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DESCRIPTION OF TWO NEW SPECIES OF BASAL PARACANTHOPTERYGIAN FISHES FROM THE PALAEOCENE OF ALBERTA, AND A PHYLOGENETIC ANALYSIS OF THE PERCOPSIFORMS (TELEOSTEI: PARACANTHOPTERYGII)

BY

ALISON M. MURRAY ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1994

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled DESCRIPTION OF TWO NEW SPECIES OF BASAL PARACANTHOPTERYGIAN FISHES FROM THE PALAEOCENE OF ALBERTA, AND A PHYLOGENETIC ANALYSIS OF THE PERCOPSIFORMS (TELEOSTEI: PARACANTHOPTERYGII) submitted by ALISON M. MURRAY in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

Mark V. H. Wilson

Dr. Mark V. H. Wilson
Supervisor

Dr. Joseph S. Nelson
Member, Supervisory Committee

Ruth A Stockey

Dr. Ruth A. Stockey
External Member, Supervisory Committee

4 October, 1994

ABSTRACT

Two new species of Palaeocene fishes from Alberta, collected by the University of Alberta Laboratory for Vertebrate Palaeontology, are described, each in its own new genus. These two new species are classified in the Family Percopsidae (Paracanthopterygii: Percopsiformes) based on their possession of that family's defining characteristic, a dorsal process on the maxilla. Although the Family Percopsidae is considered a natural (monophyletic) group, the Order Percopsiformes was disbanded in the most recent cladistic analysis including the group, as the relationships among these fish were not supported by shared derived characters. In this study, the information provided by the two new species, and other members of the Superorder Paracanthopterygii, was used to reinterpret previously used character states and to supply new character states to perform a cladistic analysis of the basal paracanthopterygians previously classified in the Order Percopsiformes. The results of this phylogenetic analysis are the restoration of the Order Percopsiformes as a monophyletic group after the removal the the Family Amblyopsidae, which is placed within the Anacanthini, tentatively as the sister group to the Order Gadiformes. The Palaeocene genus *†Mcconichthys* Grande is included in the Order Percopsiformes. The Family †Sphenocephalidae is replaced in the basal position as the sister group to the rest of the superorder.

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LIST OF ACRONYMS AND ABBREVIATIONS

† denotes fossil taxa

INSTITUTIONAL ACRONYMS:

BM(NH) - British Museum (Natural History)
CAS - California Academy of Sciences
CMN - Canadian Museum of Nature
FMNH - Field Museum of Natural History
NMC - Canadian Museum of Nature, Ichthyology Collections
NMNH - United States National Museum of Natural History
SU - Stanford University Collections, at CAS
UALVP - University of Alberta Laboratory for Vertebrate Palaeontology
UAMZ - University of Alberta Museum of Zoology

OSTEOLOGICAL ABBREVIATIONS: (terminology of bones follows Rojo, A.L. 1991. *Dictionary of Evolutionary Fish Osteology.* CRC Press Inc., Boca Raton, Florida 273 pp.)

ang	angular
ant	antorbital
boc	basioccipital
brst	branchiostegal ray
ch	ceratohyal (= anterior ceratohyal)
cl	cleithrum
cor	coracoid
den	dentary
ds	dermosphenotic
ect	ectopterygoid
eh	epihyal (= posterior ceratohyal)
end	endopterygoid
ep	epural
epo	epiotic
exoc	exoccipital
fr	frontal
hyo	hyomandibular
hy	hypural
ih	interhyal
lac	lacrimal
le	lateral ethmoid
met	metapterygoid
mx	maxilla
na	nasal
nsp	neural spine
op	opercle
pa	parietal
pal	palatine
par	parapophysis
pcl	postcleithrum
phy	parhypural
pmx	premaxilla
pop	preopercle
pr	pleural rib
psph	parasphenoid
pto	pterotic
ptt	posttemporal
pu	preural centrum
qu	quadrate
ret	retroarticular
sca	scapula
scl	supracleithrum
sn	supraneural
soc	supraoccipital
sop	subopercular
sym	symplectic
u	ural centrum
uh	urohyal
un	uroneural
v	vertebral centrum
vo	vomer (= prevomer of Rojo)

I. GENERAL INTRODUCTION

THE STUDY

Percopsiform fishes have been studied by numerous authors (*e.g.*, Cox, 1905; Gosline, 1963; Rosen, 1962) and also used as outgroups in studies of various acanthopterygian fishes (*e.g.*, Stiassny, 1990); however, the relationships of these fishes have not been satisfactorily determined (Patterson and Rosen, 1989). Various aspects of osteology (Gosline, 1963; Rosen and Patterson, 1969), nerve patterns (Freihofer, 1970), and jaw musculature (Rosen, 1962) have been examined to infer relationships, but no unique advanced characters have been found to support uniting these fish in a single lineage. New information is apparently needed to resolve better the phylogeny of the group.

In cladistic studies, the knowledge of the relative primitiveness and derivedness of character states is necessary to form hypotheses of relationships among members of a group. Basal members of a given group by definition and the nature of cladistic analysis, have fewer shared derived character states (synapomorphies) in common with the other members of the group. Although basal members may have many autapomorphies (derived character states of a single lineage), they do not possess the synapomorphies that unite the higher groups. Interrelationships of basal members are therefore important for knowledge of sequence of acquisition of synapomorphies by the group as a whole. In this study, two new fossil species of basal paracanthopterygians are described and included in the analyses, providing possible sources for new information. The relationships of Recent and fossil percopsiform fishes, the basal members of the Superorder Paracanthopterygii, are investigated using osteological features in cladistic analysis, in an effort to define better the taxa and thus provide a basis for future work on members of the superorder.

Cladograms can be viewed as hypotheses of phylogenetic relationships. The addition of new species to a previously formed framework will test the hypothesis of relationship based on shared derived character states. If the character states of a new species are consistent with the existing scheme of relationships, the validity of the cladogram is supported. If this is not the case, new hypotheses may be formed based on information from the new species regarding either previously unknown character states or new combinations of character states or both. One of the two new species described in this study, that from Joffre Bridge, possesses proposed synapomorphies that were used by Patterson and Rosen (1989) to create their cladogram, but in a combination that does not support their hypothesis of relationships.

SYSTEMATIC HISTORY

Superorder Paracanthopterygii

The Superorder Paracanthopterygii was established by Greenwood *et al.* (1966) in an effort to form more manageable, natural groups than the previous large, all-encompassing group Percomorphi of Regan (1909). Their argument for the Paracanthoptergii was that the included groups are descended from a pre-acanthopterygian radiation. The Paracanthopterygii was considered to represent "a spiny-finned radiation more or less comparable morphologically with that of the Acanthopterygii" (Greenwood *et al* 1966:387). Since the inception of this superorder, there has been some debate over its validity as a monophyletic group, and also over which orders should be included in or excluded from the superorder (*eg*. Rosen, 1985; Fraser, 1972). In fact, Greenwood *et al.* (1966) indicated that the higher taxonomic groups erected by them were not intended to be definitive.

Originally, Greenwood *et al.* (1966) considered the orders Percopsiformes, Gadiformes, Batrachoidiformes, Gobiesociformes and Lophiiformes to be members of the Paracanthopterygii. Rosen and Patterson (1969) revised the superorder, retaining within it the same orders as Greenwood *et al.* (1966) in the new Series Salmopercomorpha, and added the Polymixiiformes in a separate series, Polymixiomorpha. Freihofer (1970) added the Gobiiformes to the superorder, based on nerve patterns, and Banister (1970) added the Indostomiformes. Three years later, Fraser (1972) published a criticism of the whole superorder, removed from it both the Polymixiiformes and Indostomiformes, and suggested that the Suborder Ophidioidei be removed from the Gadiformes, to form a separate lineage of uncertain placement within the superorder.

Rosen (1985) returned to the question of the validity of the Paracanthopterygii, with his statement "Of all the proposals for subdividing the old Acanthopterygii or Percomorpha, none has been more controversial, or, in my present view, ill-fated, than the Paracanthopterygii" (1985:41). Rosen pointed out that some of the paracanthopterygian subgroups cannot be considered natural, and made special reference to the Order Percopsiformes.

Patterson and Rosen (1989), in the most recent revision of the Paracanthopterygii, strove to resolve the question of the validity of this superorder using cladistic methods, in which shared derived characters (synapomorphies) are of sole importance in inferring relationships. The result of their work was to define the Superorder Paracanthopterygii as a natural or valid monophyletic group based on four synapomorphies. Within this superorder, as the more derived members, they included two of the original paracanthopterygian orders, Lophiiformes and Batrachoidiformes, each as a monophyletic group, and a redefined Gadiformes, monophyletic after the removal of both the Bythitoidei and the Ophidioidei (separating the latter into two lineages, families Carapidae and Ophidiidae) from this order. Patterson and Rosen (1989) disbanded the Percopsiformes, in the basal position of their cladogram, into four separate lineages, †*Sphenocephalus* Agassiz, †*Libotonius* Wilson, Percopsidae and Aphredoderoidei (Aphredoderidae plus Amblyopsidae), with †*Sphenocephalus* being more closely related to higher paracanthopterygians than the rest, which form an unresolved polytomy.

The Gobiesociformes, originally included in the superorder, were removed by Gosline (1970). He was of the opinion that the morphological similarities between the Gobiesociformes and the Batrachoidiformes were a result of convergence, and listed five differences between the two orders. Patterson and Rosen (1989) supported this removal and excluded the Gobiesociformes from their review. The placement of this order is still being questioned. Jamieson (1992) provided new evidence from spermatozoa to reunite the Gobiesociformes with the Batrachoidiformes. If inclusion of the gobiesociforms in the Paracanthopterygii is appropriate, they would be placed with the more derived groups of the superorder, and therefore would be less important for this analysis of the percopsiform fishes. The Gobiesociformes have not been included in this study.

The Family Zoarcidae was also originally included in the Paracanthopterygyii in its own suborder (Zoarcoidei) of the Gadiformes (Greenwood *et al.*, 1966). Rosen and Patterson (1969) supported this placement based on jaw musculature similarities between the zoarcids and ophidioids, and the gadoid-like caudal skeleton, described by Yarberry (1965), of one particular zoarcid, *Melanostigma* Günter. Anderson and Hubbs (1981) noted that some of the apparent similarities between the gadoids and *Melanostigma* were in fact misinterpretations of the specimens of *Melanostigma* by Yarberry. Anderson and Hubbs (1981) presented several differences between the zoarcids and ophidiiform-gadiform lineage, and suggested further research is necessary before the correct placement of the Zoarcidae is known. Anderson (1984) suggested this family may be more appropriately placed in the Superfamily Zoarceoidae within the perciform Suborder Blennioidei. Patterson and Rosen (1989) found no characters of the dorsal gill arches to support inclusion of the zoarcids within the Paracanthopterygii, and they also left this group out of the superorder. Because of this removal, zoarcids have not been included in this study.

†Omosomopsis Gaudant, *†Aipichthys* Steindachner and *†Aipichthyoides* Gayet, all Cretaceous genera added to the Paracanthopterygii by Gayet (Gaudant, 1978, 1979;

Gayet, 1980), were excluded from the superorder by Patterson and Rosen (1989), the latter two genera following from the removal of the polymixiiforms, and *†Omosomopsis* based on a reexamination of the holotype. These three genera have not been included in the cladistic analyses of the present study.

