae), directly posterior to (most Galaxiidae), or directly ventral to (Lepidogalaxiidae and the galaxiid *Neochanna*) its ventral end. The other character states of this character (including the primitive one) have been discussed previo[illegible].

3. The palatoquadrate cartilage at the posterior end of the [illegible]palatine is greatly flattened, as in the Galaxiidae and Aplochitonidae, or greatly flattened and reduced (consisting of a thin, narrow strip that barely reaches the dermopalatine), as in the Lepidogalaxiidae. This cartilage is also flattened in the Retropinnidae and Prototroctidae but not to the same extent. The character state in the Galaxiidae and Aplochitonidae could be derived from an ancestor similar to the Retropinnidae and Prototroctidae by further flattening of the cartilage, and the character state in the Lepidogalaxiidae could be derived from an ancestor similar to the Galaxiidae and Aplochitonidae by further reducing the greatly flattened cartilage.

4. The teeth on the mesopterygoid are reduced in number (and in a single row along the anteromedial edge of the bone, as in the Galaxiidae and Aplochitonidae), or else lacking (Lepidogalaxiidae). Primitively in the galaxioids there is a relatively large number of ventrolaterally curved teeth, arrayed anteroposteriorly in several rows, that extend along the entire medial surface of the mesopterygoid.

A condition similar to the primitive state was probably found in the common ancestor of the galaxioids (and was retained in the Retropinnidae and Prototroctidae). The character states in the Lepidogalaxiidae and the Galaxiidae + Aplochitonidae could be derived from the primitive condition by initially losing all the teeth except those in a single row at the anteromedial edge of the bone. A single row of teeth along the anteromedial edge of the bone is hypothesized to have been present in the common ancestor of the three families. A morphoclinal series depicting the hypothetical pathways of evolutionary change of the mesopteryoid and its teeth is depicted in Fig. 98. The character state in the Lepidogalaxiidae could be derived from the hypothetical condition by losing the anterior end of the mesopterygoid (and therefore also the teeth). Supportive of this view is the observation that in the small galaxiid, *Galaxias paucispondylus*, the anterior end of the mesopterygoid is abbreviated and there is only half the number of teeth found in galaxiid species with a longer mesopterygoid. The character state in the Galaxiidae + Aplochitonidae could be derived from the hypothetical condition by changing the orientation of the teeth (from ventrolaterally directed to ventro-anterolaterally directed) and perhaps by lengthening the mesopterygoid. Associated with these changes is a loss of basihyal and basibranchial dentition in the Leipidogalaxiidae; and loss of palatine, vomerine and basibranchial dentition (but enlargement of the basihyal dentition) in the Galaxiidae and Aplochitonidae.

5. The metapterygoid is small and the endochondral portion is roughly axe-shaped (refer to Figs. 24-26). The metapterygoids in the Lepidogalaxiidae and Aplochitonidae, in particular, are very similar in shape and position and unlike those in any other salmoniform. Primitively the metapterygoid is relatively large and has an extensive endochondral portion that has a rectangular to oval to lunate shape.

A small metapterygoid with an axe-shaped endochondral portion is also found in two umbrid genera (*Novumbra* and *Dallia*) and in some Argentinoidea. However, this similarity is probably a result of convergence because there is evidence from other character states suggesting that the Argentinoidea is part of the Argentinoidei assemblage (also see Rosen 1974; Fink and Weitzman 1982), and that *Dallia* and *Novumbra* are esocoids. The metapterygoid in these fishes also differs in size, shape, and position relative to the surrounding bones.

Galaxiidae + Aplochitonidae

Within the Lepidogalaxiidae + Galaxiidae + Aplochitonidae, the Galaxiidae + Aplochitonidae constitute a holophyletic group on the basis of their sharing the following derived character states:

1. Palatine teeth (and the dermopalatine) are absent. Primitively there is a distinct dermopalatine that bears teeth on its ventral surface and lies ventral to the autopalatine (with which it is fused).

   Palatine teeth and a dermopalatine are also absent in adult *Plecoglossus*, many Platytroctidae, and some Alepocephalidae (pers. obs.; also see Parr 1960; Markle 1976). However, because there is more and stronger evidence suggesting that the aforementioned taxa belong in other assemblages, I conclude that this similarity is the result of convergence.

2. The ectopterygoid is lost and replaced by a tough ligament extending from the posteroventral end of the autopalatine to the anterodorsal corner of the body of the quadrate (see Figs. 25, 26). I know of no other teleost in which the ectopterygoid has been lost and replaced by a ligament. Other workers (for example, Chapman 1944c; McDowall 1969) have noted that an ectopterygoid is absent in these two families, but none have reported the presence of the unique ligament that replaces it.

   This character state could be derived directly from a straight and short ectopterygoid (as is hypothesized to have been present in the common ancestor of the Lepidogalaxiidae + Galaxiidae + Aplochitonidae, and is retained in the Lepidogalaxiidae) by further reduction of the bone and its gradual replacement by a ligament. Evidence for this hypothesis is also supplied by McDowall (1969, fig. 3D and p. 812) who noted that *Lovettia* (Aplochitonidae) had a "small, splint-like ectopterygoid" that lies between, but does not contact, the palatine or quadrate. As such this state would represent an intermediate condition. However, none of my specimens of *Lovettia* possessed an ectopterygoid, and it is possible that McDowall identified part of the ligament, parts of which often take on a slightly red colour after the suspensorium is stained with alizarin red) as the ectopterygoid.

The umbrid *Dallia* has a short but distinct ligament extending from the posterior tip of the fused palatine-ectopterygoid to the anterodorsal corner of the body of the quadrate. A trace of a ligament is present in *Umbra*. However, because an ectopterygoid is present in both genera, and because other characters place them within the Esocoidei, I consider this similarity to be convergent.

3. The teeth on the mesopterygoid are reduced in number and in a single row along the anteromedial edge of the bone. The primitive character state, found in the Retropinnidae, Prototroctidae, and *Hypomesus* (Osmeridae) was described previously. Mesopterygoidal teeth are reduced in number, and esentially in a single row in numerous osmeroids and in some platytroctids. However, in no other salmoniform are they restricted to the anteromedial part of the bone.
4. The teeth on the mesopterygoid curve distinctly anteriorly (and slightly laterally). Primitively the teeth curve only laterally. In some osmerids (*Osmerus*, *Allosmerus*, and *Spirinchus*) the anteriormost teeth curve slightly anteriorly while in *Thaleichthys* (Osmeridae) the entire tooth row curves slightly anteriorly. In none, however, are the teeth as anteriorly curved as they are in the Galaxiidae and Aplochitonidae. In fact, in the aforementioned osmerids part of the inclination appears to be the result of the anterodorsal curvature of the anterior end of the mesopterygoid (there is no such curvature in the Galaxiidae and Aplochitonidae). For the above reasons, and because other evidence suggests that these osmerids are relatively derived, I conclude that the slight similarities are a result of convergence.
5. The anteroventrally directed teeth on the anteromedial surface of the mesopterygoid oppose greatly enlarged posterodorsally directed teeth around the edge of the basihyal, and together form a specialized bite mechanism unlike that found in any other salmoniform (or teleost, to the best of my knowledge). Teeth are absent from the palatine, vomer, maxilla, and basibranchials, but present on the premaxilla and dentary. The primitive bite mechanism for salmoniforms with specialized mesopterygoidal teeth

has been described previously (see Osmeroidei + Galaxioidei + Argentinoidei section).

6. The lateral strut of the hyomandibular is similar in shape and position (see Figs. 25, 26). It begins near the middle of the dorsal part of the ventral arm and curves in an arc that extends to the opercular arm (it is absent, however, in the aplochitonid *Lovettia*). In its position it is roughly similar to the lateral strut in the Retropinnidae and Prototroctidae; however, it differs significantly in that it is distinctly more robust, wider, and projects farther laterally. Also, although roughly similar to that in the Retropinnidae + Prototroctidae, the struts in the Galaxiidae and Aplochitonidae are more similar to each other than they are to any other salmoniform. The primitive character state of the lateral strut was described previously.
7. The palatoquadrate cartilage at the posterior end of the autopalatine is greatly flattened. This character state was used in a broader sense to unite the five galaxioid families. However, the state in the Galaxiidae and Aplochitonidae is derived relative to that in the Retropinnidae and Prototroctidae.

<u>The Phylogenetic Position of *Lovettia*</u>. Although the genus *Lovettia* has traditionally been placed in the family Aplochitonidae and considered to be closely related to the genus *Aplochiton*, there has always been doubt as to whether or not the two genera together form a holophyletic group, partly because of morphological differences and partly because they are widely separated geographically (see Gosline 1960; McDowall 1969, 1971b; Fink 1984b; Nelson 1984). The holophyly of the Galaxiidae is assumed by most workers (see Frankenberg 1969; McDowall 1969; McDowall and Frankenberg 1981; and Fink 1984b); however, it may be that *Lovettia* is cladistically more closely related to the Galaxiidae than to *Aplochiton*. Fink (1984b) noted this uncertainty by placing *Lovettia*, *Aplochiton*, and the Galaxiidae as part of an unresolved trichotomy, stating (p. 204) that "I have been unable to find any features that link [*Aplochiton* and *Lovettia*] together ... and more work needs to be done with them."

Evidence from the bones and muscles of the suspensorium suggests that *Lovettia* and *Aplochiton* are each other's closest relatives (i.e., that the Aplochitonidae are holophyletic).

An *Aplochiton* + *Lovettia* relationship was also suggested by McDowall (1971b) when he noted (p. 43) that the "bone structure of *Lovettia* is more similar to that of *Aplochiton* than to that of any other genus." However, before firmer conclusions can be drawn more galaxiids should be examined, in particular *Paragalaxias*, which shares some features with the Aplochitonidae, and like *Lovettia* is endemic to Tasmania (see McDowall 1980, 1984; McDowall and Frankenberg 1981). The holophyly of the Galaxiidae should also be more rigorously tested.

The synapomorphies of the bones (muscle evidence is discussed in a later section) that support the hypothesis that *Lovettia* and *Aplochiton* are sister taxa include the following (I found no synapomorphies linking only *Aplochiton* with the Galaxiidae):

1. The overall shape of the suspensorium is similar: it is long, moderately wide, and relatively delicate. The suspensoria in *Lovettia* and *Aplochiton* are more similar to one another than they are to that of the galaxiids (in the Galaxiidae the suspensorium is relatively shorter anteroposteriorly and more robust).
2. The mesopterygoid is similar: it is relatively thin, narrow, and long (tapering rather abruptly anteriorly). In the Galaxiidae the bone is roughly elliptical and more robust. The teeth on the mesopterygoid are also similar in that they are long, narrow, sharply pointed, and inclined sharply anteriorly (more so in *Lovettia*). In the galaxiids examined the teeth are blunter with less of an anterior inclination.
3. The metapterygoid is similar in shape and position (but shared with the Lepidogalaxiidae). This character state was described previously.
4. The hyomandibular is similar in that the lateral foramen for the hyomandibular branch of the facial nerve is in about the same position and is visible externally. Also, the anterior lamina is absent in *Lovettia* and very narrow in *Aplochiton*. In the Galaxiidae and the other galaxioids a well-developed anterior lamina is present.

Alternate Hypotheses of Galaxioid Interrelationships.

I have no reliable derived character states that link the Retropinnidae and/or Prototroctidae with any of the other three galaxioid families. Thus my evidence strongly suggests that there are two well-defined galaxioid assemblages: the Retropinnidae + Prototroctidae, and the Lepidogalaxiidae + Galaxiidae + Aplochitonidae. However, there are three possible sets of relationships for the three families in the latter holophyletic group: the Lepidogalaxiidae and Galaxiidae as sister taxa, the Lepidogalaxiidae and Aplochitonidae as sister taxa, or the Galaxiidae and Aplochitonidae as sister taxa. Although I prefer the final hypothesis, and have outlined the seven synapomorphies supporting it, there is some evidence supporting the two alternate hypotheses.

The synapomorphies supporting the hypothesis that the Lepidogalaxiidae + Galaxiidae are sister taxa include the following:

1. The hyomandibular is roughly similar in shape: it is broad anteroposteriorly but short dorsoventrally, has a short ventral arm, a moderate-sized anterior lamina, and an expanded opercular arm (compare Fig. 24 and 26). Aside from the lateral strut (which is an autapomorphy of *Lepidogalaxias*), the hyomandibulars in the Lepidogalaxiidae and Galaxiidae are more similar to each other than they are to that of any other salmoniform.
2. The quadrate is similar in shape, especially the condyle which is unusually large relative to the rest of the bone and has a broad facet. The symplectics are also more similar to one another than they are to that of any other salmoniform.
3. The anterior lamina of the preoperculum is separated from (most Galaxiidae and the Lepidogalaxiidae), or just barely overlaps, the cartilage between the posterior end of the symplectic and the ventral end of the hyomandibular. In the other galaxioids and in most other salmoniforms the anterior lamina of the preoperculum broadly overlaps the aforementioned cartilage (i.e., the primitive character state).

The synapomorphies supporting the hypothesis that the Lepidogalaxiidae + Aplochitonidae are sister taxa include the following:

1. The metapterygoid is very similar in shape. It is almost entirely endochondral and consists

of a large axe-shaped anterior portion that narrows posterodorsally into a tube-like extension (compare Figs. 24 and 25). The metapterygoid in my specimens of *Lovettia* (Aplochitonidae) was only partly ossified, but had a shape similar to that in *Aplochiton* and especially *Lepidogalaxias*. In his figure of *Lovettia*, McDowall (1969, fig. 3D) illustrated a small but apparently ossified metapterygoid in the same position.

2. The position of the metapterygoid is similar. It is widely separated from the hyomandibular in *Lepidogalaxias* and *Lovettia*, and barely overlaps the anteroventral corner of the hyomandibular in *Aplochiton*. The wide separation of the metapterygoid from the hyomandibular in *Lepidogalaxias* and *Lovettia* is unlike that in any other salmoniform.
3. The posterior end of the palatoquadrate cartilage extends posterior to the metapterygoid and the body of the quadrate as a finger-like extension that extends towards the hyomandibular and symplectic. *Lepidogalaxias* shares this character state with *Lovettia*, but *Aplochiton* has the primitive character state in which the palatoquadrate cartilage extends only to the anterior end of the metapterygoid. A roughly similar extension of the palatoquadrate occurs in the opisthoproctid *Macropinna*; however, in this taxon the metapterygoid is absent, and the finger-like extension has a somewhat different shape and contacts the symplectic.

The two alternate hypotheses presented above are equally likely if each synapomorphy is given equal weight. Each synapomorphy supporting these alternate hypotheses is relatively simple and I see no reason to give any particular one more weight than the others.

Discussion of Galaxioid Relationships

Galaxioids

My evidence supports the hypothesis that the galaxioids are a holophyletic group made up of the five salmoniform families endemic to the southern hemisphere. Numerous other workers consider that the Retropinnidae, Prototroctidae, Galaxiidae, and Aplochitonidae are more closely related to one another than they are to the other salmoniforms (see Regan 1913;

Gosline 1960; McDowall 1969, 1984; Nelson 1970a, 1972; Fink 1984b; Nelson 1984). The Lepidogalaxiidae (= *Lepidogalaxias*), however, was only recently described (Mees 1961) and there is currently no agreement as to its phylogenetic position within the Salmoniformes, a problem that I will discuss later.

Fink (1984b) reviewed the literature (and included his own data) and listed five synapomorphies uniting the four galaxioid families: infraorbital sensory canals curve posteroventrally (versus curving posterodorsally), mesocoracoid absent, dorsal fin position posterior; principal caudal fin rays 9/9 or fewer, and palatine teeth absent. Some of these synapomorphies are of dubious value. The absence of a mesocoracoid is a loss character (i.e., weak) and shared with the Esocoidei, the Lepidogalaxiidae, the Salangidae + Sundasalangidae [illegible]ce may be present in the most primitive salangid, *Protosalanx*; see Roberts 1984), and [illegible]ous Argentinoidei (see Markle 1976; Nelson 1984). Palatine teeth are absent (another [illegible]aracter) in adult *Plecoglossus*, some salmonids, and many alepocephalids and [illegible]ids. Also, as I discussed previously, I believe the teeth on the fused palatine - [illegible]oid in the Retropinnidae and Prototroctidae to be on the palatine, not the ectopterygoid as suggested by Fink, and as such his character state (no palatine teeth) would unite only the Galaxiidae and Aplochitonidae (the Lepidogalaxiidae has palatine teeth). The posterior position of the dorsal fin is also of questionable value since the fin is distinctly posterior only in the Retropinnidae, Lepidogalaxiidae, and most Galaxiidae (the exception being the genus *Paragalaxias*, see McDowall and Frankenberg 1981). A posterior dorsal fin is also found in numerous other salmoniforms including the Esocoidei, the Salangidae + Sundasalangidae, and many Argentinoidei. Fink also used the number of principal caudal fin rays (18 or fewer) as a synapomorphy, a character state shared with the Lepidogalaxiidae (a total of 9 to 10 principal caudal rays according to Frankenberg 1969) and the derived umbrid genus *Umbra* (11 to 13 principal rays according to Wilson and Veilleux 1982). A posteroventrally curving infraorbital sensory canal is found in all galaxioids except the Lepidogalaxiidae (in which the canal is absent) and was first used as a galaxioid synapomorphy by Nelson (1972). To quote Nelson (p. 36-37), "The cephalic canal and pore patterns support the concept of the Galaxiidae [= my Retropinnidae + Prototroctidae + Galaxiidae + Aplochitonidae] as a monophyletic group. Whereas the cephalic canals tend to be subdivided into separate components in other salmoniform fishes (e.g., esocoids), in none of them is the infraorbital canal modified as in galaxiids. In galaxiids, the anterior part of the infraorbital canal, enclosed in two bones ... is posteroventrally deflected, in some species extending to or beyond the anterior limit of the preopercular canal."

Although perhaps some of the aforementioned synapomorphies uniting the families from the southern hemisphere are weak, they, together with my new synapomorphies, provide more convincing evidence of relationship than do some of the alternate hypotheses. Greenwood *et al.* (1966), for example, included the family Salangidae within the Galaxioidei (minus the Lepidogalaxiidae) but the reason they did this is unclear from their text. Weitzman (1967a, p. 533), one of the authors of Greenwood *et al.* (1966), reconsidered this position and stated that "Whether the Salangidae should be considered more closely related to the ... Osmeridae ... or galaxioids remains problematical. Perhaps it should be considered a fourth group [in addition to his osmerids, stomiatoids, and galaxioids]." McDowall (1969) concurs with this view and unequivocally states that the salangids are not galaxioids.

Patterson (1970) was the first to suggest that the Retropinnidae and Prototroctidae were more closely related to the osmerids of the northern hemisphere than to the Galaxiidae and Aplochitonidae. He noted similarities in the caudal skeleton between the retropinnids, prototroctids and osmerids as well as their sharing a short vomer, low mandible, and a cucumber odour. However, some osmerids have a relatively long vomer (*Plecoglossus* and *Hypomesus*) and some have a relatively high mandible (*Hypomesus* and *Mallotus*). A cucumber odour is found in the Osmeridae, Plecoglossidae, Retropinnidae, and Prototroctidae but absent in the Galaxiidae, Aplochitonidae, Lepidogalaxiidae, and Salangidae + Sundasalangidae (see Berra *et al.* 1982; Fink 1984b). However, it is possible that this unique odour is an osmeroid + galaxioid synapomorphy (not a retropinnid + prototroctid + plecoglossid + osmerid synapomorphy) and that it has been secondarily lost twice: once in the Salangidae + Sundasalangidae and once in the Lepidogalaxiidae + Galaxiidae +

Aplochitonidae.

The caudal skeleton evidence suggesting a relationship of the retropinnids and prototroctids with the osmeroids is more difficult to interpret (see Patterson 1970; Rosen 1974). Their primary evidence concerns sharing a unique "stegural" formed by fusion of the rudimentary neural arches of PU1 with the first uroneural. In contrast, in the Galaxiidae and Aplochitonidae the rudimentary neural arches usually fuse with the underlying centrum (PU1) and approach, but do not fuse with, the first uroneural. Rosen (1974) claimed that the former character state was derived because it formed the end point of an ontogenetic sequence that involved fusion of the rudimentary neural arch with the first uroneural. Fink and Weitzman (1982) carefully analyzed Rosen's (1974) evidence and noted a number of exceptions: some osmeroids (including the Retropinnidae and Prototroctidae) have rudimentary neural arches fused with PU1 (in addition to fusion with the uroneural), and some galaxiids and aplochitonids have fusion of the rudimentary neural arches with the first uroneural (and PU1). They state that there are two fusion patterns of these bones in the salmoniforms: in the argentinoids, galaxiids, and aplochitonids the arches fuse first with the centrum and then with the uroneural (when fusion takes place) while in the osmeroids (*sensu* Rosen 1974) the arches fuse first with the uroneural and then, sometimes with the centrum. They note that in the Salmonidae, Esocoidei, and many Argentinoidei the rudimentary neural arch does not fuse with the uroneural.

Because of the contradictory evidence that Fink and Weitzman noted and because it is uncertain as to what fusion pattern is primitive, I prefer to reject Rosen's (1974) hypothesis that the retropinnids and prototroctids are osmeroids based on caudal skeletal evidence.

Rosen (1974) also states that evidence from the hyobranchial apparatus supports his hypothesis that the retropinnids and prototroctids are osmeroids. It is difficult to tell from his text what characters he is using to support his hypothesis (also see Fink and Weitzman 1982). One appears to be the presence of (p. 313) "a blunt, somewhat elevated median ridge [on the basibranchial tooth plate] except when [the] tooth plate is greatly expanded." Upon examining specimens I found that although the toothplate is arched dorsally there is no "blunt ... median ridge." Also, an arched, similarly shaped basibranchial tooth plate is present in numerous primitive teleosts (*Elops* and *Osteoglossum*, for example) and as such the character is probably primitive (pers. obs.; also Fink and Weitzman 1982).

Rosen's (1974) other hyobranchial evidence includes similarities in the basihyal dentition and epibranchials. The basihyal dentition is similar in that the (p. 313) "Basihyal fangs in forms with unreduced dentition [are] large, arranged in alternating positions on [the] right and left side, and tending to form a single large terminal tooth." I do not find this evidence particularly convincing for a number of reasons. First, two genera, *Mallotus* and *Plecoglossus*, have reduced basihyal dentition and small teeth. Second, the teeth on the right and left sides of the basihyal do not alternate in all osmeroids (*sensu* Rosen 1974), nor do they usually all alternate when they do alternate. For example, in my specimens of *Thaleichthys* (Osmeridae) the teeth are arranged in right and left pairs (except for the anteriormost pair), and except for the anteriormost pair resemble the pattern in the Salmoninae, Galaxiidae, and Aplochitonidae. Also, when the teeth do alternate it is usually the anterior teeth; the posterior teeth are paired. The alternating anterior teeth may be simply related to the fact that in these osmeroids the anterior end of the basihyal is narrower and the anterior teeth are the same size or larger than the posterior teeth, resulting in a crowding and unequal spacing of the teeth (a feature not clearly illustrated by Rosen but visible in my specimens). The value of this character is further reduced because it is often difficult to decide whether the teeth are alternating, or paired. Also, a terminal tooth was absent in my specimens of *Hypomesus* and *Prototroctes*; instead there was a terminal pair as in the Salmoninae, Galaxiidae, and Aplochitonidae. Some salmonines (*Salvelinus fontinalis*) also have a terminal tooth, further complicating the situation.

Rosen's (1974) epibranchial evidence is also not convincing. An apparent synapomorphy is that in the osmeroids the fifth epibranchial is fused ventrally to the posteroventral end of the fourth. Primitively, the fifth epibranchial is adjacent to, but not fused with the posteroventral end of the fourth (pers. obs., also see Nelson 1967c). However, there is no fusion of epibranchial five with epibranchial four (although they are adjacent) in a number of osmeroids illustrated by Rosen, including *Stokellia* (Retropinnidae) and *Plecoglossus* (Plecoglossidae). Epibranchial five was distinctly separate from epibranchial four in both my specimens of *Prototroctes* (Prototroctidae), a taxon which Rosen did not examine. Also, in my specimens of *Retropinna retropinna* the ventral end of epibranchial five closely abuts the posteroventral end of epibranchial four; however, there was a faint line between the two, indicating that they were perhaps not fused (contradicting Rosen's fig. 16F, in which he indicates fusion in *R. retropinna*). If this were the case, then both the Retropinnidae and Prototroctidae possess the primitive character state and the character could not be used to unite them with the Osmeridae (i.e., refuting Rosen's hypothesis).

In summary, I see no reason to accept Rosen's hypothesis that the Retropinnidae and Prototroctidae are osmeroids, and prefer to consider them part of the southern hemispheric galaxioid radiation.

Retropinnidae and Prototroctidae

My evidence strongly supports the hypothesis that the Retropinnidae and Prototroctidae, together, form a holophyletic group. Evidence from numerous other recent workers using all parts of the skeleton, supports this hypothesis (see McDowall 1969, 1971b, 1976a; Patterson 1970; Nelson 1972; Rosen 1974; Berra *et al.* 1982; Fink 1984b; Nelson 1984), including the following taken from Fink (1984b): infraorbital sensory canals curved posteroventrally and extending to the preoperculum; ceratohyal ventral border deeply concave anteriorly, branchiostegals restricted to area posterior to concavity; horny abdominal keel present; only left ovary present (shared with *Plecoglossus* according to McDowall 1969); and ectopterygoid bone ventral to autopalatine (as noted before, I disagree with Fink's interpretation of this character state).

When first described by Günther in 1864, *Prototroctes* was placed in the family Aplochitonidae along with *Aplochiton* and *Lovettia*. However, the character states diagnosing the family are either shared with the Galaxiidae or are primitive. Workers after Günther unquestioningly continued to leave *Prototroctes* in the Aplochitonidae despite its obvious differences with the other two genera (see Berg 1940; Jordon 1963; Greenwood *et al.* 1966). Gosline (1960) first suggested placing *Prototroctes* in a separate family but did not because he did not want to break up the Aplochitonidae. McDowall (1969) finally removed *Prototroctes* from the Aplochitonidae and placed it in its own monotypic family, the Prototroctidae, which he considered closely related to the Retropinnidae.

Although workers since McDowall also concede that *Prototroctes* is closely related to the Retropinnidae (*Retropinna* and *Stokellia*) there is some disagreement regarding the relationships of these genera. Patterson (1970), McDowall (1969, 1984), and Berra *et al.* (1982) place *Prototroctes* in the Prototroctidae, and *Retropinna* and *Stokellia* in the Retropinnidae; Nelson (1972) places the three genera in the subfamily Retropinninae within the family Galaxiidae (along with the subfamily Galaxiinae that includes my Galaxiidae and Aplochitonidae); and Rosen (1974) and Nelson (1984) place all three genera in the Retropinnidae, with two subfamilies: the Retropinninae (*Retropinna* and *Stokellia*) and the Prototroctinae (*Prototroctes*). Although Fink (1984b) considers the three genera to form a distinct holophyletic group, he is uncertain as to their relationship to one another, and doesn't refer them to any family, preferring to consider them as an unresolved trichotomy. Since I did not examine any specimens of *Stokellia* I am unable to comment on its relationship to *Retropinna* and *Prototroctes*.

Galaxiidae and Aplochitonidae

My evidence also strongly supports the hypothesis that the Galaxiidae and Aplochitonidae, together, form a holophyletic group. Evidence from other workers supports this hypothesis (see McDowall 1969; Patterson 1970; Nelson 1972; Rosen 1974; Fink 1984b). Synapomorphies unique to the two families were listed by Fink (1984b) and include the following: posterior border of bones of suspensorium deeply incised or emarginate, principal caudal fin rays 8/8 (versus 9/9 in the Retropinnidae and Prototroctidae and 10/9 in the Salangidae, Plecoglossidae, and Osmeridae), and five hypurals (versus six in the primitive character state). The Galaxiidae and Aplochitonidae do not appear to me to have an incised or emarginate suspensorium, and Fink may be referring to the opercular series, in particular, the posterior margin of the operculum and suboperculum (in which case, this character state is also shared with the Lepidogalaxiidae and may link it with the galaxioid assemblage, as suggested by Roberts 1984).

Rosen (1974) hypothesized that the Galaxiidae (my Galaxiidae + Aplochitonidae) and Salmonidae were sister groups based primarily on hyobranchial anatomy. He noted that both groups had enlarged, fang-like teeth around the margin of the basihyal that were arranged in right and left pairs and terminated anteriorly as a single pair; and that the basibranchial was edentulous or had just a few scattered teeth. The value of this character is suspect for a number of reasons. First, other salmoniforms have enlarged marginal basihyal teeth, including the Retropinnidae, Prototroctidae, Osmeridae, and Argentinidae. As I mentioned earlier, some members of the latter families also have basihyal teeth that are arranged in right and left pairs and end anteriorly in a terminal pair. Fink and Weitzman (1982) also noted that about half the galaxiids they examined had alternating tooth pairs along the margin of the basihyal and a single terminal tooth, a state similar to the condition Rosen claimed was an osmeroid (*sensu* Rosen 1974) synapomorphy. Although the Salmoninae have paired basihyal teeth, some (*Salvelinus fontinalis, S. namaycush*) have a terminal tooth as in many osmeroids. Basibranchial teeth are absent (or represented by just a few scattered teeth) in the Salangidae + Sundasalangidae, the Lepidogalaxiidae, Argentinoidei, and stomiiforms. Also, Rosen (1974) himself notes that unlike the condition in salmonines, the basibranchial tooth plate in the Galaxiidae and Aplochitonidae is not fused with the second endoskeletal basibranchial. Overall then, the basihyal/basibranchial character state shows enough overlap with other salmoniforms to be of limited value in showing phylogenetic relationship.

I prefer the hypothesis that enlarged marginal basihyal teeth (along with an edentulous basibranchial) were developed independently in the Salmonidae and Galaxiidae. Within the Salmonidae, only the Salmoninae have this character state; the Thymallinae and Coregoninae have numerous small teeth scattered randomly over both the basihyal and basibranchials. My evidence and those of others strongly suggests that the Salmoninae are the most derived of the three salmonid subfamilies. It is more parsimonious to assume that enlarged basihyal teeth developed only in the Salmoninae and were absent in the common ancestor of the Salmonidae (which hypothetically had a condition similar to that in the Coregoninae and Thymallinae). This would take only one step (development of enlarged teeth in the Salmoninae lineage) whereas if the common ancestor of the Salmonidae had enlarged teeth three steps are needed (an initial acquisition of the teeth in the Salmonidae, then two independent losses, one in the Coregoninae and one in the Thymallinae). The condition in the Salmoninae could be derived from a state similar to that in the Thymallinae and Coregoninae by losing the basibranchial dentition (some basibranchial teeth are still found in *Hucho perryi*, *Salvelinus namaycush*, *Salvelinus confluentus*, *Salmo clarki*, and *Salmo malmo*; pers. obs., also see Norden 1961; Shaposhnikova 1968; Cavender 1978) and medial basihyal teeth (small medial basihyal teeth are retained in *Hucho* [= *Parahucho*] *perryi*, see Shaposhnikova 1968, fig. 7-3), and by enlarging the marginal basihyal teeth. The condition in the Galaxiidae and Aplochitonidae could easily be derived from a state similar to that in the Retropinnidae and Prototroctidae by losing the basibranchial and medial basihyal teeth and enlarging the remaining marginal basihyal teeth.

Rosen also cited epibranchial evidence to unite the Galaxiidae and Salmonidae. He claimed that fusion between the dorsal tip of the fifth epibranchial and the midpoint of the dorsolateral border of the fourth epibranchial was a synapomorphy uniting the two families. This is true in all the Galaxiidae and Aplochitonidae that he illustrated and in the ones I examined. However, Rosen found such fusion only in one salmonid, *Prosopium cylindraceum*, all the other species possessed the primitive character state in which the fifth epibranchial is separate from the fourth. None of the salmonids that I examined possessed fusion, including numerous specimens of *P. williamsoni* (of various sizes). This suggests that fusion in *P. cylindraceum* is an autapomorphy of this species.

All the Galaxiidae and Aplochitonidae illustrated by Rosen, and those examined by me, have fusion between the dorsal tip of the fifth epibranchial and the midpoint of the dorsolateral border of the fourth epibranchial. The ventral end of the fifth epibranchial is also fused to the posteroventral end of the fourth epibranchial so that there is a closed canal in the cartilage of epibranchial four (apparently for the passage of the fifth efferent branchial artery). No other salmoniforms that Rosen illustrated or that I examined have a similar fourth epibranchial and its shape in the Galaxiidae and Aplochitonidae may be a synapomorphy uniting the two families. The Lepidogalaxiidae lack the above closed canal and have lost the fifth epibranchial (also see Rosen 1974), a character state that could be easily derived from the state in any of the other galaxioids and is therefore congruent with my hypothesis that *Lepidogalaxias* is a galaxioid.

Another synapomorphy that Rosen uses to link the Salmonidae and Galaxiidae (*sensu* Rosen 1974) is the lack of an "uncinate process" and the lack of a "levator process" on the fourth epibranchial. However, not all galaxiids lack an uncinate process; it is present in *G. anomalous* and *G. delfini* (see Fink and Weitzman 1982) and also in *G. paucispondylus* (pers. obs.). Besides the Salmonidae, an uncinate process is absent in some umbrids (*Umbra*), some osmerids (*Hypomesus, Mallotus*, and possibly *Allosmerus*), the Salangidae, Prototroctidae, some retropinnids (absent in *Retropinna retropinna* but present in *Stokellia*); the Lepidogalaxiidae, and numerous Argentinoidei (pers. obs.; also see Rosen 1974; Greenwood and Rosen 1971). Because of the mosaic distribution of this character state within the salmoniforms I prefer to interpret the absence (loss?) of an uncinate process in the Salmonidae and some Galaxiidae as an example of convergence. The polarity of this character is also uncertain because of the mosaic distribution of its states within the salmoniforms and in other lower teleosts; for example within the Elopomorpha it is absent in *Elops* but present in *Megalops* (pers. obs.; also see Nelson 1967c).

Rosen also considered the absence of a "levator process" on the fourth epibranchial to be a salmonid + galaxiid synapomorphy. According to Rosen, the process is the insertion area for the fourth external levator muscle. This character is somewhat difficult to interpret. Fink and Weitzman (1982) questioned Rosen's definition of a "levator process" noting (p. 82) that "In many primitive euteleosts, [the dorsolateral surface of the fourth epibranchial] is separated from the ventrolateral extremity of the bone by a concavity, so that the area of [the insertion of the levator muscle] may be termed a process. Rosen's character, 'absence of a levator process,' might better be defined as loss of this concavity; the area of levator attachment remains unchanged, although in descriptive terms it is no longer a process." I tentatively concur with Fink and Weitzman's interpretation of this character. As defined by Fink and Weitzman the "Absence of this concavity" is shared by salmonids, galaxiids (*sensu* Rosen 1974), the retropinnids *Retropinna retropinna* and *Stokellia*, the Prototroctidae, *Salangichthys* (Salangidae), and by the esocoids (except *Umbra*), further limiting its usefulness as a galaxiid + salmonid synapomorphy (pers. obs.; Fink and Weitzman, p. 83).

Lepidogalaxiidae

My evidence supports the hypothesis that *Lepidogalaxias* is a galaxioid and that the Lepidogalaxiidae are the sister group of the Galaxiidae + Aplochitonidae. When Mees first described *Lepidogalaxias* in 1961, he placed it in the Family Galaxiidae; however, because of its significant differences with other galaxiids he noted (p. 38) that "it deserves to be placed at least in a genus of its own, perhaps even in a separate subfamily." Workers since then have recognized its uniqueness and most place *Lepidogalaxias salamandroides* in its own monotypic family, the Lepidogalaxiidae (e.g., see Frankenberg 1969; Rosen 1974; Berra 1981; McDowall and Pusey 1983; Nelson 1984). There is, however, considerable disagreement as to the phylogenetic position of this species. Most workers consider it, as I do, to be part of the southern hemispheric galaxioid assemblage (see Frankenberg 1969; Nelson 1972; Berra 1981; Roberts 1984). Contrary to this, Rosen (1974) considers *Lepidogalaxias* to be an esocoid, Nelson (1984) places it in its own suborder, the Lepidogalaxioidei (along with the Esocoidei, Argentinoidei, and Salmonoidei within the order Salmoniformes), and Fink (1984b) considers it to form part of an unresolved trichotomy that also includes the Salmonidae and Neoteleostei.

Although Frankenberg (1969) notes similarities of *Lepidogalaxias* with the Umbridae (especially in regards to the caudal skeleton) he prefers a galaxioid relationship primarily on the basis of similarities in the form and position of the scapular foramen and in the shape of the otoliths. Overall, he suggests that *Lepidogalaxias* is probably more closely related to the Galaxiida[illegible]plochitonidae on the basis of the aforementioned characters and on similarit[illegible] shape of the operculum and the presence of only three upper hypurals (versus four in the Retropinnidae and Prototroctidae). He proposes that the Galaxioidei (*sensu* Greenwood *et al.* 1966) be divided into two superfamilies, one containing *Lepidogalaxias* (Lepidogalaxioidea), and another containing the rest of the galaxioid families (the Galaxioidea). He suggests that similarities of *Lepidogalaxias* with the Umbridae are a result of both occupying a similar habitat and having a similar life style. Nevertheless, he does not discount the possibility that *Lepidogalaxias* might have umbrid affinities.

After studying the cephalic sensory canals and pitlines in the esocoids and galaxioids, Nelson (1972) noted that *Lepidogalaxias* resembled the Galaxiidae and Aplochitonidae (especially *Brachygalaxias*) in lacking temporal, posterior infraorbital and sometimes mandibular canals. However, he states (p. 38) that although "*Lepidogalaxias* may be the sister group of all other galaxiines (Frankenberg, MS) ... sensory canal and pore data are inconclusive." He also noted (p. 36) that "Only in *Lepidogalaxias* are pitlines well developed and distinct, resembling in general appearance those of *Dallia*."

Roberts (1984), in a comprehensive study of the salangids, examined *Lepidogalaxias* and noted (p. 216) that "I find no characters indicative of close relationship to Osmeridae or Salangidae, but the structure of the jaws and gill cover reveals specialized characters linking [*Lepidogalaxias*] to the southern galaxioid radiation." He goes on to note similarities between the galaxioids and *Lepidogalaxias* (apparently synapomorphies) in regards to the shape of the operculum, suboperculum, premaxilla and maxilla. Although his evidence is not well documented he suggests (p. 217) that *Lepidogalaxias* is related to the Galaxiidae and that it is probably a "highly specialized galaxiid or galaxioid derivative" rather than the sister group of the galaxiids or galaxioids. Also, apparently to counter Rosen's (1974) argument that *Lepidogalaxias* is an esocoid, Roberts notes a difference between the branchial arches of *Lepidogalaxias* and the Umbridae. Apparently, in *Novumbra* (p. 217) "basibranchial 5 is movably articulated to basibranchial 4" whereas in *Lepidogalaxias*, the galaxioids, osmeroids, and salangids this does not occur. He did not however examine any other esocoids. I examined *Novumbra* and *Lepidogalaxias* and would generally agree with Roberts' observation; however, it is difficult to be sure and the value of this character state is suspect. It appears to me that there is also some degree of flexibility between basibranchial four and five (as in *Novumbra*) in *Esox*, but not in *Dallia* and *Umbra*.

In contrast to the hypothesis that *Lepidogalaxias* is a galaxioid, Rosen (1974), in a very controversial paper, stated (p. 269) that "A review of the anatomy of salmoniform gill arches, caudal skeletons, and secondary sexual characters suggests that *Lepidogalaxias* is an esocoid." As I noted before, all investigators have noted similarities between *Lepidogalaxias* and the esocoids (especially the Umbridae); however, only Rosen proposed that these similarities are indicative of phylogenetic relationship. I seriously question Rosen's hypothesis, as do Fink and Weitzman (1982) who state (p. 80) that "Of the eleven characters Rosen (1974) used to place *Lepidogalaxias* in the Esocae, only four appear to be appropriate for inference of relationship between those groups: lack of a mesocoracoid, lack of pyloric caeca, a single rudimentary neural arch and spine over PU1, and a single uroneural. In view of the reductive nature of all these characters and the very small size and benthic 'habits' of *Lepidogalaxias*, and in view of the importance of the biogeographic hypothesis suggested by this hypothesis of relationships, it appears to us that a further search for characters is warranted."

It is not particularly clear to me why Fink and Weitzman (1982) singled out these four characters, and for this reason I will list the synapomorphies that Rosen (1974) proposed to link *Lepidogalaxias* with the esocoids. Many of these are shared with the galaxioids (and often other salmoniforms) and are therefore of questionable value. The character states (presumably derived) that Rosen used to place *Lepidogalaxias* in the Esocae (as taken from his key on p. 311) include the following: "Dorsal fin posterior in position, over anal fin" (but shared with the Galaxiidae, Retropinnidae, Salangidae + Sundasalangidae, and many Argentinoidei); "no adipose dorsal fin" (this character state is shared with the Galaxiidae, Sundasalangidae, and many Argentinoidei. Also, the dorsal caudal peduncle flange [there is a corresponding ventral flange] that extends from the base of the dorsal fin to the caudal fin in *Lepidogalaxias* may be homologous to an adipose fin. Frankenberg [1969] made histological transverse sections of both flanges and found that the dorsal flange had some adipose tissue at its base but that there was less or none in the ventral flange. Similar sections in a galaxiid showed no adipose tissue); "maxillary edentulous" (the maxilla is also toothless in the Galaxiidae, Aplochitonidae, Prototroctidae, most Retropinnidae, and in numerous other salmoniforms; see Nelson 1984); "with or without a supramaxilla" (Rosen lists both character states and it is unclear which is the derived state; usually the absence of a supramaxilla is derived, a character state found only in *Umbra* among the esocoids and in *Lepidogalaxias* and all the galaxioids, and numerous other salmoniforms); "endopterygoid [= mesopterygoid] edentulous" (shared with the Salmonidae, Salangidae + Sundasalangidae, Alepocephalidae, and Argentinoidea among the other salmoniforms); "no mesocoracoid" (shared with the Galaxiidae, Aplochitonidae, Retropinnidae, Prototroctidae, Salangidae + Sundasalangidae, and numerous Argentinoidei; see Markle 1976; Nelson 1984; Roberts 1984); "no pyloric caeca" (pyloric caeca are also absent in the Salangidae + Sundasalangidae, Retropinnidae and Prototroctidae. They are absent in many Galaxiidae [the range is 0-6 according to McDowall and Frankenberg 1981] and there are 0-2 in the Aplochitonidae according to McDowall [1971b]).

The other synapomorphies mentioned by Rosen concern the gill arches and caudal skeleton. He claims that the presence of "only a single large, oval, strongly dentigerous tooth plate supported by the fourth infrapharyngobranchial and fourth epibranchial" (p. 311) is a *Lepidogalaxias* + esocoid synapomorphy. A similarly shaped tooth plate occupying the same position is also found in the Salmonidae, Stomiiformes, and numerous higher teleosts (pers. obs.; also see Rosen 1973, 1974; Weitzman 1974). This suggests that convergence in this character is common and limits its value. Also, a similar tooth plate (but smaller, narrower, with smaller teeth) is found in numerous salmoniforms, including the Salangidae (it is oval with relatively large teeth in *Salanx prognathus*), most Osmeridae (*Osmerus*, *Allosmerus*, *Spirinchus, Thaleichthys*), the Plecoglossidae, Retropinnidae, and the Prototroctidae. Because of the wide distribution of this character state within the salmoniforms (and higher teleosts), it may well be primitive and is therefore not useful in suggesting relationship.

The tooth-plate character is differently expressed in the Galaxiidae and Aplochitonidae. In these families there are usually several smaller tooth plates in the area usually occupied by a single large tooth plate, except for *Lovettia* in which they have been lost (pers. obs.; also see Rosen 1974). I hypothesize that these character states were derived from a state similar to that found in the aforementioned groups by first fragmentation, then reduction in size and number, and ultimately loss of the toophplate(s). Fragmentation of the tooth plate would be a Galaxiidae + Aplochitonidae synapomorphy.

Another synapomorphy that Rosen suggested (p. 311) was that "the fourth epibranchial [is] always somewhat reduced and without a distinct posterodorsal process for the external branchial levator muscle." I have discussed this character state in detail previously in relation to the other salmoniforms (including the galaxioids, *Lepidogalaxias*, and esocoids). As defined, it is unclear to me what Rosen means by "somewhat reduced." This term is meaningless if one examines Rosen's figures of this structure in his paper. It is true that there is no distinct posterodorsal process in *Lepidogalaxias* and the esocoids (excluding *Umbra*); however, the same can be said of various other salmoniforms that he illustrates, including some salmonids, and the retropinnids. The fourth epibranchial in *Lepidogalaxias* is only broadly similar to that in the esocoids. To me, the fourth epibranchial in *Lepidogalaxias* is much more similar to that in the galaxioids, and could easily be derived from the state in most of them by losing the fifth epibranchial at the posterior end of the fourth (the fifth is usually partly fused to the posterior end of the fourth in the galaxioids; see previous discussions for details).

Rosen (p. 311) uses two synapomorphies of the caudal skeleton to unite *Lepidogalaxias* with the esocoids: "[they] never [have] more than a single rudimentary neural arch and spine over PU1, with only a single, long, straplike uroneural." The value of both these character states must be questioned because they are reductive (the primitive state is for there to be more than one rudimentary neural arch and more than one uroneural; pers. obs., also Greenwood and Rosen 1971). Rudimentary neural arches are found in numerous teleosts and their presence appears to be primitive (pers. obs.; also see Greenwood and Rosen 1971; Rosen 1974). Also, a single rudimentary neural arch is found in some Osmeridae (see Rosen 1974, fig. 28B), numerous Salmonidae (Rosen's figs. 25A, B and C), some Galaxiidae and Aplochitonidae (his figs. 18 and 19), some Argentinoidea (see Greenwood and Rosen 1971; Markle 1976), and possibly some Salangidae (see Rosen 1974, fig. 26B). It is true though that the rudimentary neural arches in the Galaxiidae and Aplochitonidae are different from those in *Lepidogalaxias* and the Esocoidei in that they are larger and usually fused ventrally with a compound centrum (however, in one of the aplochitonids illustrated by Rosen, fig. 19B, the two rudimentary neural arches are autogenous). A rudimentary neural arch is also apparently fused ventrally to the underlying centrum in some specimens of *Lepidogalaxias* (see Rosen, 1974, fig. 24C), and in this regard would resemble the galaxioids. Overall, it seems that this character state may be a *Lepidogalaxias* + esocoid synapomorphy, but a weak one. However, more detailed study of this character is required before any conclusions can be drawn.

Finally, Rosen hypothesizes that the presence of only a single, long uroneural is a synapomorphy uniting the two groups. However, a similarly shaped uroneural, in the same position, is present in numerous Alepocephalidae (pers. obs.; also see Greenwood and Rosen 1971; Markle 1976) and similar uroneurals are present in most primitive teleosts, including the leptolepids (see Monod 1968; Patterson 1968a). The presence of such a uroneural is therefore probably primitive, and the character state in effect is the presence of only a single uroneural. Although most salmoniforms (other than the esocoids and *Lepidogalaxias*) have more than one uroneural, some galaxiids and aplochitonids have one (see Rosen 1974, figs. 18D and 19C) whose shape is unlike that in *Lepidogalaxias*, but roughly similar to that in some umbrids (compare his figs. 21 and 23 with figs. 18D and 19C).

Rosen (1974, p. 293) also noted that some specimens of *Lepidogalaxias* had "anterodorsal acuminate processes" on the uroneural that resemble those in the esocoids and might be indicative of relationship. However, this similarity is rather ambiguous to me; it could be argued that similarly shaped processes are found in other salmoniforms, including galaxioids (see figs. in Rosen 1974).

Overall, it must be admitted that the caudal skeletons in *Lepidogalaxias* and the esocoids appear to be more similar to one another than they are to any other salmoniforms. However, many of the similarities are primitive for teleosts in general (as even Rosen admits) and the ones that may be derived are of questionable value and require further study. Also, because *Lepidogalaxias* displays extensive paedomorphosis, some of the similarities it shares with the esocoids (those of the caudal skeleton?) are probably paedomorphic, and therefore may not be homologous.

Another hypothesis regarding the phylogenetic position of *Lepidogalaxias* was proposed by Fink in 1984(b). Although he noted (p. 205) that it "shares a host of reductive characters with [the] galaxiids" and agrees that they "may indeed be synapomorphous traits" he gives them low weight because "in cases where extensive paedomorphosis is suspected, and this appears to be so in the morphological similarities involved, one hopes to find some innovative non-reductive characters which supply evidence for grouping." Unfortunately he does not mention any of these so-called reductive characters. However, he proposes (p. 205) that *Lepidogalaxias* "may be the sister group of the Neoteleostei" on the basis of its sharing "two non-reductive traits" with the neoteleosts: "a *retractor dorsalis* muscle and [an] occipital condyle composed of both the basioccipital and exoccipital bones." Unfortunately he does not discuss these synapomorphies. Fink and Weitzman considered the latter two features to be synapomorphies of the Neoteleostei in their 1982 paper. Fink (1984b), however, notes that because *Lepidogalaxias* lacks the two other synapomorphies that they originally used to unite the neoteleosts (a rostral cartilage or its homologue, and teeth with a unique attachment mode), it is not neoteleost. Because the Salmonidae share the occipital-condyle character with the neoteleosts, as well as what he considers to be a homologue of the rostral cartilage, Fink also considers the salmonids a possible sister group of the neoteleosts along with *Lepidogalaxias* (however, the salmonids are not neoteleosts because they lack both teeth with a unique attachment mode and a *retractor dorsalis* muscle). He reflects this ambiguity by proposing that the Salmonidae, *Lepidogalaxias*, and the Neoteleostei form an unresolved trichotomy, but does not appear overly confident with this arrangement according to his text (and pers. comm.).

It is unfortunate that Fink did not elaborate on the two non-reductive characters that he used to link *Lepidogalaxias* with the neoteleosts. Although he claims that a distinct *retractor dorsalis* (the *retractor arcuum branchialium* of some workers) is present in this genus (pers. comm.) I did not check for its presence because of a shortage of specimens. According to Winterbottom (1974a, p. 256) the *retractor dorsalis* is a "bilaterally paired muscle, which usually connects the posterior infrapharyngobranchial element(s) to the vertebral column" and apparently represents a specialization of the feeding mechanism that allows more independent movement of the dorsal gill-arch elements and their tooth plates (see Nelson 1967b, 1967c; Rosen 1973). However, assuming that Fink is correct, its presence does not necessarily link *Lepidogalaxias* with the neoteleosts because the character states in the two groups may not be homologous. This muscle has apparently developed independently a number of times during teleostean evolution, and has been recorded in the Osteoglossomorpha (*Pantodon*), some elopomorphs (the muraenid eels), the Ostariophysi (the cyprinids), *Lepidogalaxias*, the Neoteleostei, and in non-teleosts such as *Amia* and *Lepisosteus* (see Nelson 1967b; Rosen 1973, 1985; Winterbottom 1974a). Because the *retractor dorsalis* appears to be prone to independent development in unrelated lineages, and because *Lepidogalaxias* has a number of unusual and specialized features in the area where this muscle usually occurs, it is possible that its presence is an autapomorphy. For example, the position of the gill arches in *Lepidogalaxias* is unusual in that they are farther posterior than in the other teleosts (beneath the first few vertebrae and the region of the occipital condyle, in most specimens, at least in cleared and stained ones, versus beneath the posteroventral end of the skull). The dorsalmost gill-arch elements also appear to attach to the skull (via ligaments, connective tissue, and/or muscles) farther posteriorly than is usual (mainly on the basioccipital and exoccipital; in most other teleosts the more anterior prootic is also included) and this attachment area might also include the first few vertebrae, hence possibly the *retractor* *dorsalis* muscle Fink was speaking of.

The unusual position of the gill arches and the possible presence of a *retractor dorsalis* muscle may be anatomical specializations that are related, along with specializations of the occipital region (which includes Fink's other synapomorphy), to the unusual method of feeding observed in *Lepidogalaxias*, adding credence to my hypothesis that the two so-called *Lepidogalaxias* + neoteleost synapomorphies are simply autapomorphies of this unusual teleost. This is suggested by McDowall and Pusey (1983, p. 20) who state that *Lepidogalaxias* has the unusual ability of being able to "bend the 'neck' at a quite sharp angle either sideways and/or downwards" and that "This behaviour is related to food search, the fish observing moving food items on the tank bottom, moving adjacent to them, and bending the head sideways and/or down to locate the items before engulfing them." They attribute this ability to the fact that there are wide spaces between the exoccipital and the first vertebra, and the first and second vertebrae (there are also relatively wide spaces between the other cervical vertebrae, but they are not as wide, pers. obs.). They suggest (and I concur) that "the spacing of the vertebrae increases the flexibility of the vertebral column, facilitating the bending of the head sideways or downwards" (p. 21).

Related to this character state is Fink's second synapomorphy uniting *Lepidogalaxias* and the Neoteleostei: the occipital condyle is composed of both the basioccipital and exoccipital bones, versus only the basioccipital in the primitive character state. This feature was considered to be a synapomorphy uniting the neoteleosts by Fink and Weitzman (1982) and Rosen (1985), and I concur; however, it is also found in the osteoglossomorph *Hiodon* (pers. obs.), the primitive clupeomorph *Denticeps* (see Greenwood 1968), and some Salmoniformes (the Salmoninae and *Lepidogalaxias*), suggesting that it is prone to convergence, a view also held by Rosen (1985). More significant, however, is my observation that the occipital joint in *Lepidogalaxias* is morphologically unlike that in the neoteleosts, the Salmoninae, or *Hiodon* and is therefore probably not homologous. Firstly, in the latter three groups the contact of the exoccipital with the centrum of the first vertebra is via a cartilage-covered condyle or surface on each exoccipital that contacts a separate facet (usually) on the dorsolateral corners of the anterior end of the centrum. The rest of the anterior end of the centrum contacts the basioccipital. In essence therefore a distinct tripartite occipital joint exists that involves both the exoccipital and basioccipital. In *Lepidogalaxias*, however, the basioccipital forms nearly the entire joint surface, with two wing-like extensions of each exoccipital overlapping each dorsolateral corner of the anterior end of the first centrum. The contact area of the exoccipital with the vertebra is smaller than in most teleosts with such a joint and is located more laterally. In addition, the exoccipital lacks a distinct cartilage-covered condyle or facet where it contacts the first vertebra; the latter lacks a facet at the contact point. Overall it appears to me that the exoccipital may act more as a buttress to prevent excessive mediolateral movement of the relatively loose occipital condyle, rather than forming an integral part of the joint as in the other teleosts mentioned. These exoccipital "wings" are vaguely reminiscent of, and possibly derivable from, the posterolateral extensions of the exoccipitals that approach, but do not contact the first vertebra in some galaxiids (e.g., *Galaxias brevipinnis*, pers. obs.).

The exoccipitals in *Lepidogalaxias* are also unusually large and make up most of the posterior part of the cranium. The foramen magnum (bordered by the exoccipitals dorsally and laterally and the basioccipital ventrally) is larger relative to the rest of the skull than in any of the other teleosts I examined. I suggest that the large foramen magnum, which is immediately dorsal to the occipital joint, may provide extra space for the unusual vertical movements of the skull observed by McDowall and Pusey (1983).

In summary, and in view of my evidence that *Lepidogalaxias* is a galaxioid, it is more parsimonious to conclude that the two similarities that *Lepidogalaxias* shares with the neoteleosts are the result of convergence, and are probably autapomorphies of the lineage that are related to its unusual feeding behavior.

In his 1985 paper Rosen briefly mentions Fink's new hypothesis regarding *Lepidogalaxias* but does not provide any new information concerning its phylogenetic position. He does not appear to be as confident regarding his earlier hypothesis that it is an esocoid, noting (p. 37) that "Fink and Weitzman (1982) disagree with my earlier (1974) alignment of it with esocoids, partly, and I think correctly, on the grounds that my comparison of anterodorsal outgrowths of its first uroneural with those of esocoids leaves a great deal to the imagination." However, he does not discount it being an esocoid, noting that its cephalic sensory pit-lines resemble those of *Dallia* (he quotes Nelson 1972) and that it resembles "a *Novumbra* - *Dallia* esocoid subgroup defined by having a single epural and uroneural in the caudal skeleton" (p. 37). He also states (p. 37) that "A case might also be made for its original placement as a galaxiine (see Rosen, 1974) based on dorsal and caudal fin anatomy and position." Rosen sums up his current uncertainty regarding the phylogenetic position of this fish by purposely excluding it from his cladogram of euteleostean relationships (his fig. 45) and by stating (p. 37) that "Fink's (1984) statement that the 'position of *Lepidogalaxias* is controversial' is unarguable."

Argentinoidei

I have one shared derived character state that unites the Argentinoidei (*sensu* Greenwood and Rosen 1971). In the Argentinoidei there is distinct reduction and/or loss of dentition on the mesopterygoid, basihyal, and basibranchials. I hypothesized earlier that the common ancestor of the group had more extensive dentition on these and other bones. In various argentinoid lineages teeth are also lost or reduced in size or number from some or all of the following bones: the premaxillae, maxillae, vomer, and the posterior bones of the branchial arches (from the pharyngobranchials, epibranchials, and ceratobranchials). The reduction of dentition within the Argentinoidei was discussed in detail in an earlier section (refer to pages 329-332). The weight given to this synapomorphy is relatively low because it is a reduction and loss character state, and as such is more prone to convergence. For example, among the salmoniforms mesopterygoidal teeth are also absent in the Esocoidei, Salmonidae, Salangidae + Sundasalangidae, and Lepidogalaxiidae; basihyal teeth are absent in some Umbridae, the Sundasalangidae, most Salangidae, and the Lepidogalaxiidae; and basibranchial teeth are absent in most Salmonidae, the Salangidae + Sundasalangidae, and the Galaxiidae, Aplochitonidae, and Lepidogalaxiidae. However, no single assemblage within the salmoniforms shows such an extensive reduction of dentition on these three bones, or such an extensive reduction of dentition in general (except perhaps for the Lepidogalaxiidae and Salangidae + Sundasalangidae). Previously, Lauder and Liem (1983, p. 134) proposed that the absence of teeth from the basibranchials was a synapomorphy of the Argentinoidei but did not discuss the character.

Although the aforementioned synapomorphy is relatively weak, the muscles of the suspensorium support the hypothesis that the Argentinoidei is holophyletic (I will discuss this evidence later), as do Greenwood and Rosen's (1971) evidence using other parts of the skeleton. I find their overall argument convincing (but not all parts of it), and to date no one except Markle (1976) has seriously questioned it.

The crux of Greenwood and Rosen's (1971) argument supporting the holophyly of the Argentinoidei concerns the presence in the group of "a distinctive pharyngobranchial structure not known to occur in any other major group of fishes" (p. 1). They call this structure the crumenal organ, and more specifically describe it as "a complex bilaterally paired structure that takes the form of a pair of flattened, somewhat angular pouches, or purses, and that involves the last two gill arches and the anterior limits of the esophagus" (p. 5). Other teleosts (various osteoglossomorphs, clupeomorphs, ostariophysans, some salmonids, and some neoteleosts) have somewhat similar structures, usually called epibranchial organs, that apparently serve a similar function of collecting and temporarily storing small food particles (see Nelson 1967c; Bertmar *et al.* 1969; Markle 1976). However, the crumenal organ in the Argentinoidei is apparently unique in that its position is lateral, rather than dorsal or dorsolateral to the esophagus, and in that it possesses, between the posterior cartilaginous tip of ceratobranchial five and epibranchial five, a unique "accessory cartilage", which together with the latter two elements helps to support the narrow posterior margin of the pouch (see Bertmar *et al.* 1969; Greenwood and Rosen 1971; Markle 1976). The Opisthoproctidae lack an accessory cartilage (it is replaced by a cylindrical muscle); however, this state could easily have been derived from one similar to that found in the Bathylagidae (whose crumenal organ skeleton it closely resembles in every other way; compare Greenwood and Rosen's figs. 5 and 6B with fig. 6A). An accessory cartilage is also apparently absent in a few Alepocephalidae (pers. obs.; also see Greenwood and Rosen 1971; Markle 1976).

Another apparent synapomorphy of the Argentinoidei (Greenwood and Rosen 1971, p. 8) is that "the orobranchial chamber is divided longitudinally either by tissue from the floor of the mouth or by a direct upgrowth of the dermal bone over the basibranchial chain." However, the value of this character is suspect since Markle (1976, p. 32) noted that, although a well-developed basibranchial ridge is present in *Leptochilichthys* (Alepocephalidae), "In all other genera the basibranchial ridge is slight to non-existent. Instead the basibranchials are slightly arched."

Greenwood and Rosen (1971) and Rosen (1974) also noted similarities between the Alepocephaloidea and Argentinoidea in regards to their caudal skeleton anatomy. This evidence is not convincing because the character states in the two groups are quite different from each other, and neither is easily derivable from the other. Their main argument appears to concern the fact that some alepocephaloids have a character state similar to that found in the Argentinoidea (suggesting that the common ancestor of the Argentinoidei had a state similar to that in the Argentinoidea) and that the character state present in the Alepocephaloidea is the result of paedomorphosis (for which there does not appear to be much evidence).

In addition [illegible] the above evidence, Greenwood and Rosen (1971) noted similarities in jaw musculature and the structure of the anal pterygiophores that are consistent with their hypothesis (but not necessarily synapomorphies).

Markle (1976) attempted to refute Greenwood and Rosen's hypothesis that the Argentinoidei are holophyletic, suggesting (p. 85) that the crumenal organ "is a primitive feature at the salmoniform level which has been retained in the Argentinoidea and Alepocephaloidea." He does not, however, bring much new anatomical evidence to bear in his argument (other than by noting that an accessory cartilage is absent in a few Alepocephalidae and that a basibranchial ridge is absent in most) and does not attempt to evaluate Greenwood and Rosen's other evidence. The absence of an accessory cartilage in a few argentinoid lineages does not seriously threaten their hypothesis that the presence of an accessory cartilage is a synapomorphy of the Argentinoidei. In fact, all the alepocephalids that Markle claims lack the structure (*Bathylaco, Bathyprion, Mirognathus* and *Photostylus*) are rather atypical and specialized in various ways (refer to Nielsen and Larsen 1968; Markle 1976), and in the case of *Bathylaco* and *Bathyprion* there is disagreement with Greenwood and Rosen regarding its presence or absence. Perhaps significantly, Markle noted that in *Bathyprion* the fifth epibranchial is minute (Greenwood and Rosen's accessory cartilage?) while in *Mirognathus* and *Photostylus* it is either lost or fused with the fourth epibranchial. The reason why Markle rejects the presence of an accessory cartilage as a synapomorphy of the Argentinoidei is unclear, especially when he states (p. 82) that "Another possibility is that the accessory cartilage is a primitive, perhaps salmoniform, character which has remained, along with many other characters, almost unchanged in these two groups [the Alepocephaloidea and Argentinoidea]", and then attempts to prove his point by discussing the potential ease with which such a structure could be lost or gained in relation to the habitat in which a species lives. This seems to ignore the fact that no other teleost apparently has a similar accessory cartilage (see Nelson 1967c, 1969; Greenwood and Rosen 1971; Rosen 1974); therefore, it must be interpreted as a synapomorphy of the Argentinoidei.

My data define two distinctive holophyletic groups within the Argentinoidei: the Alepocephaloidea, made up of the Alepocephalidae and Platytroctidae; and the Argentinoidea, made up of the Argentinidae, Bathylagidae, and Opisthoproctidae. Within the Argentinoidea, the Bathylagidae and Opisthoproctidae, together, form a holophyletic group.

Argentinoidea

The shared derived character states of the suspensorium that unite the Argentinidae, Bathylagidae, and Opisthoproctidae are numerous, and include the following:

1. The teeth on the ventral surfaces of the palatines and vomer are closely spaced, and form a continuous, U-shaped biting surface, along the anteroventral edge of the snout, that

opposes the anterodorsal edge of dentaries that may or may not have teeth (see Figs. 28, 30, 33). The palatines firmly abut the ethmoid cartilage and the bones at the anterior end of the snout. The anterior end of the vomer (the part bearing the teeth) is also unique among salmoniforms in that it extends anterior to the ethmoid block and acts as the anteriormost biting surface. Teeth are absent from the maxillae, premaxillae, mesopterygoids, basibranchials, and usually the basihyal.

The unusual bite mechanism in the Argentinoidea is unlike that in any other salmoniform or teleost that I examined. For detailed descriptions of this character the reader is referred to the descriptive part of this thesis. The bite in other teleosts has also been previously described; in most either the premaxillae or maxillae (or both) possess teeth that are involved in the bite at the anterior end of the snout along with the palatine and vomerine dentition. In essence, in the Argentinoidea, the palatines and vomer have taken over the function of the maxillae and premaxillae.

The argentinids possess teeth on the basihyal; however, it appears that they oppose the edentulous, posteroventral surface of the vomer (there are teeth at the anteriormost end of the vomer) and not the palatine-vomerine dentition. The argentinid genus *Glossanodon* has reduced dentition on the palatines, vomer, and basihyal; the teeth are more widely spaced and there is a space between the vomerine and palatine dentition. However, because the distribution of teeth on the palatines and vomer is essentially the same as in *Argentina*, and the bite is identical, I consider the character state in *Glossanodon* to be homologous with that found in the other Argentinoidea.

Other workers have mentioned the unique bite mechanism found in the Argentinoidea, but it has not been described in much detail (see Chapman 1942a, 1942b, 1943; Cohen 1958a, 1964; Greenwood and Rosen 1971; Ahlstrom *et al.* 1984). Greenwood and Rosen (1971, p. 34) considered that the "Anterior extension of the vomer beyond the ethmoid block to act as the forward biting surface (replacing the edentulous upper jaw)" was a specialization of the Argentinoidea. Ahlstrom *et al.* (1984, p. 155) considered the Argentinoidea to be holophyletic on the basis of four derived character states, one of which was the "tendency in the group for vomer and palatines to assume the functions of the premaxillary and maxillary." However, they do not mention it any further and simply state (p. 155) that it is a "unique character, and one which never has been adequately studied and documented."

2. The anterior end of the palatine is not expanded, lacks a cartilage (a trace was present in my specimen of *Bathylagus pacificus*), and is curved anteroventrally (it is "claw-like"). In essence, the palatine is very similar within the group but is unlike that found in any other salmoniform (or teleost) examined (see Figs. 27, 29, 31, 32). *Plecoglossus* (Plecoglossidae) has a palatine that curves anteroventrally at its anterior end; however, it has an anterior cartilage and differs in numerous other ways from that in the Argentinoidea (see description of the Plecoglossidae). The palatine in *Novumbra* (Umbridae) has a very tiny cartilage at its anterior end but otherwise is unlike that in the Argentinoidea. Primitively, the palatine is straight and has an anterior expansion on which rests a relatively large cartilaginous knob (e.g., the Alepocephalidae and Platytroctidae).
3. The ectopterygoid is approximately rectangular to elliptical in shape and is straight and relatively short (anteroposteriorly) and wide (dorsoventrally). It broadly overlaps and braces the palatine and quadrate to a degree not found in most other salmoniforms (see Figs. 27, 29, 31, 32). For example, in *Argentina* (Argentinidae), *Bathylagus* (Bathylagidae), and *Dolichopteryx* (Opisthoproctidae), but in no other salmoniform that I examined (including the opisthoproctids *Macropinna* and *Opisthoproctus*), the ectopterygoid overlaps both the lateral and medial surface of the body of the quadrate.

   Although some other salmoniforms have some of these features (for example, a relatively straight ectopterygoid is found in some umbrids, some salmonids, and some galaxioids) none has all of them. The ectopterygoid in these groups also differs in other ways from that in the Argentinoidea (refer to earlier parts of this thesis for details).
4. The body of the quadrate is semicircular, with a broad rounded dorsal edge, and anterior and posterior edges that are nearly level with the horizontal (more so in the Bathylagidae

and Opisthoproctidae).

The primitive character state is found in the other salmoniforms and most other teleosts: the body is triangular with anterior and posterior edges that form a relatively sharp angle with the horizontal (for example, see Figs. 22 and 34).

5. The condyle of the quadrate and the joint with the angulo-articular bone of the lower jaw are unique (see Figs. 27, 29, 31, 32). The condyle is turned upwards so that the articular surface faces anteriorly and contacts the posteriorly-facing facet on the angulo-articular. A straight line can be drawn that passes through (from posterior to anterior): the anterior half of the symplectic and quadratojugal arm of the quadrate, the quadrate condyle, the articular facet on the angulo-articular bone of the lower jaw, and Meckel's cartilage. This line is nearly horizontal when the mouth is in the normal position (at least in specimens preserved in alcohol or cleared and stained).

The primitive character state is found in the other salmoniforms and the other teleosts examined. Primitively, the quadrate condyle projects anteroventrally so that its articular surface faces anteroventrally and contacts a posterodorsally facing facet on the angulo-articular. A line drawn through the symplectic, quadratojugal arm, and condyle runs anteroventrally, while a line drawn through Meckel's cartilage and the articular facet of the angulo-articular of the lower jaw runs posteroventrally, forming a distinct angle at their intersection (at the condyle) when the mouth is in the normal position.

6. The anterior end of the symplectic (excluding the cartilaginous knob) does not reach the posterior end of the body of the quadrate. Primitively the anterior end of the symplectic extends distinctly anterior to the posterior end of the body of the quadrate. Of the teleosts I examined, this character state was shared only with the gonorynchiform *Chanos*.

7. The metapterygoid is very small or absent. When the metapterygoid is present the endochondral portion is axe-shaped. Primitively the metapterygoid is relatively large, and has an extensive endochondral portion with a rectangular, oval, or lunate shape.

A small metapterygoid with a similar endochondral portion is found in *Novumbra* and *Dallia* (Umbridae) and in the Lepidogalaxiidae, Galaxiidae, and Aplochitonidae. The shape is most similar to that in the Lepidogalaxiidae and Aplochitonidae. However, when present, the bone in the Argentinoidea is thinner and smaller relative to the rest of the suspensorium than in any other salmoniform.

8. A possible synapomorphy that requires further documentation is the presence of a unique, oval to pear-shaped extension on the ectopterygoid that extends dorsally towards the ethmoid cartilage in some genera of each family (see Figs. 27, 32). Such an extension [illegible] found in *Argentina* (Argentinidae), *Dolichopteryx* (Opisthoproctidae), and apparently in *Nansenia* (Bathylagidae, see Chapman 1948a), but was absent in *Bathylagus* (Bathylagidae) and the two other opisthoproctids examined (*Macropinna* and *Opisthoproctus*). In *Argentina* and *Nansenia* this extension nearly reaches the lateral ethmoid bone whereas in *Dolichopteryx* it is located distinctly anterior to the lateral ethmoid.

If the common ancestor of the Argentinoidea possessed this unique feature, and if it has been secondarily lost in some Argentinoidea, then it would be a synapomorphy uniting the group. Among the other salmoniforms, only *Esox* (Esocidae) has a dorsal extension of the ectopterygoid (see Fig. 5). However, in this genus it is different in shape from that in the Argentinoidea and therefore almost certainly an example of convergence.

None of the above synapomorphies have been used previously to unite this group (except for the first one involving the palatine-vomerine bite; however, this character is here described and extensively documented). The findings of other workers, using other parts of the skeleton (primarily the caudal skeleton and features of the anal pterygiophores), other parts of the anatomy (swimbladder), and early life history stages (features of the larvae and eggs), corroborates and strengthens this hypothesis (for details see Greenwood and Rosen, 1971; Rosen 1974; Ahlstrom *et al.* 1984). My muscle evidence, which I will discuss later, also corroborates this hypothesis.

I have no reliable derived character states that [illegible] any of the families of the Argentinoidea with either the Alepocephalidae, the Platytroctidae, or both. Assuming that the Argentinoidei are holophyletic, and that specialized mesopterygoidal teeth were present in the common ancestor of the group (as I hypothesize), then a toothless mesopterygoid would be a derived character state and a synapomorphy linking the Alepocephalidae, Argentinidae, Bathylagidae, and Opisthoproctidae (teeth are present in the Platytroctidae). However, because this is an absence character state (i.e., it has low weight) and because numerous other, stronger character states support an alternate hypothesis, I consider this similarity to be convergent.

Bathylagidae [illegible]sthoproctidae

Within the Argentinoidea, the Bathylagidae and Opisthoproctidae constitute a holophyletic group (the sister group of the Argentinidae) on the basis of their sharing the following derived character states:

1. The entire dorsomedial side of the palatine closely abuts the anterolateral edge of the snout. Primary contact is made with the ethmoid cartilage but the palatine also closely approaches (or overlaps) some of the ethmoid bones (see Figs. 29-31, 33). A similar contact was not found in any other salmoniform (or teleost) examined. However, the character state in the Argentinidae is most similar; and a state similar to it could theoretically have given rise to the state in the Bathylagidae and Opisthoproctidae. In the Argentinidae the palatine also closely abuts the ethmoid block but only its anteromedial edge does so (see Fig. 27).

   Primitively, only the anteromedial surface of the cartilaginous knob at the anterior end of the palatine contacts the ethmoid cartilage (the lateral prenasal process), and in most cases, the joint formed appears to be relatively loose compared to that in the Argentinoidea.

2. The ectopterygoid is separated from the mesopterygoid by a relatively wide band of cartilage. Primitively, in the Argentinidae, and in all the other salmoniforms examined, the ectopterygoid and mesopterygoid are closely adjacent to, or overlap, each other.

3. The body of the quadrate has a distinct semicircular shape, with a very broad and rounded dorsal edge, and anterior and posterior edges that are virtually level with the

horizontal. A quadrate notch is absent. The character state in the Argentinidae is similar to that in the Bathylagidae and Opisthoproctidae, and when more broadly defined was used as a synapomorphy uniting the three families. However, in the Argentinidae the body has less of a semicircular shape, the anterior and posterior edges form a slight angle with the horizontal, and there is a shallow quadrate notch. The primitive character state was described previously.

Besides my preferred hypothesis (that the Bathylagidae and Opisthoproctidae are sister taxa) there are two possible alternate hypotheses: that the Argentinidae and Bathylagidae are sister taxa, or that the Argentinidae and Opisthoproctidae are sister taxa. In the Argentinidae (*Argentina*) and the Bathylagidae (*Bathylagus* and *Nansenia*, see Chapman 1948a) the preopercular, bony, lateral sensory canal is open along the entire length of the ventral limb, but partly closed along the dorsal limb (versus entirely open in all the opisthoproctids examined). A relatively similar character state was found in numerous alepocephaloids as was the alternate character state (entirely open). However, because it is impossible to tell whether this character state is primitive or derived I prefer not to consider its joint possession by these two families as indicative of relationship between them.

I also have no positive evidence for linking the Argentinidae and Opisthoproctidae. In *Argentina* (Argentinidae) and *Dolichopteryx* (Opisthoproctidae) the palatine has a large dorsoventrally-inclined lamina that extends posteroventrally to overlap the ectopterygoid. *Bathylagus (Bathylagidae)* lacks this lamina. However, because it is absent in the two other opisthoproctids I examined (*Macropinna* and *Opisthoproctus*) its value as an argentinid + opisthoproctid synapomorphy is questionable.

The findings of other workers corroborates my hypothesis that the Bathylagidae and Opisthoproctidae are sister taxa, and together form the sister group of the Argentinidae (see Greenwood and Rosen 1971; Rosen 1974). Their evidence primarily includes similarities in the crumenal organ and various "optical specializations." These workers considered my Bathylagidae and Opisthoproctidae to be subfamilies (the Bathylaginae and Opisthoproctinae, respectively) within the family Bathylagidae.

In contrast to these conclusions, Ahlstrom *et al.* (1984) hypothesize that the Argentinidae and Bathylagidae (my definition) are sister taxa, and together form the sister group of the Opisthoproctidae. Their evidence, however, is confusing and appears to be derived from other sources (primarily Greenwood and Rosen 1971). They cite two synapomorphies linking the Argentinidae and Bathylagidae (see their table 42 and fig. 88): "Accessory cartilage at posterior tip [of] ceratobr. [= ceratobranchial] 5" and "PU1 + U1 fused" in the caudal skeleton. However, Greenwood and Rosen (1971) considered the former character state to be a synapomorphy uniting the Argentinoidei, and as such it could not be used to unite the Argentinidae and Bathylagidae. The sharing of this character state by the latter two families would be a symplesiomorphy since the same character state is found in the outgroup of the Argentinoidea, the Alepocephaloidea. The accessory cartilage is replaced by a muscle in the Opisthoproctidae (an apparent opisthoproctid autapomorphy, see Greenwood and Rosen 1971).

Ahlstrom *et al.*'s (1984) second synapomorphy, fusion of PU1 + U1, is of questionable polarity. Such fusion occurs in the Argentinidae, Bathylagidae, and some alepocephalids and platytroctids as well as in most osmeroids and galaxioids. It is absent in the Opisthoproctidae and most alepocephalids and platytroctids (refer to Greenwood and Rosen 1971; Rosen 1974). Rosen (1974, p. 289) states that the compound centrum character (fusion) "appears to be presently of little significance in phylogenetic studies unless the consolidation occurs in unusual ways." I concur with Rosen, and pending further evidence, do not consider fusion of PU1 + U1 to be an important argentinid + bathylagid synapomorphy.

Ahlstrom *et al.* (1984) also noted that the Bathylagidae (my definition) and Opisthoproctidae share a derived character state (uncinate process lacking on fourth epibranchial), but consider this similarity to be convergent. It is uncertain to me whether or not this character state is derived at this level, since this character shows a mosaic distribution within the salmoniforms (including the Argentinoidei). I prefer to consider it of uncertain polarity.

Overall, I find Ahlstrom *et al.*'s (1984) hypothesis unfounded. A careful examination of their evidence suggests that the interrelationsips of the Argentinidae, Bathylagidae, and Opisthoproctidae are uncertain.

Alepocephaloidea

The shared derived character states of the suspensorium that unite the Alepocephalidae and Platytroctidae include the following:

1. The metapterygoid is about the same size (moderately large and robust) and shape (squarish to crescent-like), overlaps the surrounding bones in the same way, has a well-developed medial dermal ridge, and the palatoquadrate cartilage extends around its ventral edge from the anterodorsal to posterodorsal corner (see Figs. 34-46). Overall, the metapterygoids in the Alepocephalidae and Platytroctidae are more similar to one another than they are to those of any other salmoniform. In the Retropinnidae and Prototroctidae the metapterygoid is somewhat similar in shape to that in the Alepocephaloidea; in addition, the palatoquadrate cartilage occupies a similar position. However, in the Retropinnidae and Prototroctidae the metapterygoid more broadly overlaps the hyomandibular, the cartilage at the posterodorsal corner is greatly expanded and extends relatively far posteriorly, and there is no medial ridge. The Osmeridae and Plecoglossidae have a medial ridge that is similar in shape and position to the one in the Alepocephaloidea. However, in the Osmeridae and Plecoglossidae its posterior end is expanded into a laminar wing that overlaps the hyomandibular, and the *adductor arcus palatini* inserts along the entire length of the ridge. In contrast, the medial ridge is occupied by the *levator arcus palatini* in all but a few alepocephaloids, in which it is also occupied by a small part of the *adductor arcus palatini*. These differences and the unique features of the osmerid + plecoglossid metapterytoid suggest that the medial ridge in the two groups is probably convergent. Some Stomiiformes and Myctophiformes have a metapterygoid somewhat similar to that in the Alepocephaloidea (pers. obs.; also see Weitzman 1967a, 1967b, 1974); however, these similarities are also probably convergent

since there is strong evidence suggesting that both groups are holophyletic and belong in the Neoteleostei (see Fink and Weitzman 1982; Lauder and Liem 1983).

2. The medial surface of the hyomandibular usually has two ridges: one that runs dorsoventrally from near the posterodorsal corner of the head to the ventral end of the ventral arm, and one that runs anteroposteriorly from the anterior lamina or the anterior part of the head to the opercular arm (and is usually continuous with the dorsoventral ridge). The *adductor arcus palatini* inserts on, and dorsal to, the anteroposterior ridge. Although these ridges differ slightly in size and position, both are present in almost all platytroctids and alepocephalids that I examined, and at least one ridge was present in all of them (see Figs. 34-46).

Primitively the medial side of the hyomandibular lacks both ridges and has a relatively smooth surface. With one exception (some Osmeridae) medial ridges were absent in all the other salmoniforms and teleosts that I examined. Among the Osmeridae, a distinct dorsoventral ridge, similar to that in the Alepocephaloidea, is found only in the Osmerinae (*Osmerus*, *Allosmerus*, *Spirinchus*, and *Thaleichthys*) and is a shared derived character state uniting these four genera (see Figs. 16, 17). A weakly developed dorsoventral ridge, extending only along the ventral arm, is found in *Mallotus*, and a trace of a ridge is debatably present in *Hypomesus* (see Figs. 14 and 15, respectively). With the exception of *Thaleichthys*, the ridge in the osmerines is shorter than that in the alepocephaloids.

A distinct anteroposterior ridge similar to that in the alepocephaloids is absent in the Osmeridae. Some Osmerinae (*Thaleichthys* and *Osmerus*) have what might broadly be defined as such a ridge, but it is weaker and shorter than in the alepocephaloids (extending only along the opercular arm posterior to the dorsoventral ridge, versus along both the opercular arm and anterior lamina).

In summary, these similarities between the Osmerinae and Alepocephaloidea are probably a result of convergence, but... because of the differences between the medial ridges that I noted, and because there is stronger evidence suggesting that the Osmerinae and

Alepocephaloidea belong with the osmeroids and argentinoids, respectively.

Neither of the aforementioned synapomorphies has been previously used to unite the Alepocephalidae and Platytroctidae. My evidence corroborates that of numerous other workers, using other parts of the skeleton and anatomy, who consider these two groups to be each other's closest relatives (see Gosline 1960, 1969; Parr 1960; Greenwood *et al.* 1966; Marshall 1966; Nielsen and Larsen 1968; Greenwood and Rosen 1971; Markle 1976; Nelson 1984; Matsui and Rosenblatt 1987).

Although my evidence (including evidence from the muscles, which I will discuss later) supports the hypothesis that the Alepocephaloidea are holophyletic, I have no data supporting either the hypothesis that the Alepocephalidae are holophyletic, or that the Platytroctidae are holophyletic. Overall, the suspensoria in these two large families are remarkably similar to one another; in fact, there are numerous alepocephalids that more closely resemble certain platytroctids than they do other alepocephalids (and vice versa). The Platytroctidae (= Searsiidae) were actually included in the Alepocephalidae until Parr (1960) described a unique feature, called the shoulder or post-cleithral organ, that appears to be a synapomorphy of the group. Matsui and Rosenblatt (1987) recently listed more synapomorphies uniting the Platytroctidae.

The other alepocephaloids are usually placed in the family Alepocephalidae; however, it appears that this group is not holophyletic since they are usually diagnosed by the absence of character states present in the Platytroctidae (e.g., absence of the shoulder organ). In the most complete study of this group to date, Markle (1976, p. 92) notes that the Alepocephalidae "can be diagnosed from other alepocephaloids but, to date, no derived unifying character state is known although many trends are apparent." Some workers have attempted to recognize the diversity in this "family" by dividing it into subfamilies or by placing some of its more aberrant members in families of their own. For example, Nelson (1984) considered that the Alepocephalidae had four subfamilies: the Alepocephalinae, Bathyprioninae, Bathylaconinae, and Leptochilichthyinae. Workers at various times have recognized the Bathylaconidae (Nielsen and Larsen 1968), Bathyprionidae (Marshall 1966), and Leptochilichthyidae (Markle 1976), in addition to the Alepocephalidae. However, the former three families have only four genera (and perhaps six species) between them, and seem to have been created in an attempt to recognize their uniqueness, since each represents a highly specialized lineage.

No one to date has proposed a phylogenetic classification of the Alepocephalidae and the interrelationships of the various genera are very poorly known. Since the Alepocephalidae have never been shown to be holophyletic it is conceivable that some of its genera are more closely related to the Platytroctidae than they are to other alepocephalids, which is indeed suggested by my evidence. Markle (1976) divided the family (excluding *Leptochilichthys*, which he tentatively places in its own family) into five, often poorly defined "generic groups" that are really grades of development, noting (p. 93) that "They are not taxonomic equivalents. Their main value, I believe, is as a starting point for further work." Matsui and Rosenblatt (1987) present a phylogeny of the platytroctid genera in their new revision of the Platytroctidae.

I examined the suspensoria of eleven of the twenty-four genera that Markle (1976) placed in the Alepocephalidae, and seven of the thirteen platytroctid genera recognized by Matsui and Rosenblatt (1987). Of the alepocephalids that I studied I would unite only two genera with certainty, *Leptoderma* and *Conocara*. The suspensoria in these two taxa are similar to each other and unlike those found in the other alepocephalids and platytroctids. A number of the bones have features that appear to be synapomorphies, especially the metapterygoid, hyomandibular, and preoperculum. Markle's (1976) findings concur with this hypothesis: he considered that *Ericara, Aulastomatomorpha, Leptoderma*, and *Conocara* probably form a holophyletic group. I did not examine the former two genera; however, judging from the figure of the suspensorium of *Aulastomatomorpha* in Lloyd (1906), this genus is probably closely related to *Leptoderma* and *Conocara*. Any further comments I could offer concerning the phylogenetic relationships of the other alepocephalid genera would be speculative, and the same is true of the interrelationships of the Platytroctidae. However, the muscles of the suspensorium yield some insight into the interrelationships of the

Alepocephaloidea, and I will discuss this evidence later.

(OSMEROIDS + GALAXIOIDS + ARGENTINOIDS) + NEOTELEOSTS

The osmeroids, galaxioids, and argentinoids (= Argentinoidei of Greenwood and Rosen 1971), together, may form the primitive sister group of the Neoteleostei, or higher teleosts (see Fig. 94). These two assemblages are united on the basis of their sharing an open, bony, lateral sensory canal on the preoperculum. Although this character state is variable in some of these fishes, it is present in most of them, including both extant and extinct species. Primitively, the canal is enclosed in bone and opens to the exterior via a pore at each end of the preoperculum, and via pores at the ends of auxiliary canals that lead off of the main canal (e.g., see Figs. 5-7, 9-13, 47, 50).

Preopercular Canal: Derived Character State

Osmeroids + Galaxioids + Argentinoids

In the osmeroids and galaxioids (with two exceptions that I will discuss later) the bony, lateral sensory canal on the preoperculum is completely open posterior to a flange (hereafter called the anterior flange) that runs along the entire length of the anterolateral surface of the preoperculum (see Figs. 14-17, 21-23, 25, 26). The anterior edge of this flange is continuous with the anterolateral surface of the preoperculum. It projects posterolaterally from the dorsal limb and ventrolaterally from the ventral limb, and is usually slightly convex on its lateral surface. A distinct posteriorly facing groove (the open, bony, lateral sensory canal) is formed between the medial surface of the flange and the lateral surface of the preoperculum. A flange was completely absent in two of the three salangids that I cleared and stained (*Salangichthys ishikawae* and *Salanx prognathus*, see Figs. 19 and 20, respectively) but a narrow one was present in *Salangichthys microdon* (see Fig. 21). A preoperculum is absent in the Sundasalangidae (see Roberts 1984).

One highly specialized osmeroid, *Plecoglossus altivelis*, and one highly specialized galaxioid, *Lepidogalaxias salamandroides*, have a bone-enclosed preopercular canal (see Figs. 18 and 24, respectively). However, in my opinion this feature is an autapomorphy of each lineage. Unlike the esocoids, salmonids, and most other lower teleosts, the canal in *Plecoglossus* is only partly enclosed in bone, lacks distinct auxiliary canals, and has pores that are found almost directly along the main canal (compare Fig. 18 with Figs. 12 and 13 for example). The canal in the smallest specimen of *Plecoglossus* (UAMZ 5668, 55.5 mm SL) displayed even less closure than the adults, contrasting with the smallest esocoids and salmonids, which invariably had the adult character state. The canal in *Lepidogalaxias* has one auxiliary canal at the intersection of the two limbs, but it is shorter than in most species with auxiliary canals. Because of these differences with the primitive character state I conclude that a bone-enclosed canal is best interpreted as an autapomorphy of each species, and that the ancestor of each probably had an open canal as in the other osmeroids and galaxioids.

The character state in the Argentinoidei is basically similar to that in the osmeroids and galaxioids, but there is more variability. The canal in the Opisthoproctidae is entirely open posterior to a narrow anterior flange (see Figs. 31, 32). In the Argentinidae (Fig. 27) and Bathylagidae (Fig. 29) the sensory canal on the ventral limb is completely open ventral to a moderately wide flange; however, on the dorsal limb it is partly closed and opens to the exterior via a series of foramina of various sizes (*Bathylagus*), or at the end of funnel-shaped auxiliary canals (*Argentina*).

The canal was entirely open in six of the seven platytroctids that I examined, (see Figs. 42-44, 46). The anterior flange in the platytroctids is generally narrower than in the galaxioids and osmeroids, and has a slightly broken, almost porous appearance. Also, in some, there are several short flanges of bone posterior and parallel to the anterior flange that may represent remnants of what was once the posterior part of a closed canal, and short bridges of bone that join the posterior part of the anterior flange to the lateral surface of the preoperculum. The canal in *Platytroctes apus* is closed for part of its length (see Fig. 45).

However, where open, it opens directly to the exterior in a way reminiscent of that in *Bathylagus* (and unlike the primitive character state).

The canal in the Alepocephalidae (twelve genera were examined) shows considerable variability (see Figs. 34-41). Most resemble the canal found in *Talismania* (see Fig. 34), in which it is open along the ventral limb, partly closed at the intersection of the two limbs (there may be one or two funnel-shaped auxiliary canals in this area), and open along most of the dorsal limb. The canal was completely open in four genera: *Rouleina* (wide anterior flange), *Bathylaco* (relatively narrow anterior flange), *Xenodermichthys* (trace of an anterior flange), and *Photostylus* (no anterior flange). The canal in *Leptoderma* and *Conocara* (and apparently *Aulastomatomorpha*, see figure in Lloyd 1906) is open along most of the length of the bone; however, the posterior edge of the anterior flange has a scalloped appearance, and attaches to the lateral surface of the bone at various points. Overall, the canal in the Alepocephalidae most closely resembles that in the Platytroctidae; even the anterior flange has a similar porous-looking appearance.

Fossil evidence is meagre for the osmeroid + galaxioid + argentinoid assemblage; however, there are two extinct argentinoids in which the preoperculum is visible: *Glossanodon musceli* (Argentinidae) and *Carpathichthys polonicus* (Alepocephalidae), from the Upper Eocene - Lower Oligocene and Oligocene deposits of Poland, respectively (see Jerzmańska 1967, 1979). It is not clear from Jerzmańska's (1967) description and figure whether the canal is open or closed in *G. musceli*. However, in *C. polonicus* it appears to be open posterior to a flange running along the anterior edge of the bone (see Jerzmańska 1979, fig. 1).

Neoteleosts

In most higher teleosts (Neoteleostei), both extant and extinct, although there is variability similar to that in the aforementioned salmoniforms, an open, bony, lateral sensory canal on the preoperculum is present. When a bone-enclosed canal is present I hypothesize that it was ultimately derived secondarily from an ancestor with an open canal, and that this character state is not homologous with the primitive state found in the lower teleosts. Because of the size of the Neoteleosti it was impossible to check this feature in all the assemblages; however, the following account was gleaned from my own observations and the literature and covers the major groups:

Stomiiformes. The canal is completely open posterior to an anterior flange in at least some species of the following genera: *Thorophos, Araiophos, Maurolicus, Argyripnus, Sonoda, Polyipnus, Sternoptyx, Gonostoma, Diplophos* (*D. taenia*, see Fig. 51), *Argyropelecus* (*A. pacificus*), *Cyclothone*, and *Vinciguerria* (latter four genera pers. obs., others from Günther and Deckert 1955; Weitzman 1967a, 1967b, 1974; Fink and Weitzman 1982). The order Stomiiformes is moderately large (nine families and fifty-three genera according to Nelson 1984) and its interrelationships are uncertain (see Fink 1984a for the most recent account). However, from what is known it appears that many of the aforementioned genera are relatively primitive, especially *Diplophos*, which is hypothesized to be the sister group of the rest of the order (see Weitzman 1974; Fink and Weitzman 1982; Fink 1984a).

A partly closed canal is present in a number of stomiiforms, including at least some species belonging to the following genera: *Diplophos* (*D. maderensis*), *Danaphos*, *Valenciennellus*, *Argyropelecus*, (*A. aculeatus*), *Polymetme, Astronesthes, Borostomias, Heterophotus, Rhadinesthes, Neonesthes, Tactostoma*, and *Chauliodus* (latter two genera pers. obs., others from Weitzman 1967a, 1967b, 1974; Fink and Weitzman 1982). However, except for *Diplophos*, these genera appear to be relatively derived stomiiforms. In *D. maderensis* (see Fink and Weitzman 1982) the canal is closed on the dorsal limb and apparently open on the ventral one, unlike *D. taenia* in which the canal is completely open. It is difficult to tell which state is primitive for this genus; however, a completely open canal may be since the preoperculum in *D. maderensis* appears derived over that in *D. taenia* in certain features (it has a flange that extends posterolaterally from the enclosed canal that is lacking in both *D. taenia* and other stomiiforms). The canal in *Argyropelecus aculeatus* and *Polymetme* is entirely open along the ventral limb (ventral to an anterior flange) and partly open along the dorsal limb, a condition reminiscent of many Argentinoidei (see Weitzman 1967a, 1974). In

Danaphos and *Valenciennellus* the canal is "incompletely closed" according to Weitzman (1974, p. 412). In his figure of *Danaphos* (fig. 58) it appears that the canal is open posterior to the anterior flange that runs the length of the preoperculum, but may be interrupted by bridges of bone that extend between the flange and the lateral surface of the bone (a condition reminiscent of many alepocephaloids). The character state in *Valenciennellus* is apparently "very similar" to that in *Danaphos*.