The order Indostomiformes, added to the Paracanthopterygii by Banister (1970), contains the single genus *Indostomus* Prashad and Mukerji, which "...shows some affinities with the Batrachoidiform-Gobiesociform lineage..." (1970:204). Fraser (1972) felt that *Indostomus* should be left *incertae sedis*, as "Banister's arguments...for withdrawal [from the Gasterosteiformes] to another order are not compelling." Although Patterson and Rosen (1989) refered to Fraser's (1972) removal of *Indostomus* from the Paracanthoptergyii (1989: tab. 2), it was not included with the two deletions considered valid by these authors (1989:13); however, they did not mention the genus again and omitted it from their cladogram. More recently, Johnson and Patterson (1993) returned *Indostomus* to the Gasterosteiformes based on modifications of the gill filaments. *Indostomus* has not been included in this study of the Paracanthopterygii.

The gobioid fishes were given ordinal status (Order Gobiiformes) and added to the Paracanthopterygii, "with closest relationships to the Percopsiformes..." by Freihofer (1970:254) based on evidence of nerve patterns. Fraser's (1972) criticism of the superorder included the comment "wholesale transfer of a large, diverse group into another conceptual framework based on admittedly preliminary information ... is a weak practice" in referrence to Freihofer's (1970) placement of the Gobiiformes.

Patterson and Rosen (1989) cited Freihofer's (1970) addition of the Gobiiformes, but not Fraser's (1972) objections to it; however, they also left this group out of their analyses. In the present study, the Gobiiformes will not be included because of the uncertainty of their relationships.

Throughout the history of the Paracanthopterygii, the percopsiform fishes have been retained within the superorder in one form or another, although there has been much disagreement on the relationships among these fish, and also on their relationships with the rest of the groups comprising the superorder. The percopsiforms have usually been placed at or near the basal position of the Paracanthopterygii (Gosline, 1971; Jamieson, 1992; Nelson, 1984; Rosen and Patterson, 1969) and they are thus an important group to shed light on the acquisition of characters evolving in higher members of the superorder. A better understanding of these fish is therefore important for a better understanding of the superorder as a whole and the relationships of the groups contained within it.

The Percopsiform Fishes

The most recent article including a cladistic analysis of percopsiform fishes (Patterson and Rosen, 1989) disbanded the Order Percopsiformes based on its presumed paraphyletic nature. Because of this, the term "percopsiform" will be avoided for now, and the basal paracanthopterygians will be referred to by familial or generic names. These families are: Family Amblyopsidae (the extant genera *Amblyopsis* DeKay, *Chologaster* Agassiz, *Typhlichthys* Girard and *Speoplatyrhinus*

Cooper and Kuehne) Family Aphredoderidae (the extant genus *Aphredoderus* Lesueur and the Eocene genus *†Trichophanes* Cope), Family Percopsidae (the extant *Percopsis* Agassiz, and the Eocene genera *†Amphiplaga* Cope and *†Erismatopterus* Cope) and the Eocene genus *†Libotonius* Wilson in its own Family Libotoniidae. Other fossil genera such as *†Asineops* Cope, *†Sphenocephalus,* and *†Omosomopsis* have been variously included with or excluded from the percopsiforms by different authors. These fish will also be referred to by familial or generic name.

One of the first attempts at grouping some of these fish was that of Regan (1909). He grouped *Percopsis, Columbia* Eigenmann and Eigenmann and *Aphredoderus*, each a monotypic genus, together in the Order Salmopercae. *Columbia* was synonomized with *Percopsis* by Bailey *et al.* (1960) with no reason given, and later authors have followed this, so there are now two recognized species in the genus *Percopsis*. *Percopsis* and *Aphredoderus* were each classified in their own family by Regan (1911), the Percopsidae and Aphredoderidae respectively. Regan (1911:294) further alluded to the relationships of these two families by stating that these fish show resemblances to the Berycomorphi, Iniomi and Microcyprini (= Cyprinodontidae and Amblyopsidae).

Hay (1929), in his work on fossil vertebrates, related four fossil genera to the percopsids and aphredoderids. These were *†Erismatopterus* and *†Amphiplaga*, in their own family †Erismatopteridae, *†Asineops* alone in the family †Asineopidae, and *†Tricophanes* in its own subfamily, †Trichophaninae, of the Family Aphredoderidae, all of them grouped together under the newly named Order Percopsomorphi. Hay stated no reason for changing to this new ordinal name, nor for reducing Regan's Order Salmopercae to the level of family. However, he did cite Regan (1911) incorrectly as having put his listed genera (*Percopsis, Columbia* and *Aphredoderus*) in the Family Salmopercae.

While several of the percopsids and aphredoderids were classified together from the early days of their recognition, other genera caused more difficulty to early authors. In particular, the Amblyopsidae have at various times been aligned with the cyprinodontoid fishes (*eg*. Gosline, 1963). The amblyopsids were reclassified by Rosen (1962) in their own order, Amblyopsiformes, adjoining the Order Percopsiformes (percopsids and aphredoderids). In his 1985 paper, Rosen united the Amblyopsidae with the Aphredoderidae (Suborder Aphredoderoidei of Patterson and Rosen, 1989), but found no unique or derived character to unite this taxon with the Percopsidae.

THE USE OF FOSSILS IN PHYLOGENETIC RECONSTRUCTION

Patterson (1981:219) states "... a fossil cannot be legitimately interpreted until assigned to a Recent monophyletic group ..." and "When contradictions do come from fossils, they may reverse decisions on homology or polarity." He endorsed the idea that phylogenies should be made using Recent taxa, and that fossils can then be used to test hypotheses of relationship, or to determine the order in which derived characters are acquired. Although there is some merit in arguments against the use of fossils for phylogenetic reconstruction, such as the incompleteness of fossil specimens, to ignore fossils until a phylogeny based on Recent species has been made would be to ignore any information provided by those fossils.

Wilson and Williams (1993), while agreeing with many of Patterson's conclusions, disagreed with several of Patterson's objections about the use of fossils in the reconstruction of phylogenies. They cited examples of some North American freshwater fishes for which the fossil record has been important in phylogenetic reconstructions. Other authors (*e.g.*, Gauthier *et al.*, 1988; Grande, 1985) have also supported the use of fossil taxa in reconstructing phylogenies.

In this study, fossils are found to be most important for providing new information on character states. New species of animals, whether Recent or fossil, may provide states of characters, or different combinations of character states, that are not present in other members of the group (Wilson, 1992; Wilson and Williams, 1993). An example of this is the new Palaeocene species from Joffre Bridge, which has a dorsal process on the maxilla, considered advanced (Rosen and Patterson, 1969), and therefore presumably indicative of relationship with the Percopsidae, and a foreshortened second centrum, which aligns the new species with the higher paracanthopterygians (Patterson and Rosen, 1989: fig. 16). Both interpretations cannot be correct. If data from fossil groups are ignored and phylogenies are based only on Recent taxa, as proposed by Patterson (1981), valuable information may be lost, as indicated by the character state combinations of the new species from Joffre Bridge. For this reason, the many fossil representatives of the superorder were included in the analyses. Characters which were not evident on the fossil specimens were coded as missing data.

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II. MATERIALS AND METHODS

PREPARATION OF SPECIMENS

Osteology of Recent specimens was examined using several methods. X-rays of some specimens were provided by the California Academy of Sciences. Two skeletal specimens were prepared at the University of Alberta Museum of Zoology using dermestid beetles to remove flesh while keeping the bones articulated. Most Recent specimens were cleared and stained for bone and cartilage. Staining specimens with alcian blue for cartilage and alizarin red for bone, and clearing the flesh with trypsin followed the revised procedure of Taylor and Van Dyke (1985), leaving out their optional steps of degreasing and guanine removal. Some specimens had been previously stained for bone only and were not restained for cartilage.

Most of the fossil specimens consist of preserved bone in a rock matrix. These specimens were prepared by hand using fine needles to remove the matrix from around the bone. Other specimens are preserved as natural molds in the matrix, with no bone remaining. These were examined directly, and in some cases by latex peels prepared by the University of Alberta Laboratory for Vertebrate Paleontology.

Specimens were examined and, where necessary, partially dissected, using an Olympus dissecting microscope. Drawings were made using a Wild camera lucida attachment on a Wild M5 dissecting microscope. Measurements of specimens were made with KAR vernier callipers. The measurements were read in a straight line from point to point, following the standards of Hubbs and Lagler (1958). Head lengths exclude the opercular membrane. Measurements were made to the nearest tenth of a millimetre. Osteological nomenclature follows Rojo (1991) with the exception of the term "prevomer" which is replaced here with the term "vomer" following the common use in papers relating to the paracanthopterygians. The term "angular" is used, following Rojo (1991), although this bone might be more correctly referred to by the term "anguloarticular".

PHYLOGENETIC RECONSTRUCTION

Cladistic analysis

To reconstruct the phylogeny of the basal paracanthoptergyians, cladistic analysis was used. The purpose of cladistics is to find shared derived states of characters (synapomorphies) to justify forming groups. Groups of organisms united by synapomorphies are considered to be related through a common ancestor that possessed that character state. Groups united by a common ancestor, and including all the descendents from that ancester, are termed monophyletic (*sensu* Mayden and Wiley, 1992), and are considered natural groupings of a single lineage. For the purpose of this study, the term character will be used for a feature of an organism (*e.g.*, premaxilla) and the term character state will be used for one of two or more alternative conditions for the character (*e.g.*, premaxilla with postmaxillary process). Primitive or plesiomorphic states are those that arose earlier in the ancestry of the group, and states acquired later are derived or apomorphic, having evolved from the primitive states.

There are three methods for determining which character state is primitive and which derived, to define the polarity of character states. One of these methods, study of ontogeny, requires a series of specimens to establish the order in which character states are first acquired in the development of an organism. Because such developmental series were not available to me, and also because of the large numbers of fossil taxa in this study, the ontogenetic method was not used.

The other two methods to determine polarity are stratigraphic (palaeontological) and outgroup comparison. The stratigraphic method uses older fossil species to determine polarity of character states. Species that diverged earlier in the evolution of their lineage tend to have more primitive character states than later species, but these primitive forms are often lost through extinction (Wilson, 1992); therefore older extinct species tend to be more primitive than Recent species.

While there are objections to the use of fossils to determine polarity, because a fossil species is not necessarily more primitive than a living species (*e.g.*, Schaeffer *et al.*, 1972), in this study the oldest fossils date to Late Cretaceous marine deposits, about 100 mya, with a gap of about 40 my before the next oldest fossils in freshwater Palaeocene deposits. The relative age of the fossil species of paracanthopterygians was not used by Patterson and Rosen (1989), who placed the oldest known fossils (Cretaceous *†Sphenocephalus*) in a more derived position than younger fossil species and the extant percopsids, aphredoderids and amblyopsids. Although geological age has been shown to be correlated with primitiveness (Wilson, 1992), the stratigraphic method will not be used to polarize characters in this study because of the controversy surrounding this method. Instead, the relative ages of the fossil specimens will be considered after the phylogeny has been made, as a test of the possible validity of the hypothesised relationships.

The third method, outgroup comparison, will be used to resolve questions of character state polarity. When using the outgroup comparison method, one starts with a group presumed to be monophyletic on the basis of previous work. This group is termed the ingroup, and its members are the ones whose relationships are to be studied. In this case, as the percopsiforms have uncertain interrelationships, the encompassing group, the Superorder Paracanthopterygii, believed to be monophyletic based on four synapomorphies (Patterson and Rosen, 1989), can be considered the ingroup. Character states of the ingroup are compared to the states in several outgroups. The taxa of both the ingroup and outgroups are united in subgroups based on shared character states. After the taxa have been united, polarity of the character states can be determined. If one of the states in the ingroup is unique, it is considered derived.

In some cases, the polarity of states of one character will indicate a relationship that is not consistent with the polarity of a second character's states. For example, as stated above, the foreshortened second centrum used as a synapomorphy by Patterson and Rosen (1989) is present in the new species from Joffre Bridge, and links it with †*Sphenocephalus* and the Anacanthini within the Paracanthopterygii. However, the new species from Joffre Bridge also has a dorsal process on the maxilla, which is considered derived for the Percopsidae (Rosen and Patterson, 1969). In a situation such as this, if both character states are derived, only one of them can be indicative of the correct placement of the new species from Joffre Bridge; therefore, the other derived character state must have been independantly acquired (*i.e.*, be homoplastic) in both the Joffre Bridge species and the clade for which it is autapomorphous (an autapomorphy is a derived character state defining a single lineage). The character state which is considered indicative of relationship, and not the result of homoplasy, is determined using parsimony. Parsimony, as it relates to cladistics, is interpreted as the fewest possible changes in the states of all characters in all taxa in the cladogram. The number of character state changes in a cladogram is expressed as the tree length. The most parsimonious cladogram is the one with the fewest instances of independantly derived character states or homoplasy.

Character states can in theory be weighted according to the likelihood of homoplasy. Character states that are complex are theoretically less likely to evolve many times, and therefore are given a high weight. Simple character states are given less weight, and loss or reduction character states are often given the least weight as theoretically these are often considered to be most prone to homoplasy. It is considered unlikely that a complex character once lost will be reacquired (Mayr and Ashlock, 1991).

Several computer programmes are available for phylogenetic reconstruction. For this study, two programmes were used, Phylogenetic Analysis Using Parsimony (P.A.U.P.) 3.1 (Swofford, 1993), to find the shortest trees using the branch and bound method, and MacClade 3.04 (Maddison and Maddison, 1994), for entering data, to create figures for the trees generated by P.A.U.P, and for manual manipulations of the trees to aid understanding of alternatives.

GENERA IN STUDY

Ingroups

The basal paracanthopterygians include the Recent genera *Amblyopsis, Aphredoderus, Chologaster, Percopsis, Speoplatyrhinus* and *Typhlichthys*, and the fossil genera *†Amphiplaga, †Erismatopterus, †Libotonius* and *†Trichophanes. Speoplatyrhinus* was originally described in the Amblyopsidae (Cooper and Kuehne, 1974) but its osteology is not known and no specimens were available. This genus is excluded from the analyses. The two new Palaeocene species are also basal paracanthoptergyians and are included in the analyses. Because the percopsiform fishes are considered paraphyletic (Patterson and Rosen, 1989) several other groups within the Superorder Paracanthopterygii will be included in the analyses for comparisons. Following Patterson and Rosen (1989, fig. 16) and the cladogram in Fig. II-1, *†Sphenocephalus*, and the recently described related genera, *†Xenyllion* (Wilson and Murray, in press), and a representative genus of the Ophidiidae will be included in the study. The ophidiids are proposed to be basal anacanthines (Patterson and Rosen, 1989: fig.16), and closest to the percopsiforms within the Paracanthopterygii. Unfortunately, no representatives of the Carapidae or Bythitoidea were available for this study. The Order Gadiformes has at times been given sister group relationship with the percopsiforms (*e.g.*, Lauder and Liem, 1983:150). For this

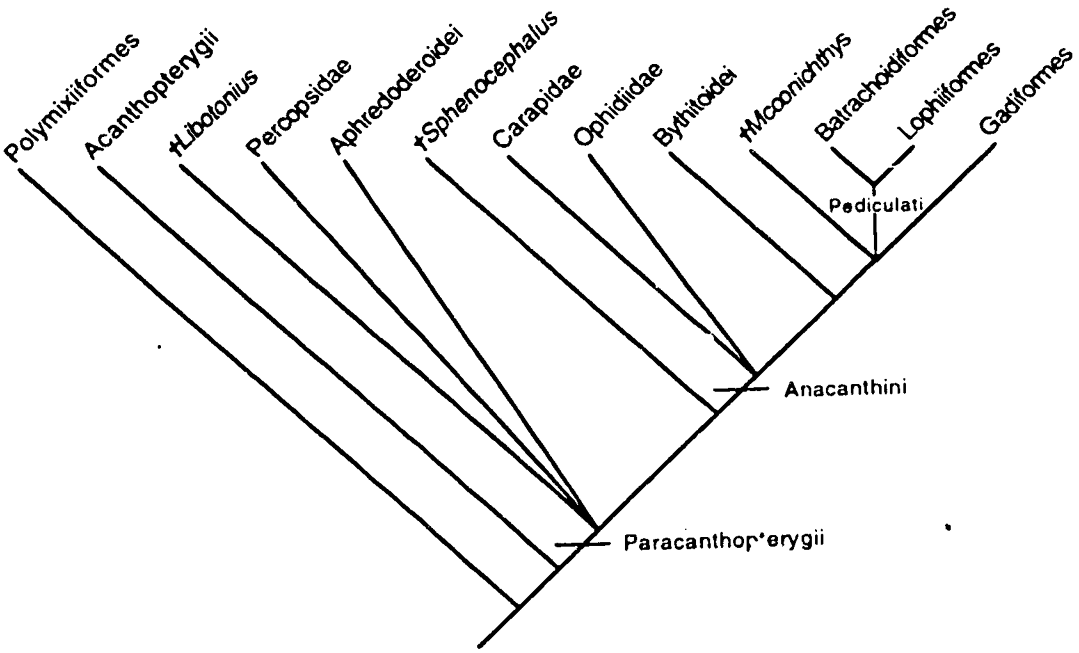

Figure II-1. Cladogram of proposed paracanthopterygian relationships. Redrawn from Patterson and Rosen (1989:fig. 16), with the addition of *†Mcconichthys* by Grande (1988:fig. 7).

reason, representative species of the gadiforms will also be included. †*Mcconichthys*,a presumed fossil anacanthine, will also be included, as it was placed in that group in the cladogram by Grande (1988), but it does not have all of the features of the Anacanthini (*e.g.* there is no postmaxillary process and therefore no "gadoid notch").

The Batrachoidiformes and Lophiiformes are combined in the Pediculati (Patterson and Rosen, 1989). These fishes are considered advanced paracanthopterygians (Fig. II-1) and have remained in the derived position within the superorder with only slight controversy (*eg.*, Greenwood *et al.*, 1966). Although they are the most derived paracanthopterygians, and therefore not of great importance to this study of the relationships of lower paracanthopterygians, a representative of each has been included in this study.

Outgroups

Good outgroups to use for comparison are from lineages closely related to the ingroup. The most closely related lineage, sharing a single ancestor only with the ingroup, is called the sister group. Following the cladogram in Fig. II-2 (from Johnson and Patterson 1993:fig. 24), the sister group to the Paracanthopterygii is thought to be the Acanthopterygii, and the two together are classified as the Holacanthopterygii. Sister to the Holacanthopterygii is the Order Polymixiiformes; these two together form the Euacanthomorpha. The sister group to this is the Order Lampridiformes, and together they form the Acanthomorpha. Following Rosen (1973), the sister group to the Acanthomorpha is the Order Myctophiformes, the two together

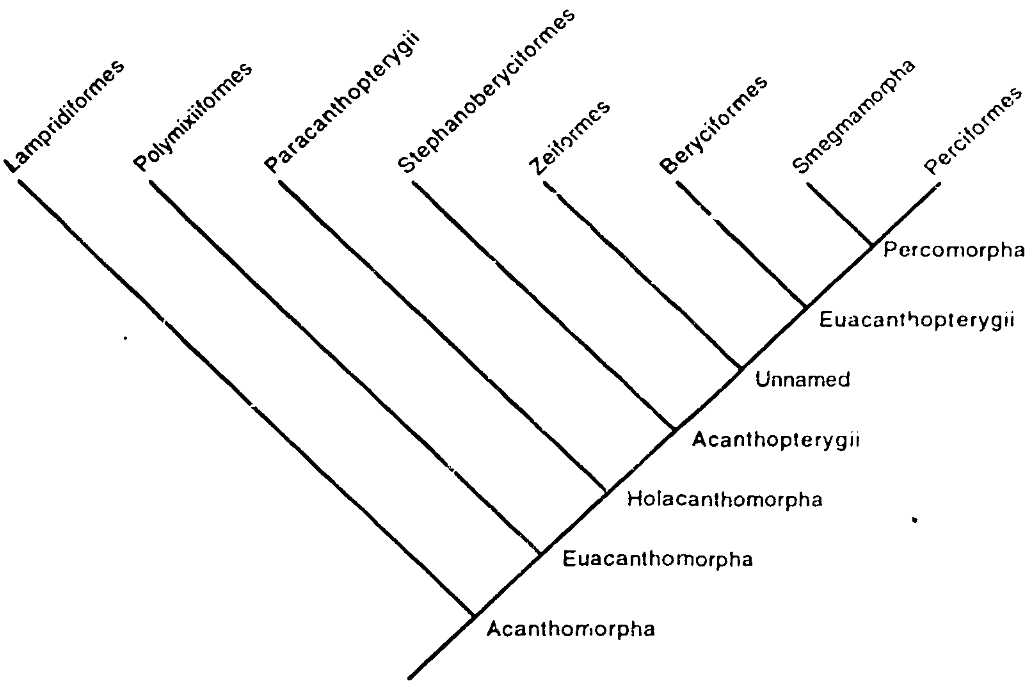

Figure II-2. Cladogram of acanthomorph relationships. Redrawn from Johnson and Patterson (1993:fig. 24).

forming the Subsection Ctenosquamata.

A second specification for choosing outgroups for this study was to find basal members of the closely related lineages listed above. Basal members by definition have fewer synapomorphies of the higher members of a lineage, and thus are more likely to display primitive states of characters. Although recent literature (*e.g.*, Johnson and Patterson, 1993) provides a variety of new hypotheses regarding the organization of groups related to the Paracanthopterygii, the choice of outgroups is unaffected. For example, Parenti (1993) suggested that only one of two subgroups of the Acanthopterygii, the Atherinomorpha, should be the sister group to the Paracanthopterygii. Parenti (1993) proposed eight synapomorphies to support this relationship, but recommended that the relationship between the two acanthopterygian groups (Atherinomorpha and Percomorpha) and the Paracanthopterygii be left as an unresolved trichotomy. Whether the Atherinomorpha are the sister group to the paracanthopterygians or the percomorphs, basal members have been included in the comparative material. Similarly, the Lampridiformes are alternately considered basal acanthopterygians (Jamieson, 1992) or the sister group to the Euacanthomorpha (Johnson and Patterson, 1993). Either way, this order will be considered as a relevent outgroup for comparative analysis.