The character state in *Astronesthes, Borostomias, Heterophotus, Rhadinesthes, Neonesthes, Tactostoma,* and *Chauliodus* is unlike that found in the other stomiiforms (latter two genera pers. obs., others from Weitzman 1967b). In this assemblage the canal is enclosed in bone for most of the length of the preoperculum, but opens to the exterior via a number of irregularly placed foramina that open directly off of the main canal in a way reminiscent of the state in some Argentinoidei. Although the canal is completely enclosed in bone, there are three reasons why I suggest that this condition was secondarily derived from an ancestor with an open or partly open canal. First, this assemblage represents a rather specialized, and apparently phylogenetically derived lineage within the stomiiformes (see Weitzman 1967b, 1974; Fink 1984a). The shape of the suspensorium, in particular, is highly atypical. The preoperculum is virtually straight, very narrow, and inclined anterodorsally (as is the rest of the suspensorium). Second, although the canal is enclosed in bone, it does not resemble the primitive character state found in the lower teleosts. Primitively, the pores leading to the exterior are generally found at the end of auxiliary canals leading off of the main canal, and are not found along its posterior and lateral surface, as in the aforementioned genera. Finally, because most stomiiforms (including most primitive ones) have a canal that is completely open or mostly open, it is more likely that this state is primitive for the order.

Although there are some fossil stomiiforms from the Oligocene and Miocene (see Jerzmańska 1960; Crane 1966) it is unclear from their descriptions whether the preopercular canal is open or closed.

Aulopiformes. Information concerning the preopercular canal in this order (twelve families with forty genera according to Nelson 1984) is scarce. However, it appears that an open canal may be primitive for the assemblage. Most workers agree that the genus *Aulopus* (of the monotypic family Aulopodidae) is the most primitive and generalized aulopiform, and that a species similar to it may have given rise to the other aulopiforms (see Goody 1969a; Rosen and Patterson 1969; Rosen 1973; Sulak 1977). In *Aulopus filamentosus* (pers. obs.) the preopercular canal is rather unusual and might be interpreted as an intermediate character state. It is almost completely open along the dorsal two thirds of the dorsal limb (posterior to an irregular anterior flange that does not extend to the dorsal tip of the bone). The canal on the ventral third of the dorsal limb is enclosed in bone (but there are two wide foramina along its posterior side) and there is a single short auxiliary canal at the intersection of the two limbs. Although the canal on the ventral limb is enclosed in bone, when viewed laterally it resembles the wide anterior flange found in some galaxioids (i.e., the derived charater state), but opens to the exterior via three or four moderately wide foramina along its ventromedial edge instead of being completely open ventral to the flange. Because this "anterior flange" slightly overlaps the foramina laterally they are visible only when the bone is viewed ventrolaterally.

It is difficult to tell if the character state in *Aulopus* is primitive or derived for the aulopiforms; however, evidence from other primitive and generalized aulopiforms, such as *Chlorophthalmus* (see Sulak 1977), as well as fossil evidence, suggests that a more open canal may have been present in the ancestor of the group. For example, in *Chlorophthalmus agassizi* (pers. obs.) the preopercular canal is completely open posterior to an anterior flange that runs the length of the bone, except for a short section at the intersection of the two limbs. At this point a series of irregular bony bridges extend from the posterior edge of the anterior flange to the lateral surface of the preoperculum (as in numerous alepocephaloids).

Rosen and Patterson (1969) described and illustrated the extinct species *Nematonotus longispinus* from the Upper Cretaceous of Lebanon, claiming that it was a relative of the recent genus *Aulopus* (and more primitive than it). In their figures 66 and 68 they illustrated a preoperculum that appeared to be closed, with five relatively long auxiliary canals (four on the ventral limb and one on the dorsal limb) but do not mention this in their description. I examined a specimen of *Nematonotus* sp. (UAVP 13362, 89 mm SL) in which the entire medial surface of the right preoperculum was visible. It is obvious in this specimen that the canal is completley open posterior to a well-developed anterior flange (there was no evidence of auxiliary canals, or even grooves that might indicate their presence). It is difficult to interpret Rosen and Patterson's figures in light of this evidence. However, it is possible that the artist was unsure as to the presence of the canals (they are only lightly outlined) but included them anyway. In any case, Rosen (1973, p. 462), based upon additional evidence, was less certain that *Nematonotus* is a close relative of *Aulopus* and states that "The two species [of *Nematonotus*] can be regarded as members, *incertae sedis*, of the aulopoid assemblage [one of two suborders belonging to the Aulopiformes, *sensu* Rosen 1973], but only with the understanding that this assignment is provisional and that phyletic arguments based on their position are futile."

The canal in the other extant aulopiforms is variable. In many (most?), the canal is similar to that in the specialized stomiiforms described previously (*Astronesthes, Borostomias,* etc.): it is enclosed in bone for most of the length of the preoperculum, but opens to the exterior via a series of foramina of variable size, shape, and position, that open directly along the main canal (e.g., *Synodus* and *Saurida*, pers. obs.; also see Günther and Deckert 1960; Goody 1969a; Sulak 1977; Johnson 1982). In some the canal is open along most of the bone (posterior to a flange) but partly closed at its ventral end (e.g., all the evermannellid genera illustrated by Johnson 1982, fig. 12). Some may have a completely open canal (e.g., *Scopelarchus and Scopelarchoides*; see Parr 1929, figs. 2 and 5, respectively). Interestingly, and perhaps significantly, a juvenile specimen of *Bathypterois grallator* (43 mm standard length) possessed what appears to be an open canal (see Sulak 1977, fig. 20C), whereas an adult of the same species had a bone-enclosed canal with foramina opening along it (his fig. 12A). The suspensorium was inclined distinctly obliquely in the adult, but was nearly vertical in the juvenile (the primitive character state). Sulak in fact noted that the condition in the juvenile approached that of more primitive aulopiforms such as *Chlorophthalmus* and *Aulopus* in many respects. These facts suggest that a bone enclosed canal with foramina opening along it may have been derived from a form with an open canal, and as such would add credibility to my hypothesis that the latter character state is primitive for the aulopiforms.

Goody (1969a) described a number of extinct Upper Cretaceous "salmoniforms" that Rosen (1973) subsequently placed in the Aulopiformes (mainly in the derived suborder Alepisauroidei). Of those in which the preoperculum was adequately figured or described, most have a canal that is either entirely open (*Apateodus* and *Halec*) or partly open (*Enchodus, Eurypholis*, and *Phylactocephalus*). *Ichthyotringa* had a closed canal with "several openings to the external surface throughout its length" (p. 17).

Myctophiformes. This order has two families: the Myctophidae with about thirty-two genera, and the Neoscopelidae with three genera (see Nelson 1984). According to Paxton (1972) the preopercular canal is completely open posterior to a well-developed anterior flange in all myctophids (also pers. obs. of *Myctophum, Protomyctophum, Symbolophorus*, and *Stenobrachius*). The character state in the Neoscopelidae is unknown to me. The extinct myctophiform from the Upper Cretaceous, *Sardinioides*, has an open canal similar to that found in modern myctophids (see Goody 1969a; Rosen 1973).

Paracanthopterygii. It was impossible to examine or find data on many lineages, mainly because of the size of this group (thirty-three families according to Nelson 1984). However, rather extensive information was available on what is thought to be the most primitive order, the Percopsiformes (*Percopsis, Chologaster*, pers. obs.; also see Rosen 1962; Rosen and Patterson 1969), and their sister group according to Lauder and Liem (1983), the Gadiformes (*Lota, Microgadus*, pers. obs.; also see Mujib 1967; Rosen and Patterson 1969). Some data were also available on the more derived lineages, the Batrachoidiformes, Lophiiformes, and Gobiesociformes (*Porichthys, Ogilbia*, pers. obs.; also see Rosen and Patterson 1969). All Paracanthopterygii (for which information was available) have a preopercular canal that is completely open posterior to a well-developed anterior flange (this flange is apparently reduced in some derived lineages, for example, the Amblyopsidae). In a few species narrow bridges of bone appear to extend from the posterior edge of the anterior flange to the lateral surface of the preoperculum at the intersection of the two limbs. Other than this, I found no case in which the canal was even partly closed (the character state in most species closely resembles that found in the Myctophiformes).

The Percopsiformes and Gadiformes have a rather extensive fossil record, and in most cases the preoperculum is well-preserved (the fossil record of the three other more derived orders, however, is very poor). The oldest known, and osteologically the most primitive paracanthopterygian, the percopsiform *Sphenocephalus* (from the Upper Cretaceous of Europe), has a preopercular canal that is completely open posterior to a wide anterior flange (see Rosen and Patterson 1969). Another recently discovered, and yet unnamed percopsiform from the Palaeocene of North America has a similar canal (pers. obs., UAVP 17741). The four other fossil percopsiform genera (*Trichophanes*, from the Oligocene-Miocene, pers. obs.; and *Erismatopterus*, *Amphiplaga*, and *Libotonius* from the Eocene, see Rosen and Patterson 1969 and Wilson 1979) have the same character state. According to Rosen and Patterson (1969) the oldest known gadiform (from the lower Palaeocene of Greenland, no name given) has a properculum that is similar to that found in the gadoids (i.e., it has an open canal?). The canal is completely open posterior to a wide anterior flange in the Eocene gadoid *Rhinocephalus*, but there are three narrow bridges of bone extending from the posterior edge of the anterior flange to the lateral surface of the preoperculum at the intersection of the two limbs (see Rosen and Patterson 1969, fig. 52).

†<u>Ctenothrissiformes</u>. This extinct order contains the marine Upper Cretaceous genera *Aulolepis* and *Ctenothrissa* (see Rosen 1973). The phylogenetic position of the ctenothrissiforms is uncertain. Nelson (1984) placed them in the Paracanthopterygii whereas Rosen (1971) placed them in the Acanthopterygii. However, in his 1973 paper Rosen states (p. 504) that "Available evidence ... suggests that *Ctenothrissa* and *Aulolepis* are related and

that together they form a primitive sister-group of the Paracanthopterygii + Acanthopterygii." The observation that in both genera the preopercular canal is entirely open posterior to an anterior flange (see Patterson 1964) suggests that the common ancestor of the latter assemblage might have had a similar character state (if Rosen's hypothesis is correct).

Acanthopterygii. Because of its large size (fifteen orders and two hundred and forty-six families according to Nelson 1984) it was impossible to examine, or to obtain information on more than a small percentage of these fishes. The bony, lateral sensory canal in this assemblage shows considerable variation, ranging from being completely open to closed with short auxiliary canals. However, evidence from both fossils and extant species suggests, that a completely open canal may be primitive for this group.

The Beryciformes are considered to be the basal group of acanthopterygian evolution since they are structurally the most primitive acanthopterygians and are the first to appear in the fossil record (see Patterson 1964, 1967a, 1968b; Greenwood *et al.* 1966; Rosen and Patterson 1969; Rosen 1973; Zehren 1979; Lauder and Liem 1983; Nelson 1984). Almost all beryciforms, both extant and extinct species, have a bony, lateral sensory canal on the preoperculum that is completely open posterior to well-developed anterior flange (pers. obs. of *Plectrypops, Melamphaes, Photoblepharon*; also see Patterson 1964, 1967a; Zehren 1979). This includes *Lissoberyx dayi*, from the lowest part of the marine Upper Cretaceous of Lebanon, that Patterson (1967a, p. 69) considers to be "the most primitive berycoid yet known, and ... near the origin of the suborder." In a few species narrow bridges of bone extend from the posterior edge of the anterior flange to the lateral surface of the preoperculum at the intersection of the two limbs (for example: †*Homonotichthys,* †*Stichocentrus, Anoplogaster, Monocentris,* and *Paratrachichthys*; see Patterson 1964, 1967a; Zehren 1979). The most complete closure is found in *Photoblepharon* (pers. obs.) and *Diretmus* in which the canal is closed on the dorsal limb (see Zehren 1979). However, since the latter five extant genera are members of the most derived beryciform lineage (see Zehren 1979; Keene and Tighe 1984) and the majority of beryciforms (including the most primitive species) have a completely open canal it is more parsimonious to conclude that the canal was completely open in the common ancestor of the group and became partly closed secondarily in some of the more derived beryciforms. The "beryciform" *Polymixia*, which Rosen (1985) considered to form the sister group of the Acanthomorpha (the Paracanthopterygii + Acanthopterygii), also has a preopercular canal that is completely open posterior to an anterior flange (see Zehren 1979), as do the fossil polymixiids described by Patterson (1964).

The other acanthopterygians exhibit a variety of character states of the preopercular bony lateral sensory canal. Unfortunately, the interrelationships of this huge assemblage are poorly known, and for this reason it is often difficult to polarize the data regarding the canal. Overall, however, an open canal is relatively common in the groups hypothesized to be more primitive, and even when a closed canal is present it is usually structurally unlike that found in most lower teleosts.

Most recent workers divide the Acanthopterygii into two series: the Atherinomorpha and Percomorpha, of which only the holophyly of the Atherinomorpha is well-documented (see Rosen and Parenti 1981; Lauder and Liem 1983; Nelson 1984). Within the Atherinomorpha (two orders and eighteen families according to Nelson 1984) data were available for members of seven families: the Exocoetidae, Belonidae, and Hemiramphidae of the suborder Exocoetoidei, order Cyprinodontiformes (see Parin and Astakhov 1982); the Cyprinodontidae and Poeciliidae, suborder Cyprinodontoidei, order Cyprinodontiformes (pers. obs.); and the Atherinidae and Melanotaeniidae of the order Atheriniformes (pers. obs.). All the specimens that I examined from the latter four families (*Fundulus* and *Cyprinodon; Xiphophorus; Menidia, Thyrina,* and *Hypoatherina*; and *Melanotaenia*, respectively) had a completely open bony canal posterior to an anterior flange. However, the former three families exhibited a variety of character states (see Parin and Astakhov 1982). In the Belonidae (five genera seen) the canal on the ventral limb was completely open in *Strongylura* and *Tylosurus* but closed in *Belone, Platybelone*, and *Ablennes*. In the latter three genera the canal on the ventral limb opened to the exterior at the end of auxiliary canals of various shapes (very short in *Platybelone* but relatively long in the other two genera). The canal on the dorsal limb was almost completely open in *Platybelone* and *Tylosurus* but was closed in the other three genera shown. Only in *Tylosurus* was the canal open on both limbs. Similar variation was seen in the Exocoetidae and Hemiramphidae.

Because the interrelationships of the atherinomorph families are poorly known (and the fossil record is relatively poor) it is difficult to hypothesize as to what character state of the bony canal is primitive for the group. Rosen and Parenti (1981) and White *et al.* (1984) hypothesized that the atheriniforms are the primitive sister group of the cyprinodontiforms. All the Atheriniformes that I examined (four species) had a completely open canal. This fact combined with the observation that a closed canal (and then usually only partly closed) was found in relatively derived cyprinodontiform lineages (the Belonidae, Hemiramphidae, and Exocoetidae; see Collette *et al.* 1984) suggests that an open canal may be primitive for the Atherinomorpha.

The character states of the bony preopercular canal in the other acanthopterygian series, the Percomorpha (thought to be paraphyletic by most workers, see Lauder and Liem 1983), are also variable and it is difficult to tell what state is primitive in most lineages. The interrelationships of this assemblage are poorly known. However, an open canal is common in a number of lineages that are relatively primitive (including the Beryciformes that were described previously), and as such it may represent the primitive character state for the group. For example, the suborder Percoidei of the order Perciformes (the largest acanthopterygian order) is thought to be the basal group from which the other perciforms, and several other orders, evolved (Gosline 1968; Smith 1971; Nelson 1984). Data were available for the following percoid families: Centropomidae, Percichthyidae, Serranidae, Grammistidae, Grammidae, Kuhliidae, Centrarchidae, Percidae, Sciaenidae, and Haemulidae. In the Centropomidae (with three genera) the canal in *Psammoperca* and *Lates* is closed on the dorsal limb and partly open on the ventral limb; there are no auxiliary canals, simply wide foramina that open directly off of the main canal (see Greenwood 1976). However, the canal is completely open along its entire length in what Greenwood considers to be the sister genus of the latter two genera, *Centropomus*, suggesting that the common ancestor of the

Centropomidae may have had a similar character state. *Ambassis*, which some workers place in the Centropomidae (e.g., Nelson 1984), has a canal similar to that in *Centropomus* (pers. obs.). All Percichthyidae for which data were available had a completely open bony canal (*Morone*, pers. obs.; *Perchichthys*, *Polyprion*, and *Percilia*, see Arratia 1982). The extinct species *Percichthys hondoensis* (Eocene), *P. lonquimayiensis* and *P. sandovali* (both Upper Palaeocene), and *Priscacara* (Eocene) all have a completely open canal (data for the first three species from Arratia 1982; *Priscacara*, pers. obs.). A few narrow bridges of bone appear to extend from the anterior flange to the lateral surface of the ventral limb in *Polyprion oxigeneius* (extant) and the Upper Tertiary species *Santosius antiquus* (see Arratia 1982). The canal in the Serranidae is more variable. In *Paralabrax* and *Hemilutjanus* it appears to be completely open (see Arratia 1982, figs. 104 and 105). However, in *Caprodon*, *Centropristis*, and *Epinephelus* it is closed to varying degrees (all pers. obs.). In *Caprodon* and *Centropristis* most of the dorsal limb is open; however, on the ventral limb and at the intersection of the two limbs the canal is closed but opens directly to the exterior via a number of foramina; there are no auxiliary canals. The canal in *Epinephelus* is similar to that found in the latter two genera except that the canal on the dorsal limb is completely closed. The canal in *Rypticus* (Grammistidae) and *Gramma* (Grammidae) is similar to that in *Epinephelus* (all pers. obs.). In *Kuhlia* (Kuhliidae) the canal on the dorsal limb is closed but is almost entirely open on the ventral limb (pers. obs.). Data were available for all nine centrarchid genera (*sensu* Nelson 1984). The canal is completley open only in *Elassoma* (see Branson and Moore 1962). However, in *Centrarchus*, *Micropterus*, *Lepomis*, *Pomoxis*, and *Ambloplites* it is open along most of its length except for bridges of bone that extend from the posterior edge of the anterior flange to the lateral surface of the preoperculum at the intersection of the two limbs and on the ventral limb (*Pomoxis*, pers. obs., other genera from Branson and Moore 1962). In *Archoplites*, *Acantharchus*, and *Enneacanthus* the canal is closed more than the other genera but opens to the exterior via foramina along the length of the main canal; there are no auxiliary canals (see Branson and Moore 1962). In the Percidae there is also considerable variability. In *Perca* (pers. obs.) the canal is closed but opens to the exterior via large foramina along its length (there are no auxiliary canals). In *Gymnocephalus* the canal is mostly open except for equally spaced bridges that extend from the posterior edge of the anterior flange to the lateral surface of bone (see Elshoud-Oldenhave and Osse 1976). In *Etheostoma* and the extinct *Mioplosus* (Eocene) the canal is completely open (both pers. obs.). In *Stizostedion* the canal is mostly closed but opens to the exterior via narrow foramina along its length (pers. obs.). In the five sciaenid genera illustrated by Kim and Kim (1965) the canal was completely open except for widely spaced narrow bridges extending from the posterior edge of the anterior flange to the lateral surface of the bone. The canal in adult specimens of *Anisotremus* (Haemulidae) is closed on the dorsal limb, but almost completely open on the ventral limb except for three narrow bridges of bone that extend from the ventral edge of the anterior flange to the lateral surface of the preoperculum (see Potthoff *et al.* 1984, fig. 30). Perhaps significantly, in small specimens the canal is completely open posterior to a well-developed anterior flange, with some closure visible on the dorsal limb of a specimen 20.4 mm SL.

The Pomacentridae, Cichlidae, Embiotocidae, and Labridae form a holophyletic group within the Perciformes according to Lauder and Liem 1983. The Cichlidae, both extinct and extant species, have a closed canal that opens to the exterior via pores at the end of short auxiliary canals that lead off of the main canal, resembling the character state found in most lower teleosts (*Hemichromis*, pers. obs.; also see Stiassny 1981; Van Couvering 1982). However, this character state may be secondarily derived from an ancestor with an open canal because the Pomacentridae, considered to be the primitive sister group of the other three families, has a completely open canal interrupted by a few bony bridges in some species (*Pomacentrus* and *Stegastes*, pers. obs.; also see Stiassny 1981).

The character states of the preopercular canal in other major percomorph assemblages exhibits variability similar to that previously described. For example, in the Scorpaeniformes that I examined (the scorpaenid *Sebastes*, the cottids *Chitonotus* and *Cottus*, the Psychrolutid *Malacocottus*, and the cyclopterid *Liparis*) the canal was partly closed: wide bony bridges extend from the posterior edge of the anterior flange to the lateral surface of the preoperculum along the entire length of the preoperculum (also see Nelson 1982). None had auxiliary canals. In the Gasterosteiformes the canal ranges from an open, shallow groove (an anterior flange is absent) in *Gasterosteus aculeatus* (pers. obs.) to a completely enclosed canal with a few small foramina opening along it, as in *Pungitius platygaster* (pers. obs.).

In summary, a completely, or mostly open canal may be primitive for the Acanthopterygii. If this is the case then the closed canal found in many species would have been secondarily derived from an ancestor with an open canal. Very few acanthopterygians have a closed canal with well-developed auxiliary canals similar to that found in the lower teleosts. When such a canal is present (e.g., the Cichlidae) it is usually found in more derived acanthopterygians in which the hypothesized primitive sister group possessed an open canal.

Preopercular Canal: Primitive Character State

Lower Teleosts

In the primitive character state for the Teleostei, the preopercular canal is enclosed in bone, and opens to the exterior via a pore at each end of the preoperculum, and via pores at the end of auxiliary canals that lead off of the main canal (e.g., see Figs. 5-7, 9-13, 47, 50). This character state, or a variant of it, is found in most species, both extant and extinct, belonging to the Salmonidae, Esocoidei, Ostariophysi, Clupeomorpha, Elopomorpha, and Osteoglossomorpha, and is hypothesized to have been present in the common ancestor of each. Significantly, it is also found in the extinct Ichthyodectiformes, Aspidorhynchiformes, Leptolepidiformes, and Pholidophoriformes. The latter two orders are considered to be paraphyletic by most workers, but are thought to contain the basal, and osteologically the most primitive teleosts (see Patterson and Rosen 1977; Nelson 1984). In some lower teleosts the auxiliary canals are reduced and/or lost, and foramina open almost directly along the main canal (for example, some elopomorphs). Sometimes the entire canal is open posterior to an anterior flange, but this invariably occurs in the more derived lineages of an assemblage (for example, in the Engraulidae of the Clupeomorpha). In the latter two exceptions there is relatively strong evidence that the common ancestor of each group possessed distinct auxiliary canals.

The character states of the preopercular canal in the lower teleostean assemblages are briefly described in the following account.

Salmonidae. In all the salmonids the preopercular canal is enclosed in bone, and opens to the exterior via a pore at each end of the preoperculum, and via pores at the end of auxiliary canals that are short to moderately long (see Figs. 10-13; also see Shaposhnikova 1968, 1970; Cavender 1970; Gorshkov *et al.* 1979). The canal is similar in the oldest known salmonid, *Eosalmo driftwoodensis*, from the Eocene of British Columbia (pers. obs.; also see Wilson 1974, 1979), and in all other known fossil salmonids (e.g., see Cavender and Miller 1972; Smith 1975).

Esocoidei. In all extant esocoids (Esocidae + Umbridae) the preopercular canal is enclosed in bone and opens to the exterior via a pore at each end of the preoperculum, and via pores at the end of auxiliary canals that are short, as in *Esox* and *Novumbra*, or long, as in *Dallia* and *Umbra* (see Figs. 5-7, 9; also see Nelson 1972; Jollie 1975; Sytchevskaya 1976; Wilson and Veilleux 1982). The canal is similar in fossil esocoids, including the oldest known esocoids, *Esox tiemani* (pers. obs.) and *Boltyshia* (see Sytchevskaya 1976) from the Palaeocene (also see Cavender 1969; Wilson 1984).

†Gaudryella and †Humbertia. Patterson (1970) placed the extinct, marine, Upper Cretaceous genera *Gaudryella* and *Humbertia, incertae sedis* in the order Salmoniformes (which at this time included the Stomiiformes of Rosen 1973). If this placement is correct, they would be the oldest known salmoniforms. Both genera have a bone-enclosed lateral sensory canal on the preoperculum with long, to moderately long, auxiliary canals leading off of the main canal. Because of this they probably do not belong in the (osmeroid + galaxioid + argentinoid) + neoteleost assemblage, which share an open, bony, lateral sensory canal on

the preoperculum. They are also probably not neoteleosts (which includes the stomiiforms) or salmonines because their first vertebra articulates with only the basioccipital bone (not with both the basioccipital and exoccipital, which Fink and Weitzman [1982] consider to be a synapomorphy of the Neoteleostei, but is also found in the Salmoninae). Some evidence from the suspensorium suggests that they may belong in the esocoid + salmonid group: *Humbertia* (but not *Gaudryella*) has what appears to be an anteroventral wing on the hyomandibular (a derived character state that I hypothesize to be a synapomorphy uniting the esocoids and salmonids), the palatine in both is reminiscent of some coregonines (as is the shape of the mandible), and the mesopterygoid in both is edentulous as in the esocoids and salmonids. Furthermore, Patterson (1970, p. 253) noted that in both genera the skeleton is "almost entirely acellular." Parenti (1986) considered acellular bone to be derived relative to cellular bone in the Teleostei, and noted that it was found in the neoteleosts, osmeroids (*sensu* Fink and Weitzman 1982), and esocoids, but not in most lower teleosts (including the Argentinoidei). The salmonids, like *Gaudryella* and *Humbertia* but unlike most other teleosts, have both types of bone, suggesting a possible relationship; but in the salmonids most of the skeleton is cellular. Patterson argued that *Gaudryella* and *Humbertia* are not salmonids or esocoids because their first preural and first ural caudal centra are fused, unlike the latter two taxa, in which they are separate. The phylogenetic position of *Gaudryella* and *Humbertia* is still uncertain, and in light of the new evidence accumulated since their original description, needs to be reinvestigated.

Ostariophysi. Most Ostariophysi appear to have a bone-enclosed lateral sensory canal on the preoperculum similar to that found in the Esocoidei and Salmonidae. Although because of its size (over six thousand species according to Nelson 1984) it was impossible to obtain data on more than a small percentage of these fishes, there is good evidence suggesting that a bone-enclosed canal is primitive for the Ostariophysi. The most primitive members (both extant and extinct) of each of the major assemblages have a bone-enclosed canal. For example, the genus *Chanos*, hypothesized by Fink and Fink (1981) to be the sister group of all other gonorynchiforms (the Gonorynchiformes in turn are the primitive sister group of the three other ostariophysan orders, the Cypriniformes, Characiformes, and Siluriformes), has a bone-enclosed canal and numerous auxiliary canals (see Fig. 50). The gonorynchiform *Gonorynchus* also appears to have a closed canal (but no auxiliary canals? see the figure in Ridewood 1905c) as does the extinct Eocene genus *Notogoneus* (pers. obs.).

The Cypriniformes are hypothesized to be the sister group of the Characiformes + Siluriformes (see Fink and Fink 1981). The interrelationships of this order are uncertain; however, a number of genera are considered to be morphologically primitive, including *Opsariichthys, Zacco, Luciosoma, Barilius,* and *Engraulicypris*, all of which apparently have a bone-enclosed canal with pores opening along it (see Howes 1980; Fink and Fink 1981). The genera *Notropis* (see Harrington 1955), *Labeo* (see Sarbahi 1933), *Osteochilus* (see Karnasuta 1981), and *Couesius* (pers. obs.) have a similar canal.

The characiformes are the sister group of the specialized Siluriformes (Siluroidei + Gymnotoidei) according to Fink and Fink 1981; however, traditionally this group has been considered to be more primitive than both the Cypriniformes and Siluriformes. Characiformes hypothesized by various workers to be primitive include *Hoplias* (see Fuiman 1984), *Hepsetus* (see Roberts 1969), *Brycon* (see Weitzman 1962), and *Xenocharax* (hypothesized by Fink and Fink to be morphologically the most primitive member of the distichondontid-citharinid lineage, which they consider to be the primitive sister group of all other characiforms), all of which have a bone-enclosed canal (with auxiliary canals). Other characiforms with a bone-enclosed canal include members of the Citharinidae and Distichodontidae (see Vari 1979), *Lepidarchus* (see Roberts 1966), *Acestrorhynchus* and *Ctenolucius* (see Roberts 1969), and *Paracheirodon* (see Weitzman and Fink 1983). A partly or completely open canal apparently occurs in some characiforms; however, this appears to be the exception. For example, in the Gasteropelecidae (three genera) the canal is open along the ventral limb in *Thoracocharax* and *Gasteropelecus* whereas it is completely open in *Carnegiella* (see Weitzman 1954). However, because the gasteropelecids are highly specialized characiforms, and because most other Ostariophysi have a closed canal, I conclude that the open canal in this family is simply an autapomorphy.

The fossil evidence also supports the hypothesis that a bone-enclosed canal is primitive for the Ostariophysi. The canal is enclosed in bone in the three ostariophysans (*Judeichthys*, *Ramallichthys*, and *Lusitanichthys*) that Gayet (1985, 1986) described from the marine Upper Cretaceous, opening to the exterior via a pore at each end of the bone, and via pores at the end of short to moderately short auxiliary canals that lead off of the main canal. A similar character state is found in *Chanoides*, described from marine Eocene deposits by Patterson (1984a). However, in this genus the auxiliary canals are more numerous and longer. The fact that Patterson considers *Chanoides* to be the sister group of all Recent Otophysi (the Cypriniformes + Characiformes + Siluriformes) suggests that the common ancestor of the Otophysi might have had a similar character state.

Clupeomorpha. A bone-enclosed lateral sensory canal (with numerous long auxiliary canals leading off of the main canal) was probably present in the common ancestor of the Clupeomorpha because this character state is present in the oldest (Lower Cretaceous), and morphologically the most primitive clupeomorphs, as well as in the most primitive extant species.

The extinct genera *Erichalcis* (Lower Cretaceous), *Armigatus* (Upper Cretaceous), *Diplomystus* (Upper Cretaceous to Eocene), and *Ellimmichthys* (Lower Cretaceous) are all more primitive morphologically than the extant species and represent the oldest known clupeomorphs (see Patterson 1967b; Forey 1973b, 1975; Grande 1982a, 1985). The extinct Upper Cretaceous genus *Ornategulum* was once thought to be the sister group of all the other clupeomorphs (see Forey 1975; Grande 1982a) but on the basis of new and better-preserved material Grande (1985, p. 238) states that it "is probably not a clupeomorph" and places it in the Clupeocephala (the Clupeomorpha + Euteleostei) *incertae sedis*. In Grande's (1985) new scheme *Erichalcis* is the sister group of the other clupeomorphs and *Armigatus*, *Diplomystus* + *Ellimmichthys*, and the extant clupeomorphs (the Clupeiformes) form an unresolved trichotomy. All five extinct genera have a bone-enclosed canal with numerous, long auxiliary canals (pers. obs. of *Diplomystus*; also see the aforementioned authors). Also, and perhaps significantly, a similar canal is found in the extinct species *Leptolepides sprattiformis* (Upper Jurassic), which Patterson and Rosen (1977) consider to be the sister group of the Clupeocephala (Clupeomorpha + Euteleostei).

The interrelationships of the extant clupeomorphs (the Clupeiformes) are poorly known; however, most workers place the Denticipitidae (=Denticipitoidei), containing one extant and one similar extinct species, as the sister group of the other extant clupeomorphs (see Greenwood 1968; Lauder and Liem 1983; Grande 1985). Unfortunately, denticipitids are specialized in several ways, one of which is the shape of the preoperculum and its canal (this appears to be an autapomorphy of the family since a similar preoperculum is not found in any other clupeomorphs, extinct or extant). The preopercular canal is enclosed in bone on the dorsal limb, has a few auxiliary canals at the intersection of the two limbs, and forms a partly open trough on the ventral limb intersected by bridges of bone. Greenwood (1968) noted similarities between this preoperculum and certain osteoglossomorphs (especially *Scleropages* and *Osteoglossum*).

The interrelationships of the other extant clupeomorphs, the clupeoids, are uncertain (see Lauder and Liem 1983). Because of this and because the preopercular canal in this assemblage shows considerable variation, it is difficult to tell what is the primitive character state for the Clupeoidei. However, the observation that the outgroups of this assemblage have a bone-enclosed canal, as do a number of clupeoids, suggests that a closed canal is the primitive character state, and that the partly or completely open canal found in numerous species is secondarily derived from an ancestor with a closed canal. For example, a bone-enclosed canal with moderately long auxiliary canals is found in the clupeoids *Dussumieria* and *Etrumeus* whereas in *Chirocentrus* the auxiliary canals are lacking and there are pores along the main canal (all pers. obs.). Most clupeoids I examined (which included specimens from all major groups) had a partly closed canal; usually the canal on the ventral limb was completely open and the dorsal limb showed various degrees of closure, for example: *Ilisha, Odontognathus, Alosa, Dorosoma, Nematalosa, Hyperlophus, Harengula,* and

Clupea (see Fig. 49). In the extinct genus *Knightia* (Palaeocene-Eocene) the canal on the dorsal limb appears to be closed, whereas that on the ventral limb is open (pers. obs.), an observation that corroborates Grande's (1982b) hypothesis that this genus belongs in the Clupeoidei and is not related to †*Diplomystus* (which has a bone-enclosed canal with numerous auxiliary canals). A completely open canal (posterior to a well-developed anterior flange), similar to that found in the higher teleosts, was present in *Jenkinsia* (pers. obs.), and all the engraulids I examined (*Anchoa, Amentum, Cetengraulis, Thryssa,* and *Engraulis*).

Elopomorpha. A bone-enclosed canal was almost certainly present in the common ancestor of the Elopomorpha. Almost all fossil species (the fossil record extends to the Upper Jurassic), and most primitive extant species, have a bone-enclosed preopercular canal that opens to the exterior via a pore at each end of the bone, and via pores that are found directly along the ventral part of the main canal (pers. obs of *Elops* and *Megalops*, see Fig. 48; also see Goody 1969b; Forey 1973a, 1973c; Greenwood 1977). Distinct auxiliary canals are not present, a character state that is derived relative to the state with auxiliary canals, and may be an elopomorph autapomorphy (also see Forey 1973a, 1973c). Auxiliary canals, however, may have been present in the common ancestor of the Elopomorpha since some species belonging to the oldest known (Upper Jurassic) elopomorph genus, *Anaethalion*, apparently have a few according to Forey (1973a, p. 39).

Some elopomorphs (members of the family Albulidae, *sensu* Nelson 1984) have a canal that is completely open posterior to an anterior flange, including: *Albula, Pterothrissus,* and species belonging to the Upper Cretaceous fossil genera *Istieus* and *Lebonichthys* (see Forey 1973a). However, because the Albulidae are a relatively derived lineage, because the primitive sister group of the Albulidae (the extinct family †Osmeroididae) has a bone-enclosed canal with pores along it (except for †*Osmeroides latifrons*, in which the canal along the ventral limb is open), and since the other primitive elopomorphs have a bone-enclosed canal, it is more parsimonious to conclude that the open canal in the Albulidae was secondarily derived from an ancestor with a closed canal, and that it is an albulid autapomorphy (see Greenwood 1977; Forey 1973a).

Osteoglossomorpha. The preopercular lateral sensory canal shows some variability within the Osteoglossomorpha (pers. obs. of the osteoglossoids *Osteoglossum* and *Pantodon* and the notopteroids *Xenomystus*, *Hiodon*, and †*Eohiodon*; also see Gaudant 1968; Wilson 1974, 1980; Taverne 1977, 1978, 1979); however, evidence suggests that a bone-enclosed canal with auxiliary canals leading off of the main canal was probably present in the common ancestor of the group.

There are essentially two character states of the preopercular canal in the Osteoglossomorpha (excluding the highly specialized Mormyridae, *sensu* Lauder and Liem 1983). In *Osteoglossum*, *Scleropages*, *Pantodon*, the three notopterid genera, and the four Eocene fossil genera *Phareodus*, *Phareoides*, *Brychaetus*, and *Musperia* (all four of which are considered to be closely related to *Osteoglossum* and *Scleropages* by Taverne 1977) the canal on the dorsal limb is enclosed in bone, whereas the canal on the ventral limb is open and trough-like (in some genera bridges of bone extend from the unusually wide anterior flange to the lateral surface of the canal). The other character state is found in *Arapaima*, *Heterotis*, *Hiodon* (see Fig. 47), the Eocene fossil *Eohiodon*, and the Upper Jurassic fossil *Lycoptera*. In these genera the entire canal is enclosed in bone with auxiliary canals leading off of the main canal (except in *Arapaima*, in which pores open directly along the main canal). I suggest that a bone-enclosed canal with auxiliary canals was present in the common ancestor of the Osteoglossomorpha and that the partly open canal found in some was secondarily derived from such an ancestor. First, the oldest known osteoglossomorph (by far), *Lycoptera* has the former character state. Secondly, the primitive outgroups of the Osteoglossomorpha (all other lower teleosts) and the more derived Elopomorpha, Clupeomorpha, Ostariophysi, and Esocoidei + Salmonidae have a bone-enclosed canal. Also, Taverne (1979, fig. 13) illustrates the upper Palaeocene genus *Opsithrissops*, which he considers to be related to *Osteoglossum* and *Scleropages* (which have a partly open canal), as having what appears to be a bone-enclosed canal with auxiliary canals.

Early Fossil Teleosts. The Osteoglossomorpha is the most primitive teleostean group with living representatives. The oldest (Middle Triassic) and morphologically the most primitive teleosts are represented only by fossils. These extinct species have been assigned at various times to the following taxa, not all of which are holophyletic (in order of increasing primitiveness): Ichthyodectiformes, Leptolepidiformes, Pholidophoriformes, Aspidorhynchiformes (= Aspidorhynchidae), and Pachycormiformes (= Pachycormidae) (see Patterson and Rosen 1977; Lauder and Liem 1983; Nelson 1984). The Ichthyodectiformes are hypothesized to be holophyletic whereas the Leptolepidiformes and Pholidophoriformes are not (see Patterson and Rosen 1977).

Extensive information was available concerning the character states of the preopercular canal in these lower teleosts. Because all species (without exception) had a bone-enclosed canal that opened to the exterior via a pore at each end of the preoperculum and via pores at the end of numerous, long auxiliary canals (nineteen in one specimen of *Pholidophorus bechei*, see Nybelin 1966) that lead off of the main canal (refer to Saint-Seine 1949; Griffith and Patterson 1963; Nybelin 1966, 1974; Wenz 1967; Patterson and Rosen 1977; Arratia 1981; Schaeffer and Patterson 1984) this is undoubtedly the primitive character state for the Teleostei.

Summary. An open, bony, lateral sensory canal on the preoperculum may be a synapomorphy uniting the osmeroids, galaxioids, and argentinoids with the higher teleosts (the neoteleosts). Some members of these lineages have a bone-enclosed canal (the primitive character state for the Teleostei), but it appears that this character state was ultimately derived from an ancestor within this assemblage with an open canal. The oldest fossils, and the primitive members of the major lineages in this assemblage, have an open canal or a variant of it (e.g., the Beryciformes). The opposite condition is found in the esocoids, salmonids, and lower teleosts. In these fishes, the oldest fossils and the most primitive extant species have a bone-enclosed canal (usually with auxiliary canals). Although an open canal has evolved independently in a number of lower teleostean species, it is usually in the more derived lineages, the ancestors of which appear to have had a bone-enclosed canal.

RECENT ALTERNATE HYPOTHESES OF EUTELEOST RELATIONSHIPS; A CRITIQUE.

Fink and Weitzman (1982) and Fink (1984b) recently suggested that the Salmonidae may form the sister group of the Neoteleostei on the basis of sharing a similar occipital condyle with the higher teleosts, and because some salmonids possess cartilaginous structures that they believed were homologous with the rostral cartilage found in the neoteleosts. Partly in response to these claims, Rosen (1985) presented a detailed account of the anatomy of the occipital region and the rostral cartilage in the euteleosts, and concluded that these similarities are probably convergent, a conclusion that my own observations corroborate.

Fink and Weitzman (1982) united the neoteleosts partly on the basis of their sharing an occipital condyle that is composed of both the basioccipital and the exoccipital bones. Rosen (1985) termed this structure a tripartite occipital condyle because there are three articular surfaces, one on the basioccipital (ventral) and one on each exoccipital (dorsal). In primitive teleosts the entire occipital condyle is formed by the basioccipital. I agree, as does Rosen (1985), that a tripartite occipital condyle is a synapomorphy of the Neoteleostei; however, Fink and Weitzman (1982) also state (p. 76) that "In salmonids, the neurocranial articulation is virtually the same as that of neoteleosts, with the basioccipital and exoccipitals articulating with the anterior vertebra, and it may be that the two are sister groups." Upon closer examination it appears that a distinct tripartite occipital condyle is present only in the subfamily Salmoninae within the Salmonidae, and that it is probably a salmonine autapomorphy (assuming that the Salmonidae are holophyletic, for which there is evidence) and convergent with the feature in the neoteleosts.

In the Coregoninae (the sister group of the Thymallinae + Salmoninae) all workers agree that *Coregonus* and *Stenodus* have an occipital condyle composed only of the basioccipital (pers. obs.; also see Pokrovsky 1966; Fink 1984b; Rosen 1985). However there is some disagreement as to the character state in *Prosopium* (hypothesized by most workers to be the sister group of the other two coregonine genera) and *Thymallus*. Fink (1984b) claimed that the latter two genera had a tripartite condyle, as did ~~the~~ Salmoninae, and because of this the tripartite state was primitive for the Salmonidae, and could be used to link the Salmonidae with the Neoteleostei. However, according to Rosen (1985) there was no exoccipital participation in the joint surface in either *Prosopium williamsoni* or *P. cylindraceum* (see his figs. 8 and 13), and my own observations of *P. williamsoni* (UAMZ 518, 3400, 2828, 3320; 32.1, 77.4, 98.1, 143.2 mm SL, respectively) confirm this. The fossil record also supports this view. Smith (1975) described the extinct Pliocene species *Prosopium prolixus* and illustrated (his fig. 7H) an occipital condyle in which only the basioccipital appears to contribute to the articular surface.

Fink and Weitzman (1982) and Fink (1984b) also claimed that the exoccipital contributed to the occipital condyle in *Thymallus*. However, again Rosen disagreed with this, stating that (p. 8) "the condition in *Thymallus* is hardly different from that of *Albula* (fig. 9) and *Pterothrissus*, among other teleosts, in which only a small extension of the exoccipital is visible posteriorly without noticeably affecting the shape of the basioccipital." My own observations tend to confirm Rosen's view and more or less agree with his fig. 7B. The articular surface of the condyle in *Thymallus* appears to be formed entirely by the basioccipital (pers. obs. UAMZ 3449, 3425; 67.2, 95.2 mm SL, respectively); however, the section of the basioccipital that extends dorsally between the first vertebra and the exoccipitals to form the articular surface is very thin and it appears that if it were lost, contact with the exoccipitals would occur. In this sense the state in *Thymallus* might be interpreted as somewhat intermediate. However, unlike the salmonines, the first vertebra lacks articular facets for the reception of the exoccipital condyles and in this sense resembles the coregonines.

The character state of the occipital condyle in the salmonines is unlike that in *Thymallus* or the coregonines and appears to be a salmonine autapomorphy. All extant salmonines have a well-developed triple joint in which two large, and separate, exoccipital condyles (one on each exoccipital) contact correspondingly large facets on the anterodorsal surface of the centrum of the first vertebra (pers. obs.; also see Pokrovsky 1966; Rosen

1985). The basioccipital forms only the ventral half of the joint, lacking the dorsal extension at its posterior end that fits between the exoccipital and the first vertebra to form the dorsal half of the condyle in the other salmonids and primitive teleosts. *Eosalmo driftwoodensis*, the oldest known fossil salmonid (Eocene) may have a tripartite occipital condyle (pers. obs. UAVP 13482, 379 mm SL), an observation that if true would corroborate Wilson's (1974) placement of it in the Salmoninae. Although all recent salmonines have a tripartite occipital condyle this is not true of all fossil species since in the Pliocene salmonine *Smilodonichthys rostratus* the condyle is formed only by the basioccipital and resembles that in the coregonines, especially *Coregonus* and *Stenodus* (see Cavender and Miller 1972; Rosen 1985). Cavender and Miller considered *Smilodonichthys* to be closely related to the extinct salmonine genus *Oncorhynchus* which has a distinct tripartite condyle.

In light of these facts it appears that a tripartite occipital condyle is diagnostic only of a derived subgroup within the Salmonidae, the Salmoninae (and even then it is lacking in some fossils) and as such does not link the Salmonidae with the neoteleosts but is an example of convergence. Further evidence for convergence is provided by the observation that a similar tripartite occipital condyle has developed independently in other teleosts, including the osteoglossomorph *Hiodon* (pers. obs.), the clupeomorph *Denticeps* (see Greenwood 1968), and debatably in the salmoniform *Lepidogalaxias*. Even more significant is Rosen's (1985) observation that the tripartite condyle in the salmonines is derived over that in the primitive neoteleosts, most closely resembling that in various advanced percomorphs such as *Lutjanus*. As such it is difficult to imagine the salmonine occipital condyle giving rise to the condition found in primitive neoteleosts since the two character states are anatomically very different. Rosen (1985) hypothesizes that a character state similar to that found in some osmerids (e.g., *Osmerus*) could more easily have given rise to the primitive neoteleostean condition, adding credibility to his more recent hypothesis that the osmerids are the sister group of the neoteleosts.

The other synapomorphy that Fink and Weitzman (1982) used to unite the salmonids with the neoteleosts was the presence in some salmonids of paired cartilaginous nodules, lying between the ethmoid and premaxillae, that they believed were the precursor of, and homologous with the single median rostral cartilage found in the neoteleosts. They speculated that fusion of these nodules would result in a structure identical with a rostral cartilage (which they consider to be a synapomorphy of the Neoteleostei), a hypothesis that Fink (1984b) seems to confirm when he examined small juvenile cichlids and noted (p. 204) that "the rostral cartilage appears to develop ontogenetically from bilateral cartilage bodies which fuse at the midline." However, Fink and Weitzman's synapomorphy has a number of serious drawbacks (also see Rosen 1985). Firstly, cartilaginous nodules are not present in all salmonids, and within the family the distribution is mosaic: in the Coregoninae they are present in *Prosopium* (pers. obs) but absent in *Coregonus* (pers. obs.; also see Fink 1984b) and *Stenodus* (see Fink 1984b); they are absent in *Thymallus* (pers. obs.); and within the Salmoninae they are present in *Salma trutta* (pers. obs.), *Salmo gairdneri* (pers. obs.; also see Rosen 1985), and *Salvelinus fontinalis* (pers. obs., contrary to Rosen who stated that he did not find these cartilages in any species of *Salvelinus* that he examined), but absent in *Salvelinus namaycush* (pers. obs.) and *Oncorhynchus nerka* (pers. obs.). Because of this mosaic distribution and the lack of a well-tested hypothesis of salmonid interrelationships it is unwise to speculate that nodules were present in the common ancestor of the Salmonidae and then lost in some species. It seems just as likely, or even more likely, that they evolved independently in various salmonid lineages. Virtually identical cartilages were also found in one osmerid that I examined, *Osmerus mordax* (but absent in all others), suggesting that they may be subject to independent development (also see Rosen 1985). Fink and Weitzman (1982) also pointed out that similar, but more laterally located "cartilage bodies" are found between the palatine, maxilla, and ethmoid in a number of other primitive teleosts (including various ostariophysans, osteoglossomorphs, and esocoids).

The main salmonid with cartilaginous nodules that Fink and Weitzman (1982) cite to support their hypothesis is *Prosopium* (apparently because it belongs to the most primitive salmonid subgroup, of which it is hypothesized to be its most primitive member). They state (p. 86) that "Among the fishes we examined, the largest of these bodies were found in

Prosopium; in this fish they are paired blocks which meet at the midline." In none of my specimens, however, did the cartilages meet medially (although they are relatively close to each other). Instead, they are separated by a narrow anterior projection of the ethmoid cartilage, suggesting that the nodules may simply represent a fragmentation of the anterior end of the ethmoid block, and are an autapomorphy of this lineage. In the two smallest specimens of *Prosopium williamsoni* that I examined (UAMZ 2828, 518; 29.5, 32.1 mm SL, respectively), nodules were absent, and the anterior extension of the ethmoid block was broader than in the larger specimens (UAMZ 3400, 2828, 3369; 77.4, 98.1, 151.5 mm SL, respectively). Larger specimens of *Prosopium* also exhibited a number of other types of reduction including loss of teeth on the maxillae, premaxillae, vomer, and palatine; a narrowing of the anterior end of the snout; and a greatly reduced palatine (more so than in the other coregonines). Although these trends also are found in the other coregonines they are more pronounced in *Prosopium*, and at least in this instance the skeleton of *Prosopium* appears to be more derived than the other coregonines.

Further evidence suggesting that fragmentation of the ethmoid block may occur and result in separate cartilaginous nodules is provided by another teleost, *Plecoglossus*, in which even more extreme morphological changes occur in the region of the snout during ontogeny. In a small specimen of *Plecoglossus* (UAMZ 5668, 55.5 mm SL) the ethmoid cartilage was in one piece; however, in larger specimens (UAMZ 5669, 3505; 77.9 and 160.6 mm SL, respectively) the anterolateral section is lost with only a small, separate cartilaginous knob remaining that is attached to the mid anterior edge of the vomer.

It also appears doubtful to me that the cartilaginous nodules found in some salmonids could have given rise to the rostral cartilage of the higher teleosts since there is such a large morphological difference between the two structures. Rosen (1985) also pointed out that the rostral cartilage in higher teleosts does not necessarily form by fusion of paired cartilaginous nodules as noted by Fink (1984b), but may also arise from three distinct cartilages (see his figs. 42 and 43). In addition, Rosen does not appear to agree that the rostral cartilage, as defined by Fink and Weitzman (1982), is a synapomorphy of the Neoteleostei since he noted a number of exceptions within the lower neoteleosts, especially within the Stomiiformes. Instead he redefines it in such a way that it unites all neoteleosts excluding the stomiiforms and alepisauroids.

In conclusion, I conclude that the Salmonidae are not the sister group of the Neoteleostei, and that the two similarities that Fink and Weitzman (1982) proposed to link the two groups are the result of convergence. I came to a similar conclusion in an earlier section concerning Fink's (1984b) hypothesis that *Lepidogalaxias* might form the sister group of the Neoteleostei.

In addition to reviewing the anatomy of the occipital region and rostral cartilage in the euteleosts, and discussing some of Fink and Weitzman's earlier hypotheses, Rosen (1985) presented a new scheme of euteleostean relationships based on his new evidence and that from other sources. On his cladogram he still considers the Neoteleostei to be holophyletic (albeit rearranged internally somewhat). He rejects Fink and Weitzman's hypothesis that the Salmonidae are the neoteleostean sister group and states (p. 34) that "an equally good case can be made for the Osmeridae, which incidentally show the same spottiness of character distribution. For example, *Spirinchus* shows the primitive neoteleostean cervical gap between the occiput and the first vertebra ... and has, as a consequence, exoccipitals that have exposed posterior condyle-like faces, and *Osmerus mordax* has the paired premaxillary cartilages ... developed to the same extent as they are in *Prosopium williamsoni* ... But if we must make a choice from amongst the old 'salmoniforms' for a neoteleostean sister group, then the Osmeroidei, or at least *Spirinchus*, is a better choice than the salmonids." On his cladogram he places the "osmeroids" as the sister group of the neoteleosts (parentheses apparently because he now questions the holophyly of the osmeroids). Although Rosen's "osmeroids" appear to include the galaxiids and aplochitonids (i.e., the osmeroids *sensu* Fink and Weitzman 1982), this is not completely clear from his text. Rosen (p. 52) unites the osmeroids with the neoteleosts on the basis of three synapomorphies: the presence of "Acellular endoskeletal bone," "A toothed alveolar process on the premaxilla which lies under the maxilla, completely so in galaxioids," and "In the caudal skeleton, NPU2 [the neural spine on the second preural centrum] is shorter than NPU3 [the neural spine on the third preural centrum] and bladelike."

The value of Rosen's first character state (acellular bone) is difficult to evaluate since he states that only two osmeroids were examined for bone type, *Osmerus mordax* and a species of *Galaxias*. However, apparently the osmerids *Hypomesus pretiosus* and *Thaleichthys pacificus* also have acellular bone (see Moss 1965), and furthermore, in a more recent paper Parenti (1986) discusses the use of this character in detail, adding credibility to Rosen's hypothesis (see pages 423-424 for a discussion of her paper).

Rosen's second synapomorphy, ("A toothed alveolar process on the premaxilla which lies under the maxilla, completely so in galaxioids") is rather difficult to evaluate because of its vagueness and lack of background data. He mentions this feature on page 37 when he states that in osmeroids "The premaxillary has an alveolar process of sorts ... under which there are no maxillary teeth ... in other words, they show a simple tandem arrangement of these bones as opposed to their more primitive serial alignment in salmonids." This character appears to be more of a teleostean trend towards exclusion of the maxilla from the gape by the premaxilla rather than a crucial synapomorphy, an observation that appears to be confirmed if one examines an earlier paper by Rosen (1982) in which he depicts a gradual transformation series of the anatomical changes of the two bones and their relation to one another in the Teleostei (see his figs. 9 and 10). Although it is true that the osmeroids and galaxioids (including *Lepidogalaxias*) do have an alveolar process that is similar to that in some of the lower neoteleosts (in particular, the Stomiiformes) so do most of the Alepocephalidae that I examined (but not the other Argentinoidei). If one accepts Rosen's synapomorphy, then one could conceivably expand it to include the Argentinoidei (if the character state in the alepocephalids is primitive for the Argentinoidei), in which case the osmeroids + galaxioids + argentinoids would form the sister group of the Neoteleostei, as I hypothesize.

Rosen's final synapomorphy uniting the osmeroids with the neoteleosts (the neural spine on the second preural centrum is shorter than the neural spine on the third preural centrum and is bladelike) is also problematical because there is doubt regarding the polarity of the character (contrast Rosen 1973 and 1985 with Patterson 1968b and 19[illegible] short laminar spine is also present in various primitive salmonids such as *Prosopium* (pers. obs.; also see Rosen's fig. 44), *Coregonus* (pers. obs.), and *Stenodus* (see Kendall and Behnke 1984) and appears to be be present in the alepocephalid *Bathylaco* (see Markle 1976, fig. 13A). A similar structure is also found in various extinct primitive teleosts illustrated by Patterson and Rosen (1977), including *Thrissops formosus* (see their fig. 14), *Crossognathus sabaudianus* (their fig. 21), *Leptolepis coryphaenoides* (their fig. 33B), *Diplomystus longicostatus* (their fig. 37), various species of *Anaethalion* (their figs. 39, 41, 42, 43), and "*Leptolepis*" *talbragarensis* (their fig. 46A), plus in the extant elopomorphs *Elops hawaiensis* (pers. obs.) and *E. lacerta* (see Monod 1968, figs. 20-24). In addition, within the Neoteleostei there are numerous species that have a long and relatively narrow neural spine on the second preural centrum that is virtually the same length as that on the third preural centrum (i.e., the primitive character state according to Rosen) including: the cetomimoids and both Recent and fossil polymixioids (see Rosen 1973), all the percopsiforms (Recent and fossil) illustrated by Rosen and Patterson (1969), and the stomiiforms (see Weitzman 1974, Fink and Weitzman 1982). A similar character state is also found in the Galaxiidae, Aplochitonidae, Lepidogalaxiidae, and various salangids among the osmeroids (pers. obs.; also see figures in Rosen 1974 and Roberts 1984). The character may also vary within a species since in the osmerid *Osmerus eperlanus*, Patterson (1970, p. 273) noticed that the neural spine on the second preural centrum was short in one specimen but long in two others.

In conclusion, the mosaic distribution of this character within the Teleostei and the resulting controversy regarding its polarity (contrast Rosen 1973 with Patterson 1970) limits its utility as a synapomorphy uniting the osmeroids with the neoteleosts.

The phylogenetic position of the other salmoniforms are not discussed in any great detail in Rosen's (1985) paper. He places the Salmonidae as the sister group of the osmeroids + neoteleosts on the basis of two synapomorphies (p. 52): "Paired stegural outgrowths of the first uroneural" and "At least some parts of the endoskeleton with aceullar bone." In both cases insufficient information is provided to properly evaluate the characters. The former synapomorphy in particular is too vaguely defined to be of any value, a number of esocoids and argentinoids might be interpreted as having "Paired stegural outgrowths of the first uroneural" (see figs. in Rosen 1974 and Markle 1976, respectively).

Rosen does not provide any new information regarding the phylogenetic position of the Argentinoidei and Esocoidei. He considers the Argentinoidei, Ostariophysi, and salmonids + osmeroids + neoteleosts to form an unresolved trichotomy and unites them on the basis of their sharing "an adipose dorsal fin". This entire assemblage in turn forms an unresolved trichotomy along with the esocoids and clupeomorphs (refer to Fig. 2D). The adipose fin character must be treated with much suspicion since this fin is absent in numerous salmoniforms and higher teleosts, and might just as easily have been lost in the esocoids, especially in light of the posterior position of the dorsal fin in this group.

In a recent paper Parenti (1986) discusses bone type in euteleostean fishes and its bearing on their interrelationships. She concludes that acellular bone (identified by the lack of enclosed osteocytes in mature matrix) is derived relative to cellular bone in the Teleostei, and that its presence in the Esocae (= Esocoidei), Osmeroidei (*sensu* Fink and Weitzman 1982), and Neoteleostei is reason for uniting them into a single holophyletic group (however, she does not suggest how these three taxa are related to one another). As a rule (there are exceptions), cellular bone is typical of lower teleosts (the osteoglossomorphs, elopomorphs, clupeomorphs, ostariophysans, and the Argentinoidei among the salmoniforms) and acellular bone is typical of higher teleosts. The Salmonidae are apparently intermediate because they have both cellular (mostly) and acellular bone (also see Moss 1965). Partly for this reason Rosen (1985) considers the Salmonidae to be the sister group of the osmeroids + neoteleosts.

Parenti's new data are not completely inconsistent with my hypothesis of salmoniform relationships (refer to Fig. 94). I agree with Parenti that the presence of acellular bone is probably the derived character state. However, it could be argued that the development of acellular bone in the euteleosts is just a trend, and that it has developed independently in various salmoniform lineages, and in the Neoteleostei as well. Interpreted in this way the presence of acellular bone would be an autapomorphy of the Esocoidei, and a synapomorphy uniting the osmeroids with the galaxioids, hence resolving my trichotomy involving the osmeroids, galaxioids, and Argentinoidei. The mixture of cellular and acellular bone in the salmonids could be viewed as a second derived character state, and an autapomorphy of the Salmonidae. Evidence that acellular bone has developed independently is provided by the observation that it is found in several unrelated lower teleostean lineages, including: the osteoglossomorph *Hiodon* (see Moss 1965), the clupeomorph *Anchoviella* (see Moss 1961), and the ostariophysan *Trichomycterus* (see Kölliker 1859). Like the salmonids, the elopomorph *Albula vulpes* has both acellular and cellular bone (see Parenti 1986).

B. RELATIONSHIPS: MUSCLES OF THE SUSPENSORIUM

In addition to studying the bones of the suspensorium I examined the muscles that are associated with it. This information was used to test the phylogeny I had reconstructed using the bones and to help clarify interfamilial relationships. It also provided basic anatomical information that was lacking, and yielded insight into the functional significance of some of the osteological character states.

In the following account I will first discuss a morphocline involving the character states of the *adductor mandibulae* and its tendons and ligaments, and then present the shared derived character states that unite various taxa. The term tendon is usually synonymized with ligament, primarily because these two elements are not readily distinguishable in this group.

MORPHOCLINE: ADDUCTOR MANDIBULAE

The largest, most variable, and phylogenetically speaking, the most interesting muscle of the suspensorium is the *adductor mandibulae*. It is primarily responsible for closing the jaws. It originates from the lateral surface of the suspensorium and inserts onto the lower jaw, and in some species, onto the upper jaw.

Morphoclines depicting the hypothetical pathways of evolutionary change of the *adductor mandibulae* within the salmoniforms are presented in Figs. 99-103. Although these morphoclines are not a phylogeny, they suggest possible evolutionary pathways within the salmoniforms, from a primitive ancestral condition to more derived descendant states.

The primitive pattern of the *adductor mandibulae*, from which the patterns in the salmoniforms were derived, was probably similar to that found in the more generalized and primitive members of the primitive outgroups, represented by the Clupeomorpha and Elopomorpha (see Fig. 99). The pattern in the Ostariophysi is too specialized to be ancestral, and apparently is an autapomorphy of this assemblage (also see Fink and Fink 1981; Howes 1985).

Primitively, there is only one external division of the *adductor mandibulae*, termed section A2. Section A2 inserts onto the lower jaw (primarily on the medial surface) and is connected to the maxilla at the same time via the maxilla-mandibular ligament (or *ligamentum primordium*, labelled as sections L.x, L.y, and L.z on Fig. 99). The supramaxillary ligament (labelled L.smx on Fig. 99) extends posteriorly from the anterior tip of the posterior supramaxilla (primitively there are two) to join the maxilla-mandibular ligament. The reasons for selecting this character state as the primitive one for the elopomorphs, clupeomorphs, and salmoniforms are outlined in a previous section.

There are three main patterns of the *adductor mandibulae* in the Salmoniformes, each derivable from the primitive pattern: one in the Esocoidei and most Salmonidae; one in the osmeroids and galaxioids; and one in the Argentinoidei (see Figs. 99-103).

Esocoidei

In the Esocoidei (Esocidae + Umbridae) the *adductor mandibulae* inserts directly onto the lower jaw, and unlike the primitive condition, has no ligamentous connection with the maxilla-mandibular ligament (see Fig. 99). As in the primitive condition, the Esocidae have a well-developed maxilla-mandibular ligament (L.mm); however, unlike the ancestor, it is not connected with the *adductor mandibulae* (i.e., it lacks section L.z). The Umbridae have no maxilla-mandibular ligament. A single, oval supramaxilla is present in the Esocidae (moderately large), *Novumbra* (small), and *Dallia* (tiny), but absent in *Umbra*; however, no esocoid has a supramaxillary ligament (supramaxillae are not drawn on Fig. 99). All esocoids have a coronoid-maxilla ligament (L.cm) that extends from the lateral surface of the coronoid process (dentary and/or angulo-articular bones) of the lower jaw to the middle or posterior third of the maxilla. This ligament is unique to the esocoids and separate from, and not homologous with, the maxilla-mandibular ligament (both occur together in the Esocidae).

The pattern of the *adductor mandibulae* in the esocoids could be derived from the primitive condition by initially losing the supramaxillary ligament, losing the connection of the maxilla-mandibular ligament with the *adductor mandibulae* (i.e., losing section L.z), and developing the unique coronoid-maxilla ligament, as found in the Esocidae (see Fig. 99). The pattern in the Umbridae could then be derived from the esocid pattern by initially losing the rest of the maxilla-mandibular ligament (i.e., losing section L.x-L.y), as found in *Novumbra hubbsi* and *Umbra krameri*. The pattern in *Umbra limi* and *Umbra pygmaea* could be derived from the pattern in *Novumbra hubbsi* and *Umbra krameri* by developing a tendon (L.A2) that extends from the *adductor mandibulae* to the lateral surface of the angulo-articular bone of the lower jaw. The pattern in *Dallia pectoralis* could also be derived from a pattern like *Novumbra hubbsi* and *Umbra krameri* by enlarging section A2 of the *adductor mandibulae*, and have it develop a dorsomedial subdivision (A2.dm).

Salmonidae

The pattern in the Salmonidae could be derived from the primitive condition by initially losing the supramaxillary ligament and retaining the maxilla-mandibular ligament and its connection to the *adductor mandibulae*, as found in *Prosopium* and *Stenodus* (see Fig. 100). All salmonids have only one supramaxilla and lack a distinct supramaxillary ligament.

The pattern in *Stenodus*, in which the ligamentous connection of the *adductor mandibulae* with the maxilla-mandibular ligament (i.e., section L.z) is present, but narrow, could be derived from the pattern in *Prosopium* by a reduction of section L.z.

The other salmonids (*Coregonus*, *Thymallus*, and the Salmoninae) resemble the esocoids in that the *adductor mandibulae* inserts directly (and only) onto the lower jaw. This state could be derived from a pattern similar to *Stenodus* by losing the ligamentous connection with the maxilla-mandibular ligament (i.e., losing section L.z). As in the Esocidae (but unlike the Umbridae), the aforementioned salmonids still retain part of the maxilla-mandibular ligament (section L.x-L.y). The pattern in most Salmoninae could then be derived from the pattern in *Coregonus*, *Thymallus*, or the salmonine *Brachymystax* by enlarging section A2 of the *adductor mandibulae*. The observation that *Brachymystax* has what appears to be the primitive character state of the *adductor mandibulae* (relatively small size) in the Salmonidae adds credibility to Norden's (1961) hypothesis that this genus may be the most primitive extant salmonine. In all the other salmonines that I dissected the *adductor mandibulae* was large and bulbous.

The similar pattern of the *adductor mandibulae* in the esocoids and many salmonids suggests a possible relationship between the two groups. However, these similarities are mainly between more derived salmonids and the esocoids. Two of the three genera in the Coregoninae (*Prosopium* and *Stenodus*), the most primitive salmonid subfamily, have an *adductor mandibulae* that is similar to the primitive condition (i.e., it is ligamentously connected to the maxilla via the maxilla-mandibular ligament). This includes *Prosopium*, which appears to be the most primitive genus in the Coregoninae (also see Norden 1961; Kendall and Behnke 1984). These observations suggest that the *adductor mandibulae* may have independently lost its ligamentous connection with the maxilla and mandible in the two groups, and therefore the similarity may not be indicative of relationship. Regardless, the pattern in the Esocoidei can hypothetically be derived from a pattern similar to that in *Prosopium* or *Stenodus* by initially losing the ligamentous connection between the *adductor mandibulae* and the maxilla-mandibular ligament (i.e., losing section L.z), and by developing a coronoid-maxilla ligament, as in the Esocidae (see Fig. 101).

Osmeroids and Galaxioids

The patterns of the *adductor mandibulae* in the osmeroid and galaxioid families form another group that can be derived from the primitive condition (see Fig. 102). The osmerids *Mallotus, Osmerus, Allosmerus,* and *Spirinchus starksi* have the primitive pattern of the *adductor mandibulae*. The pattern in the other osmerids (*Hypomesus* and possibly *Thaleichthys* and *Spirinchus thaleichthys*) is similar to that in the primitive condition except that the supramaxillary ligament has lost its connection with the maxilla-mandibular ligament. The latter character state is found in some salangids (*Salangichthys ishikawae*, among the salangids that I examined) and may be found in other salangids that possess a supramaxilla (three of the four salangid genera have a single supramaxilla, including *Protosalanx, Neosalanx*, and *Salangichthys*; the other genus, *Salanx* lacks one). All Osmeridae have one supramaxilla, unlike the primitive condition in which there are two (presumably the anterior supramaxilla has been lost in the osmerids and salangids).

The pattern in the Retropinnidae, Prototroctidae, some salangids (*Salanx*), and the Sundasalangidae differs from the Osmeridae and most salangids (probably) only in that the supramaxilla, and consequently the supramaxillary ligament, are lost. Because the pattern in these taxa is otherwise the same as in the outgroups (i.e., primitive), I do not consider it to be strongly indicative of closer relationship between them.

The pattern in the Plecoglossidae can be derived from the aforementioned retropinnid-prototroctid-salangid pattern. In the Plecoglossidae, section A2 of the *adductor mandibulae* has developed a dorsomedial subdivision (A2.dm) that passes medial to the *levator arcus palatini*. There is also a partial dorsolateral subdivision (A2.pa) adjacent to it that lies lateral to the *levator arcus palatini* and converges onto the same tendon (L.z). The anterior end of the maxilla-mandibular ligament has also developed a side branch that extends anteromedially to attach to the anterolateral surface of the palatine (a unique feature of the

Plecoglossidae among the salmoniforms).

The patterns found in the Lepidogalaxiidae, Galaxiidae, and Aplochitonidae can also be derived from the retropinnid-prototroctid-salangid pattern and corroborate the hypothesis, based on the bones of the suspensorium, that *Lepidogalaxias* is not an esocoid. In these three families the posterior part of the maxilla-mandibular ligament that attaches onto the lower jaw (section L.y on Fig. 102) is reduced in size so that the section extending directly from the *adductor mandibulae* to the maxilla (section L.x-L.z) is prominent. Also, there is a short, tough ligament (L) that extends from the middle of the medial surface of the posterior end of the maxilla to the coronoid process (dentary) of the lower jaw. Finally, the mandibularis branch of the trigeminal nerve (md V) passes medial to the *adductor mandibulae* before running medial to the lower jaw (versus passing lateral to the *adductor mandibulae* in most other salmoniforms). The character state in the Aplochitonidae and Galaxiidae can then be derived from the pattern in the Lepidogalaxiidae by having the dorsomedial part of the *adductor mandibulae* either partially subdivide as in the Aplochitonidae, or completely subdivide as in the Galaxiidae.

Argentinoidei

The patterns of the *adductor mandibuale* in the five argentinoid families can also be derived from the primitive condition (see Fig. 103). Initially, the posterior part of the maxilla-mandibular ligament, the part that attaches onto the lower jaw (section L.y), is lost, so that the *adductor mandibulae* inserts directly onto the maxilla via the remaining ligament (section L.x-L.z). The supramaxillary ligament (L.smx) is also lost, as is the anterior supramaxilla in some. These character states are found in most Alepocephalidae and some Platytroctidae. Perhaps significantly, three relatively primitive alepocephalids: *Rouleina, Narcetes,* and *Xenodermichthys*, possess a narrow, delicate "ligament" (a remnant of section L.y, in the process of being lost?) that extends from the posterior end of section L.x-L.z to the angulo-articular bone, as in the primitive condition (refer to Figs. 74, 75). The platytroctid, *Mirorictus* also has a similar "L.y-section", but it is better deve[illegible]efer to Fig. 85). No alepocephalid or platytroctid that I examined had what I would call a distinct supramaxillary ligament, except for the alepocephalid *Photostylus*. However, because the anterior ligaments in this genus are unusual in other ways, this may be an autapomorphy of the genus (see Fig. 79 and compare to Figs. 73-75).

The pattern found in most platytroctids and some alepocephalids can be derived from the aforementioned pattern by having the dorsolateral part of section A2 of the *adductor mandibulae* completely subdivide to produce a separate A1 subdivision that inserts ligamentously onto the upper jaw. Section A2 now inserts only onto the lower jaw (see Fig. 103). A separate A1 subdivision is present in only four (of twenty-five) alepocephalid genera: *Talismania, Binghamichthys, Bathylaco,* and *Leptochilichthys* (see Figs. 76-78 and Markle 1976) but was found in five of the seven platytroctid genera that I examined (the exceptions being *Mirorictus* and *Pellisolus*). The direction of evolutionary change is suggested by the fact that in some alepocephalids (*Alepocephalus*) the dorsolateral part of section A1 is partly subdivided (an incipient A1 subdivision ? see Fig 103).

In the Argentinoidea (Argentinidae + Bathylagidae + Opisthoproctidae) the *adductor mandibulae* is undivided (i.e., there is no A1 subdivision) and inserts only onto the lower jaw (see Fig. 103). There is no maxilla-mandibular ligament nor are there supramaxillae or a supramaxillary ligament. This pattern can be derived from that found in most Alepocephalidae (and some Platytroctidae) by losing the ligament that extends directly from the *adductor mandibulae* to the maxilla (losing section L.x-L.z, and having the muscle insert only onto the lower jaw), and by losing the supramaxillae. The *adductor mandibulae* also expands anteroposteriorly. The polarity is suggested by the character state in the Bathylagidae. In *Bathylagus pacificus* some of the anteroventral fibres of the *adductor mandibulae* converge onto what might be interpreted as a remnant of a maxilla-mandibular ligament (refer to Fig. 88). This thin and delicate ligament extends ventrally to the angulo-articular bone of the lower jaw, and to the middle of the medial surface of the maxilla. An even thinner "ligament" extends from the anterodorsal corner of the *adductor mandibulae* ventrally to the angulo-articular and anteriorly to end in loose connective tissue between the maxilla and lower jaw. However, these ligaments are of doubtful significance because of their unusual position and small size, and because the *adductor mandibulae* inserts mainly onto the lower jaw, as in the other Argentinoidea. Therefore, it appears that this "maxilla-mandibular" ligament is in the process of being lost and represents an intermediate condition between that found in most alepocephalids and the Argentinoidea.

Neoteleostei

The pattern of the *adductor mandibulae* in the higher teleosts is, as expected, variable and often complicated. However, primitively (e.g., in the Stomiiformes, Aulopiformes, and Myctophiformes) there is a distinct maxilla-mandibular ligament extending from the anterior end of the maxilla to the lateral surface of the angulo-articular bone. There are often two supramaxillae, plus a supramaxillary ligament that may or may not be connected with the posterior end of the maxilla-mandibular ligament. However, unlike the salmoniforms and lower teleosts, part of the *adductor mandibulae* usually inserts directly along the posterior end of the maxilla-mandibular ligament (in addition to inserting onto the lower jaw). In addition, the *adductor mandibulae* is almost always subdivided (e.g., see Figs. 92, 93; also refer to Rosen and Patterson 1969; Rosen 1973; Winterbottom 1974a).

The pattern of the *adductor mandibulae* in the primitive neoteleosts could conceivably be derived from one similar to that found in salmoniforms, that approach the primitive state (found in the clupeomorphs and elopomorphs), including: the salmonids *Prosopium* and *Stenodus*, the Osmeridae, some Salangidae, and perhaps the Retropinnidae, Prototroctidae, and some primitive alepocephaloids. Possible steps in this sequence might begin with the encroachment of the anterior fibres of the *adductor mandibulae* onto the maxilla-mandibular ligament, and then subsequent division of the muscle into the various subdivisions. The pattern found in other salmoniforms is more derived, and is less likely to have given rise to the neoteleost arrangement because more steps would be required to achieve the neoteleostean state. For example, in the Argentinoidea, the maxilla-mandibular ligament, and the supramaxillae and supramaxillary ligament would have to be reacquired (a reversal) and then the *adductor mandibulae* would have to encroach upon it.

SUMMARY OF SHARED DERIVED CHARACTER STATES OF THE MUSCLES OF THE SUSPENSORIUM

I did not find any shared derived character state that unites the families traditionally placed in the order Salmoniformes. However, within the order the muscles proved particularly useful in clarifying interfamilial relationships, helped to better define a number of subgroups, and served as a test of the phylogeny reconstructed using the bones. In most cases evidence from the muscles corroborated this phylogeny (for example, the myological evidence supports the hypothesis that the Esocoidei are holophyletic).

In the following account I will discuss the shared derived character states of the muscles of the suspensorium, and whether or not they corroborate or refute the hypothesis reconstructed using the bones.

ESOCOIDEI + SALMONIDAE

If we assume that the Esocoidei and Salmonidae are both holophyletic, the Esocoidei and Salmonidae can arguably be united on the basis of their sharing an *adductor mandibulae* that inserts directly onto the lower jaw and has no ligamentous connection with the maxilla (see Figs. 52-57, 59-61). Primitively, the *adductor mandibulae* inserts onto the lower jaw and is connected to the maxilla at the same time via the maxilla-mandibular ligament (e.g., see Figs. 62, 67, 91). All esocoids, and most salmonids (*Coregonus*, the Thymallinae, and the Salmoninae) share the derived character state. However, two salmonid genera, ***Prosopium*** (see Fig. 58) and *Stenodus* (see Fig. 100), have the primitive character state. Because ***Prosopium*** is thought to be the most primitive coregonine, and the Coregoninae are usually considered to be the most primitive of the three salmonid subfamilies (see Norden 1961; Cavender 1970; Kendall and Behnke 1984), it may be that the character state in *Prosopium* is primitive for the Salmonidae, and that the *adductor mandibulae* has independently lost its connection with the maxilla-mandibular ligament in the esocoids and most salmonids. Unfortunately, the intergeneric relationships of the Salmonidae are still uncertain, although most workers consider the family to be holophyletic (see Norden 1961; Cavender 1970; Fink 1984b; Kendall and Behnke 1984).

The Esocoidei and Salmonidae might also be united on the basis of their having lost the supramaxillary ligament that extends from the anterior tip of the supramaxilla to the lower jaw. However, because this character state is shared with numerous other salmoniforms (from each major assemblage), and is therefore prone to convergence, it is of little use in inferring phylogenetic relationship.

Overall then, the evidence from the muscles of the suspensorium weakly supports the hypothesis that the Esocoidei and Salmonidae form a clade.

Conclusions: The Phylogenetic Relationships of the Esocoidei

I tentatively accept the hypothesis that the Esocoidei and Salmonidae form a clade based on evidence from the suspensorium and its muscles. Some earlier workers such as Gosline (1960) and Weitzman (1967a) have suggested that the esocoids and salmonids may be related, and consider the two groups to be more primitive than the other salmoniforms; however, their data are difficult to evaluate because it is not particularly clear what evidence they are using.

The phylogenetic position of the esocoids has always been controversial, and is even more so today (refer to Gosline 1960; Weitzman 1967a; McDowall 1969; Nelson 1970a; Rosen 1973, 1974, 1985; Patterson and Rosen 1977; Fink and Weitzman 1982; Lauder and Liem 1983; Fink 1984b; Nelson 1984; Parenti 1986). All that can be said with certainty is that they are positioned somewhere at the base of the Euteleostei (the Ostariophysi + Salmoniformes +

Neoteleostei), and are relatively distantly related to the other salmoniforms. Even their position as euteleosts is questionable since they lack two of the three synapomorphies that Patterson and Rosen (1977) used to unite the group, and there is debate as to whether the third one applies to esocoids (see Rosen 1974, 1985). Rosen (1985) reflected this ambiguity by placing the esocoids, clupeomorphs, and euteleosts (minus the esocoids) as an unresolved trichotomy on his latest cladogram of euteleostean relationships (refer to Fig. 2D). However, this is not particularly satisfactory because he excludes the esocoids from the euteleosts solely on the basis of their lacking an adipose fin (the only synapomorphy that he uses to unite all the other euteleosts). The esocoids could not have an adipose fin because of the posterior position of the dorsal fin in all their members. In addition, an adipose has almost certainly been secondarily lost in numerous euteleosts with similar posterior dorsal fins (e.g., the alepocephaloids).

In an earlier paper Rosen (1974) placed the esocoids in the order Salmoniformes (at this time he considered the order to be holophyletic, although doubtfully so), but noted the uncertainty of their position when he stated (p. 310) that "The present evidence for regarding esocoids as members of the Salmoniformes is slight." In his preferred hypothesis of salmoniform relationships he considers the esocoids to be the primitive sister group of the other salmoniforms "on the basis of the exceedingly primitive aspect to the basihyal and basibranchial tooth plates and dentition" (p. 310). In Rosen's alternate hypothesis, based on evidence from the caudal skeleton, the esocoids are the sister group of the salmonids + osmeroids (my osmerids, plecoglossids, retropinnids, prototroctids, and salangids), whereas either the galaxiids (my galaxiids and aplochitonids) or Argentinoidei could be the primitive sister group of the esocoids + (salmonids + osmeroids). However, placement of the esocoids was based on their having reduced the number of rudimentary neural arches to one, evidence that Rosen considers to be weak, and I agree.

Fink and Weitzman (1982) reviewed Rosen's data and presented some of their own. They concluded that esocoids were not salmoniforms and state (p. 86) that "Esocoids seem to share no unique specializations with the other [salmoniforms]; we could list esocoids as *sedis* *mutabilis* at the euteleostean level or as the sister group of all other euteleosts, depending on the placement of the ostariophysans." On their cladogram of relationships (refer to Fig. 2B) and Fink's (1984b) recent one (refer to Fig. 2C) the esocoids form the sister group of all other euteleosts, and in turn the clupeomorphs form the sister group of the Euteleostei (also see Lauder and Liem 1983). However, this arrangement is largely the result of elimination since the other euteleosts (the Ostariophysi + the salmoniforms minus the esocoids + the neoteleosts) are united because they "lack ... a toothplate on the fourth endoskeletal basibranchial" (Fink and Weitzman, p. 81). Although the esocoids possess such a tooth-plate, and its absence appears to be derived, excluding the esocoids from the other euteleosts solely on this basis is not convincing.

Most recently, Parenti (1986) studied type of bone in euteleostean fishes, and concluded that because the esocoids, osmeroids (*sensu* Fink and Weitzman 1982), and neoteleosts share acellular bone, they form a single holophyletic group (refer to pages 423-424 for details and a critique). She does not, however, suggest how these three taxa are related to one another.

In conclusion, I agree with McDowall (1969, p. 817) who suggested that the "esocoids probably form an offshoot of very early salmoniform stock." This in fact is suggested by my hypothesis that the Esocoidei and Salmonidae are sister groups. In view of the recent confusion over esocoid relationships my hypothesis deserves further testing using other parts of the anatomy.

Esocoidei

In agreement with the evidence from the bones, the Esocidae and Umbridae are united in the Esocoidei because they share the following derived character states:

1. There is a unique coronoid-maxilla ligament that extends from the lateral surface of the coronoid process (from the dentary in the Esocidae and *Novumbra*, from both the dentary and angulo-articular in *Umbra*, and from the angulo-articular in *Dallia*) to the

dorsomedial surface of the posterior part of the maxilla (about the middle of the maxilla in the Esocidae and *Umbra* compared with the posterior third in *Novumbra* and *Dallia*; see Figs. 52-56). Eaton (1935) described and illustrated such a ligament (but did not name it) in *Umbra*, but its presence in the Esocidae, and in *Novumbra* and *Dallia* has never been mentioned in the literature. This ligament is found only in the Esocoidei among the salmoniforms, and was not present in any other teleosts that I examined. It is completely separate from, and does not appear to be homologous with the maxilla-mandibular ligament in the Esocidae (see Fig. 52). In *Esox* the maxilla-mandibular ligament is broader and longer than the coronoid-maxilla ligament, and originates from (the posteroventral corner of the lateral surface of the angulo-articular) and inserts upon (the dorsolateral edge of the anterior end of the maxilla) a completely different area. In the Umbridae the maxilla-mandibular ligament is absent (and presumed to be lost) but a distinct coronoid-maxilla ligament is present in essentially the same location as in the Esocidae (and presumed to be homologous with it).

2. The *adductor arcus palatini* inserts on the posterodorsal surface of the mesopterygoid (in addition to the hyomandibular and metapterygoid). This character state is, however, shared with three other salmoniform lineages: the Salmoninae (Salmonidae), the Lepidogalaxiidae + Galaxiidae + Aplochitonidae, and the Argentinoidea (Argentinidae + Bathylagidae + Opisthoproctidae).

   Primitively in the Salmoniformes (and the teleosts in general) the *adductor arcus palatini* is located posteriorly and inserts onto the hyomandibular, and usually the metapterygoid. In more derived teleosts the muscle is expanded farther anteriorly (onto the mesopterygoid) so that it lines the floor of the orbit between the skull and the suspensorium (pers. obs.; also see Winterbottom 1974a). This seems to be the case in the Salmoniformes; the lineages in which the *adductor arcus palatini* is expanded anteriorly onto the mesopterygoid are the more derived and specialized lineages within their respective assemblages.

3. The *adductor mandibulae* inserts directly onto the lower jaw, and has no ligamentous

connection with the maxilla. This character state was discussed previously and applies here only if it was derived independently in the Esocoidei, *Coregonus*, and the Salmoninae, and is not a synapomorphy uniting the Esocoidei + Salmonidae. It is also shared with the Argentinoidea.

Esocidae

The derived character states unique to the family Esocidae are numerous (for example, the presence of two subdivisions of each of: section A2 of the *adductor mandibulae*, the *levator arcus palatini*, and the *levator operculi*). Because the family contains only the genus *Esox*, and I examined only two of the five extant species, I will not discuss them here.

Umbridae

The Umbridae are holophyletic on the basis of two derived character states that all species share:

1. The maxilla-mandibular ligament is completely lost. This character state is shared with the Argentinoidea. However, this is probably a result of convergence because stronger evidence links the latter with the alepocephaloids, and the umbrids with the esocids. Primitively in the salmoniforms this ligament is either complete (connecting the maxilla, mandible, and *adductor mandibulae*; e.g., the Osmeridae) or at least part of it is present. For example, in the Esocidae, the immediate outgroup of the Umbridae, the ligament has lost its connection with the *adductor mandibulae* (section L.z on Fig. 99) and extends only between the maxilla and mandible. The character state in the Umbridae could be derived directly from the state in the Esocidae by then losing the remaining section (L.x-L.y).
2. The *adductor arcus palatini* is expanded far anteriorly (farther than in the Esocidae) so that it lines the floor of the posterior half of the orbit and inserts on about the posterior third of the dorsal surface of the mesopterygoid.
3. Section A2 of the *adductor mandibulae* is expanded posteriorly onto the cheek so that the

area of origin includes a large part of the lateral surface of the preoperculum (see Figs. 53-56). The entire anterior lamina is covered in all species; however, the area of origin on the limbs is variable and increases in approximately the following sequence: *Novumbra* → *Umbra krameri / U. pygmaea* → *U. limi* → *Dallia*. Virtually the entire lateral surface of the preoperculum is covered in *Umbra limi* and *Dallia* (especially). The large area of origin of this muscle on the preoperculum in *Umbra* and *Dallia* corresponds with the unusually broad preoperculum in these two genera. A character state somewhat similar to the umbrid one is found in the Lepidogalaxiidae, the Aplochitonidae, some galaxiids, the Argentinidae, and the Bathylagidae among the other salmoniforms.

Primitively only a small part of the *adductor mandibulae* originates on the preoperculum. In the Esocidae the origin includes only the lateral surface of the small anterior lamina and the anterolateral edge of the limbs, but not their lateral surface. The primitive character state for the Teleostei appears to be for the muscle to originate only along the anterolateral edge of the bone, and not the lateral surface of the anterior lamina, even if it is present. This state is found in all salmonids, the osmeroids, and the alepocephaloids among the salmoniforms.

Interrelationships of the Umbridae. As was discussed in a previous section, the interrelationships of the three umbrid genera have been the subject of numerous disagreements. My findings, using the bones of the suspensorium, more or less equally supported the hypothesis that *Umbra* and *Dallia* are sister taxa, and the hypothesis that *Novumbra* and *Dallia* are sister taxa. However, evidence from the muscles, in particular the *adductor mandibulae*, proved to be useful in resolving the problem. This new evidence suggests that *Umbra* and *Dallia* probably form a sister group, yet does not discount the hypothesis that *Novumbra* and *Dallia* are sister taxa. As with the bones, there were no shared derived character states uniting *Umbra* and *Novumbra*.

The derived character states shared by *Novumbra* and *Dallia* include the following:

1. The *levator arcus palatini* does not insert on the metapterygoid (shared with the

Lepidogalaxiidae and the Argentinoidea). In most salmoniforms, including *Umbra* and the Esocidae, the insertion includes both the hyomandibular and the metapterygoid. However, this synapomorphy is relatively weak because the character state appears to be related to the size of the metapterygoid; in all the salmoniforms sharing it the metapterygoid is reduced in size (it is tiny or absent in the Bathylagidae and Opisthoproctidae).

2. The coronoid-maxilla ligament inserts about one-third of the way from the posterior end of the maxilla. In the Esocidae and *Umbra* the insertion is about the middle of the maxilla.

The derived character states shared by *Umbra* and *Dallia* are more numerous and include the following:

1. The anterolateral fibres of section A2 of the *adductor mandibulae* converge onto the dorsal and ventral sides of a well-developed, anteroposteriorly oriented ridge of tissue on the lateral surface of the tendinous aponeurosis that overlies the metapterygoid and quadrate (and extends anteriorly medial to the lower jaw). No part of section Aw inserts along the ridge.

   The ridge is absent in the Esocidae and *Novumbra* and in the other salmoniforms that I examined. However, in both *Esox* and *Novumbra* the anteriormost fibres of section A2 insert partly onto the posterior surface of a thin sheet of fascia that is continuous with the tendinous aponeurosis, and extends diagonally across its lateral surface. The posteriormost fibres of section Aw originate on this fascia. Whether or not the fascia in the Esocidae and *Novumbra* is homologous with the well-developed ridge of tissue found in *Umbra* and *Dallia*, and represents an incipient ridge, is uncertain.

2. Only a small part of the *adductor mandibulae* (section Aw) inserts onto the medial surface of the lower jaw (i.e., fills the Meckelian fossa). This corresponds to the relatively small size of the Meckelian fossa in *Umbra* and *Dallia* when compared with that in the Esocidae, *Novumbra*, and most other salmoniforms (the exceptions being the Plecoglossidae, Lepidogalaxiidae, Bathylagidae, and Opisthoproctidae). Primitively, the Meckelian fossa is relatively large, as is the part of the *adductor mandibulae* inserting into

it.

Section Aw is small in *Umbra*. If section Aw in *Dallia* is only the portion found medial to the lower jaw, and does not include the subdivision medial to section A2 (see pages 228-231 for a discussion of this issue), then the Aw section would be even smaller than in *Umbra*. If this is the case, then the small size of section Aw would also be a synapomorphy uniting *Umbra* and *Dallia*. However, there is evidence suggesting that the "subdivision" medial to A2 represents a posterior expansion of section Aw, in which case section Aw in *Dallia* would be larger than in the other umbrids.

3. The coronoid-maxilla ligament originates from the lateral surface of the angulo-articular bone (the dentary and angulo-articular in *Umbra* and only the angulo-articular in *Dallia*). The primitive character state, found in *Novumbra* and the Esocidae, is for the origin to include only the lateral surface of the dentary.

   This difference might be partly related to differences in the shape of the mandible in the three genera. In all esocoids the ligament originates from the lateral edge of the dorsalmost part of the mandible. However, the bone that forms the dorsalmost part of the mandible is different in each genus, and this difference corresponds to the difference in origin. For example, in the Esocidae and *Novumbra* it is the dentary (as is the case in most salmoniforms and lower teleosts), in *Dallia* it is the angulo-articular, and in *Umbra* the condition is somewhat intermediate, with the dentary being slightly more dorsal than the angulo-articular.

Conclusions. Although the evidence from the bones of the suspensorium is equivocal, the evidence from the muscles suggests that the *Dallia* is probably more closely related to *Umbra* than to *Novumbra* (i.e., that *Umbra* and *Dallia* are sister taxa). The two synapomorphies supporting the alternate hypothesis are of relatively low weight. The first one – the *levator arcus palatini* does not insert on the metapterygoid – is shared with several other salmoniform lineages and appears to be directly related to the size of the metapterygoid in all of them. The polarity of the second synapomorphy — the point of insertion of the coronoid-maxilla ligament on the maxilla — is questionable.

The first two synapormorphies supporting the preferred hypothesis should be given more weight. This includes the well-developed ridge of tissue on the tendinous aponeurosis, onto which part of section A2 of the *adductor mandibulae* inserts, that is unique to *Umbra* and *Dallia*. The second synapomorphy — the insertion of only a small part of the *adductor mandibulae* onto the medial surface of the lower jaw — is almost certainly the derived character state, but is shared with a few other relatively derived salmoniforms and should be given less weight than the first one. The final synapomorphy — [illegible] point of origin of the coronoid-maxilla ligament — is given relatively low weight becau[illegible] some doubt as to its polarity, and because it appears to be related to which bo[illegible] dorsalmost part of the mandible, since its geometric point of origin does not vary (the dorsalmost part of the lower jaw).

To sum up, my evidence suggests that *Umbra* and *Dallia* are sister groups, but does not rule out the possibility that *Novumbra* and *Dallia* are each other's closest relatives. Combining evidence from the bones and muscles, there are a total of seven synapomorphies supporting the preferred hypothesis, and five supporting the alternate. The evidence supporting the preferred hypothesis includes most parts of the suspensorium whereas that supporting the alternate is essentially related to the shape of the metapterygoid and the parts adjacent to it. These conclusions essentially support the findings of Nelson (1972) and Wilson and Veilleux (1982), but disagree with those of Cavender (1969) and Reist (1987).

Salmonidae

Although the bones of the suspensorium support the holophyly of the Salmonidae, I did not find any shared derived character state of the muscles that unites the family.

Evidence from the muscles, however, corroborated the hypothesis that the Thymallinae + Salmoninae are sister groups. As with the bones there was no evidence supporting the two alternate hypotheses (the Coregoninae + Thymallinae are sister taxa, or the Coregoninae + Salmoninae are sister taxa). The shared derived character states uniting the Thymallinae + Salmoninae include the following:

1. A separate *adductor hyomandibulae* is present. It is closely associated with, but separate from, the posterior end of the *adductor arcus palatini*, originating from the ventrolateral surface of the pterotic and inserting mainly on the dorsomedial surface of the opercular arm of the hyomandibular. Other salmoniforms with a separate *adductor hyomandibulae* include *Esox*, *Dallia*, some Osmeridae, the Retropinnidae and Prototroctidae, and most Alepocephalidae and Platytroctidae.
2. The area of insertion of the *levator arcus palatini* (LAP) on the medial surface of the metapterygoid is extensive, especially in the Salmoninae, and includes the entire surface of the unique posterodorsal dermal lamina. It is common for the LAP to insert on the medial surface of the metapterygoid (a medial insertion of the LAP on the metapterygoid appears to be primitive for the Teleostei, but there is so much variation that it is difficult to be sure); however, usually the area of insertion is smaller and does not include a dermal lamina.
3. The *adductor mandibulae* inserts directly onto the lower jaw, and has no ligamentous connection with the maxilla. This character state was discussed previously and applies here only if it was achieved independently in the Esocoidei, *Coregonus*, and the Thymallinae + Salmoninae, and is not a synapomorphy uniting the Esocoidei + Salmonidae. It is also shared with the Argentinoidea.