LIST OF MATERIAL EXAMINED

Wherever possible, specimens were examined for the necessary features. For some genera, however, specimens were not available or actual specimens did not provide the information needed. In these cases descriptions and illustrations from other authors were used. Following the name of each of these species is the reference predominantly used. The abbreviation "c&s" indicates material cleared and double stained unless "bone only" is noted.

Aulopiformes

Suborder Alepisauroidei, Family Synodontidae, Subfamily Harpadontinae

Saurida tumbil (Bloch) - 2 c&s (bone only), UAMZ 4046

Suborder Aulopoidei, Family Aulopidae

Aulopus japonica Günter - 3 x-rays, CAS 17550 (East China Sea), SU 22626 (Japan, Misaki), SU 53425 (Tokyo Market)

Myctophiformes, Family Myctophidae

Myctophum sp. - 1 c&s, UAMZ 2689 (Bellairs, Barbados)

Myctophum punctatum Rafinesque - 3 c&s, NMC 70-0244 (North Atlantic Ocean)

Lampanyctus leucopsarus (Eigenmann and Eigenmann) - Jollie, 1954

Superorder Paracanthopterygii

new species from Smoky Tower - UALVP 21541, 22870, 34771, 34772

new species from Joffre Bridge - UALVP 21627, 21660, 21758, 23534, 23535, 23538, 23553, 25325, 25417, 25480, 25614, 25833, 25834, 27144, 27145, 30842a/b, 30846a, 30899a, 31683, 32554, 39089, 39090, 39091, 39092, 39093, 39094

Amblyopsidae

Amblyopsis spelaea Dekay - 3 c&s, CAS 78143 (Mitchell, Indiana)

Chologaster agassizi Putnam - 3 x-rays, CAS 57170 (Kentucky), 3 alcohol preserved, UAMZ 7635 (Bowling Green, Kentucky)

C. cornutus Agassiz - 2 x-rays, CAS 78371 (no data)

C. papilliferus Forbes (= *C. agassizi*) - 5 x-rays, SU 63331 (Illinois)

Typhlichthys subterraneus Girard - 3 x-rays, one CAS 78370 (Kentucky), two SU 01310 (Indiana)

Aphredoderidae

Aphredoderus sayanus (Gilliams) - 3 c&s, CAS 57257 (Alachua Co., Florida)

†*Trichophanes foliarum* Cope - latex peel, UALVP 17741 (Florissant Lake, Colorado); Rosen and Patterson, 1969

Percopsidae

Percopsis omiscomaycus (Walbaum) - 3 c&s, UAMZ 3062 (Hay River, NWT), UAMZ 5274, 5275 (no data)

P. transmontana (Eigenmann and Eigenmann) - Rosen and Patterson, 1969

†*Amphiplaga brachyptera* Cope - UALVP 13400, 13401 (Eocene, Green River Formation, Fossil Butte, Wyoming); Rosen and Patterson, 1969

†*Erismatopterus levatus* Cope - UALVP 12358, 12362 (Eocene, Bridger Formation, Labarge, Wyoming); Rosen and Patterson, 1969

†*E. rickseckeri* Cope (=*E. levatus*) UALVP 12363 (Eocene, Bridger Formation,

Labarge, Wyoming)

†Libotoniidae

†Libotonius blakeburnensis Wilson - Wilson, 1977 and 1979

†L. pearsoni Wilson - UALVP 13466 (holotype), 13469 (paratype, 14765a and b (paratype), 14769 a and b (Middle Eocene, Klondike Mountain Formation, Resner Canyon, Washington)

†Sphenocephaloidei, Family †Sphenocephalidae

†Sphenocephalus fissicaudus Agassiz - Patterson, 1964; Rosen and Patterson, 1969

†Xenyllion zonensis Wilson and Murray - UALVP 32133 (holotype) (Cenomanian, Peace River, Alberta)

Family †Mcconichthyidae

†Mcconichthys longipinnis Grande - Grande, 1988

Gadiformes, Family Lotidae

Lota lota (Linnaeus) - skeletal preparations, UAMZ 571 (Lac Ste. Anne, Alberta), UAMZ 7595 (Red Deer River, Alberta), and UAMZ 7596 (Cold Lake, Alberta); Mujib, 1967

Family Gadidae

Microgadus proximus (Girard) - 2 c&s (bone only), UAMZ 7594 (Strait of Juan de Fuca, British Columbia)

Ophidiiformes, Family Ophidiidae, Subfamily Ophidiinae

Ophidion welshi (Nichols and Breder) - 3 c&s, UAMZ 6597 (Gulf of Mexico)

Family Carapidae - Markle and Olney, 1990; Rosen and Patterson, 1969

Batrachoidiformes, Family Batrachoididae

Porichthys notatus Girard - 2 c&s, (bone only) UAMZ 2011 (Strait of Juan de Fuca, British Columbia)

Lophiiformes

Family Lophiidae - 1 skeletal preparation UAMZ 1572

Superorder Acanthopterygii

Lampriformes

Suborder Veliferoidei, Family Veliferidae - x-ray, CAS 31492 (Arabian Sea)

Velifer hypselopterus Bleeker - x-ray, CAS 15865 (Taiwan Strait)

Velifer africanus Smith (= *V. hypelopterus*) - Rosen, 1973

Suborder Lamproidei Family Lampridae

Lampris - Oelschläger, 1983

Cyprinodontiformes

Fundulus diaphanus (Lesueur) - 2 c&s, UAMZ 6629; Parenti, 1981

Fundulus heteroclitus (Linnaeus) - 3 c&s UAMZ 3948.1 (Branx River and Sprain Brook, Winchester Co., Bronxville, New York)

Menidia menidia (Linnaeus) - 1 c&s, UAMZ 6631

Beryciformes - Patterson, 1964; Zehren, 1979

Suborder Polymixioidei, Family Polymixiidae

Polymixia japonica Günter - 3 c&s, NMC 79-0001 (Pacific Ocean, Japan)

Suborder Berycoidei, Family Berycidae

Beryx affinis Günter (= *Centroberyx affinis* (Günter)) - x-ray, SU 24124 (Tokyo Market)

Suborder Stephanoberycoidei, Family Melamphaidae

Melamphaes lugubris Gilbert - 1 c&s, 2 alcohol preserved UAMZ 1388

Incertae sedis

Family †Asineopidae, †*Asineops squamifrons* Cope, 1870 - UALVP 17829, expoxy cast of FMNH PF 9900, both from Green River Formation, Wyoming

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III. A NEW PALAEOCENE GENUS AND SPECIES OF PARACANTHOPTERYGIAN (TELEOSTEI: ACANTHOMORPHA) FROM SMOKY TOWER, ALBERTA

INTRODUCTION

The Palaeocene rocks of Alberta are represented by rocks of the Paskapoo Formation. Most of the exposed surface bedrock for several hundred kilometres northwest of the Red Deer River is part of this formation. The Paskapoo Formation has been dated in several areas, using fossils and potassium-argon dating techniques, as of middle Tiffanian age, with dates of 62.5, 61.8 and 61.5 million years old (Christophel, 1976); such dates place it in the Palaeocene Epoch of the early Tertiary.

Smoky Tower, named for a nearby fire tower, is an important plant and fish locality in the Paskapoo Formation. The locality was discovered in the early 1960's when Atlantic Richfield Oil Company began excavation in the area (Christophel, 1976). A road was constructed for access to a well site near Smoky Tower, and during, or shortly after, this construction the fish fossils were discovered. The site, north of the fire tower, is located about 123 km north and slightly west of Hinton, in LSD 10-6-63-2-W6 (Christophel, 1976). Fossil remains from Smoky Tower include plant material (Christophel, 1976); two species of salamanders (Naylor and Fox, 1993; L.A. Lindoe, pers. comm.); more than fifteen specimens of the pike, †*Esox teimani* (Wilson, 1980); a single osteoglossomorph fish (Li Guo-Qing, pers. comm.); and four specimens of the new species described here. All of the fish and salamander specimens were found in a single slab of sandstone, collected in fragments by the late B. Tieman of Grande Prairie, Alberta.

Among the fish which have at one time or another been grouped in the Order Percopsiformes, only members of the †Sphenocephalidae are from rocks older than those of Smoky Tower. *†Sphenocephalus* Agassiz is from Cretaceous marine deposits of Europe, and the recently described *†Xenyllion zonensis* Wilson and Murray (in press), is from Cretaceous marine deposits of Alberta. Other fossils that appear to belong to a sphenocephalid closely related to *†Xenyllion zonensis* have been found in Cretaceous marine deposits in the United States (Stewart, in press). The rest of the North American fossil genera previously described in the Order Percopsiformes are all from freshwater deposits in rocks of Eocene or later age (Rosen and Patterson, 1969).

The earliest freshwater paracanthopterygian known is *†Mcconichthys longipinnis* Grande from early Palaeocene deposits in Montana. Although Grande (1988) placed this species in the Anacanthini, not in the Order Percopsiformes, it is closely related to the new species from Smoky Tower (Ch. V) and is older than the new species.

Previously the Order Percopsiformes contained the families Percopsidae, Aphredoderidae and Amblyopsidae (Rosen and Patterson, 1969), along with the fossil genus *†Libotonius* (Wilson, 1977) and *†Sphenocephalus* (Rosen and Patterson, 1969), but Patterson and Rosen's (1989) revision of this group suggested that the order is paraphyletic, united only by features they believed to be symplesiomorphies. The Percopsidae, Amblyopsidae, Aphredoderidae, and *†Libotonius* are, however, each considered to be monophyletic, based on one or more synapomorphies per group (Patterson and Rosen, 1989). The new species of Palaeocene freshwater paracanthopterygian fish described here is classified in the Family Percopsidae based on the distinguishing characteristic of the dorsal process on the maxilla.

ACRONYMS

CAS, California Academy of Sciences; SU, Stanford University Collections at CAS; UALVP, University of Alberta Laboratory for Vertebrate Paleontology; UAMZ, University of Alberta Museum of Zoology.

ABBREVIATIONS

† - denotes fossil taxa

ang, angular; brst, branchiostegal; ch, ceratohyal; cl, cleithrum; cor, coracoid; den, dentary; ect, ectopterygoid; fr, frontal; ep, epural; hy, hypural; hyo, hyomandibula; lac, lacrimal; mx, maxilla; nsp, neural spine; op, opercle; pcl, postcleithrum; phy, parhypural; pmx, premaxilla; pop, preopercle; psph, parasphenoid; ptt, posttemporal; pu, preural centrum; qu, quadrate; ret, retroarticular; sca, scapula; scl, supracleithrum; sn, supraneural; sop, subopercle; sym, symplectic; u, ural centrum; uh, urohyal; un, uroneural.

MATERIAL AND METHODS

The four specimens of the new species from Smoky Tower are in the collections of the University of Alberta Laboratory for Vertebrate Paleontology. The fossils were prepared by hand by technician L.A. Lindoe, using fine needles to remove the matrix from around the preserved bone. Drawings have been made from photographs and/or with the aid of a Wild camera lucida on a Wild M5 dissecting microscope.