OSMEROIDS + GALAXIOIDS + ARGENTINOIDS

Although I united the osmeroids, galaxioids, argentinoids on the basis of their sharing specialized teeth on the mesopterygoid I did not find any evidence from the muscles to unite this assemblage. However, there are some general observations that can be made concerning the muscles that might be associated with the function of these teeth. First, in all species that have the teeth the *adductor mandibulae* has a ligamentous connection with the maxilla.

Second, in all species that have teeth on the posterior surface of the mesopterygoid (the Plecoglossidae, Osmeridae, Retropinnidae, Prototroctidae, and Platytroctidae), the *adductor arcus palatini* (AAP), the muscle that adducts the suspensorium, originates far posteriorly on the skull (entirely, or almost entirely from the prootic) and the anteriormost fibres extend anterolaterally to insert onto the medial surface of the hyomandibular and metapterygoid (only the hyomandibular in the Platytroctidae). However, this character state appears to be primitive for the Teleostei and is also found in the Salmonidae, Alepocephalidae, Salangidae, various higher teleosts (e.g., the relatively primitive stomiiforms *Diplophos* and *Vinciguerria*), most clupeoids, and the primitive elopomorphs *Elops* and *Megalops*. In the Galaxiidae and the Aplochitonidae, the only two lineages in which the teeth are restricted to the anterior half of the mesopterygoid, the AAP originates farther anteriorly (along the posterolateral edge of the parasphenoid, to a point level with the condyle of the quadrate) and inserts onto the posterodorsal surface of the mesopterygoid (as well as on the medial surfaces of the metapterygoid and hyomandibular).

Interrelationships. There is some evidence from the muscles that suggests that the osmeroids and galaxioids may be sister groups. In the osmeroids (including the Salangidae) and most galaxioids the *levator arcus palatini* (LAP) inserts on the dorsolateral surface of the metapterygoid rather than on the dorsomedial surface (which appears to be the primitive character state). The exceptions are *Lepidogalaxias* and *Lovettia* (Aplochitonidae); however, in these fish the LAP does not insert on the metapterygoid at all. In *Aplochiton* (Aplochitonidae) the insertion is on the dorsal surface of the posterior half of a posterior, tube-like extension of the metapterygoid. Among other salmoniforms the metapterygoid does not serve as part of the insertion area in two umbrids (*Novumbra* and *Dallia*) and in the Argentinoidea, but in these the metapterygoid is reduced in size or lost altogether (some opisthoproctids). In all the other salmoniforms (the Salmonidae, Esocidae, *Umbra*, Alepocephalidae, and Platytroctidae) the LAP inserts on the dorsomedial surface of the metapterygoid. This character state is also found in the primitive ostariophysan *Chanos*, the clupeoids (in the sister group of the clupeoids, the Denticipitidae, the insertion is only on the hyomandibular; see Greenwood 1968), the primitive elopomorphs *Elops* and *Megalops*, as well as numerous relatively primitive higher teleosts (e.g., the primitive stomiiforms *Diplophos* and *Vinciguerria*). In none of the teleosts that I examined, other than the osmeroids and galaxioids, did the LAP insert on the dorsolateral surface of the metapterygoid. For these reasons it appears that having part of the *levator arcus palatini* insert on the dorsolateral surface of the metapterygoid may be a synapomorphy uniting the osmeroids and galaxioids. However, since this evidence is far from conclusive and is not corroborated by any other, I still consider the osmeroids, galaxioids, and argentinoids to form an unresolved trichotomy.

It may be that the dorsolateral insertion of the LAP on the metapterygoid is related to the function of the specialized teeth on the mesopterygoid found in the osmeroids and galaxioids. However, the Platytroctidae (Argentinoidei) have similar teeth, but the LAP inserts on the dorsomedial surface of the metapterygoid, apparently contradicting this hypothesis.

Osmeroids

Evidence from the muscles supports the hypothesis that the Osmeridae + Plecoglossidae form a holophyletic group. The shared derived character states uniting the Osmeridae + Plecoglossidae include the following:

1. The *levator arcus palatini* (LAP) inserts along and dorsal to a moderate (*Hypomesus*, *Mallotus*), to well-developed (*Osmerus*, *Allosmerus*, *Spirinchus*, *Thaleichthys*, and *Plecoglossus*) ridge on the lateral surface of the posterodorsal part of the metapterygoid. The insertion area dorsal to this ridge is primarily on the lateral surfaces of the hyomandibular, and the posterior dermal lamina of the metapterygoid (less so in *Plecoglossus*). As I discussed previously (see page 333) the lateral ridge on the metapterygoid is a synapomorphy uniting the two families and is unique to this

assemblage. Although the LAP also inserts on the lateral surface of the metapterygoid in most galaxioids (see previous section), in none does it insert onto a ridge similar to that found in the Osmeridae and Plecoglossidae. However, in *Galaxias maculatus* (but not in the other four galaxiid species examined) part of the LAP inserted onto and dorsal to a short (anteroposteriorly), rounded ridge on the lateral surface of the posteroventral part of the metapterygoid (the ridge was distinctive only in one of two specimens examined).

2. Part of the *adductor arcus palatini* (AAP) inserts along and dorsal to a well-developed ridge on the medial surface of the metapterygoid that extends posteroventrally from the anterodorsal corner towards the posteroventral corner. Among the other salmoniforms, a similar medial ridge is present only in the Alepocephalidae and Platytroctidae. However, in most alepocephalids and [illegible] the AAP inserts only on the hyomandibular, and the ridge is occupied by the *levator arcus palatini* (see later section for details).

Interrelationships. Although I did not find any evidence to unite the Salangidae + Sundasalangidae with either the Osmeridae or Plecoglossidae I tentatively place them as part of an unresolved trichotomy, along with the latter two families, based on evidence from other sources (see pages 340-343 for details).

I also did not find any evidence linking the six osmerid genera, suggesting that the Osmeridae, as traditionally defined, may not be holophyletic. Within the Osmeridae, there is evidence supporting my hypothesis that *Spirinchus* and *Thaleichthys* form a sister group: they share a separate *adductor hyomandibulae* (AH) that originates from the posteroventral surface of the pterotic and inserts onto the dorsomedial surface of the long opercular arm of the hyomandibular. Although a separate AH is found in numerous other salmoniforms (the Esocidae, *Dallia*, Thymallinae, Salmoninae, Retropinnidae, Prototroctidae, most Alepocephalidae, and most Platytroctidae) it is absent in all other osmeroids and is therefore a synapomorphy uniting the two genera.

Galaxioids

Although evidence from the bones of the suspensorium supports the holophyly of the galaxioids (Retropinnidae + Prototroctidae + Lepidogalaxiidae + Galaxiidae + Aplochitonidae) I did not find any reliable features of the muscles to unite this assemblage.

Two possible synapomorphies are shared by all five families, but because they are also shared with numerous other salmoniforms and teleosts I do not consider them to be reliable indicators of phylogenetic relationship. First, all galaxioids lack supramaxillae, and consequently the supramaxillary ligament (primitively in the Teleostei there are two supramaxillae, and a supramaxillary ligament extends from the anterior tip of the posterior one to the lower jaw). This character state is shared with the Plecoglossidae (but one supramaxilla was present in the smallest specimen of *Plecoglossus* that I cleared and stained and a vestige was found in the next smallest one), some Salangidae (the Salanginae), and the Argentinoidea, as well as the Ostariophysi and Osteoglossomorpha among the lower teleosts. One supramaxilla is present, but the supramaxillary ligament is lost in the Esocoidei (*Umbra* has no supramaxilla) and Salmonidae. Alepocephalids and platytroctids usually have one or two supramaxillae; however, of all the ones I examined, only *Photostylus* (Alepocephalidae) had a distinct supramaxillary ligament. The ease with which the supramaxillae can be lost is also demonstrated by the fact that in the Alepocephalidae about half the genera have one supramaxilla, the other half have two, and some have both character states.

The second possible synapomorphy uniting the galaxioids is that the origin of the *adductor mandibulae* includes the entire lateral surface of the anterior lamina of the preoperculum (the anterior lamina is virtually absent in the Lepidogalaxiidae; but the area of origin on the anterolateral surface of the preoperculum is about the same as the other galaxioids). This character state is shared with the Esocoidei and Argentinoidea among the other Salmoniforms, as well as with *Chanos*, *Hiodon*, and numerous higher teleosts (e.g., the aulopiform *Aulopus* and the paracanthopterygian *Percopsis*). The primitive character state appears to be for the *adductor mandibulae* to originate only along the anterolateral edge of the preoperculum, and not on the lateral surface of the anterior lamina, even if it is present (as in the salmonids, osmeroids, alepocephaloids, and various more primitive teleosts including the clupeoids and the elopomorphs *Elops* and *Megalops*).

Retropinnidae + Prototroctidae

Evidence from [illegible] muscles supports the hypothesis that the Retropinnidae + Prototroctidae form a holophyletic group. Both share a separate *adductor hyomandibulae* that is closely adjacent to, but separate from, the posterior end of the *adductor arcus palatini*. It originates from the lateral surface of the posteroventral part of the pterotic [illegible] on the dorsomedial edge of the opercular arm of the hyomandibular. Other salmoniforms with a separate *adductor hyomandibulae* include the osmerids *Spirinchus* and *Thaleichthys*, most Alepocephalidae and Platytroctidae, the Esocidae, and *Dallia* (Umbridae).

There is one derived character state that contradicts this hypothesis, and possibly links the Prototroctidae with the Lepidogalaxiidae + Galaxiidae + Aplochitonidae. However, because I believe this feature evolved independently in the two groups (and is a synapomorphy uniting the latter three families) I will discuss it in the following section.

Lepidogalaxiidae + Galaxiidae + Aplochitonidae

In agreement with the evidence from the bones, the Lepidogalaxiidae + Galaxiidae + Aplochitonidae are united because they share the following derived character states:

1. Section A2 of the *adductor mandibulae* inserts onto the maxilla and lower jaw via a maxilla-mandibular ligament unlike that found in the other salmoniforms or teleosts that I examined. In all species the ligament extends from the anterolateral end of section A2 to the maxilla (the primitive character state). However, the posterior part of the ligament that attaches to the lower jaw is unusual. Unlike the outgroups, the section that extends to the angulo-articular bone (section L.y on Fig. 102) is reduced and extends ventrally from the posteriormost end of the main ligament (nearly at the point where it joins the muscle) to join the angulo-articular bone almost immediately dorsal to the joint (see

Figs. 70-72). Because this section (L.y) extends from the posteriormost end of the main ligament there is virtually no separate section (L.z on Fig. 102) that extends from the *adductor mandibulae* to join the main part (section L.x-L.y on Fig. 102) of the maxilla-mandibular ligament. In essence, the part of the ligament that extends directly from the muscle to the maxilla is prominent, and the part attaching to the angulo-articular is reduced in size and importance. In the primitive character state, exemplified by *Hypomesus* (Osmeridae) and *Retropinna* (Retropinnidae) all parts of the maxilla-mandibular ligament (L.x, L.y, L.z) are present and equally well-developed, and section L.y does not insert adjacent to the joint on the angulo-articular, but farther anteriorly (refer to Figs. 62 and 67, respectively).

Another unique feature is the presence of a ligament (a new part of the maxilla-mandibular ligament) that extends anteroventrally from the intersection of sections L.x and L.y and inserts onto the coronoid process (the posterodorsal corner of the dentary) of the lower jaw (L.w on Figs. 69-72). This ligament is moderately long and narrow in *Galaxias maculatus* (see Fig. 70) but shorter and broader in *G. paucispondylus*. In the Aplochitonidae (both *Aplochiton* and *Lovettia*) it is similar to *G. maculatus* but is thinner. In the other galaxiids that I examined (*G. brevipinnis, G. fasciatus, Neochanna apoda*, and *Brachygalaxias bullocki*), and in the Lepidogalaxiidae, the character state is modified, but appears to be homologous with that in the other species because it occupies the same position. In these fish, the new ligament (L.w) is shorter and much broader, forming a tough ligamentous "glove" that broadly inserts directly onto the dentary (see Figs. 69, 71). In *G. brevipinnis, G. fasciatus* (see Fig. 71), and *Brachygalaxias* a separate L.y section, similar to that in *G. maculatus* (see Fig. 70), *G. paucispondylus*, and the aplochitonids (see Fig. 72), is also present (but in *G. fasciatus* it is shorter, probably because its dorsal part has become incorporated into the unusually broad ligamentous glove). In *Neochanna* the ligamentous glove is broader than the other genera, and is expanded ventrally onto the angulo-articular bone in the area normally occupied by ligament L.y (in addition to inserting onto the dentary). A distinct L.y ligament is absent, but I hypothesize that it has been incorporated into the ligamentous glove. Evidence is provided by the observation that a vestige of section L.y was present on one side of each of the two specimens that I examined. Because *Neochanna* is specialized (both ecologically and morphologically) relative to the other galaxiids this character state is probably an autapomorphy of the genus. *Lepidogalaxias*, a fish that converges on *Neochanna* in a number of features, has a similar character state except that the ligamentous glove inserts only onto the dentary.

In no other salmoniforms (or teleosts) that I examined did the *adductor mandibulae* have a similar ligamentous attachment onto the coronoid process of the lower jaw, and at the same time have a direct ligamentous connection with the maxilla, and a reduced L.y section of the maxilla-mandibular ligament. A hypothetical transformation series depicting how this ligamentous arrangement might have evolved is depicted in Fig. 104.

Associated with the aforementioned features is the observation that in this assemblage section A2 of the *adductor mandibulae* extends farther anteriorly than in most other salmoniforms (including the immediate outgroups, the Retropinnidae + Prototroctidae). In some cases, the anterior end of the muscle actually overlaps the posterolateral surface of the lower jaw and obscures the posterior ligaments (e.g., *Galaxias maculatus* and *G. fasciatus*, see Figs. 70 and 71, respectively).

2. The tendinous aponeurosis, onto which the medial fibres of section A2 of the *adductor mandibulae* insert, is either not connected with (and completely separate from) the posteriormost end of the ligament that connects section A2 to the upper jaw, as in the Galaxiidae and Lepidogalaxiidae, or else just barely connected with the ligament, as in the Aplochitonidae (because of the small size of the specimens it was impossible to tell in *Lovettia*). Among the other salmoniforms in which section A2 is connected ligamentously to the maxilla only *Bathylagus* (Bathylagidae) shared this character state. Primitively, there is a distinct connection between the anterodorsal edge of the tendinous aponeurosis (before it bifurcates anteriorly) and the posteriormost end of the ligament that extends to

the maxilla. This character state was found in the Retropinnidae + Prototroctidae, osmeroids, alepocephaloids, *Prosopium*, *Stenodus*, and the primitive teleosts *Clupea* and *Megalops*.

3. The mandibular branch of the trigeminal nerve first passes between the anterolateral surface of the tendinous aponeurosis and the anteromedial surface of section A2 of the *adductor mandibulae* before running medial to the lower jaw (i.e., the nerve passes medial to section A2 before running medial to the lower jaw, see Figs. 69-72). In the primitive character state the nerve passes lateral to the anterior end of section A2 (usually lying at the intersection of sections A2 and Aw) before running medial to the lower jaw (e.g., see Figs. 52, 57, 62, 67, 91). The primitive character state was found in most salmoniforms (the Esocoidei, Salmonidae, Osmeridae, Plecoglossidae, most Salangidae, Retropinnidae, Alepocephalidae, Platytroctidae, and Opisthoproctidae); most lower teleosts examined, including *Chanos* (Ostariophysi), *Clupea* (Clupeidae), *Amentum* (Engraulidae), *Hiodon* (Osteoglossomorpha), and the elopomorphs *Elops* and *Albula* (see Greenwood 1977); and the primitive higher teleosts *Diplophos* (Stomiiformes), *Argyropelecus* (Stomiiformes), *Vinciguerria* (Stomiiformes), *Aulopus* (Aulopiformes), and *Myctophum* (Myctophiformes).

Within the salmoniforms the derived character state (the nerve passes medial to section A2 before running medial to the lower jaw) was shared with the Prototroctidae, Argentinidae, and Bathylagidae (see Figs. 68, 87, 88). I conclude that the state in the latter two families is an example of parallelism because other, more extensive and convincing evidence suggests that they belong in the Argentinoidei. The character also possibly links the Prototroctidae (a galaxioid) with the Lepidogalaxiidae, Galaxiidae, and Aplochitonidae; however, again there is more and better evidence suggesting that the Retropinnidae + Prototroctidae are sister taxa, and together form the primitive sister group of the other three galaxioid families. I conclude that the character state of the nerve in the Prototroctidae was derived independently of that in the other galaxioids with the same character state (i.e., it is an autapomorphy of the Prototroctidae).

Also, in two umbrids, *Umbra limi* and *U. pygmaea*, the mandibular branch of the trigeminal nerve passes medial to the anterior end of section A2 (but only medial to part of it) before running medial to the lower jaw. This appears to be related to a unique feature of the *adductor mandibulae* found in the aforementioned species. In *U. limi* and *U. pygmaea* the anterolateral fibres of section A2 converge onto a tendon (L.A2) that extends anteriorly to attach to the lateral surface of the angulo-articular bone of the lower jaw (see Fig. 54 of *U. limi* and compare it to Fig. 55 of *U. krameri*). This character state is unique to these two esocoids among the teleosts that I examined, corroborating Wilson and Veilleux's (1982) hypothesis that *U. limi* + *U. pygmaea* are sister species, and that *U. krameri* is the most primitive species of *Umbra*. The nerve in *U. limi* and *U. pygmaea* rests lateral to the anterior end of section A2 at the division of sections A2 and Aw (as in the primitive character state represented by the other esocoids, see Figs. 52, 53, 55, 56); however, it lies medial to the new tendon and the anterolateral fibres of section A2 that converge onto it (see Fig. 54). Thus, although technically the nerve passes medial to section A2, it occupies the same relative position as the other esocoids. However, it should be noted that in one specimen of *U. limi* that I examined (UAMZ 3725, 68.0 mm SL) the nerve did pass medial to the main muscle mass of A2, as in the galaxioids.

4. The *adductor arcus palatini* inserts on the posterodorsal surface of the mesopterygoid (in addition to the hyomandibular and metapterygoid). This character state is shared with the Argentinoidea, Salmoninae (Salmonidae), and Esocoidei.

5. A relatively short, narrow, but well-defined ligament, somewhat rounded in cross-section, extends medially from the medial surface of the expanded posterior end of the maxilla to the lateral surface of the coronoid process (dentary) of the lower jaw (L on Fig. 102). This ligament passes through a sheet of connective tissue that extends between the same points. Although the posteromedial surface of the maxilla is connected to the coronoid process via connective tissue in all salmoniforms, and the other teleosts examined, and in many cases (e.g., some salmonids) the tissue could be broadly defined as a ligament, a

similarly shaped structure was found only in the Lepidogalaxiidae + Galaxiidae + Aplochitonidae. This ligament differs from the coronoid-maxilla ligament found in the Esocoidei and described in an earlier section. In the Esocoidei the coronoid-maxilla ligament is longer and flatter, and extends anteroposteriorly (rather than mediolaterally), and inserts farther anteriorly on the maxilla. Also, at the same time a sheet of connective tissue extends between the medial surface of the posterior end of the maxilla and the coronoid process in the esocoids, but no ligament is present.

Hypotheses of Lepidogalaxiid + Galaxiid + Aplochitonid Interrelationships

Assuming that the Aplochitonidae and Galaxiidae each form a holophyletic group (the Lepidogalaxiidae contain only one species) there are three possible hypotheses of how these taxa are related to one another: the Lepidogalaxiidae + Aplochitonidae are sister taxa, the Lepidogalaxiidae + Galaxiidae are sister taxa, or the Galaxiidae + Aplochitonidae are sister taxa. In the account that follows, evidence from the muscles supporting each hypothesis is discussed.

Lepidogalaxiidae + Aplochitonidae. There is only one possible synapomorphy of the muscles uniting the Lepidogalaxiidae + Aplochitonidae, and this was only shared by *Lepidogalaxias* and one aplochitonid, *Lovettia*: the insertion area of the ***adductor arcus palatini*** (AAP) includes the entire lateral surface of the metapterygoid. The metapterygoid in my specimens of *Lovettia* was only partly ossified, but McDowall (1969, fig. 3D) illustrated an ossified metapterygoid in the same position in his figure of *Lovettia*. Primitively (including *Aplochiton*), the AAP inserts on the dorsomedial surface of the metapterygoid, and occasionally onto part (but not all) of the lateral surface.

Lepidogalaxiidae + Galaxiidae. There is some evidence from the muscles supporting the hypothesis that the Lepidogalaxiidae + Galaxiidae are sister taxa. Although these derived character states were usually shared with only some galaxiids that I examined, the resemblances were often striking. This suggests that perhaps *Lepidogalaxias* is more closely related to some galaxiids than to others if the Galaxiidae can be shown to be paraphyletic. However, more galaxiids need to be examined and the holophyly of the family rigorously tested before any conclusions can be drawn. The synapomorphies uniting *Lepidogalaxias* with the Galaxiidae include the following:

1. The part of the maxilla-mandibular ligament that extends directly from the *adductor mandibulae* to the maxilla is relatively short and inserts about one third to one half of the way from the posterior end of the maxilla. *Lepidogalaxias* shared this character state with *Galaxias paucispondylus*, *G. fasciatus*, *G. brevipinnis*, *Brachygalaxias*, and *Neochanna apoda*. The ligament is longer and inserts farther anteriorly in *G. maculatus*. Primitively (including the Aplochitonidae), the ligament is longer than in the galaxiids and *Lepidogalaxias* and inserts near the anterior end of the maxilla.
2. The tendinous aponeurosis onto which the medial fibres of section A2 of the *adductor mandibulae* insert is not connected with the posteriormost end of the ligament that connects section A2 to the upper jaw. Primitively, there is a distinct connection between the anterodorsal edge of the tendinous aponeurosis and the posteriormost end of the ligament that extends to the maxilla. However, the state in the Aplochitonidae approaches the derived state in that there is a slight connection between the two elements.
3. The new part of the maxilla-mandibular ligament (L.w) that extends from the intersection of sections L.x and L.y to insert onto the coronoid process of the lower jaw is short, broad, and forms a tough ligamentous "glove" that broadly inserts onto the coronoid process (dentary). *Lepidogalaxias* shares this character state with *Galaxias brevipinnis*, *G. fasciatus*, *Neochanna apoda*, and *Brachyglaxias bullocki* (compare Figs. 69 and 71). However, in the Aplochitonidae and the galaxiids *G. paucispondylus* and *G. maculatus* ligament L.w is relatively long and narrow. I hypothesize that the latter character state is the primitive one, since it hypothetically could form the beginning of a transformation series that ultimately could lead to a character state similar to that found in *Lepidogalaxias* and the galaxiids with a "glove-like" ligament.

4. The *levator arcus palatini* (LAP) is barrel-shaped, laterally bulbous, and expanded dorsally onto the dorsolateral surface of the skull so that its origin includes the lateral surfaces of the sphenotic (the spine and the area anterior and dorsal to it), pterosphenoid, prootic, and the lateral edges of the frontal and parietal. This character state was found in *Lepidogalaxias* and all the galaxiids that I examined except for *Brachygalaxias bullocki*. *B, bullocki* and most salmoniforms possessed the primitive character state in which the LAP is roughly conical, and originates only from the lateral surface of the sphenotic (the spine and the surface anteroventral to it).

   Although other salmoniforms have roughly a barrel-shaped LAP (the Salangidae, Argentinidae, and the umbrid *Dallia*), in none does the muscle extend as far dorsally onto the skull and originate from exactly the same area. In *Esox* the origin also includes the sphenotic, pterosphenoid, prootic, and frontal (but not the parietal). However, the area of origin on the frontal is different (from the ventrolateral surface at the back of the orbit) and the muscle is not expanded dorsally onto the dorsolateral surface of the skull (it does not extend dorsal to the spine on the sphenotic). Also, the LAP in *Esox* has two subdivisions, versus only one in the galaxiids and *Lepidogalaxias*.

Also worth noting is the observation that the general shape of the *adductor mandibulae* in some galaxiids, in particular *Galaxias fasciatus*, *G. brevipinnis*, and less so *Neochanna*, is quite similar to that in *Lepidogalaxias* (compare Figs. 69 and 71).

Galaxiidae + Aplochitonidae. Two shared derived character states of the muscles unite the Galaxiidae and Aplochitonidae, corroborating my preferred hypothesis that they are sister groups:

1. Section A2 of the *adductor mandibulae* either has a small dorsomedial subdivision, as in the Galaxiidae, or a partial (incipient?) dorsomedial subdivision, as in the Aplochitonidae (*Aplochiton*). In the Galaxiidae the subdivision is slightly visible externally, passes medial to the *levator arcus palatini* (LAP) and only its anteroventral fibres are continuous with those of the main muscle mass (see Figs. 70, 71). In *Aplochiton* the subdivision is partial;

its lateral fibres can be separated from those of the main muscle mass, but its ventral fibres are continuous with it. Unlike the Galaxiidae, it is not visible externally and does not pass medial to the LAP (although the medialmost fibres run in the same direction; i.e., posteromedially). However, homology is suggested by the observation that the origin is essentially the same (primarily from the lateral surface of the metapterygoid) as is the insertion (the surface of the tendinous aponeurosis that extends anteriorly to the lower jaw). There does not appear to be a partial subdivision in the other aplochitonid, *Lovettia*, although because of the small size of the specimens it is difficult to be sure. Primitively in the salmoniforms and lower teleosts section A2 is not subdivided.

[illegible] significantly, in the larger specimen of *Lepidogalaxias* [illegible] dae) that I examined, there was what might be interpreted as a partial [illegible] somedial subdivision of section A2 similar to that described for [illegible] ver, it appears to originate from the symplectic and the LAP. More [illegible] be examined before conclusions can be drawn, but this evidence might [illegible] *Lepidogalaxias* with the Galaxiidae and Aplochitonidae.

Among the other salmoniforms, the osmerid *Plecoglossus* has a dorsomedial subdivision of section A2 that is similar to the one in the Galaxiidae (refer to Fig. 63). However, it does not appear to be homologous because, unlike the Galaxiidae, its fibres converge anteriorly onto a separate ligament that extends anteriorly to join the ligament onto which the dorsolateral fibres of the main muscle mass converge, which in turn extends anteriorly as section L.z of the maxilla-mandibular ligament. The only other salmoniform with a dorsomedial subdivision (and there is some doubt as to whether or not it is part of section A2 or is section Aw) is found in the umbrid *Dallia* (see Fig. 56). However, even if this part is derived from section A2, it is unlike that in either the Galaxiidae or *Plecoglossus* because it originates primarily from the hyomandibular (versus the metapterygoid) in a highly unusual way, and inserts onto a separate ligament that inserts on the medial surface of the lower jaw. In addition, the position of the mandibularis branch of the trigeminal nerve relative to the subdivision is different in

Dallia than in *Plecoglossus* and the galaxiids, suggesting that it may be a posteromedial expansion of section Aw (see pages 228-231 for a discussion of this issue).

2. Part of section A2 of the *adductor mandibulae* originates from the posterior surface of the unique arc-shaped lateral strut of the hyomandibular (the strut is absent in *Lovettia*). Primitively, the *adductor mandibulae* originates from the anteriorly facing surface of the lateral strut. Among the other salmoniforms, the derived character state was found only in *Leptoderma* (Alepocephalidae), which has a similarly shaped lateral strut. As[illegible] with this character state was the observation that in these species the *levator arcus palatini* inserted upon the entire anterior surface of the lateral strut (versus most, or only part of it in the other salmoniforms).

<u>The Phylogenetic Position of *Lovettia*</u>. Evidence from the muscles corroborates and strengthens my hypothesis that *Lovettia* and *Aplochiton* are sister taxa (i.e., that the Aplochitonidae are holophyletic). *Lovettia* and *Aplochiton* share a new ligament (L.m on Fig. 72), separate from the maxilla-mandibular ligament (but continuous with it at both ends, and possibly derived from it), that extends from the ventral end of section L.y of the maxilla-mandibular ligament (on the angulo-articular) to a flange on the dorsolateral surface of the anterior end of the maxilla, where it is continuous with the anterior end of the maxilla-mandibular ligament. No other salmoniforms that I examined possessed a similar ligament in conjunction with a maxilla-mandibular ligament, with the exception of a few alepocephaloids (e.g., see Figs. 79, 83). However, unlike the aplochitonids, in these alepocephaloids the maxilla-mandibular ligament was incomplete in that the section (L.y) that inserts onto the angulo-articular bone is absent.

In conclusion, I accept the hypothesis, based on evidence from both the bones and muscles, that *Lovettia* + *Aplochiton* are sister taxa and therefore that the Aplochitonidae are holophyletic.

<u>Preferred Hypothesis.</u> Evidence from the muscles of the suspensorium supports basically two

hypotheses: the Galaxiidae + Aplochitonidae are holophyletic, or the Lepidogalaxiidae + Galaxiidae are holophyletic. If each synapomorphy were given equal weight, then the latter is preferred (four synapomorphies versus two). However, the nature of the synapomorphies and the amount of confidence that can be placed in them precludes such an easy decision. For instance, nearly every synapomorphy does not apply to all members of one of the groups examined (the origin and shape of the *levator arcus palatini*, for example, was similar in *Lepidogalaxias* and most, but not all galaxiids, the exception being *Brachygalaxias*). Also, in some of the smaller species (especially *Lovettia*) it was difficult to be sure of some of the character states (for example, the presence or absence of a dorsomedial subdivision of the *adductor mandibulae*). For these reasons evidence from the muscles appears to marginally support the hypothesis that the Lepidogalaxiidae + Galaxiidae are sister taxa.

In contrast, evidence from the bones relatively strongly supports the hypothesis that the Galaxiidae + Aplochitonidae are sister taxa. The synapomorphies supporting this hypothesis are more numerous (seven versus three for the alternate), more clearly definable, and among the most distinctive and complex in all the Salmoniformes (in particular, the unique ligament extending between the palatine and quadrate, and the highly specialized mesopterygoidal teeth and bite). Because complex character states are less likely to have evolved more than once (and therefore are less likely to exhibit parallelism) they are more reliable indicators of phylogenetic relationships. Therefore, based primarily on the evidence from the bones, I prefer the hypothesis that the Galaxiidae + Aplochitonidae are sister taxa, and that the Lepidogalaxiidae are their sister group. However, because *Lepidogalaxias* closely resembles some galaxiids in numerous characters, especially those of the muscles, more galaxiids should be examined before firmer conclusions can be drawn. In particular, the holophyly of the Galaxiidae should be rigorously tested, since if they are not holophyletic, *Lepidogalaxias* may prove to be more closely related to some galaxiids than to others.

Argentinoidei

The bones of the suspensorium weakly support the hypothesis that the Argentinoidei (*sensu* Greenwood and Rosen 1971) are holophyletic. However, the muscles, in particular the *adductor mandibulae*, corroborate and strengthen this hypothesis.

The *adductor mandibulae* in the Argentinoidei is unique, and exhibits a number of character states that can ultimately be derived from the primitive (ancestral) state found in the outgroups. The morphoclinal series depicting the hypothetical pathways of evolutionary change of this muscle, and its ligaments, was discussed in an earlier section. The primitive character state, from which the patterns in the Argentinoidei were ultimately derived, was probably similar to that in the Osmeridae, Salangidae, Retropinnidae, Prototroctidae, and some Salmonidae (*Prosopium* and *Stenodus*) among the salmoniforms (which in turn is similar to that in the primitive clupeomorphs and elopomorphs). Primitively, there is only one external division of the *adductor mandibulae* (section A2) that inserts onto the lower jaw, and is connected to the maxilla at the same time via the maxilla-mandibular ligament (refer to Fig. 103). A posteroventral extension of this ligament also directly connects the *adductor mandibulae* (and the maxilla) to the lateral surface of the angulo-articular bone of the lower jaw (L.y on Fig. 103). The character states in the Argentinoidei can be derived from this primitive pattern by initially losing the L.y section of the maxilla-mandibular ligament, so that the muscle inserts directly onto the maxilla via the remaining ligament (L.x-L.z on Fig. 103). This character state is found in most Alepocephalidae and some Platytroctidae. Three alepocephalids that I examined (*Rouleina, Narcetes,* and *Xenodermichthys*, see Figs. 74, 75), and one platytroctid (*Mirorictus*, see Fig. 85) appear to represent an intermediate condition in which section L.y is in the process of being lost: in these genera it is present but is thin, delicate, and indistinct (less so in *Mirorictus*).

The loss of the posteroventral extension (section L.y on Fig. 103) of the maxilla-mandibular ligament, the part that is connected to the lateral surface of the angulo-articular bone of the lower jaw, is therefore a synapomorphy uniting the Argentinoidei because it is the first step in the transformation series. Once section L.y has been lost, the patterns in the other Argentinoidei can be derived by: having the dorsolateral part of section A2 of the *adductor mandibulae* completely subdivide to produce a separate A1 subdivision that inserts ligamentously onto the upper jaw, with section A2 inserting onto the lower jaw (as in most Platytroctidae and some Alepocephalidae); or else having the *adductor mandibulae* remain undivided, and losing the entire maxilla-mandibular ligament, so that section A2 inserts only onto the lower jaw (as in the Argentinidae, Bathylagidae, and Opisthoproctidae).

The synapomorphy uniting the Argentinoidei (loss of section L.y of the maxilla-mandibular ligament) is not shared with any other salmoniforms. It is also unlike the character state found in the more primitive higher teleosts, such as the Stomiiformes, Aulopiformes, and Myctophiformes (see Figs. 92, 93; also see Rosen 1973; Winterbottom 1974a; Fink and Weitzman 1982). Primitively in these groups there is a complete maxilla-mandibular ligament that extends from the maxilla to the angulo-articular bone, with a subdivision of the *adductor mandibulae* inserting directly along it. In other words, sections L.x and L.y are present, but the separate L.z section, which connects it to the anterior end of the *adductor mandibulae* in the primitive teleosts, is absent because the muscle has encroached onto section L.x-L.y

The Argentinoidei might also be united on the basis of their having lost the supramaxillary ligament that extends from the anterior tip of the supramaxilla to the lower jaw. This ligament was present only in *Photostylus* and *Platytroctes* among the alepocephaloids I examined (what might be called vestiges were found in a few others). However, because this character state was found in numerous other salmoniforms, from each major assemblage, and is prone to parallelism, it is not a reliable indicator of phylogenetic relationship.

Alepocephaloidea

Evidence from the muscles supports the hypothesis that the Alepocephaloidea (Alepocephalidae + Platytroctidae) are holophyletic.

The shared derived character states that unite the Alepocephalidae + Platytroctidae include the following:

1. The *adductor arcus palatini* (AAP) inserts only on the medial surface of the hyomandibular, onto and dorsal to a ridge (Hm.ap on Figs. 34 and 42) that is oriented roughly anteroposteriorly from the anterior lamina to the opercular arm. No other salmoniforms shared this character state. Primitively the AAP inserts on both the hyomandibular and metapterygoid, and there is no anteroposterior ridge on the medial surface of the hyomandibular. In some salmoniforms (the umbrids *Novumbra* and *Dallia*) the AAP did not insert onto the metapterygoid, but in these species the insertion included the mesopterygoid and hyomandibular (the metapterygoid was reduced), and there was no anteroposterior ridge on the hyomandibular. In no other teleosts that I examined did the AAP insert exclusively on the medial surface of the hyomandibular and onto a distinct anteroposterior ridge on the hyomandibular at the same time. In some stomiiforms (*Diplophos, Vinciguerria, Argyropelecus*) the AAP inserts only onto the hyomandibular but there was no anteroposterior ridge on the medial surface of the bone (pers. obs.). In addition, in other stomiiforms (*Chauliodus* and *Tactostoma*) the insertion was on both the hyomandibular and metapterygoid, suggesting that perhaps the former character state is an autapomorphy within the order. An anteroposterior ridge onto which the AAP inserted was also present on the medial surface of the hyomandibular in two relatively derived osmerids, *Thaleichthys* (see Fig. 16) and *Osmerus*; however, in both the ridge was shorter than in most alepocephaloids (extending only along the opercular arm) and the AAP inserted extensively on the medial surface of the metapterytoid.

   In three of the twelve alepocephalid genera (*Talismania, Binghamichthys*, and *Leptoderma*) and one of the platytroctid genera (*Mirorictus*) that I examined the AAP inserted onto the medial surface of the posterodorsal part of the metapterygoid, in addition to the hyomandibular. However, in these genera the AAP inserted onto a ridge on the hyomandibular as in the other alepocephaloids. In the primitive sister genus of *Leptoderma, Conocara*, the AAP inserted only on the hyomandibular but was adjacent to the metapterygoid, suggesting that the character state in *Leptoderma* might be an autapomorphy. An anteroposterior ridge of some kind was present on the medial surface of the hyomandibular in all alepocephaloids that I examined except for the platytroctid *Pellisolus facilis*.

2. The *levator arcus palatini* (LAP) inserts along and dorsal to a well-developed ridge (Mt.m on Figs. 34 and 42) on the medial surface of the metapterygoid that extends posteroventrally from near the anterodorsal corner to the posterior edge of the bone. Primitively the LAP inserts onto the medial surface of the metapterygoid, but not onto a well-developed ridge. Among the other salmoniforms a similar ridge was found only in the Osmeridae and Plecoglossidae; however, it differs from that in the Alepocephaloidea in that the *adductor arcus palatini* (AAP), instead of the LAP, inserts along it. In addition, the posterior end of the medial ridge in the Osmeridae and Plecoglossidae is expanded into a laminar wing that overlaps the ventral arm of the hyomandibular.

There were a few exceptions in the Alepocephaloidea. In the alepocephalids *Talismania*, *Bathylaco* ...

There were a few exceptions in the Alepocephaloidea. In the alepocephalids *Talismania*, *Binghamichthys*, and the platytroctid *Mirorictus*, the medial ridge on the metapterygoid is occupied by the AAP, and the LAP is restricted to the posterodorsal corner of the metapterygoid. This character state is somewhat reminiscent of that in the Osmeridae and Plecoglossidae, except that in the latter two families the LAP inserts on the lateral surface of the metapterygoid, unlike the alepocephaloids in which it inserts only on the medial side. The medial ridge is reduced in the alepocephalid *Conocara* and its sister genus *Leptoderma* (see Fig. 41). In *Leptoderma* the LAP does not insert onto the metapterygoid at all, whereas in *Conocara* the insertion of the LAP includes the medial surface of the posterodorsal corner of the bone (but not the "ridge").

No other salmoniform had a character state like that found in the alepocephaloids, nor did any other teleost. The character state in some stomiiforms (*Diplophos* and *Vinciguerria*) and the Myctophiformes that I examined was superficially similar but, upon closer examination, the insertion is on the medial surface of a triangular, dorsolaterally directed flange (Mt.d on Fig. 51) on the posterodorsal corner of the metapterygoid, and on the laminar expansion medial to it. In no stomiiform or myctophiform was there a medial dermal ridge on the metapterygoid similar to that in the alepocephaloids.

Evolutionary trends in the Alepocephaloidea

In addition to the aforementioned synapomorphies, there are two evolutionary trends in the Alepocephaloidea that suggest that it is a holophyletic group: most Alepocephalidae and Platytroctidae have a separate *adductor hyomandibulae*; and most Platytroctidae, and some Alepocephalidae, have a separate dorsolateral (A1) subdivision of the *adductor mandibulae* that inserts ligamentously onto the upper jaw.

Adductor Hyomandibulae. Of the twelve alepocephalid genera that I examined, eight (*Alepocephalus, Rouleina, Xenodermichthys, Narcetes, Photostylus, Bathylaco, Talismania,* and *Binghamichthys*) had a sepatate *adductor hyomandibulae* (AH), it was debatably incipient in one (*Conocara*), two (*Bathytroctes, Leptoderma*) lacked an AH, and in one (*Bajacalifornia*) the *adductor operculi* was fused with the AH. Markle (1976) also claimed that a separate AH was present in *Asquamiceps, Einara, Ericara, Bathyprion,* and *Leptochilichthys*, and contrary to my observations, in *Bathytroctes, Leptoderma,* and *Conocara*. Of the six platytroctid genera that I examined, four (*Holtbyrnia, Pellisolus, Mirorictus,* and *Searsia*) had a separate AH, one lacked it (*Platytroctes*), and it was debatably incipient in another (*Searsioides*). Among the other salmoniforms, a separate AH was found in the esocoids *Esox* and *Dallia*, the Thymallinae and Salmoninae among the salmonids, the osmerids *Spirinchus* and *Thaleichthys*, and the Retropinnidae and Prototroctidae.

Because of the mosaic distribution of the AH in the alepocephaloids (and in the other salmoniforms), and because the interrelationships of its genera are poorly known, it is difficult to speculate as to whether or not it was present in the common ancestor of the group, and was then lost independently in some lineages (i.e., it is a synapomorphy of the Alepocephaloidea); or was absent in the common ancestor and evolved independently in the various lineages (as appears to be the case in some of the other salmoniforms).

A1 Subdivision of the *Adductor Mandibulae*. Another evolutionary trend is for the development of a separate dorsolateral (A1) subdivision of the *adductor mandibulae* that inserts ligamentously directly (and only) onto the upper jaw (when an A1 subdivision is present section A2 inserts only onto the lower jaw). A separate A1 subdivision is found in four (*Talismania*, *Binghamichthys*, *Leptochilichthys*, and *Bathylaco*) of the twenty-six alepocephalid genera (pers. obs.; Markle 1976, 1980; Markle and Merrett 1980) and was present in five (*Holtbyrnia*, *Platytroctes*, *Sagamichthys*, *Searsia*, and *Searsioides*) of the seven platytroctid genera that I examined (see Figs. 76-78, 82-84). As I discussed earlier, section A1 could be derived directly from a character state similar to that found in most alepocephalids and some platytroctids by having the dorsolateral part of section A2 completely subdivide.

If one accepts the hypothesis that the Platytroctidae are holophyletic (as I tentatively do), then one must conclude that section A1 was independently evolved in the platytroctids and in the alepocephalids. Because of this, the presence of section A1 cannot be used as a synapomorphy uniting the two families; however, one can state that there is a definite tendency in the Alepocephaloidea for the development of this muscle.

No other salmoniform has a separate A1 subdivision of the *adductor mandibulae*. Section A1 is present in a few lower teleosts, and in most higher teleosts. However, these character states do not appear to be homologous with that in the alepocephaloids, primarily because of differences in position, and because other evidence suggests the other teleosts with section A1 belong in other assemblages.

Among the lower teleosts, most Ostariophysi have an A1 subdivision, but it is located ventrolateral to section A2 (rather than dorsolateral as in the alepocephaloids), and appears to be a synapomorphy of the group (see Winterbottom 1974a; Fink and Fink 1981; Howes 1985). A similar subdivision is present in the derived elopomorph family Notacanthidae (see Greenwood 1977). Some engraulids (Clupeomorpha) have an A1 subdivision that lies lateral to the middle (*Amentum devisi*) or ventral two thirds (*Anchoa mundeoloides*) of section A2 and inserts ligamentously onto the maxilla (pers. obs.). However, its presence may be an autapomorphy of some engraulids since it was absent in the engraulid *Thryssa hamiltoni* and the other clupeomorphs that I examined. Apparently, it is also absent in the Denticipitidae, the primitive sister group of all other extant clupeomorphs (see Greenwood 1968).

An A1 subdivision of some kind is present in most higher teleosts (pers. obs.; also see Rosen 1964; Rosen and Patterson 1969; Rosen 1973; Winterbottom 1974a; Stiassny 1981; Fink and Weitzman 1982). However, the character state in most (including the more primitive neoteleosts) is unlike that found in the alepocephaloids. For example, in all Stomiiformes and the Myctophidae (Myctophiformes) section A1 is found medial to section A2, rather than dorsolateral to it (pers. obs.; also see Rosen 1973; Winterbottom 1974a; Fink and Weitzman 1982). In addition, in most Stomiiformes the muscle inserts directly along the posterior end of the maxilla-mandibular ligament that extends between the maxilla and lower jaw (see Figs. 92, 93). The Aulopiformes and the Neoscopelidae (Myctophiformes) as well as numerous Acanthopterygii and Paracanthopterygii have an A1 section that lies dorsolateral to section A2, but it also inserts directly along the posterior end of the maxilla-mandibular ligament (e.g., see Rosen 1973; Winterbottom 1974a).

Alepocephaloid Interrelationships

Although my data support the hypothesis that the Alepocephaloidea are holophyletic, there is no evidence from either the bones or muscles supporting the hypothesis that the Alepocephalidae are holophyletic, or that the Platytroctidae are holophyletic. I tentatively accept the hypothesis that the Platytroctidae are holophyletic, primarily on the basis of their possessing a unique character called the "shoulder organ" (see Matsui and Rosenblatt 1987). However, because there is no evidence of any kind supporting the holophyly of the Alepocephalidae (also see Markle 1976), it is possible that some alepocephalids are more closely related to the Platytroctidae than are others (i.e., the Alepocephalidae are probably a paraphyletic group).

If the Platytroctidae are assumed to be holophyletic, then a rough phylogeny of the seven platytroctid genera that I examined emerges, based on the muscles. Because I examined [illegible] half of the genera in the family this phylogeny is not definitive, but should serve as a [illegible] point for future work. This evidence suggests that *Mirorictus* is the primitive sister group of the other six genera, and that *Pellisolus* in turn is the sister group of *Searsia* + *Searsioides* + *Holtbyrnia* + *Sagamichthys* + *Platytroctes*. *Pellisolus* and the latter five genera are united on the basis of their lacking the posteroventral part of the maxilla-mandibular ligament (L.y on Fig. 103) that attaches to the angulo-articular bone (see Figs. 82-84, 86). Section L.y was present, but poorly-developed, in *Mirorictus* (see Fig. 85). Another possible synapomorphy uniting *Pellisolus* + *Searsia* + *Searsioides* + *Holtbyrnia* + *Sagamichthys* + *Platytroctes* is the shape of the *levator arcus palatini*; in *Mirorictus* it is conical (the primitive character state) whereas in the other genera it is barrel-shaped. *Searsia* + *Searsioides* + *Holtbyrnia* + *Sagamichthys* + *Platytroctes* are united on the basis of their having an A1 subdivision of the *adductor mandibulae*, but their relationships to one another remain unresolved, and hence they form an unresolved polychotomy.

Among the Alepocephalidae, the muscles helped to define a few subgroups within the family, and suggested possible future areas of research. For example, evidence from the muscles corroborated my hypothesis that *Leptoderma* + *Conocara* are sister taxa, including:

1. The *levator operculi* (LO) is unusually narrow and inserts onto a small area on the dorsomedial edge of the middle of the operculum. In the other alepocephalids (i.e., the primitive character state) the LO is broader and inserts onto a much larger area of the operculum (at least the posterior half of its dorsomedial edge, but usually more).
2. The anterior end of the maxilla-mandibular ligament (that connects the similarly shaped *adductor mandibulae* directly with the maxilla) inserts onto a well-developed, and similarly-shaped knob on the dorsolateral surface of the anterior end of the maxilla (compare Figs. 80 and 81). In the other alepocephaloids, and most Stomiiformes, the insertion is farther posteriorly, and not onto a knob. However, the polarity of this character state is somewhat uncertain since it appears that primitively in the

salmoniforms, and the other lower teleosts, the insertion is similar to that in *Leptoderma* and *Conoçara*.

Among the other alepocephalids, my evidence suggests that *Narcetes* + *Rouleina* may be sister groups. They share a *levator operculi* (LO) with a posterior subdivision that originates from the lateral surface of the supracleithrum of the pectoral girdle and inserts on the medial surface of the posterodorsal corner of the operculum, and a larger anterior subdivision (the LO found in most salmoniforms) whose origin includes the lateral surface of the epaxial muscle mass next to the pterotic. The only other salmoniform with a posterior subdivision of the LO is the esocoid *Esox* (but the origin was on the post-temporal). However, part of the LO originates from the epaxial muscles in the alepocephalid *Bathylaco*, suggesting that *Bathylaco* may be related to *Narcetes* and *Rouleina*.

It may be that *Talismania* + *Binghamichthys* + *Bathylaco* + *Leptochilichthys* form a holophyletic group since they share an A1 subdivision of the *adductor mandibulae*. However, section A1 in *Bathylaco* is different from that in the other three genera; it is much narrower and is subdivided, at least in smaller specimens (see Fig. 78). In addition, in larger specimens of *Bathylaco* section A1 (Markle calls it the α subdivision of section A2) is apparently broader, not subdivided, and inserts directly along the maxilla (see Markle 1976). This suggests that the character state in *Bathylaco* may not be homologous with that in the other three genera and may not be indicative of relationship with them. Section A1 in *Leptochilichthys* (see Markle, fig. 5A) is similar to that in *Talismania* and *Binghamichthys* (both pers. obs.), but unlike the latter two genera (and all other salmoniforms except for *Esox*), section A2 is subdivided. Markle placed *Leptochilichthys* in its own family; however, it may be that it is more closely related to some alepocephalids (*Talismania* and *Binghamichthys*?) than to others since the Alepocephalidae appear to be paraphyletic.

Argentinoidea

Evidence from the muscles supports the hypothesis that the Argentinidae + Bathylagidae + Opisthoproctidae form a holophyletic group (the Argentinoidea) within the

Argentinoidei. The shared derived character states of the muscles that unite the Argentinoidea include the following:

1. The *adductor mandibulae* inserts directly onto the lower jaw, and has no ligamentous connection with the maxilla (see Figs. 87-89). Associated with this character state is the absence of supramaxillae (and of course, the supramaxillary ligament). *Bathylagus* has a remnant of the maxilla-mandibular ligament that joins the *adductor mandibulae* to the maxilla. However, this ligament is of doubtful functional significance because of its position and size, and appears to be in the process of being lost. Primitively in the salmoniforms, the *adductor mandibulae* inserts onto the lower jaw and is connected to the maxilla at the same time via a well-developed maxilla-mandibular ligament. In addition, two supramaxillae (one or two in the alepocephaloids) are present and there is a supramaxillary ligament (but not in the alepocephaloids).

   The derived character state is shared with the Esocoidei and most Salmonidae; however, in these salmoniforms one supramaxilla is present (except for the esocoid *Umbra*, which has none).

2. The *adductor arcus palatini* inserts on the dorsal surface of the mesopterygoid (in addition to the hyomandibular and metapterygoid). However, this character state is shared with three other salmoniform lineages: the Esocoidei, the Salmoninae, and the Lepidogalaxiidae + Galaxiidae + Aplochitonidae. The primitive character state was discussed earlier.

3. The tendinous aponeurosis onto which the medial fibres of section A2 of the *adductor mandibulae* inserts does not bifurcate anteriorly and inserts only onto the coronomeckelian bone on the medial surface of the lower jaw. This character state is shared only with *Lepidogalaxias* among the other salmoniforms. In the primitive character state the tendinous aponeurosis bifurcates anteriorly: the anterior end of the longer dorsal section inserts onto Meckel's cartilage and parts of the angulo-articular and dentary (usually) bones, whereas the ventral section inserts primarily on the coronomeckelian bone.

4. The area of origin of the *adductor mandibulae* includes part of the dorsolateral surface of the mesopterygoid. The only other salmoniform with this character state was *Esox* (Esocidae).

Bathylagidae + Opisthoproctidae

Two shared derived character states of the muscles unite the Bathylagidae and Opisthoproctidae, corroborating my preferred hypothesis that they are sister groups:

1. The *adductor arcus palatini* (AAP) inserts on a large part of the dorsal surface of the mesopterygoid (most of the dorsomedial surface in the Bathylagidae, see Fig. 88; the posterior half of the dorsomedial surface in the Opisthoproctidae, see Fig. 89). The AAP inserts onto the mesopterygoid in the Argentinidae, but the area is much smaller, as is the case in most other salmoniforms in which the AAP inserts onto the mesopterygoid (the Esocoidei, Salmoninae, Lepidogalaxiidae, Galaxiidae, and Aplochitonidae). In the primitive character state the AAP does not insert on the mesopterygoid.
2. Only a small part (the Bathylagidae), or none (the Opisthoproctidae) of the *adductor mandibulae* inserts directly onto the medial surface of the lower jaw. This corresponds to the relatively small size of the Meckelian fossa in these two families when compared with that in the Argentinidae, and most other salmoniforms (the exceptions being the Lepidogalaxiidae, Plecoglossidae, and the umbrids *Dallia* and *Umbra*). In the Opisthoproctidae the entire *adductor mandibulae* is posterior to the lower jaw and the muscle inserts in the Meckelian fossa via tendons that pass into the Meckelian fossa. Primitively, the Meckelian fossa is relatively large, as is the part of the *adductor mandibulae* inserting into it.

I found no evidence from the muscles to link the Argentinidae and Opisthoproctidae. However, there was one synapomorphy uniting the Argentinidae + Bathylagidae: the ramus mandibularis of the trigeminal nerve first passes between the anterolateral surface of the tendinous aponeurosis and the anteromedial surface of section A2 of the *adductor mandibulae* before running medial to the lower jaw (i.e., the nerve passes medial to A2 before running medial to the lower jaw). This character state was shared with the Prototroctidae, Lepidogalaxiidae, Galaxiidae, and Aplochitonidae. Primitively, the nerve passes lateral to the anterior end of section A2 before running medial to the lower jaw. The primitive character state was found in the Opisthoproctidae and most other teleosts that I examined.

However, overall I prefer the hypothesis that the Bathylagidae + Opisthoproctidae are sister groups. Five synapomorphies (three from bones, and two from the muscles) support this hypothesis whereas only one (the path of the nerve) supports the alternate (that the Argentinidae + Bathylagidae are sister taxa). In addition to being more numerous, the synapomorphies of the bones that unite the Bathylagidae + Opisthoproctidae are not shared with the other salmoniforms. These facts suggest that the Bathylagidae + Opisthoproctidae are sister groups, and that the similarity that the Argentinidae shares with the Bathylagidae is an example of convergence.

(OSMEROIDS + GALAXIOIDS + ARGENTINOIDS) + NEOTELEOSTS

Although the bones of the suspensorium support the holophyly of this group I did not find any shared derived character state of the muscles that unites it. However, the pattern of the *adductor mandibulae* in the primitive neoteleosts could conceivably be derived from one similar to that found in the primitive members of the osmeroid + galaxioid + argentinoid assemblage, including: the Osmeridae, some Salangidae, the Retropinnidae, the Prototroctidae, and some primitive alepocephalids.

FIGURES

Figure 1. Cladistic relationships of the Teleostei. Hypothesis of euteleostean relationships is based on Rosen (1973); non-euteleostean relationships hypothesized by Patterson and Rosen (1977).

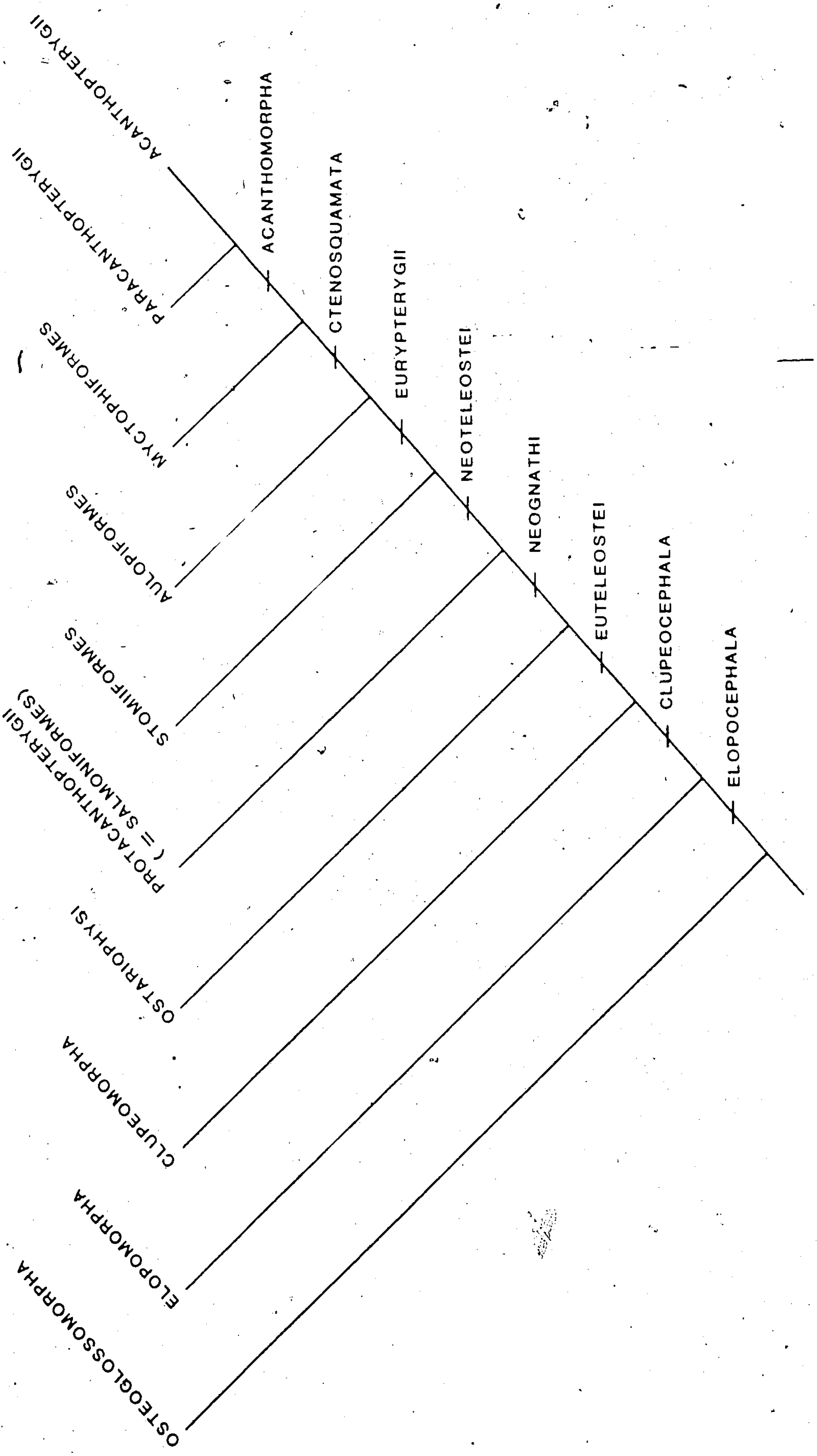

ACANTHOPTERYGII
PARACANTHOPTERYGII
MYCTOPHIFORMES
AULOPIFORMES
STOMIIFORMES
PROTACANTHOPTERYGII
(= SALMONIFORMES)
OSTARIOPHYSI
CLUPEOMORPHA
ELOPOMORPHA
OSTEOGLOSSOMORPHA
ACANTHOMORPHA
CTENOSQUAMATA
EURYPTERYGII
NEOTELEOSTEI
NEOGNATHI
EUTELEOSTEI
CLUPEOCEPHALA
ELOPOCEPHALA

Figure 2. Current hypotheses of the cladistic relationships of the salmoniform fishes (indicated by asterisks): (A) Rosen, 1974; (B) Fink and Weitzman, 1982; (C) Fink, 1984b; (D) Rosen, 1985. Hypothesis A is the only one that considers the order Salmoniformes to be holophyletic. In A the Esocae includes *Lepidogalaxias*, the Galaxiidae includes the aplochitonids, and the Osmeroidea includes the osmerids, *Plecoglossus*, the salangids, the retropinnids, and the prototroctids. In B the Osmeroidei includes the Osmeroidea and Galaxiidae of A. In C *Lepidogalaxias* is removed from the Esocae of hypotheses A and B, otherwise the species composition of the taxa is the same as in hypothesis B. In D *Lepidogalaxias* is excluded because its position is uncertain, otherwise the salmoniform taxa are as in hypothesis C; parentheses indicate Rosen's uncertainty about the holophyly of a taxon.

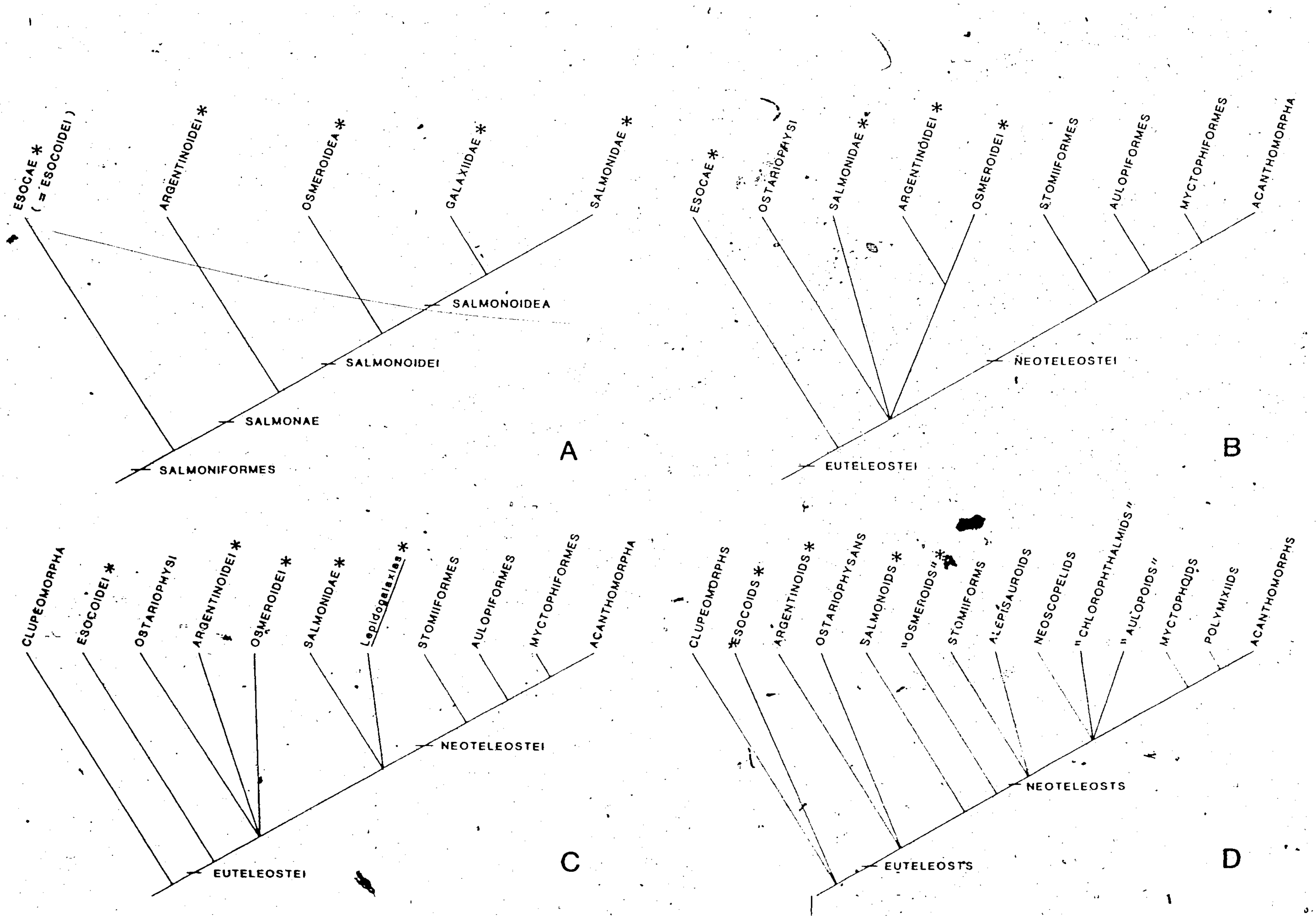
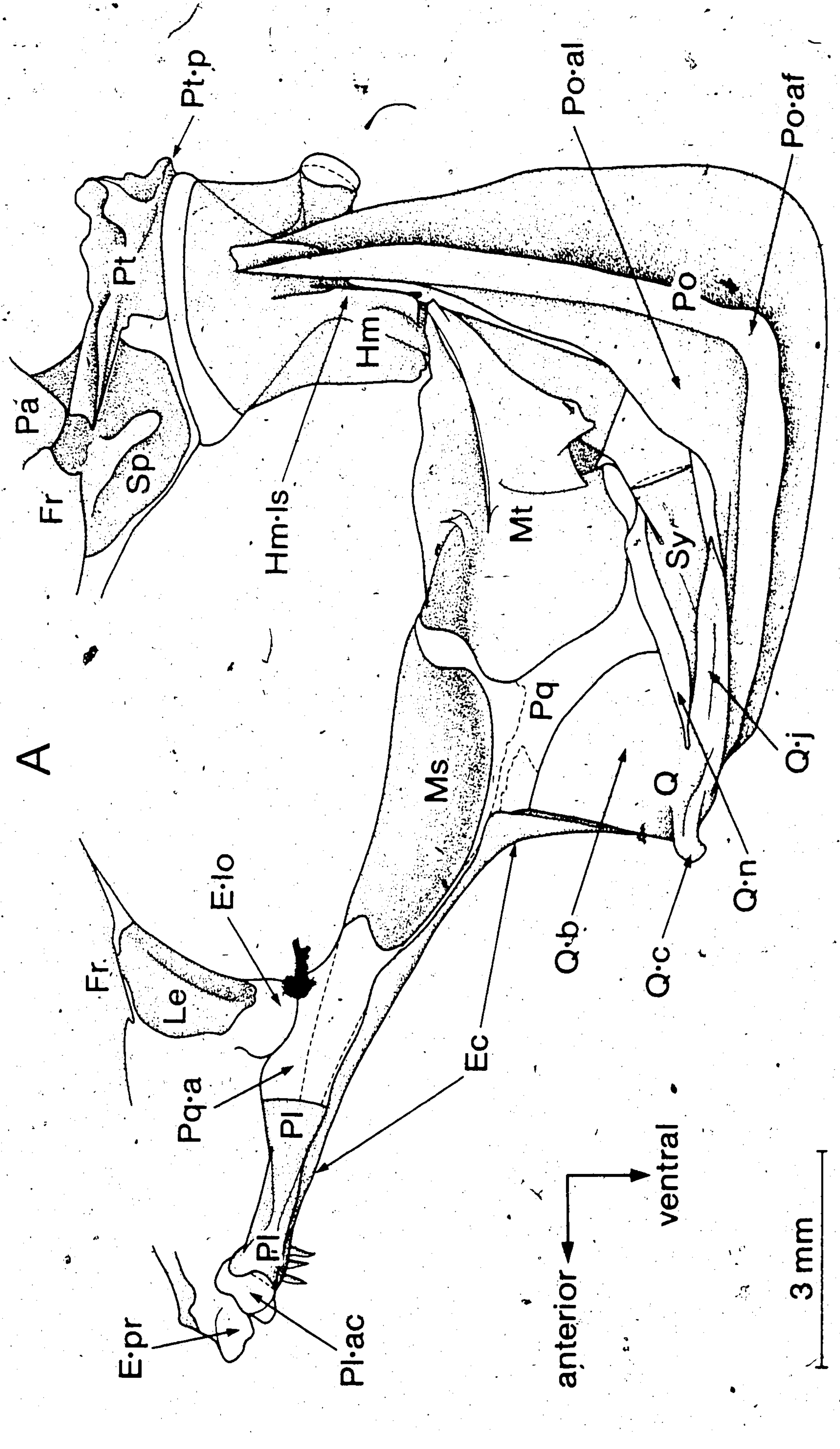

ESOCAE *
(= ESOCOIDEI)
ARGENTINOIDEI *
OSMEROIDEA *
GALAXIIDAE *
SALMONIDAE *
SALMONOIDEA
SALMONOIDEI
SALMONAE
SALMONIFORMES
A
ESOCAE *
OSTARIOPHYSI
SALMONIDAE *
ARGENTINOIDEI *
OSMEROIDEI *
STOMIIFORMES
AULOPIFORMES
MYCTOPHIFORMES
ACANTHOMORPHA
NEOTELEOSTEI
EUTELEOSTEI
B
CLUPEOMORPHA
ESOCOIDEI *
OSTARIOPHYSI
ARGENTINOIDEI *
OSMEROIDEI *
SALMONIDAE *
Lepidogalaxias *
STOMIIFORMES
AULOPIFORMES
MYCTOPHIFORMES
ACANTHOMORPHA
NEOTELEOSTEI
EUTELEOSTEI
C
CLUPEOMORPHS
ESOCOIDS *
ARGENTINOIDS *
OSTARIOPHYSANS
SALMONOIDS *
"OSMEROIDS" *
STOMIIFORMS
ALEPISAUROIDS
NEOSCOPELIDS
"CHLOROPHTHALMIDS"
"AULOPOIDS"
MYCTOPHOIDS
POLYMIXIIDS
ACANTHOMORPHS
NEOTELEOSTS
EUTELEOSTS
D

Figure 3. Lateral (A) and medial (B) views of the left suspensorium in *Hypomesus pretiosus* (Osmeridae) to illustrate the bones, cartilages, and subdivisions of both commonly referred to in the text. Bone is indicated by stippling, while clear areas on and around bones that are bordered by lines indicate cartilage. Lateral view is of the suspensorium attached to the skull, medial is after it was removed from the skull.


A
Pt·p
Pt
Pa
Fr
Sp
Hm·ls
Hm
Po·al
Po
Po·af
Mt
Sy
Pq
Ms
Q
Q·j
Q·n
Q·c
Q·b
Ec
E·lo
Fr
Le
Pq·a
Pl
Pl
Pl·ac
E·pr
anterior
ventral
3 mm

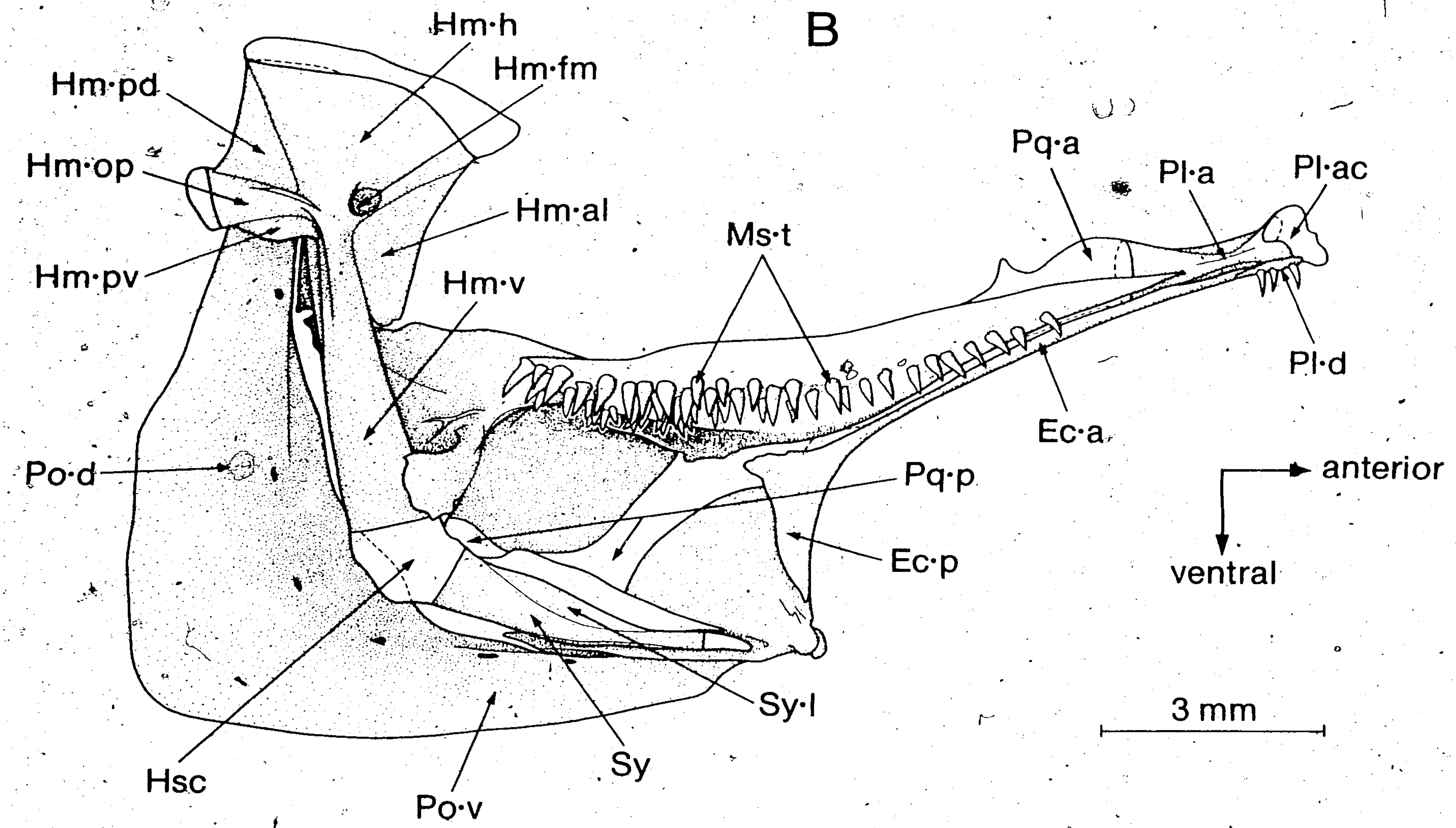
B
Hm·h
Hm·fm
Hm·pd
Hm·op
Hm·al
Hm·pv
Hm·v
Ms·t
Pq·a
Pl·a
Pl·ac
Pl·d
Ec·a
Po·d
Pq·p
Ec·p
anterior
ventral
Sy·l
Sy
Hsc
Po·v
3 mm

Figure 4. Lateral view of the external muscles of the left suspensorium in *Hypomesus pretiosus* (Osmeridae) to illustrate the elements commonly referred to in the text. Muscles are indicated by closely spaced lines (often curving) that run parallel to one another, ligaments and tendons are shown as short, closely spaced dashes, the mandibular branch of the trigeminal nerve is a thick black line, and bones are simply outined.

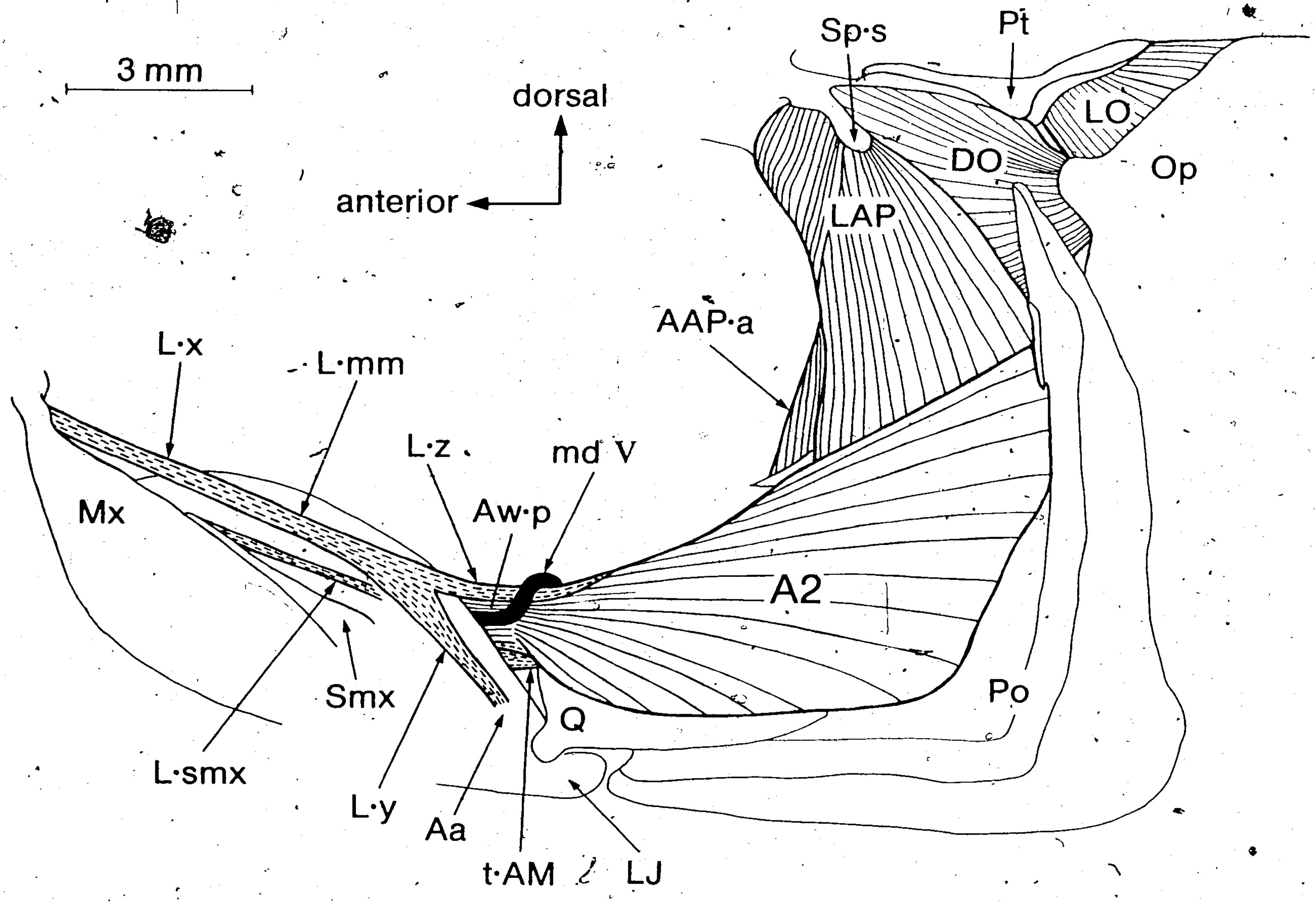
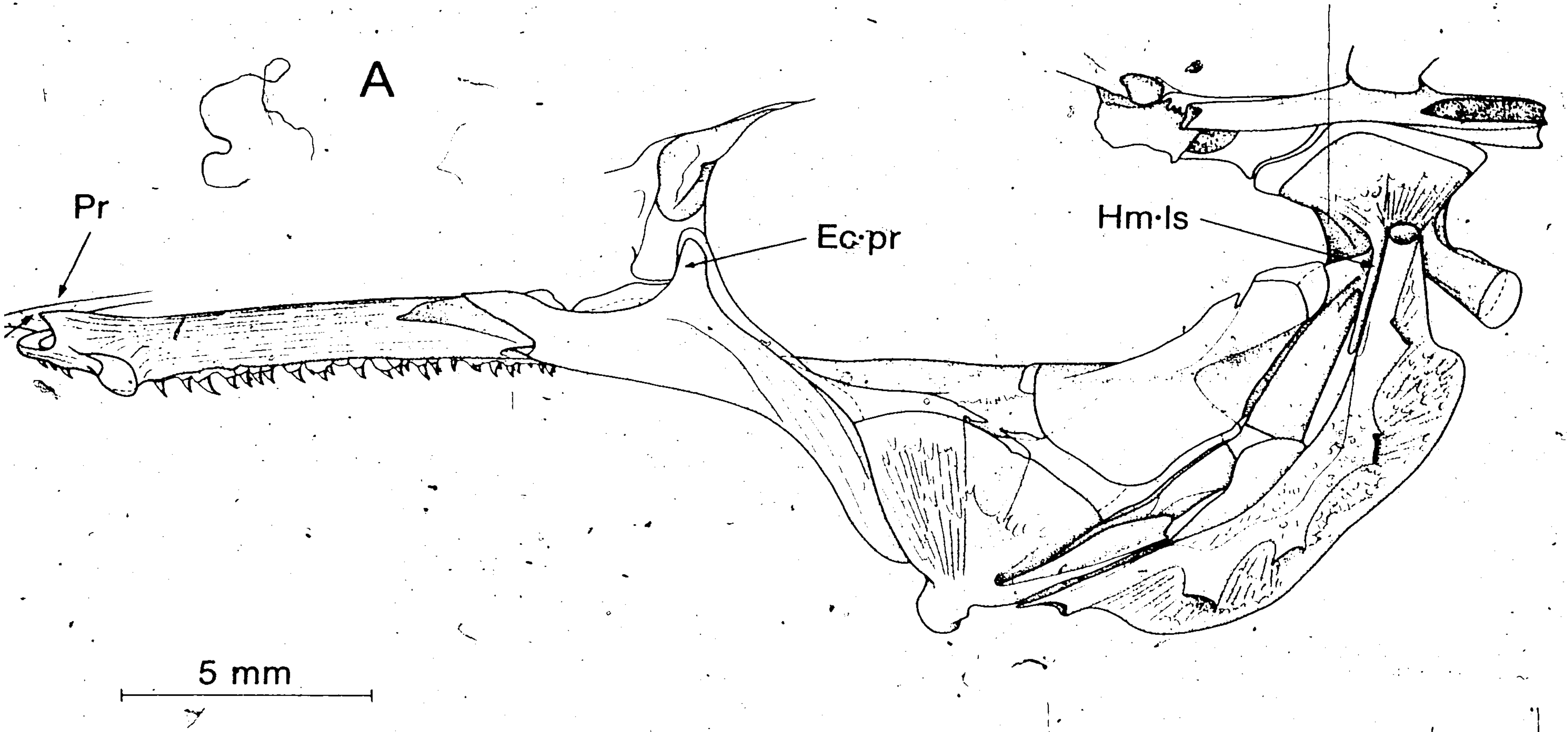
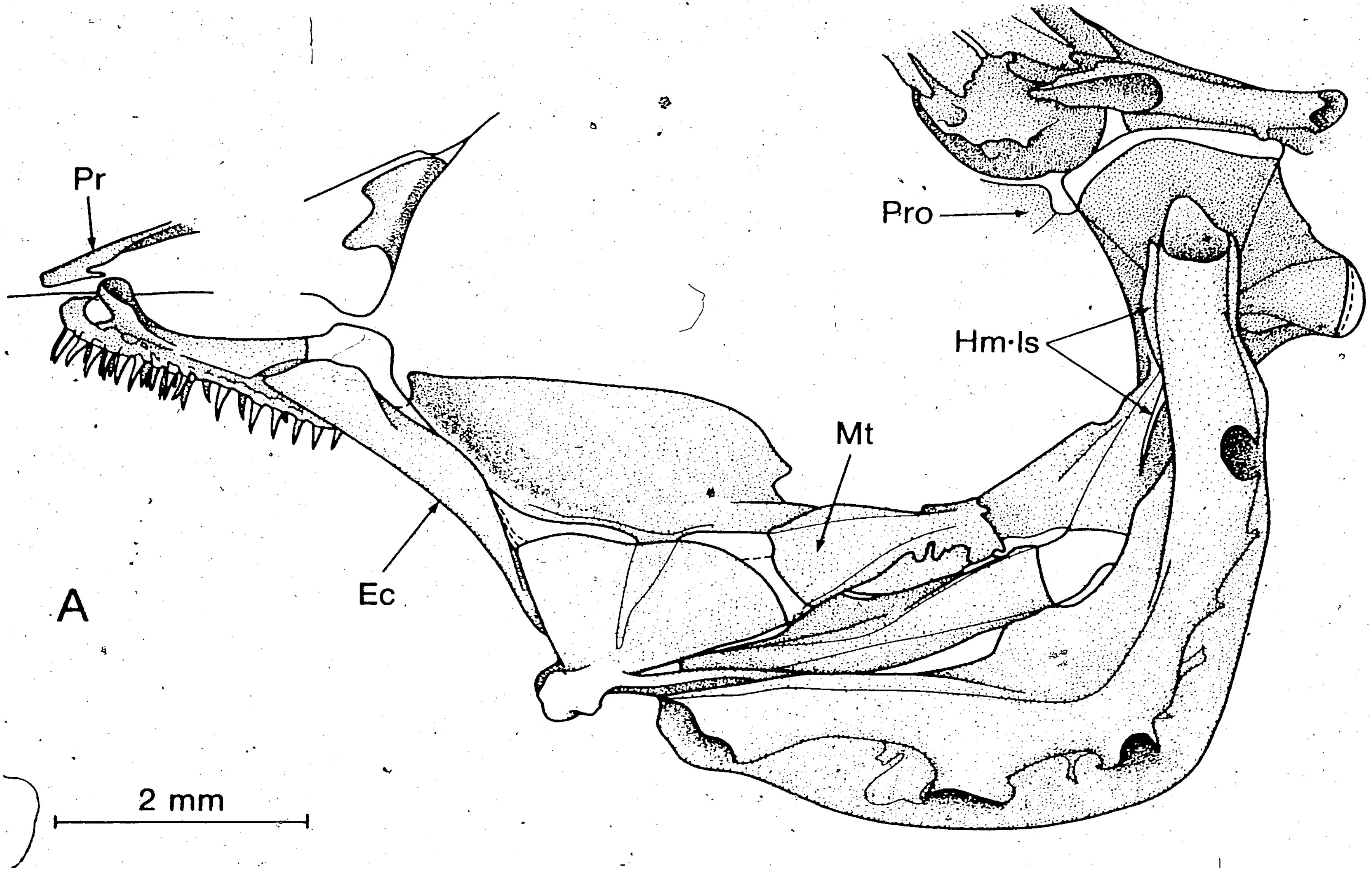

3 mm
dorsal
anterior
Sp·s
Pt
LO
DO
Op
LAP
AAP·a
L·x
L·mm
L·z
md V
Aw·p
Mx
A2
Smx
Po
Q
L·smx
L·y
Aa
t·AM
LJ

Figure 5. Lateral (A) and medial (B) views of the left suspensorium in *Esox lucius* (Esocidae).


A
Pr
Ec·pr
Hm·Is
5 mm


B
5 mm
Hm·aw

Figure 6. Lateral (A) and medial (B) views of the left suspensorium in *Novumbra hubbsi* (Umbridae).


Pr
Pro
Hm·Is
Mt
Ec
A
2 mm

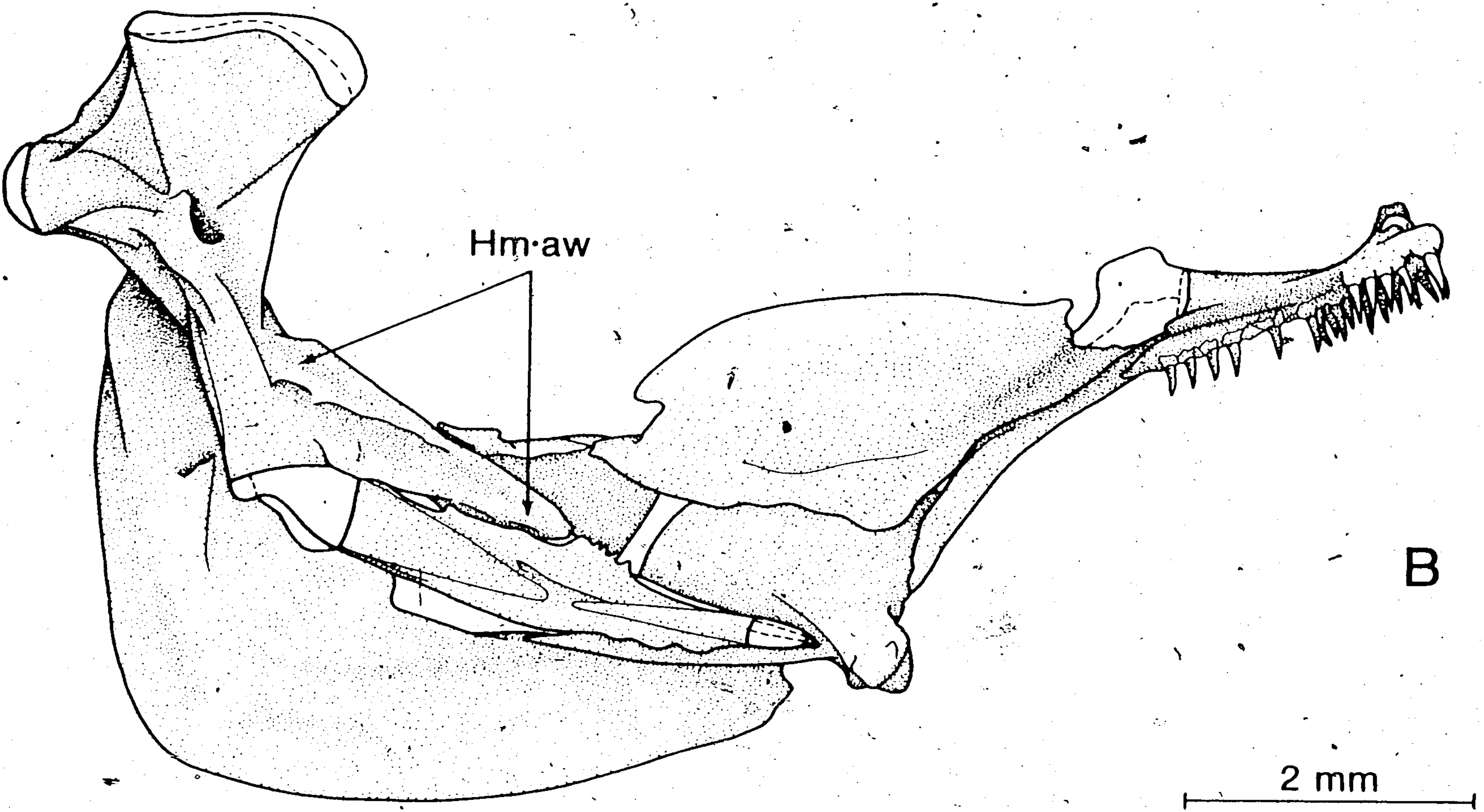
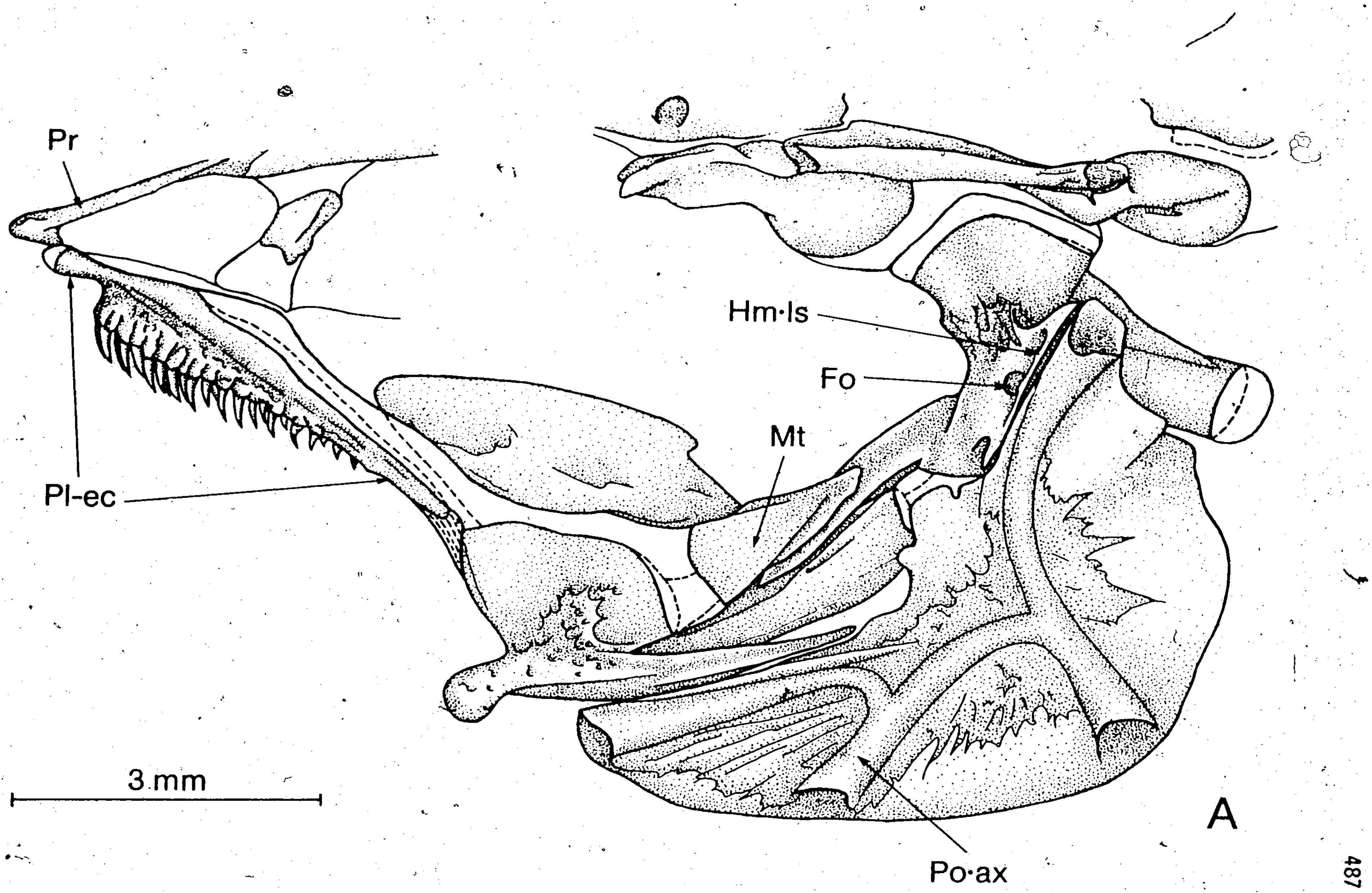

Hm·aw
B
2 mm

Figure 7. Lateral (A) and medial (B) views of the left suspensorium in *Dallia pectoralis* (Umbridae).


Pr
Pl-ec
Hm·Is
Fo
Mt
Po·ax
3 mm
A

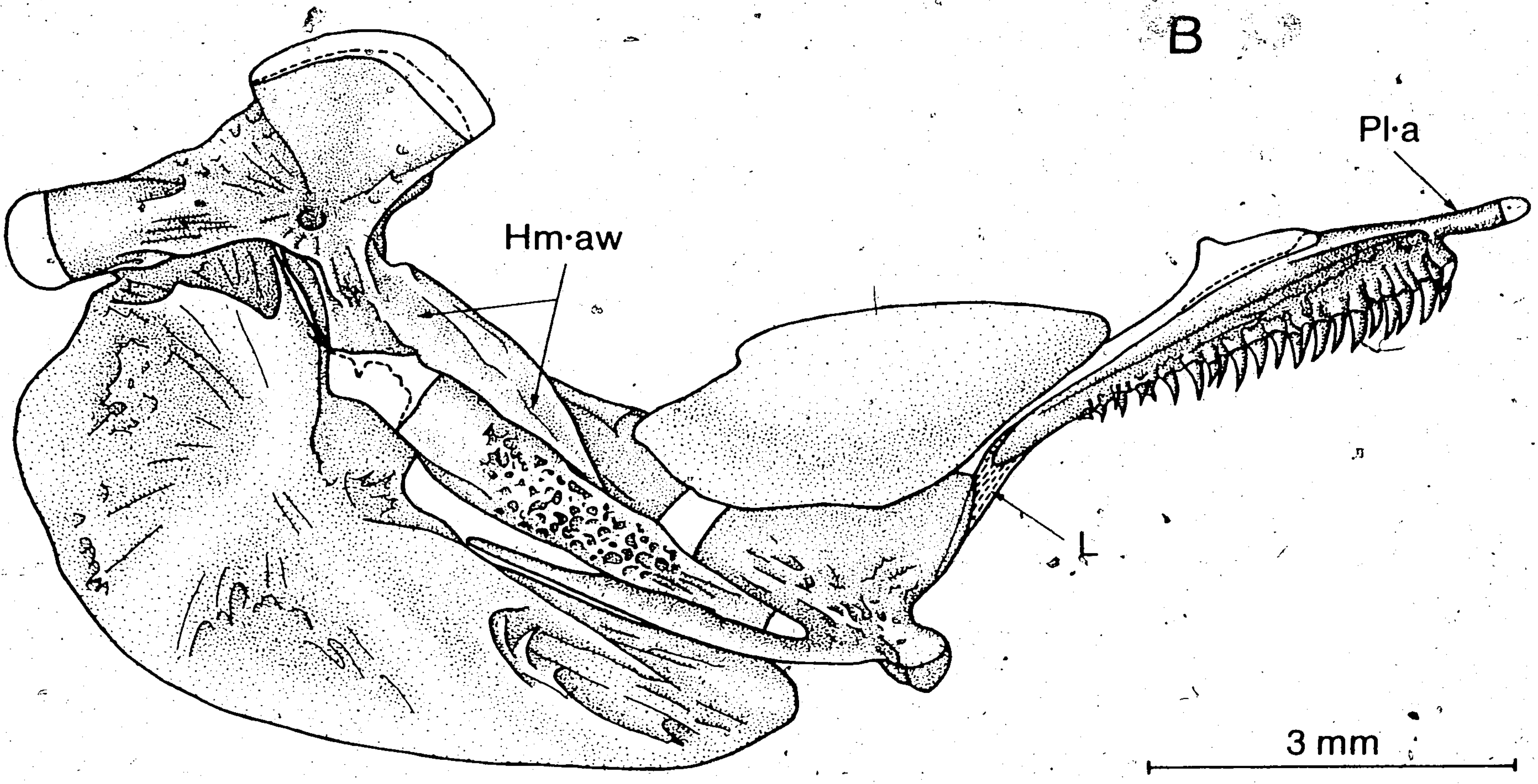

B
Pl·a
Hm·aw
L
3 mm

Figure 8. Left, fused palatine-ectopterygoid in *Dallia pectoralis* (Umbridae): (A) dorsolateral view; palatine-ectopterygoid attached to skull, nasal and circumorbitals obsuring its view omitted; (B) ventral view; suspensorium removed from skull.

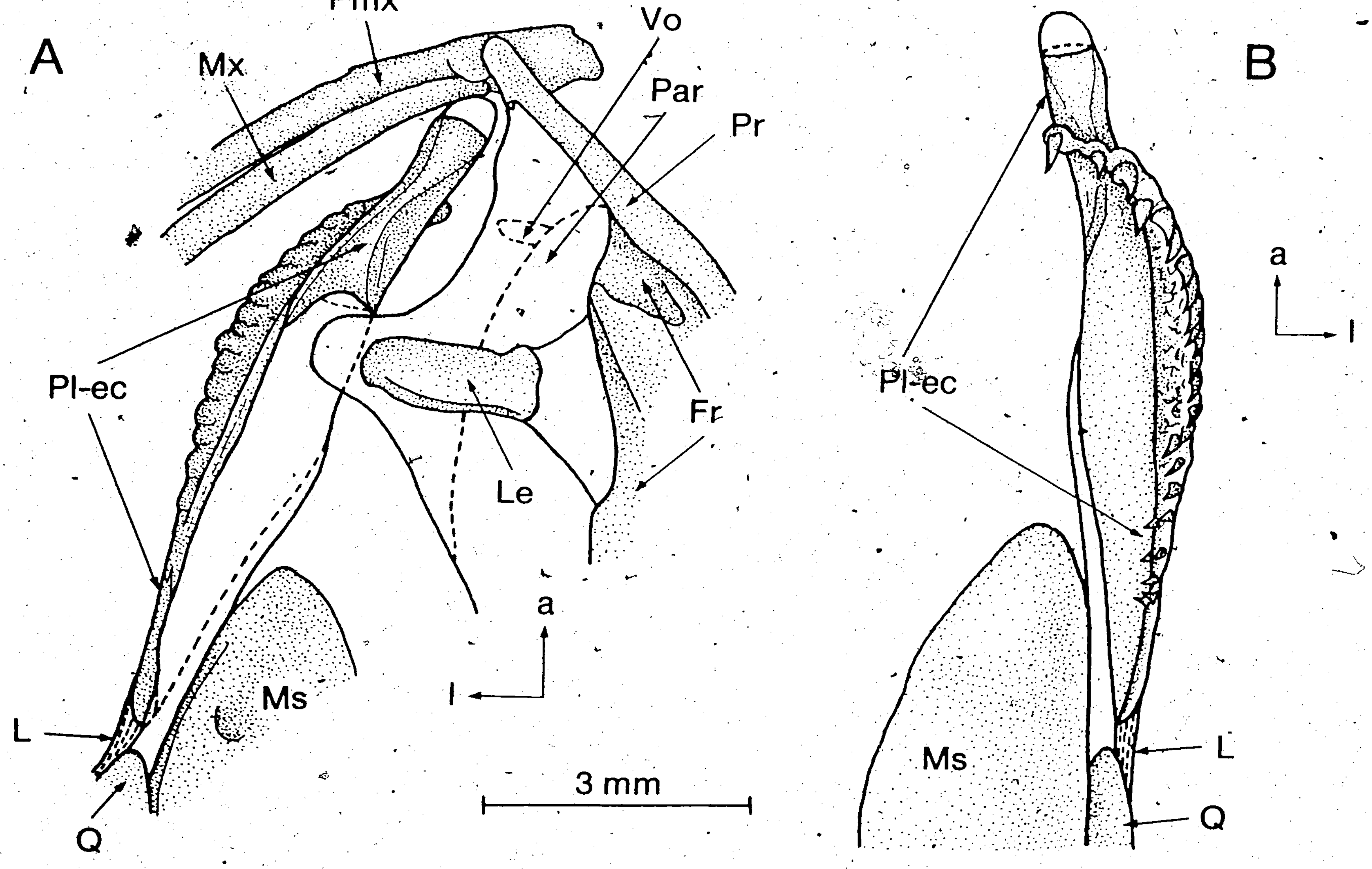
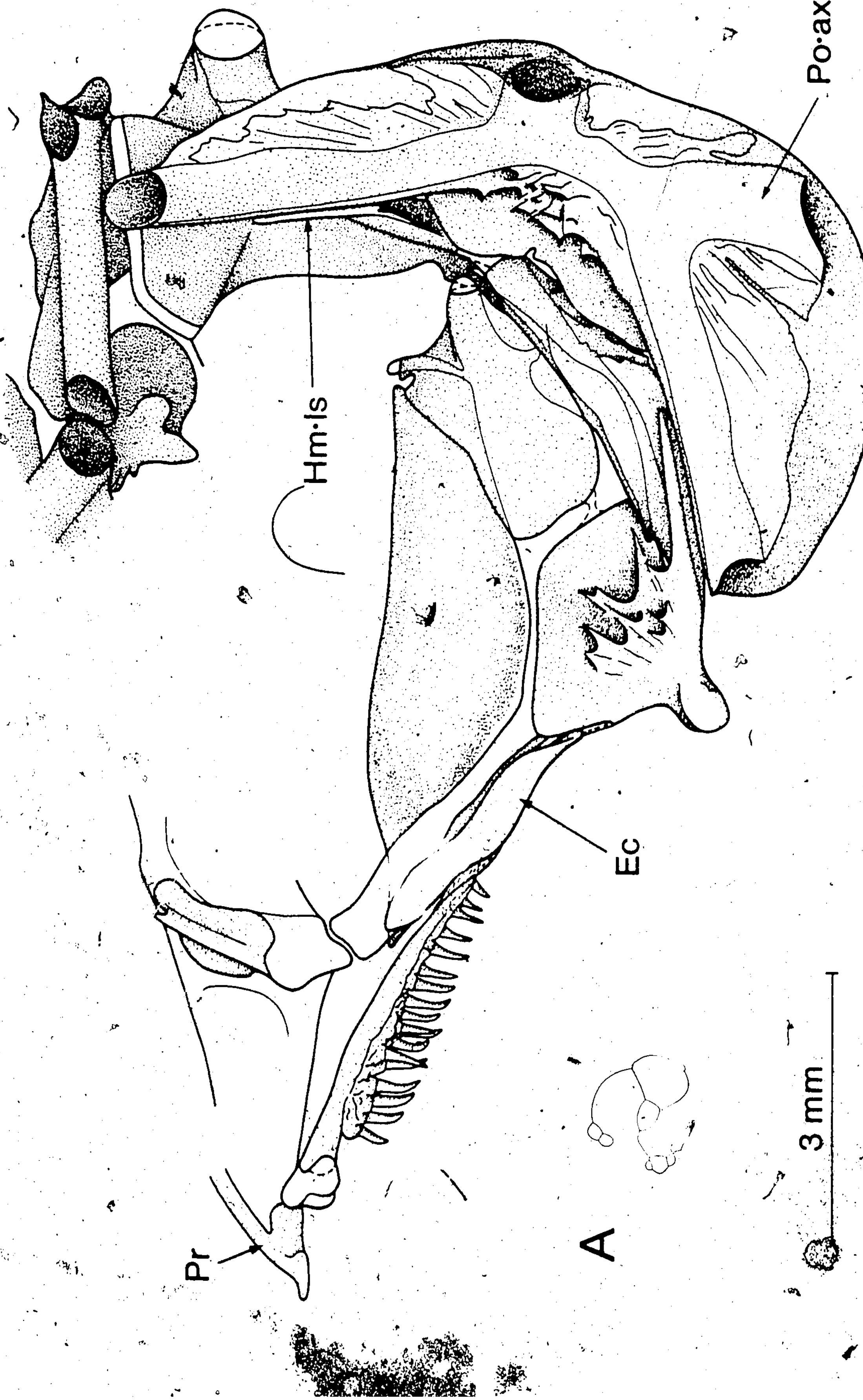

A
Pmx
Mx
Vo
Par
Pr
Pl-ec
Fr
Le
a
l
Ms
L
Q
3 mm
B
Pl-ec
a
l
Ms
L
Q

Figure 9. Lateral (A) and medial (B) views of the left suspensorium in *Umbra limi* (Umbridae).


Po·ax
Hm·ls
Ec
Pr
A
3 mm

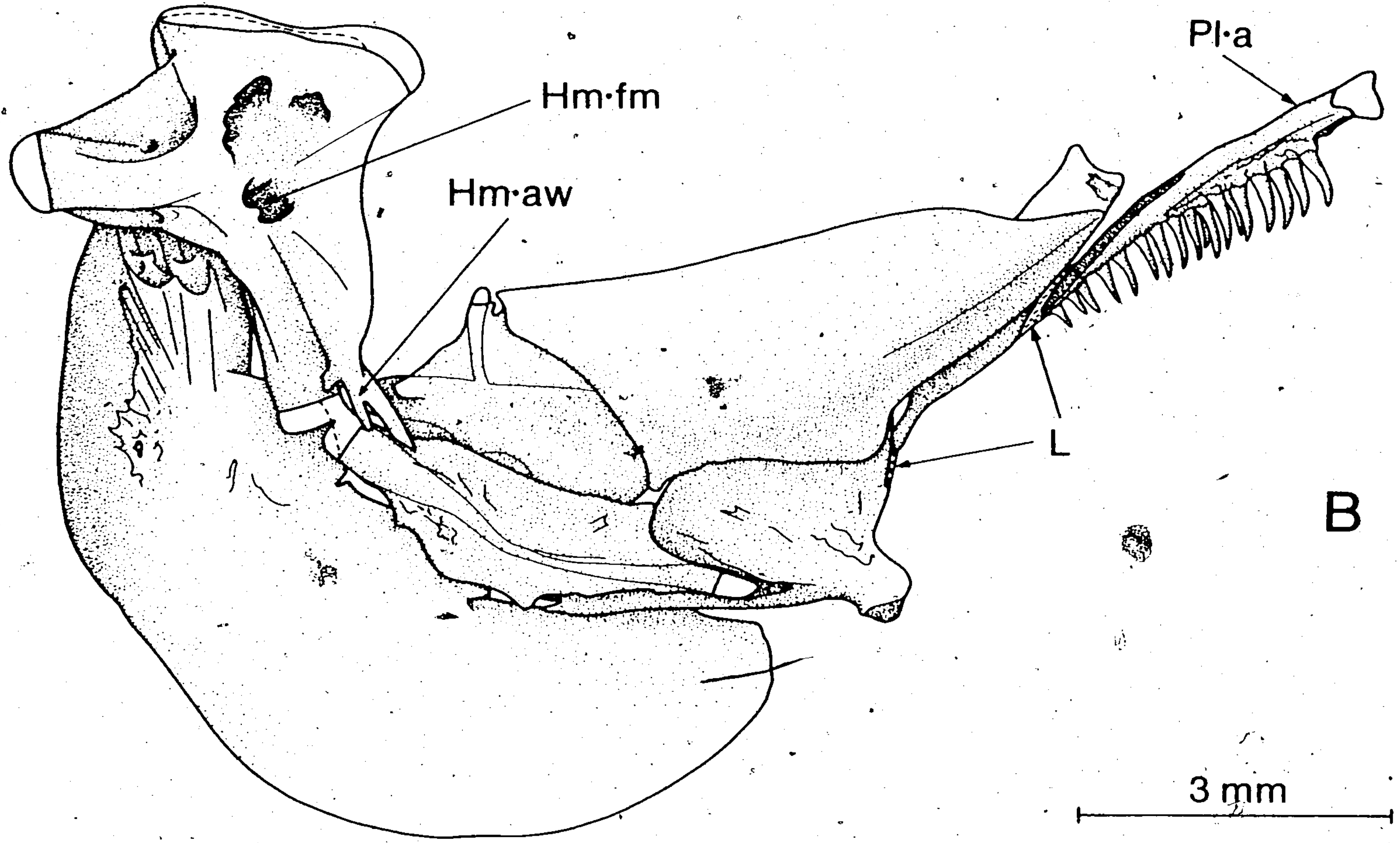
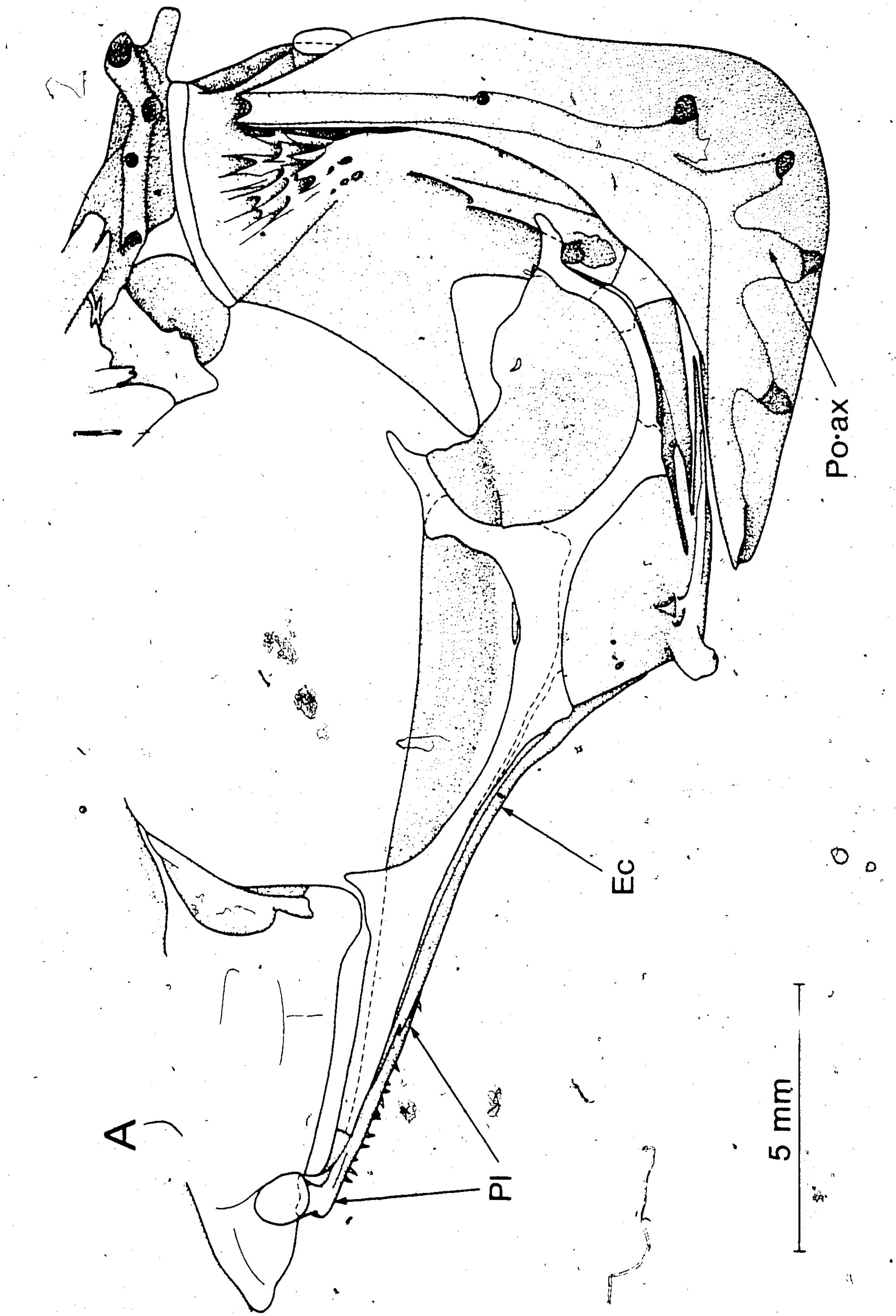

Hm·fm
Hm·aw
Pl·a
L
B
3 mm

Figure 10. Lateral (A) and medial (B) views of the left suspensorium in *Coregonus artedii*. (Salmonidae).


A
Pl
Ec
Po·ax
5 mm

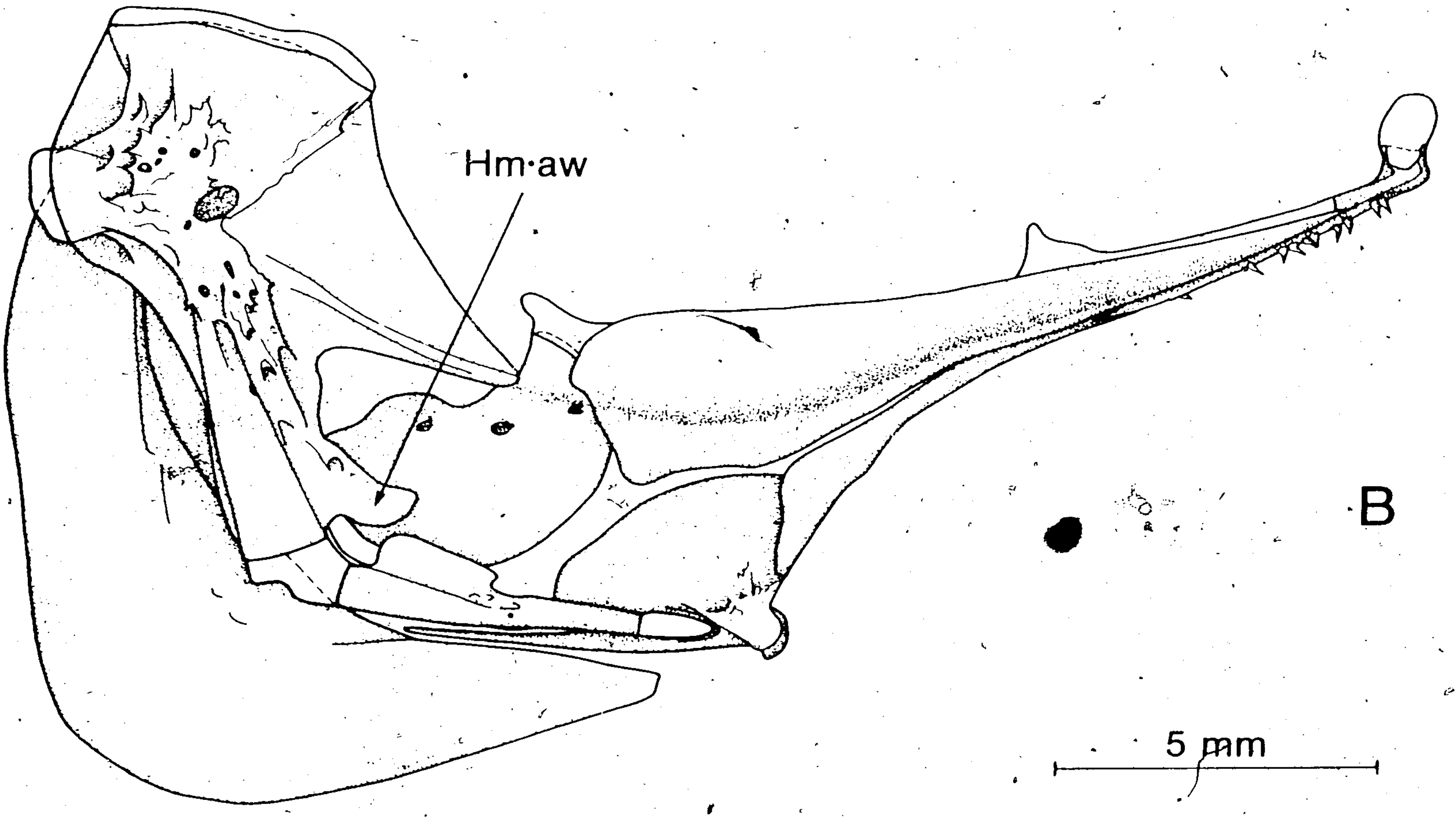

Hm·aw
B
5 mm

Figure 11. Lateral (A) and medial (B) views of the left suspensorium in *Prosopium williamsoni* (Salmonidae).

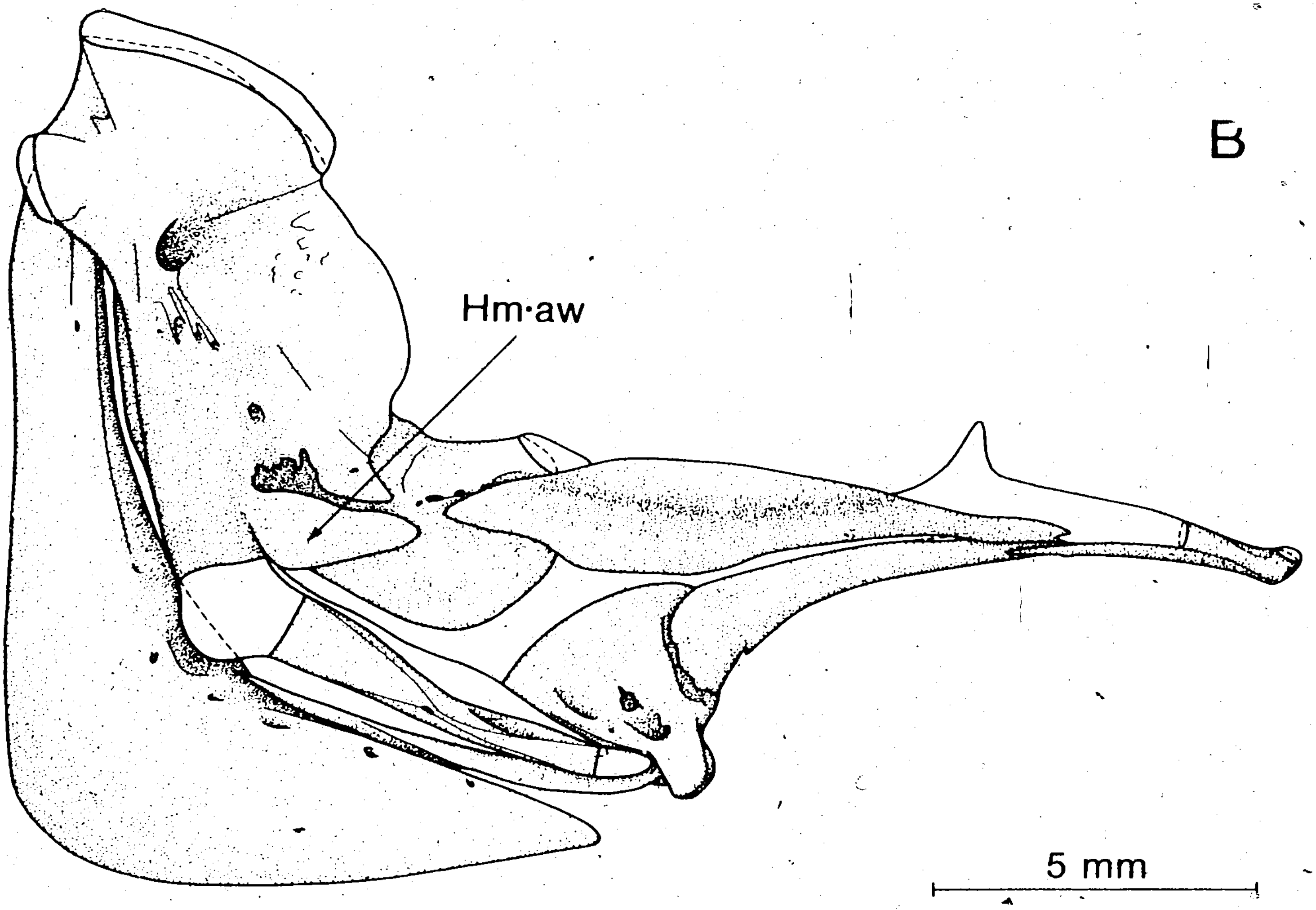
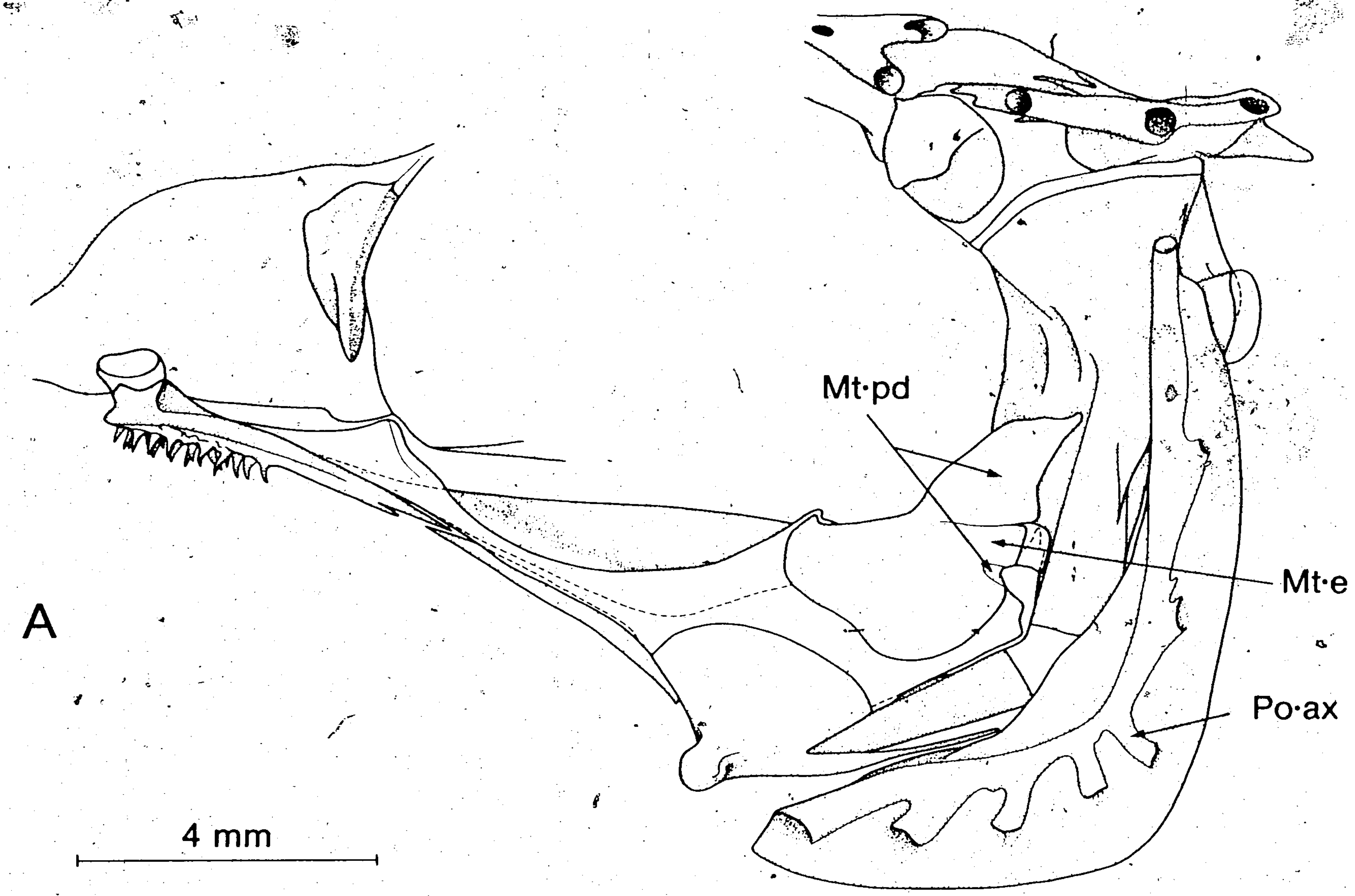

B
Hm·aw
5 mm

Figure 12. Lateral (A) and medial (B) views of the left suspensorium in *Thymallus arcticus* (Salmonidae); UAMZ 3425, 95.2 mm SL; (C) is a dorsal view of the left palatine attached to the skull, nasal and circumorbital bones obscuring its view omitted; UAMZ 3421, 110 mm SL.


Mt·pd
Mt·e
A
Po·ax
4 mm

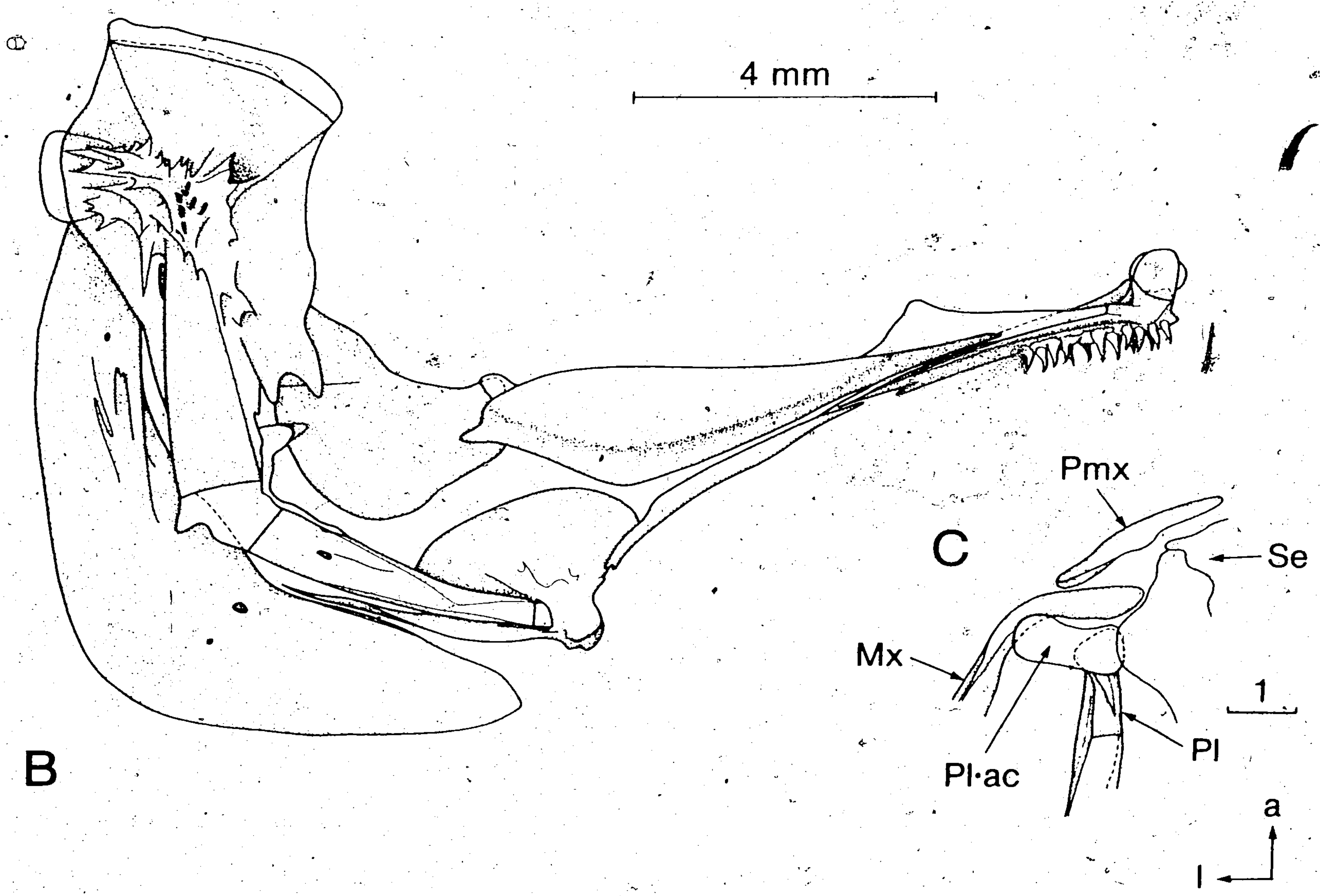

4 mm
B
C
Pmx
Se
Mx
Pl·ac
Pl
1
a
l

Figure 13. Lateral (A) and medial (B) views of the left suspensorium in *Salvelinus fontinalis* (Salmonidae); UAMZ 3349, 76.0 mm SL; (C) is a dorsal view of the left palatine attached to the skull, nasal and circumorbital bones obscuring its view omitted; UAMZ 3349, 90.3 mm SL. On A the small, separate suprapreopercular bone found immediately dorsal to the dorsal tip of the dorsal limb of the preoperculum is omitted.

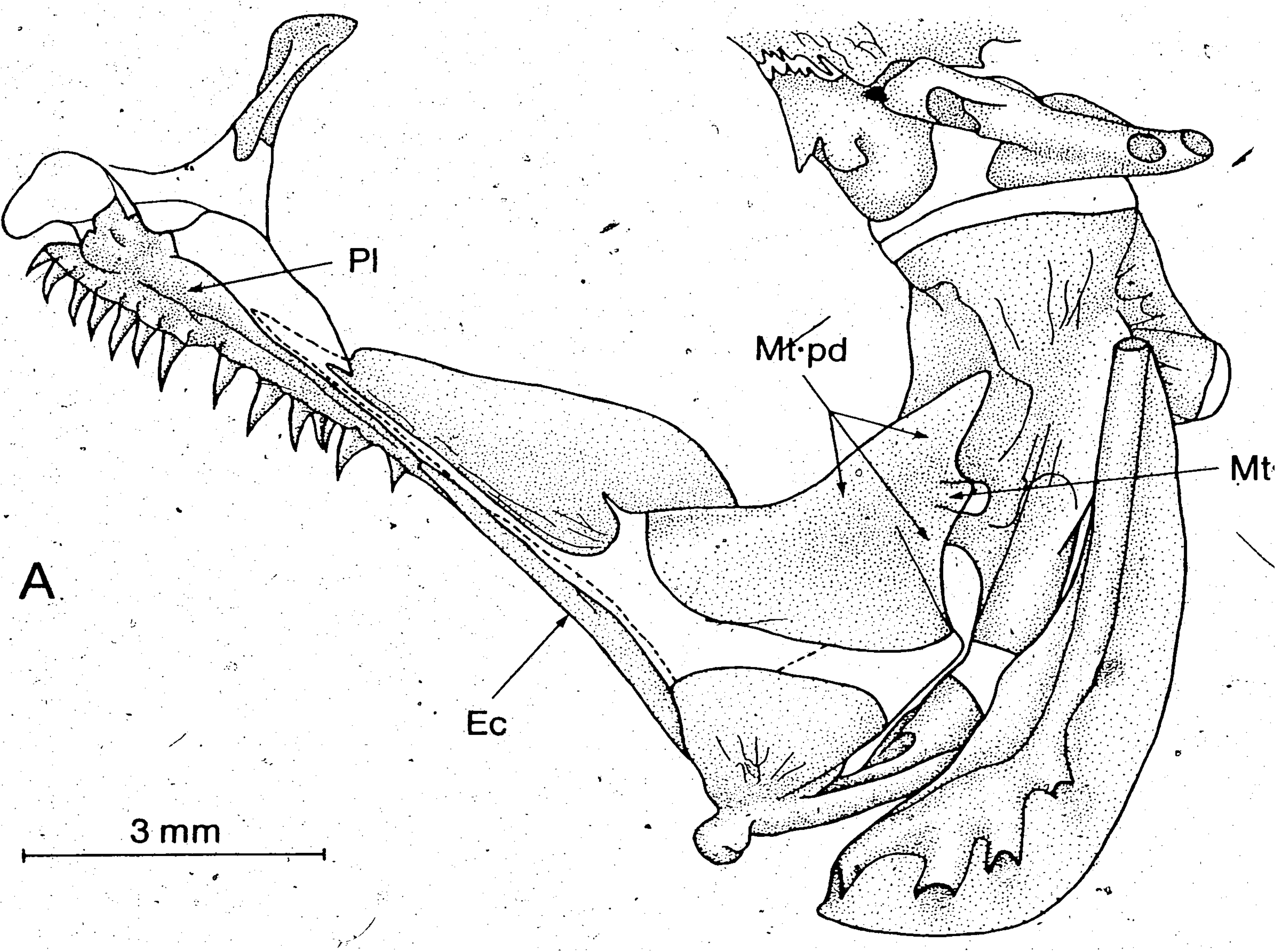

Pl
Mt·pd
Mt
A
Ec
3 mm

Figure 14. Lateral (A) and medial (B) views of the left suspensorium in *Mallotus villosus* (Osmeridae). Both drawings are of the suspensorium after its removal from the skull.

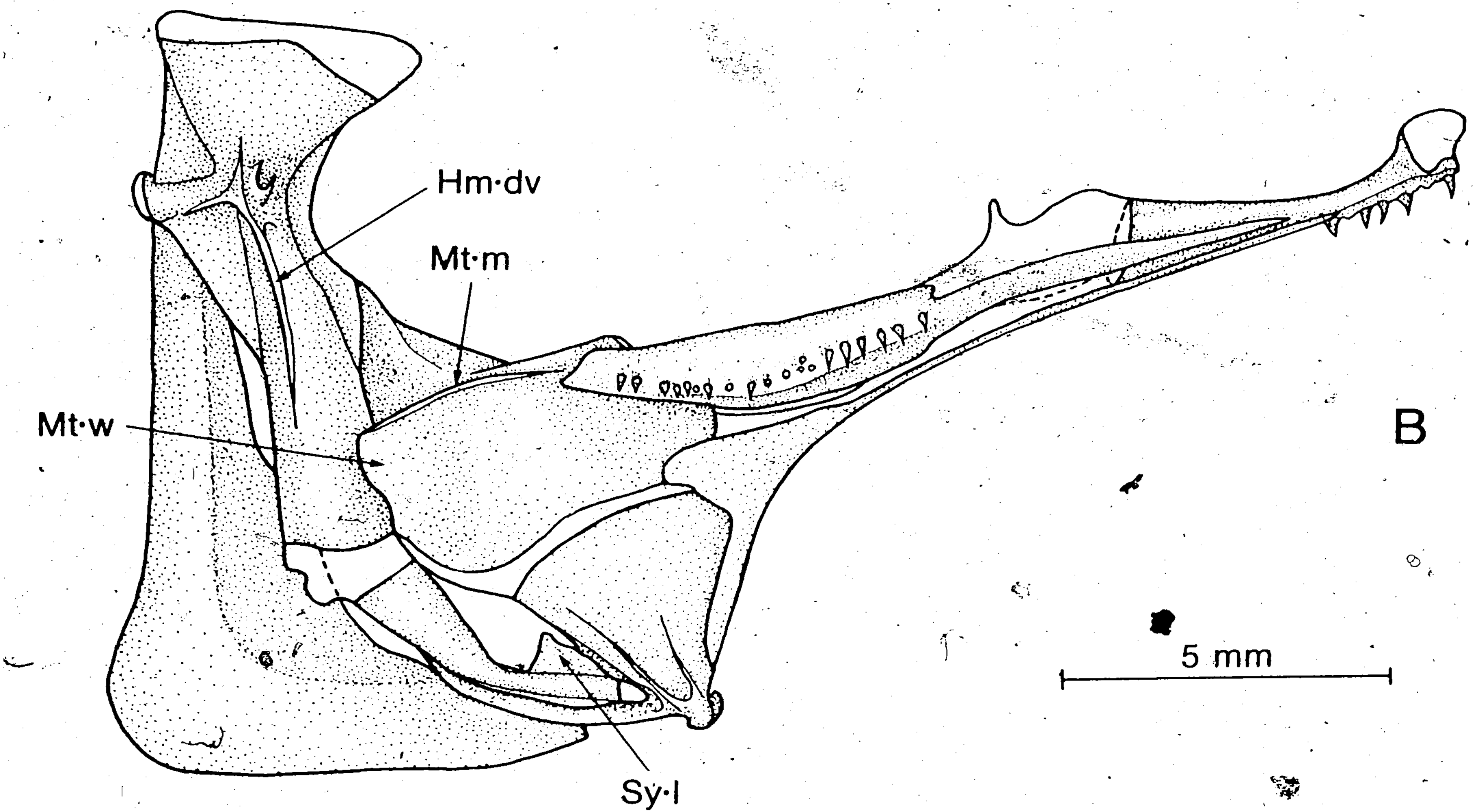

Hm·dv
Mt·m
Mt·w
B
5 mm
Sy·l

Figure 15. Lateral (A) and medial (B) views of the left suspensorium in *Hypomesus pretiosus* (Osmeridae).

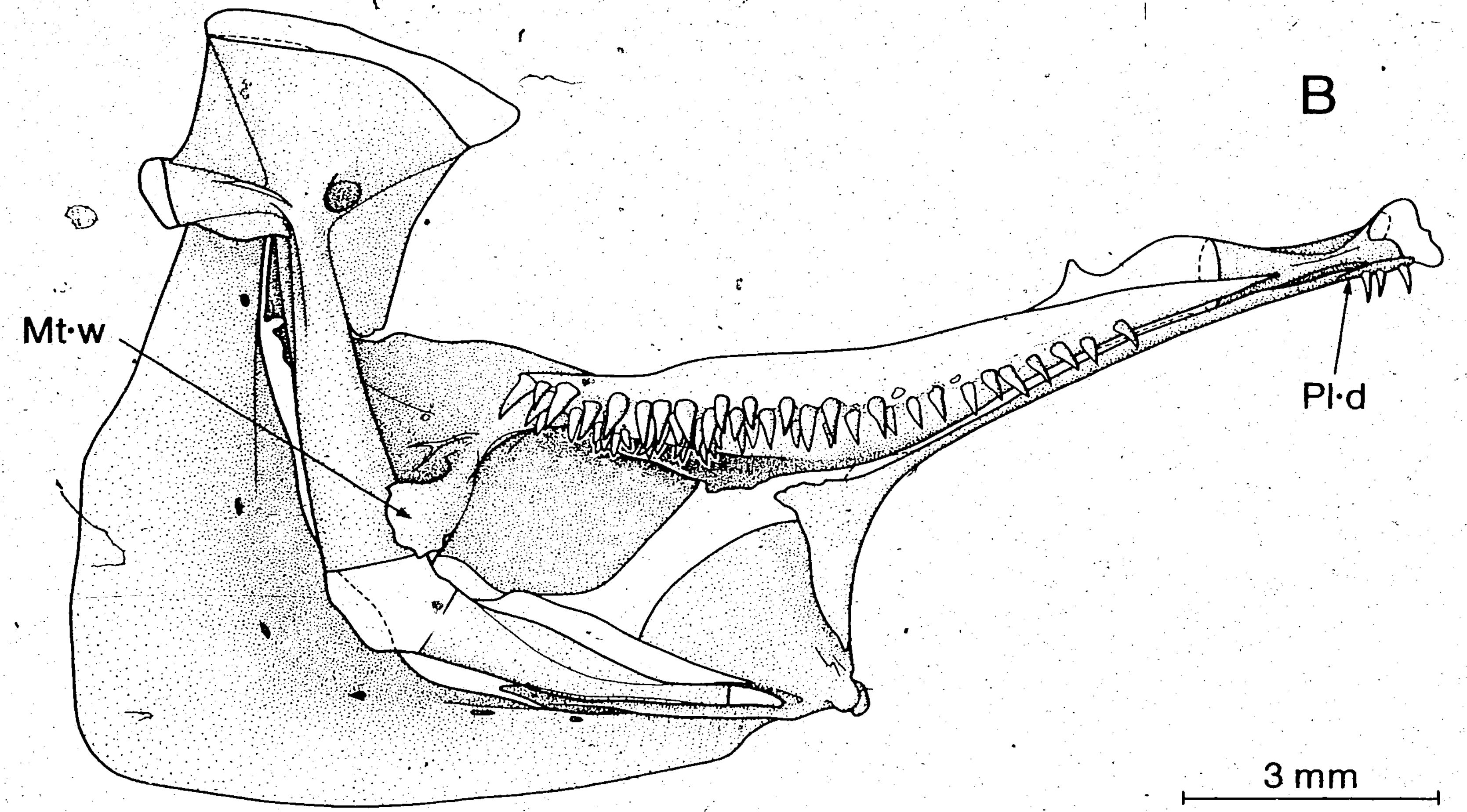
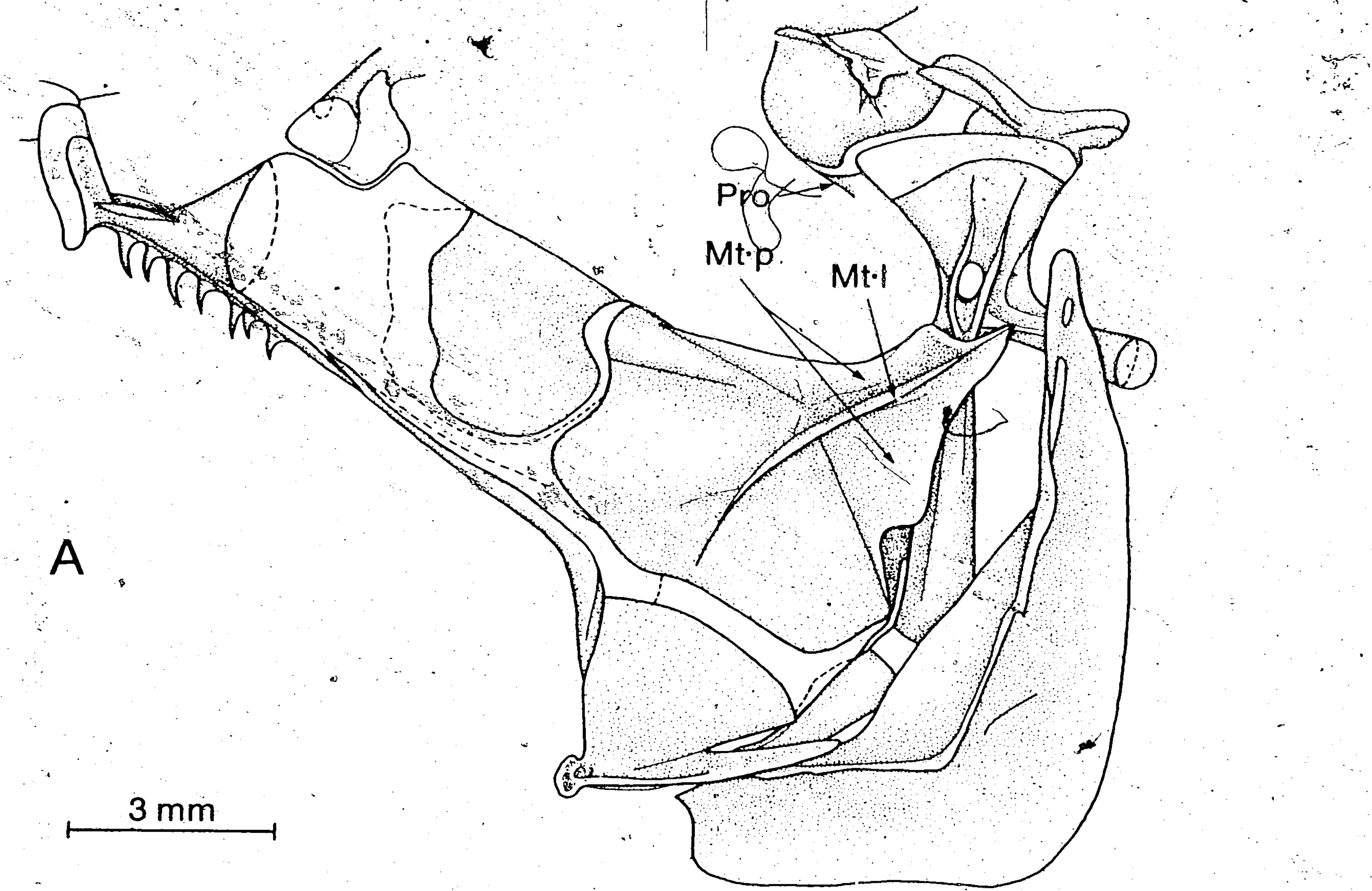

B
Mt·w
Pl·d
3 mm

Figure 16. Lateral (A) and medial (B) views of the left suspensorium in *Thaleichthys pacificus* (Osmeridae).


Pro
Mt·p
Mt·l
A
3 mm

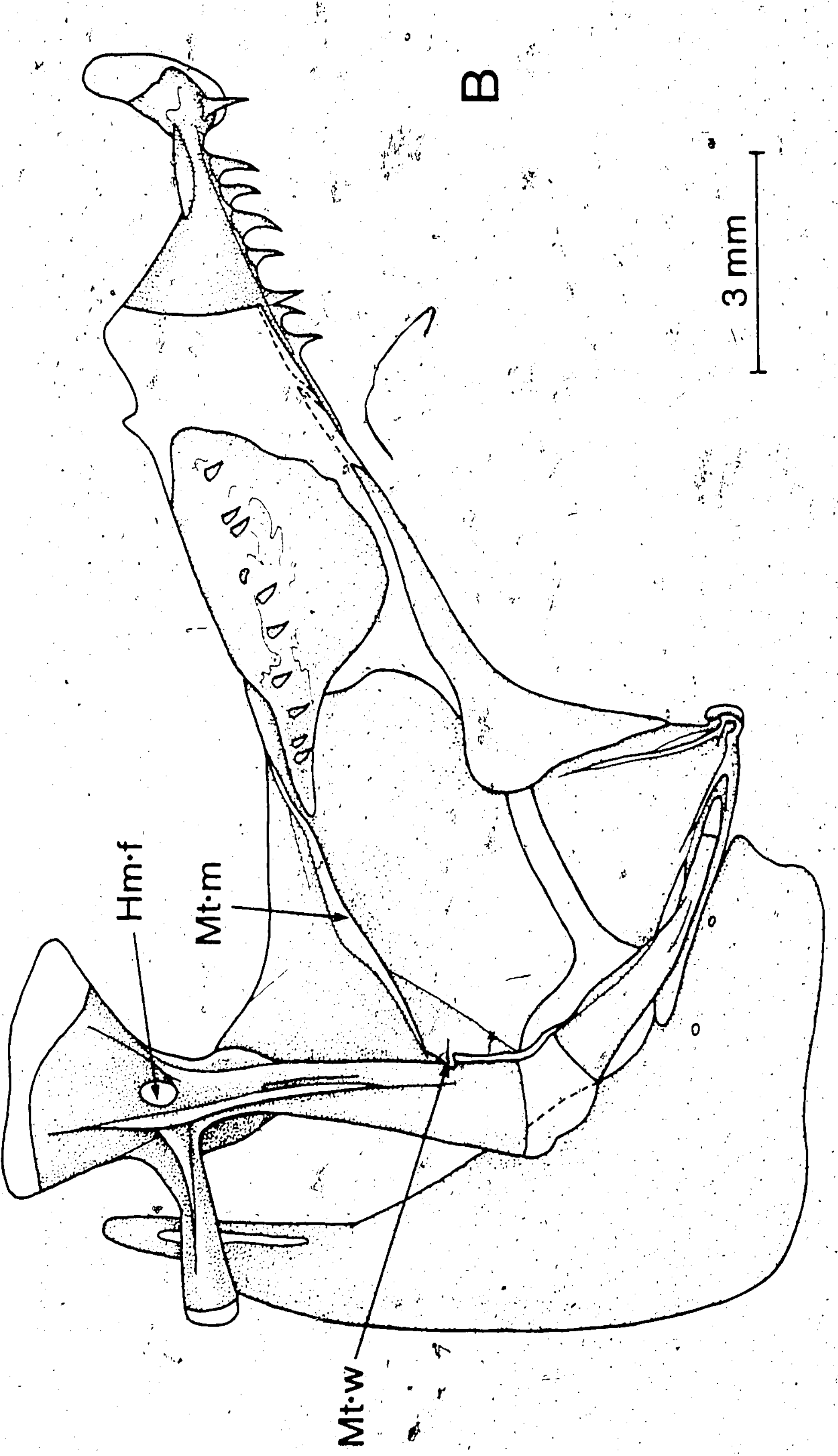
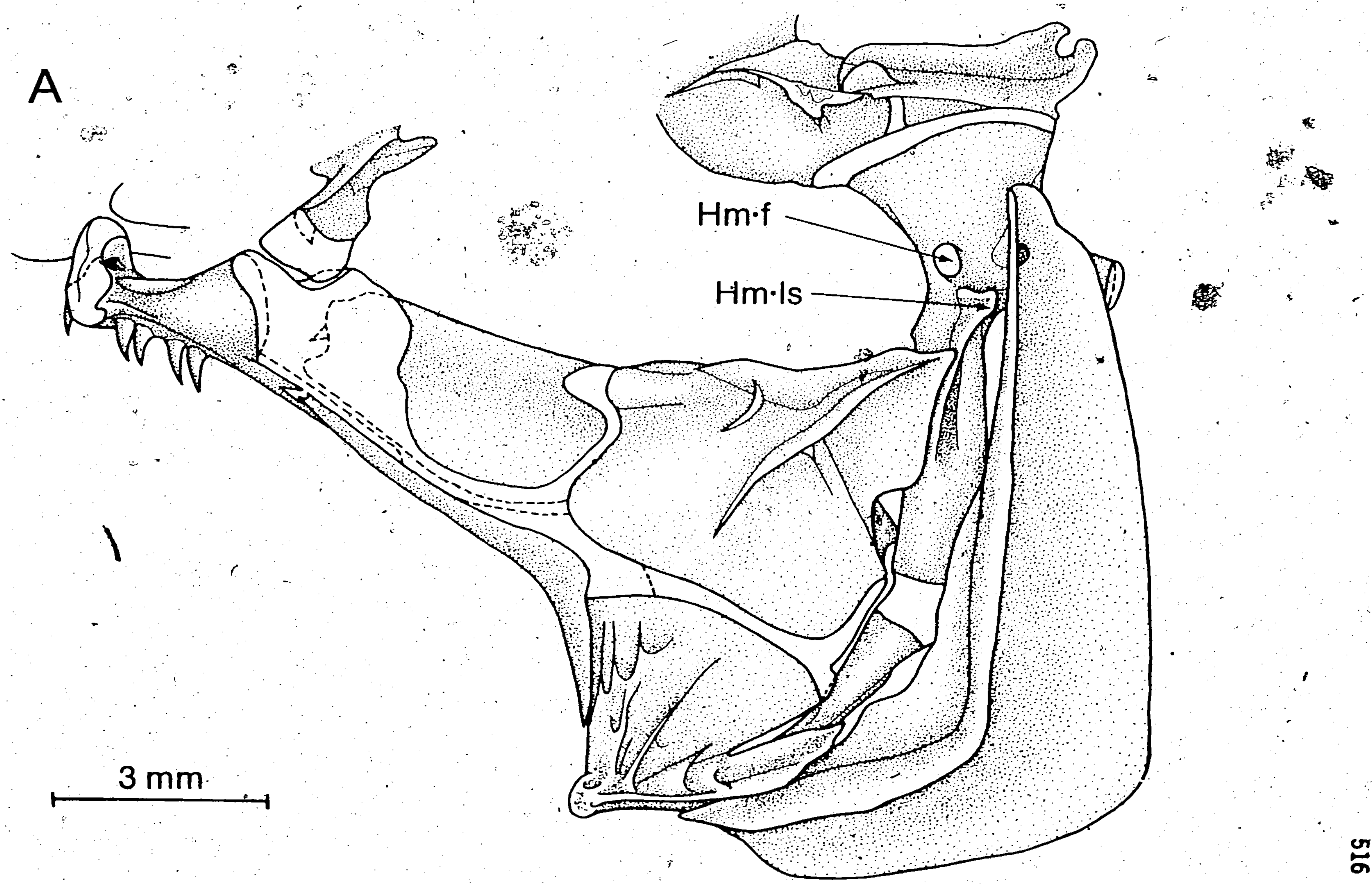

B
3 mm
Hm·f
Mt·m
Mt·w

Figure 17. Lateral (A) and medial (B) views of the left suspensorium in *Spirinchus thaleichthys* (Osmeridae).


A
Hm·f
Hm·ls
3 mm

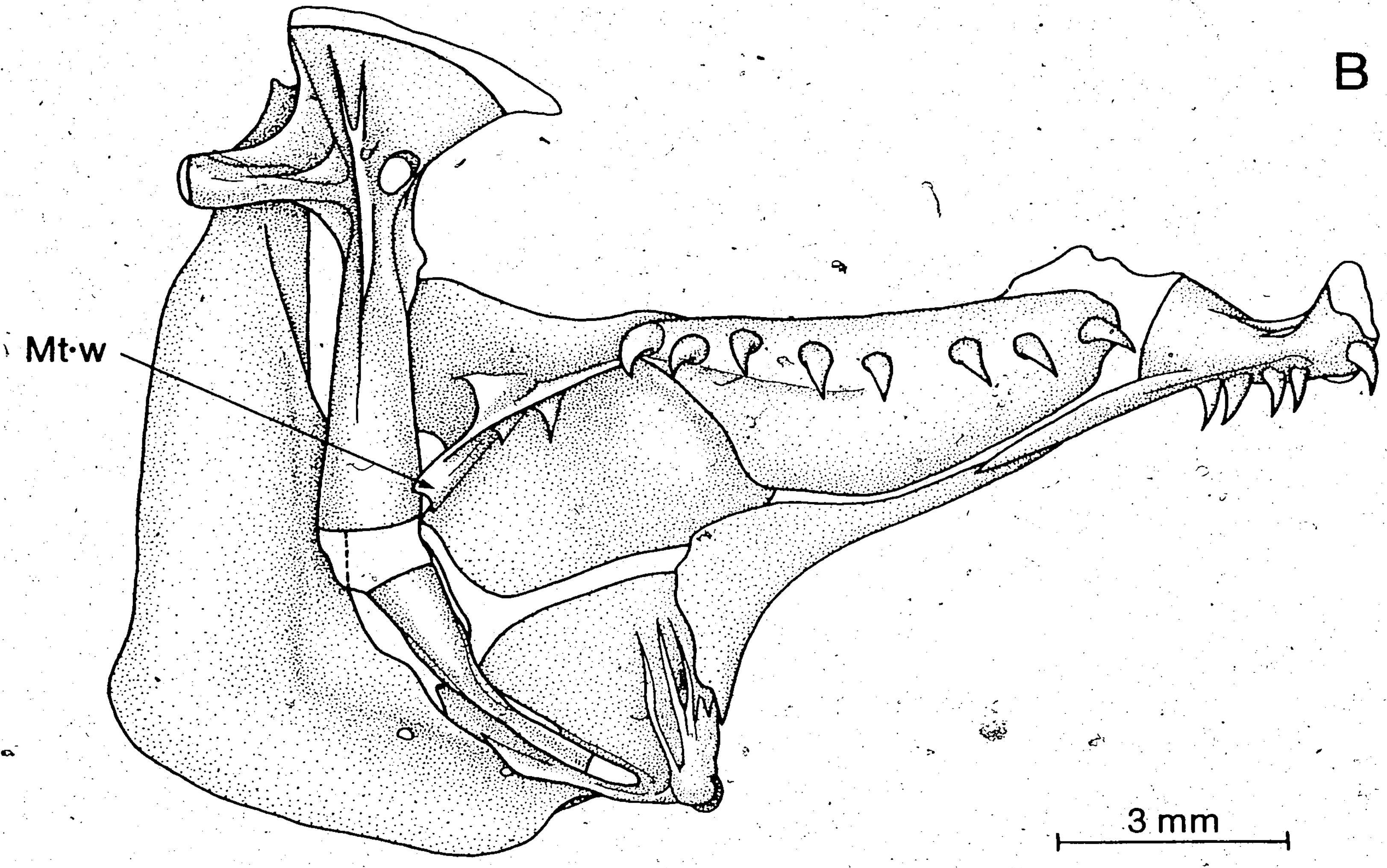
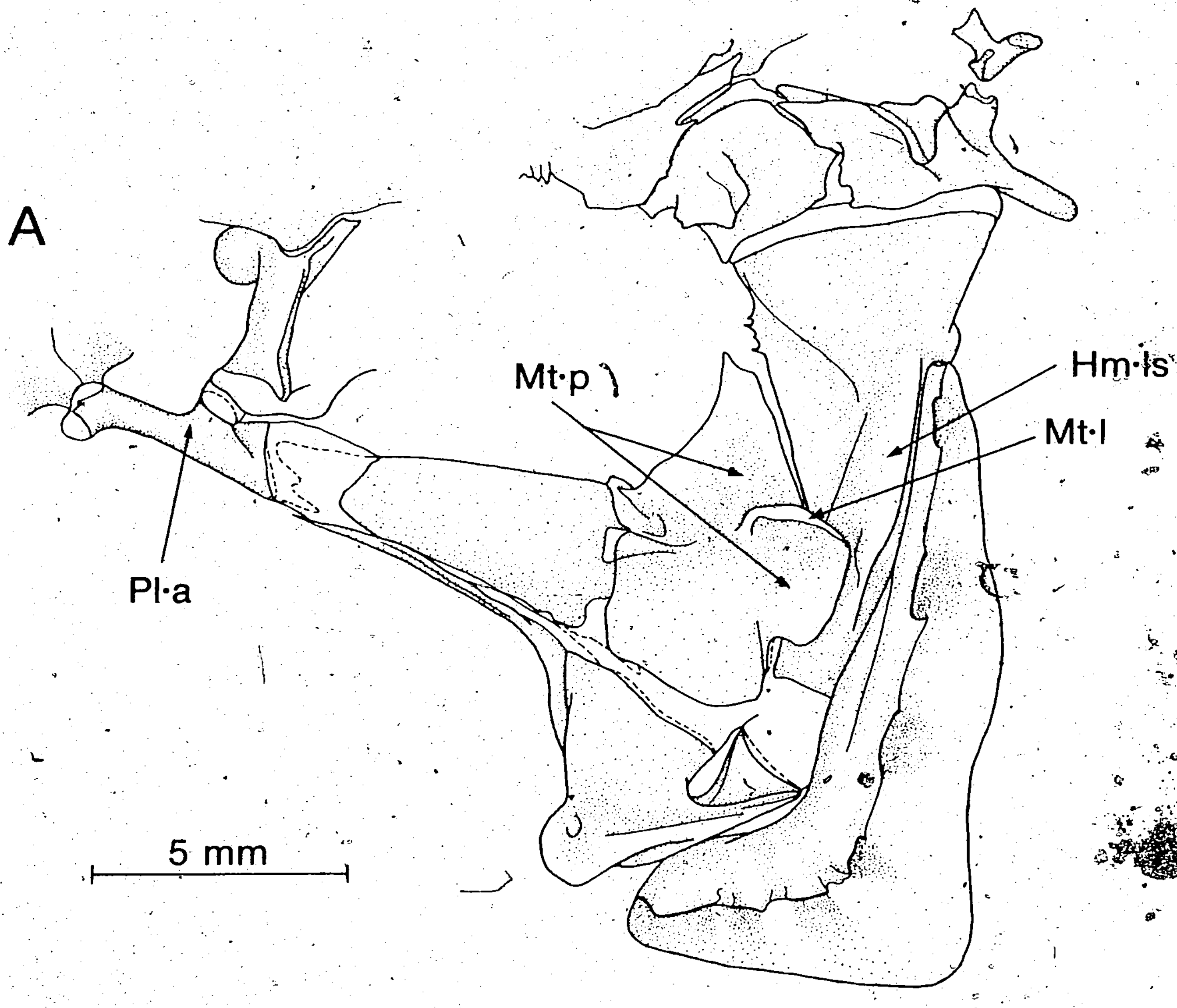

B
Mt·w
3 mm

Figure 18. Lateral (A) and medial (B) views of the left suspensorium in *Plecoglossus altivelis* (Plecoglossidae). On A the small, separate suprapreopercular bone found immediately dorsal to the dorsal tip of the dorsal limb of the preoperculum is omitted.


A
Mt·p
Hm·Is
Mt·I
Pl·a
5 mm

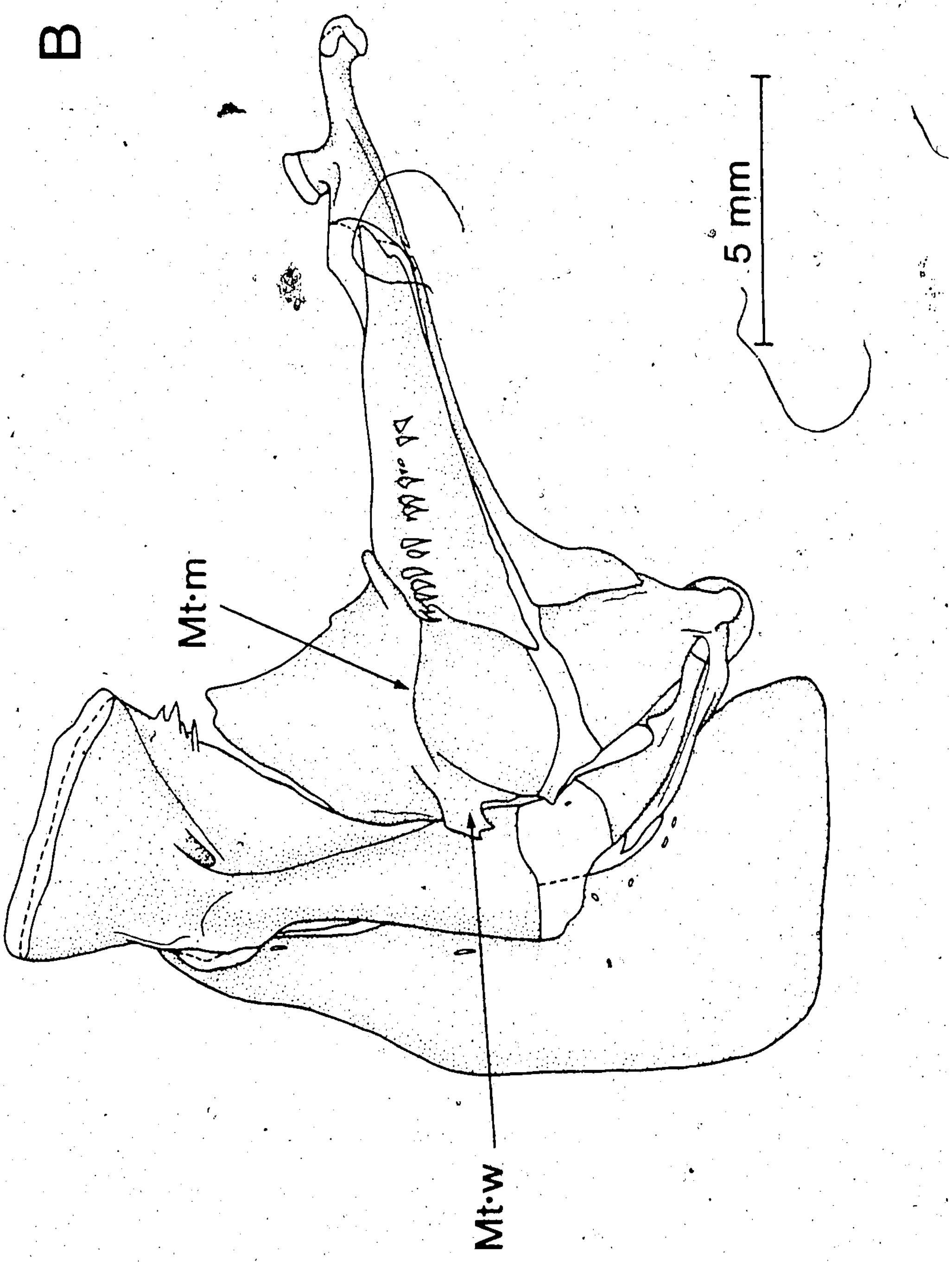
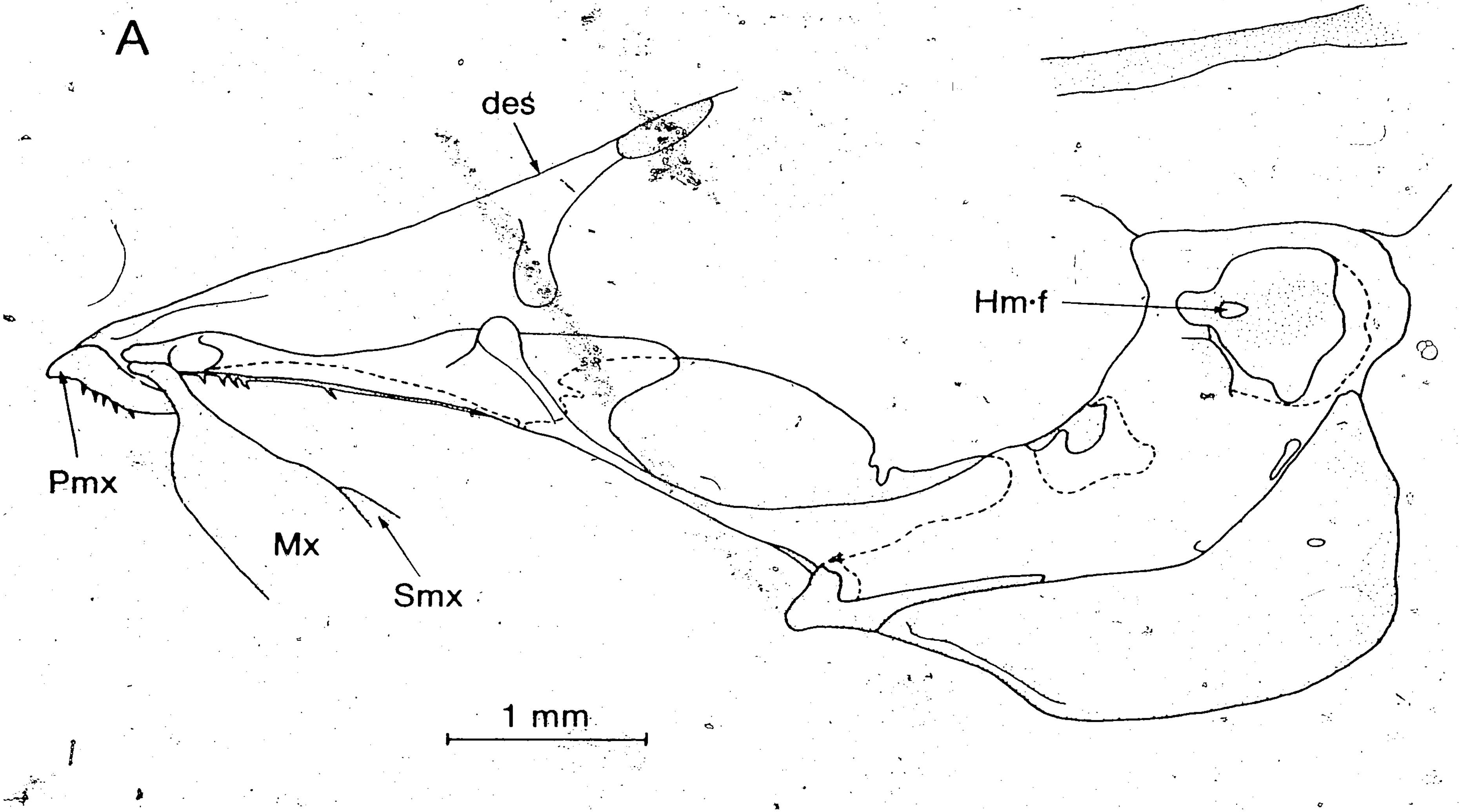

B
5 mm
Mt·m
Mt·w

Figure 19. Lateral (A) and medial (B) views of the left suspensorium in *Salangichthys ishikawae* (Salangidae).


A
des
Hm·f
Pmx
Mx
Smx
1 mm

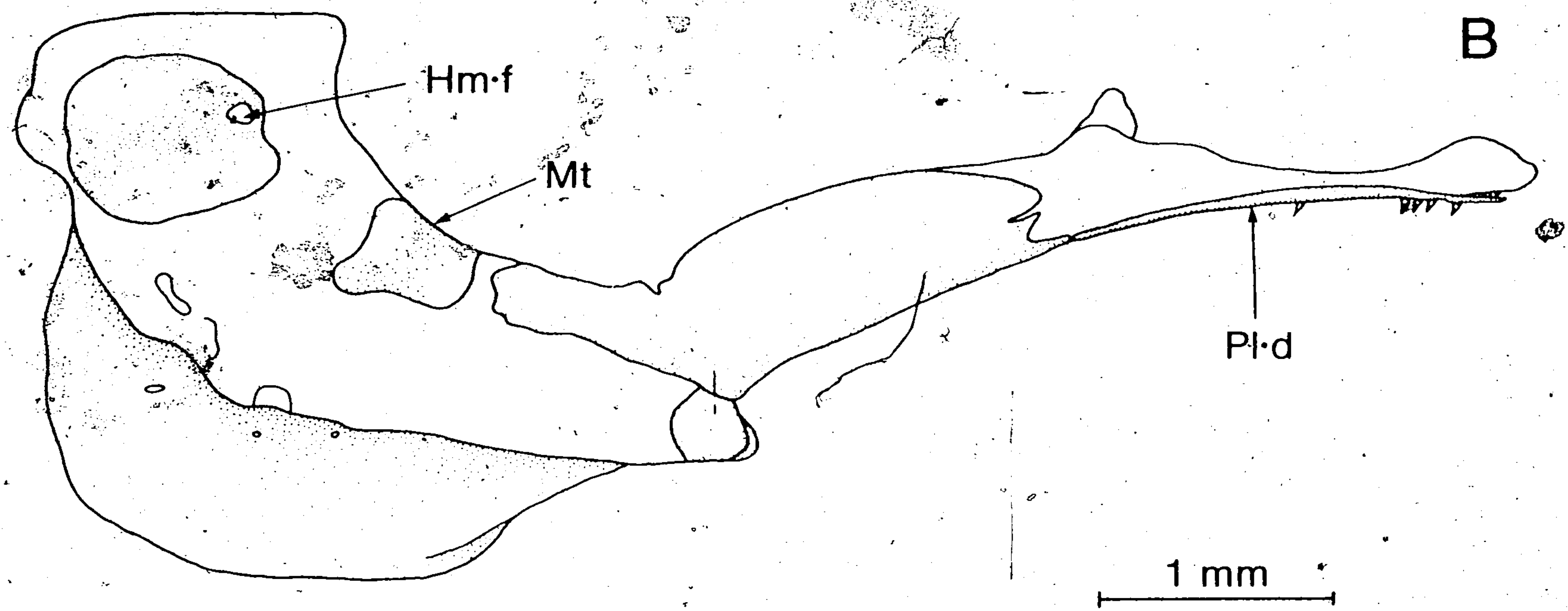
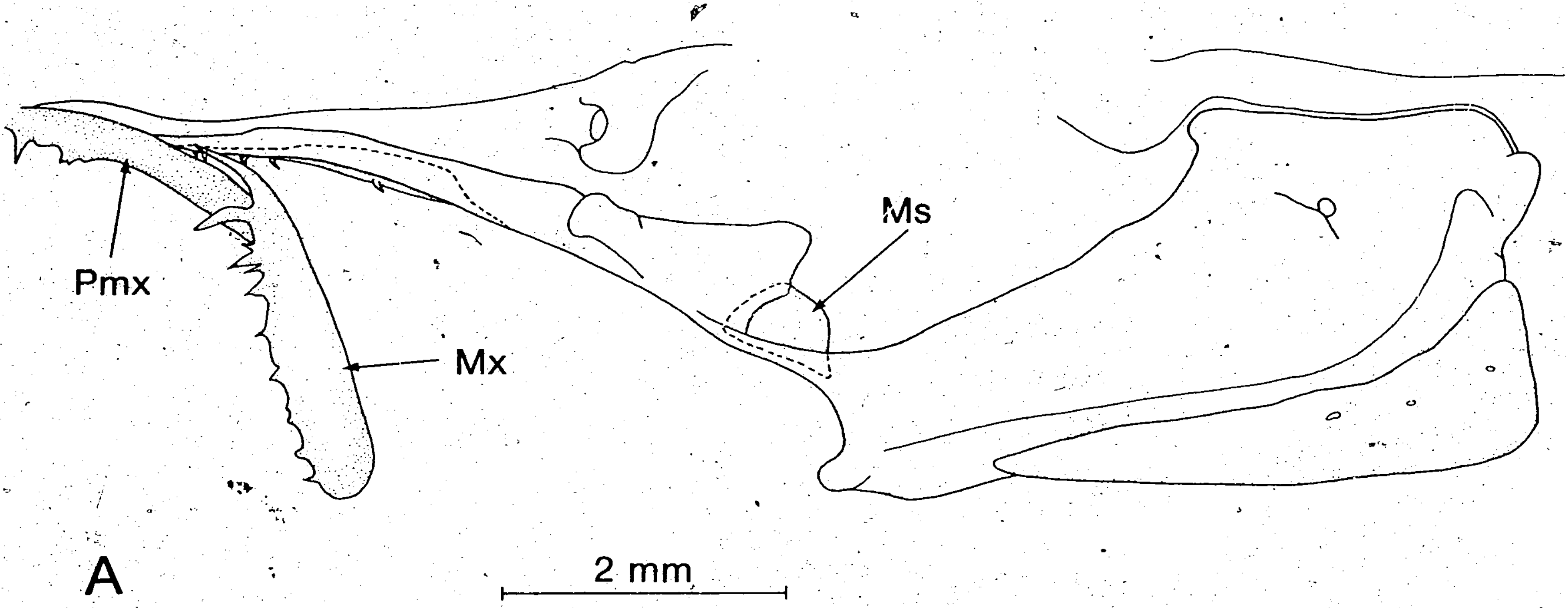
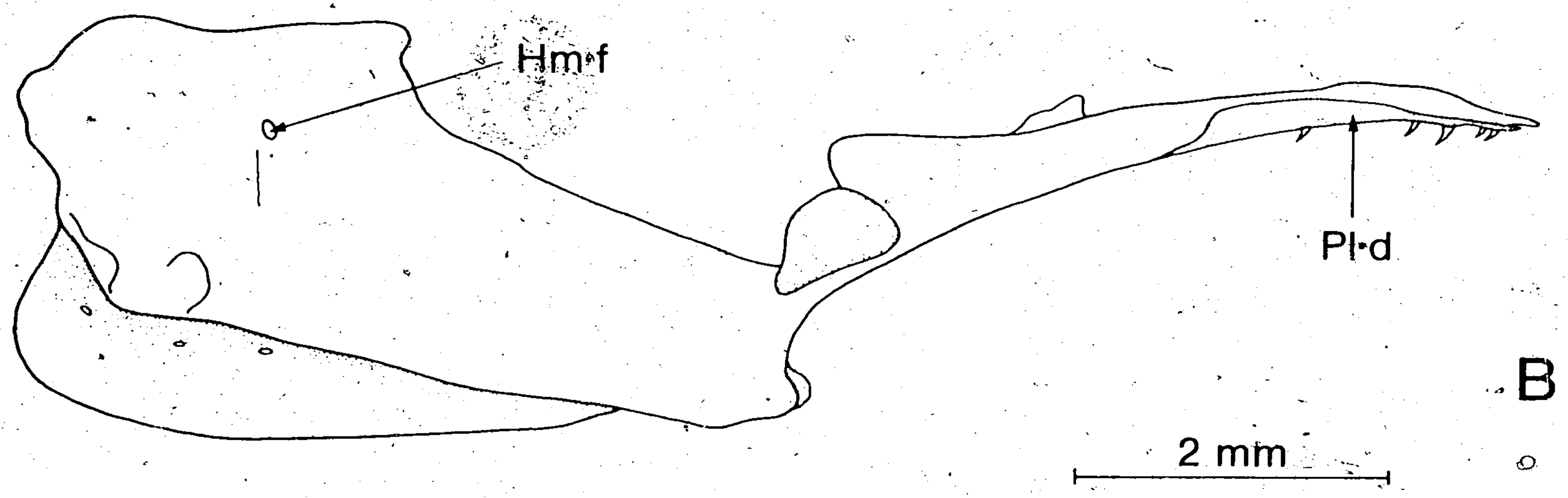
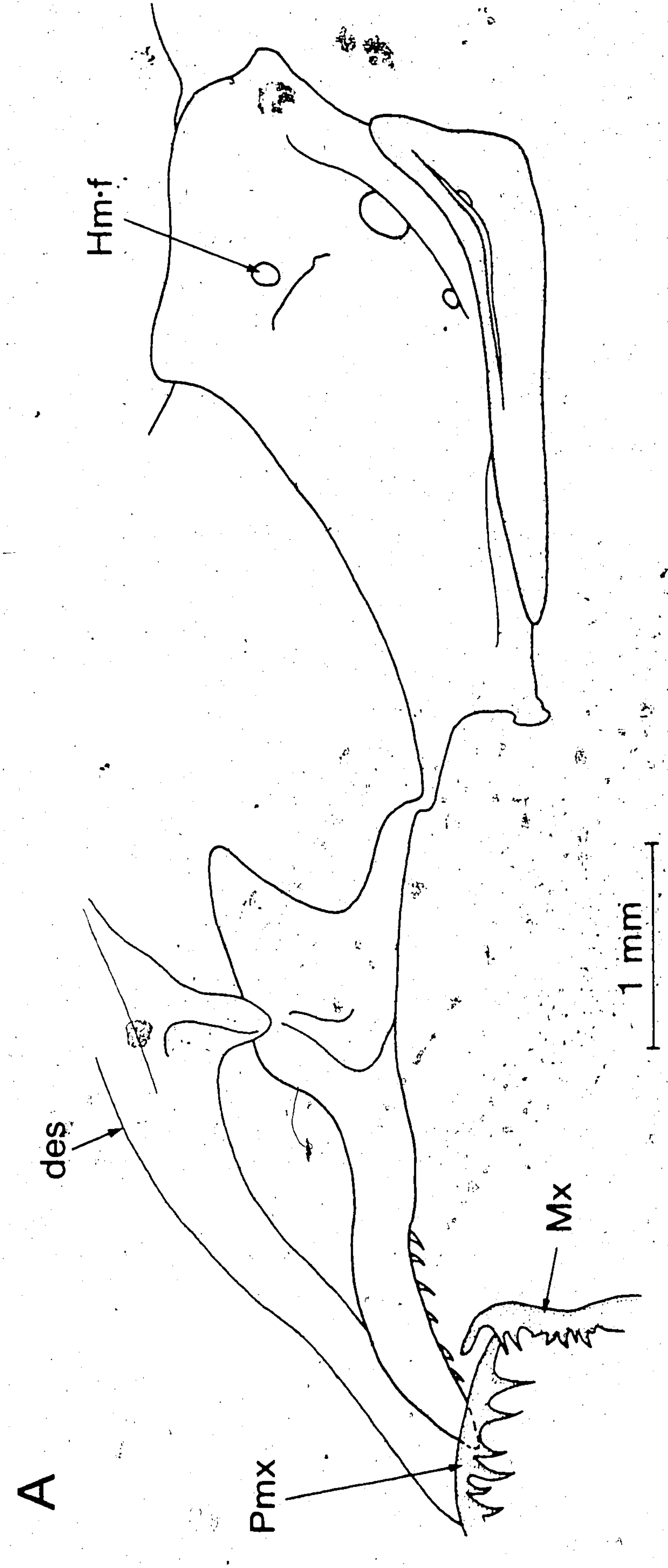

B
Hm·f
Mt
Pl·d
1 mm

Figure 20. Lateral (A) and medial (B) views of the left suspensorium in *Salanx prognathus* (Salangidae).


Ms
Pmx
Mx
A
2 mm


Hm·f
Pl·d
B
2 mm


A
Hm·f
des
Mx
Pmx
1 mm

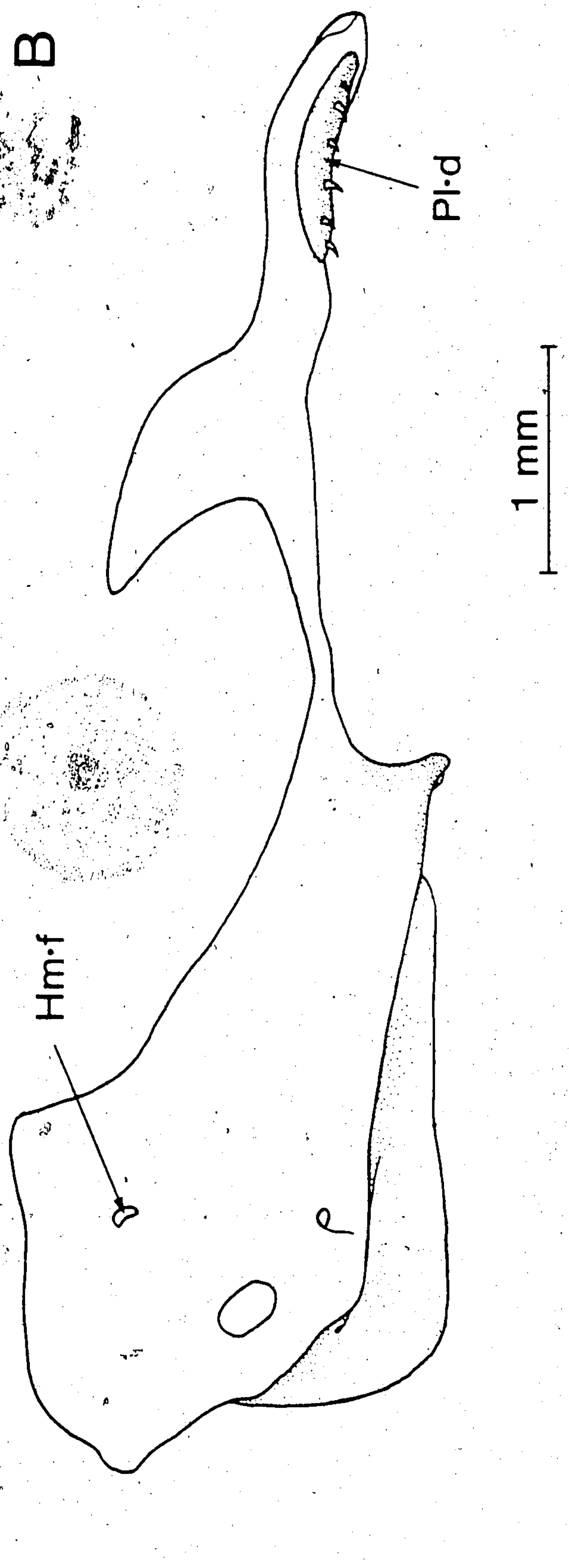
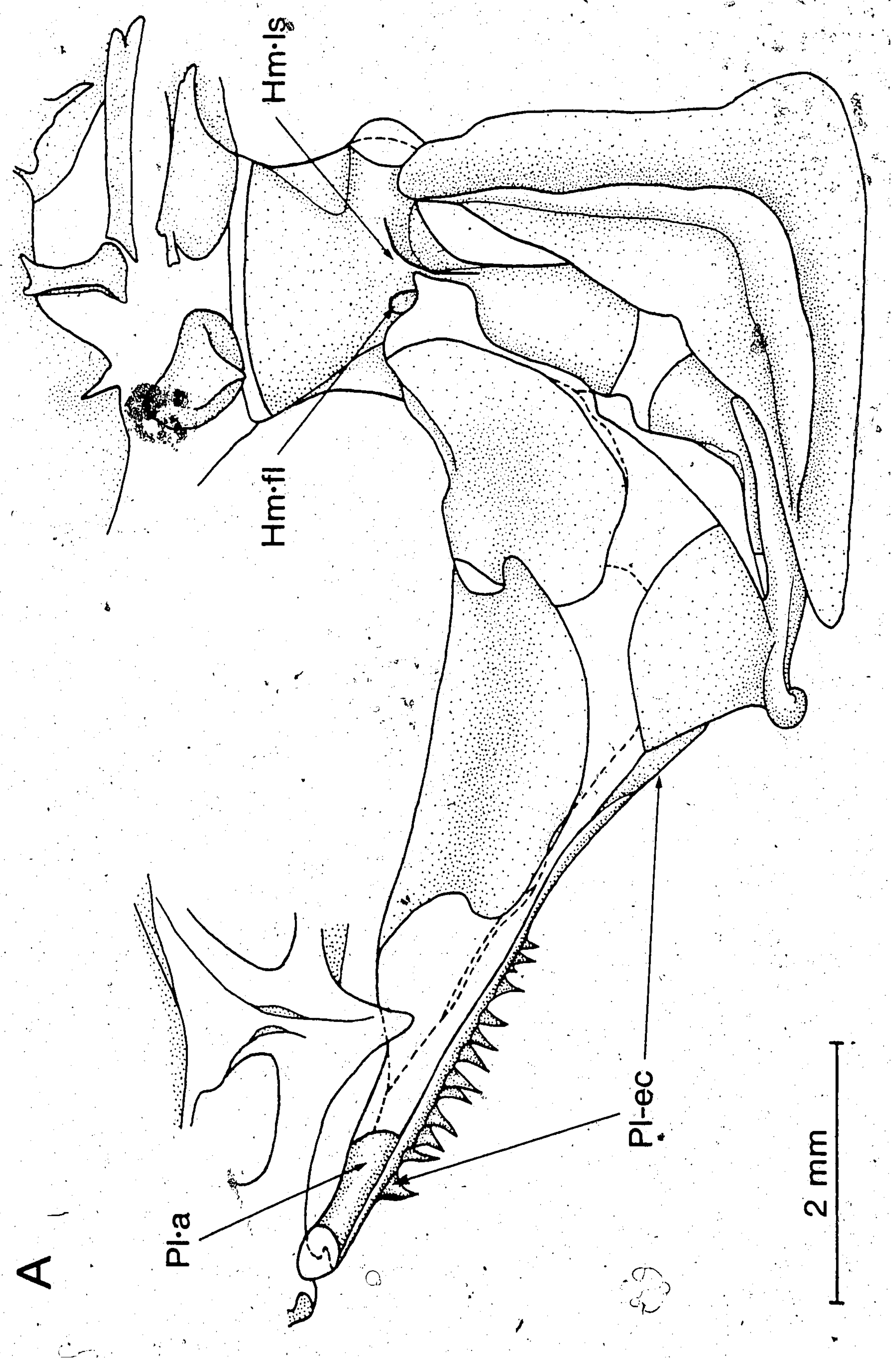

B
Pl·d
1 mm
Hm·f

Figure 22. Lateral (A) and medial (B) views of the left suspensorium in *Retropinna retropinna* (Retropinnidae).