Recent specimens used for comparison of osteological material, to clarify or verify characters from the work of previous authors, were cleared and stained following Taylor and Van Dyke (1985), (*Percopsis omiscomaycus, Amblyopsis spelaea* and *Aphredoderus sayanus*), or x-rayed (*Chologaster cornutus, C. papilliferus, C. agassizi* and *Typhlichthys subterraneus*).

Material Examined

Percopsis omiscomaycus UAMZ 5274, 5275 and 3062; *Aphredoderus sayanus* CAS 57257; *Amblyopsis spelaea* CAS 78143; *Chologaster cornutus* CAS 78371; *C. papilliferus* SU 63331; *C. agassizi* CAS 57170; *Typhlichthys subterraneus* CAS 78370, SU 1310. Fossil specimens of *†Amphiplaga, †Erismatopterus* and *†Libotonius* were also used for comparisons.

SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII (*sensu* Nelson, 1994)

Subdivision TELEOSTEI: (*sensu* Patterson and Rosen, 1977)

Infradivision EUTELEOSTEI (*sensu* Greenwood *et al.*, 1967)

Sept ACANTHOMORPHA (*sensu* Stiassny, 1986)

Superorder PARACANTHOPTERYGII (*sensu* Patterson and Rosen 1989)

Order PERCOPSIFORMES (*sensu* Ch. V)

Family PERCOPSIDAE Regan, 1911

Emended diagnosis - Paracanthopterygian fish with dorsal process on maxilla; caudal fin with 18 principal rays, 16 branched; palatine with or without teeth; 28-45 vertebrae.

Included genera - *Percopsis, †Amphiplaga, †Erismatopterus*

†Lateopisciculus gen. nov.

Type and Only Species - *†Lateopisciculus turrisfumosus* gen. et sp. nov.

Diagnosis - As for species.

Etymology - From the Latin "lateo" lie hidden, and "pisciculus" (masculine) little fish. These little fish lay hidden in the strata for many years.

†Lateopisciculus turrisfumosus sp. nov.

Figs. III-1A and B

Diagnosis - Percopsid fish with unique distally tapering parhypural. Percopsoid projections (McAllister, 1968) on second, third and fourth branchiostegal rays; 27-29 vertebrae; dorsal fin with three spines and seven rays.

Holotype - UALVP 3477, Fig. III-1A and B.

Paratypes - UALVP 21541, 22870, 34772.

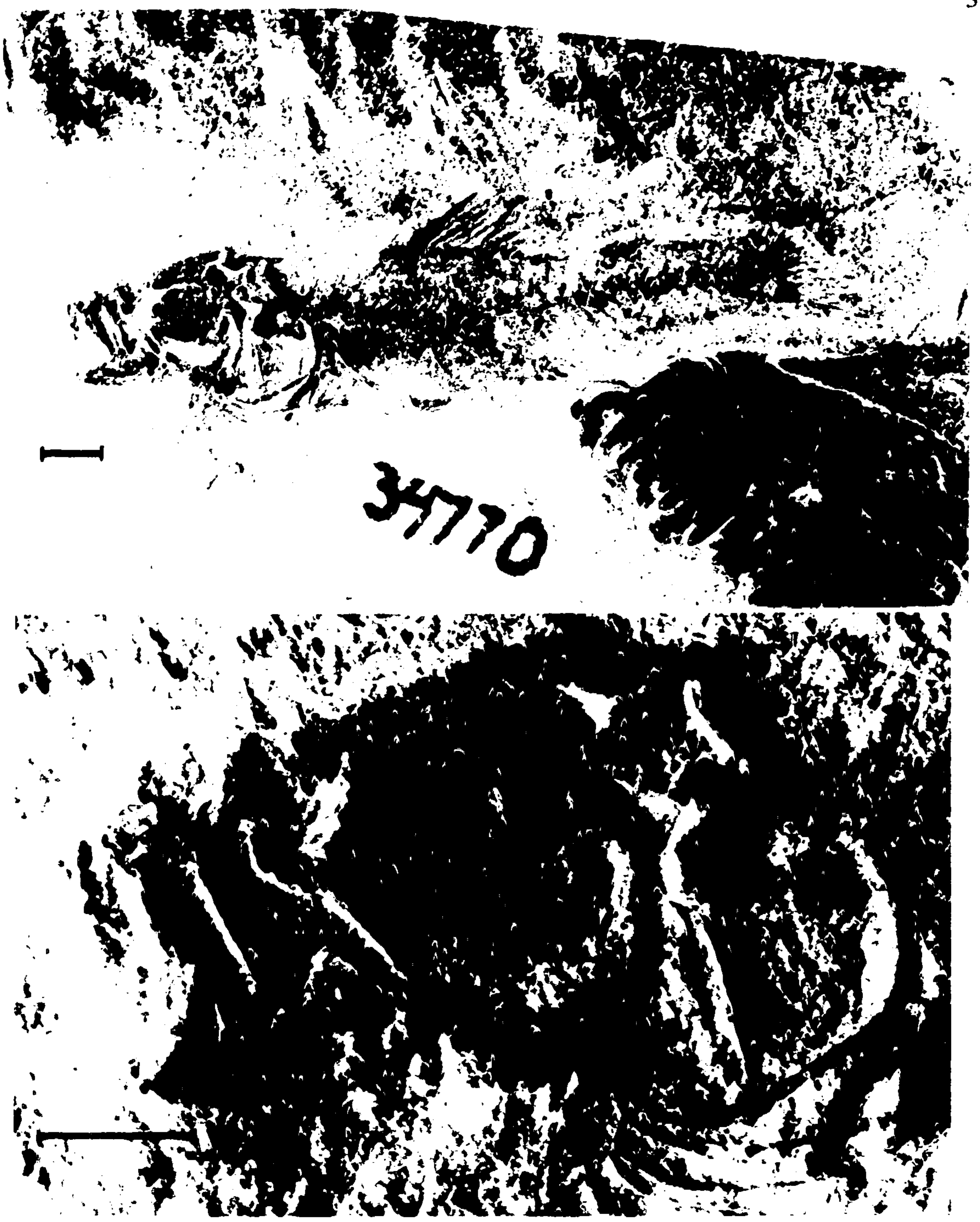

Figure III-1. †*Lateopisciculus turrisfumosus* gen. et sp. nov., holotype UALVP 34771. A. whole specimen, B. skull. Fish at lower right of top photograph is an osteoglossomorph (Li Guo-Qing, pers. comm.). Scale bars = 2 mm.

Locality - Smoky Tower site #1 (Wilson, 1980), N.E. 1/4, S6, T63, W6 Alberta, Canada.

Horizon - Paskapoo Formation, late Palaeocene based on plant material (Dawson *et al.*, 1994) and radiometric dates of 61.5-62.5 my (Christophel, 1976).

Etymology - The specific epithet is named for the type locality of these specimens, Smoky Tower, Alberta, from the Latin "turris" tower, and "fumosus" smoky.

DESCRIPTION

Body form

These are small fish, with a standard length (SL) about 25 mm (measured from the anteriormost point of the protruding premaxilla to the posteriormost end of the hypurals in UALVP 34771 (Fig. III-1A). Meristics are given in Table III-1, and measurements in Table III-2. The maximum depth of the body is at the second branched ray of the dorsal fin and represents about 25% of SL. Head length is about one third SL, and head depth is close to the maximum body depth. The dorsal fin is situated midway along the back. The predorsal length on the holotype represents 40% of the estimated SL. The origin of the anal fin is slightly posterior relative to the insertion of the dorsal fin. The caudal fin, preserved in UALVP 21541, is clearly forked. The length of the caudal fin from the posterior edge of the hypurals to the distal point of the longest ray, measured diagonally, is about 20% SL. The pectorals are inserted slightly below the middle of the body. The distal tips of the pectoral rays reach or just pass a vertical through the origin of the dorsal fin. The pelvic fin base is

Table III-1. Meristics for †*Lateopisciculus turrisfumosus* gen. et sp. nov.

specimen:	22870	21541	34772	34771
dorsal fin rays	III,7	III,9	III,8	-
anal fin rays	IV,6	IV,5	-	-
pectoral fin rays	12	10+	10+	12
pelvic fin rays	7+	7+	9	-
caudal fin principle rays	-	18	18	-
vertebrae total	30+1	26+	28+	28+
predorsal vertebrae	3 or 4	-	3+	-
postanal vertebrae	20	19	17+	-
dorsal pterygiophores	12	12	13	-
anal pterygiophores	8	8	-	-
branchiostegal rays	5/6	2+	5/6	4+

Table III-2. Measurements for †*Lateopisciculus turrisfumosus* gen. et sp. nov.

specimen:	22870	21541	34772	34771
(mm)				
standard length	31.0	-	23.2	25.9
total length	-	-	>26.8	-
head length	10.1	-	8.6	8.8
upper jaw lgth	3.3	-	3.1	>1.8
mandible length	4.2	-	3.1	3.5
body depth	8.5	>6.6	6.0	-
prepectoral length	11.9	-	9.6	10.0
prepelvic length	16.1	-	12	-
predorsal length	13.4	-	11.5	-
longest pectoral ray	2.3	-	>2.1	>2.4
dorsal fin base	5.9	6.0	>4.7	-
anal fin base	-	5.7	-	-
caudal peduncle length	-	12.0	-	-
caudal peduncle depth	-	2.7	2.8	-
snout length	3.4	-	2.1	-
orbit	2.9	-	2.8	-
dorsal fin to hypurals	17.8	16.2	12.4	-

situated at about one third of the distance between the pectoral fin base and anal fin origin. A reconstruction of the whole fish is shown in Figure III-2. In the following description, comparison to other genera is based on personal observations of specimens unless otherwise noted.

Neurocranium and Skull Roof

None of the specimens has all the bones of the skull preserved, but many features can be seen in one specimen or another. The roof of the cranium is not completely visible but in UALVP 22870 one can distinguish a stocky frontal that appears very similar to that of *Percopsis omiscomaycus*, which is termed "truncated anteriorly" by Rosen and Patterson (1969). The frontal, well preserved on UALVP 34772 (Fig. III-3), is about one third as wide as it is long; left and right frontals on this same specimen meet medially to form a ridge. The parasphenoid in UALVP 22870 (Fig. III-4) crosses the orbit near its ventral rim, just above the quadrate, from the posterior edge of the second infraorbital bone to the angle formed by the horizontal and vertical branches of the preopercle. It is slender with a low dorsal ridge as in *Percopsis*. The parasphenoid is also well preserved in the holotype (Fig. III-1B). On the dorsal surface of this parasphenoid can be seen one of the lateral triangular processes, just anterior to the forked posterior end.