A
Pl·a
Pl-ec
2 mm
Hm·ls
Hm·fl

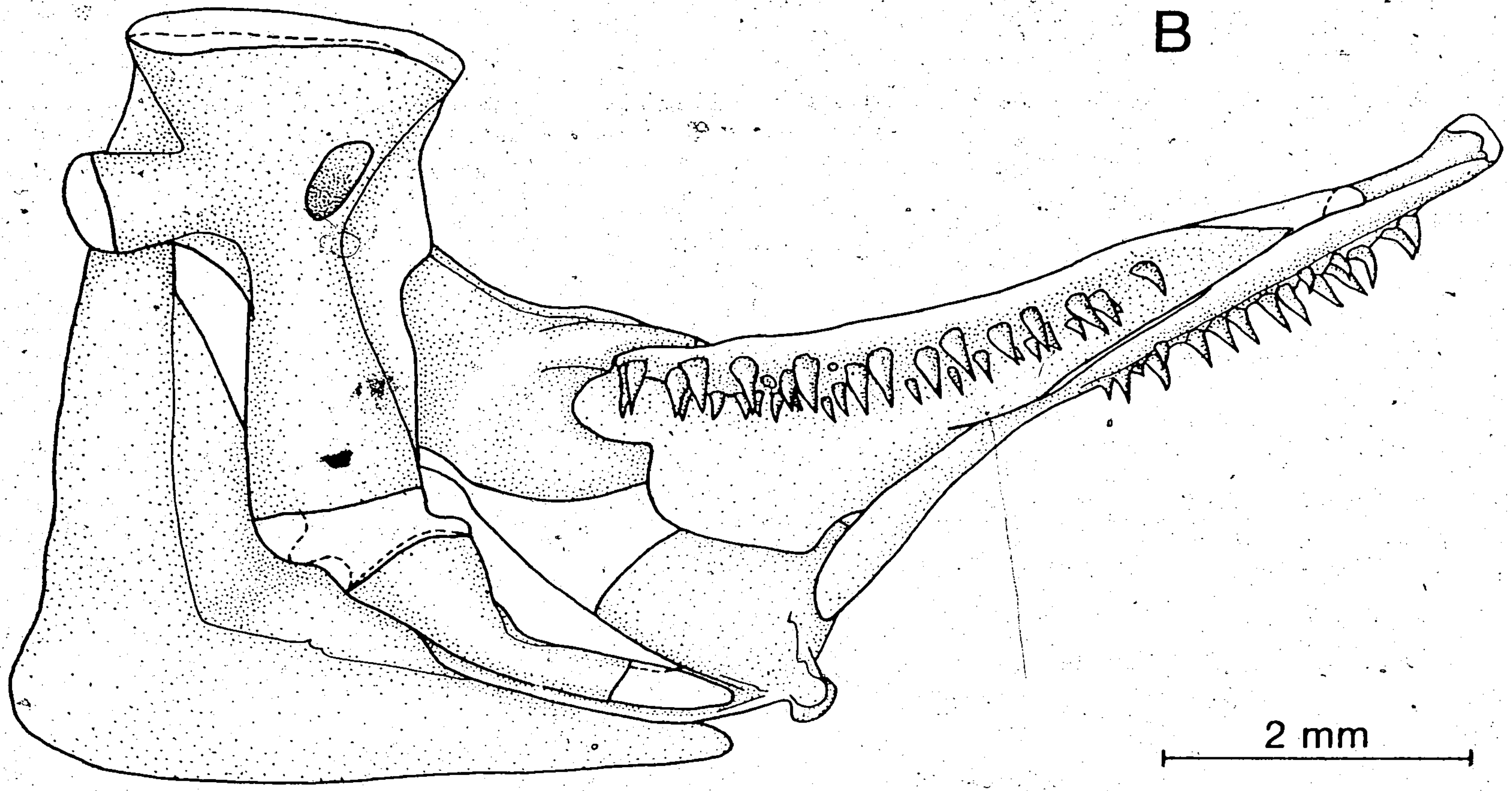
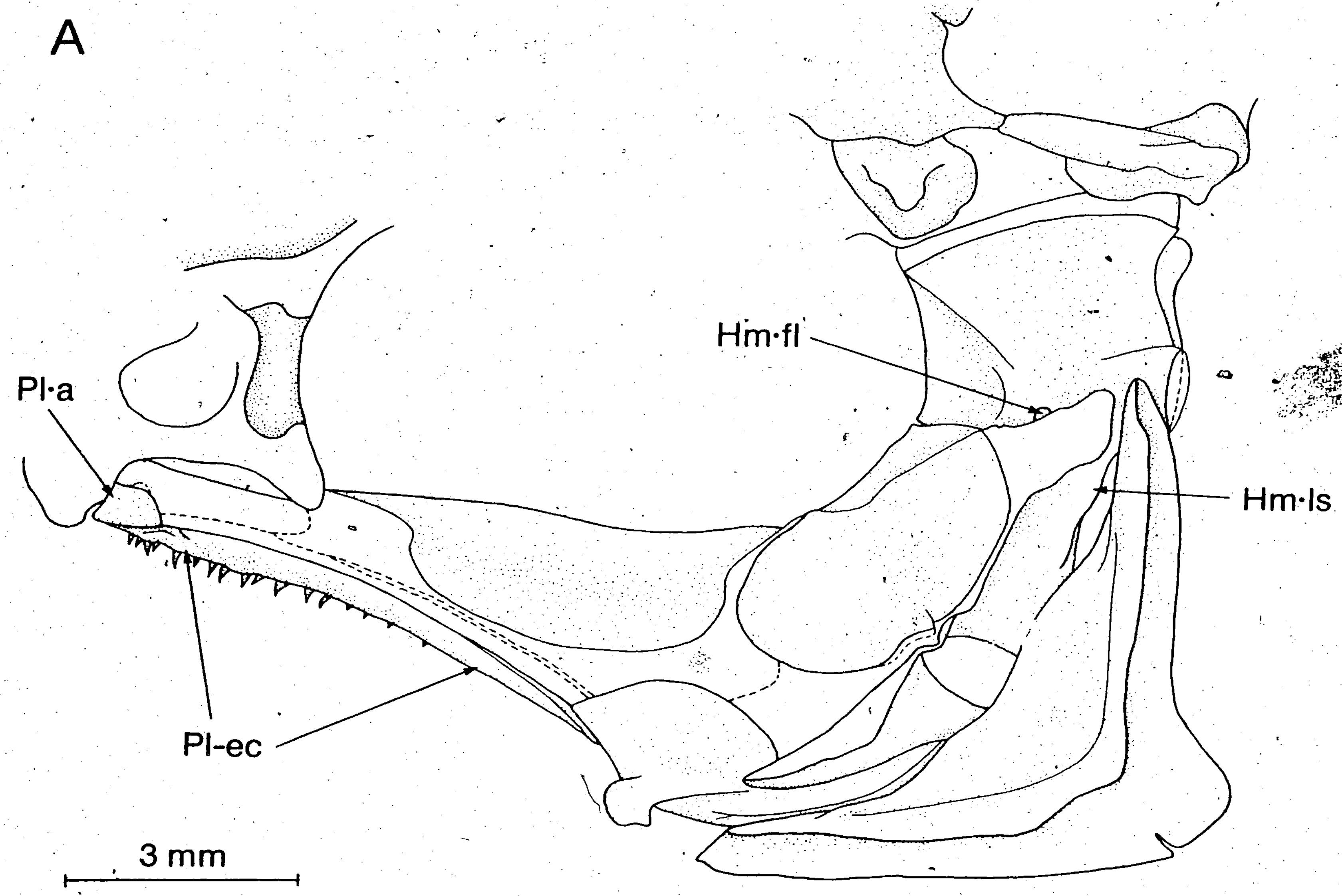

B
2 mm

Figure 23. Lateral (A) and medial (B) views of the left suspensorium in *Prototroctes maraena* (Prototroctidae).


A
Pl·a
Pl-ec
3 mm
Hm·fl
Hm·ls

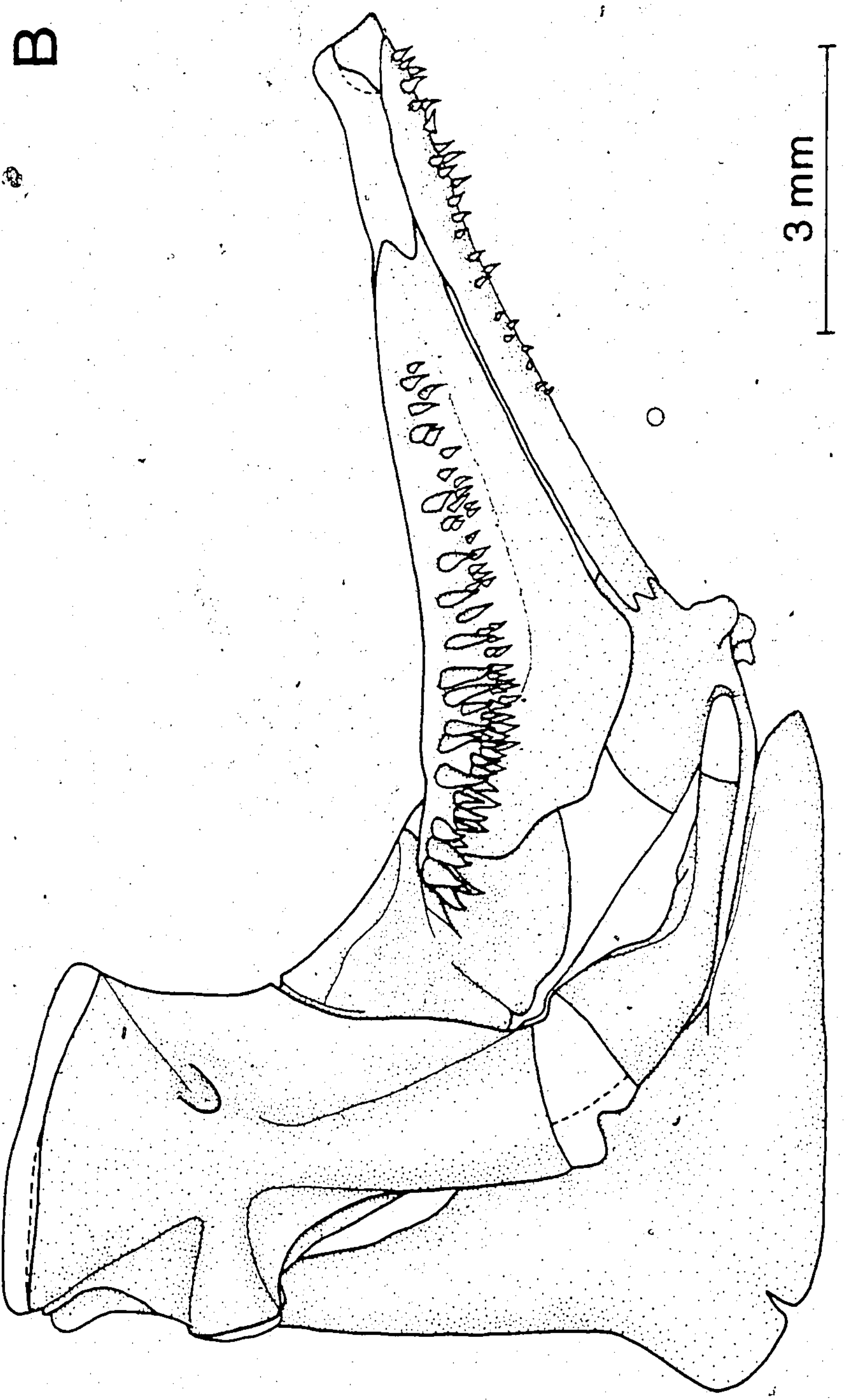

B
3 mm

Figure 24: Lateral (A) and medial (B) views of the right suspensorium in *Lepidogalaxias salamandroides* (Lepidogalaxiidae).

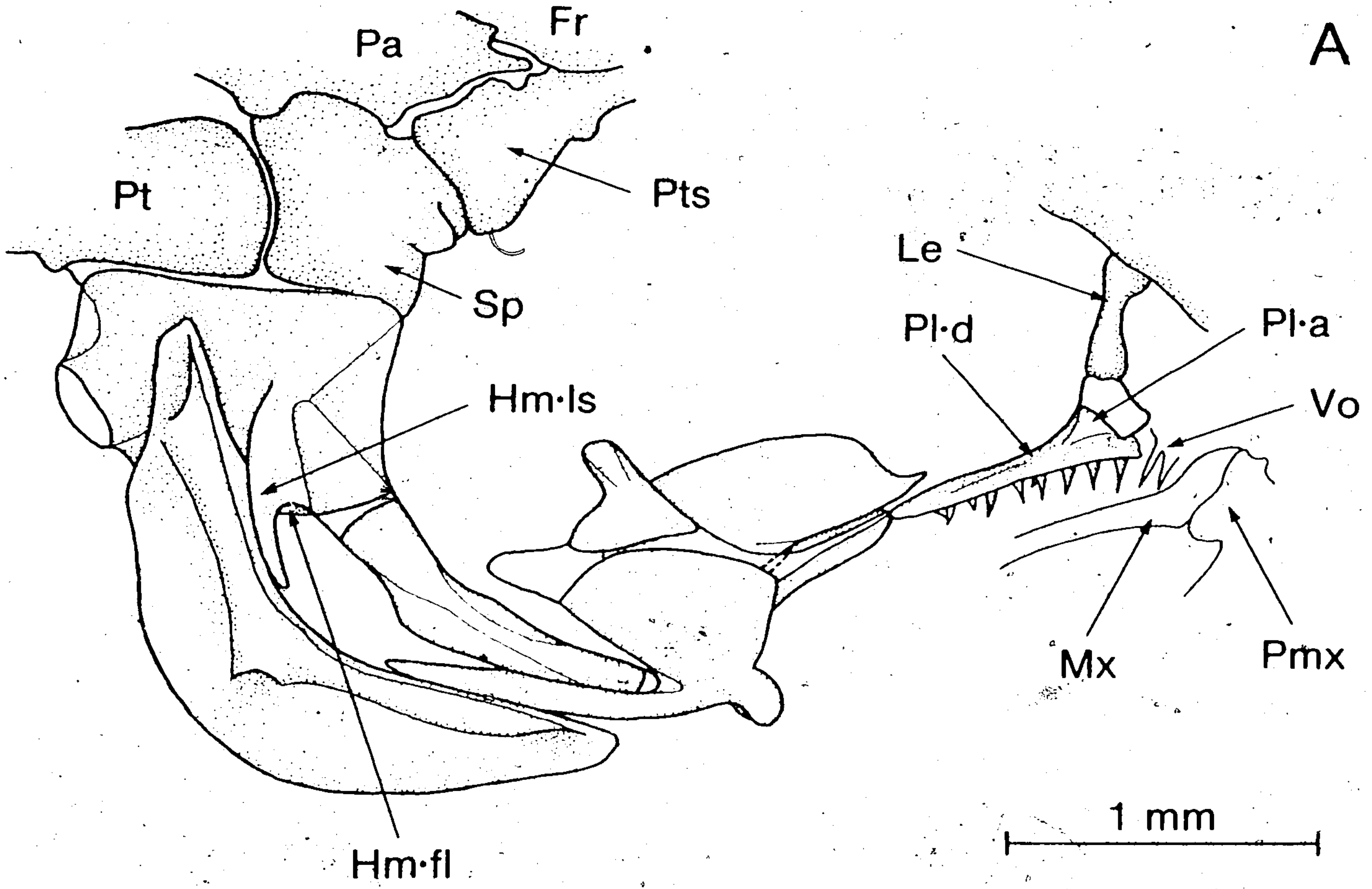
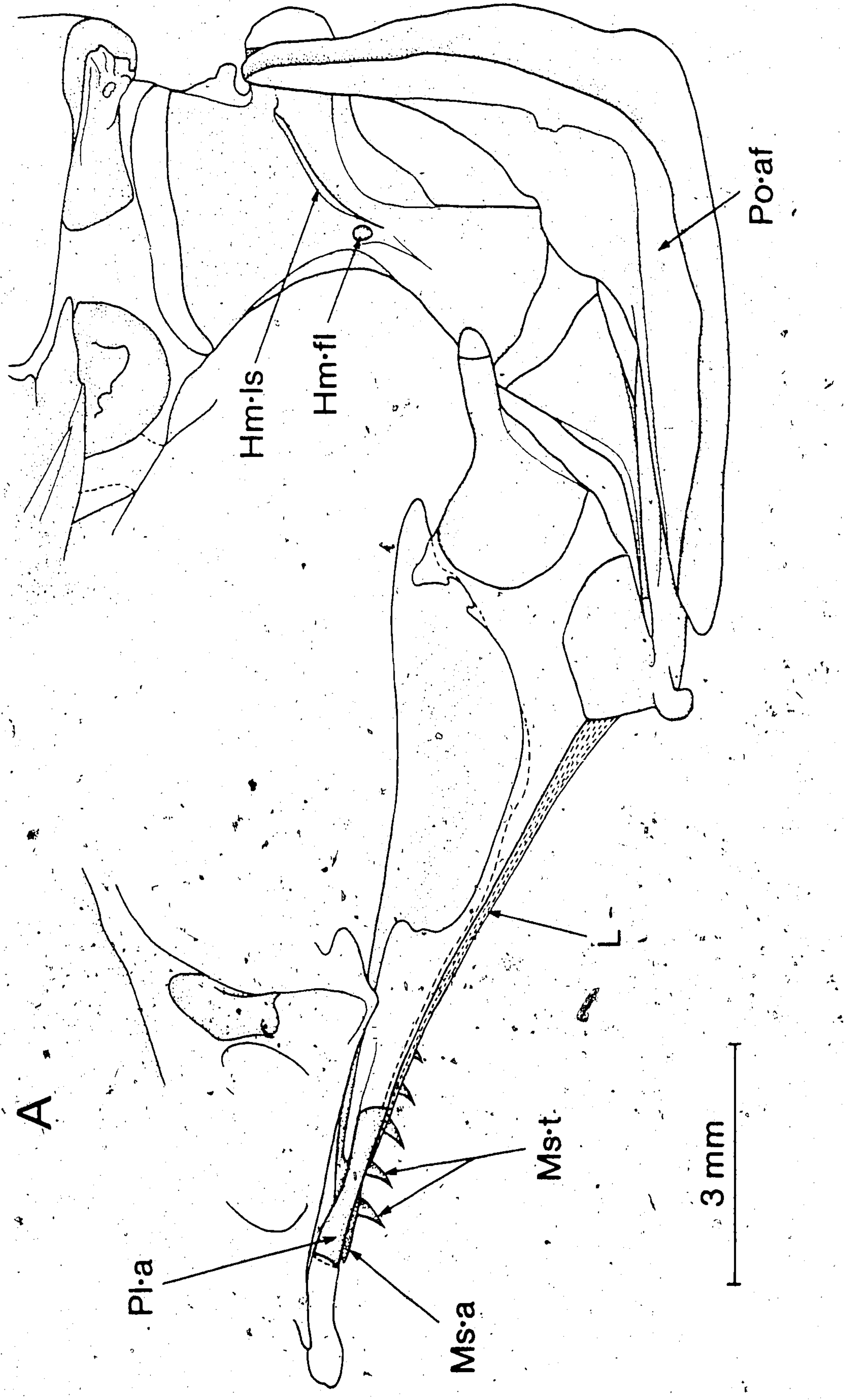

A
Fr
Pa
Pts
Pt
Sp
Hm·ls
Hm·fl
Le
Pl·d
Pl·a
Vo
Mx
Pmx
1 mm

Figure 25. Lateral (A) and medial (B) views of the left suspensorium in *Aplochiton taeniatus* (Aplochitonidae).


A
Hm·ls
Hm·fl
Po·af
L
Ms·t
Pl·a
Ms·a
3 mm

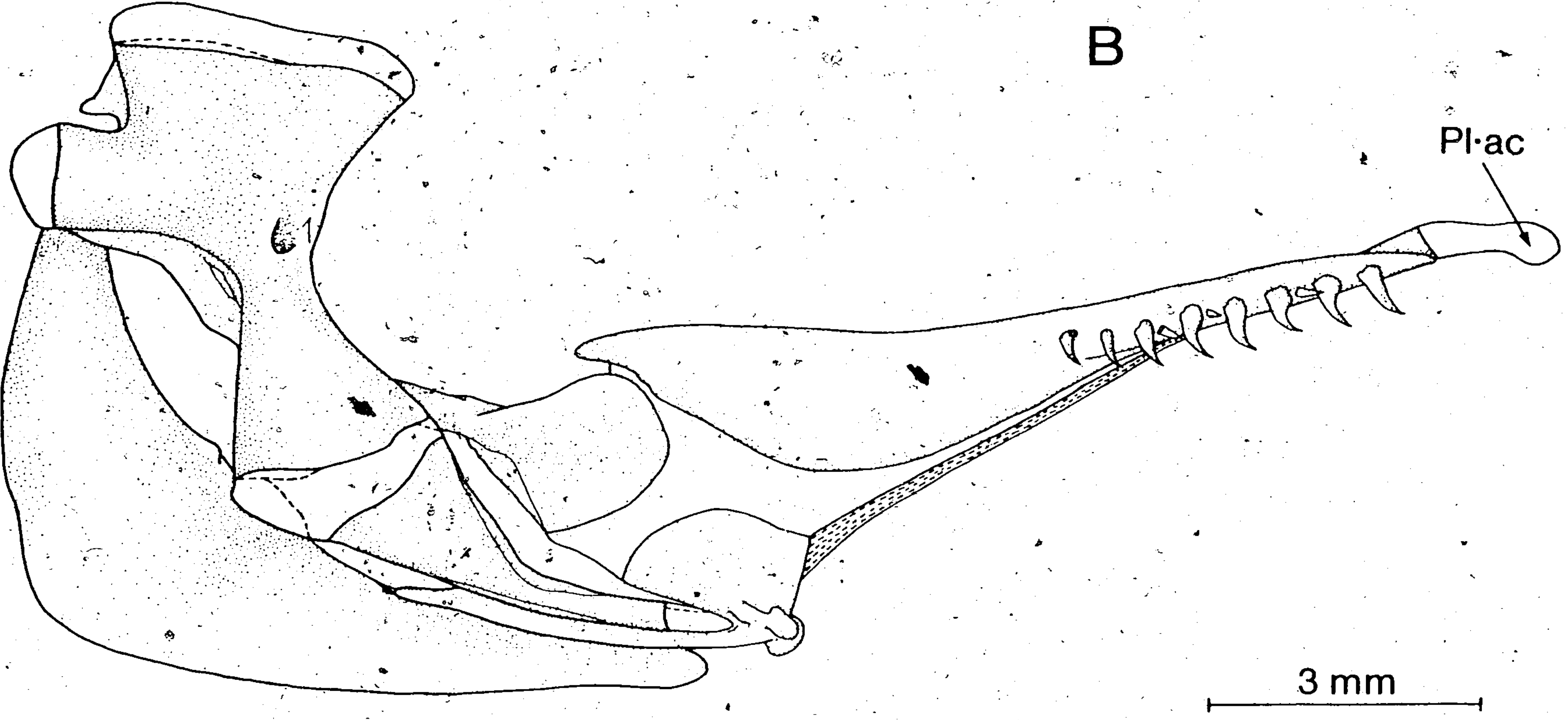
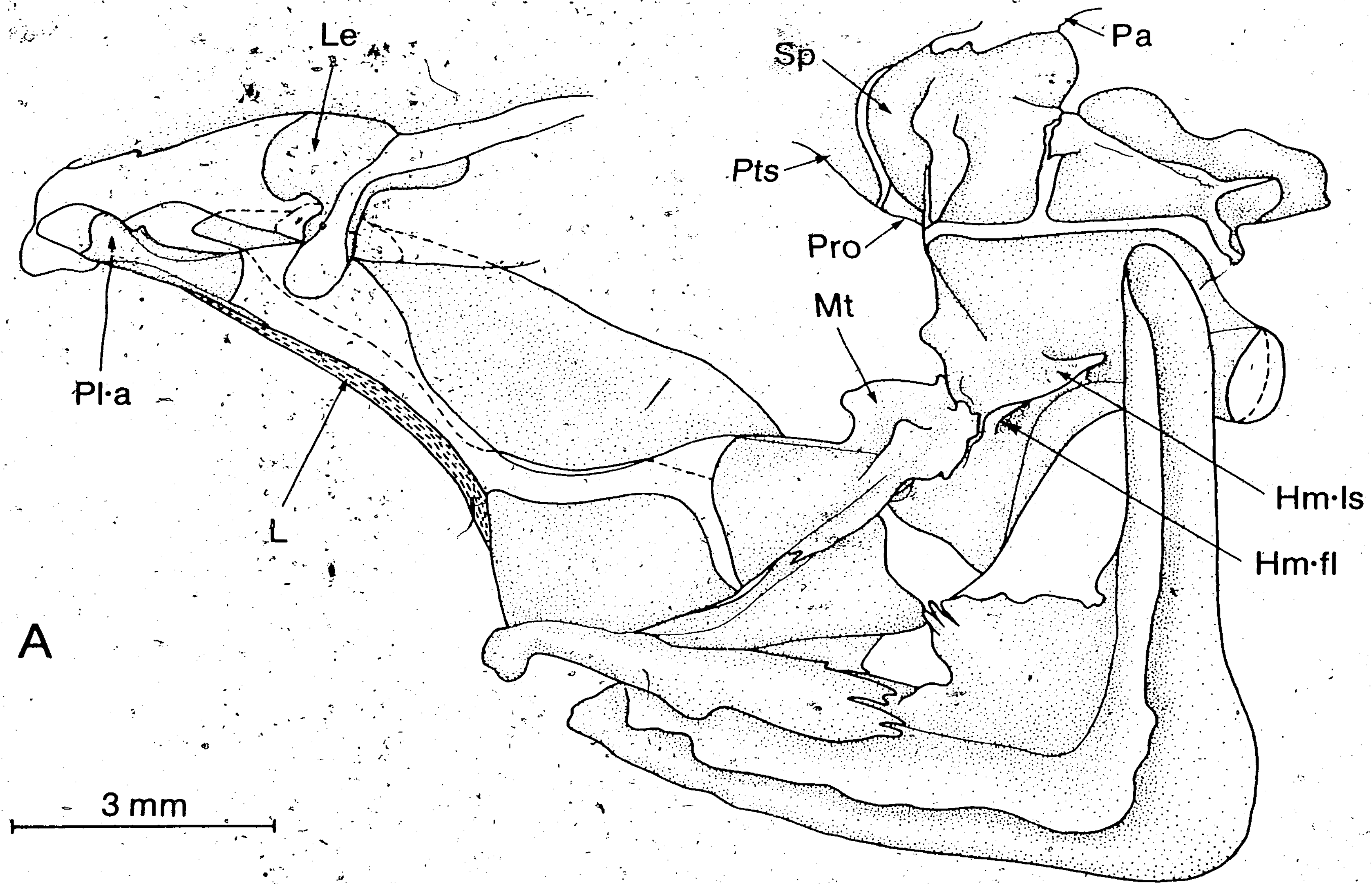

B
Pl·ac
3 mm

Figure 26. Lateral (A) and medial (B) views of the left suspensorium in *Galaxias maculatus* (Galaxiidae).


Le
Pa
Sp
Pts
Pro
Mt
Pl·a
L
Hm·ls
Hm·fl
A
3 mm

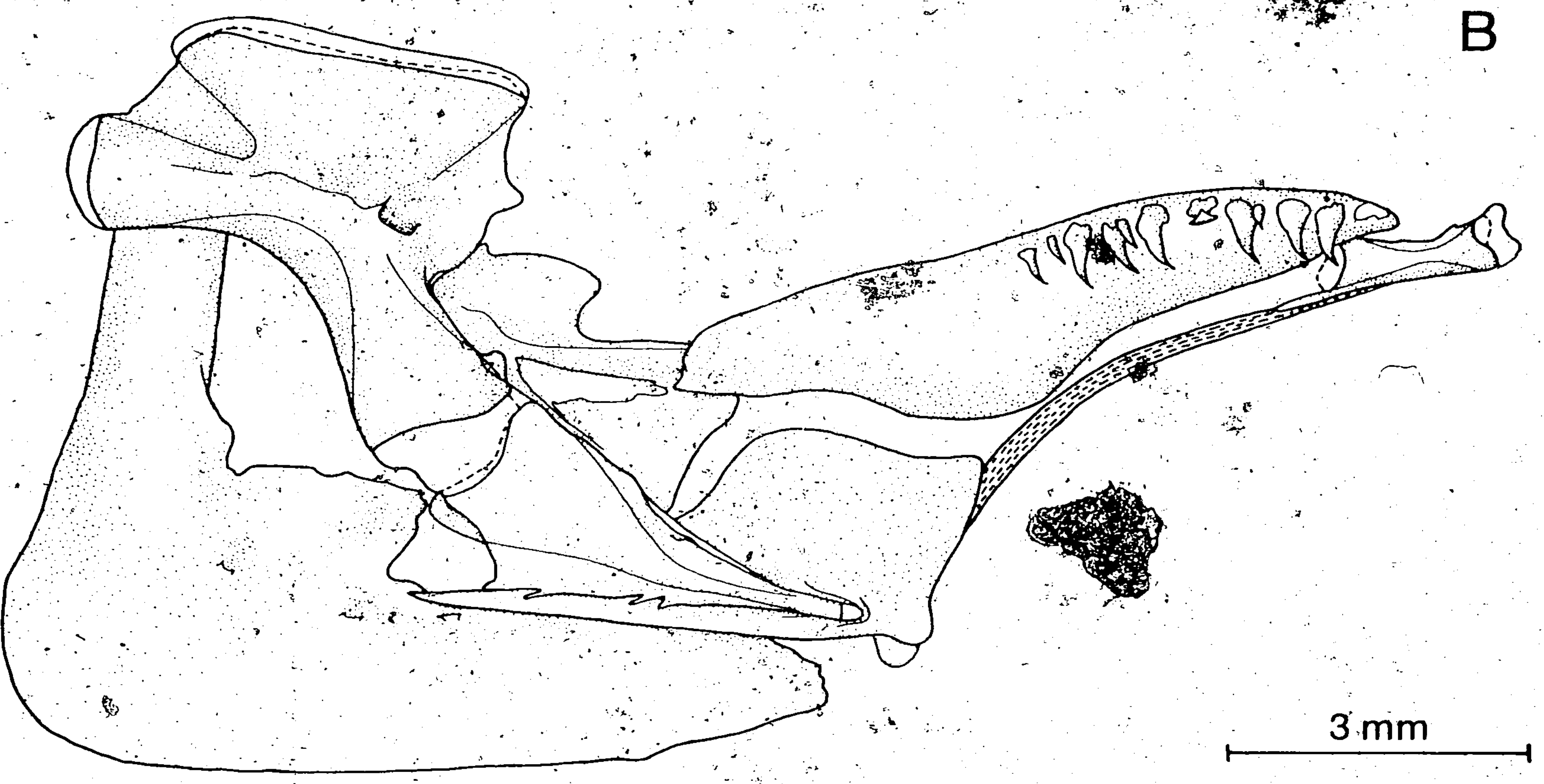
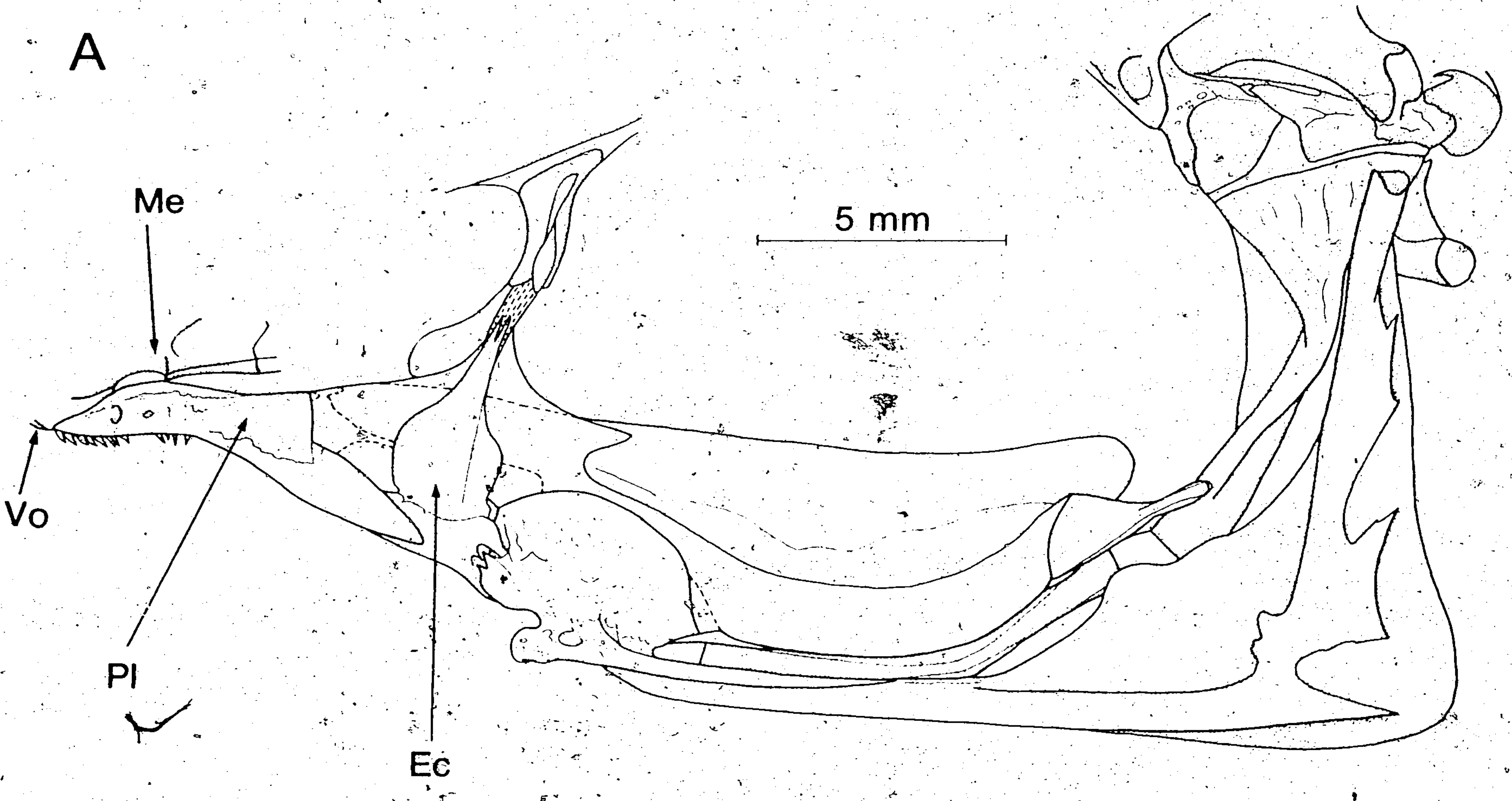

B
3 mm

Figure 27. Lateral (A) and medial (B) views of the left suspensorium in *Argentina silus* (Argentinidae).


A
Me
5 mm
Vo
Pl
Ec

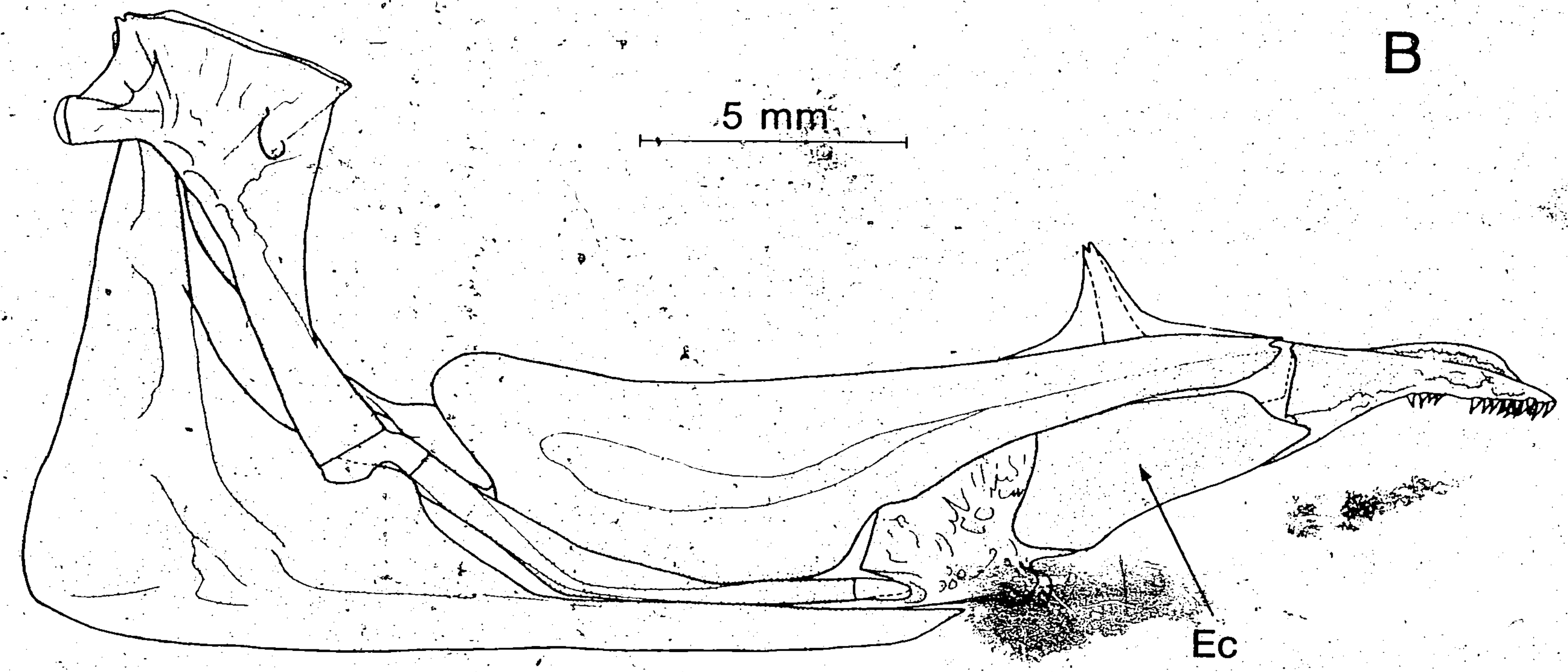

B
5 mm
Ec

Figure 28. Ventral view of the left palatine, *in situ*, in *Argentina silus* (Argentinidae) to show both its articulation with the anterior end of the snout and the palatine-vomerine biting surface. The premaxilla and maxilla are omitted. Anterior is to the top of the page, lateral is to the right.

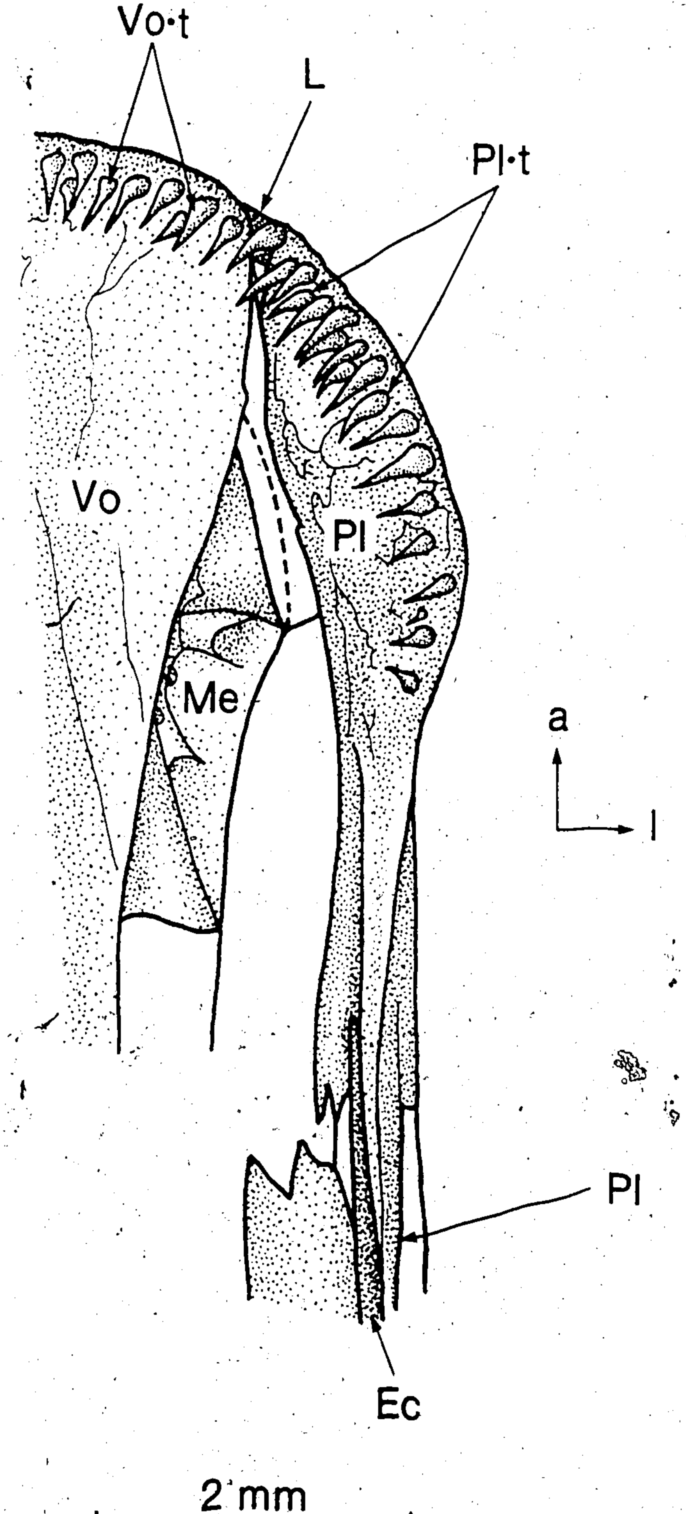
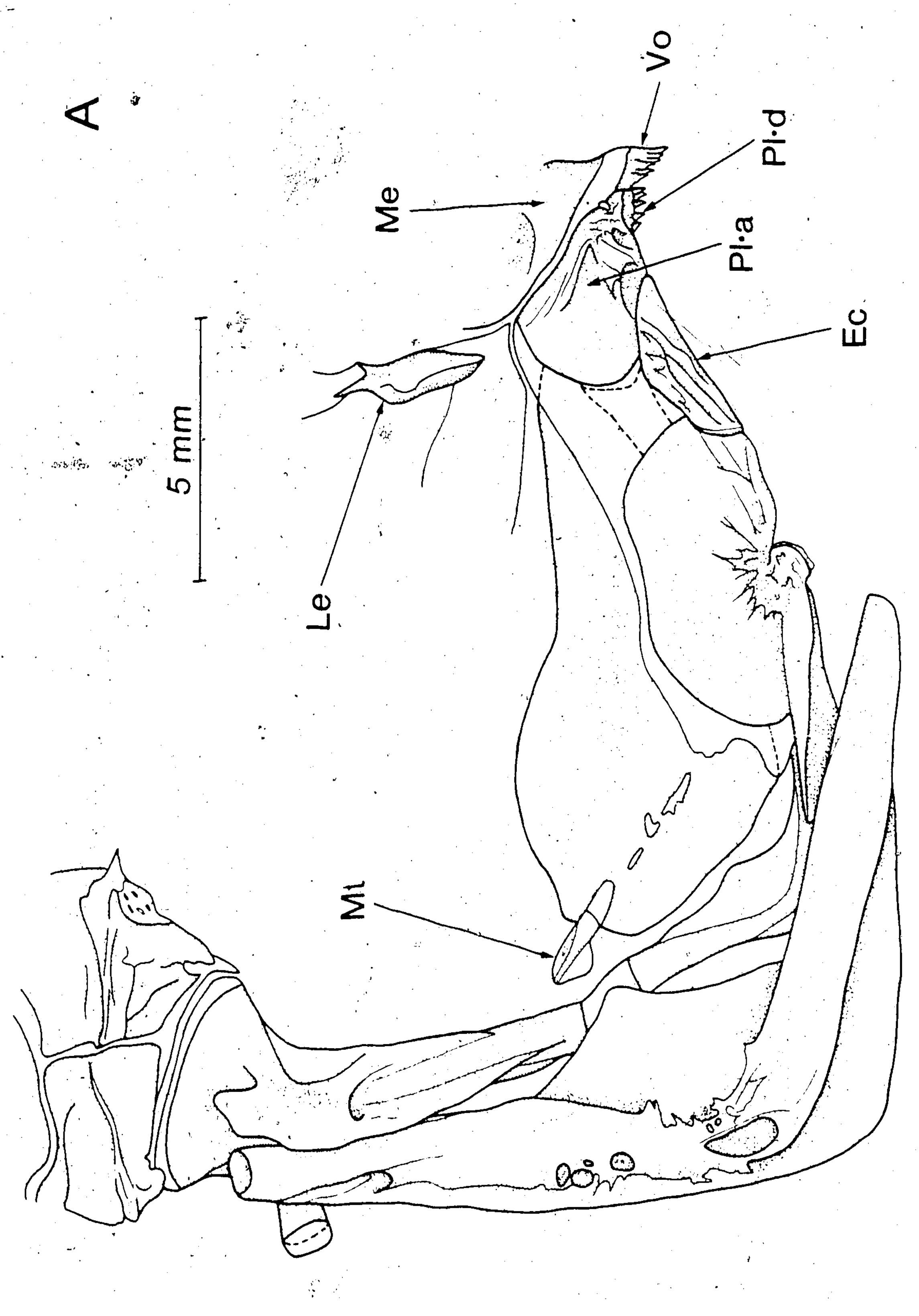

Vo·t
L
Pl·t
Vo
Pl
Me
a
l
Pl
Ec
2 mm

Figure 29. Lateral (A) and medial (B) views of the right suspensorium in *Bathylagus pacificus* (Bathylagidae).


A
Vo
Pl·d
Me
Pl·a
Ec
5 mm
Le
Ml

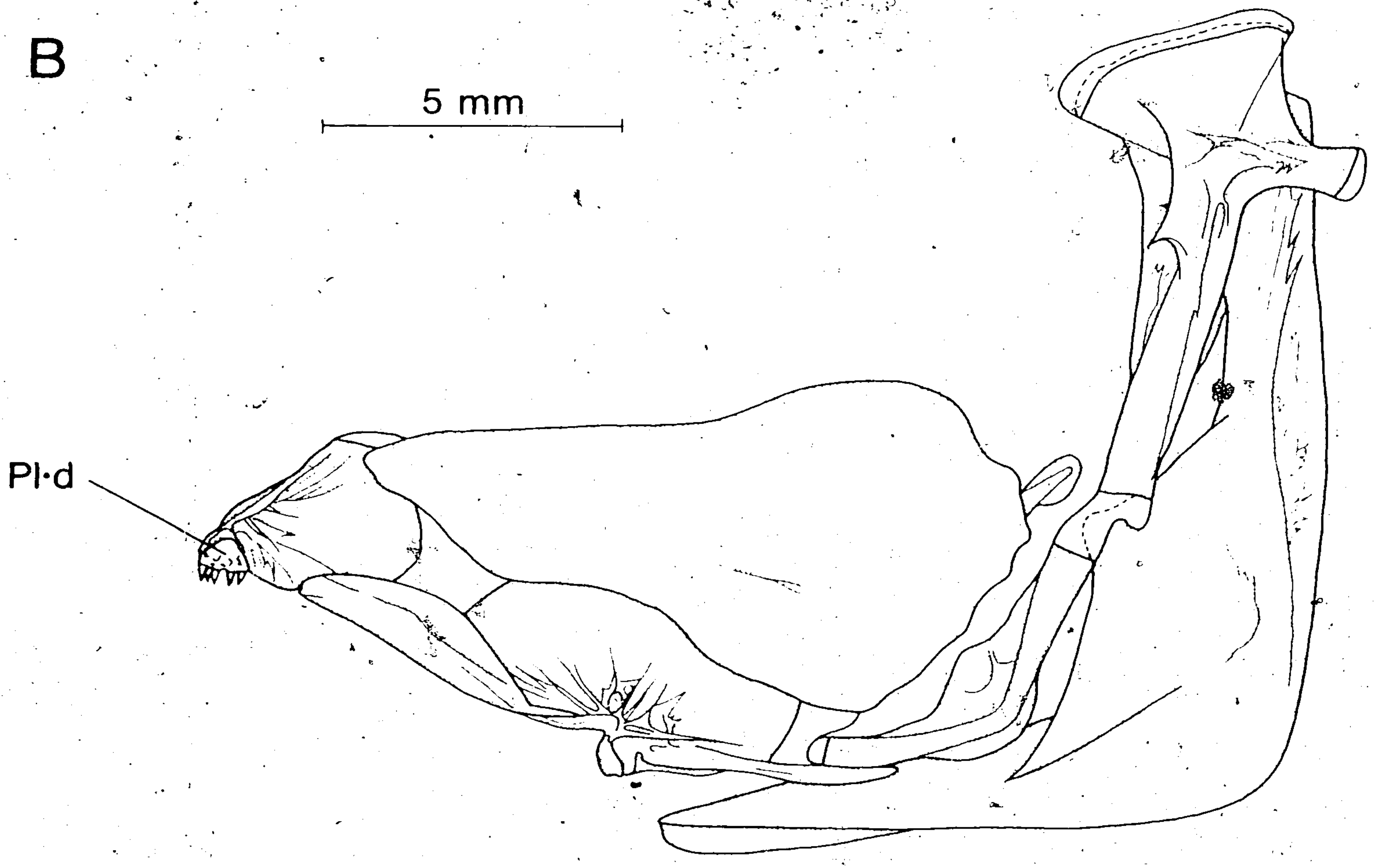

B
5 mm
Pl·d

Figure 30. Ventral view of the left palatine, *in situ*, in ***Bathylagus pacificus*** (Bathylagidae) to show both its articulation with the anterior end of the snout and the palatine-vomerine biting surface. The premaxilla and maxilla are omitted. Anterior is to the top of the page, lateral is to the right.

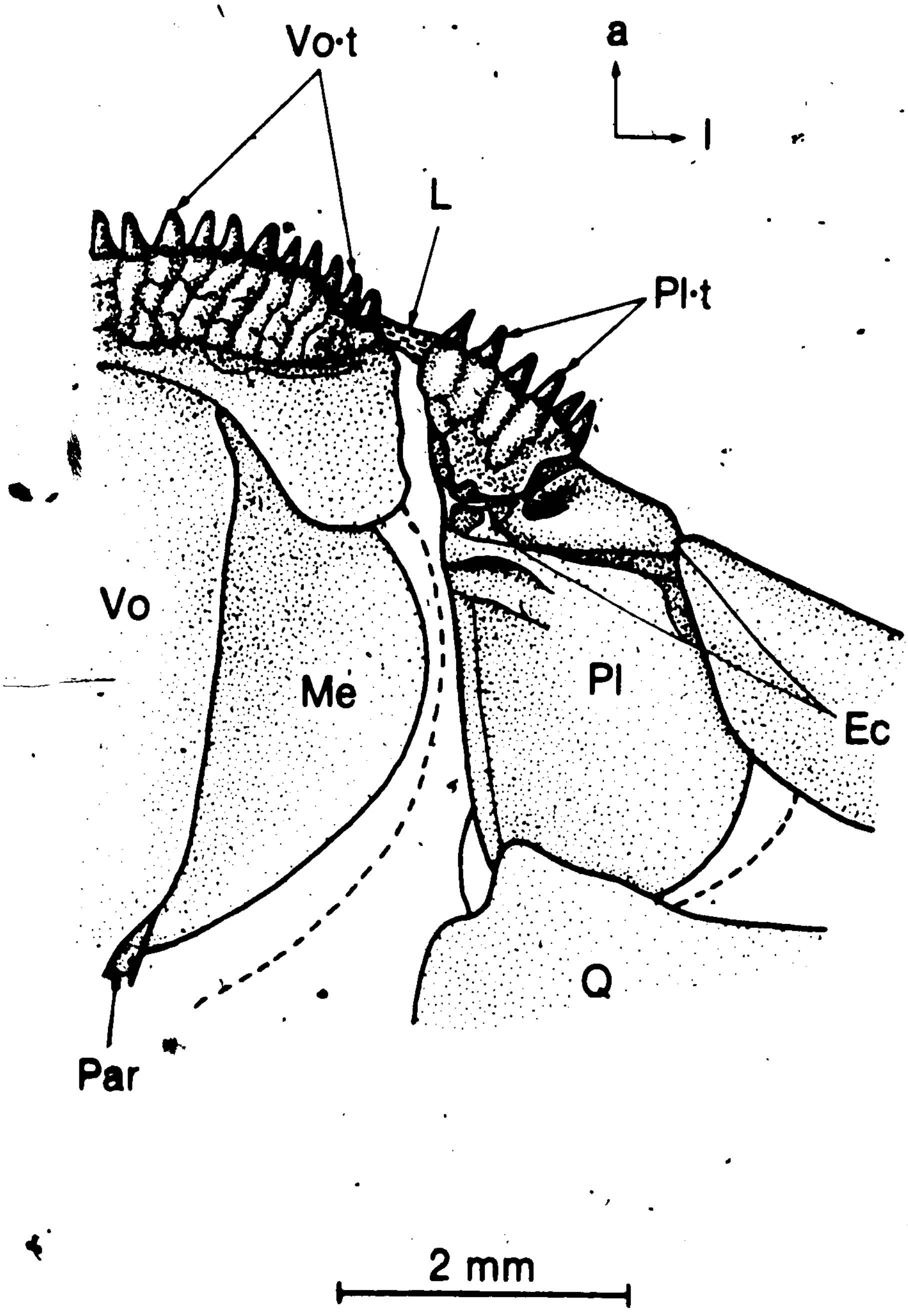
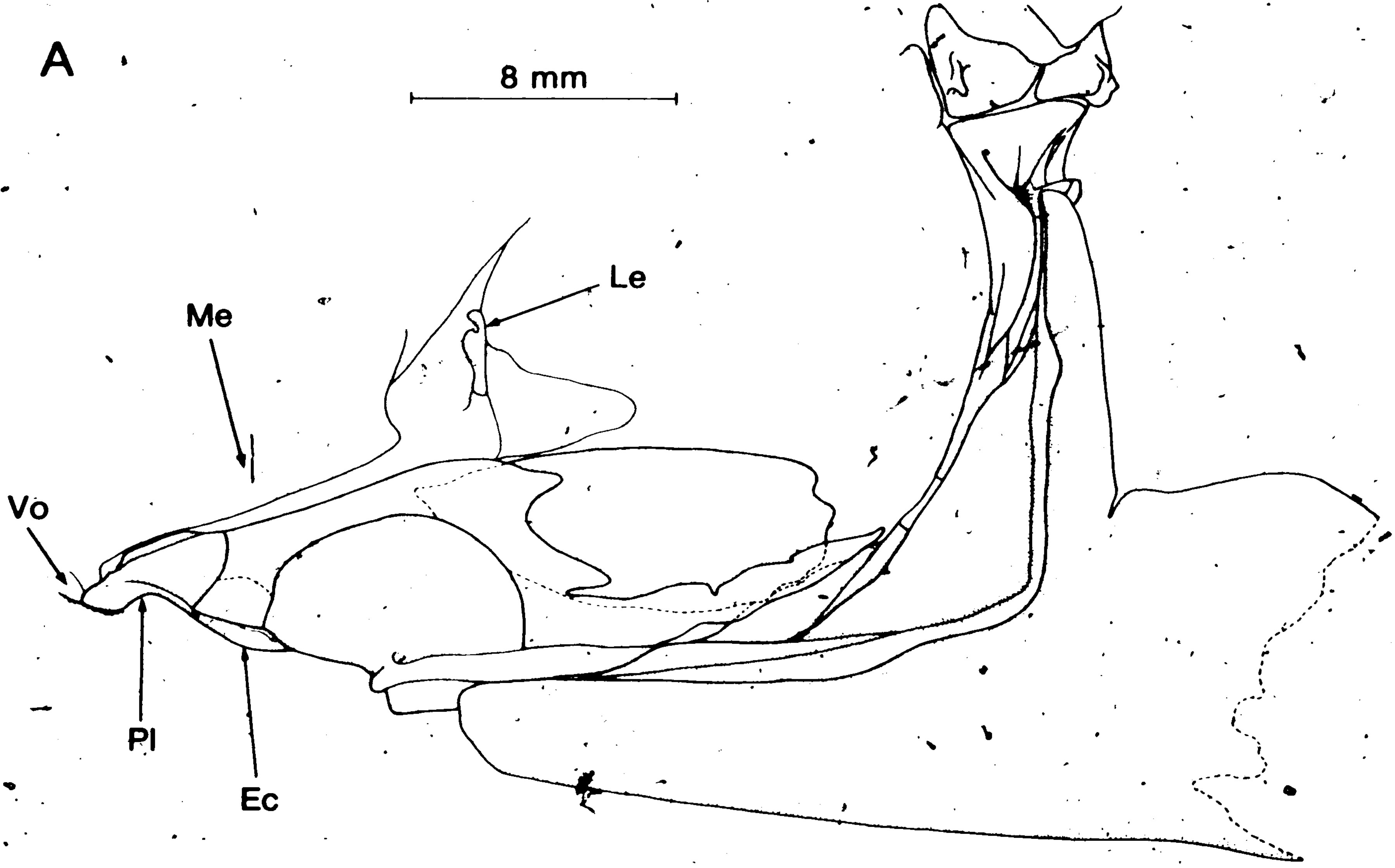

Vo·t
a
l
L
Pl·t
Vo
Me
Pl
Ec
Q
Par
2 mm

Figure 31. Lateral (A) and medial (B) views of the left suspensorium in *Macropinna microstoma* (Opisthoproctidae). The posteroventral corner of the preoperculum, indicated by the dashes, was broken off and is therefore not shown.


A
8 mm
Le
Me
Vo
Pl
Ec

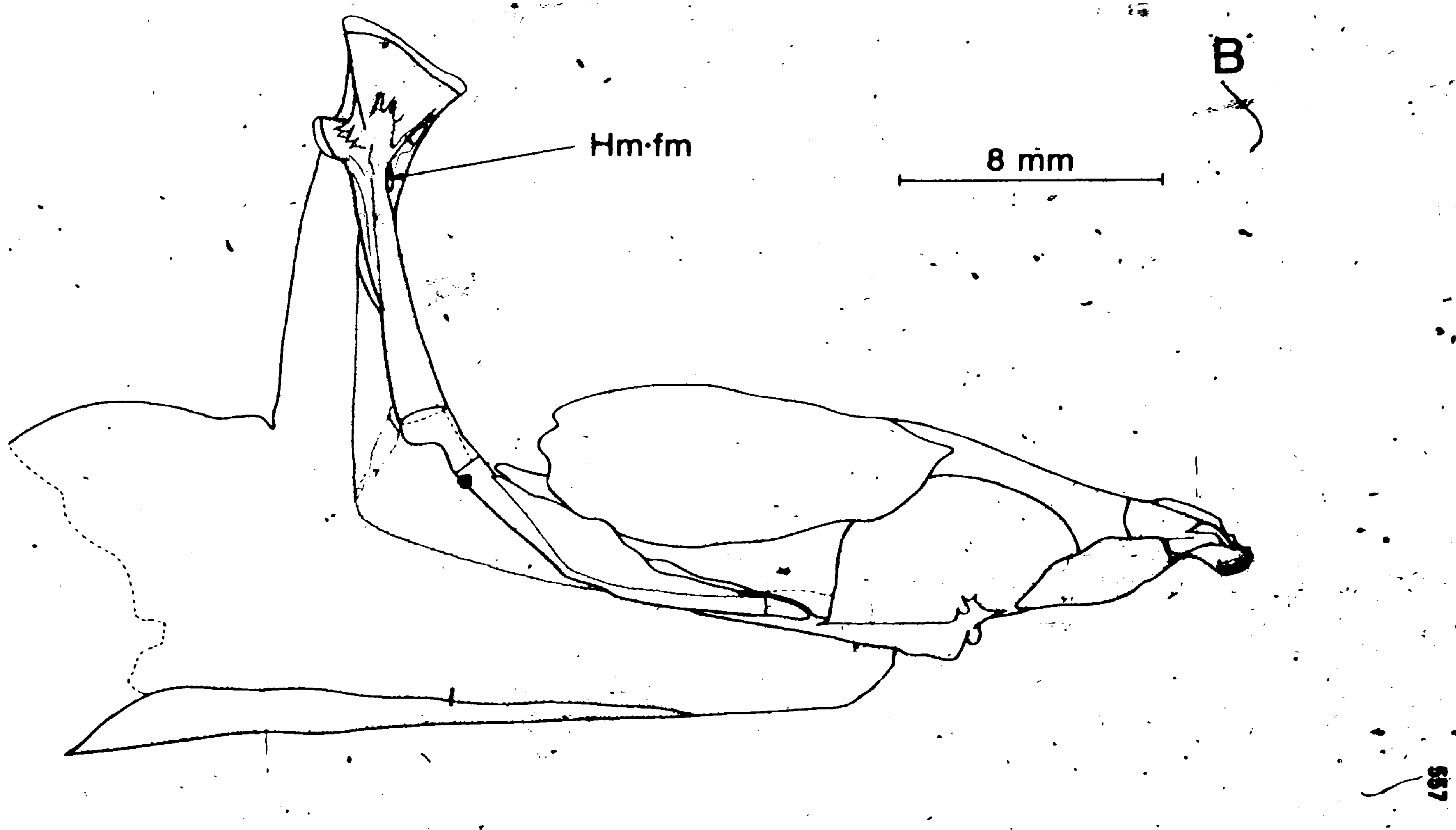
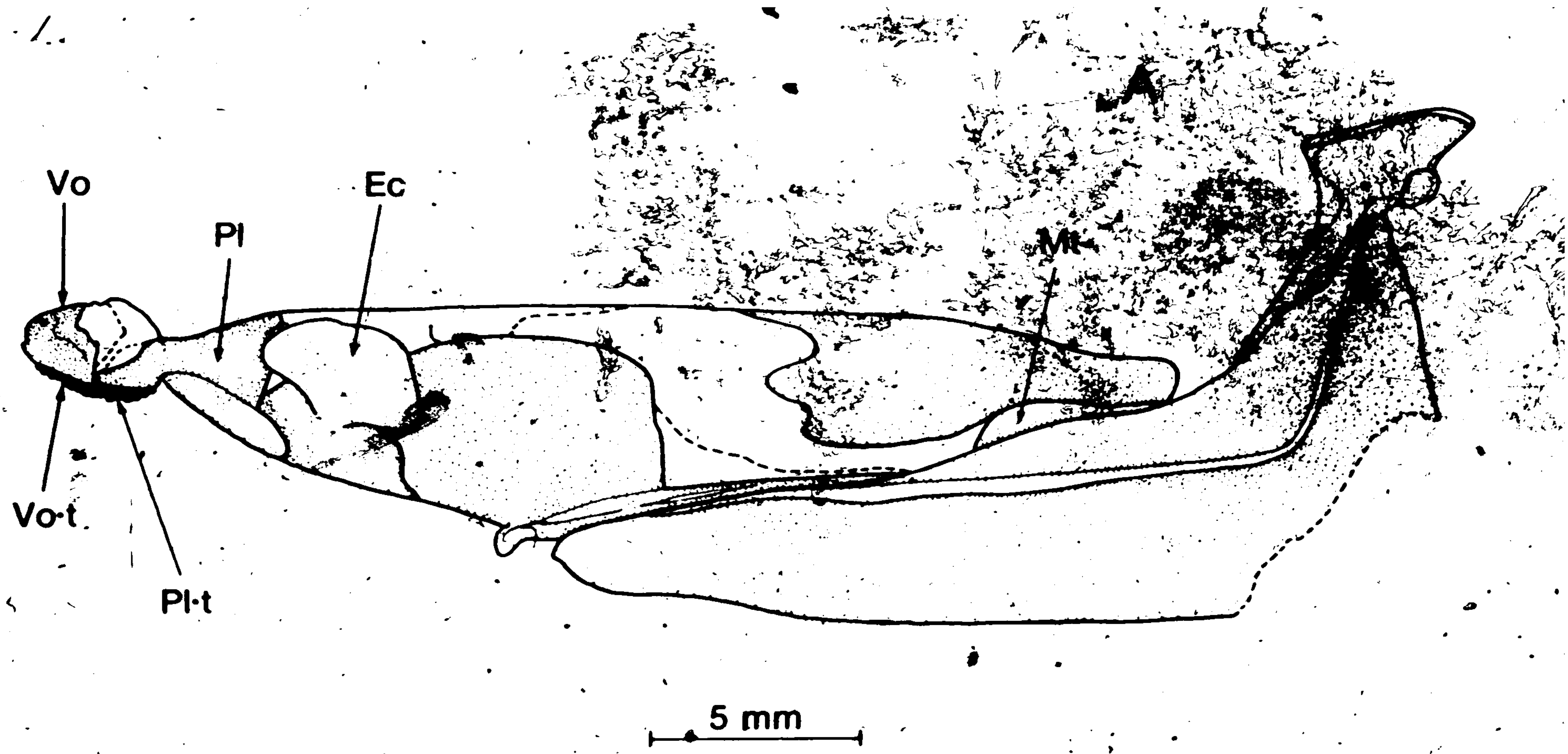
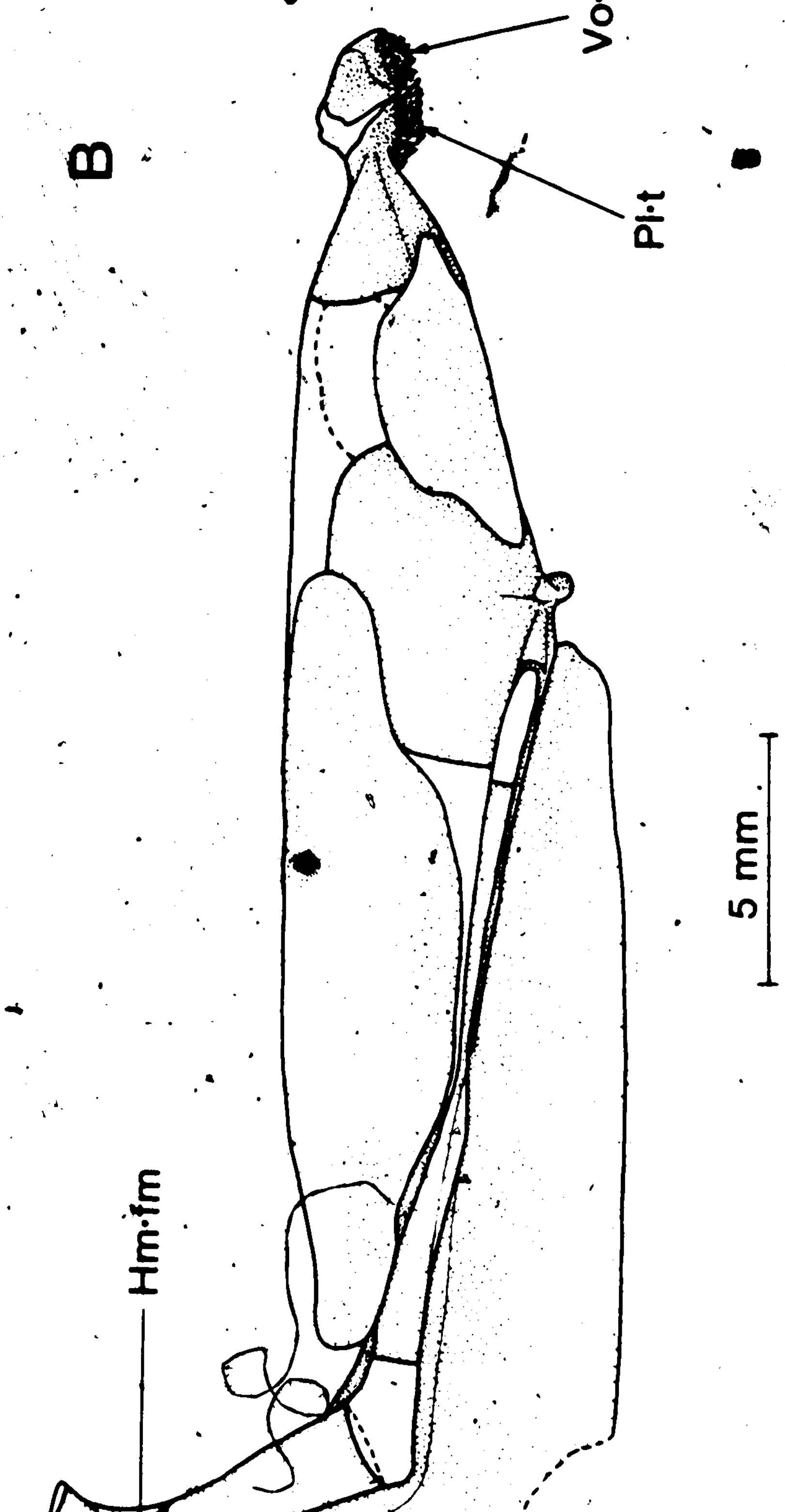

B
Hm·fm
8 mm
557

Figure 32. Lateral (A) and medial (B) views of the left suspensorium in *Dolichopteryx longipes* (Opisthoproctidae). Both drawings are of the suspensorium after its removal from the skull. The part of the vomer shown was broken away from the skull. because the palatine and vomer are inseparable. The posteroventral corner of the preoperculum, indicated by the dashes, was broken off and is therefore not shown.


Vo
Pl
Ec
Mt
Vo·t
Pl·t
5 mm


B
Vo·t
Pl·t
Hm·fm
5 mm

— Figure 33. Ventral view of the left palatine, *in situ*, in *Macropinna microstoma* (Opisthoproctidae) to show both its articulation with the anterior end of the snout and the palatine-vomerine biting surface. The maxilla is omitted (the premaxilla is absent). Anterior is to the top of the page, medial is to the left.

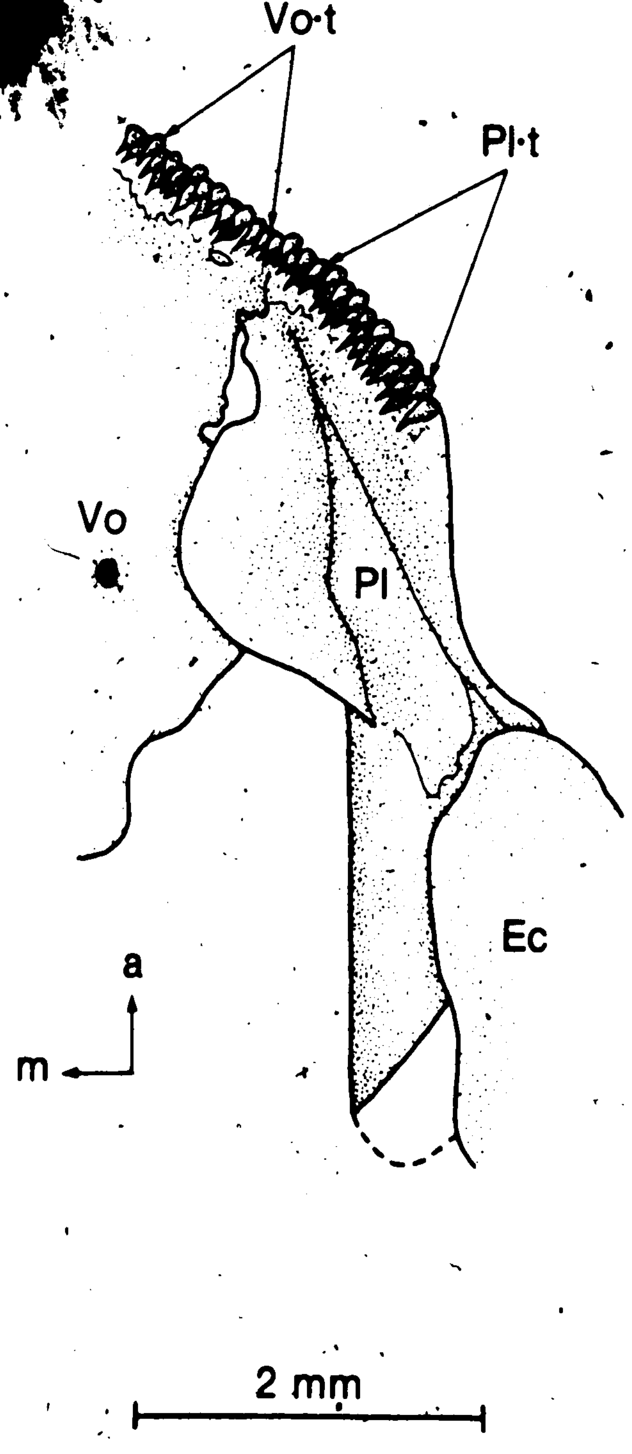
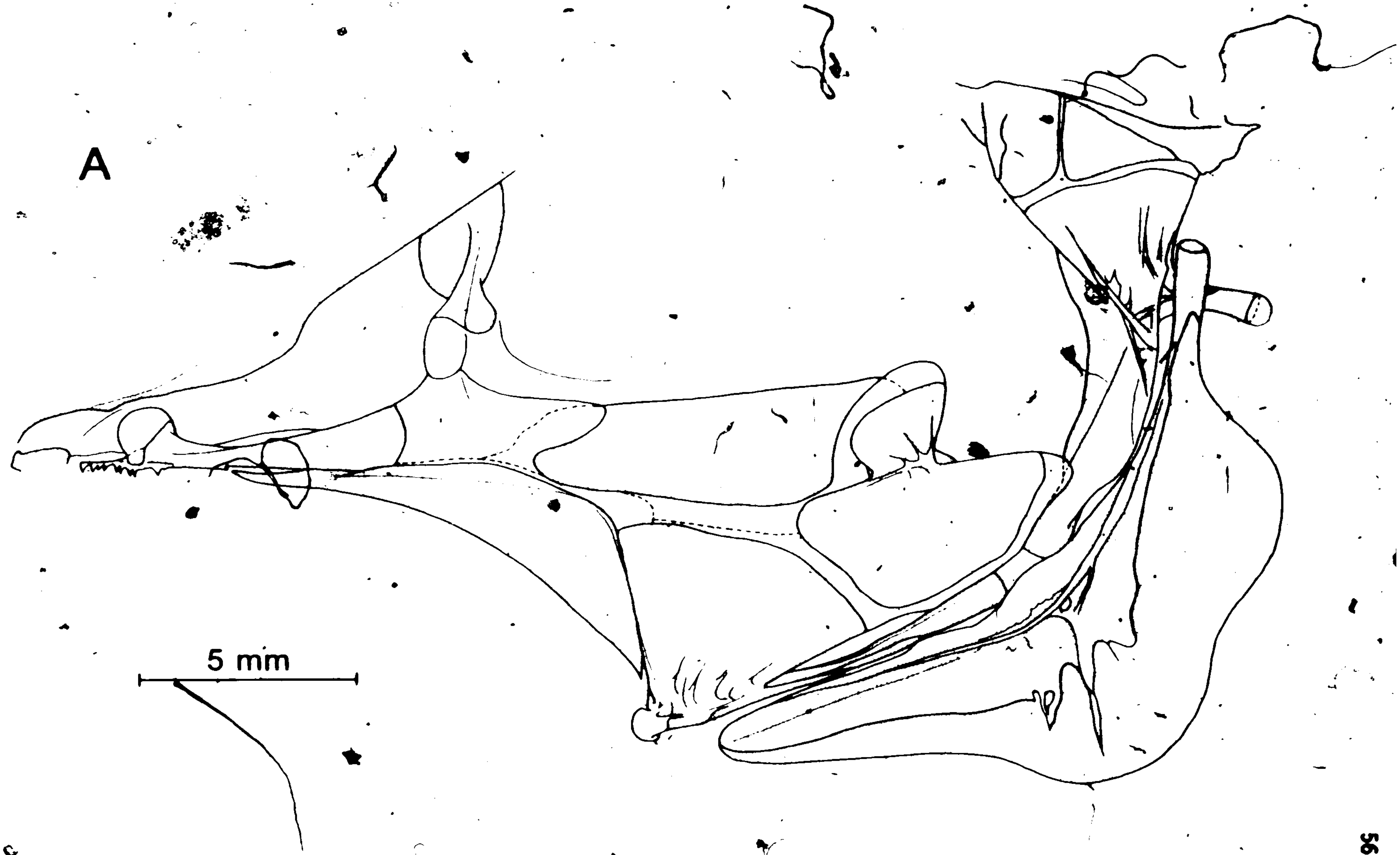

Vo·t
Pl·t
Vo
Pl
Ec
a
m
2 mm

Figure 34. Lateral (A) and medial (B) views of the left suspensorium in *Talismania antillarum* (Alepocephalidae).


A
5 mm

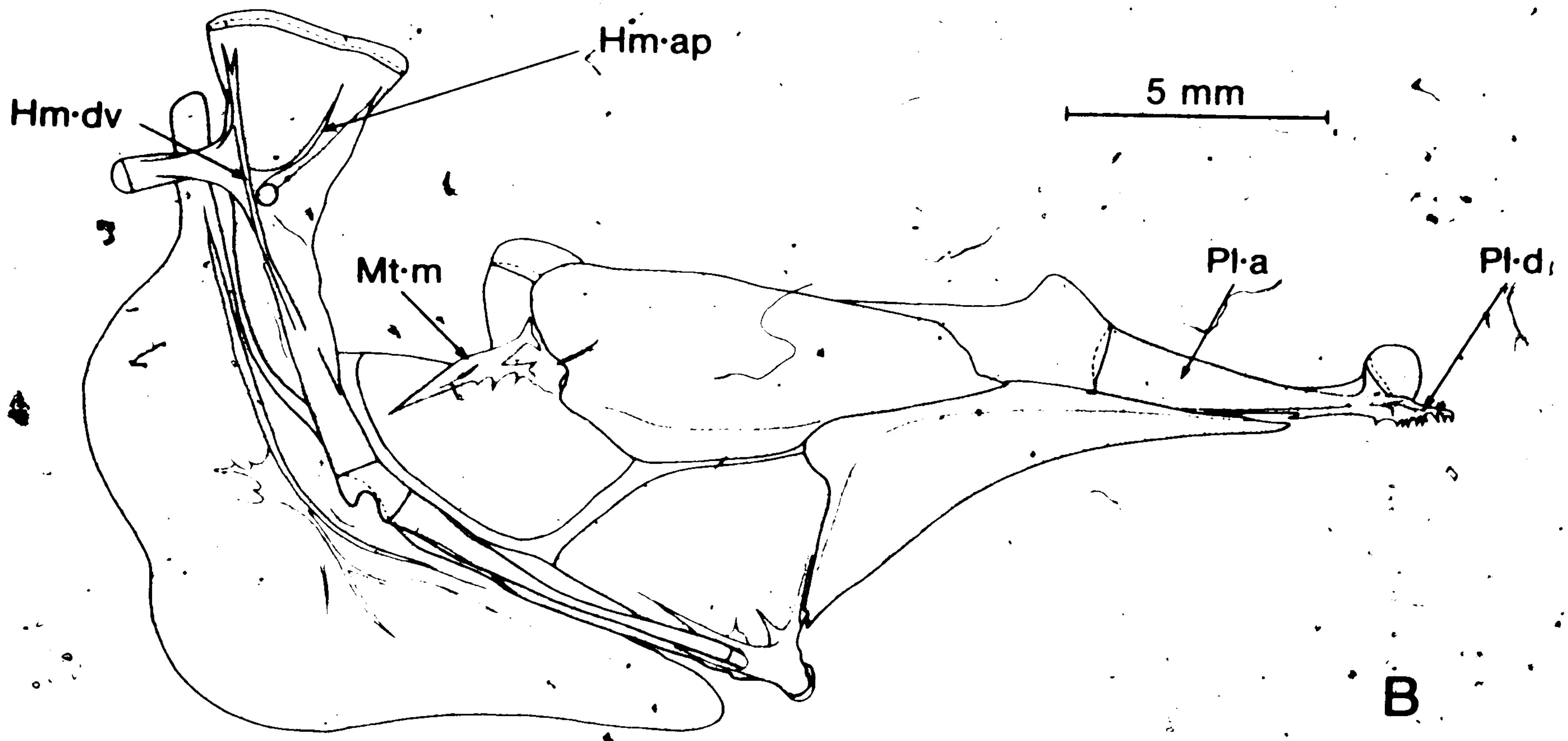
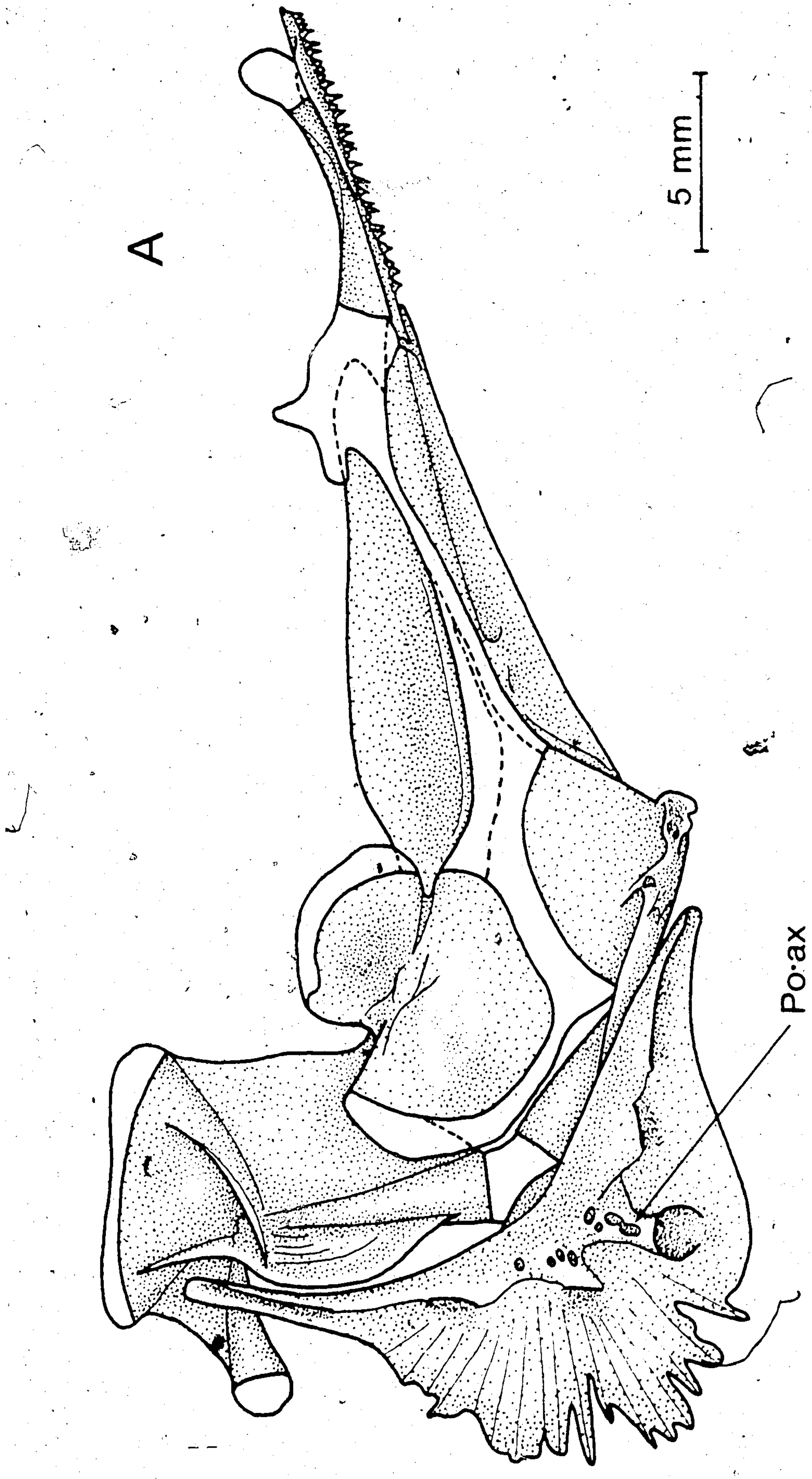

Hm·ap
Hm·dv
5 mm
Mt·m
Pl·a
Pl·d
B

Figure 35. Lateral (A) and medial (B) views of the right suspensorium in *Alepocephalus bairdii* (Alepocephalidae). Both drawings are of the suspensorium after its removal from the skull. Most of the posterior edge of the preoperculum was broken off, but was reconstructed using the left preoperculum.


A
5 mm
Po·ax

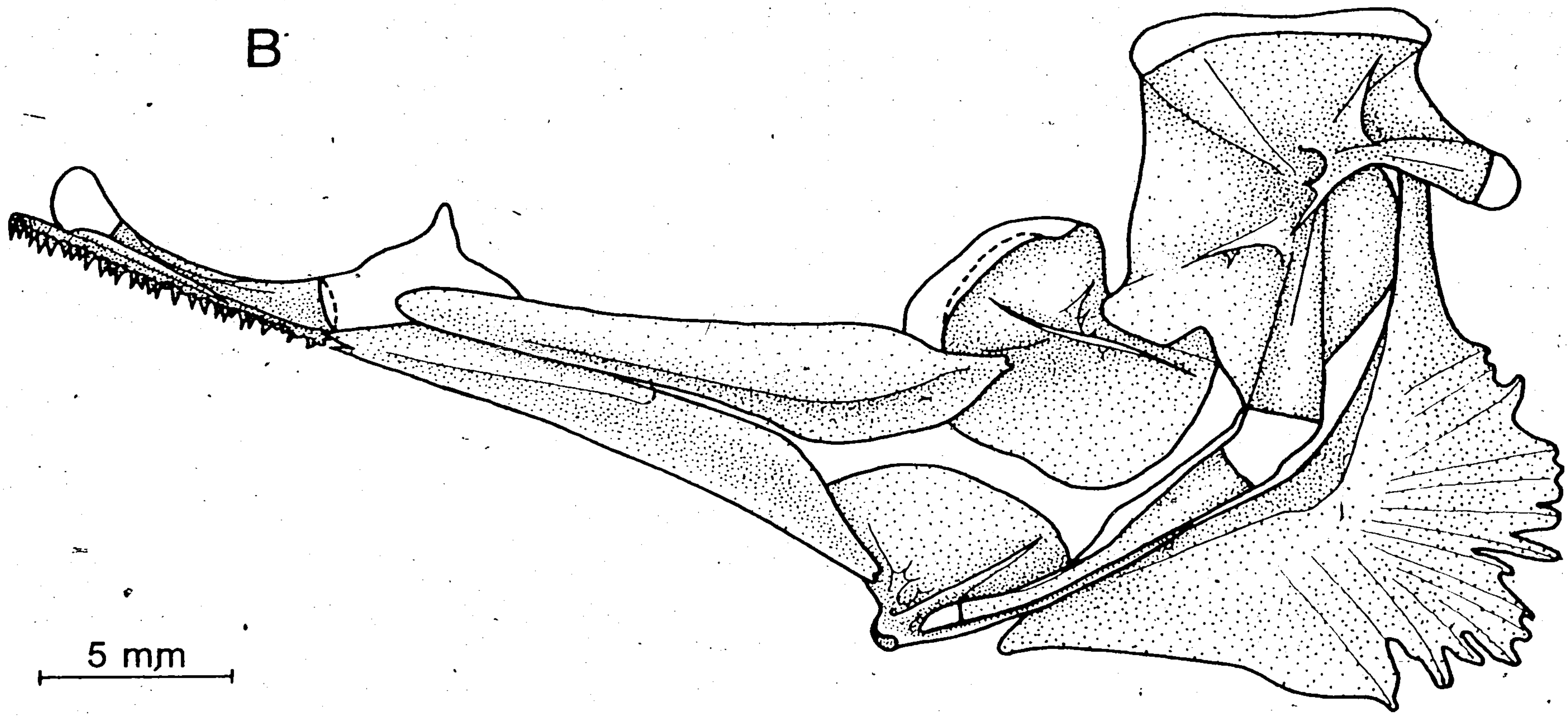
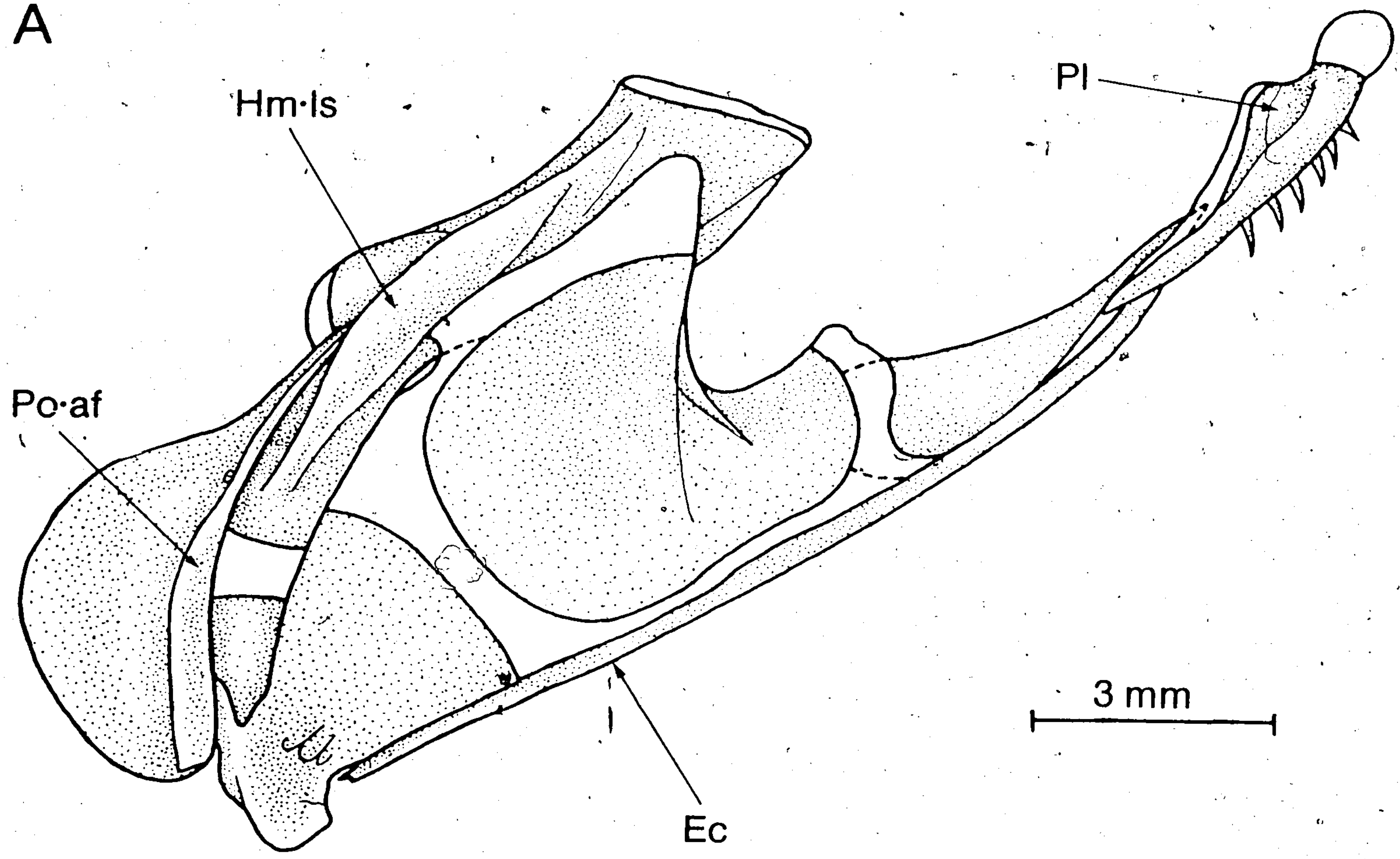

B
5 mm

Figure 36. Lateral (A) and medial (B) views of the right suspensorium in *Bathylaco nigricans* (Alepocephalidae). Both drawings are of the suspensorium after its removal from the skull.


A
Hm·Is
Pl
Po·af
Ec
3 mm

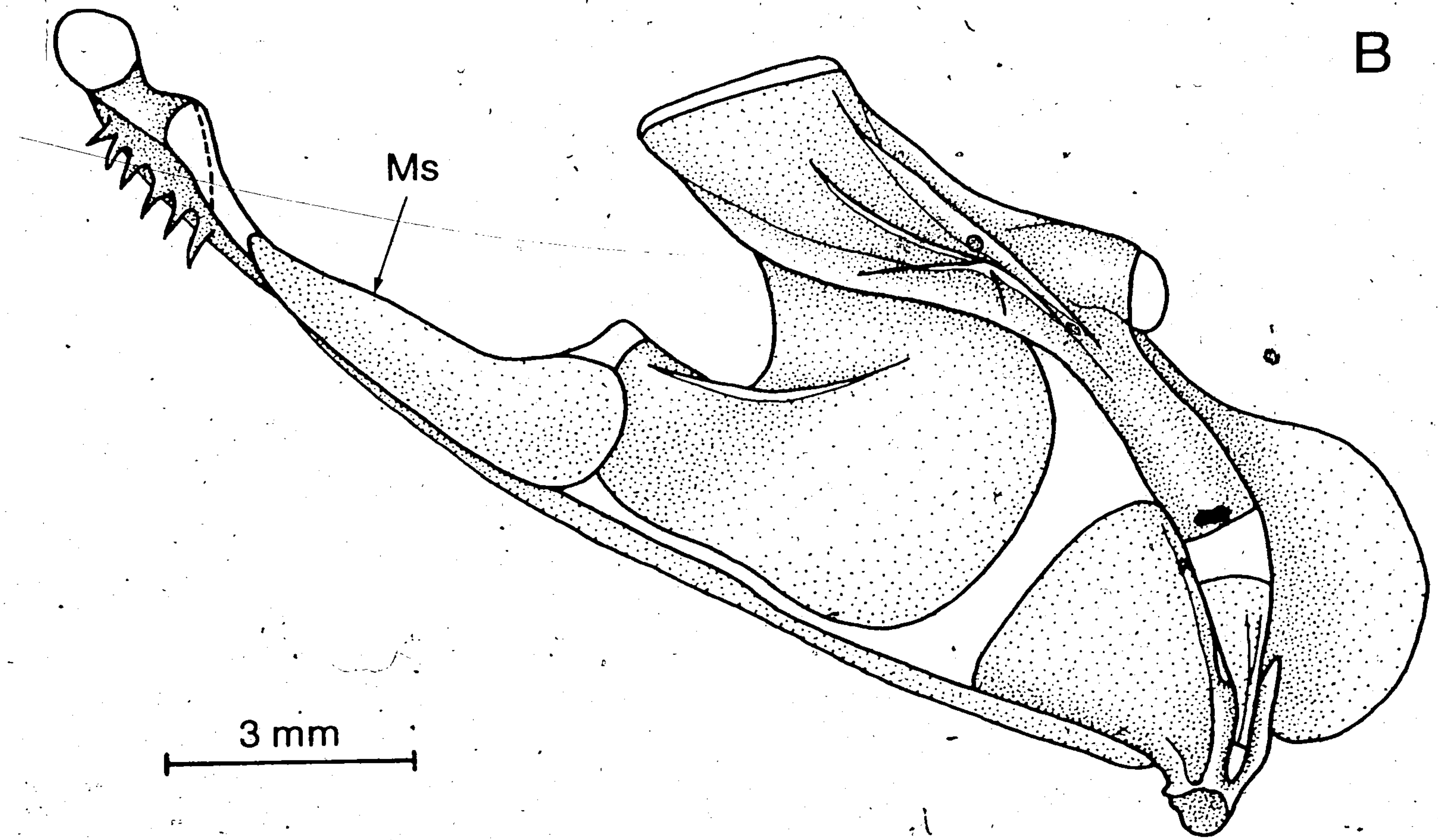
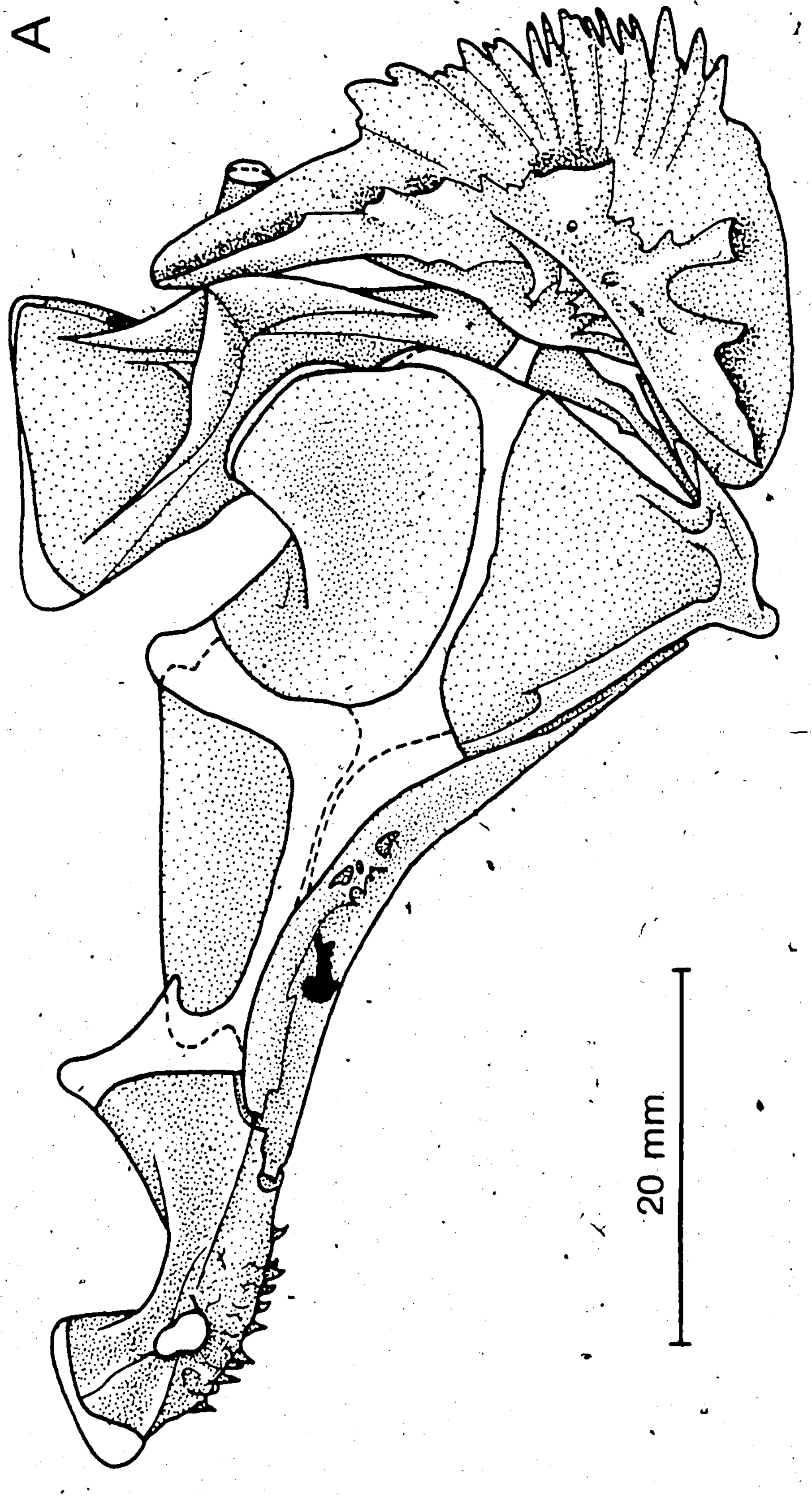

B
Ms
3 mm

Figure 37. Lateral (A) and medial (B) views of the left suspensorium in *Narcetes stomias* (Alepocephalidae). Both drawings are of the suspensorium after its removal from the skull.


A
20 mm

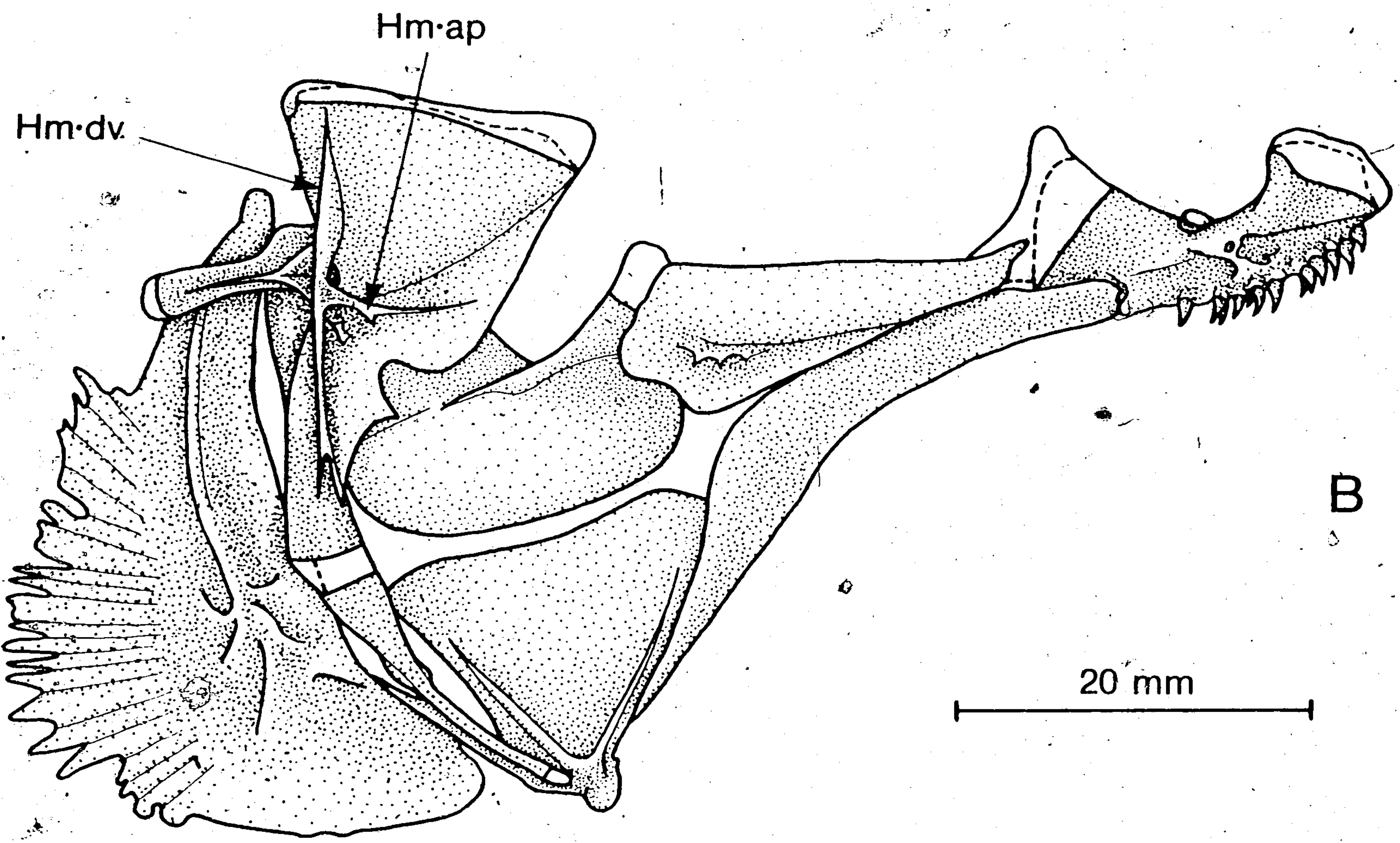
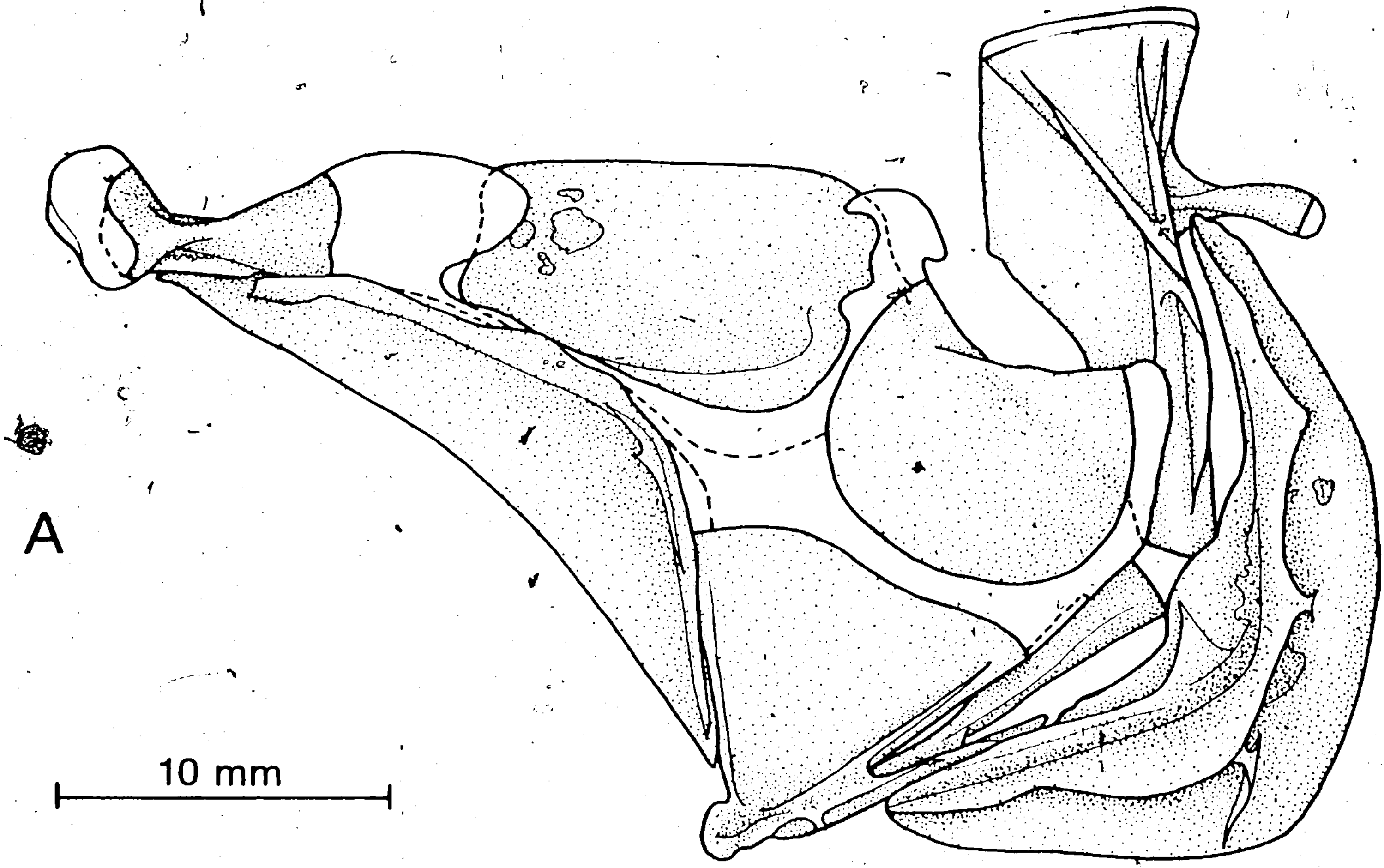

Hm·ap
Hm·dv.
B
20 mm

Figure 38. Lateral (A) and medial (B) views of the left suspensorium in *Rouleina maderensis* (Alepocephalidae). Both drawings are of the suspensorium after its removal from the skull.


A
10 mm

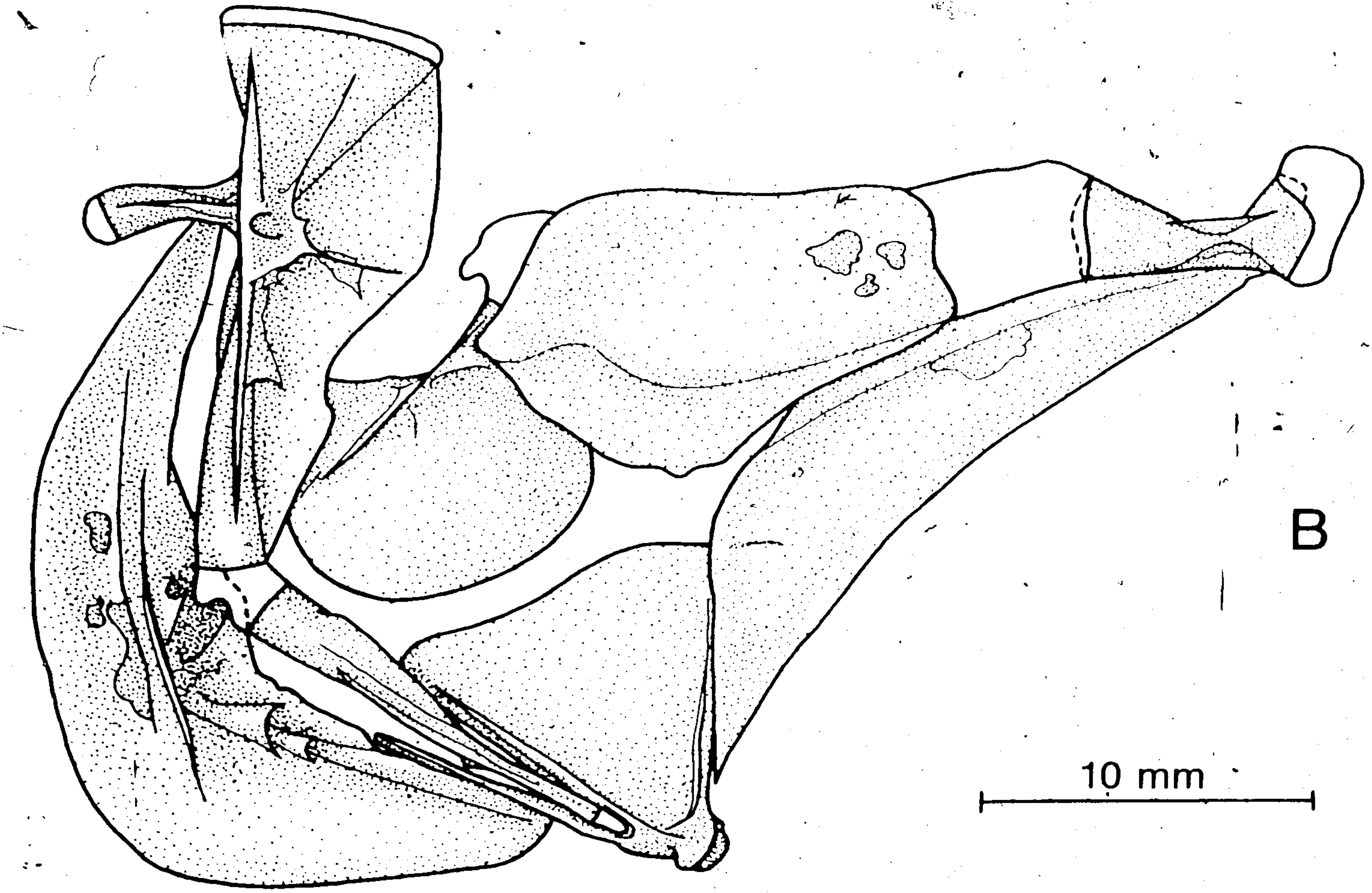
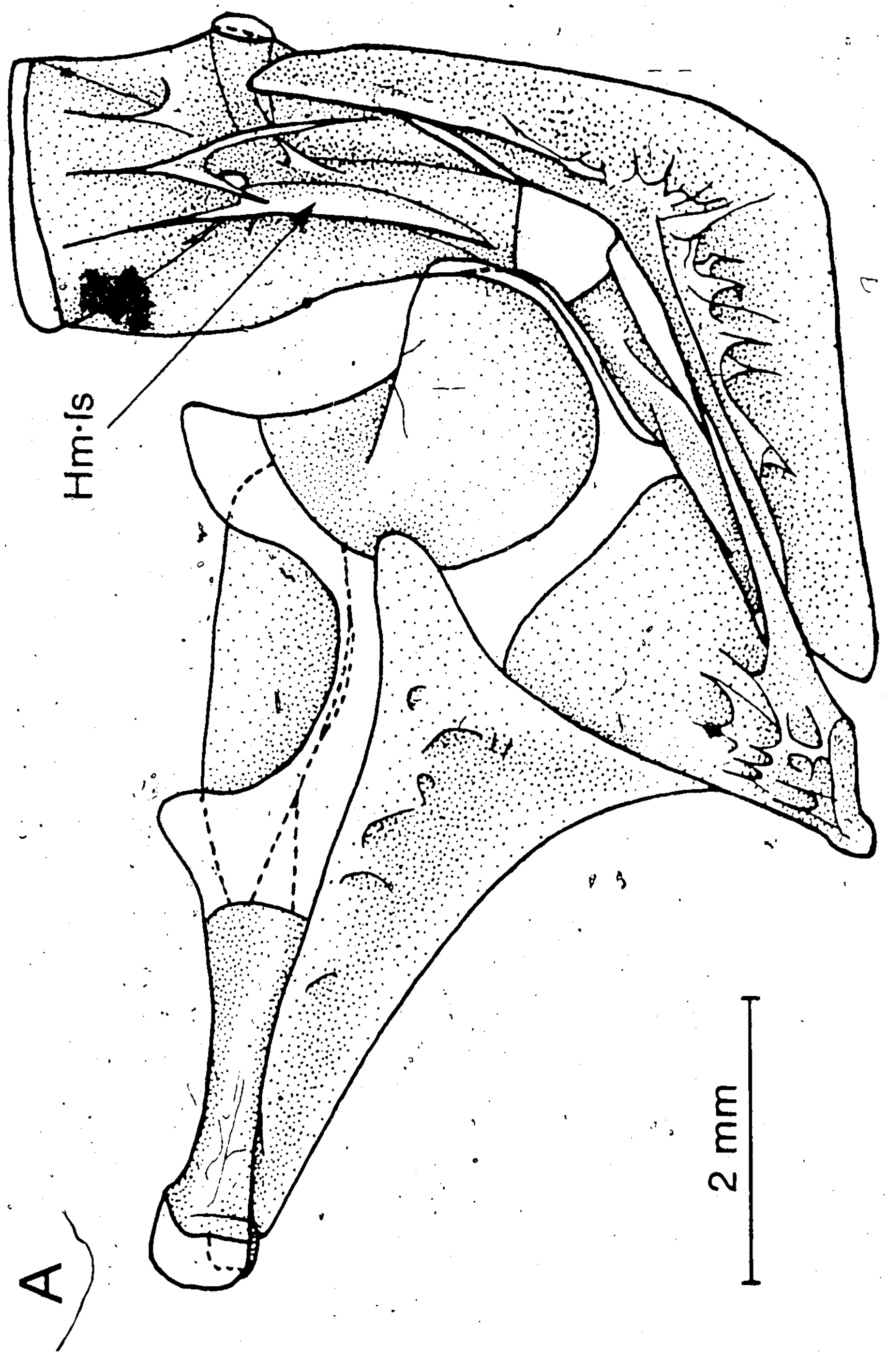

B
10 mm

Figure 39. Lateral (A) and medial (B) views of the left suspensorium in *Photostylus pycnopterus* (Alepocephalidae). Both drawings are of the suspensorium after its removal from the skull.


Hm·Is
2 mm
A

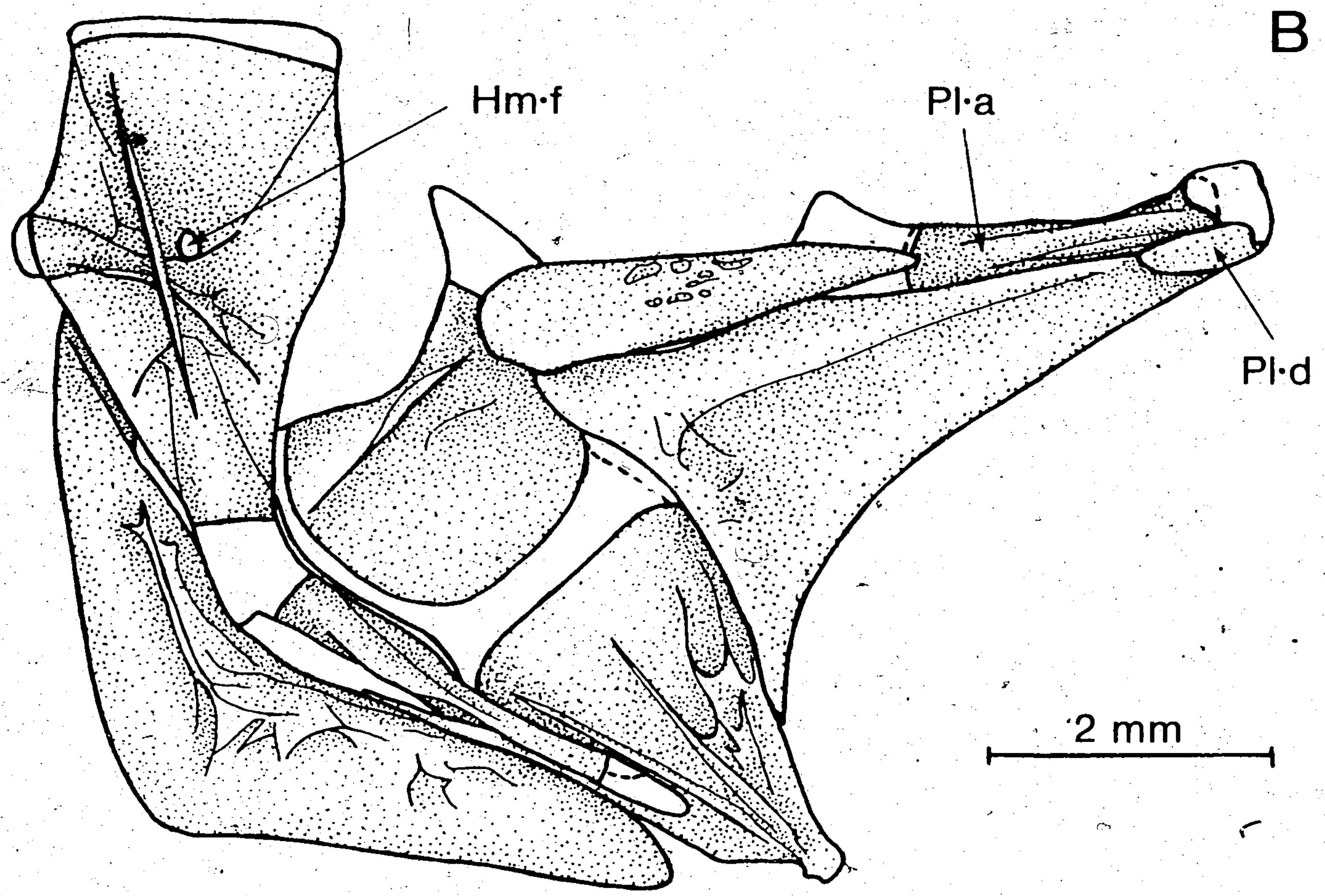
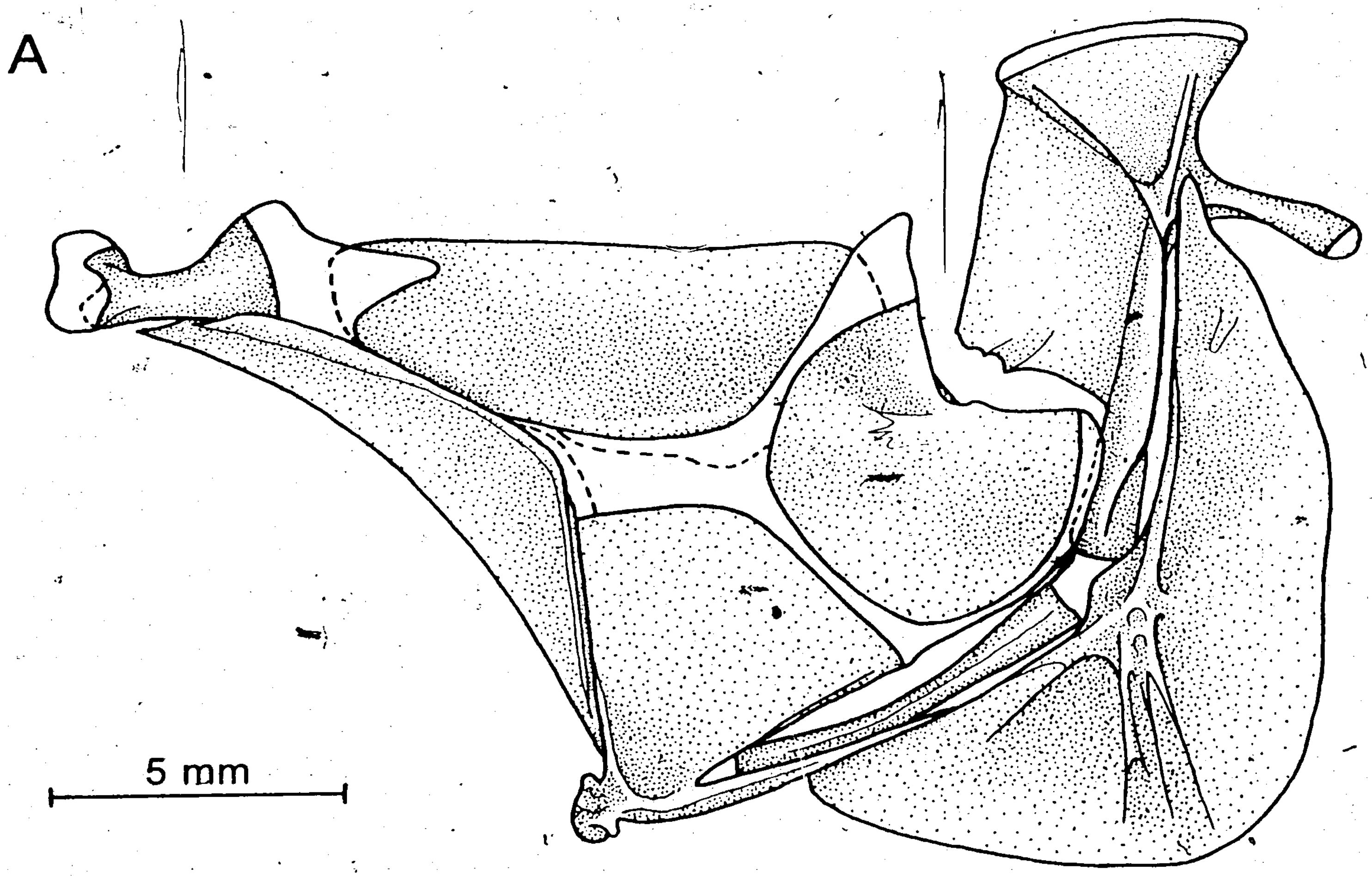

B
Hm·f
Pl·a
Pl·d
2 mm

Figure 40. Lateral (A) and medial (B) views of the left suspensorium in *Xenodermichthys copei* (Alepocephalidae). Both drawings are of the suspensorium after its removal from the skull.


A
5 mm

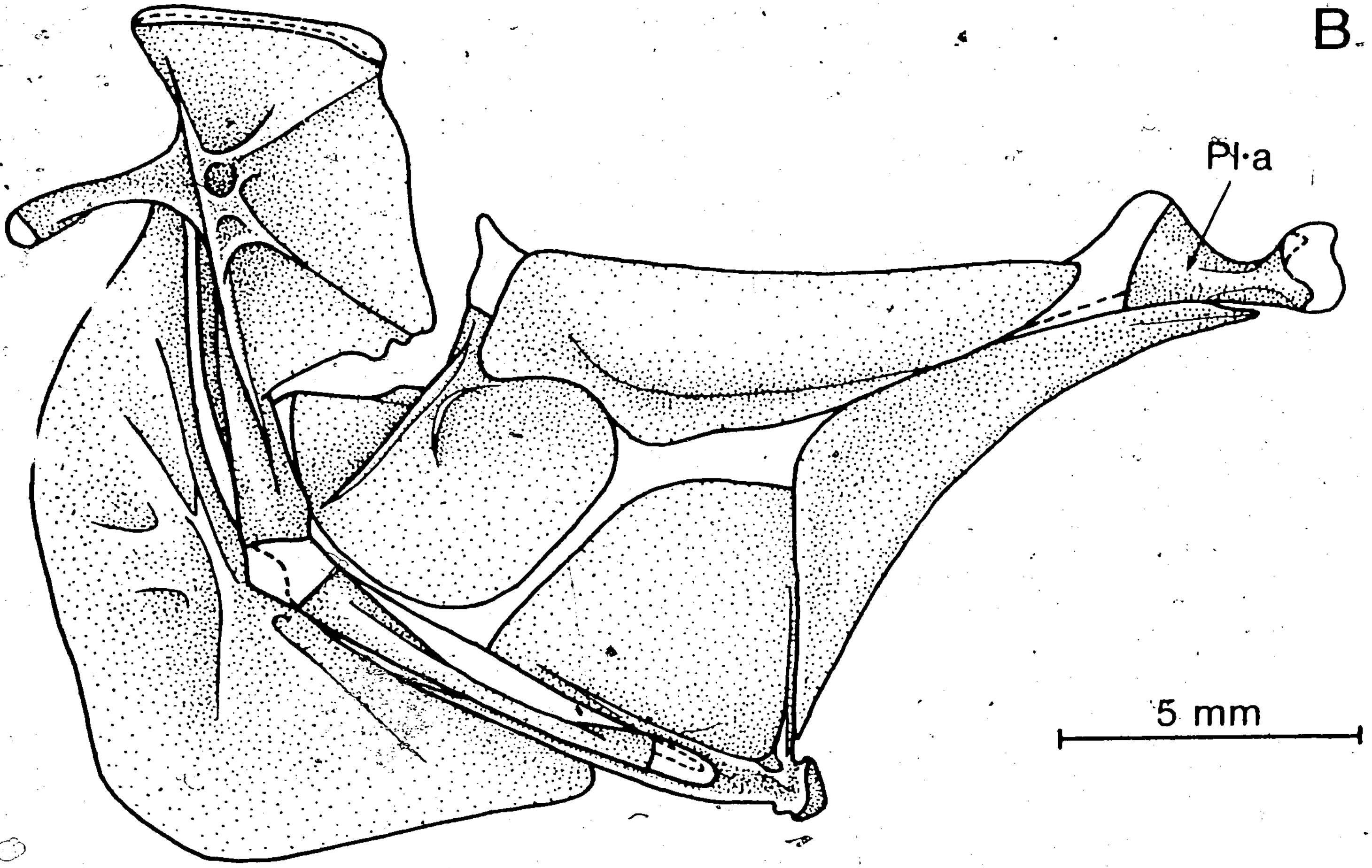
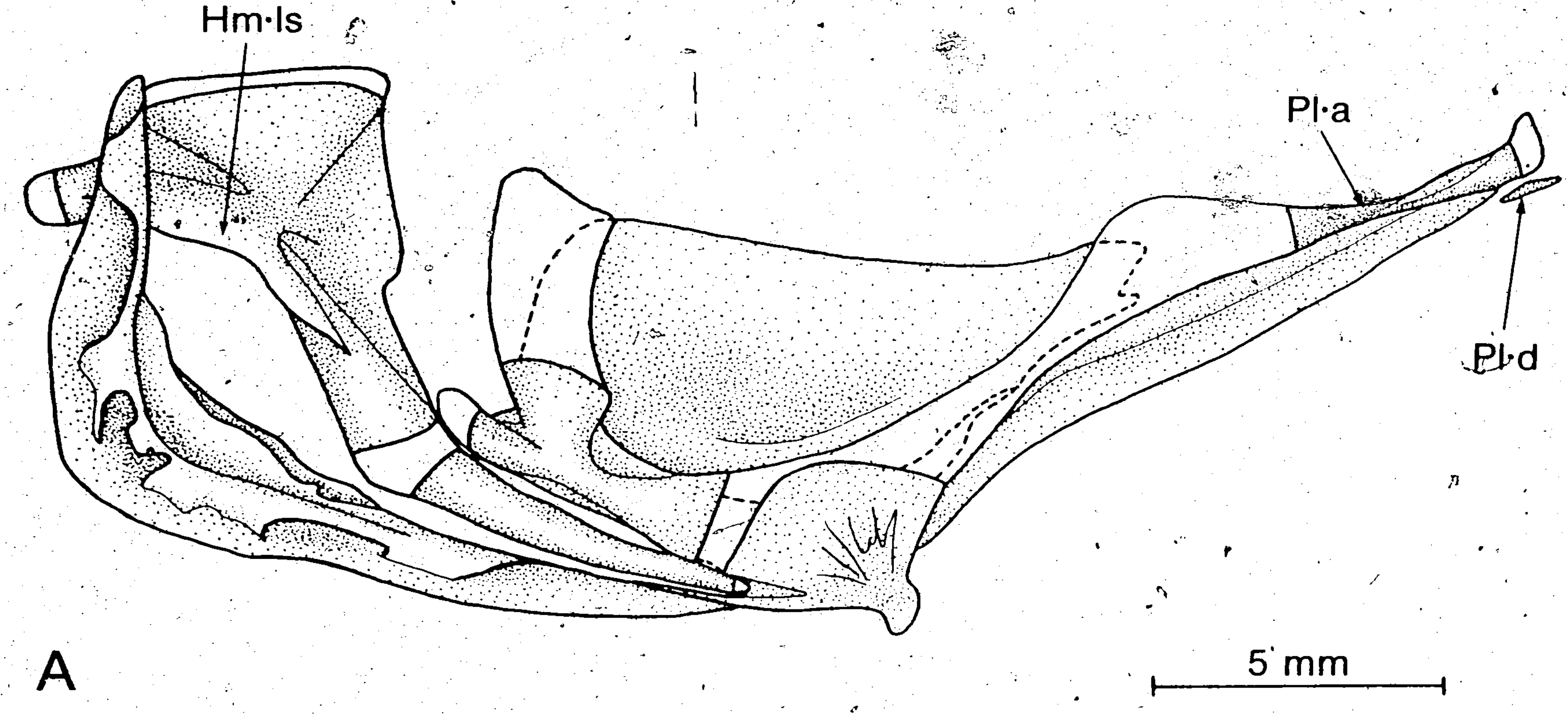

B
Pl·a
5 mm

Figure 41. Lateral (A) and medial (B) views of the right suspensorium in *Leptoderma macrops* (Alepocephalidae). Both drawings are of the suspensorium after its removal from the skull.


Hm·ls
Pl·a
Pl·d
5 mm
A

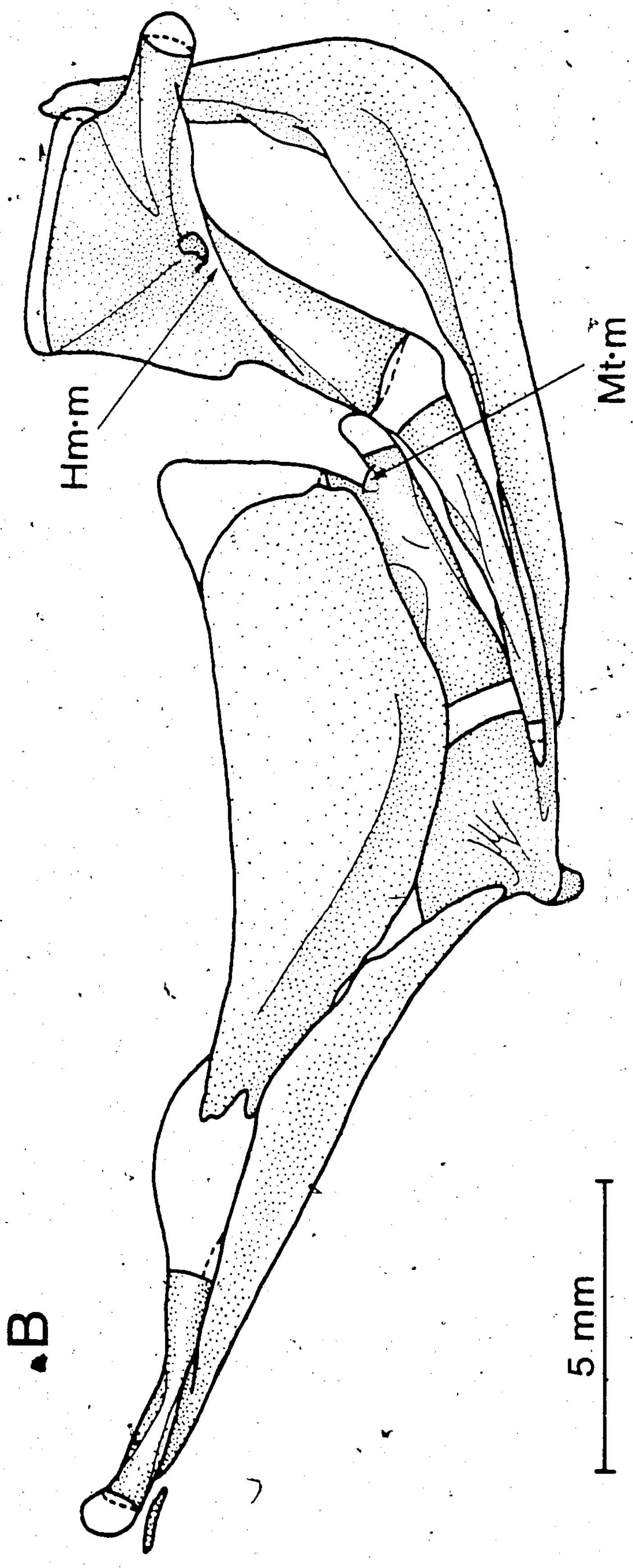
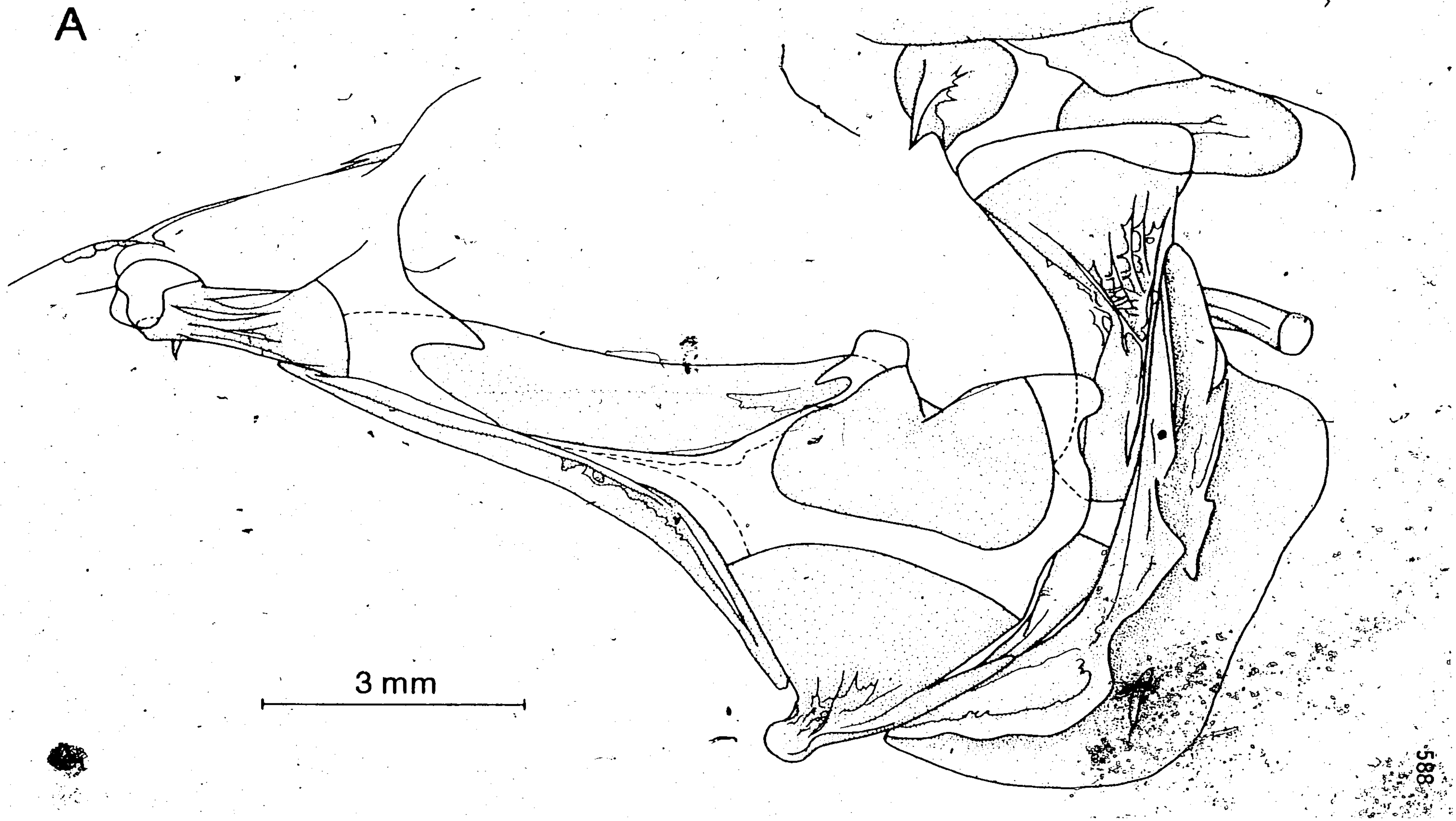

B
Hm·m
Mt·m
5 mm

Figure 42. Lateral (A) and medial (B) views of the left suspensorium in *Sagamichthys abei* (Platytroctidae).


A
3 mm
588

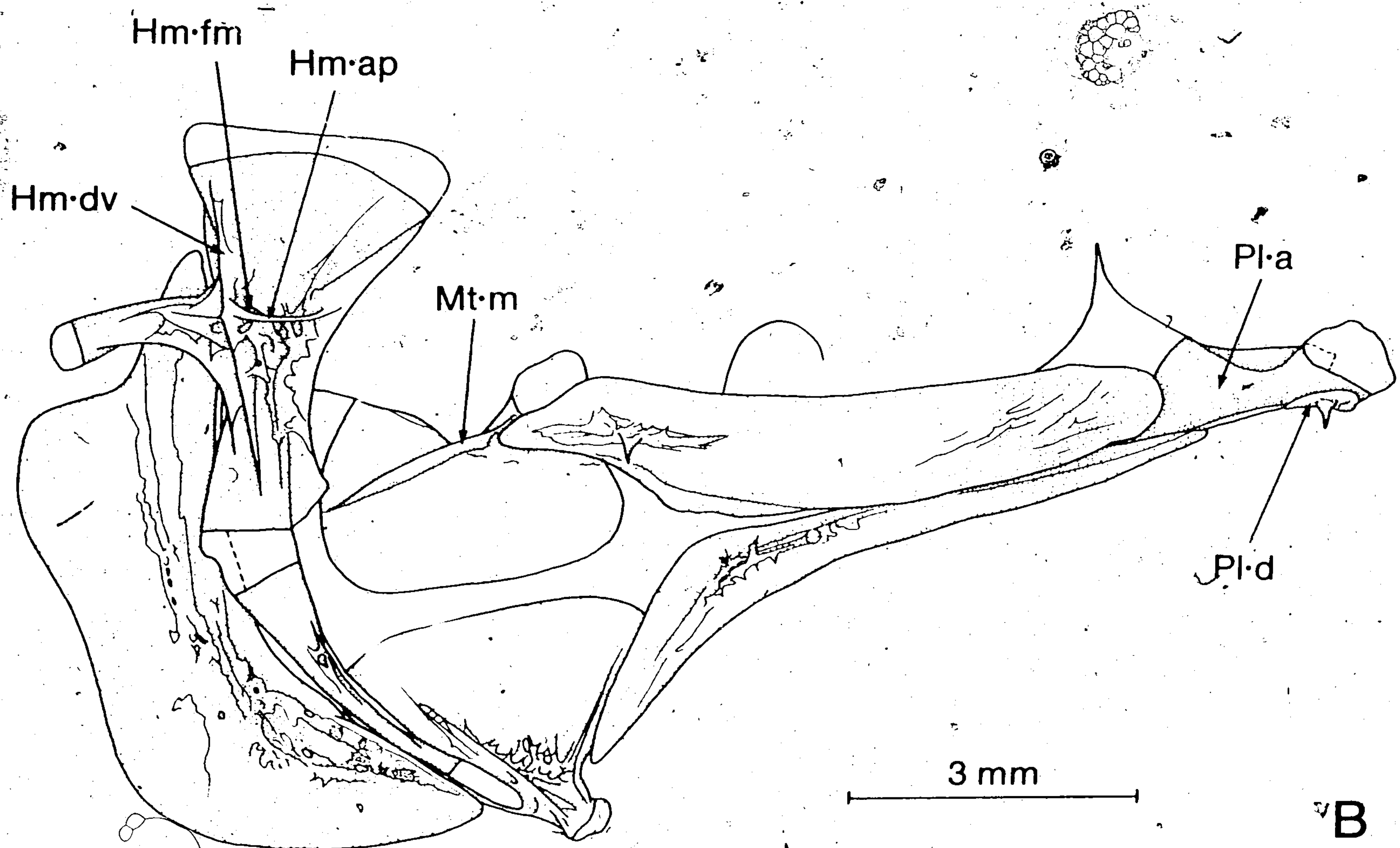
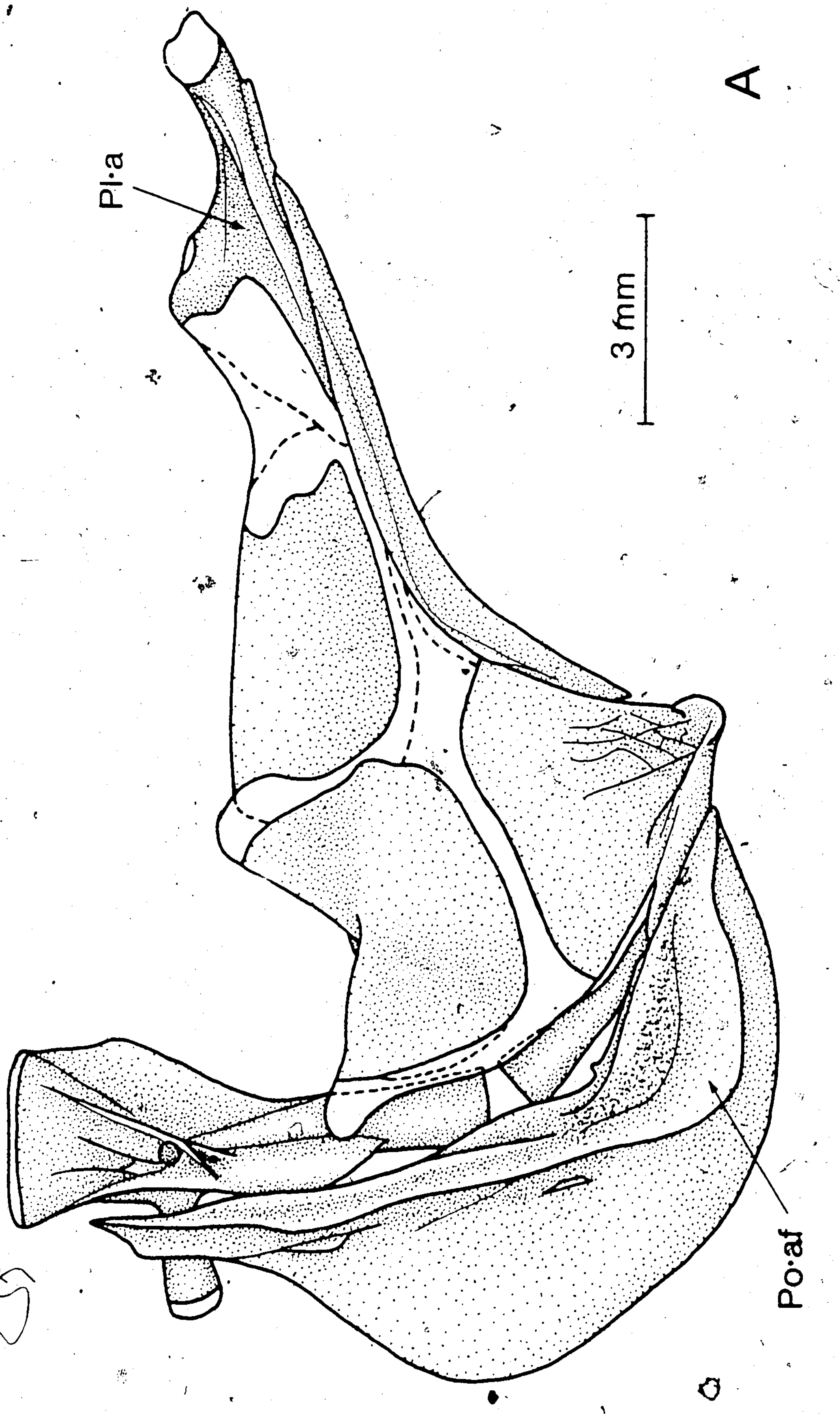

Hm·fm
Hm·ap
Hm·dv
Mt·m
Pl·a
Pl·d
3 mm
B

Figure 43. Lateral (A) and medial (B) views of the right suspensorium in *Searsia koefoedi* (Platytroctidae). Both drawings are of the suspensorium after its removal from the skull.


Pl·a
3 mm
A
Po·af

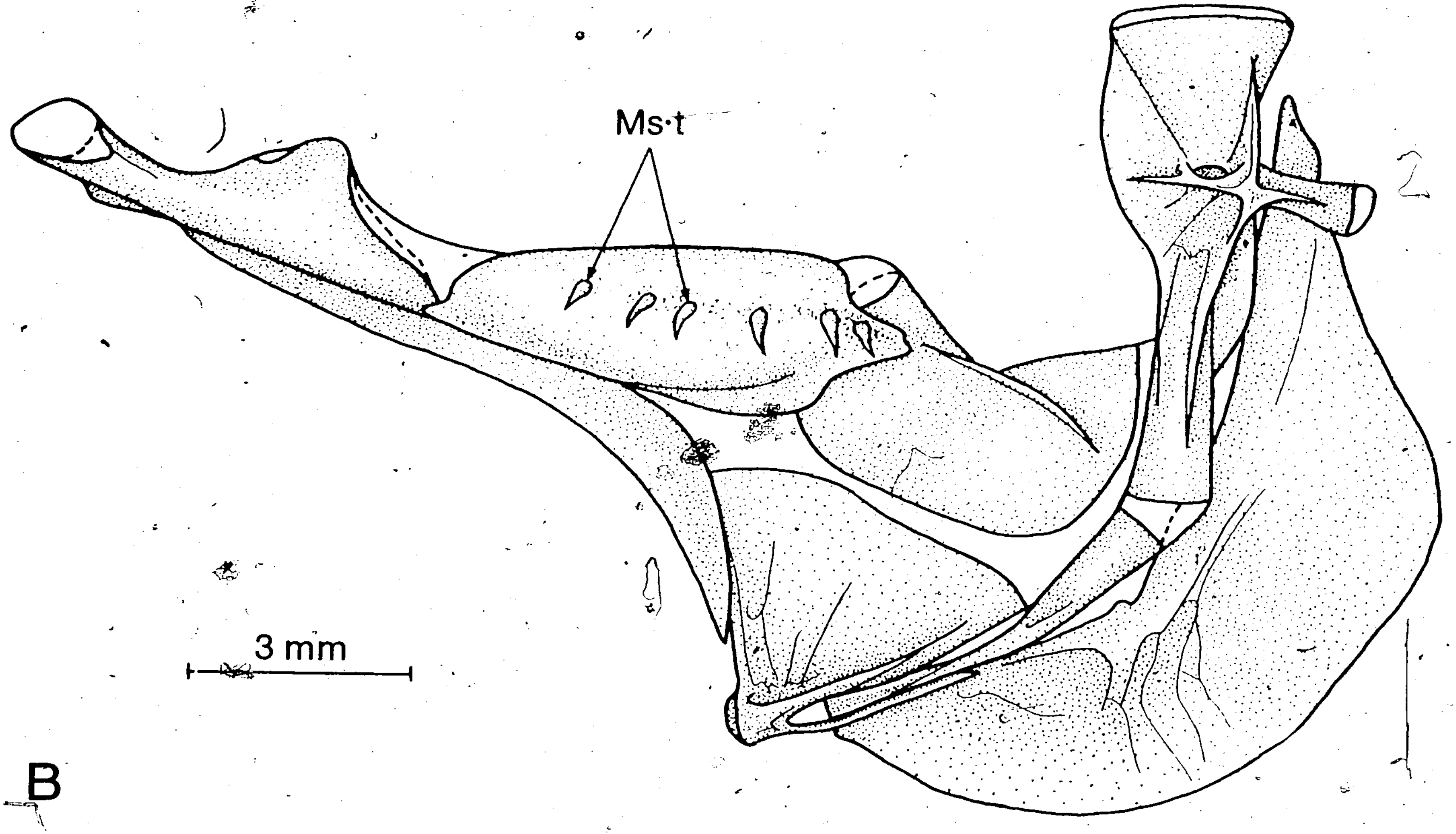
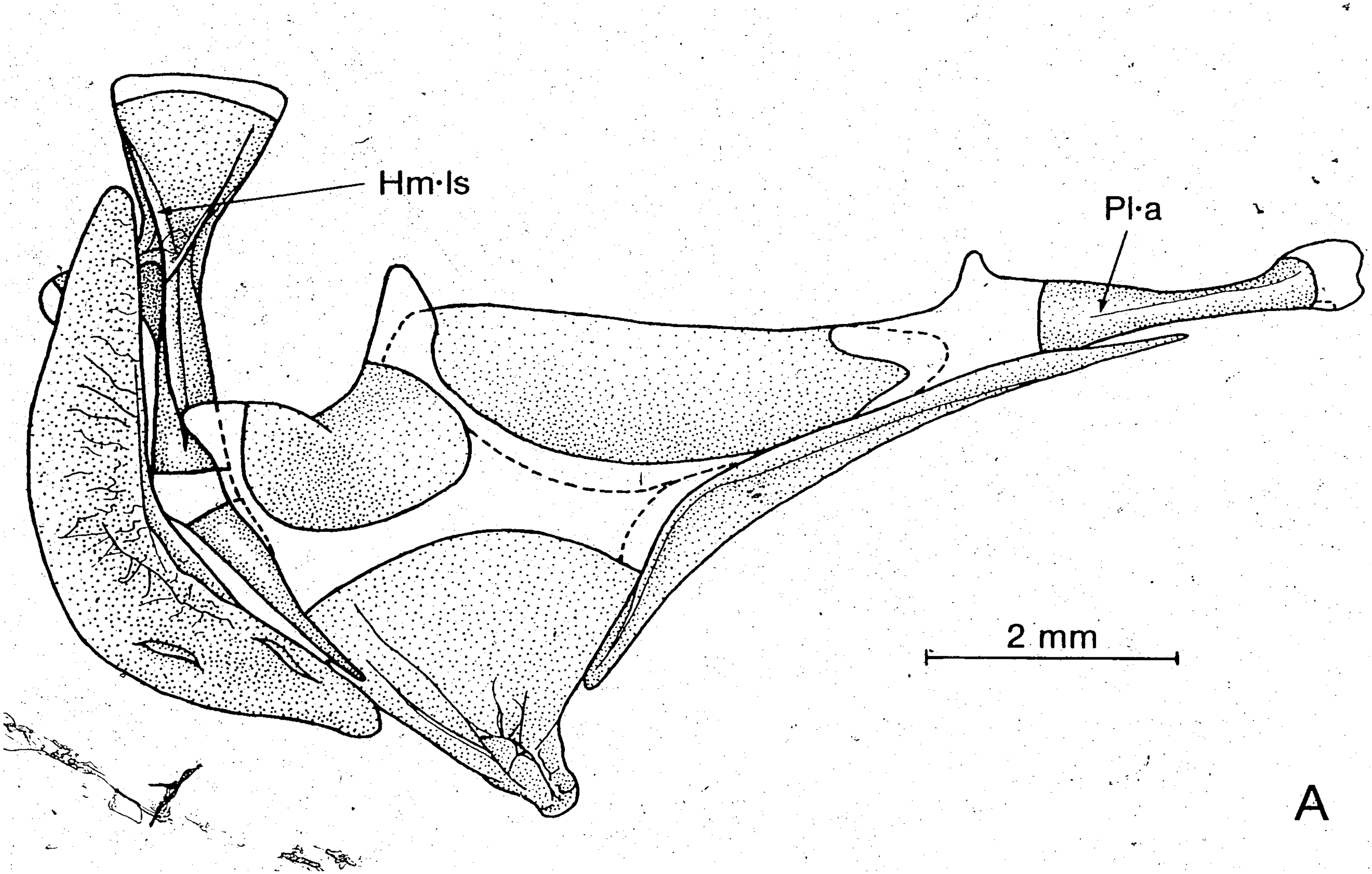

Ms·t
3 mm
B

Figure 44. Lateral (A) and medial (B) views of the right suspensorium in *Searsioides multispinus* (Platytroctidae); SIO 61-32, 40.8 mm SL. Both drawings are of the suspensorium after its removal from the skull. Because the preopercula in this specimen were detached during clearing and staining the position of the preoperculum was estimated using specimen SIO 61-32, 54.0 mm SL. Also, the anterior end of the ectopterygoid became slightly separated from the palatine during clearing and staining, and this is shown on the drawing.


Hm·ls
Pl·a
2 mm
A

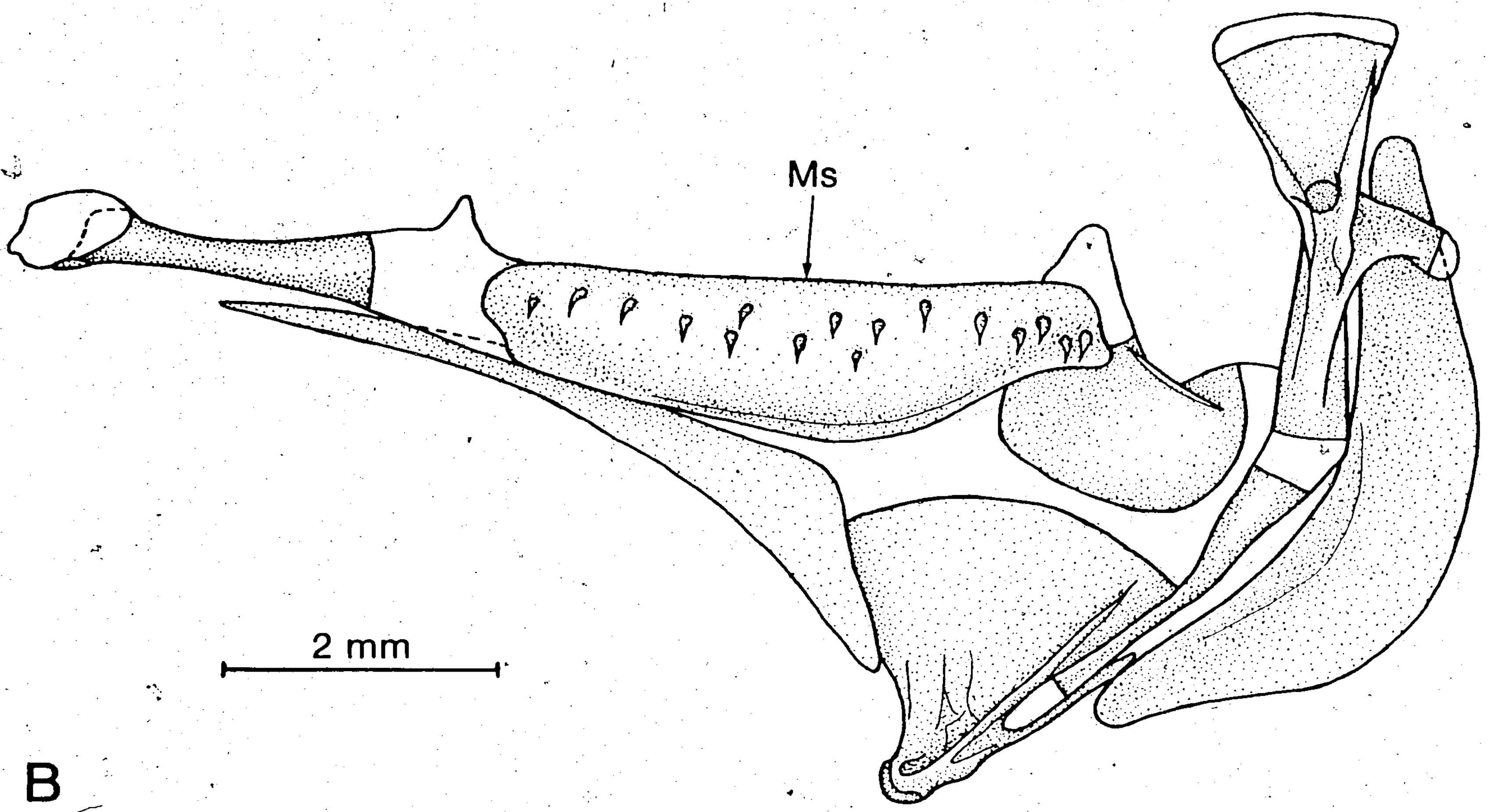

Ms
2 mm
B

Figure 45: Lateral (A) and medial (B) views of the left suspensorium in *Platytroctes apus* (Platytroctidae), SIO 55-246, 136.0 mm SL. Both drawings are of the suspensorium after its removal from the skull. The anterior end of the left ectopterygoid was broken and lost, but was reconstructed using the right ectopterygoid and those in specimen SIO 55-244, 141.1 mm SL. Because both preopercula were lost in specimen SIO 55-246, the left preoperculum was reconstructed using the preopercula in specimen SIO 55-244. For this reason, the preoperculum drawn is probably slightly larger relative to the other bones than it actually is.

Figure 46. Lateral (A) and medial (B) views of the left suspensorium in *Mirorictus taningi* (Platytroctidae). Both drawings are of the suspensorium after its removal from the skull.

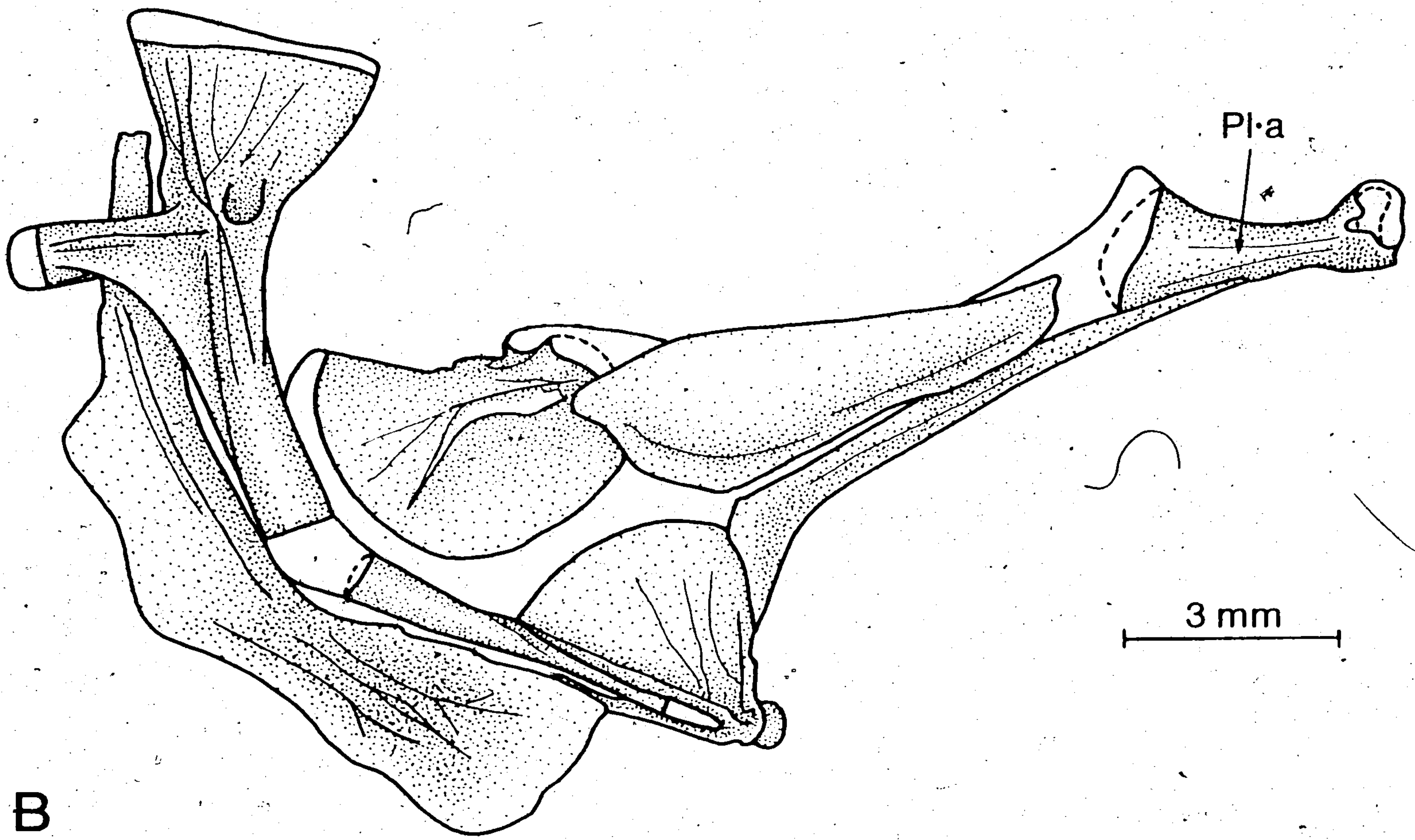
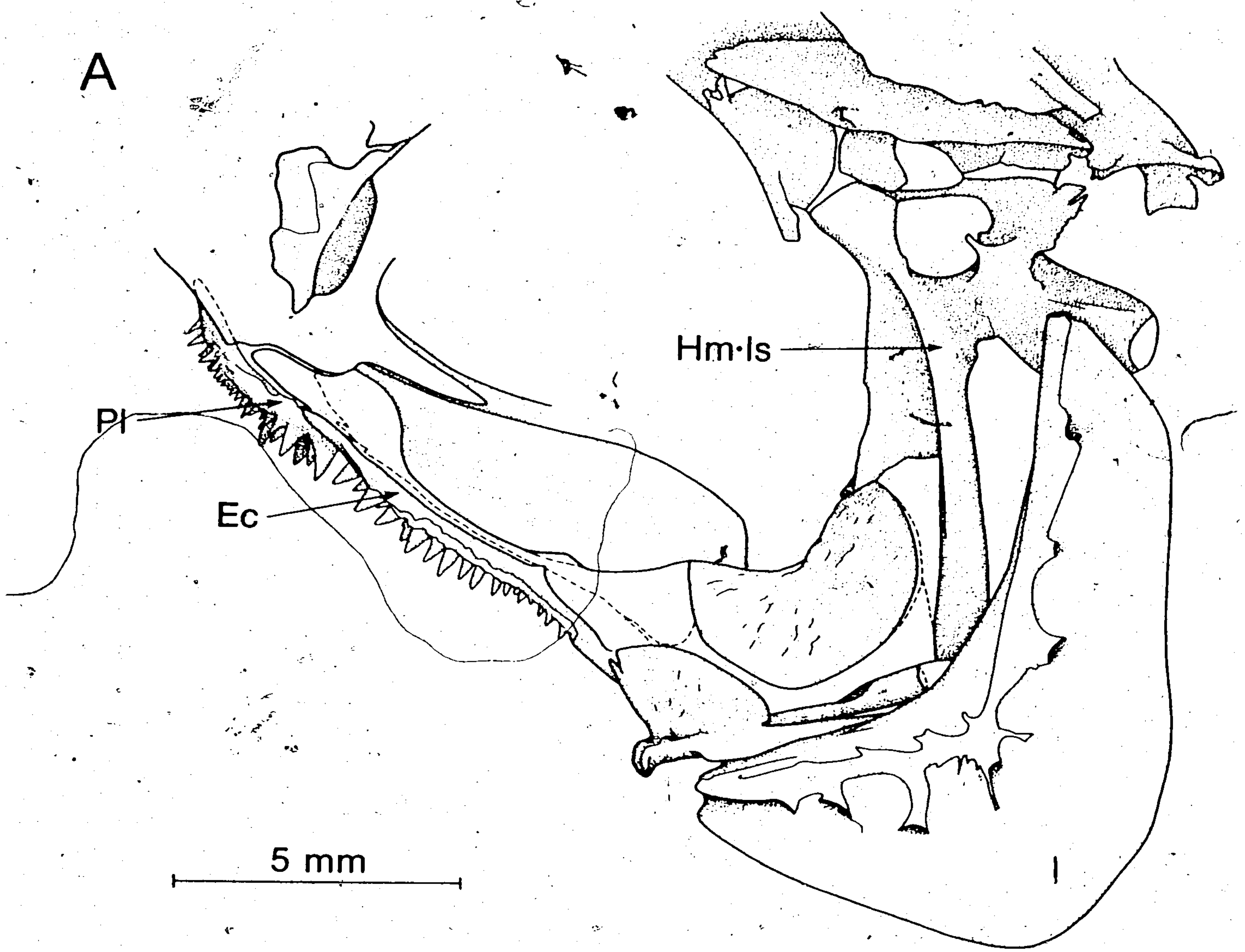

Pl·a
3 mm
B

Figure 47. Lateral (A) and medial (B) views of the left suspensorium in *Hiodon alosoides* (Hiodontidae, Osteoglossiformes).


A
Hm·Is
Pl
Ec
5 mm

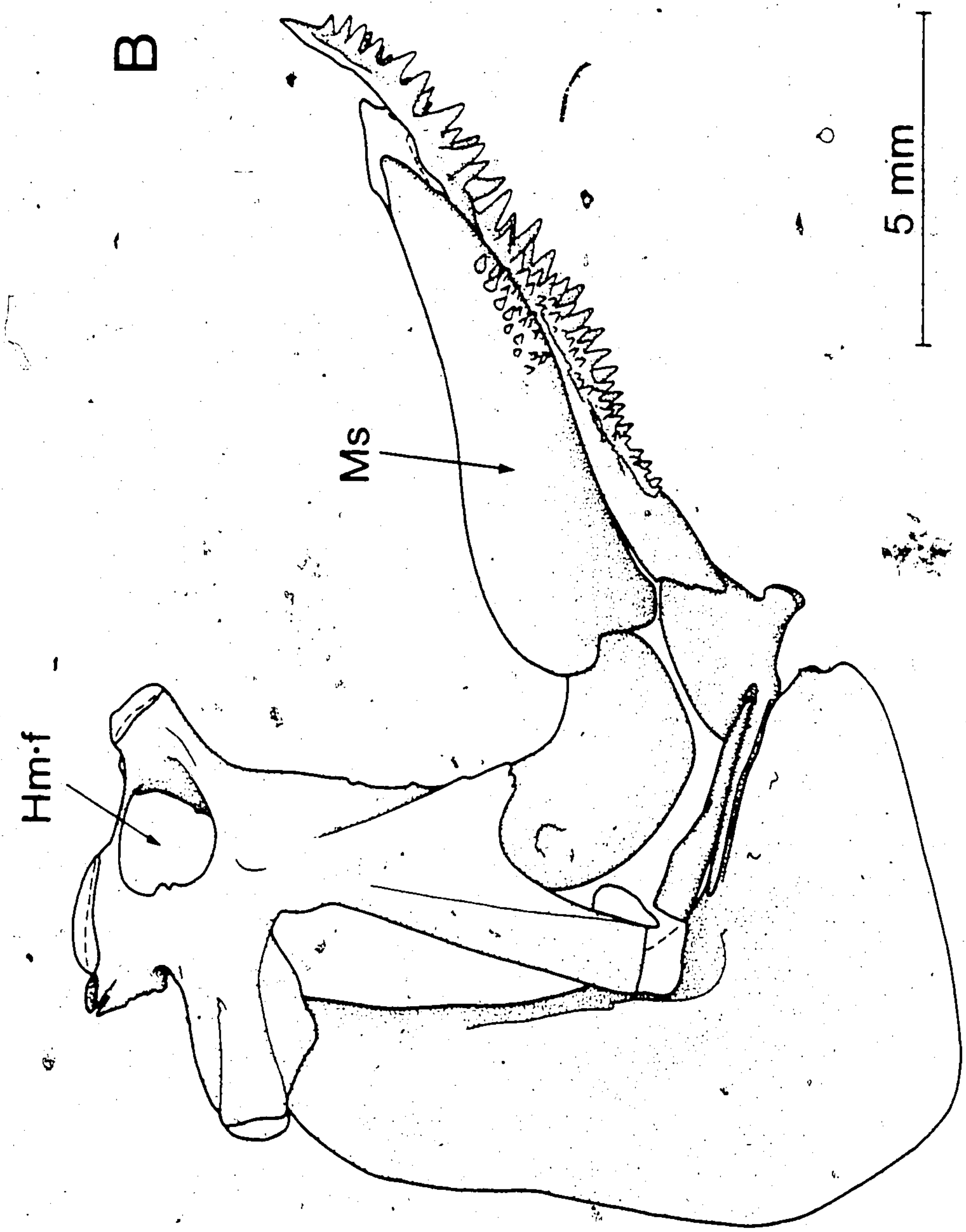

B
Ms
Hm·f
5 mm

Figure 48. Lateral (A) and medial (B) views of the left suspensorium in *Megalops cyprinoides* (Megalopidae, Elopiformes). The ectopterygoid was broken in half, at the intersection of the two arms, but was reconstructed using the right ectopterygoid.

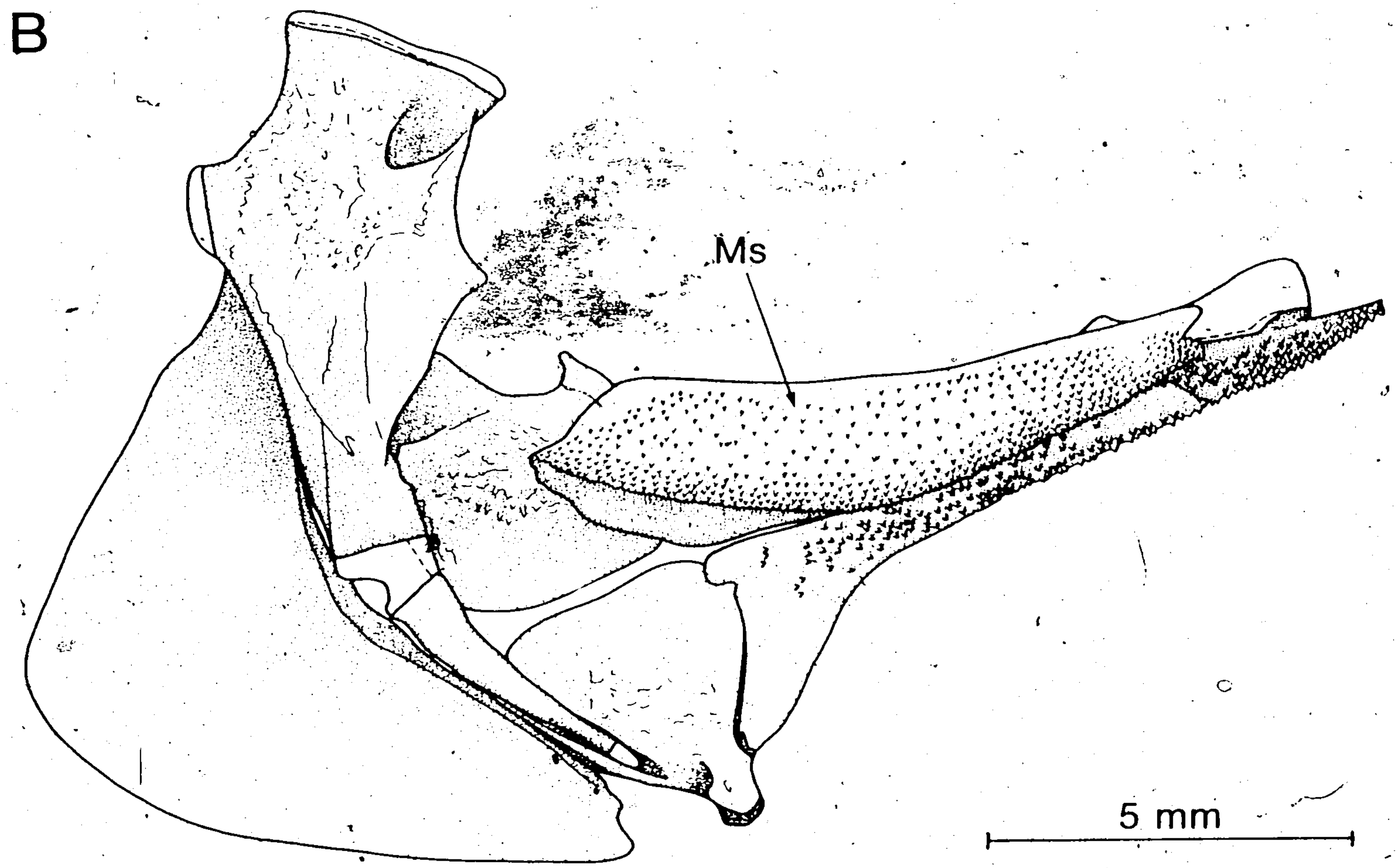
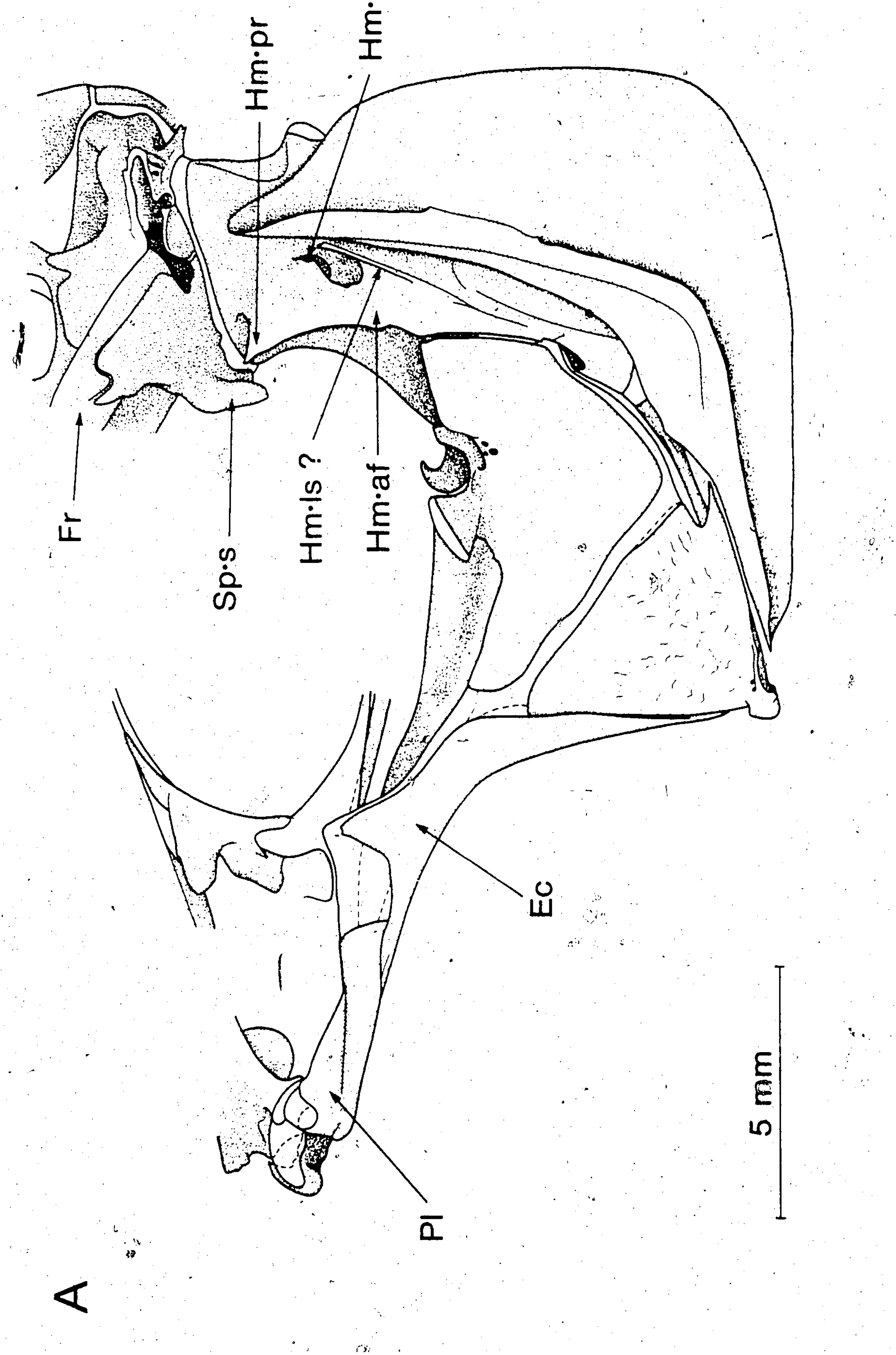

B
Ms
5 mm

Figure 49. Lateral (A) and medial (B) views of the left suspensorium in *Clupea harengus* (Clupeidae, Clupeiformes).


A
Fr
Sp·s
Hm·pr
Hm·fl
Hm·ls ?
Hm·af
Ec
Pl
5 mm

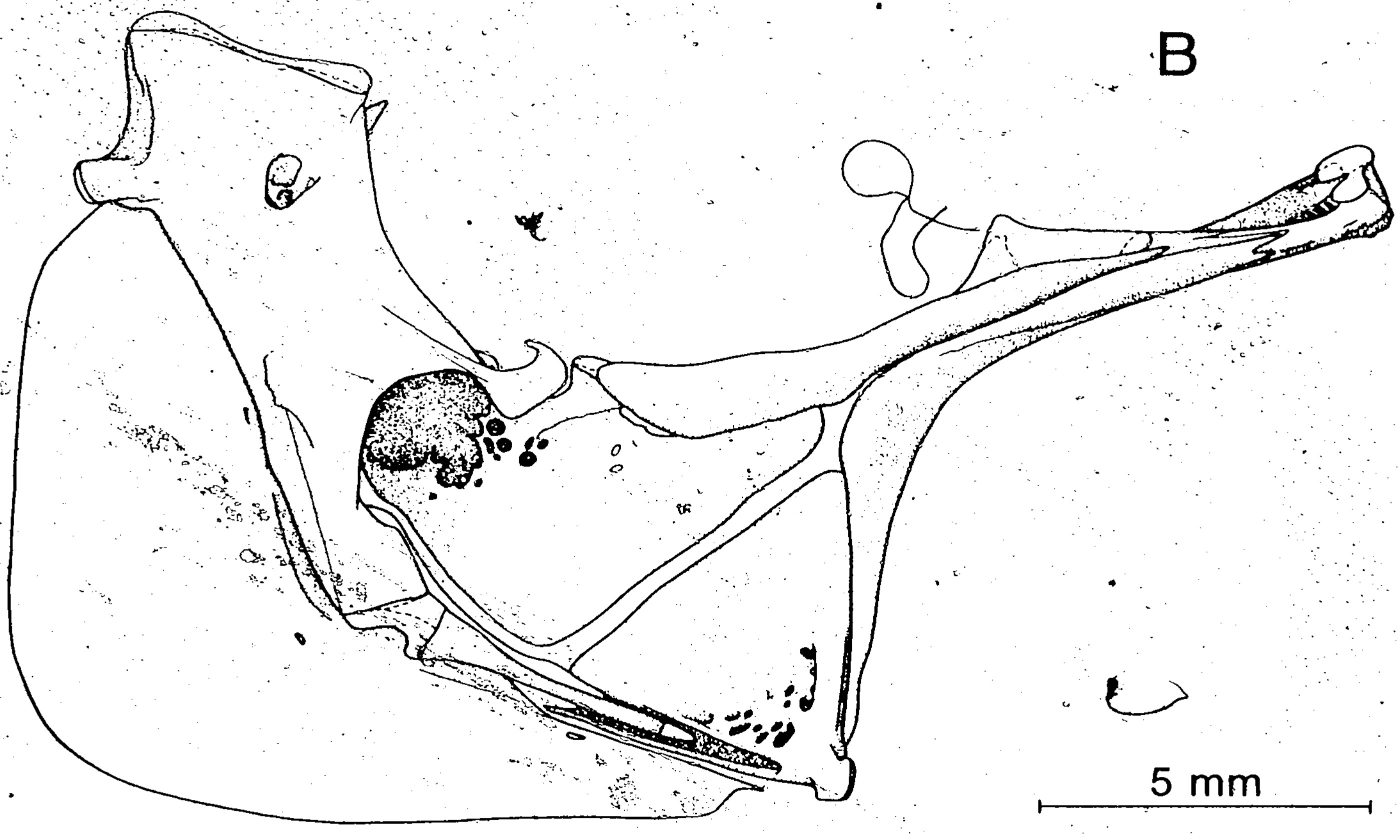
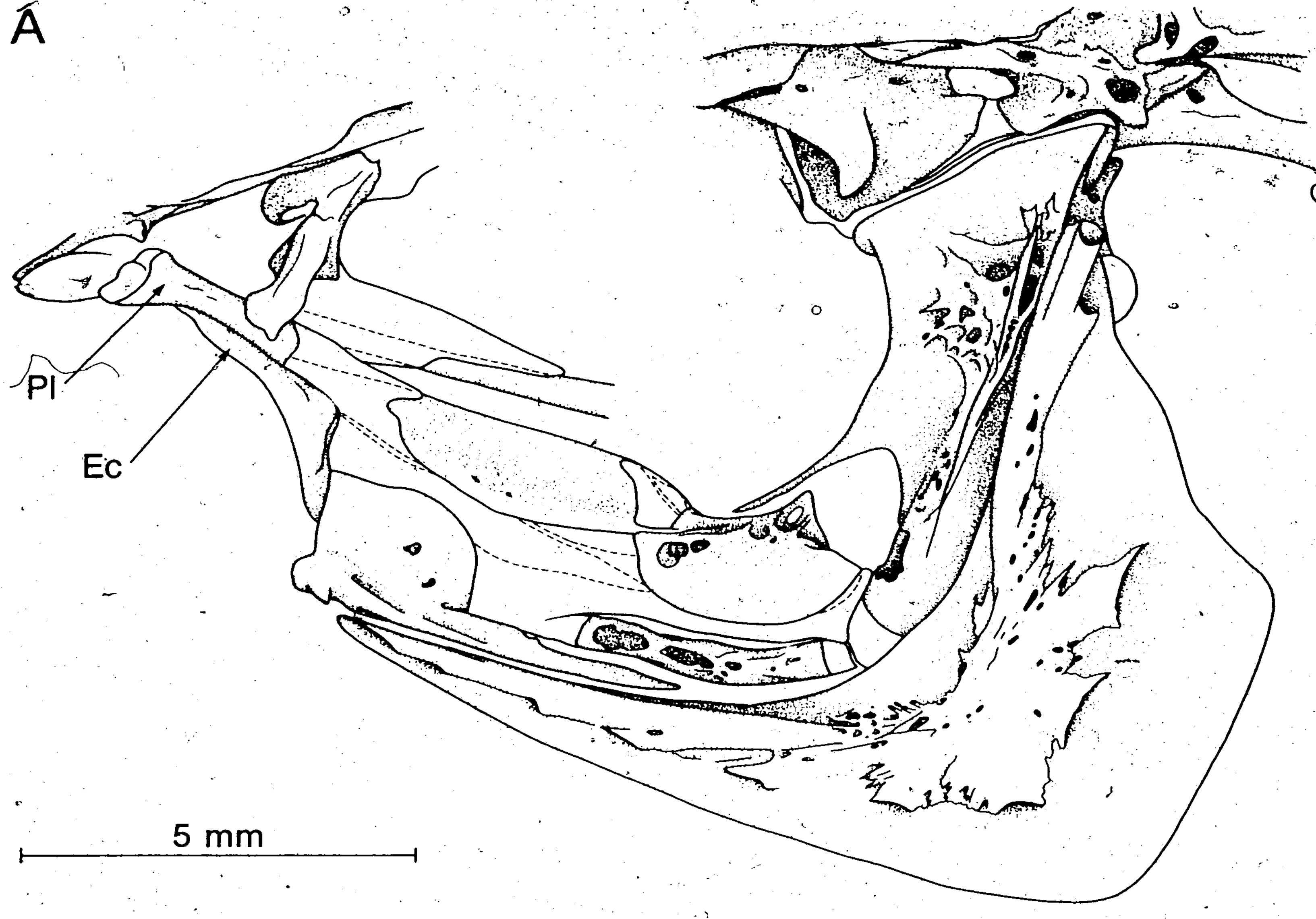

B
5 mm

Figure 50. Lateral (A) and medial (B) views of the left suspensorium in *Chanos chanos* (Chanidae, Gonorynchiformes).