The orbit is covered in black pigment in UALVP 34771. The horizontal diameter of the orbit represents one fifth of the head length including the protruding premaxilla. Of the infraorbital series, only the lacrimal and the second infraorbital are

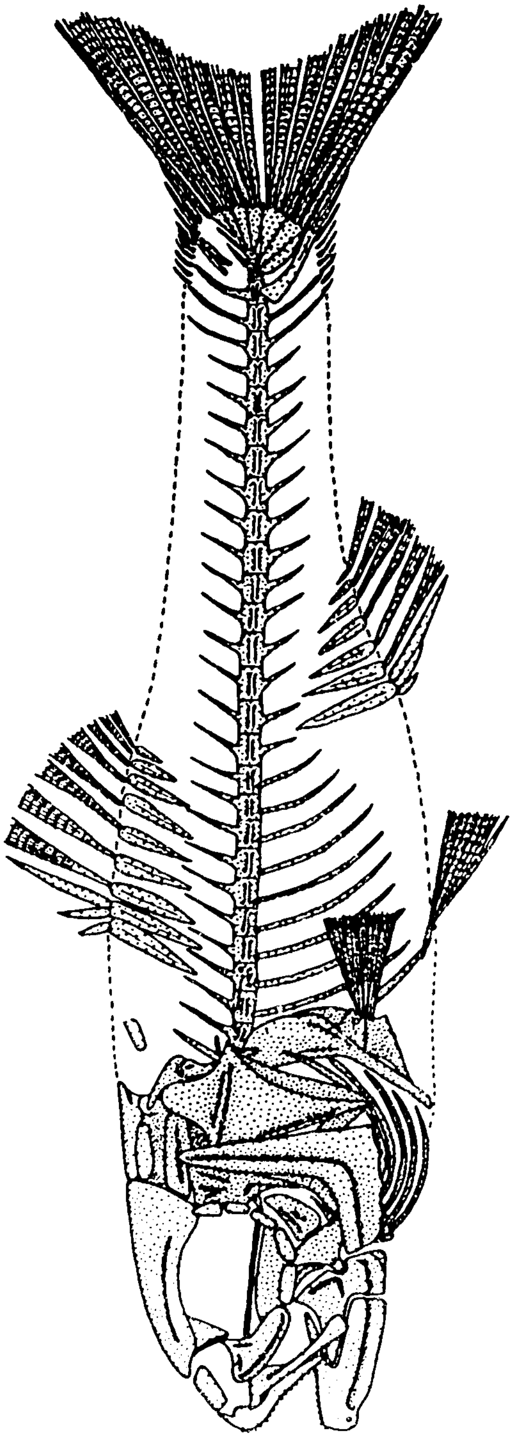

Figure III-2. Reconstruction of †*Lateopisciculus turrisfumosus* gen. et sp. nov.

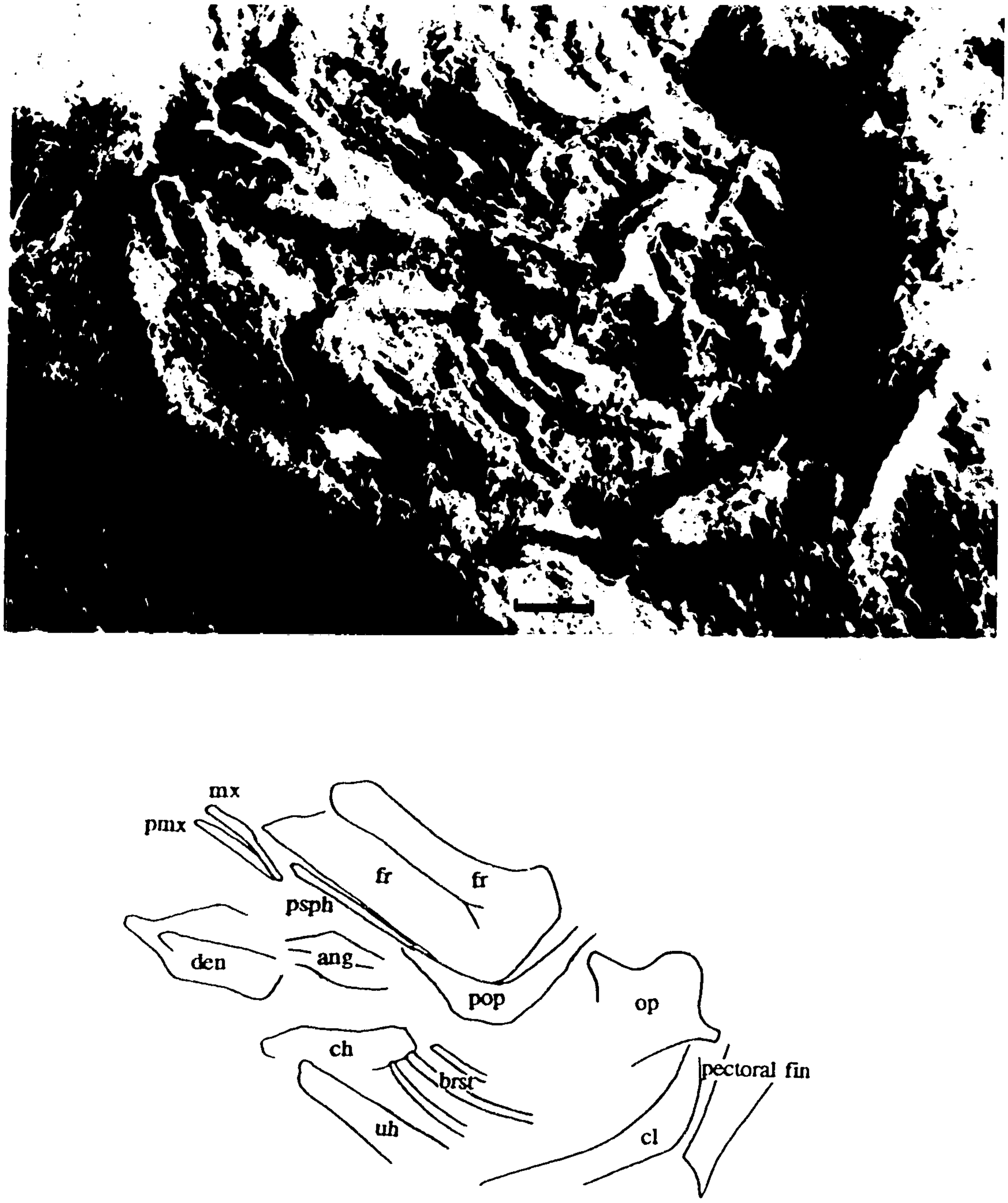

Figure III-3. †*Lateopisciculus turrisfumosus* gen. et sp. nov., photograph and camera lucida drawing of the skull in laterodorsal view, UALVP 34772. Anterior to left. Scale bar = 1 mm.

Figure III-4. †*Lateopisciculus turrisfumosus* gen. et sp. nov., photograph and camera lucida drawing of the skull in lateral view, UALVP 22870. Anterior to left. Scale bar = 1 mm.

visible (UALVP 22870). The lacrimal has a slightly crescentic ventral outline, and a dorsal margin that is rolled laterally to form a shelf, less pronounced at both anterior and posterior ends than it is in the middle. There are a few weak serrations visible on the lateral edge of the lacrimal shelf, but the ventral edge of the bone is smooth. A tapered dorsal process is present just anterior to the middle of the dorsal surface of the lacrimal. It is slightly longer and more pointed than that of *Percopsis*, being more similar to that of *†Amphiplaga* (Percopsidae) (Rosen and Patterson, 1969: fig. 20). The posterior end of the lacrimal reaches a point above and just anterior to the articulation between the quadrate and angular bones. There is no evidence of an antorbital in any specimen.

Jaws and suspensorium

A reconstruction of the jaws and parts of the suspensorium is shown in Figure III-5. The quadrate is not completely visible in UALVP 22870; the dorsal edge is not exposed. The quadrate is triangular with a thickened postero-ventral edge. The posterior part of the quadrate and the symplectic are covered by the preopercle. The ectopterygoid, endopterygoid, metapterygoid and hyomandibula are not visible.

The maxilla is clearly visible in UALVP 22870 and 34771, where it is preserved in lateral view, and in 34772 where it is preserved in ventrolateral view. On the dorsal surface of the maxilla is the process for the attachment of the muscle that Rosen (1962) called the *levator maxillae superioris* muscle, now deemed to be the A1ß (Rosen, 1973:417). This process is similar to that of *Percopsis*, although in

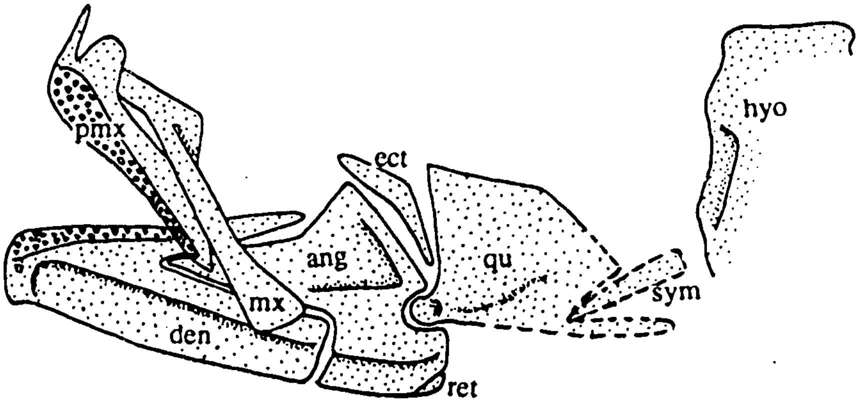

Figure III-5. †*Lateopisciculus turrisfumosus* gen. et sp. nov., reconstruction of the jaws and suspensorium, based on UALVP 22870. Anterior to left.

Percopsis the maxillary head is less sharply angled than it is in the new species. The posterior end of the maxilla is expanded, more so than in *Percopsis*, and reaches a point dorsal to the posterior edge of the angular. There are no supramaxillaries and no teeth on the maxilla.

The premaxilla is 0.78 the length of the maxilla, proportionally longer than in *Percopsis*. The articular process is rounded, broad, and well developed, but the ascending process is broken in UALVP 22870 and not visible in the other specimens.

Ventrally the alveolar process of the premaxilla is arched and dorsally it is also slightly arched, as in *Percopsis*. The alveolar process tapers towards the posterior end. It is not segmented as in amblyopsids and aphredoderids, and there is no postmaxillary process. The premaxilla excludes the maxilla from the gape, and bears sharp, thin, conical teeth, a few of which are visible in UALVP 22870.

The mandible, measured from the anterior tip of the dentary to the posteriormost end of the angular in the UALVP 22870, fits 2.5 times in the head length. The dentary is a triangular bone in which the posterior border is indented to receive the anterior tip of the angular. The oral border of the dentary has fine teeth in a broad band visible in UALVP 22870. The angular is also triangular, with the anteroventral corner articulating with the dentary. The dorsal edge of the angular, visible in UALVP 22870, is thickened, and the ventral edge, visible in UALVP 34771, is thickened, as are both edges in *Percopsis*. The angular terminates near the rear in a lateral articular facet in which fits the condylar process of the quadrate. A separate retroarticular is visible at the posteroventral corner of the angular in UALVP 22870.