A
Pl
Ec
5 mm

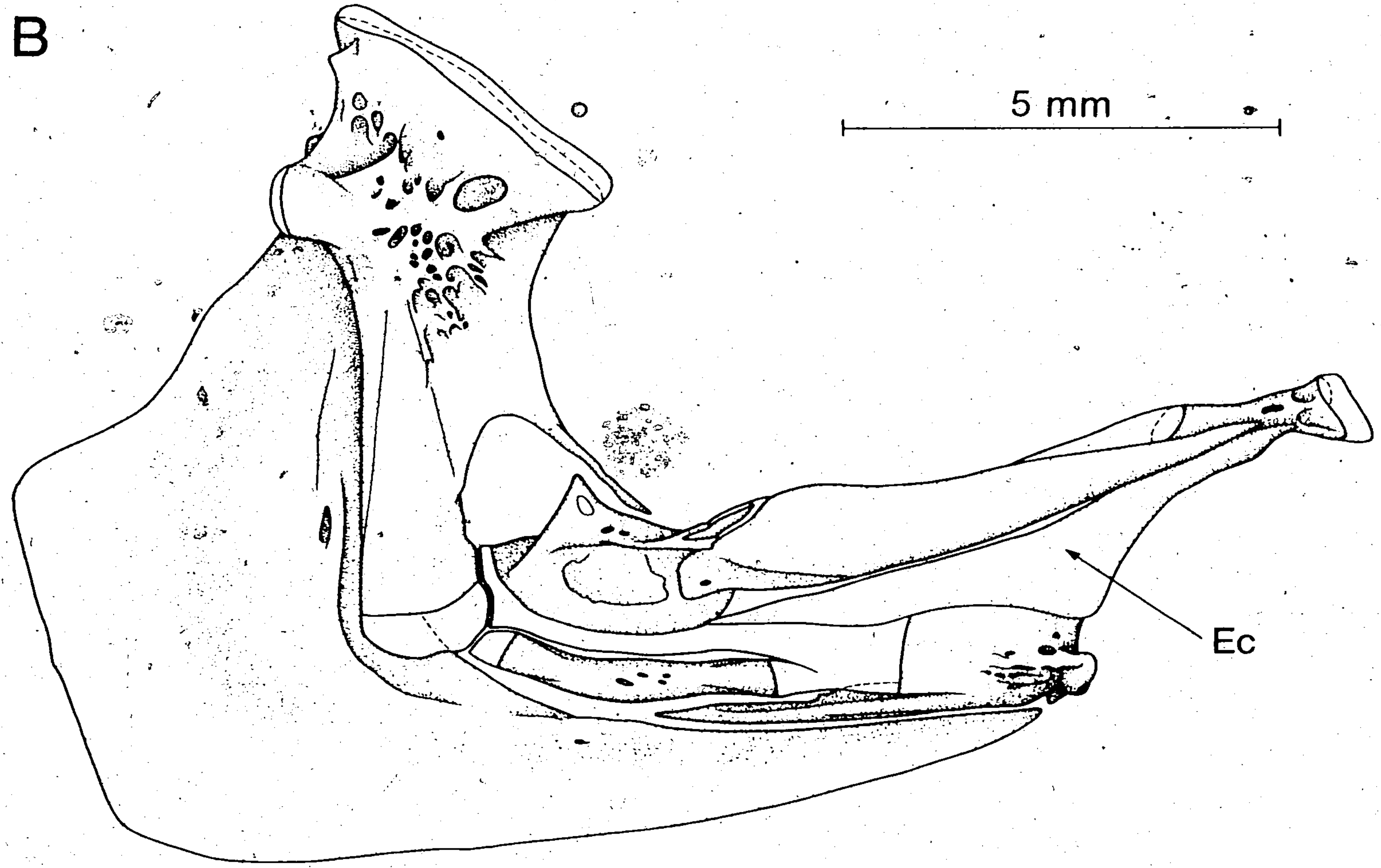
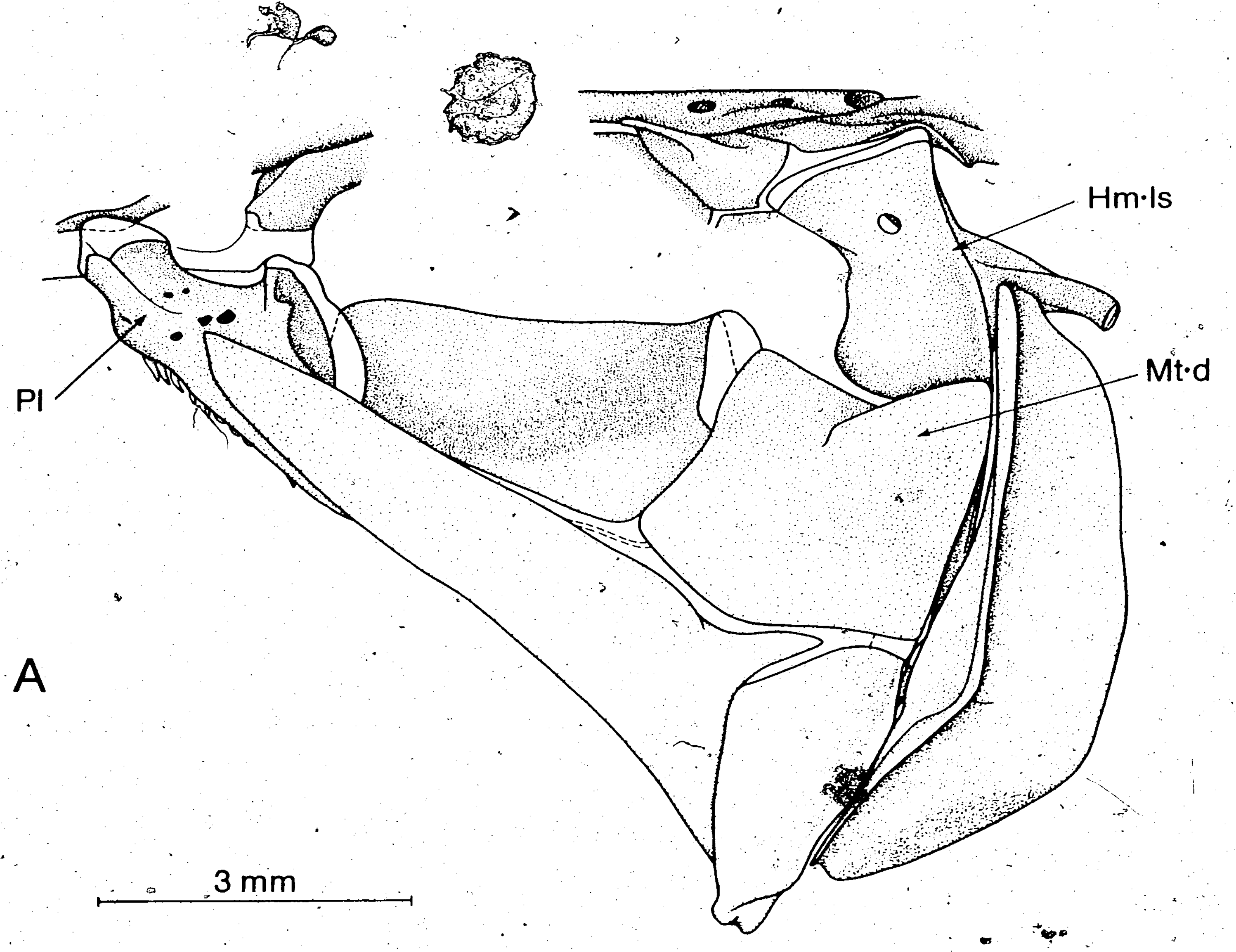

B
5 mm
Ec

Figure 51. Lateral (A) and medial (B) views of the left suspensorium in *Diplophos taenia* (Gonostomatidae, Stomiiformes).


Hm·ls
Mt·d
Pl
A
3 mm

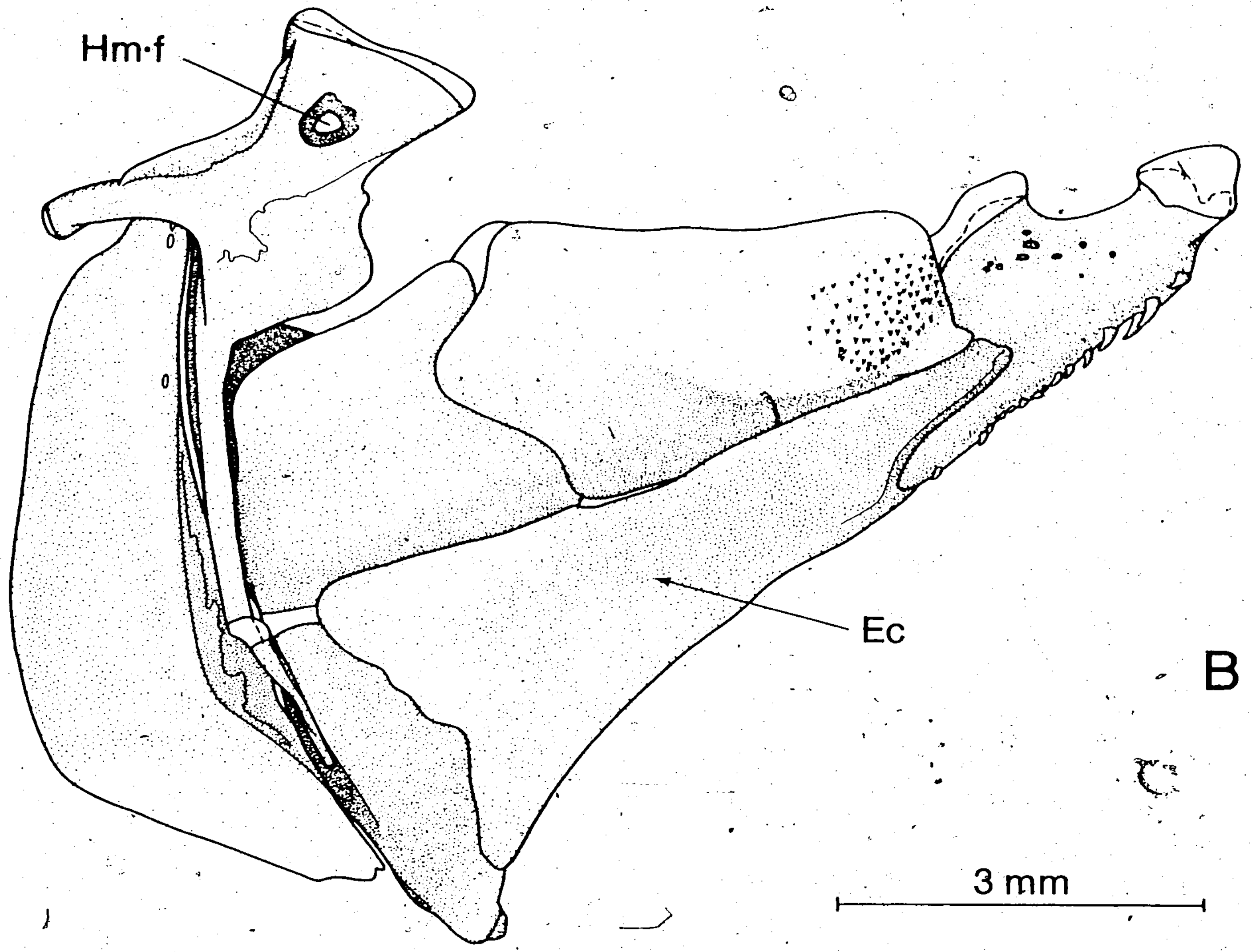

Hm·f
Ec
B
3 mm

Figure 52. Lateral view of the external muscles of the left suspensorium in *Esox lucius* (Esocidae). The supramaxilla is omitted because it obscures the anterior end of the coronoid-maxilla ligament.

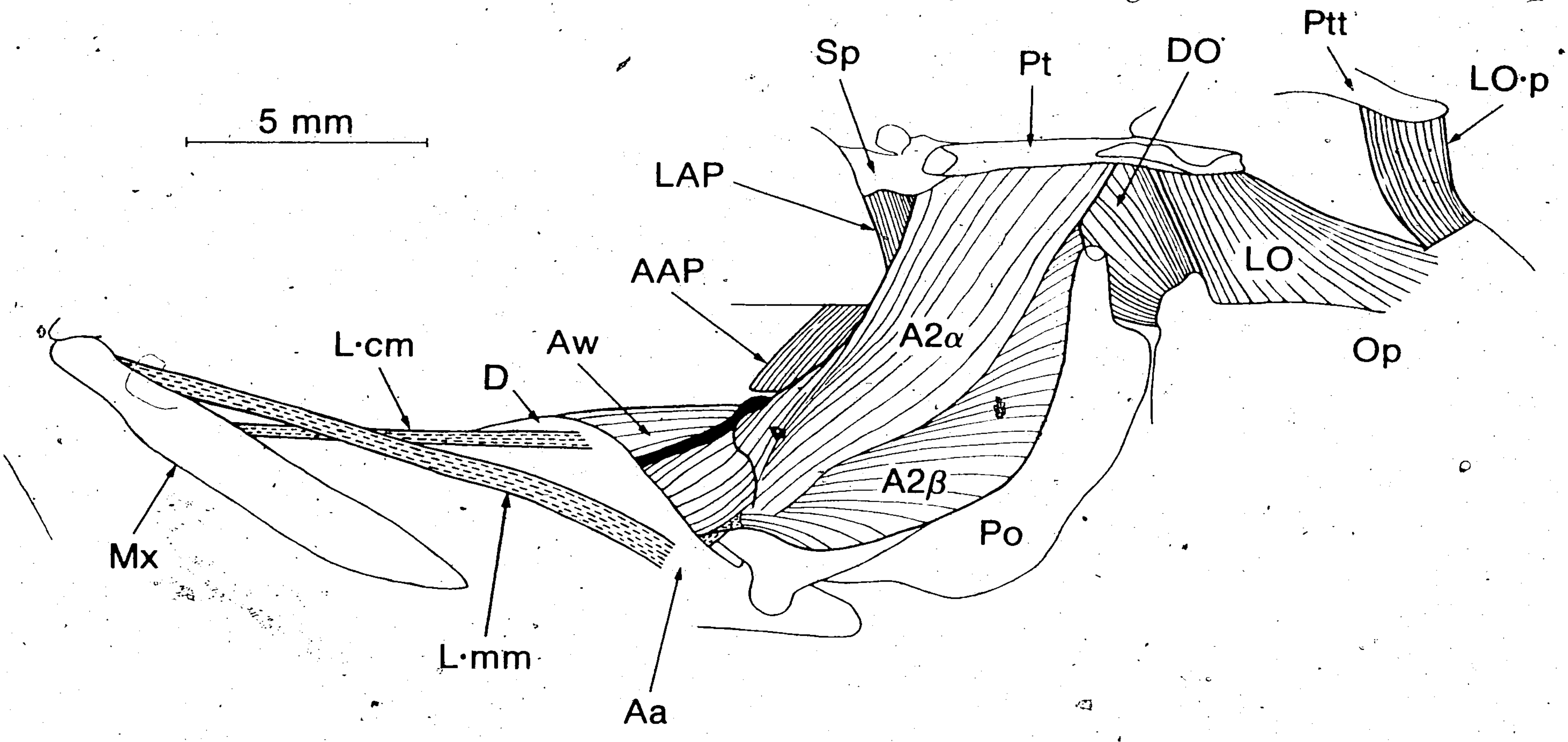

5 mm
Sp
Pt
DO
Ptt
LO·p
LAP
AAP
LO
L·cm
Aw
A2α
Op
D
A2β
Mx
Po
L·mm
Aa

Figure 53. Lateral view of the external muscles of the left suspensorium in *Novumbra hubbsi* (Umbridae).

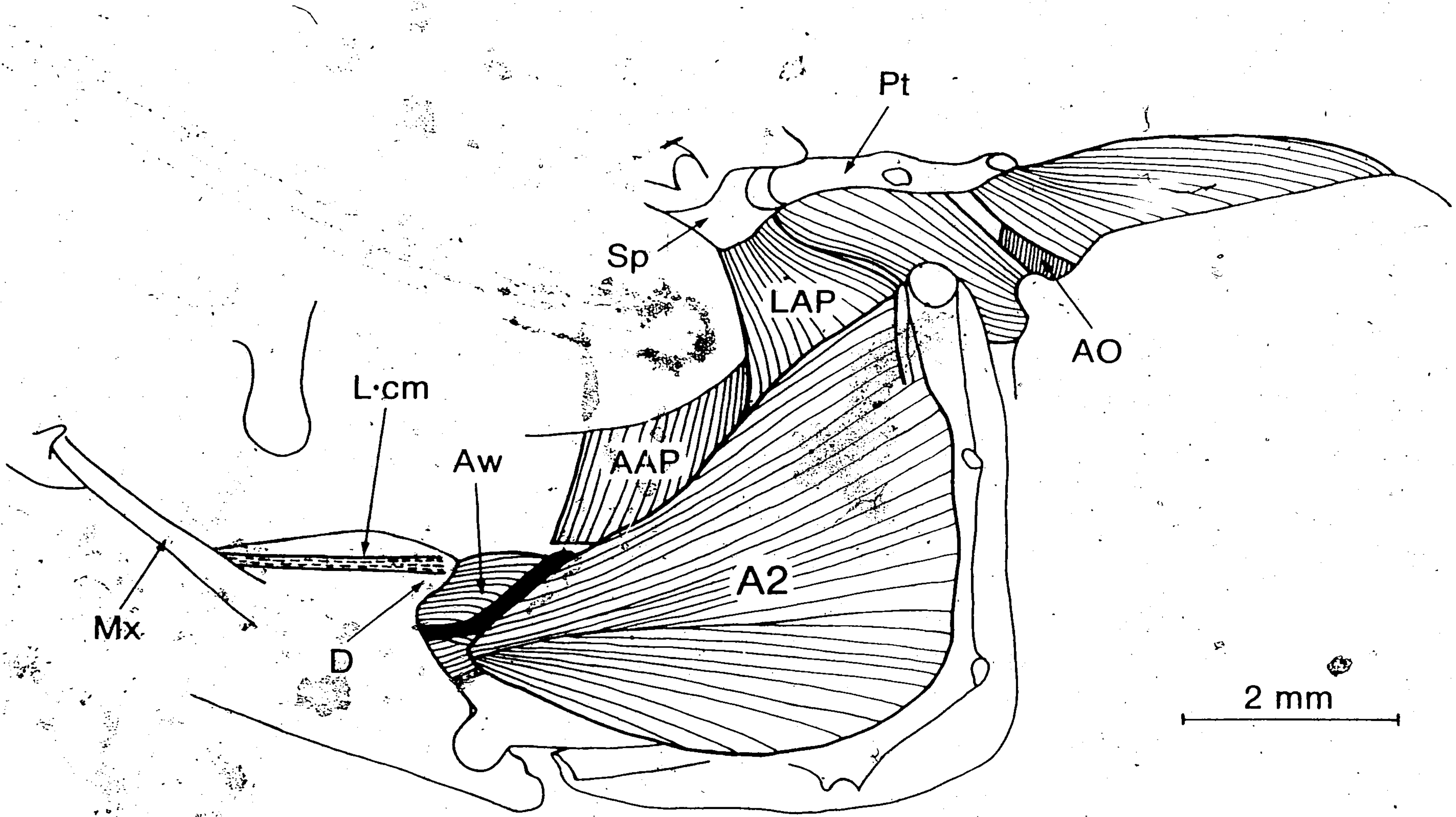

Pt
Sp
LAP
AO
L·cm
Aw
AAP
A2
Mx
D
2 mm

Figure 54. Lateral view of the external muscles of the left suspensorium in *Umbra limi* (Umbridae).

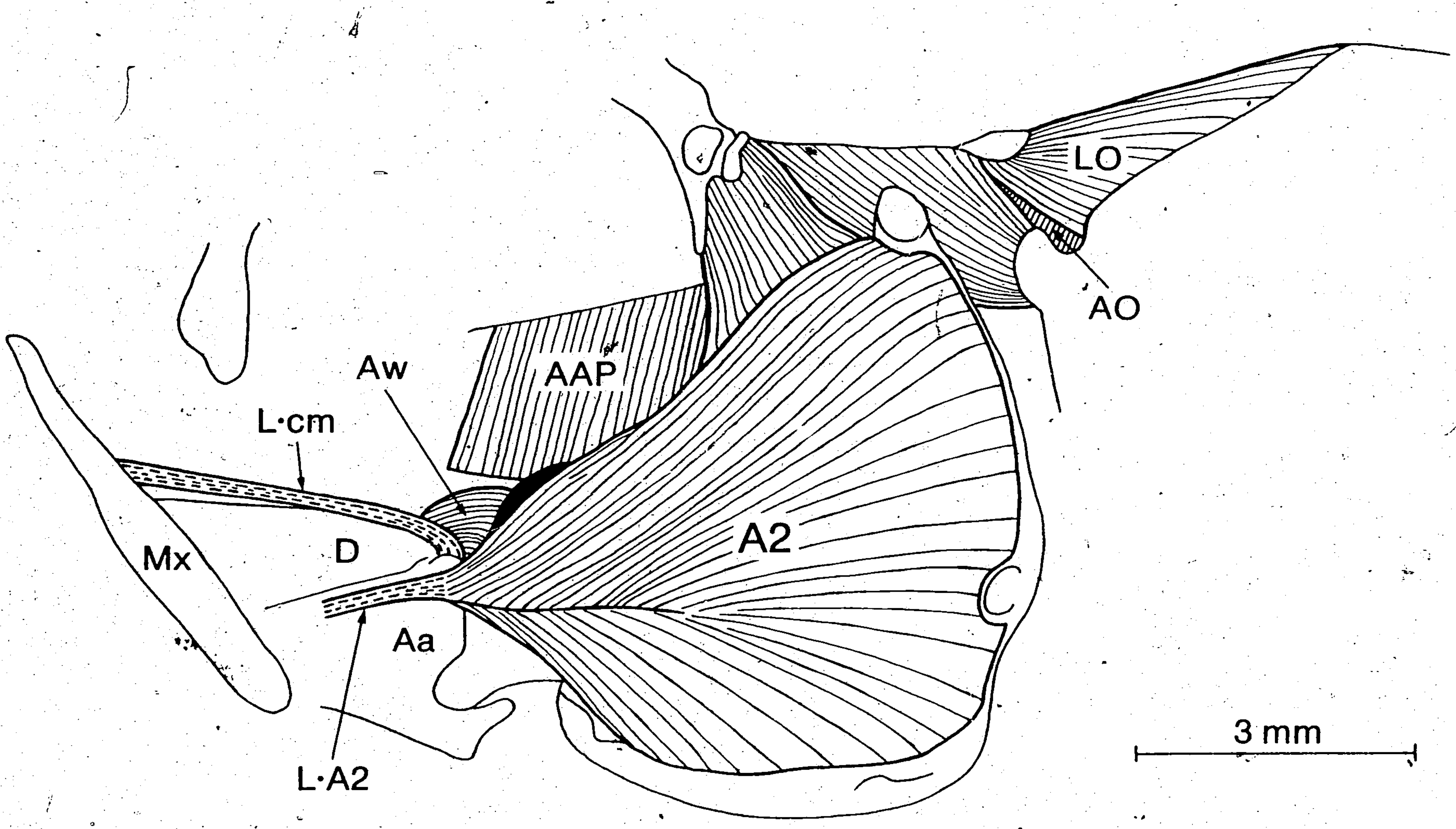

LO
AO
AAP
Aw
L·cm
A2
Mx
D
Aa
L·A2
3 mm

Figure 55. Lateral view of the external muscles of the left suspensorium in *Umbra krameri* (Umbridae).

Figure 56. Lateral (slightly dorsal) view of the external muscles of the left suspensorium in *Dallia pectoralis* (Umbridae).

Figure 57. Lateral view of the external muscles of the left suspensorium in *Coregonus artedii* (Salmonidae).

Figure 58. Lateral view of the external muscles of the left suspensorium in *Prosopium williamsoni* (Salmonidae).

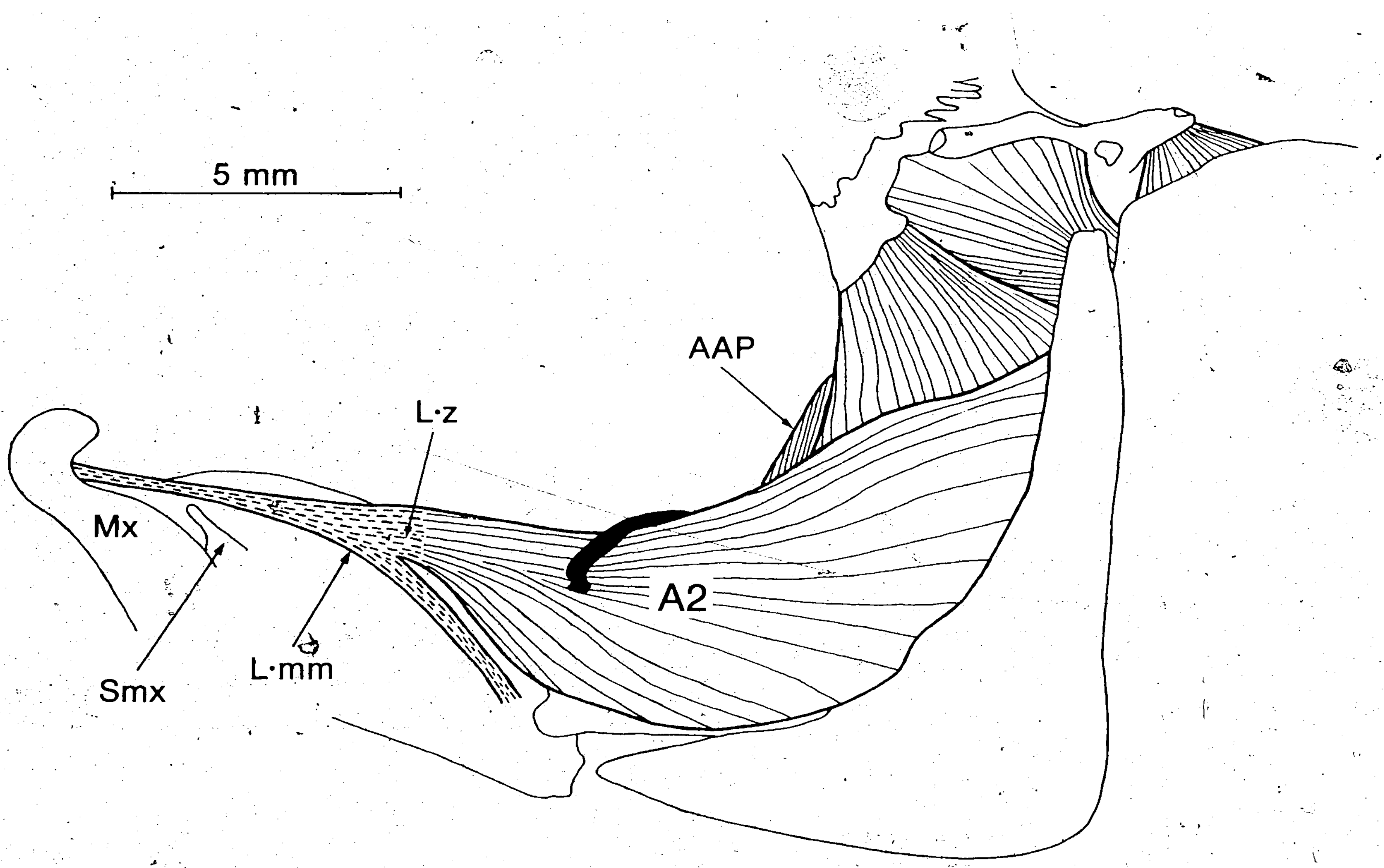

5 mm
AAP
L·z
Mx
A2
Smx
L·mm

Figure 59. Lateral view of the external muscles of the left suspensorium in *Thymallus arcticus* (Salmonidae).

Figure 60. Lateral view of the external muscles of the left suspensorium in *Salvelinus fontinalis* (Salmonidae).

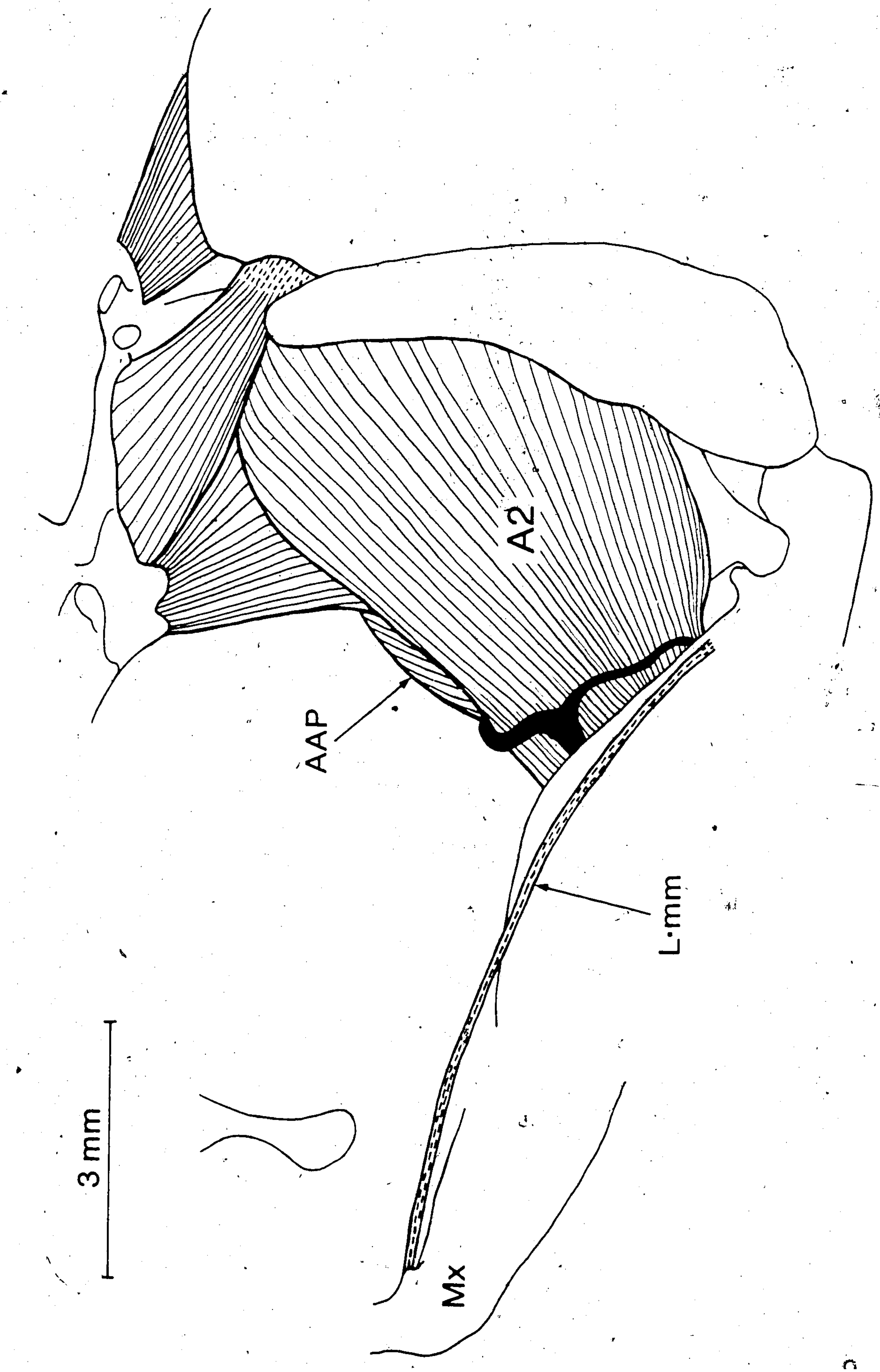

A2
AAP
L·mm
3 mm
Mx

Figure 61. Lateral view of the external muscles of the left suspensorium in *Brachymystax lenok* (Salmonidae).

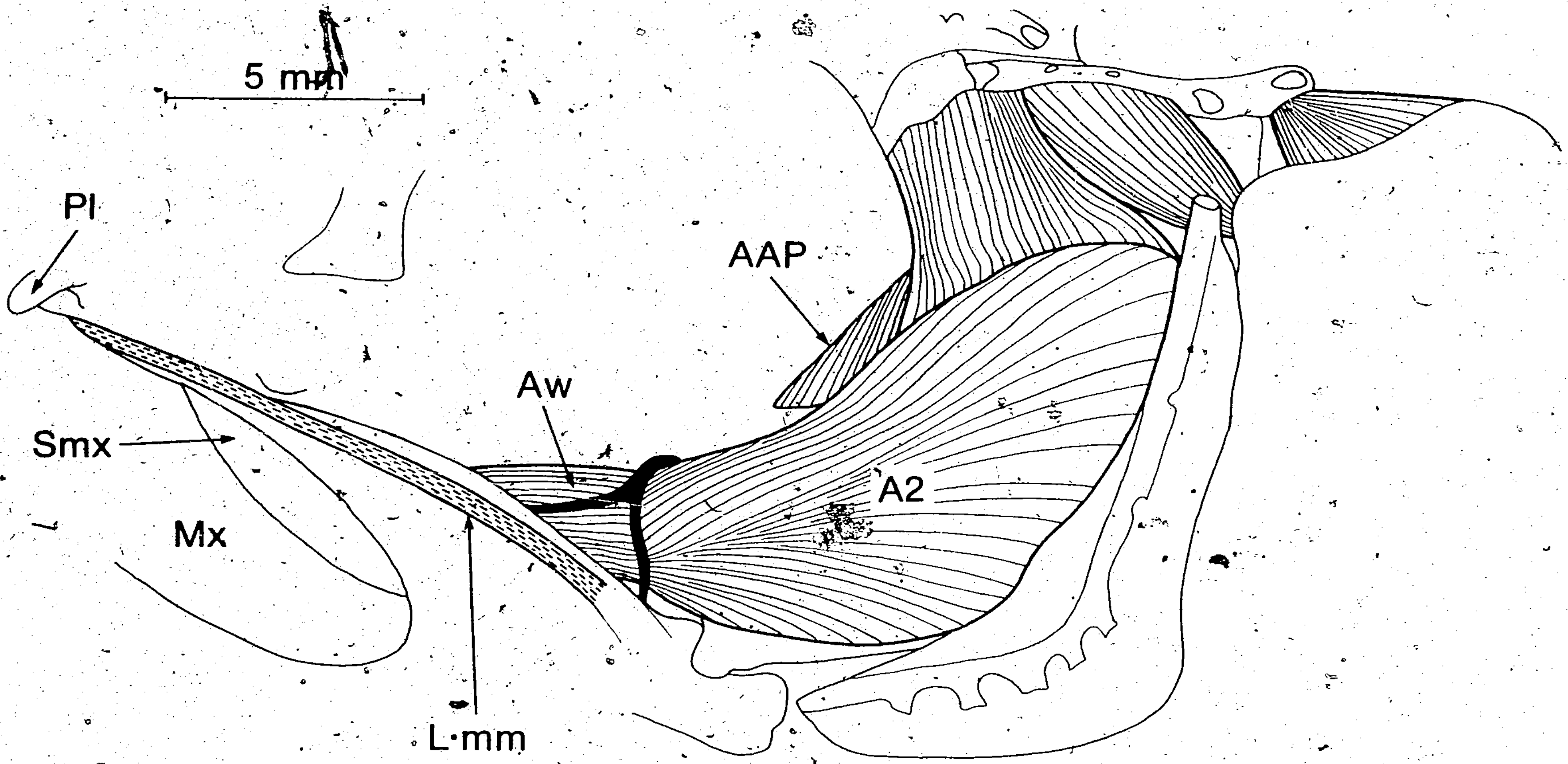

5 mm
Pl
AAP
Aw
A2
Smx
Mx
L·mm

Figure 62. Lateral view of the external muscles of the left suspensorium in *Hypomesus pretiosus* (Osmeridae).

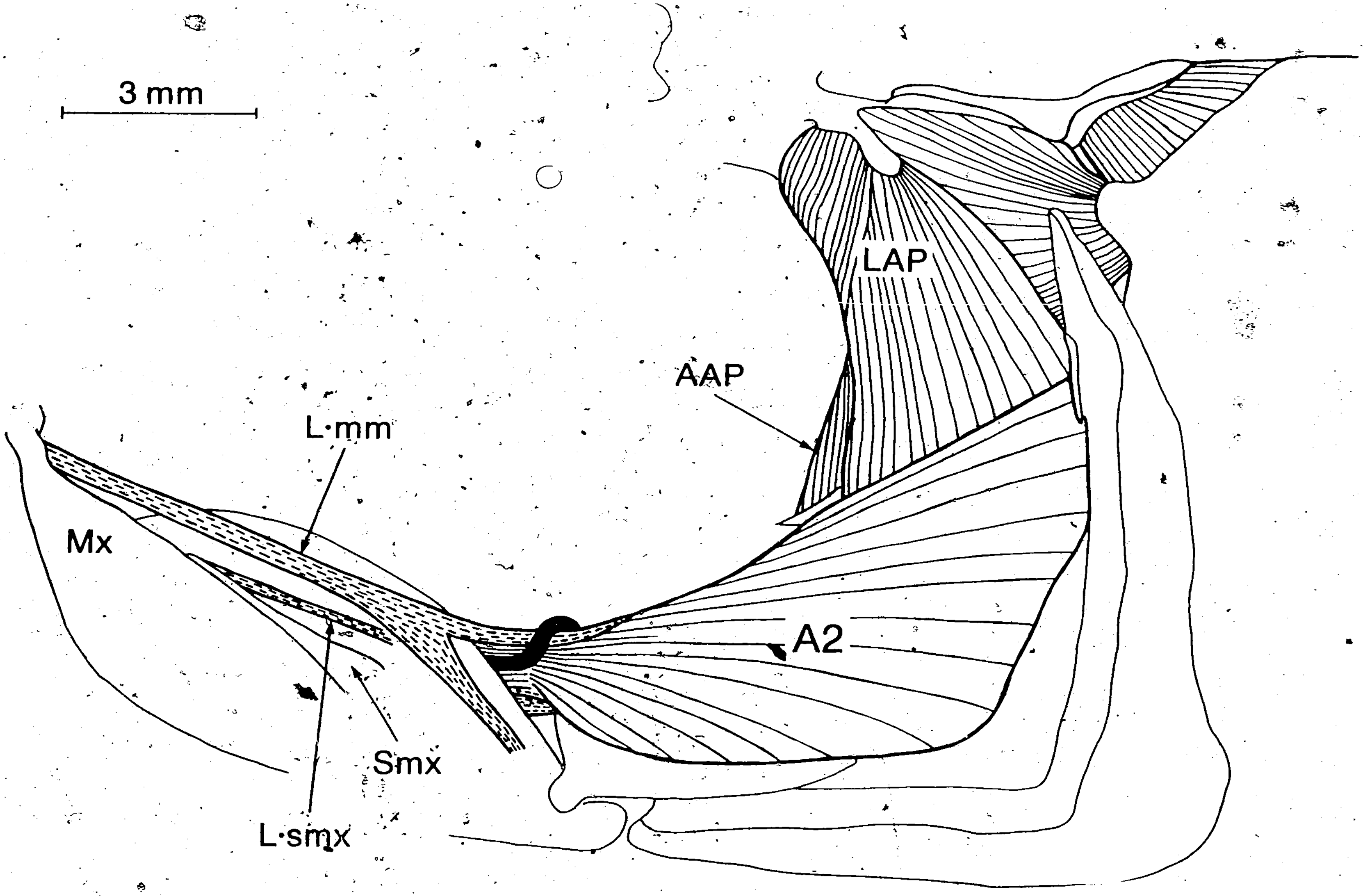

3 mm
LAP
AAP
L·mm
Mx
A2
Smx
L·smx

Figure 63. Lateral view (slightly dorsal) of the external muscles of the left suspensorium in *Plecoglossus altivelis* (Plecoglossidae).

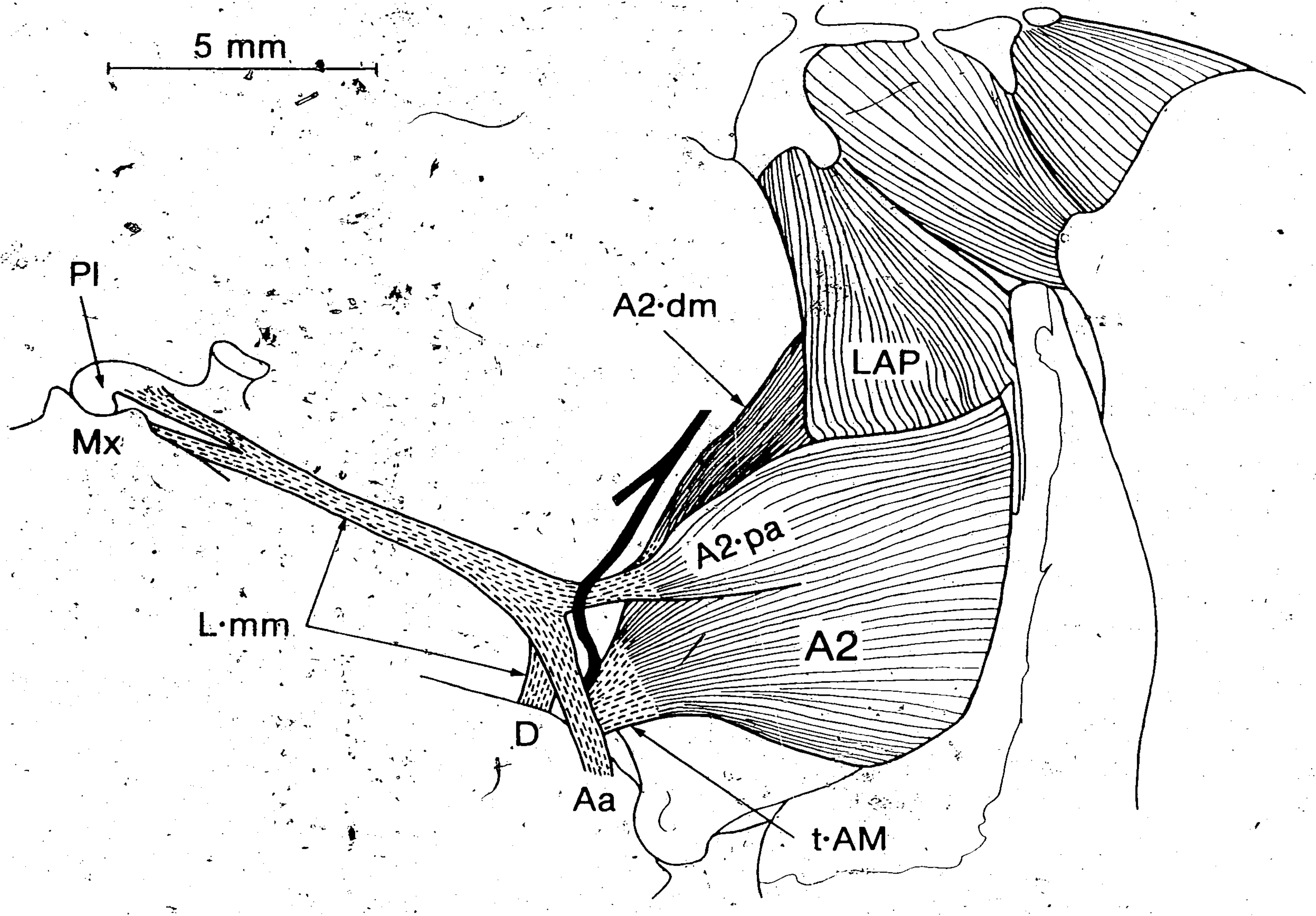

5 mm
Pl
Mx
A2·dm
LAP
A2·pa
L·mm
A2
D
Aa
t·AM

Figure 64. Lateral view of the external muscles of the right suspensorium in *Salangichthys ishikawae*.

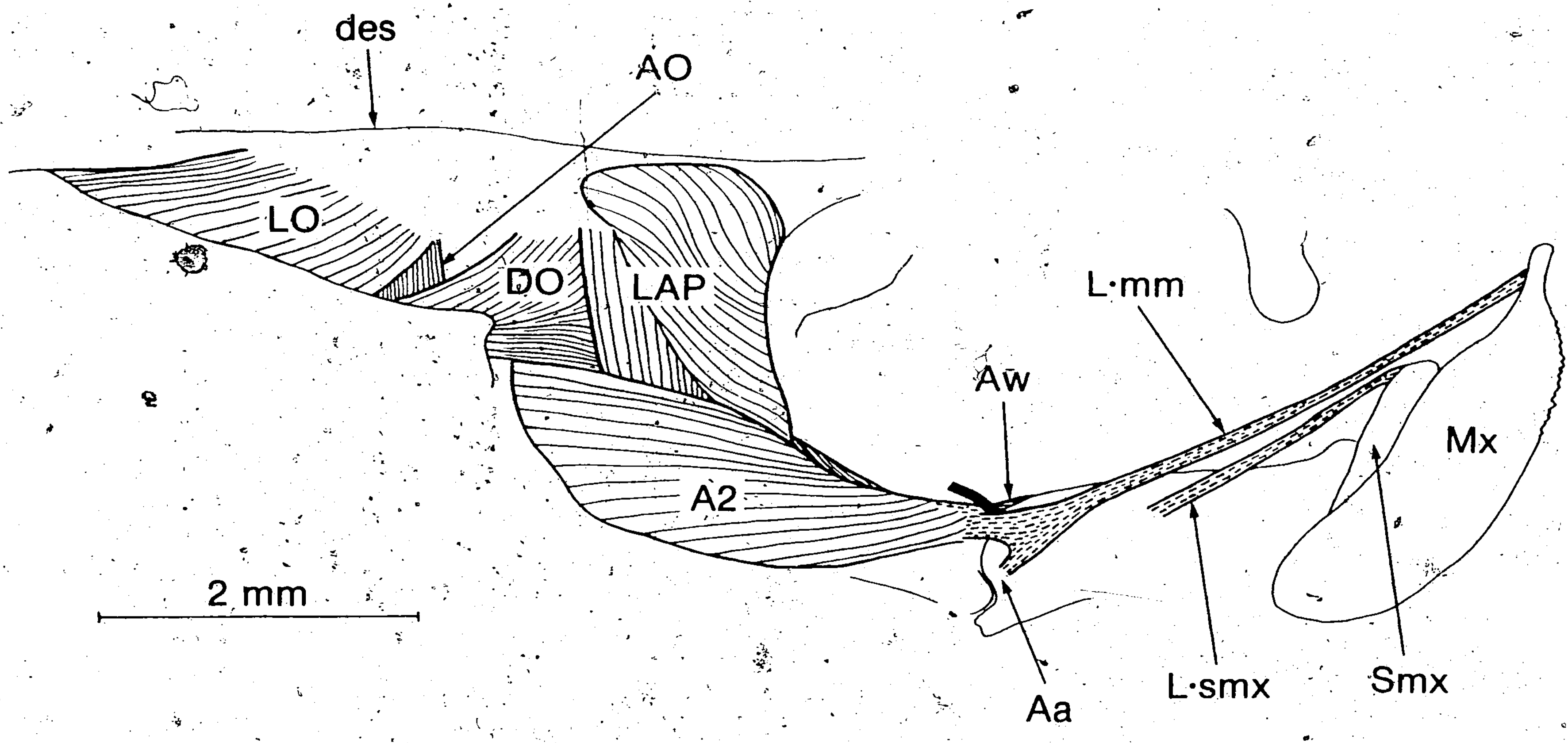

des
AO
LO
DO
LAP
L·mm
Aw
Mx
A2
2 mm
Aa
L·smx
Smx

Figure 65. Lateral view of the external muscles of the left suspensorium in *Salangichthys microdon* (Salangidae).

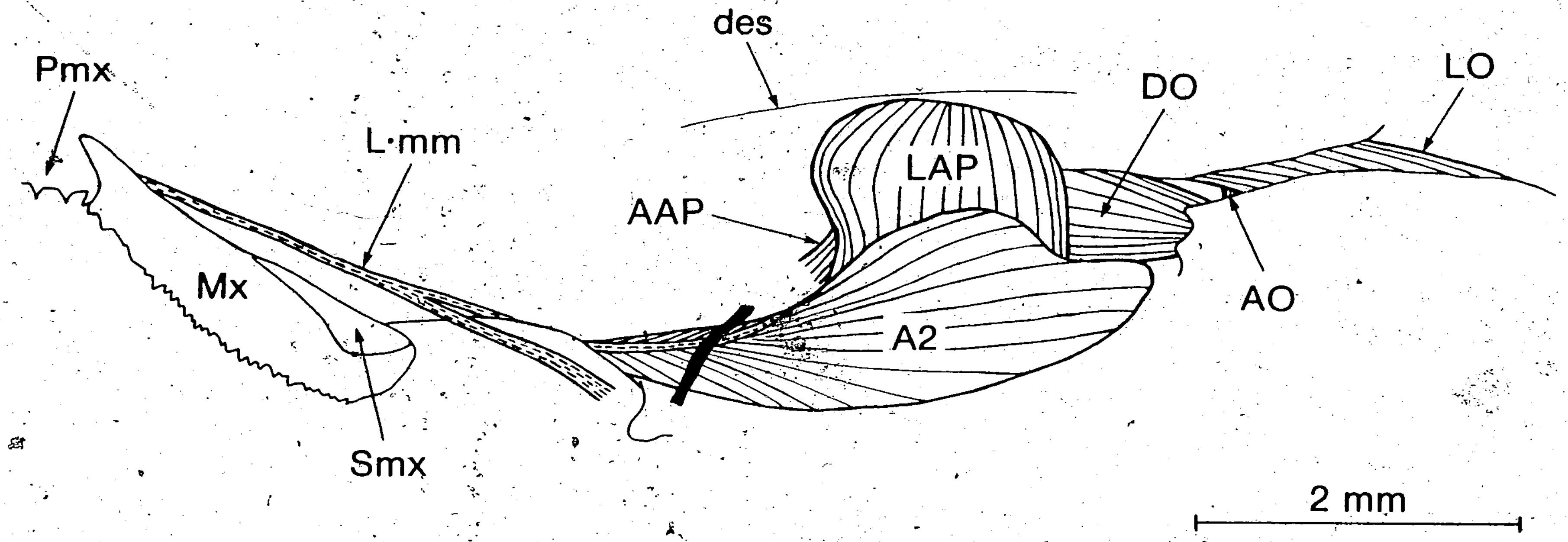

Pmx
L·mm
des
LAP
AAP
DO
LO
Mx
A2
AO
Smx
2 mm

Figure 66. Lateral view of the external muscles of the right suspensorium in *Salanx prognathus* (Salangidae).

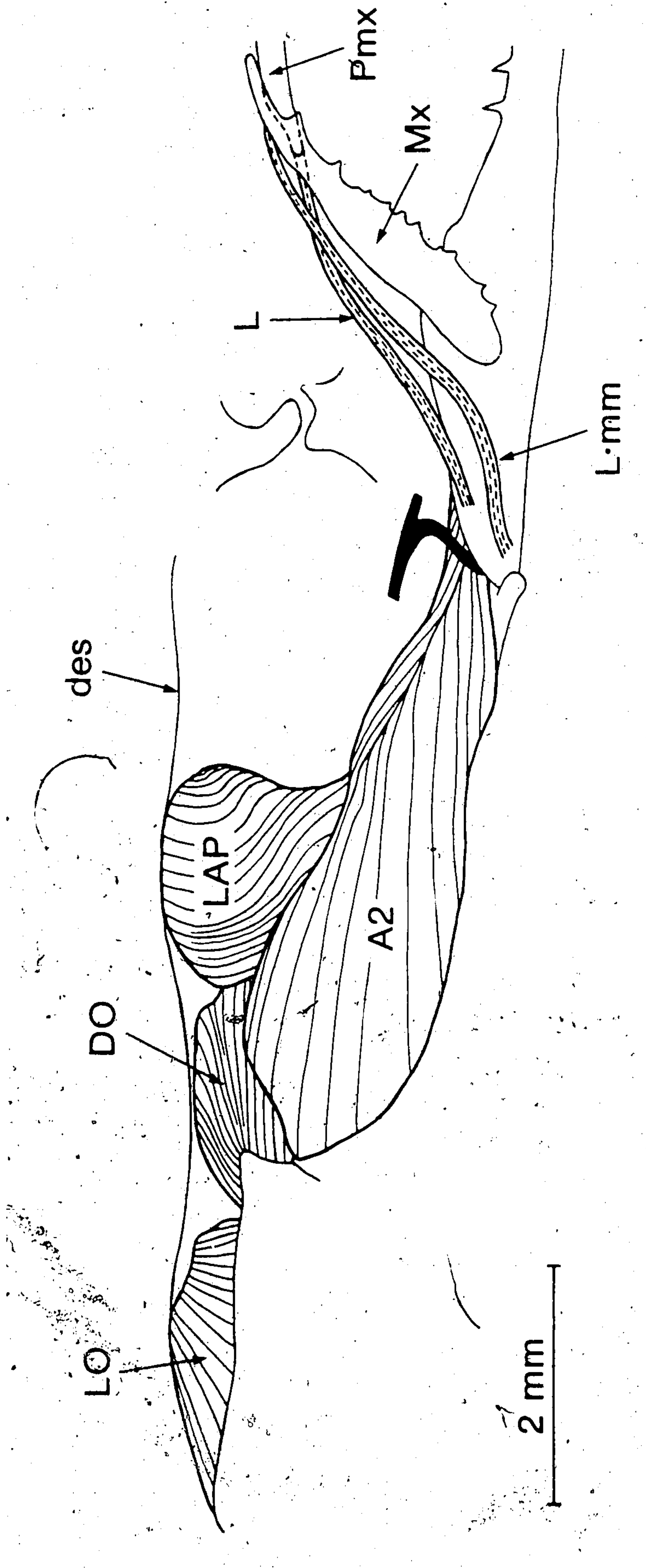
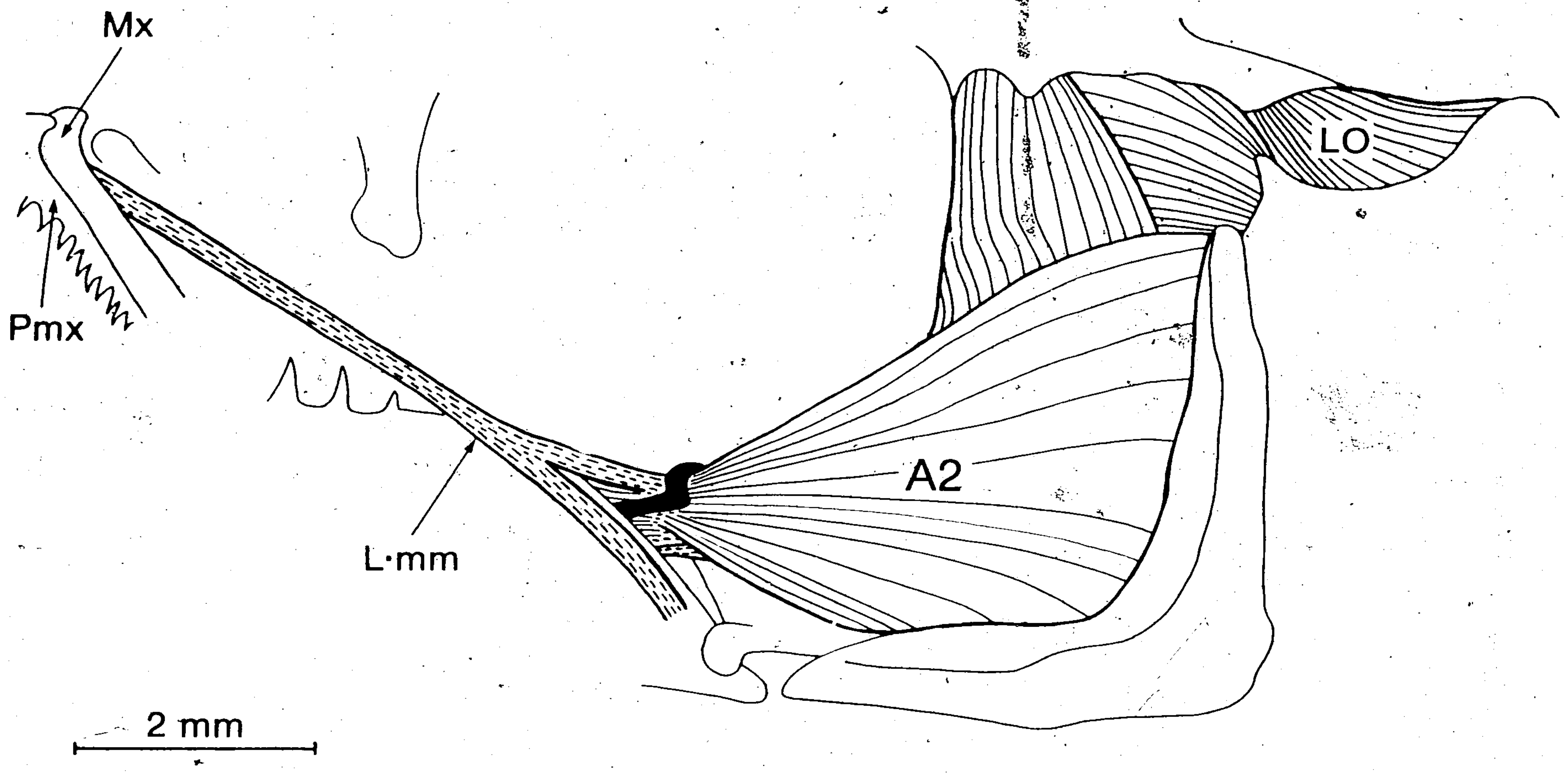

Pmx
Mx
L
L·mm
des
LAP
A2
DO
LO
2 mm

Figure 67. Lateral view of the external muscles of the muscles of the left suspensorium in *Retropinna retropinna* (Retropinnidae).


Mx
Pmx
LO
A2
L·mm
2 mm

Figu[illegible] external muscles of the left suspensorium in *Prototroctes*

Figure 69. Lateral view of the external muscles of the left suspensorium in *Lepidogalaxias salamandroides* (Lepidogalaxiidae).

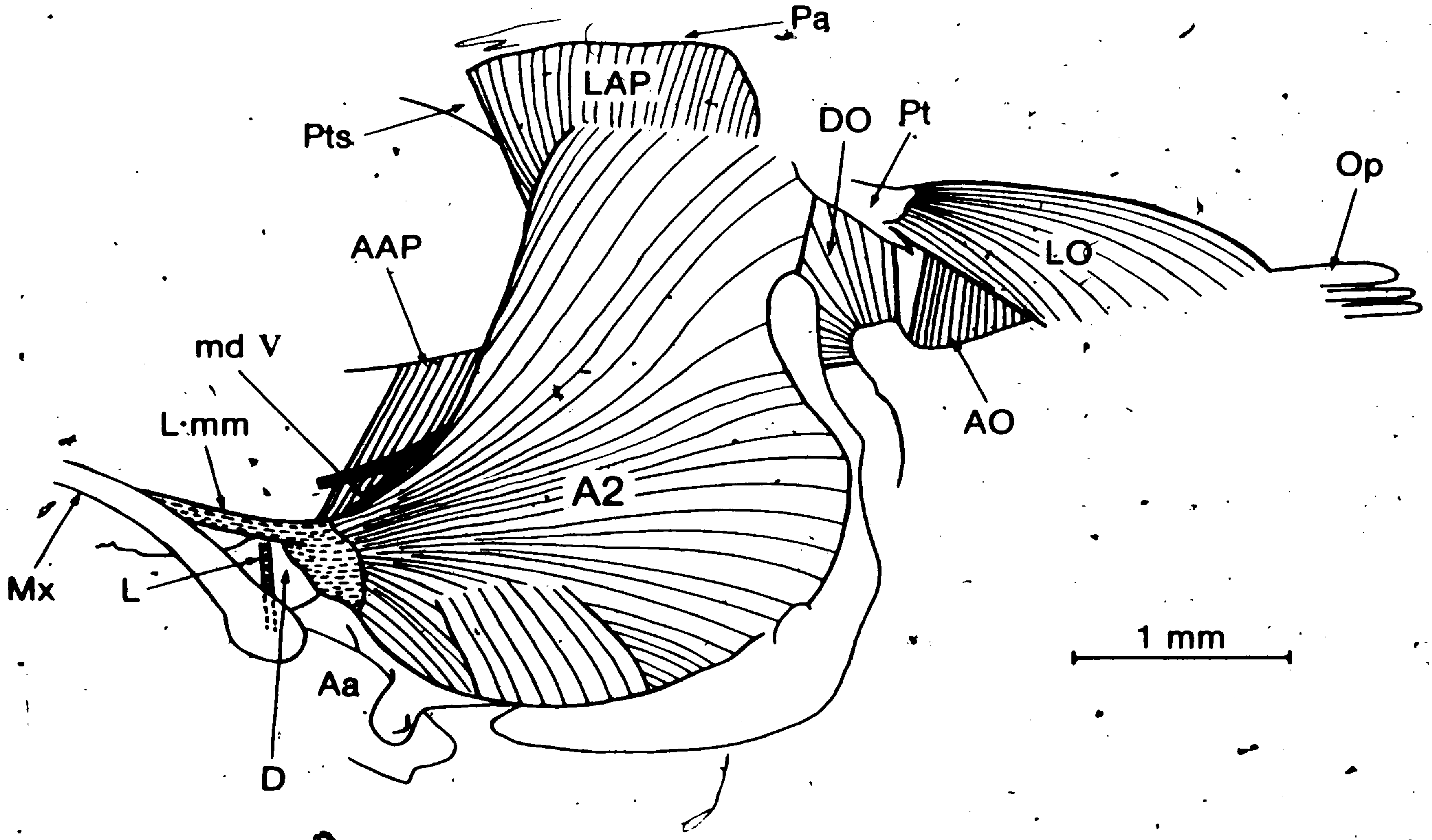

Pa
LAP
Pts
DO
Pt
Op
LO
AAP
md V
AO
L·mm
A2
Mx
L
Aa
D
1 mm

Figure 70. *Galaxias maculatus* (Galaxiidae): (A) lateral view of the external muscles of the left suspensorium; (B) ventrolateral (slightly posterior) view of the ligaments (=tendons) attaching section A2 of the *adductor mandibulae* onto the maxilla and lower jaw, the anterolateral fibres of section A2 that insert onto the ligaments are removed to clearly show the ligamentous pattern. The posterior end of the maxilla and the ligament extending from its posteromedial surface to the dentary (see Fig. 69) are not drawn.

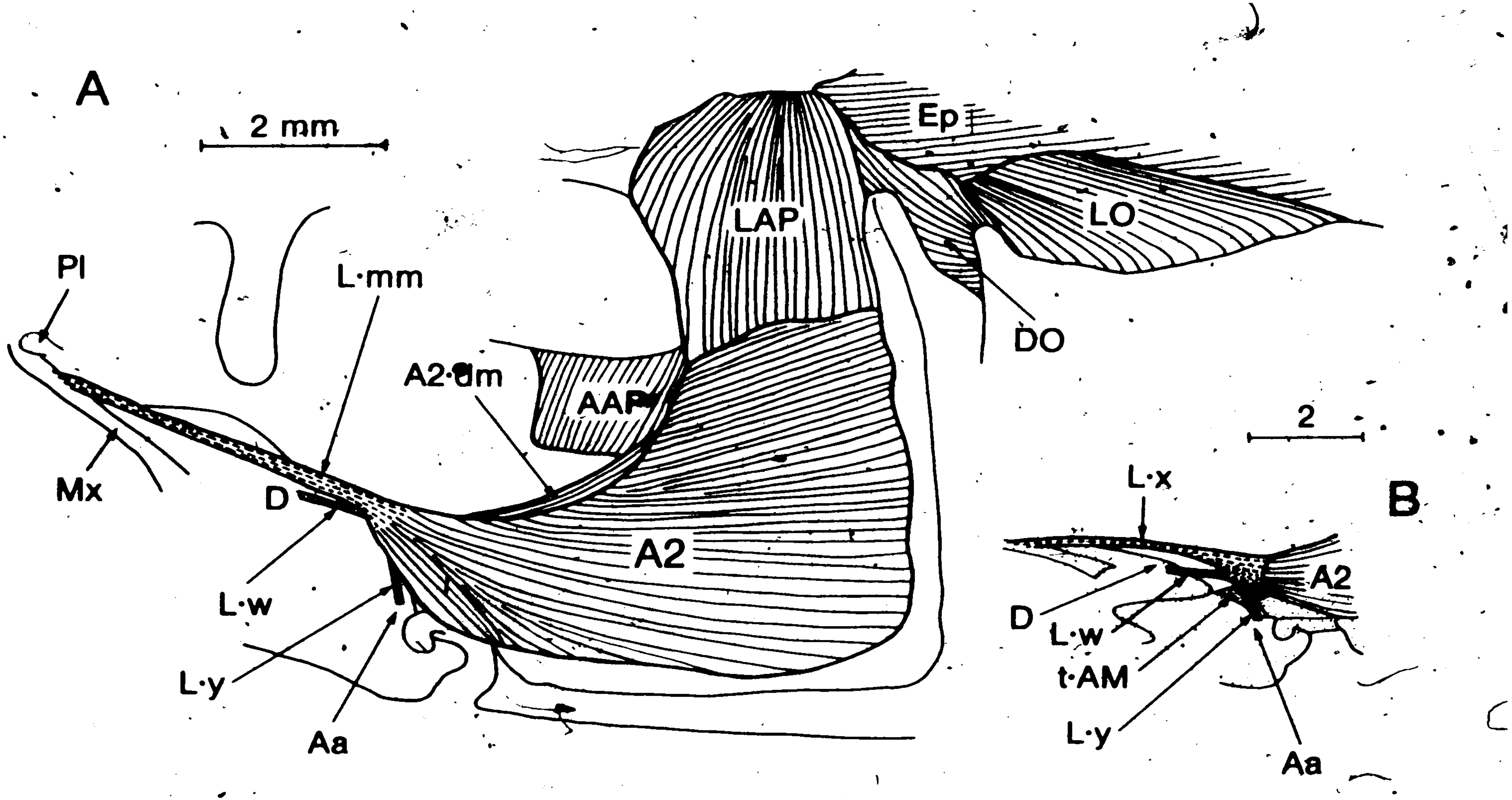

A
2 mm
Pl
Mx
L·mm
D
L·w
L·y
Aa
A2·dm
AAP
A2
LAP
Ep
LO
DO
2
B
L·x
A2
D
L·w
t·AM
L·y
Aa

Figure 71. *Galaxias fasciatus* (Galaxiidae): (A) lateral view of the external muscles of the left suspensorium; (B) ventrolateral (slightly posterior) view of the ligaments (=tendons) attaching section A2 of the *adductor mandibulae* onto the maxilla and lower jaw, the anterolateral fibres of section A2 that insert onto the ligaments are removed to clearly show the ligamentous pattern. The short ligament extending from the posteromedial surface of the maxilla to the dentary (see Fig. 69) is not drawn.

Figure 72. Lateral view of the external muscles of the left suspensorium in *Aplochiton taeniatus* (Aplochitonidae). The short ligament extending from the posteromedial surface of the maxilla to the dentary (see Fig. 69) is not drawn.

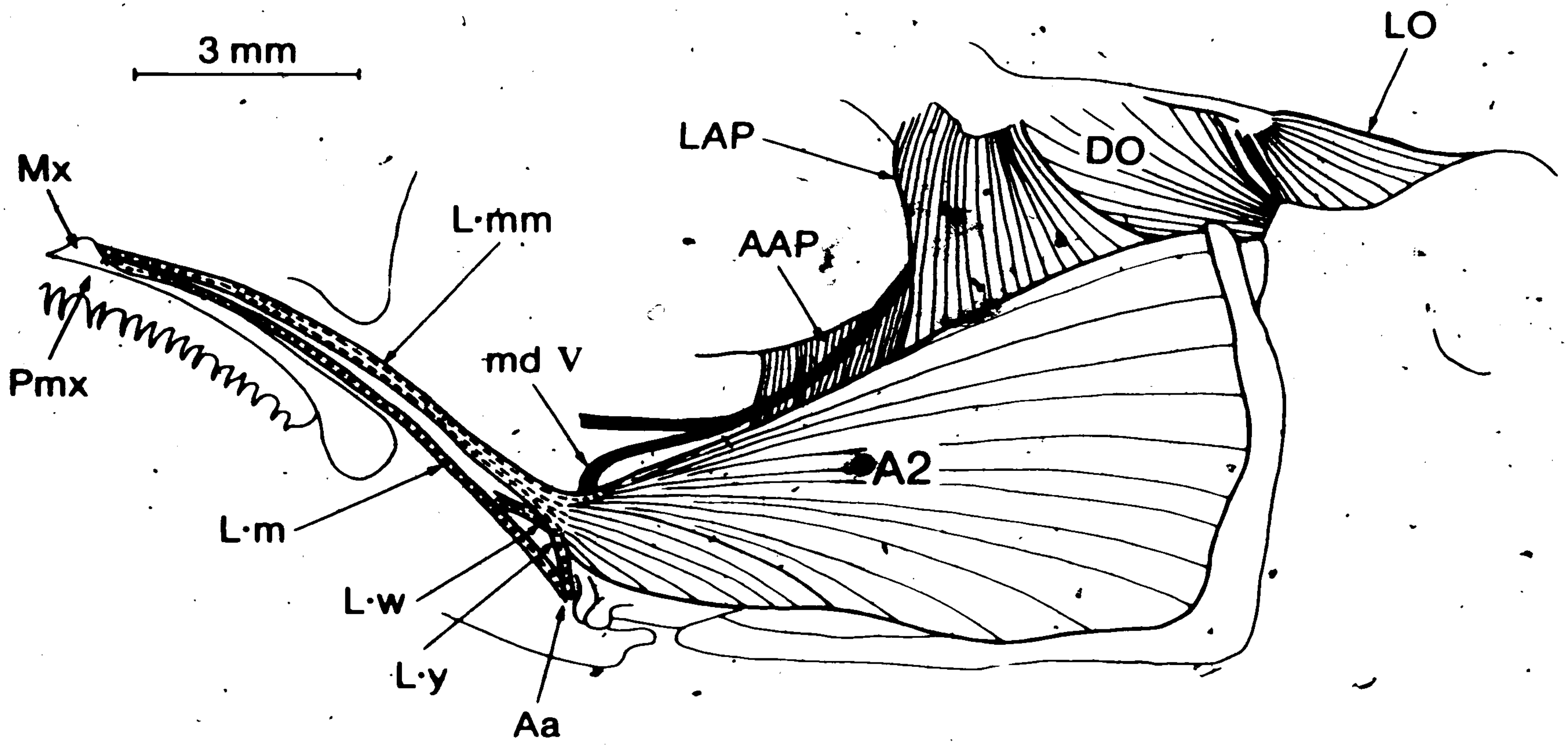

3 mm
Mx
Pmx
L·mm
L·m
L·w
L·y
Aa
md V
AAP
LAP
A2
DO
LO

Figure 73. Lateral view of the external muscles of the right suspensorium in *Alepocephalus tenebrosus* (Alepocephalidae).

Figure 74. Lateral view of the left *adductor mandibulae* in *Rouleina nudus* (Alepocephalidae).

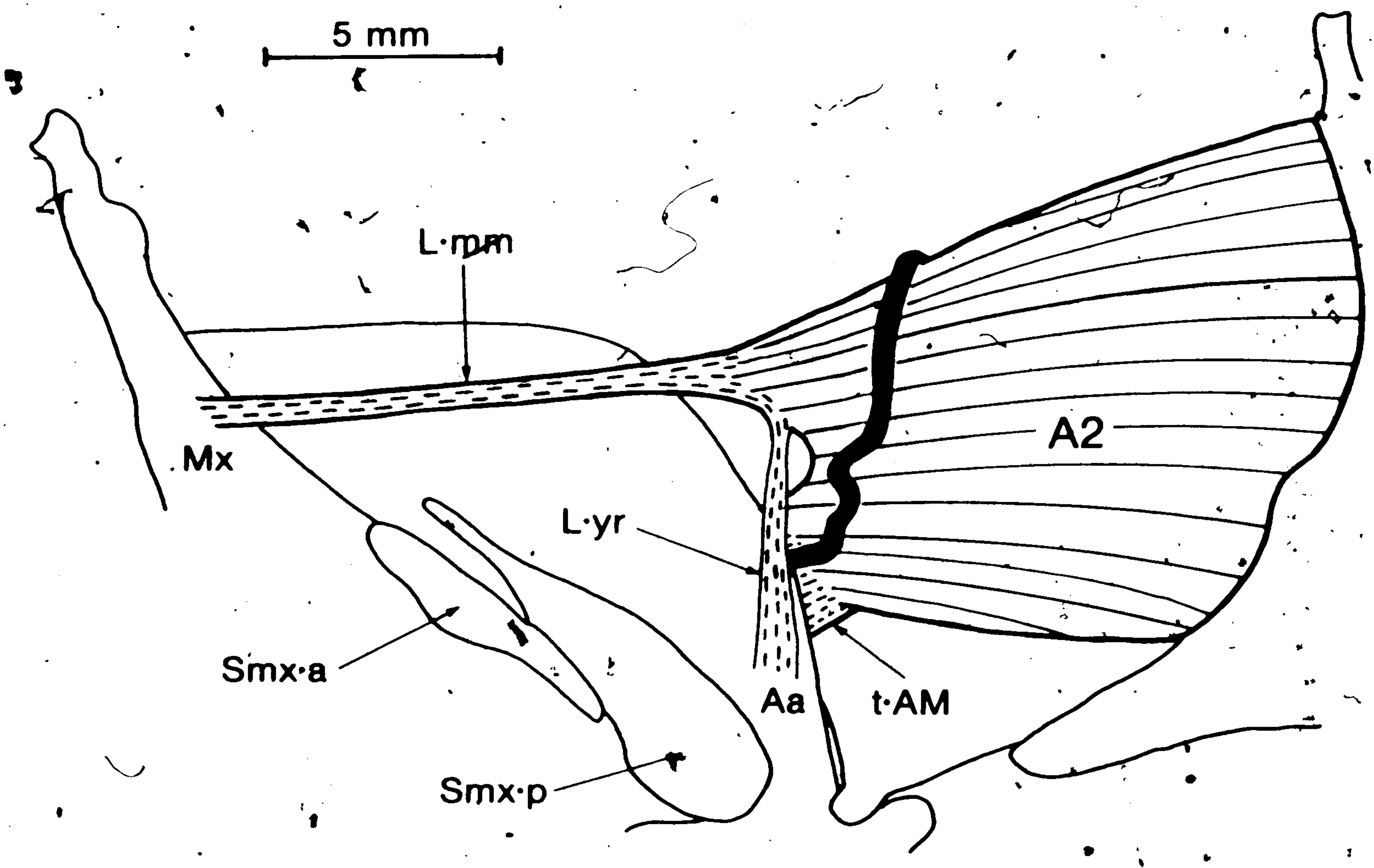

5 mm
L·mm
Mx
A2
L·yr
Smx·a
Aa
t·AM
Smx·p

Figure 75. Lateral view of the left *adductor mandibulae* in *Narcetes stomias* (Alepocephalidae).

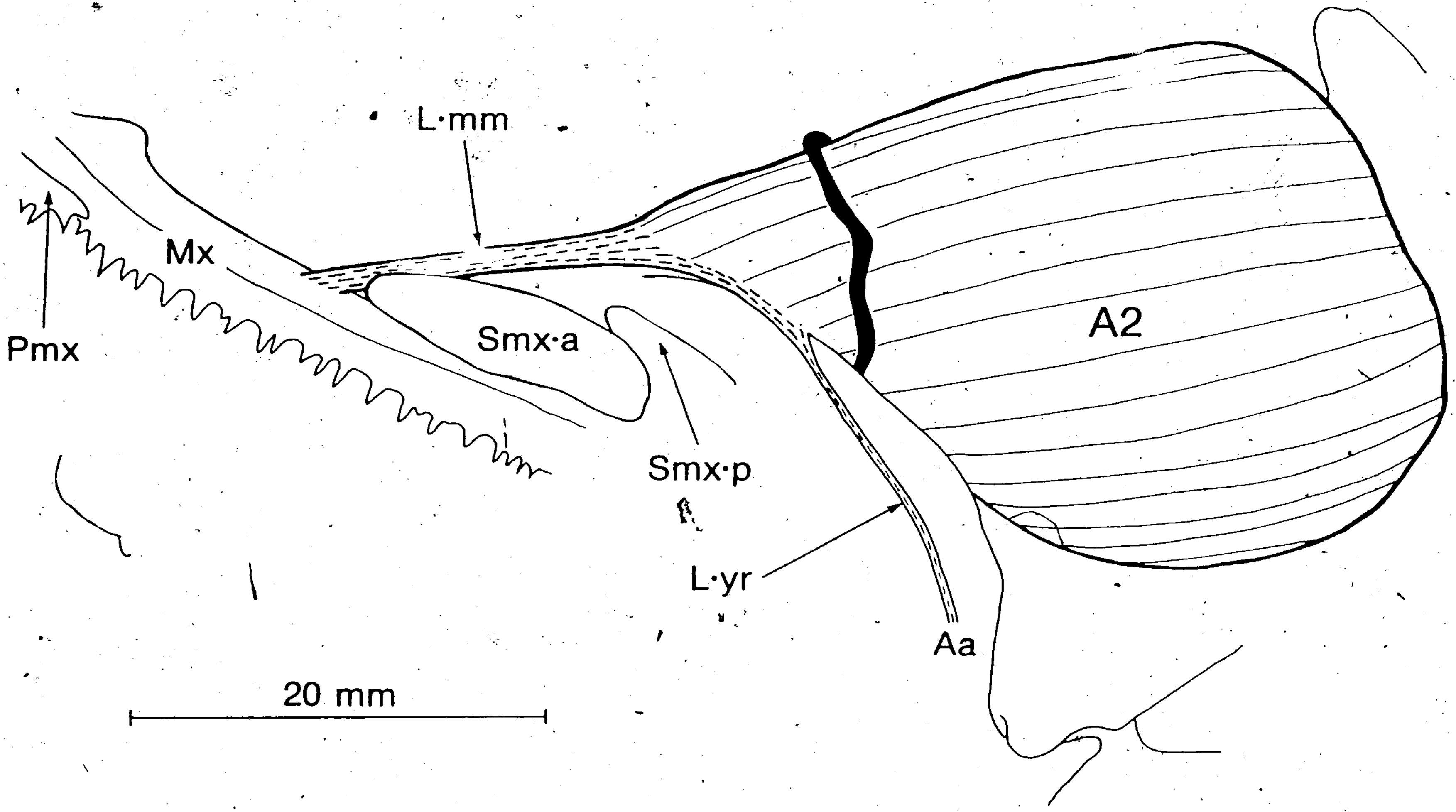

L·mm
Mx
Pmx
Smx·a
A2
Smx·p
L·yr
Aa
20 mm

Figure 76. Lateral view of the right *adductor mandibulae* in *Talismania antillarum* (Alepocephalidae).

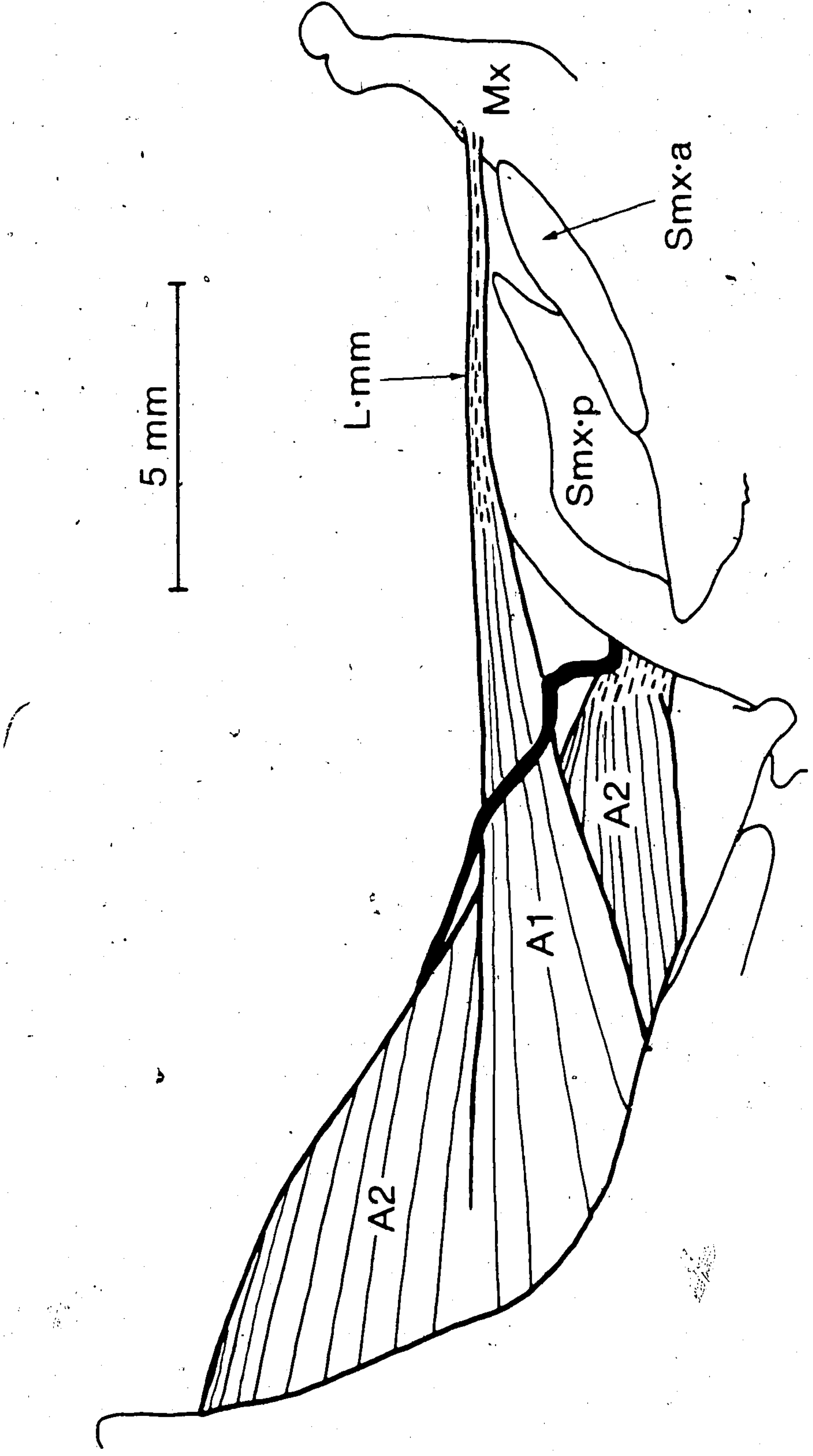

Mx
Smx·a
Smx·p
L·mm
5 mm
A2
A1
A2

Figure 77. Lateral view of the left *adductor mandibulae* in *Binghamichthys aphos* (Alepocephalidae).

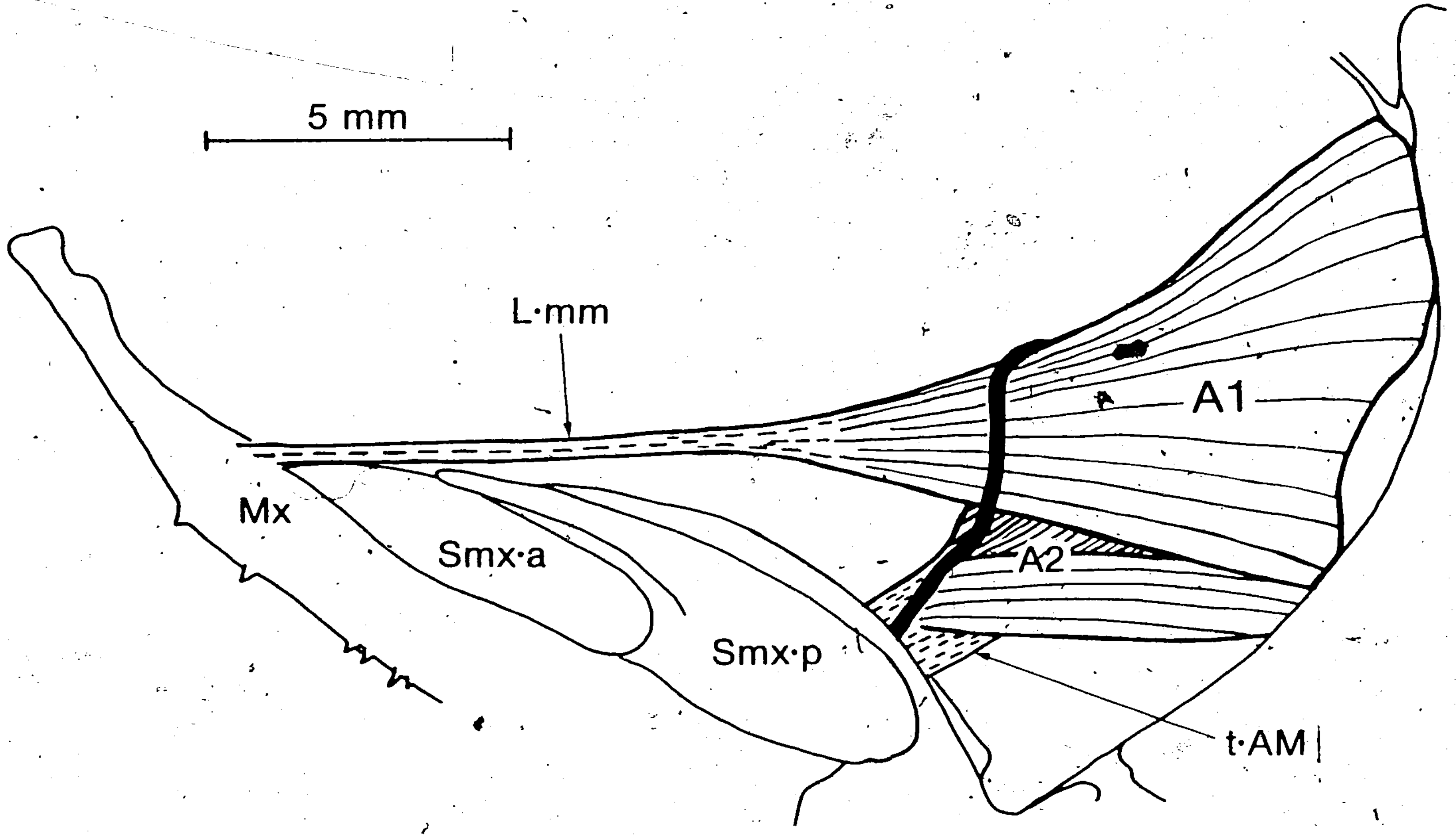

5 mm
L·mm
A1
Mx
Smx·a
A2
Smx·p
t·AM

Figure 78. Lateral view of the external muscles of the left suspensorium in *Bathylaco nigricans* (Alepocephalidae).

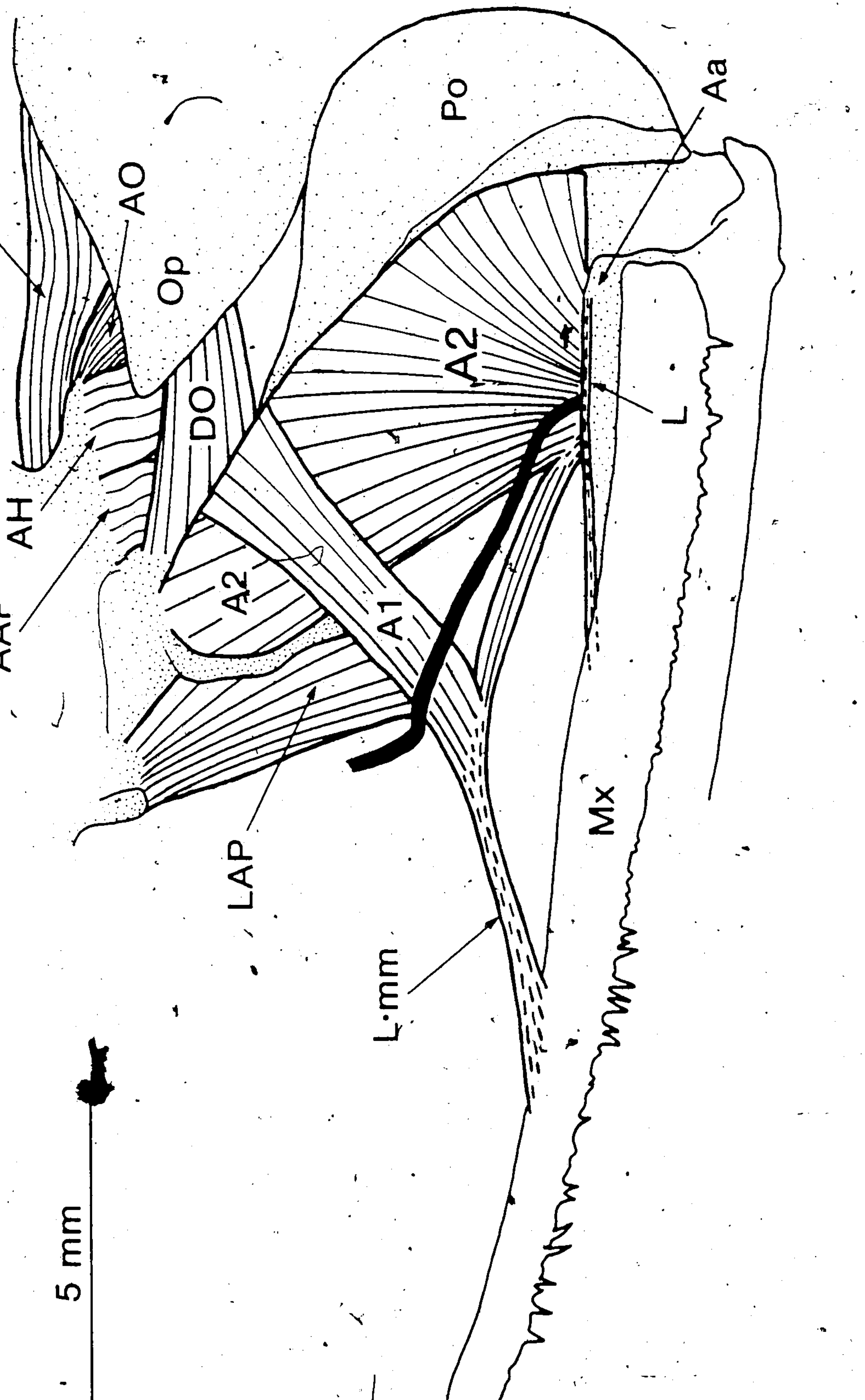

LO
AO
Op
Po
Aa
A2
L
DO
AH
AAP
A2
A1
LAP
Mx
L·mm
5 mm

Figure 79. Lateral view of the left *adductor mandibulae* in *Photostylus pycnopterus* (Alepocephalidae).

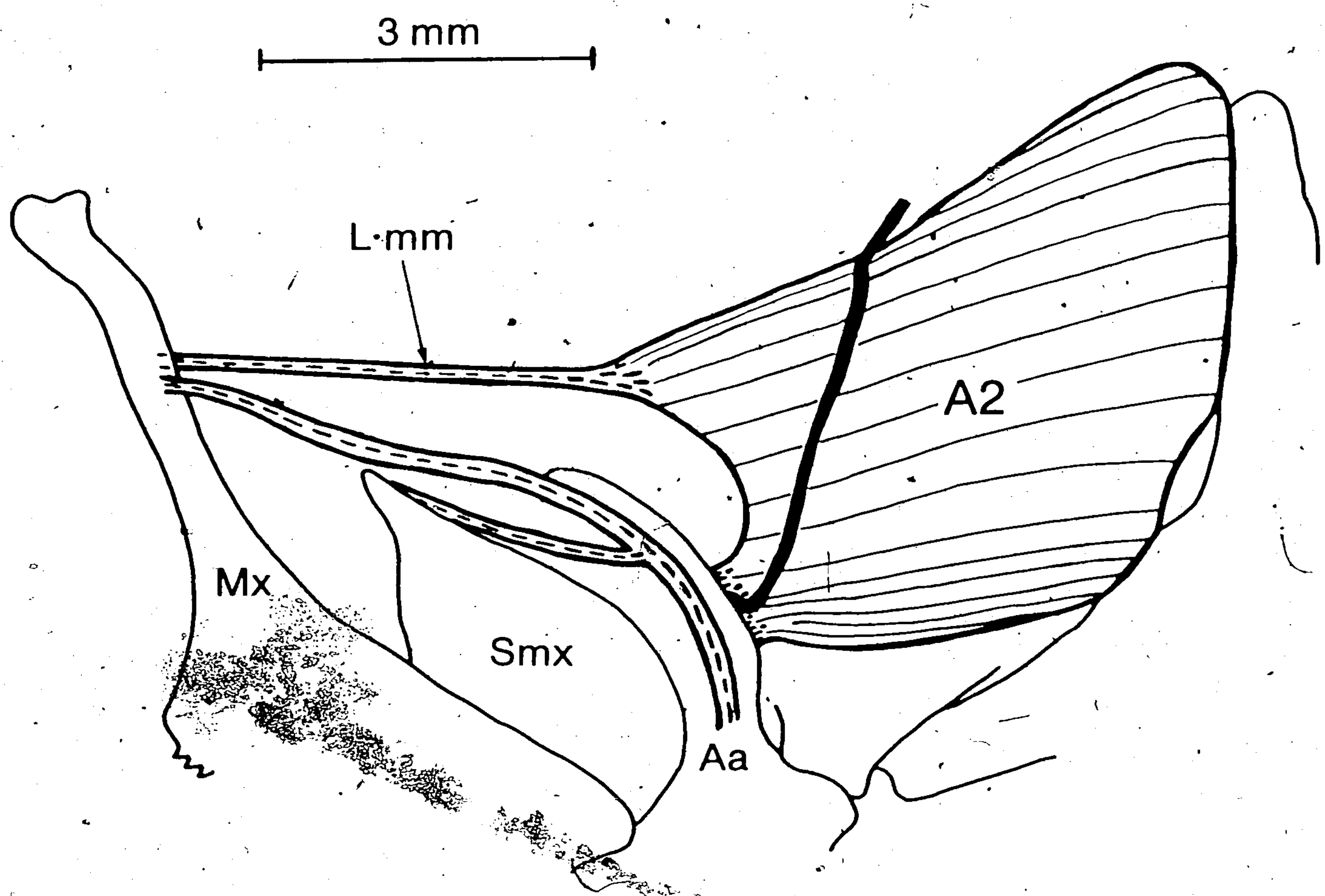

3 mm
L·mm
A2
Mx
Smx
Aa

Figure 80. Lateral view of the right *adductor mandibulae* in *Conocara mcdonaldi* (Alepocephalidae).

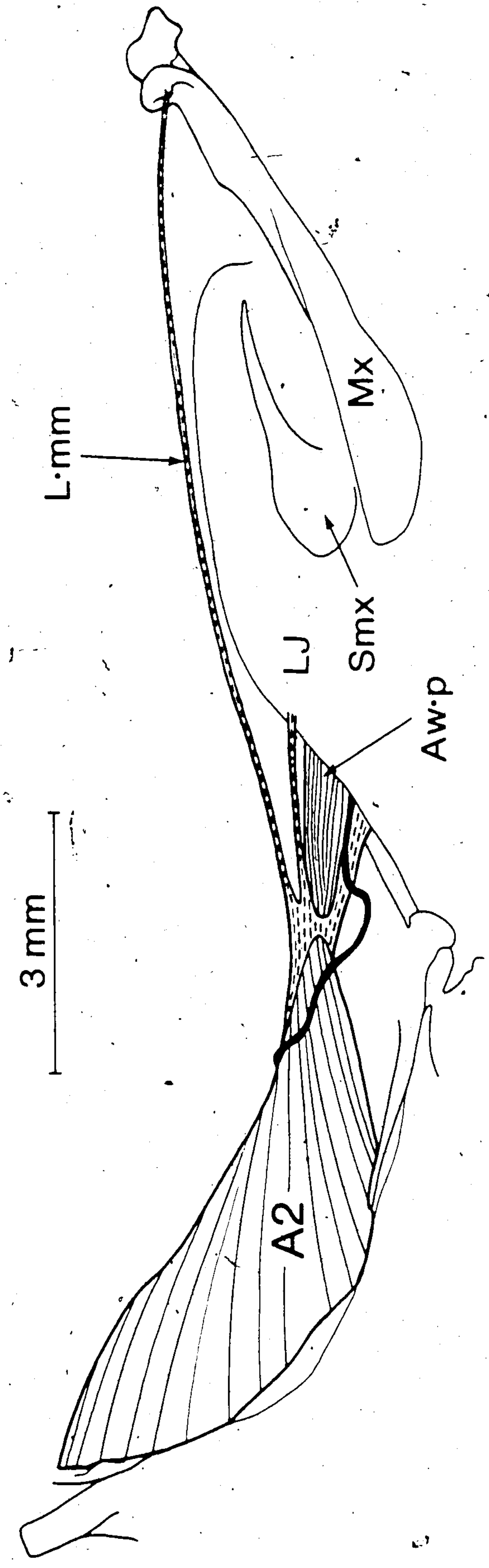

L·mm
Mx
Smx
LJ
Aw·p
A2
3 mm

Figure 81. Lateral view of the right *adductor mandibulae* in *Leptoderma macrops* (Alepocephalidae).

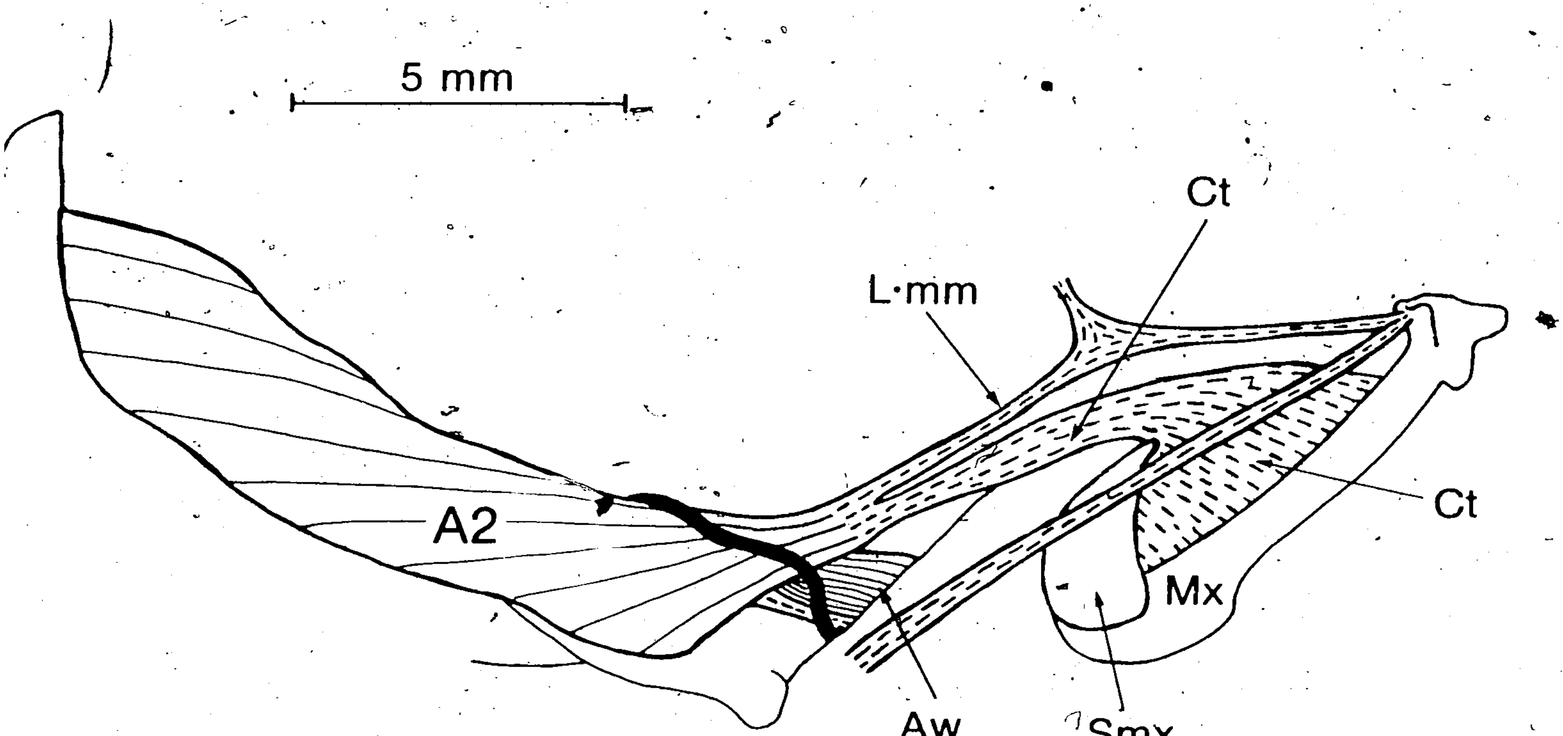

5 mm
Ct
L·mm
Ct
A2
Mx
Aw
Smx

Figure 82. Lateral view of the external muscles of the left suspensorium in *Holtbyrnia latifrons* (Platytroctidae).

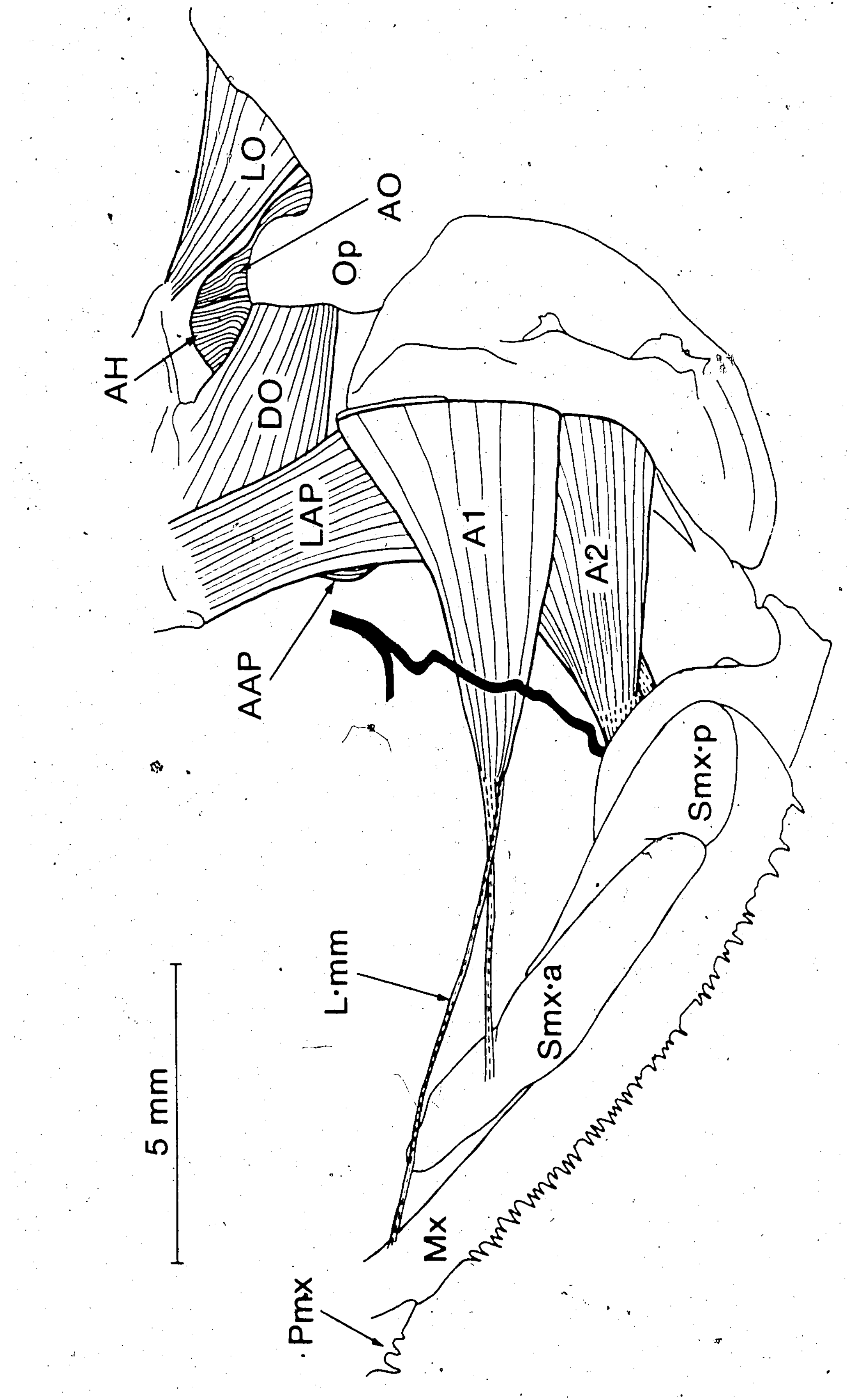

LO
AO
Op
AH
DO
LAP
A1
A2
AAP
Smx·p
Smx·a
L·mm
5 mm
Mx
Pmx

Figure 83. Lateral view of the right *adductor mandibulae* in *Platytroctes apus* (Platytroctidae).

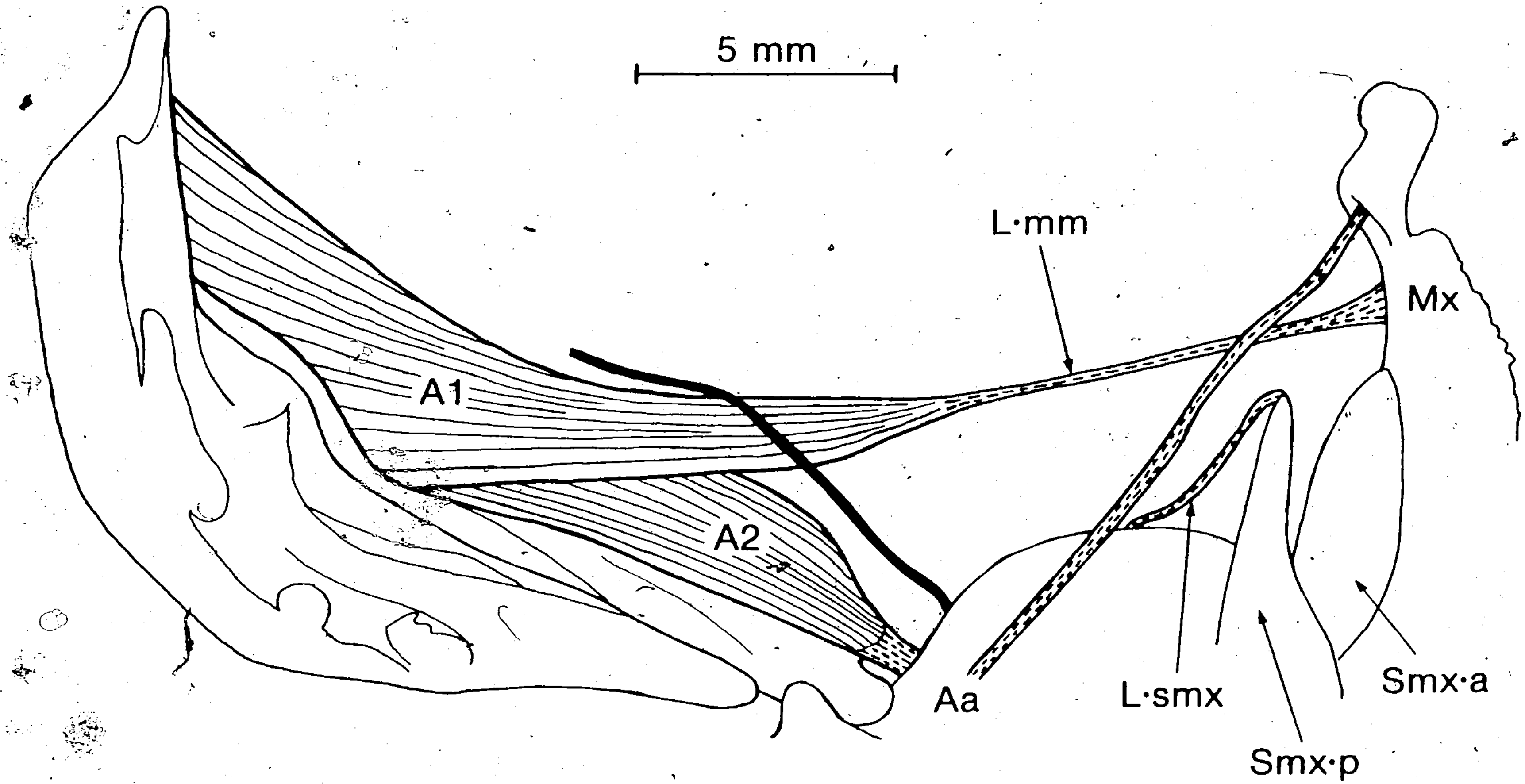

5 mm
L·mm
Mx
A1
A2
Aa
L·smx
Smx·a
Smx·p

Figure 84. Lateral view of the right *adductor mandibulae* in *Searsia koefoedi* (Platytroctidae).

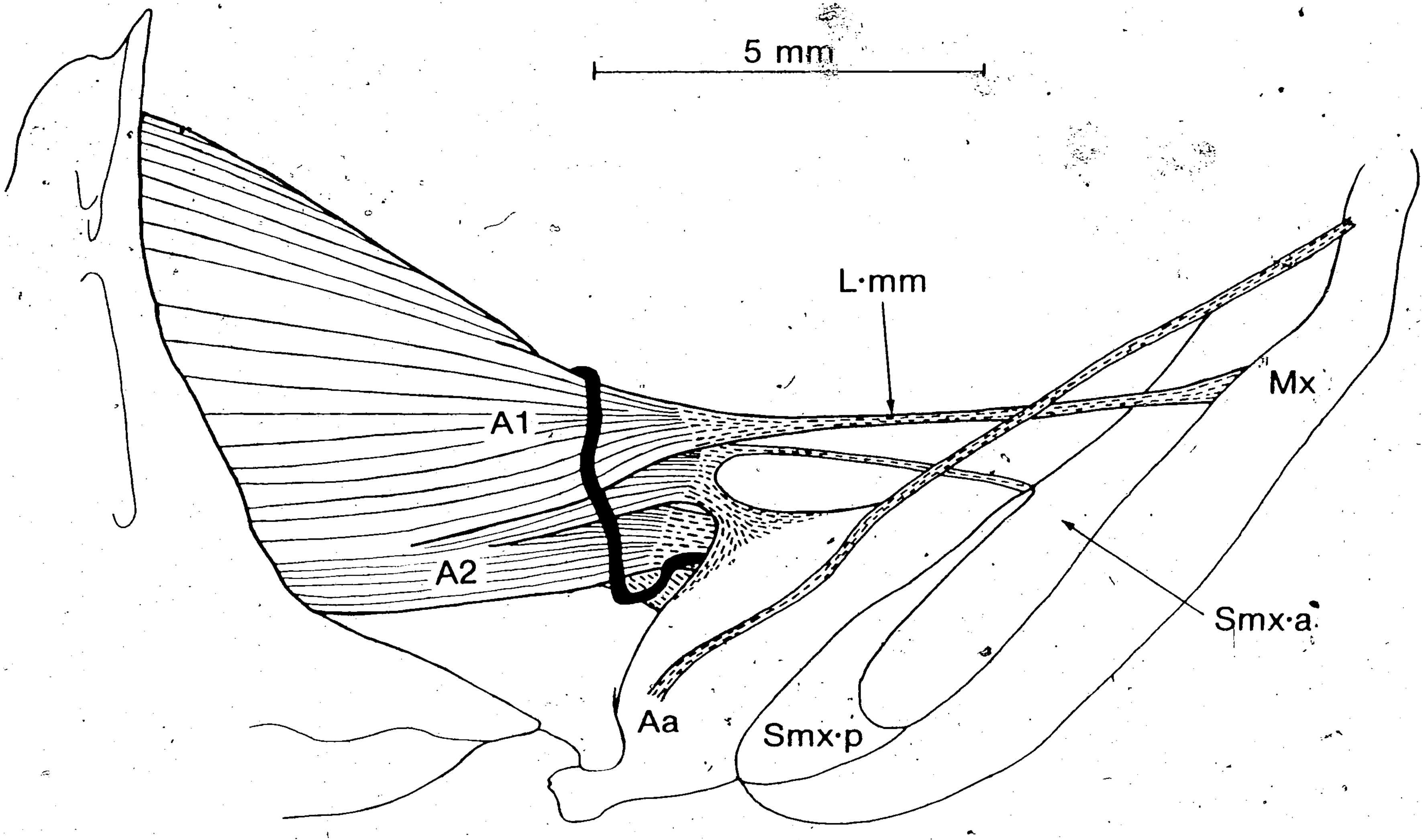

5 mm
L·mm
Mx
A1
A2
Smx·a.
Aa
Smx·p

Figure 85. Lateral view of the external muscles of the left suspensorium in *Mirorictus taningi* (Platytroctidae).

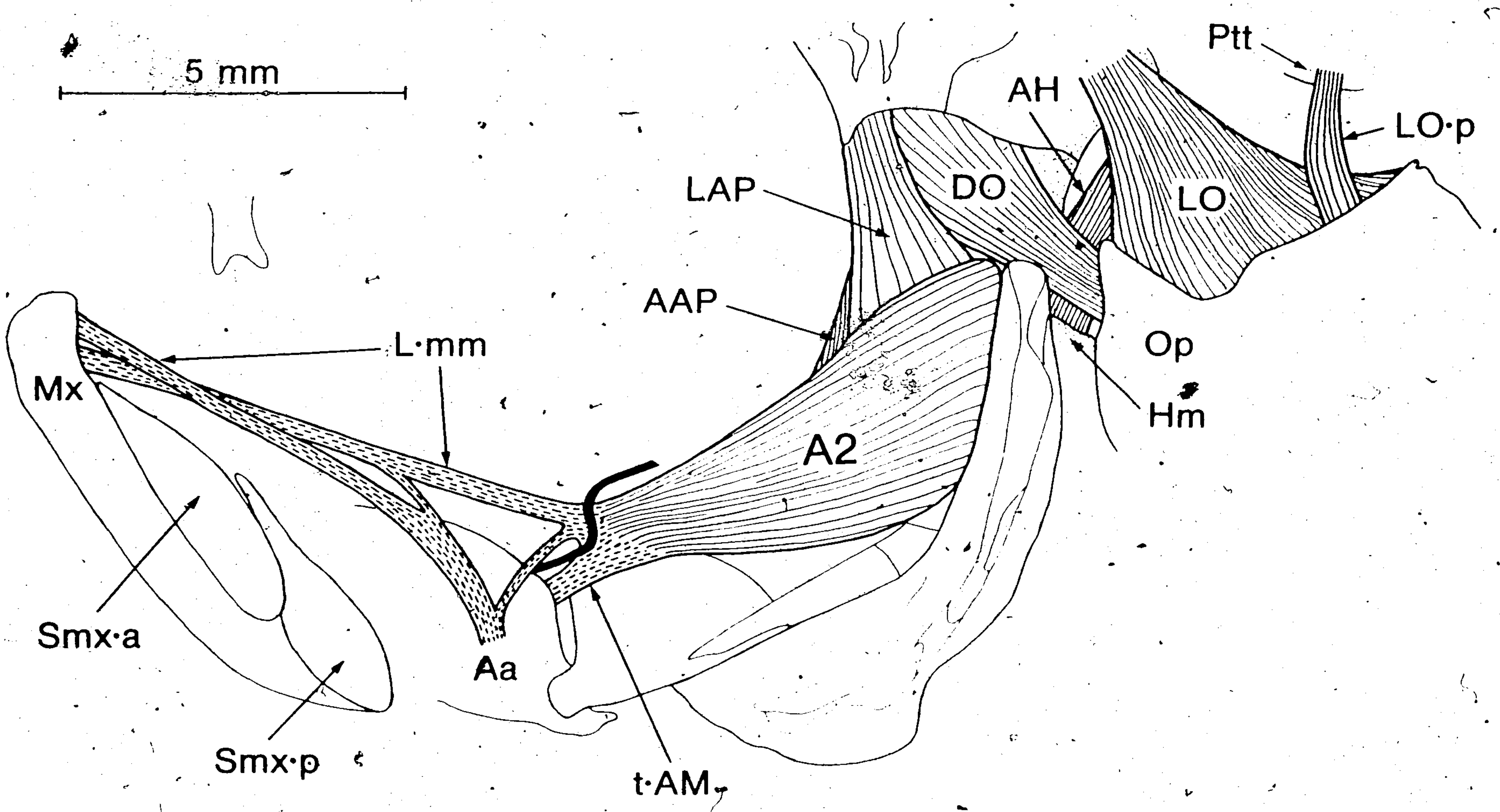

5 mm
Ptt
LO·p
AH
LAP
DO
LO
AAP
Op
L·mm
Mx
Hm
A2
Smx·a
Aa
Smx·p
t·AM

Figure 86. Lateral view of the right adductor *mandibulae* in *Pellisolus facilis* (Platytroctidae).

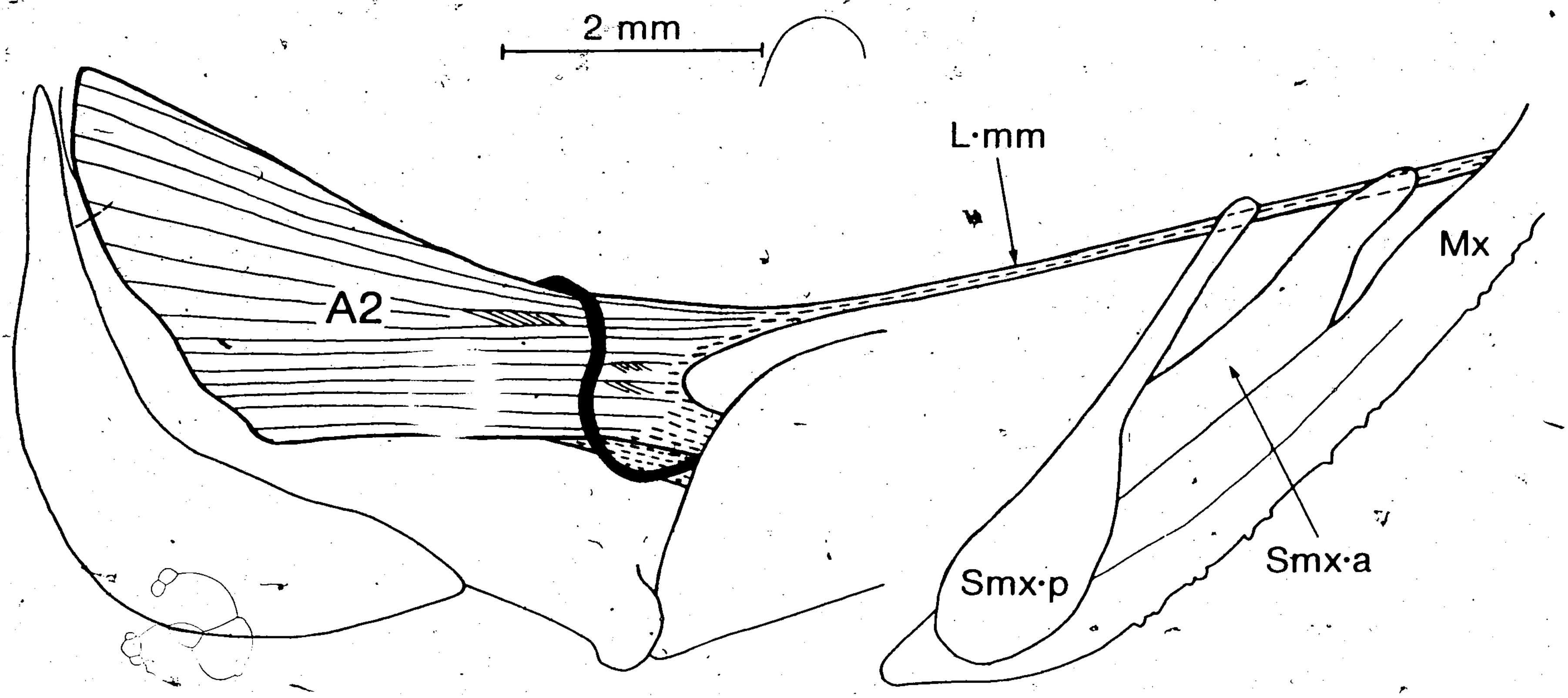

2 mm
L·mm
Mx
A2
Smx·a
Smx·p

Figure 87. Lateral view of the external muscles of the right suspensorium in *Argentina silus* (Argentinidae).

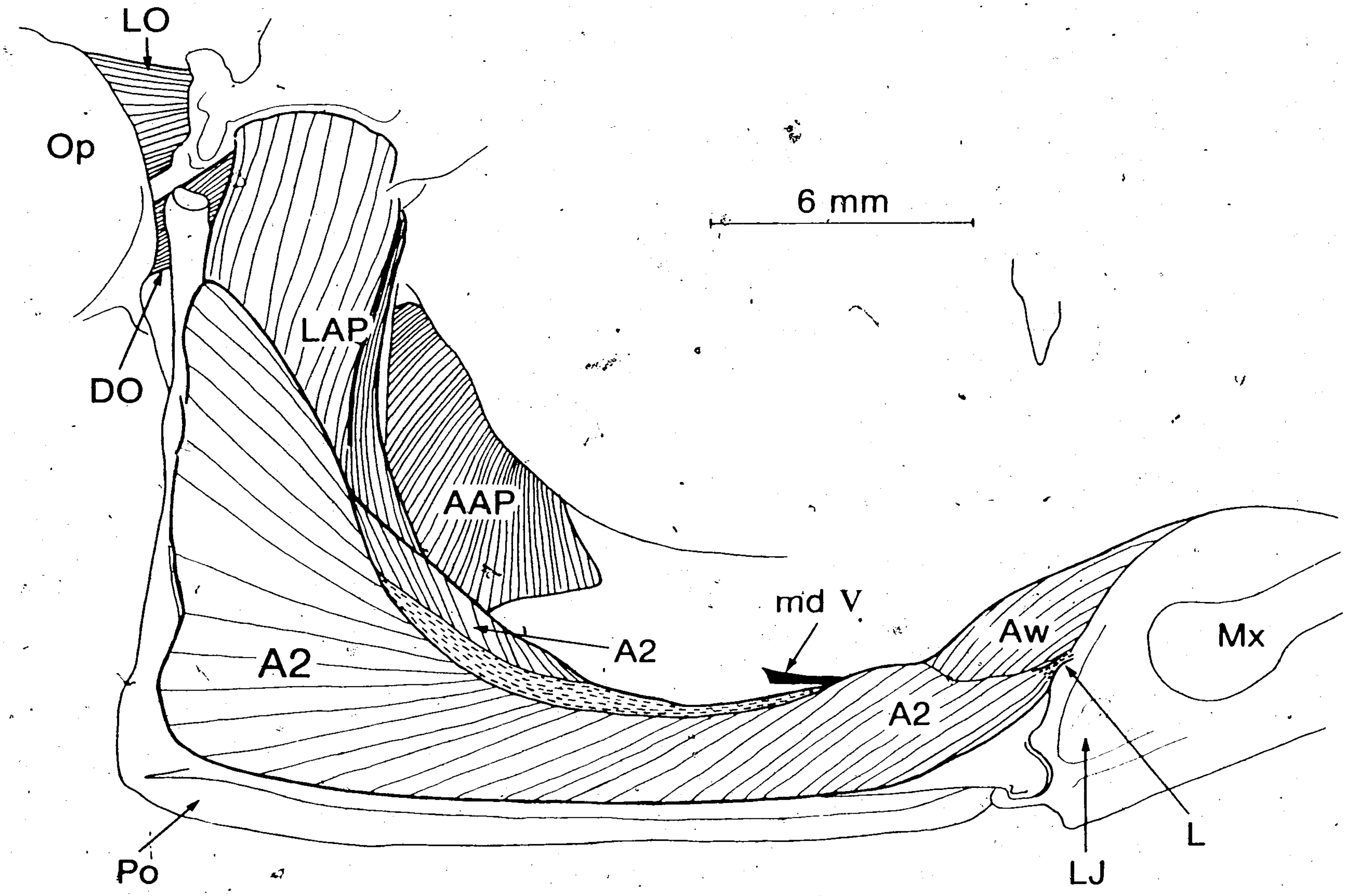

LO
Op
DO
LAP
AAP
6 mm
md V
A2
A2
A2
Aw
Mx
L
LJ
Po

Figure 88. Lateral view of the external muscles of the right suspensorium in *Bathylagus pacificus* (Bathylagidae).

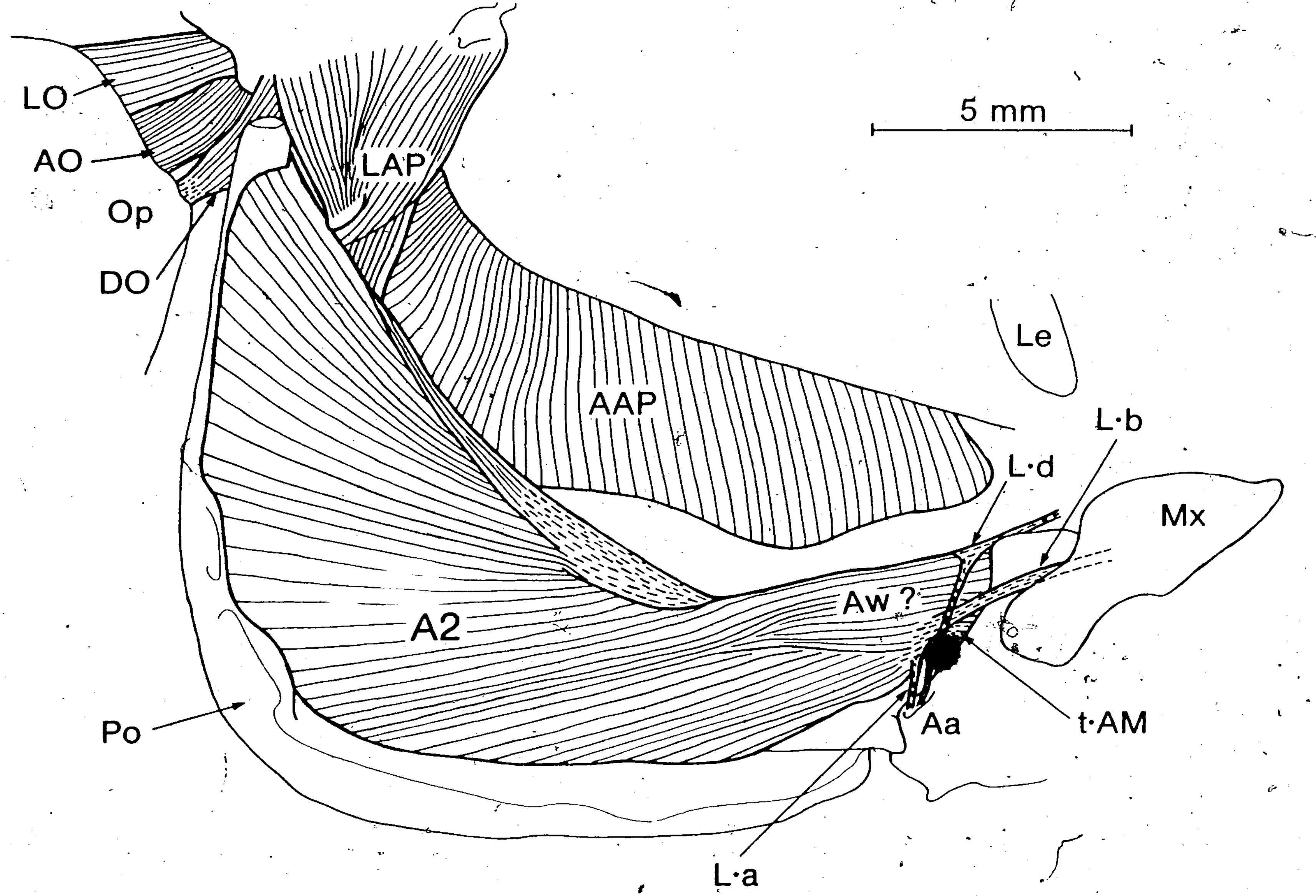

5 mm
LO
AO
Op
DO
LAP
AAP
Le
L·b
L·d
Mx
Aw ?
A2
Po
Aa
t·AM
L·a

Figure 89. Lateral view of the external muscles of the left suspensorium in *Dolichopteryx longipes* (Opisthoproctidae).

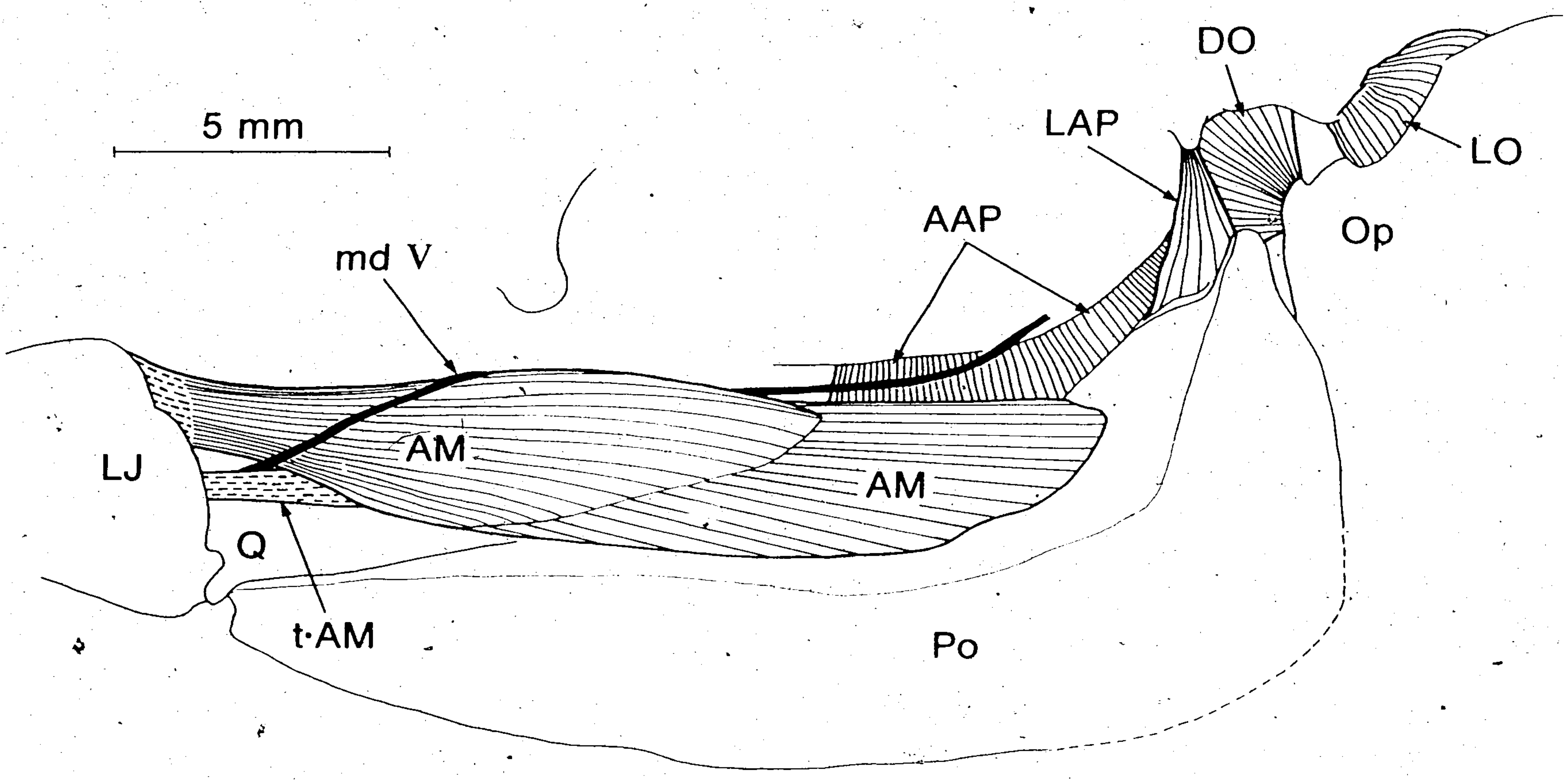

DO
LAP
LO
AAP
Op
md V
5 mm
AM
AM
LJ
Q
t·AM
Po

Figure 90. Lateral view of the external muscles of the left suspensorium in *Megalops cyprinoides* (Megalopidae, Elopiformes).

Figure 91. Lateral view of the external muscles of the left suspensorium in *Clupea harengus* (Clupeidae, Clupeiformes).

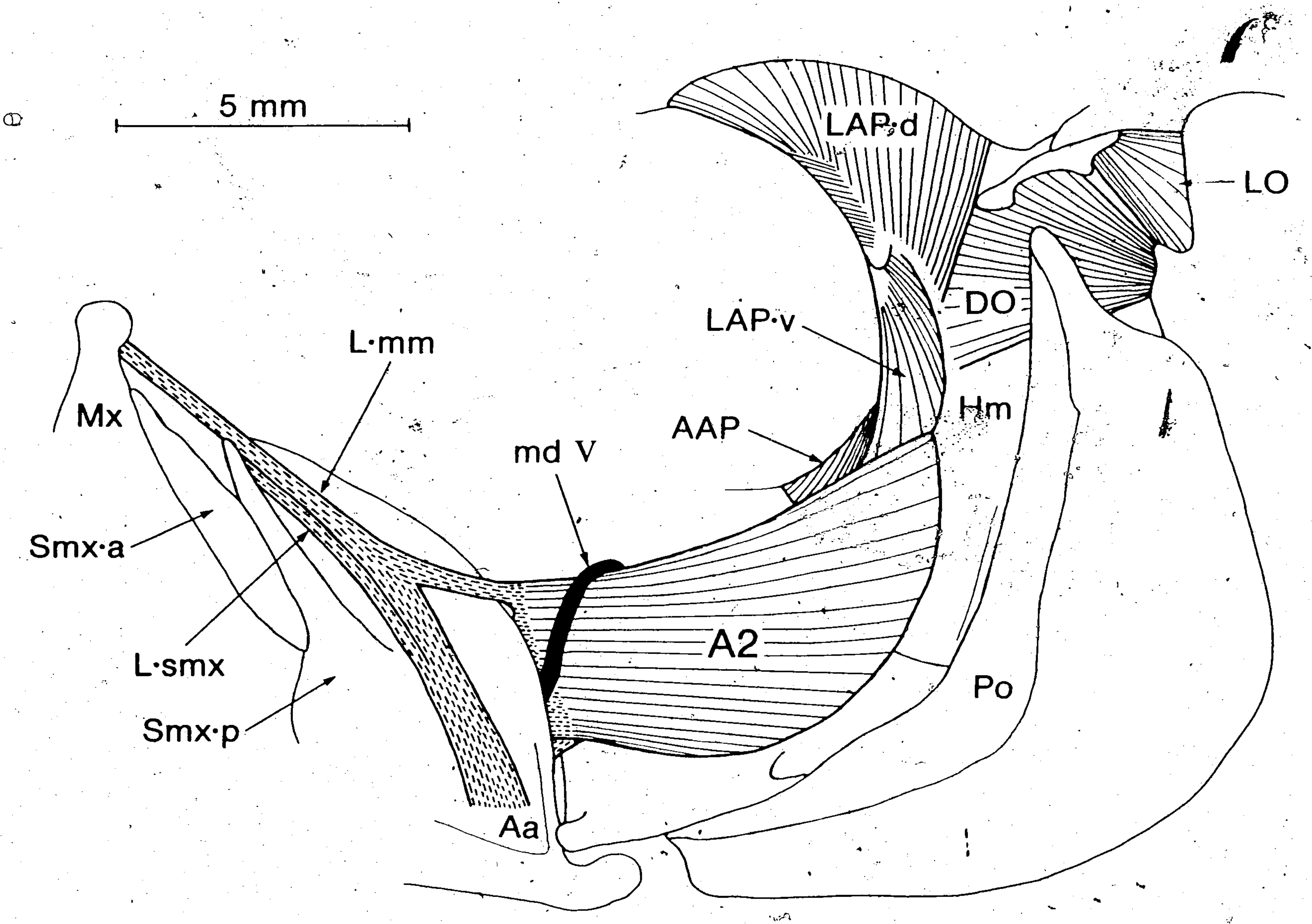

5 mm
LAP·d
LO
DO
LAP·v
L·mm
Mx
Hm
AAP
md V
Smx·a
A2
L·smx
Po
Smx·p
Aa

Figure 92. Lateral view of the anterior end of the right *adductor mandibulae* in *Diplophos taenia* (Gonostomatidae, Stomiiformes) to show how it attaches onto the upper jaw. The supramaxillae and supramaxillary ligament are not drawn.

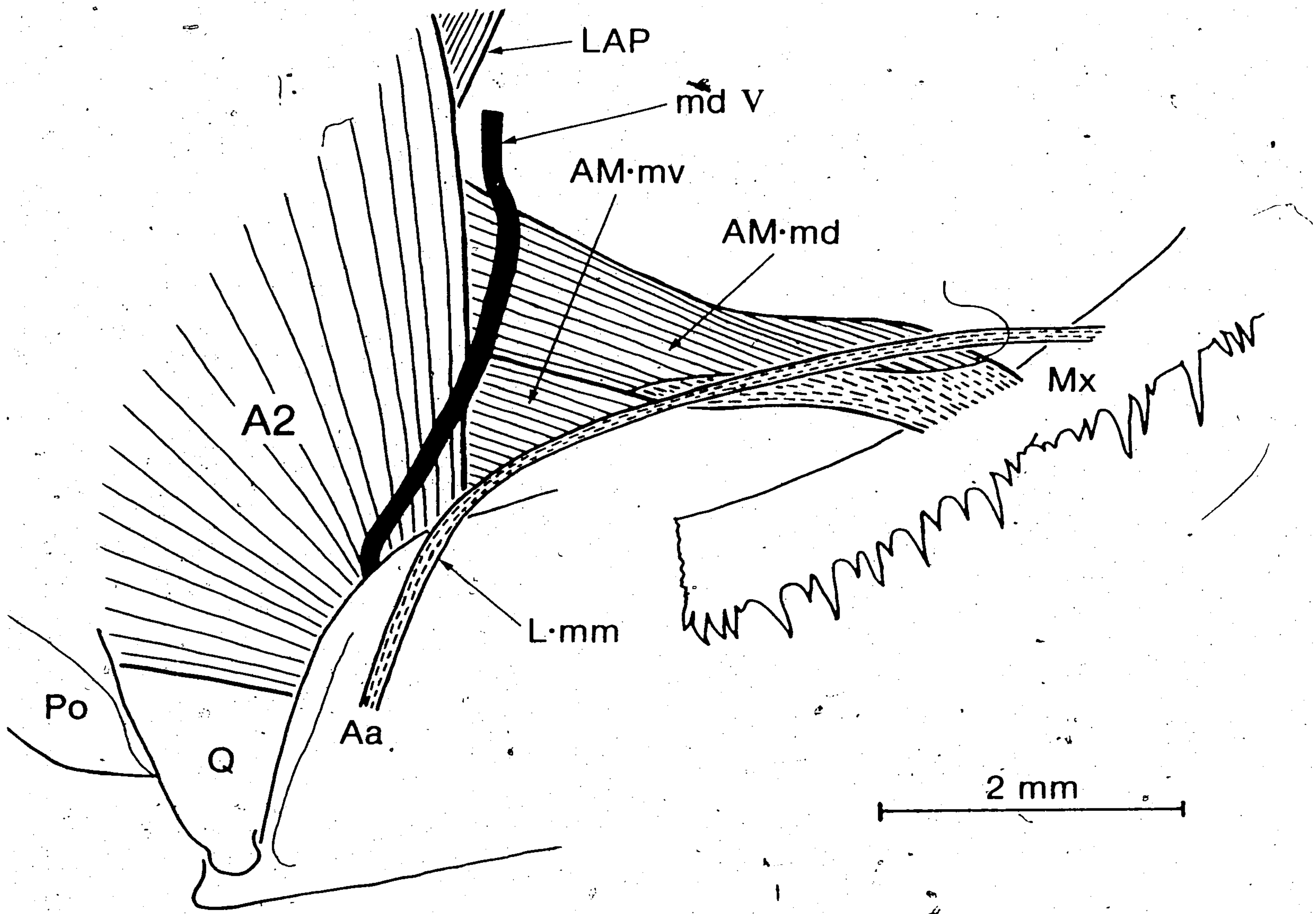

LAP
md V
AM·mv
AM·md
A2
Mx
L·mm
Po
Q
Aa
2 mm

Figure 93. Lateral view of the external muscles of the left suspensorium in *Vinciguerria nimbaria* (Photichthyidae, Stomiiformes). The supramaxillae and supramaxillary ligament are not drawn.

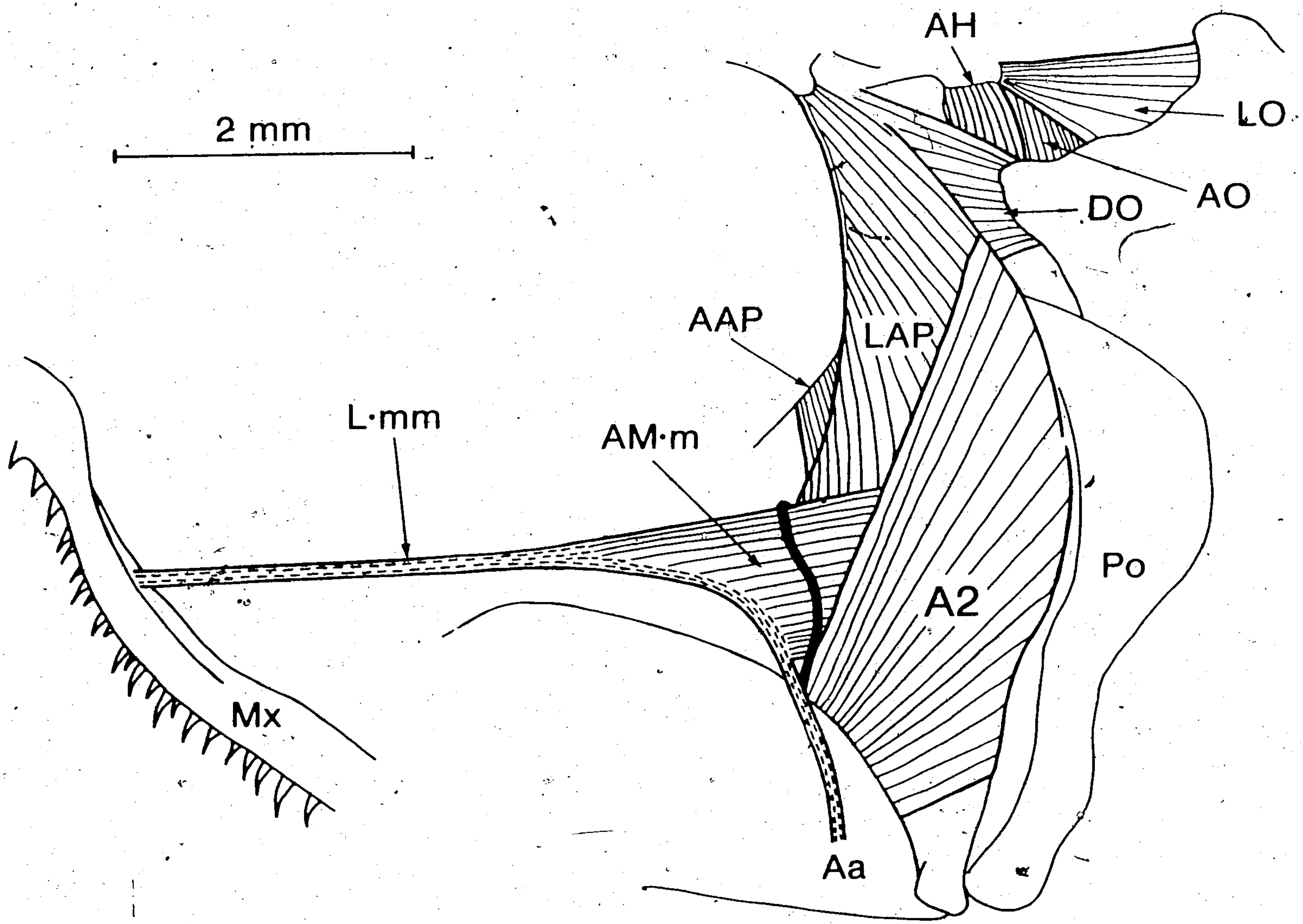

AH
LO
AO
DO
2 mm
AAP
LAP
L·mm
AM·m
A2
Po
Mx
Aa

Figure 94. Hypothesis of the cladistic relationships of the salmoniform fishes (indicated by asterisks) based on evidence from the suspensorium and its muscles. Synapomorphies supporting this phylogeny are discussed in the text, those supporting the holophyly of the Clupeocephala, Clupeomorpha, Euteleostei, Ostariophysi, and Neotoleostei, respectively, are from other sources (e.g., see Lauder and Liem 1983).

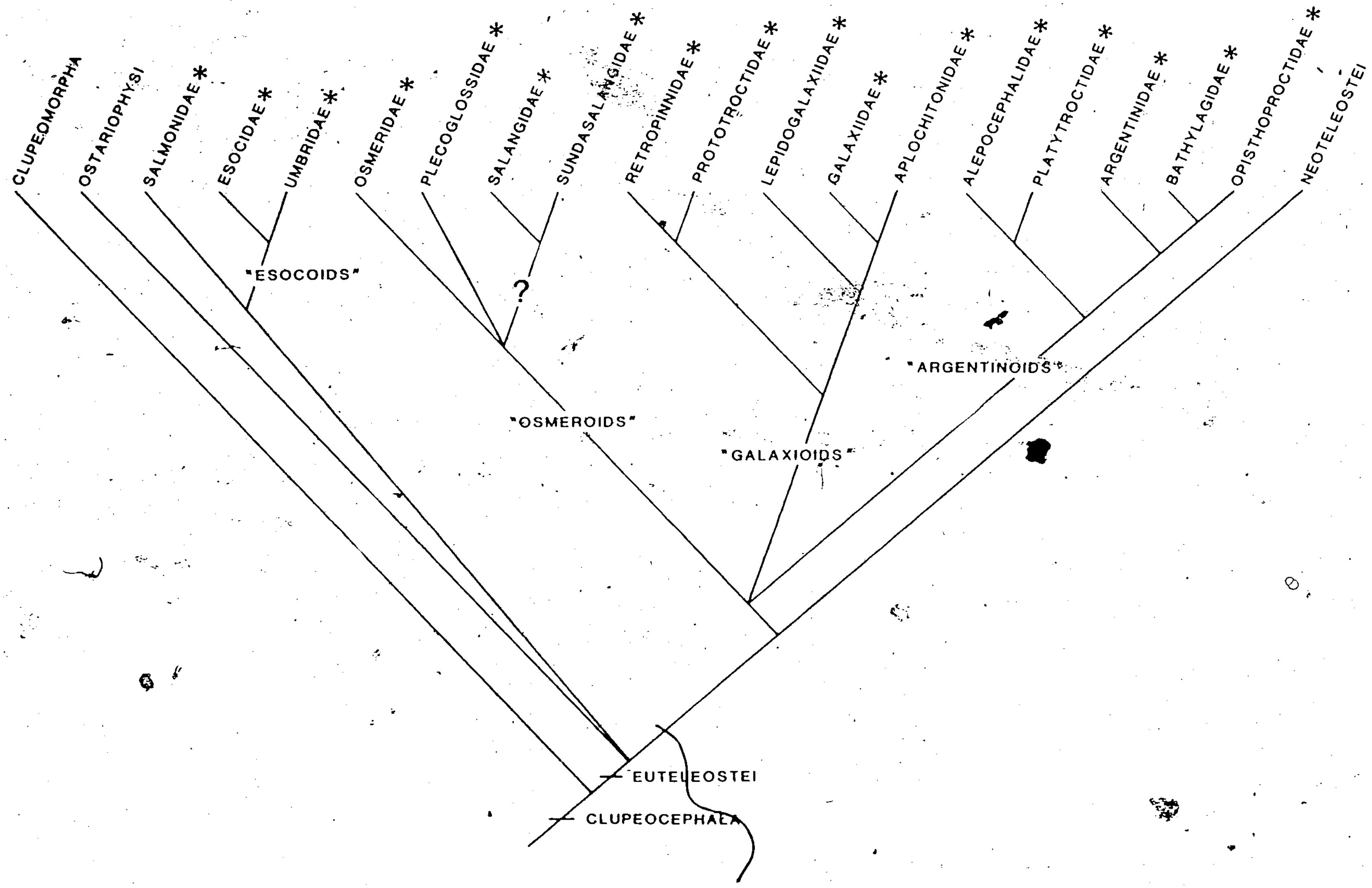

CLUPEOMORPHA
OSTARIOPHYSI
SALMONIDAE *
ESOCIDAE *
UMBRIDAE *
OSMERIDAE *
PLECOGLOSSIDAE *
SALANGIDAE *
SUNDASALANGIDAE *
RETROPINNIDAE *
PROTOTROCTIDAE *
LEPIDOGALAXIIDAE *
GALAXIIDAE *
APLOCHITONIDAE *
ALEPOCEPHALIDAE *
PLATYTROCTIDAE *
ARGENTINIDAE *
BATHYLAGIDAE *
OPISTHOPROCTIDAE *
NEOTELEOSTEI
"ESOCOIDS"
?
"OSMEROIDS"
"GALAXIOIDS"
"ARGENTINOIDS"
EUTELEOSTEI
CLUPEOCEPHALA

Figure 95. Ventral view of the left mesopterygoid and its teeth in *Saurida tumbil* (Synodontidae, Aulopiformes); UAMZ 4046, 155 mm SL.

Figure 96. Preferred hypothesis of the cladistic relationships of *Plecoglossus* and the six osmerid genera based on evidence from the suspensorium and its muscles. Synapomorphies supporting this hypothesis are discussed in the text.

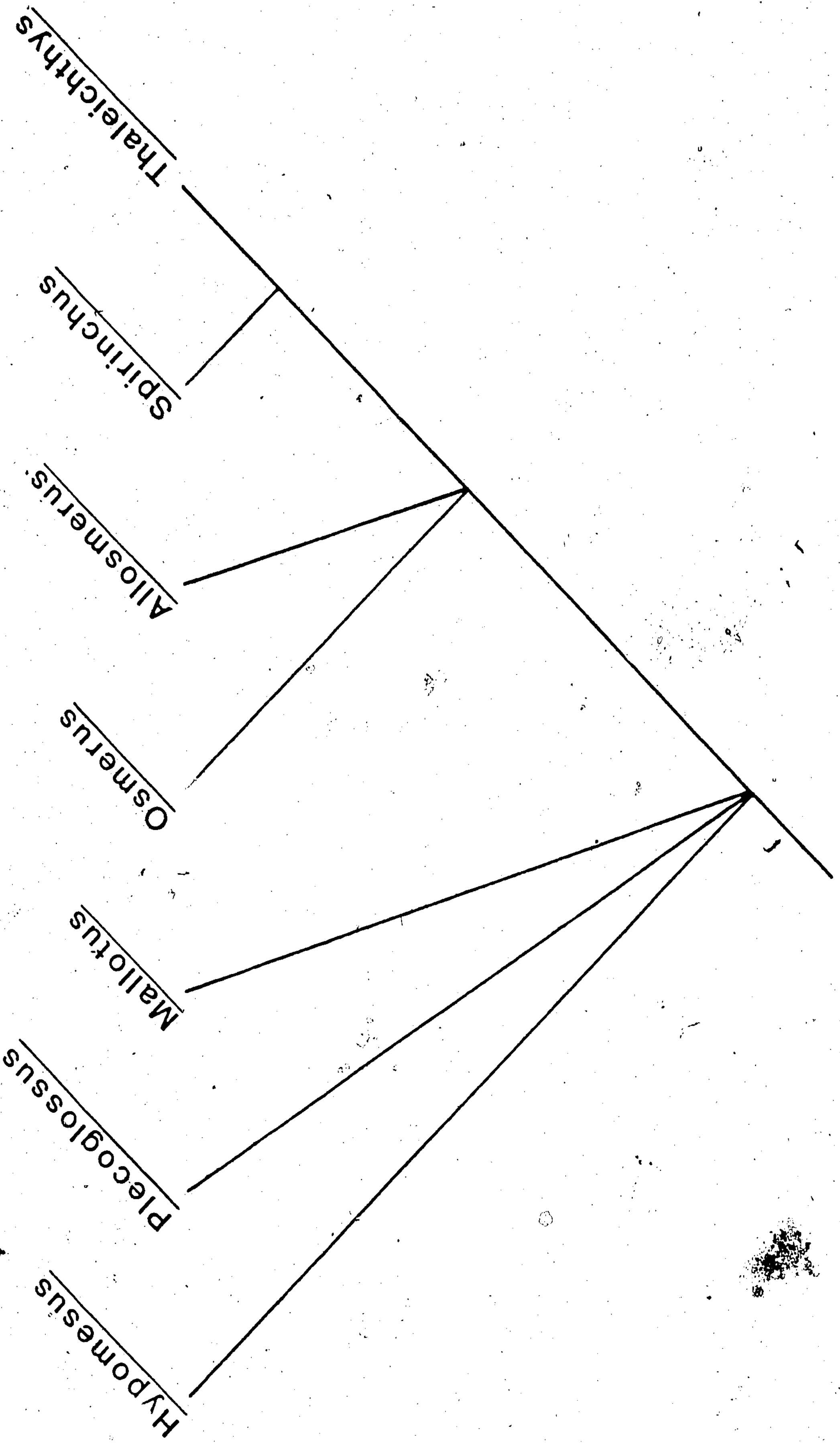

Thaleichthys
Spirinchus
Allosmerus
Osmerus
Mallotus
Plecoglossus
Hypomesus

Figure 97. Morphocline depicting hypothetical pathways of evolutionary change (indicated by arrows) of the ectopterygoid in the galaxioids.

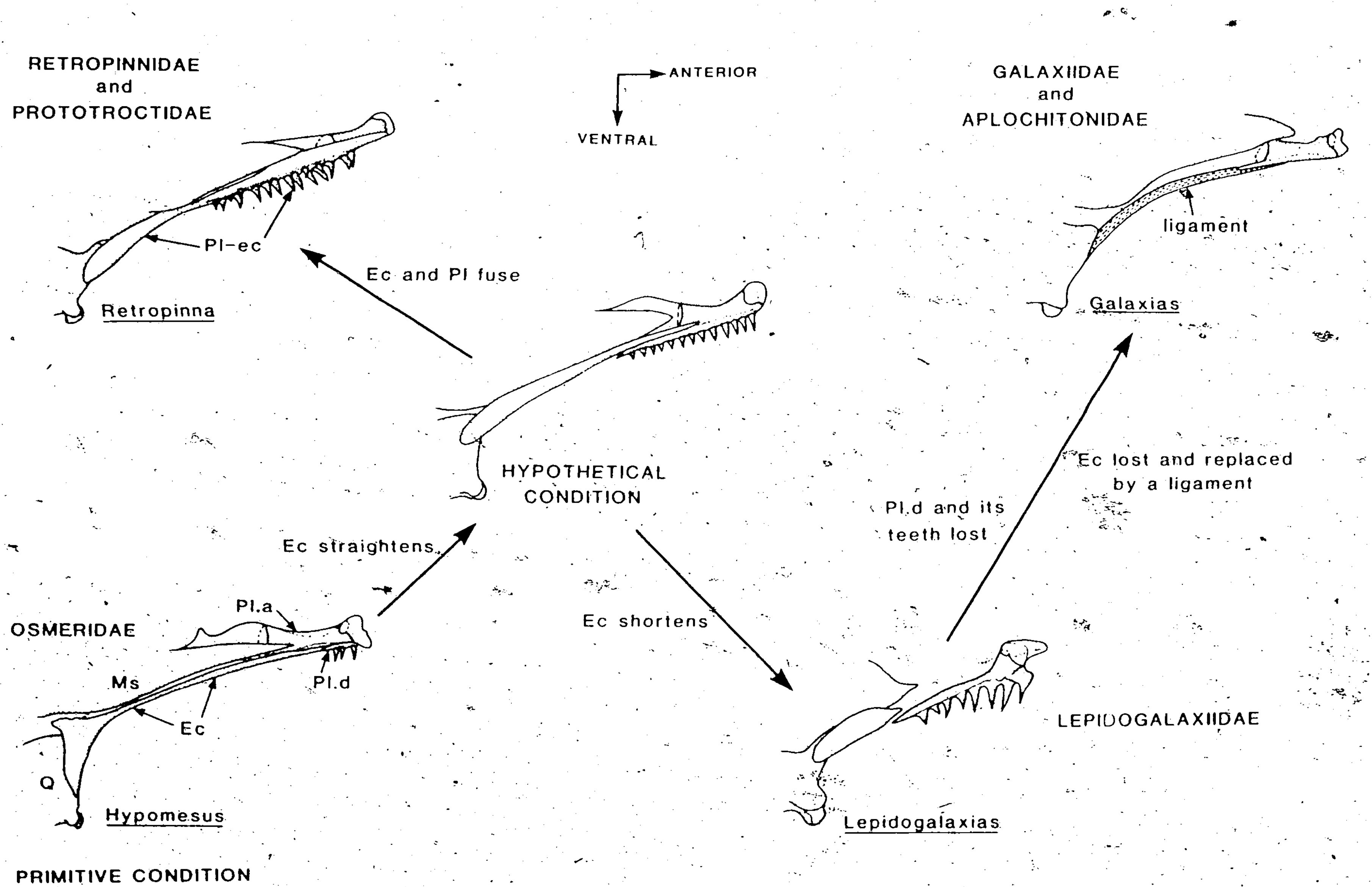

RETROPINNIDAE
and
PROTOTROCTIDAE
Pl-ec
Retropinna
ANTERIOR
VENTRAL
GALAXIIDAE
and
APLOCHITONIDAE
ligament
Galaxias
Ec and Pl fuse
HYPOTHETICAL
CONDITION
Ec lost and replaced
by a ligament
Pl.d and its
teeth lost
Ec straightens
Ec shortens
OSMERIDAE
Pl.a
Ms
Pl.d
Ec
Q
Hypomesus
PRIMITIVE CONDITION
LEPIDOGALAXIIDAE
Lepidogalaxias

Figure 98. Morphocline depicting hypothetical pathways of evolutionary change (indicated by arrows) of the mesopterygoid and its teeth in the galaxioids.

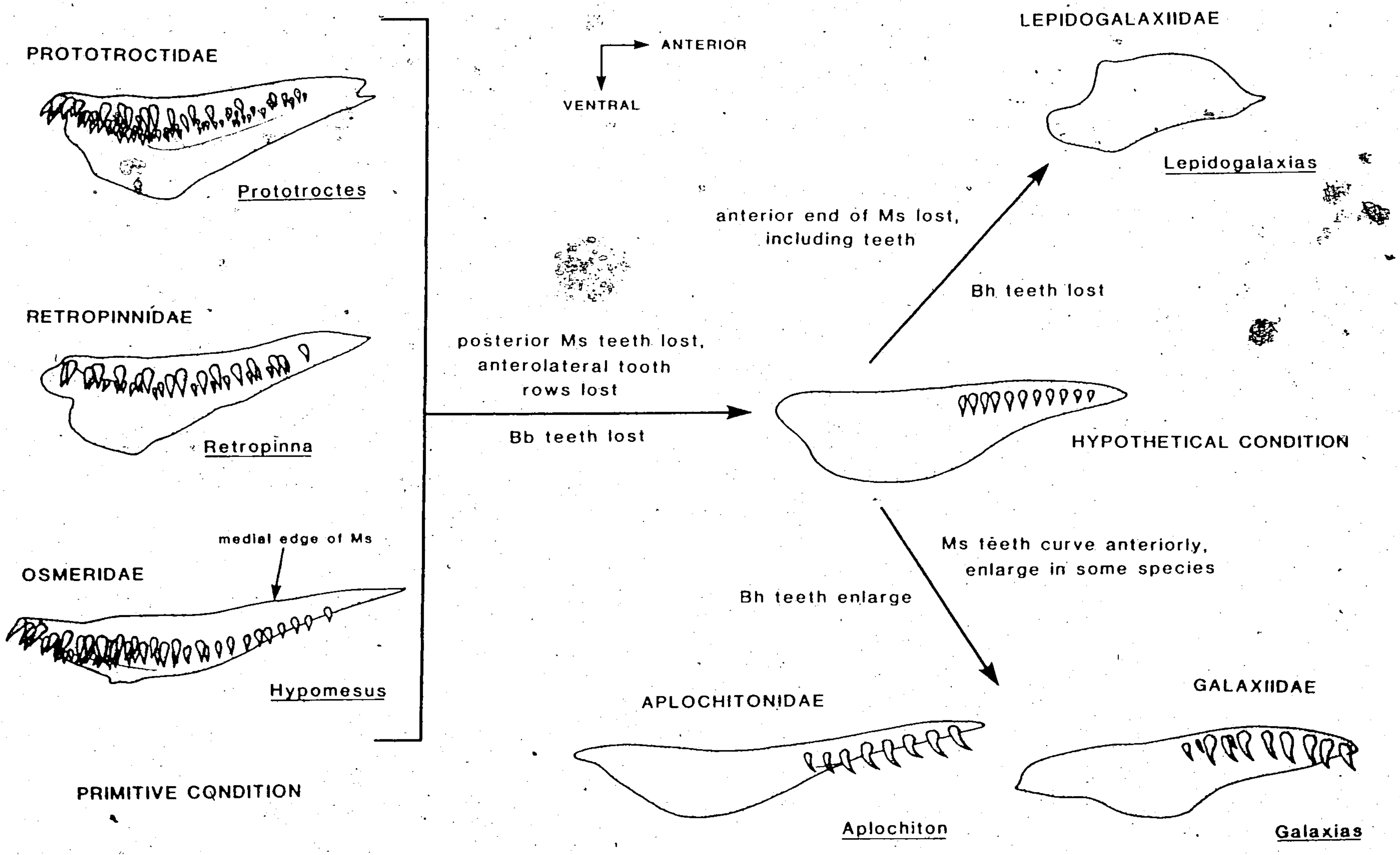

ANTERIOR
VENTRAL
PROTOTROCTIDAE
Prototroctes
RETROPINNIDAE
Retropinna
OSMERIDAE
medial edge of Ms
Hypomesus
PRIMITIVE CONDITION
posterior Ms teeth lost, anterolateral tooth rows lost
Bb teeth lost
HYPOTHETICAL CONDITION
anterior end of Ms lost, including teeth
Bh teeth lost
LEPIDOGALAXIIDAE
Lepidogalaxias
Ms teeth curve anteriorly, enlarge in some species
Bh teeth enlarge
APLOCHITONIDAE
Aplochiton
GALAXIIDAE
Galaxias

Figure 99. Morphocline depicting hypothetical pathways of evolutionary change (indicated by arrows) of the *adductor mandibulae* and its ligaments (=tendons) in the Esocoidei.

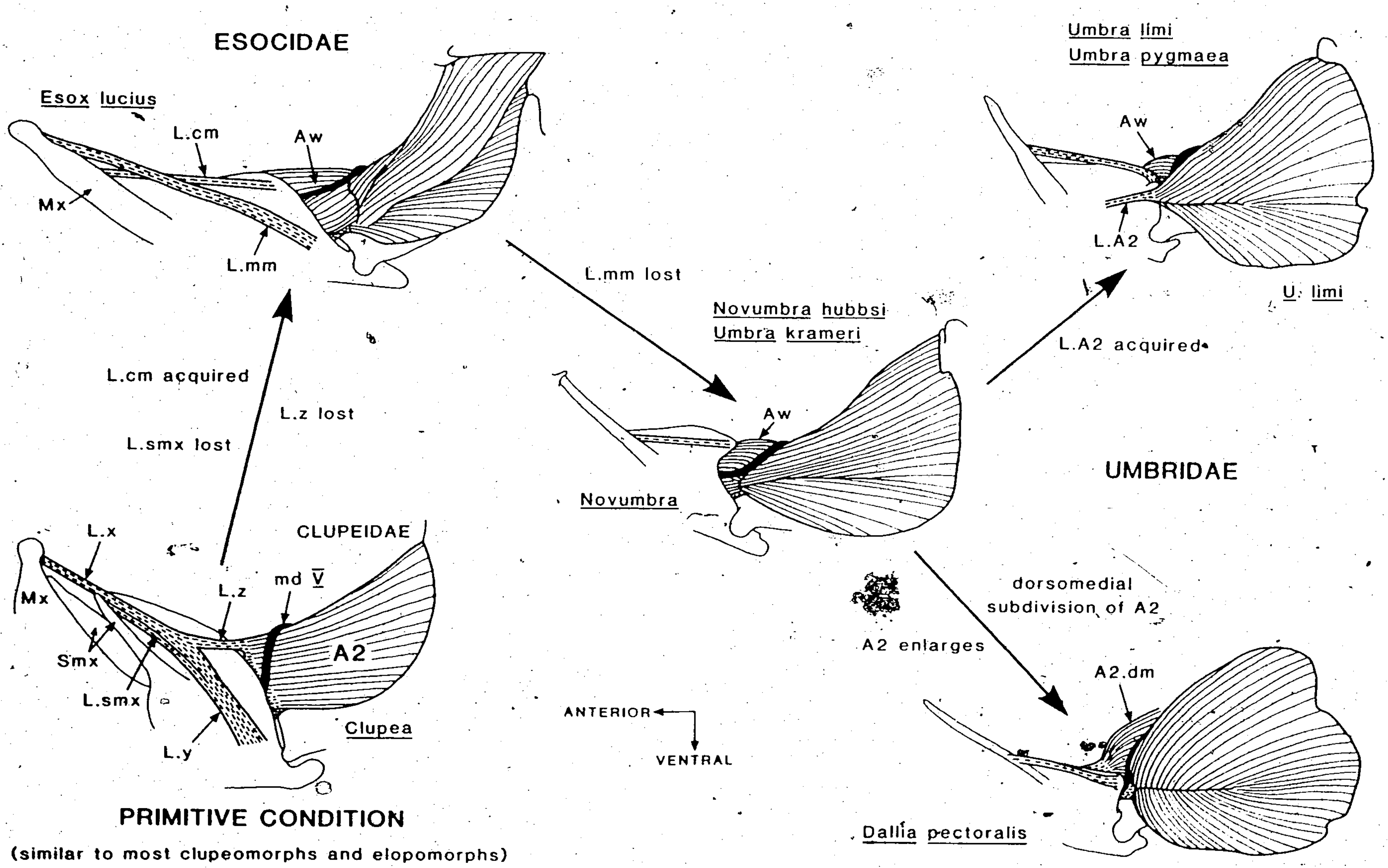

ESOCIDAE
Esox lucius
L.cm
Aw
Mx
L.mm
L.mm lost
Umbra limi
Umbra pygmaea
Aw
L.A2
U. limi
L.A2 acquired
Novumbra hubbsi
Umbra krameri
Aw
Novumbra
UMBRIDAE
L.cm acquired
L.z lost
L.smx lost
CLUPEIDAE
L.x
Mx
L.z
md V
A2
Smx
L.smx
L.y
Clupea
PRIMITIVE CONDITION
(similar to most clupeomorphs and elopomorphs)
ANTERIOR
VENTRAL
dorsomedial
subdivision of A2
A2 enlarges
A2.dm
Dallia pectoralis

Figure 100. Morphocline depicting hypothetical pathways of evolutionary change (indicated by arrows) of the *adductor mandibulae* and its ligaments (=tendons) in the Salmonidae.

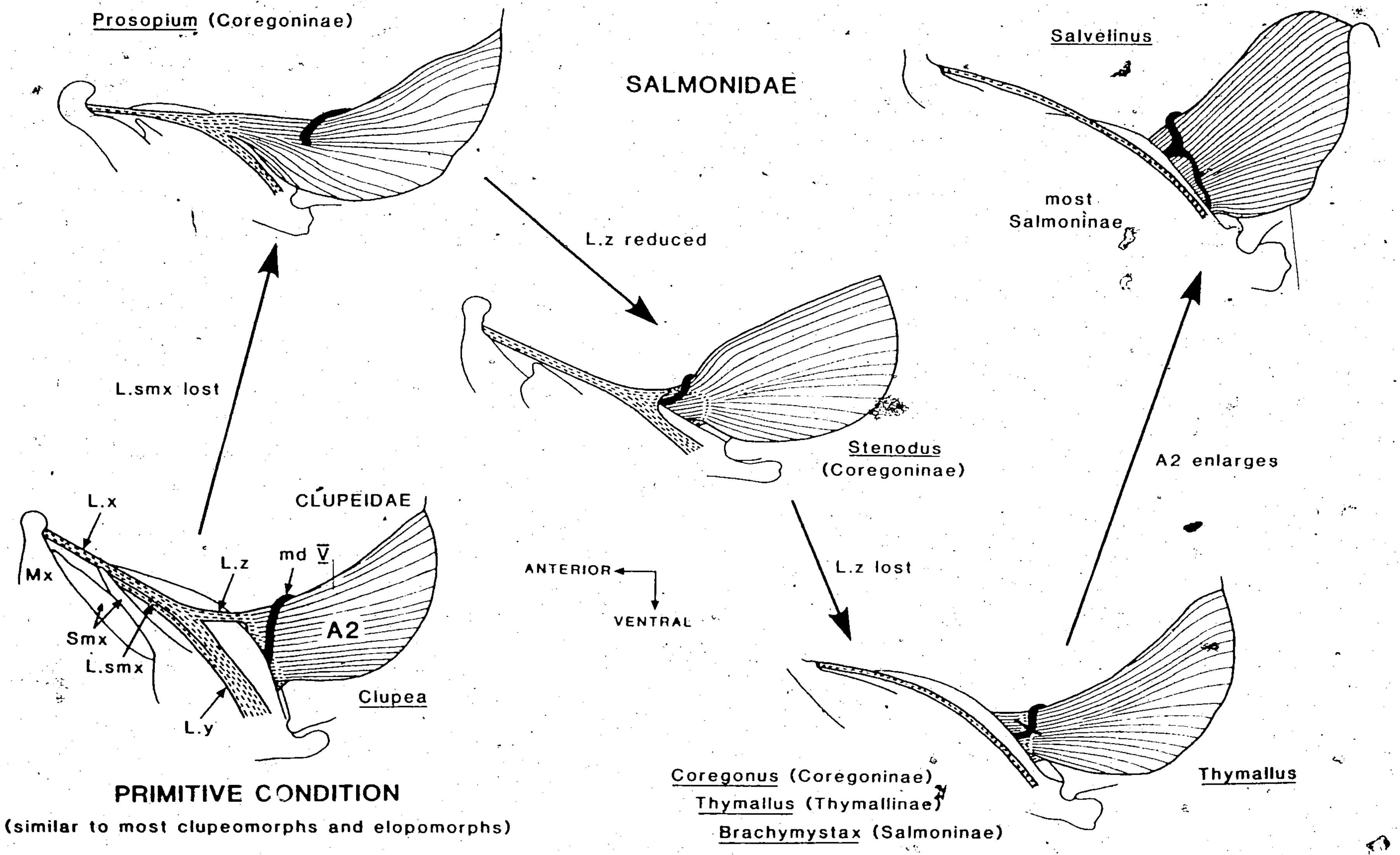

SALMONIDAE
Prosopium (Coregoninae)
Salvelinus
most Salmoninae
L.z reduced
Stenodus (Coregoninae)
L.smx lost
A2 enlarges
L.z lost
ANTERIOR
VENTRAL
CLUPEIDAE
L.x
Mx
Smx
L.smx
L.z
md V
A2
L.y
Clupea
PRIMITIVE CONDITION
(similar to most clupeomorphs and elopomorphs)
Coregonus (Coregoninae)
Thymallus (Thymallinae)
Brachymystax (Salmoninae)
Thymallus

Figure 101. Morphocline depicting hypothetical pathways of evolutionary change (indicated by arrows) of the *adductor mandibulae* and its ligaments (=tendons) in the Esocoidei + Salmonidae.

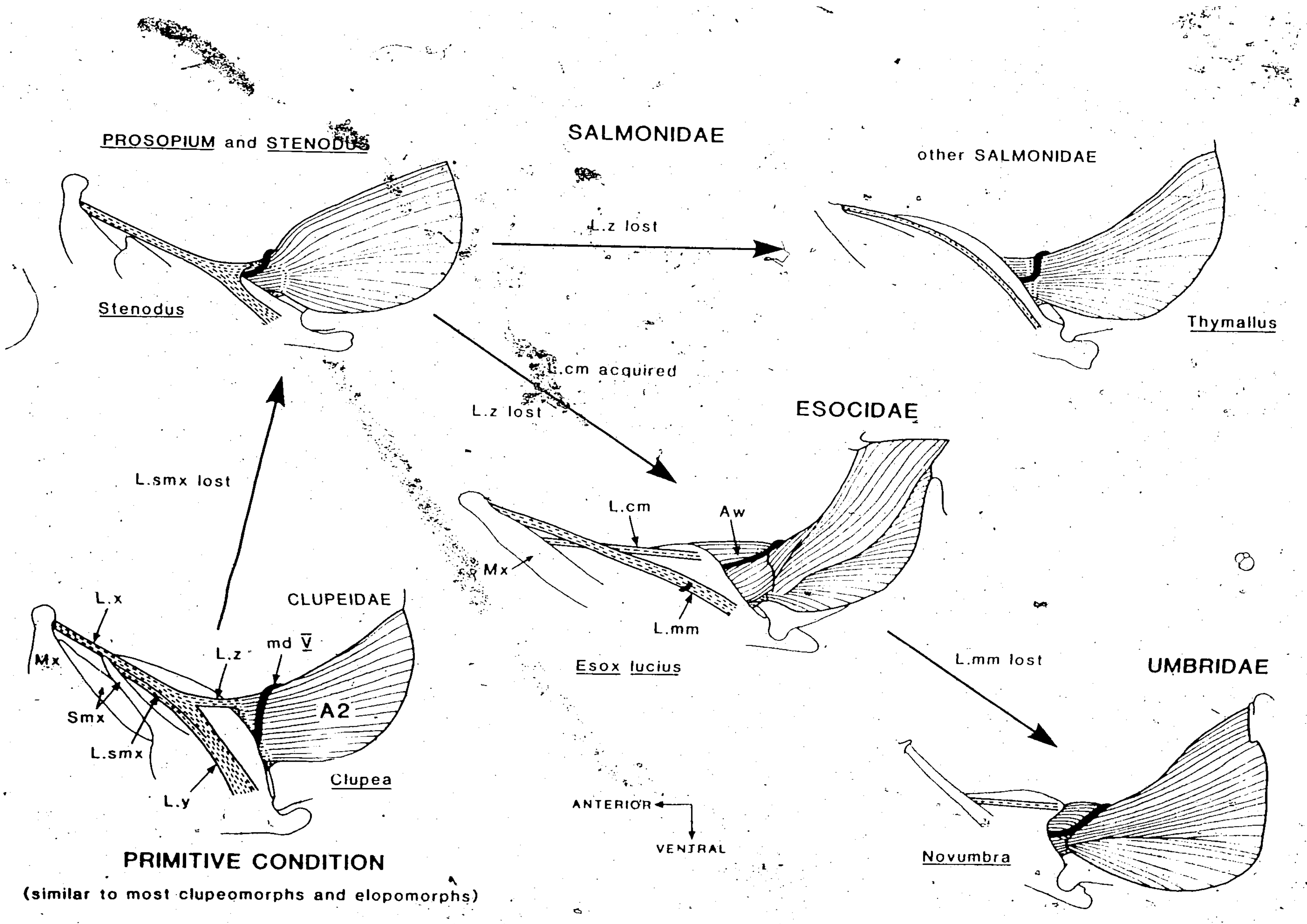

PROSOPIUM and STENODUS
Stenodus
SALMONIDAE
L.z lost
other SALMONIDAE
Thymallus
L.cm acquired
L.z lost
ESOCIDAE
L.cm
Aw
Mx
L.mm
Esox lucius
L.smx lost
L.x
CLUPEIDAE
Mx
L.z
md $\underline{V}$
A2
Smx
L.smx
L.y
Clupea
PRIMITIVE CONDITION
(similar to most clupeomorphs and elopomorphs)
ANTERIOR
VENTRAL
L.mm lost
UMBRIDAE
Novumbra

Figure 102. Morphocline depicting hypothetical pathways of evolutionary change (indicated by arrows) of the *adductor mandibulae* and its ligaments (=tendons) in the osmeroids and galaxioids.

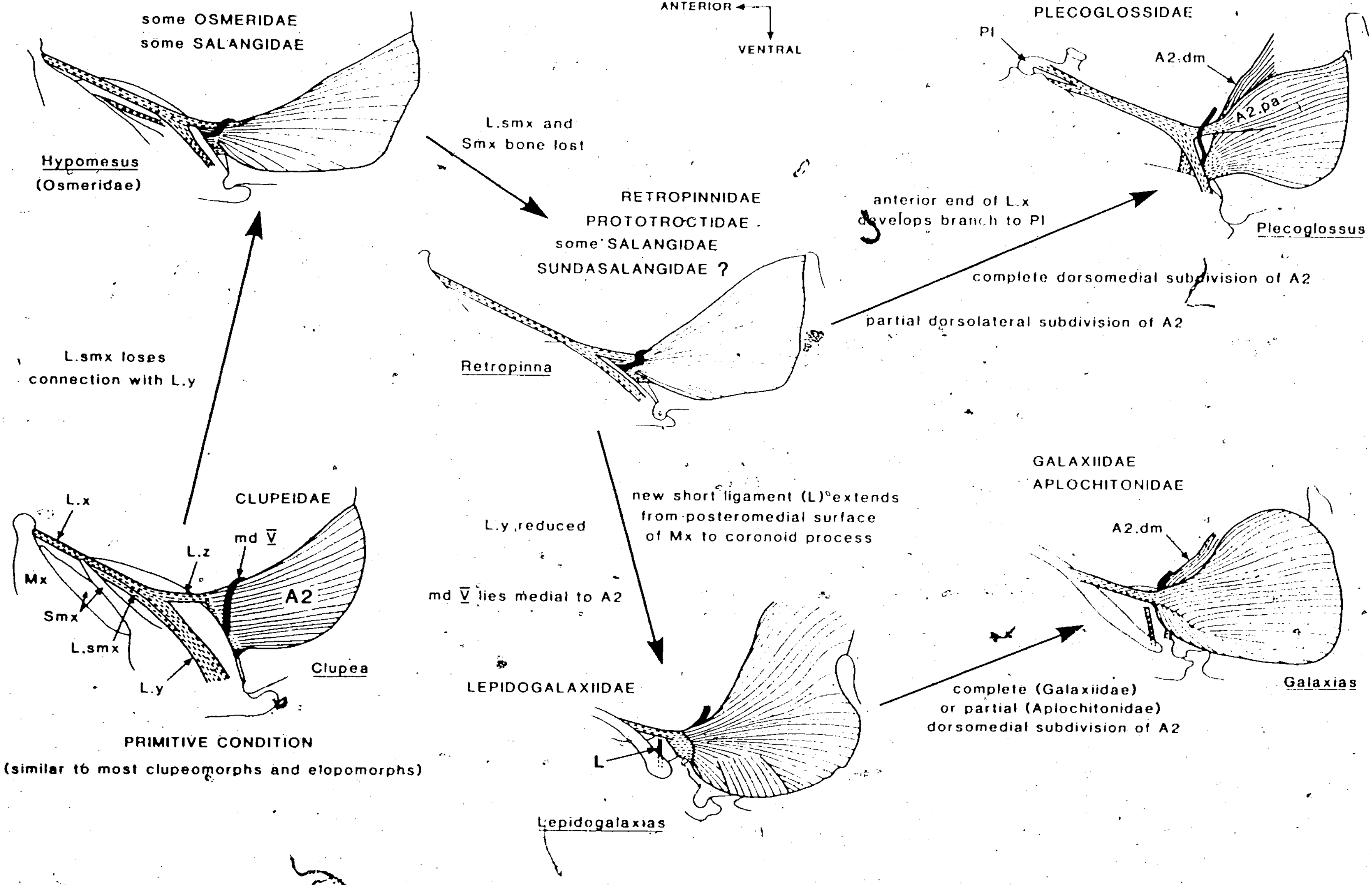

some OSMERIDAE
some SALANGIDAE
Hypomesus
(Osmeridae)
ANTERIOR
VENTRAL
PLECOGLOSSIDAE
Pl
A2.dm
A2.pa
Plecoglossus
L.smx and
Smx bone lost
RETROPINNIDAE
PROTOTROCTIDAE
some SALANGIDAE
SUNDASALANGIDAE ?
Retropinna
anterior end of L.x
develops branch to Pl
complete dorsomedial subdivision of A2
partial dorsolateral subdivision of A2
L.smx loses
connection with L.y
CLUPEIDAE
L.x
Mx
Smx
L.smx
L.y
L.z
md V̄
A2
Clupea
PRIMITIVE CONDITION
(similar to most clupeomorphs and elopomorphs)
L.y reduced
md V̄ lies medial to A2
new short ligament (L) extends
from posteromedial surface
of Mx to coronoid process
LEPIDOGALAXIIDAE
L
Lepidogalaxias
GALAXIIDAE
APLOCHITONIDAE
A2.dm
Galaxias
complete (Galaxiidae)
or partial (Aplochitonidae)
dorsomedial subdivision of A2

Figure 103. Morphocline depicting hypothetical pathways of evolutionary change (indicated by arrows) of the *adductor mandibulae* and its ligaments (=tendons) in the argentinoids.

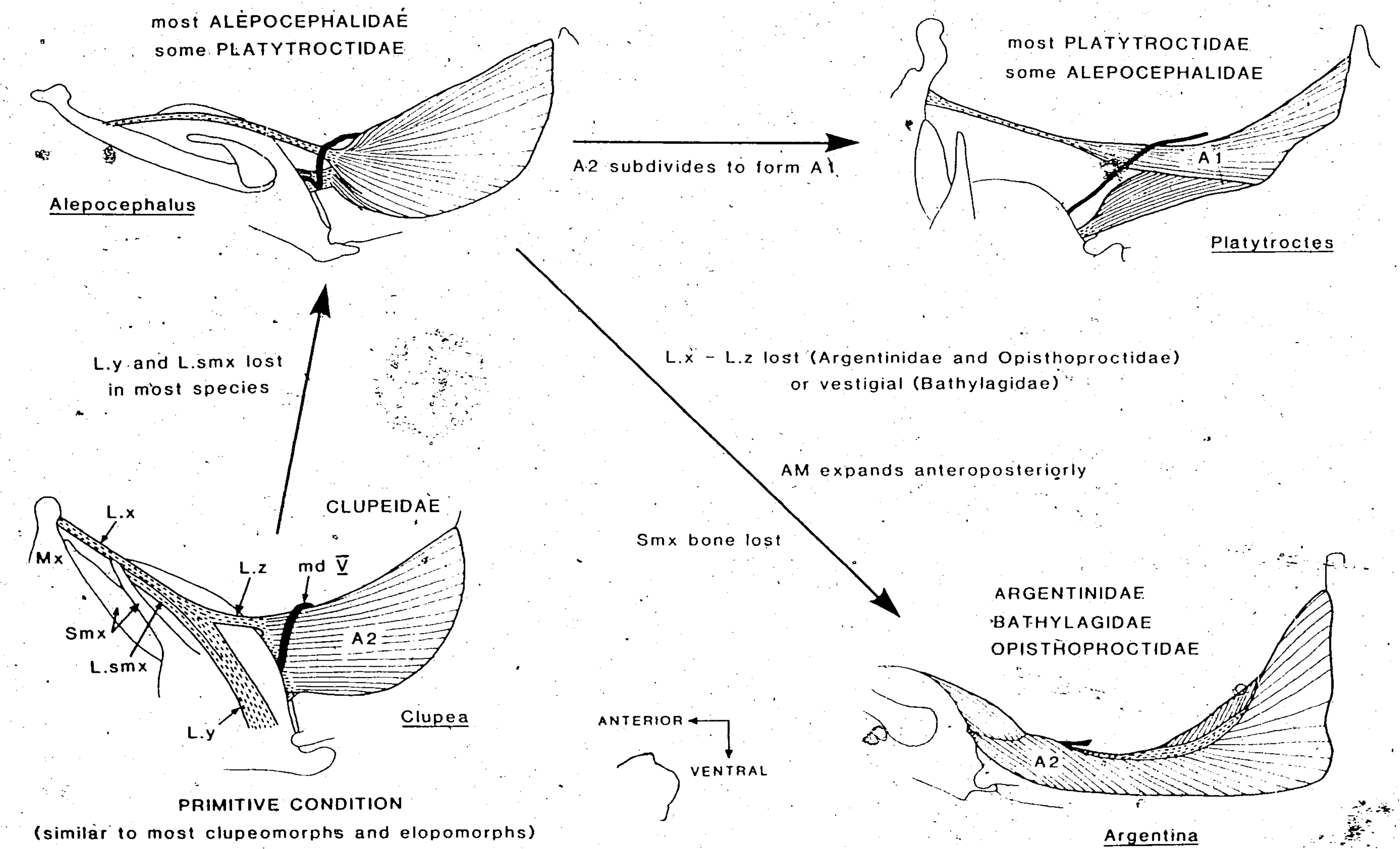
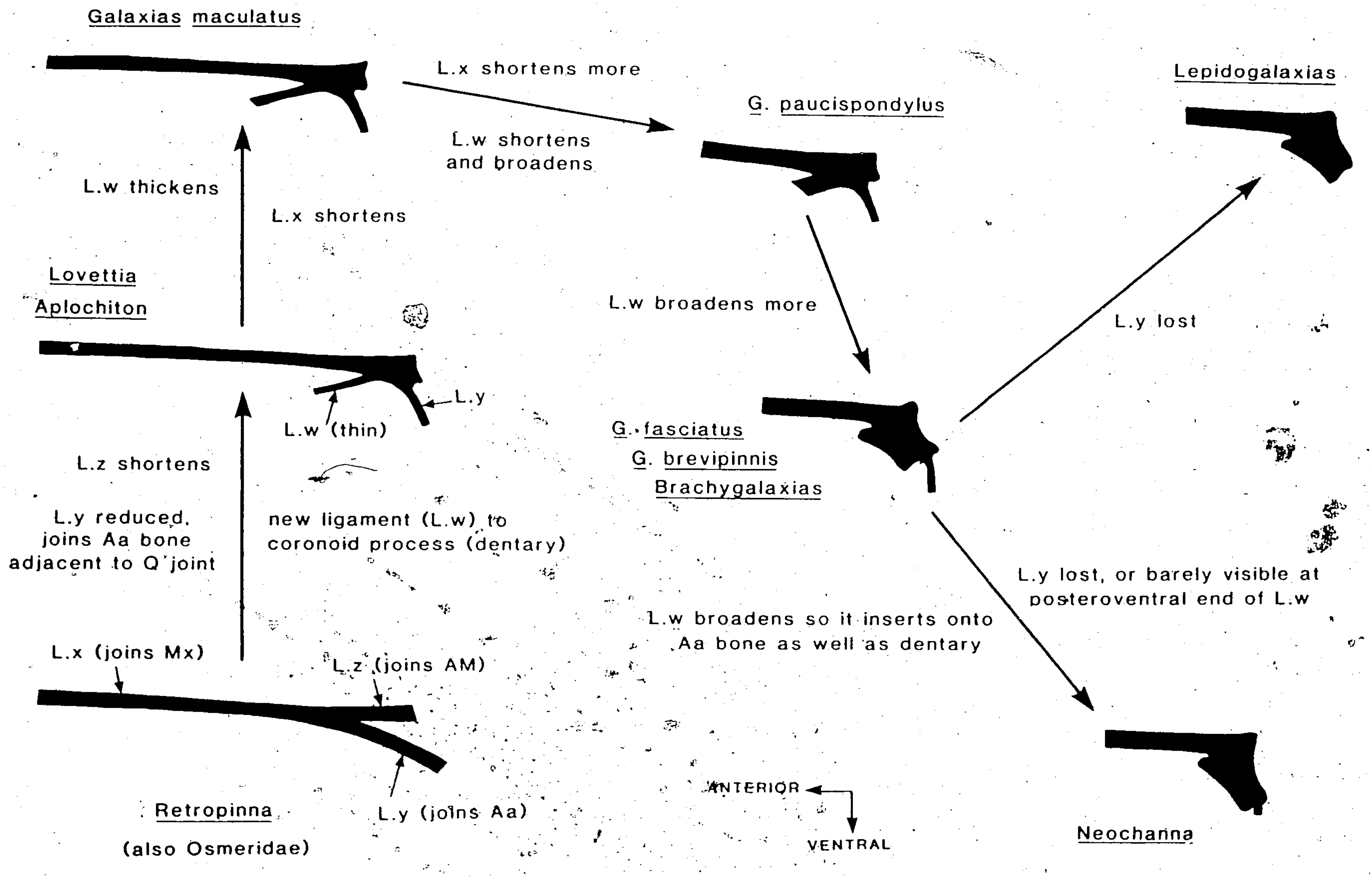

most ALEPOCEPHALIDAE
some PLATYTROCTIDAE
Alepocephalus
A2 subdivides to form A1
most PLATYTROCTIDAE
some ALEPOCEPHALIDAE
A1
Platytroctes
L.y and L.smx lost
in most species
L.x – L.z lost (Argentinidae and Opisthoproctidae)
or vestigial (Bathylagidae)
AM expands anteroposteriorly
Smx bone lost
CLUPEIDAE
L.x
Mx
L.z
md V
A2
Smx
L.smx
L.y
Clupea
PRIMITIVE CONDITION
(similar to most clupeomorphs and elopomorphs)
ANTERIOR
VENTRAL
ARGENTINIDAE
BATHYLAGIDAE
OPISTHOPROCTIDAE
A2
Argentina

Figure 104. Morphocline depicting hypothetical pathways of evolutionary change (indicated by arrows) of the maxilla-mandibular ligament in the galaxioids.


Galaxias maculatus
L.x shortens more
L.w shortens
and broadens
G. paucispondylus
Lepidogalaxias
L.w thickens
L.x shortens
Lovettia
Aplochiton
L.w broadens more
L.y lost
L.y
L.w (thin)
G. fasciatus
G. brevipinnis
Brachygalaxias
L.z shortens
L.y reduced,
joins Aa bone
adjacent to Q joint
new ligament (L.w) to
coronoid process (dentary)
L.y lost, or barely visible at
posteroventral end of L.w
L.w broadens so it inserts onto
Aa bone as well as dentary
L.x (joins Mx)
L.z (joins AM)
Retropinna
(also Osmeridae)
L.y (joins Aa)
ANTERIOR
VENTRAL
Neochanna

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