Hyoid arch and opercular region

Of the distal part of the hyoid arch only the imperforate ceratohyal is clearly visible in UALVP 22870. The hypohyals are not distinct, and the epihyal and interhyal are hidden by the preopercle. Tooth plates on the dorsal edge of the ceratohyal are present in *Percopsis* and *Aphredoderus* and would be expected for the Percopsidae and Aphredoderidae and are present in *†Sphenocephalus* according to

Rosen and Patterson (1969); however, there are none visible on any of the fossil specimens. At least five branchiostegal rays articulate with the posteroventral edge of the ceratohyal. All five are acinaciform, with "percopsoid projections" (McAllister, 1968) visible on the second, third, and fourth ray. A trace of bone ventral to all five branchiostegals in UALVP 22870 may be the remains of a sixth.

Most of the urohyal is visible in lateral view in UALVP 22870, just below the branchiostegal rays. The urohyal is roughly rectangular; the posterior depth fits about 2.5-3 times into the length of the bone. At the anterior end, there appears to be a dorsal flange, more pronounced than that of *Percopsis*.

The preopercle consists of two perpendicular branches. The horizontal branch is slightly shorter but deeper than the vertical branch, which narrows near the top. There are four spines on the posterior and ventral edges starting at the angle between the vertical and horizontal limbs and continuing along the horizontal limb. Behind a broad flange there is a groove for the sensory canal, which is not enclosed by bone anywhere along the preopercle.

The opercle, visible in UALVP 22870, is triangular, but the dorsal part of the anterior edge is hidden by the preopercle. The postero-ventral edge is concave, but of larger radius than in *†Amphiplaga*, and greater curvature than *Percopsis*. The anterior edge of the superior border is excavated just anterior to the large dorsal projection of the opercle, as in *Percopsis*. This feature is also visible in UALVP 34772. The large distinctive dorsal projection, which is proportionally slightly larger than that of *Percopsis*, appears slightly broken on both the anterior and posterior edges in both

UALVP 22870 and 34772. The vertical ventral spine-like projection of the opercle is pronounced and its tip extends just beyond the level of the ventral edge of the preopercle in UALVP 22870. The posterior spine of the opercle is well developed and longer than that of *Percopsis*. The subopercle can be seen in UALVP 22870 and 34772 where the anterior end of this bone appears to have a blunt process. An interopercle is not visible.

Vertebral Column

The axial skeleton of UALVP 22870 contains 30 vertebrae of which 18, including the second ural centrum, are behind the first anal pterygiophore. The neural and haemal spines are long, with their distal tips reaching about one half to two thirds of the distance separating dorsal and ventral regions of the centra from the animal's dorsal and ventral edges respectively. Neural spines are longer in the caudal region than in the trunk. The anterior neural spines are not broad but thin and pointed, as are all the others. The first neural spine is not sutured to or in close articulation with the supraoccipital crest, but is clearly distinct. Pleural ribs are visible on vertebrae 4-11.

Some short epipleurals (or epineurals following the nomenclature of Johnson and Patterson, 1993), whose length is little more than that of one centrum, are present on centra 1-3 and possibly 4. One supraneural can be seen in front of the dorsal fin above the first neural spine. It is slightly arched and may have a dorsal projection. It is more similar to the rectangular supraneural of *Percopsis* than to that of other fossil percopsiform fishes.

Caudal Skeleton

The caudal fin is best preserved in UALVP 21541 (Fig. III-6), to which all of the following description applies. The caudal fin is clearly forked, as in *Percopsis*, not truncated, as in *Aphredoderus* (Family Aphredoderidae). There are 18 principal rays, with 16 branched (I,8,8,I). In front of the two lobes there are 11 dorsal and 10 ventral procurrent rays; the anteriormost dorsal ones articulate with the neural spine on the fourth preural centrum.

Posterior to the parhypural is a large triangular hypural plate (Hy1) and a much narrower one (Hy2) which contribute, with the parhypural, to support the ventral lobe of the caudal fin. The parhypural articulates with the centrum as in *Percopsis* and in †*Trichophanes* (Family Aphredoderidae). Hypurals one and two and the parhypural articulate, as expected, on the fused first preural plus first ural centrum (PU1+U1). The parhypural tapers to a narrow point at its distal end.

The dorsal lobe of the fin is supported by four upper hypural plates (Hy3-6), which articulate with the second ural centrum (U2), with the exception of hypural six, which does not articulate with any centrum. Between the second uroneural (UN2) and the neural spine of the second preural centrum (NPU2) lie two epurals, which are slender and about half the length of the neural spine on PU2. The second uroneural is the same length as the epurals and straight, not curving as are most of the posterior neural spines. The first uroneural (UN1) is shorter, about half the length of UN2, but also straight.

The most posterior free preural centrum (PU2) has a full neural spine, as is

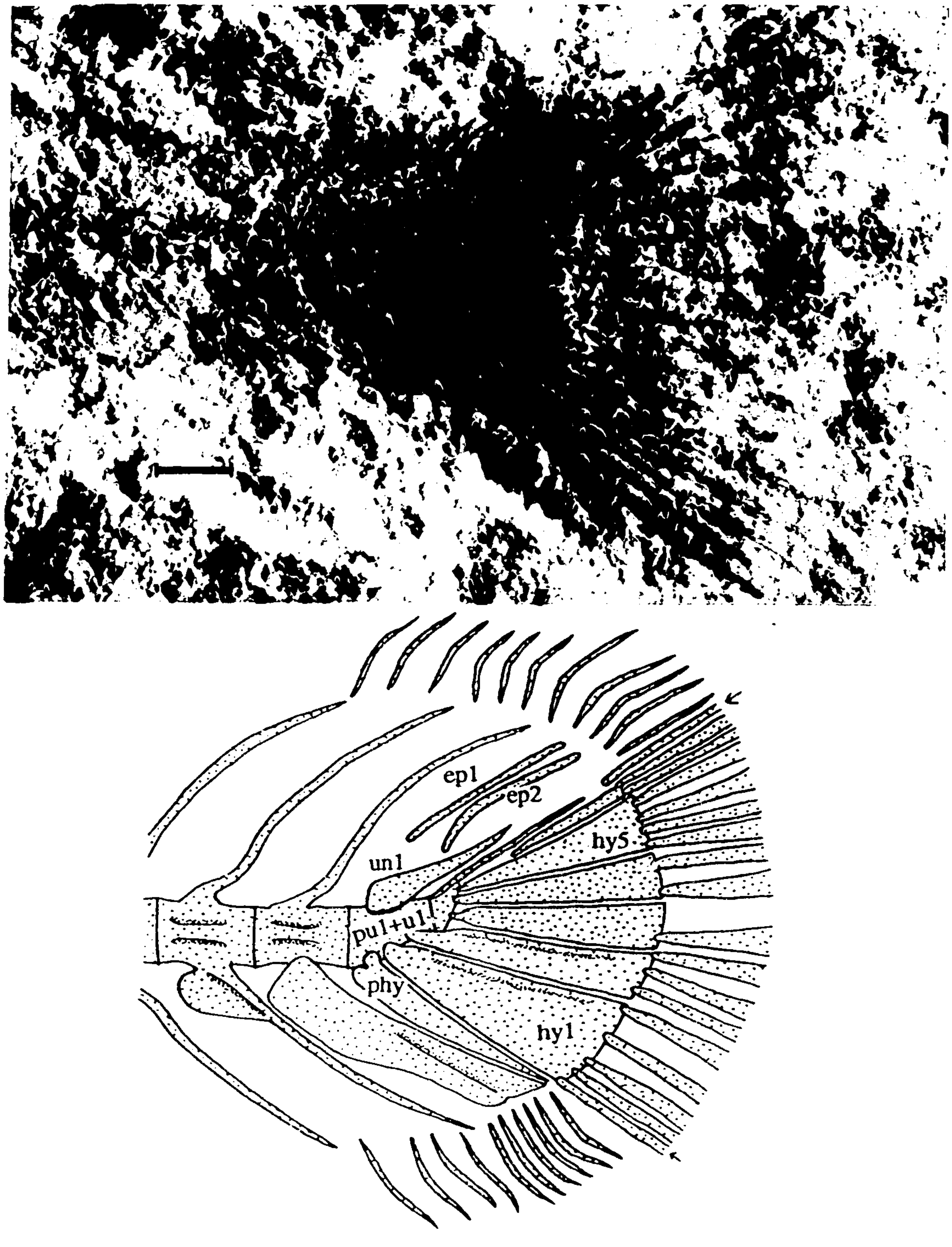

Figure III-6. *†Lateopisciculus turrisfumosus* gen. et sp. nov., photograph and reconstruction of the caudal skeleton, UALVP 21541. Anterior to left. Scale bar = 1 mm.

characteristic of paracanthopterygians, and the haemal spine on this centrum has a broad anterior flange. The third and fourth preural centra (PU3 and PU4) have long neural and haemal spines which, along with those of PU2, support the dorsal and ventral procurrent rays of the caudal fin. The neural spine on PU2 is not doubled as Rosen and Patterson (1969:386) reported for *Percopsis, Aphredoderus, Chologaster* and *Amblyopsis* (the latter two in the Family Amblyopsidae). However, of the four cleared and stained specimens of *Percopsis* I examined, only one had a double neural spine on PU2, as did one of two *Chologaster agassizi* specimens examined. No doubling was seen in three *Amblyopsis* and three *Aphredoderus* specimens.

In addition to the anterior midsagittal flange on the proximal portion of the haemal spine of PU2, there appears to be a small flange on the proximal end of the haemal spine of PU3, but no flanges are visible on any of the neural spines. In *Percopsis* and *†Amphiplaga*, there are anterior flanges on the proximal parts of the haemal and neural spines of PU2 and PU3, and a small posterior flange on PU4. Small midsagittal expansions are also found in *†Libotonius blakeburnensis* (Wilson, 1977).

Dorsal Fin

Clearly visible in UALVP 22870 and well preserved on UALVP 21514, the dorsal fin is situated midway along the fish, originating slightly anterior relative to the distal tips of the pectoral fin rays. It is composed of three spines and seven soft rays. The first spine is very short, the second about three times as long as the first, and the third is the longest and stoutest of the three. The first of the soft rays is the longest ray of the fin, but only slightly longer than the longest spine. The length of the longest ray represents about half the body height measured at the level of the ray's insertion. All seven rays are branched, and the last one is doubled in UALVP 21514. Their lengths progressively diminish towards the rear. The margin of the fin is not falcate, being straight or, if anything, slightly convex.

The endoskeleton of the dorsal fin is composed of 11 pterygiophores, all of roughly triangular shape. The longer anterior pterygiophores just pass the distal tip of the corresponding neural spines. The length and degree of development of the last five pterygiophores diminish progressively towards the rear. The very last pterygiophore in UALVP 22870 and 21514 has no associated soft ray. The first pterygiophore is between the third and fourth neural spines, and the last pterygiophore is between the eleventh and twelfth neural spines. Although *Percopsis* has an adipose fin, and therefore one may be expected in the new species, its presence cannot be confirmed in any of the four specimens.

Anal Fin

The origin of the anal fin is at a point slightly farther back on the body relative to the insertion of the dorsal fin. The anal fin is composed of three robust spines and at least six soft rays. In neither specimen UALVP 22870 nor UALVP 21541, where the anal fin is relatively clear, are the fin rays well preserved.

The endoskeleton of the anal fin is made up of eight or nine pterygiophores, the first two well developed and triangular, the rest less so. The distal tip of the most anterior pterygiophore reaches almost to the vertebral column; the rest are progressively shorter.

Pectoral Girdle and Fins

A reconstruction of the pectoral girdle is shown in Figure III-7. The supracleithrum is a stout, rod-like bone lying lateral to the anterior end of the vertebral column. There is a posterior flange at the dorsal end of the supracleithrum. The dorsal part of the cleithrum is broad and plate like, with thicker anterior and posteroventral edges. The ventral portion of the cleithrum extends anteroventrally, is fairly broad, and is similar in appearance to that of *Percopsis*. The postcleithrum also

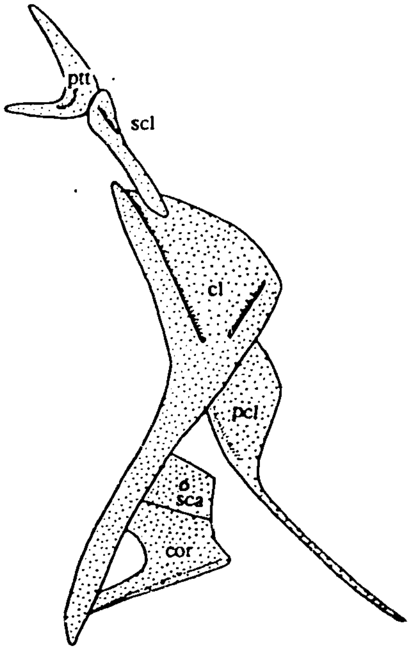

Figure III-7. †*Lateopisciculus turrisfumosus* gen. et sp. nov., reconstruction of the pectoral girdle, based on UALVP 22870 and 34771. Anterior to left.

has an expanded dorsal plate (postcleithrum 2 of Gottfried, 1989), best seen in the holotype, fused to the ventral rod-like part (postcleithrum 3 of Gottfried, 1989). In *Percopsis* the postcleithra do not reach the pelvic girdle, whereas in *†Lateopisciculus turrisfumosus* gen. et sp. nov. they do, a feature that is more similar to the other fossil taxa.

The pectoral fins insert low on the flank, closer to the ventral surface of the body than to the vertebral column. This is relatively lower than the pectorals of *Percopsis*, *†Erismatopterus*, *†Amphiplaga*, and *†Trichophanes*. The distal tips of the longest rays do not reach the pelvic origin. There are 11 pectoral rays.

Pelvic Girdle and Fins

A reconstruction of the pelvic girdle is shown in Figure III-8. The pelvic fins are situated under the dorsal fin, the origin just posterior to a vertical through the dorsal origin. They are about the same length as the pectorals and have six or seven rays, the first of which appears to be unbranched, as in many paracanthopterygians. There may be a pelvic splint, but it is difficult to be sure. The pelvic girdle is not well preserved. The radials are only vaguely seen on UALVP 34772.

Scales

On the counterpart of UALVP 22870, near the anal fin, small, round scales can be seen. These scales appear to be finely ctenoid, and are about 0.45 mm in diameter.

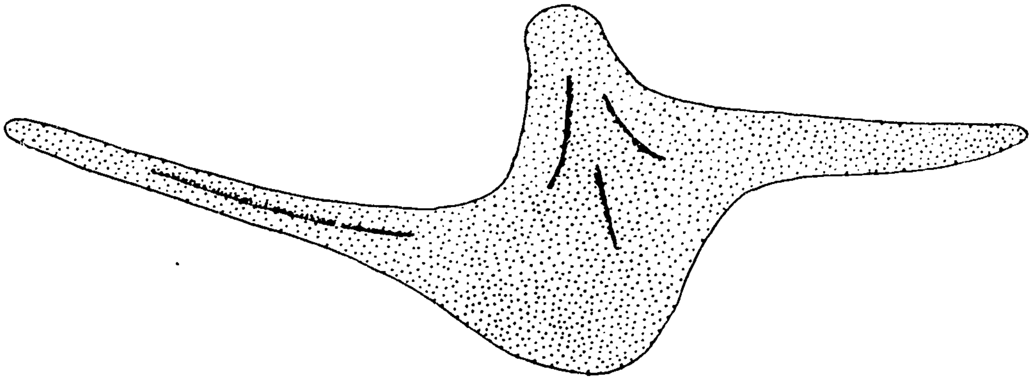

Figure III-8. †*Lateopisciculus turrisfumosus* gen. et sp. nov., reconstruction of the left half of the pelvic girdle based on UALVP 21541. Anterior to left.

THE RELATIONSHIPS OF THE NEW SPECIES FROM SMOKY TOWER

The most recent cladistic analysis of the Paracanthopterygii is that of Patterson and Rosen (1989). From their analysis, it follows that the European Cretaceous genus, *†Sphenocephalus* (Family †Sphenocephalidae), is considered closer to the higher paracanthopterygians (Anacanthini) than the Percopsidae, Aphredoderoidei (aphredoderids plus amblyopsids) and *†Libotonius*. This change in the placement of *†Sphenocephalus* consequently altered the polarity of the character states previously used to unite all these fish in the Order Percopsiformes. The change in polarity also causes the character states previously used to support relationships to be viewed as symplesiomorphies, and hence not useful to support the monophyly of this order. Thus, Patterson and Rosen (1989:fig. 20) proposed a scheme in which the Percopsiformes are not accepted as valid (*i.e.*, are not monophyletic). They include in their paper a proposed cladogram based on twenty synapomorphies (their figure 16) to organize the Paracanthopterygii. Grande (1988) used those character states to insert another species of Palaeocene paracanthopterygian, *†Mcconichthys longipinnis*, in its own family, †Mcconichthyidae, into their cladogram. The following is an attempt, similar to that of Grande, to insert the new species from Smoky Tower into Patterson and Rosen's cladogram (Fig. II-1). Of the twenty characters used by Patterson and Rosen (1989:fig. 16), the states for eleven (numbers 4, 6, 8, 9, 10, 11, 12, 15, 16, 19, and 20) cannot be determined for the new species, and these characters will not be discussed further.

The derived states of characters one, two and three (presence of a full neural spine on the second preural centrum; presence of two epurals in the caudal skeleton; and presence of a single supraneural behind the first or second neural spine) are present in the new species. This places it within the Superorder Paracanthopterygii.

The absence of synapomorphies five and seven separate *†Libotonius*, Percopsidae and Aphredoderoidei from the rest of the superorder in Patterson's and Rosen's scheme. The fifth proposed synapomorphy is foreshortening of the second, or second and third, centra to become much shorter than the first and third or fourth. The first two or three centra on the new species are not visible in any of the specimens, but from the position of the neural spines, foreshortening of the second does not seem likely. The seventh synapomorphy given is the presence of a "gadoid notch", an excavation behind the postmaxillary process of the premaxilla. This is considered not present in the new species because there is no postmaxillary process. Conversely, Grande (1988) used the absence of the postmaxillary process in *†Mcconichthys* to discount the lack of a "gadoid notch" as an informative character when he placed Mcconichthys with the anacanthines, which have a "gadoid notch".

Derived states of characters eight through twenty are synapomorphies for the Anacanthini and subgroups within it. Although numbers eight, nine, ten, eleven, twelve, fifteen, sixteen, nineteen and twenty cannot be analysed in the new species, it seems unlikely that this fish should be placed with any of these more advanced groups based on the previous character states, which were present, and the remaining derived states of characters thirteen, fourteen, seventeen and eighteen (respectively the first neural arch sutured to or in close articulation with the occipital crest; a suite of features including no endopterygoid, posttemporal fused to the skull, no ribs, no intercalar; X and Y bones present in the caudal skeleton; and no epipleurals on the first two vertebrae), all of which are seen to be absent in the new species from Smoky Tower.

From the above, and following the scheme of Patterson and Rosen (1989), the new species from Smoky Tower belongs in the basal paracanthopterygian area of the cladogram, within the trichotomy of *†Libotonius*, Percopsidae and Aphredoderoidei, and below the level of *†Sphenocephalus*. In other words, this fish belongs with the other fish that were traditionally classified as the Order Percopsiformes, considered by Patterson and Rosen (1989) to be a paraphyletic group.

An analysis of character states for each group within the trichotomy can be made to further narrow the placement of the new species into one of the three groups. The Family Percopsidae consists of living members *Percopsis transmontanus* and *P. omiscomaycus*, and fossil members in the genera *†Amphiplaga* and *†Erismatopterus*. *†Libotonius* was originally described in the Percopsidae (Wilson, 1977), but following Patterson and Rosen (1989), I will leave it as a separate lineage. The Aphredoderoidei contains the amblyopsids and aphredoderids, including the fossil genus *†Tricophanes*.

Rosen (1985) chose two characters in particular to indicate a relationship between *Percopsis*, *†Amphiplaga* and *†Erismatopterus*, as the Family Percopsidae. The first is a dorsal process on the maxilla, and the second is a broadly arched alveolar process of the premaxilla. The former is present in the new species from Smoky Tower and is here considered indicative of relationship. As for the latter, the alveolar process of the premaxilla is arched in the new species, much more so than in *Percopsis*. A comparison of the new species to Rosen and Patterson's table of characters (1969:382, table 1) shows that this fish also shares with the Percopsidae anteriorly truncated frontals and similar opercle shape, postcleithrum shape, epipleural number, parhypural articulation and forked caudal fin. *†Lateopisciculus* does not have the segmented alveolar process of the premaxilla, which is considered characteristic of the aphredoderids and amblyopsids (Rosen, 1985:43). With the Aphredoderidae, the new species shares the character of spines present around the angle of the preopercle, but it has no character solely in common with the Amblyopsidae. As for *†Libotonius*, following the description of Wilson (1977), this genus has no features in common with the new species that are not also found in the percopsids. Therefore, *†Lateopisciculus turrisfumosus* gen. et sp. nov. is classified in the Percopsidae.

DEPOSITIONAL ENVIRONMENT

The fish fauna found at the Smoky Tower locality (Esocidae, Osteoglossomorpha and Percopsidae) may be indicative of the type of environment that this locality represents. Members of the Family Esocidae in Canada all tend to inhabit small streams, ponds, rivers or lakes that are sluggish and have heavy vegetation (Scott and Crossman, 1973). The two extant hiodontids (Osteoglossomorpha) in Canada also prefer quieter waters of rivers, lakes or ponds and marshy areas. The extant percopsids are found in similar habitats to the esocids. Based on the habitats of the extant relatives of the Smoky Tower fish fauna, this locality possibly represents a small, quiet lake with shallow waters. The cross-bedded sandstone in which the fish specimens were preserved, are similar to the Mass Death Layer of the Joffre Bridge Roadcut locality (Ch. IV) (M.V.H. Wilson, pers. comm.). It is possible that the cross-bedded sandstone indicates a crevasse splay from a stream or river into an oxbow lake or shallow swamp, that enabled the fish to enter the area where they then died after spawning, or from extreme temperatures or low oxygen. The crevasse splay may then have provided the sediment to cover the fish.

The new species of percopsid from Smoky Tower extends the geological history of this family into the middle of the Palaeocene. Previously the oldest known members of the Percopsidae were *†Amphiplaga* and *†Erismatopterus* from early to middle Eocene deposits in the Green River Formation.

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IV. A NEW PALAEOCENE GENUS AND SPECIES OF PARACANTHOPTERYGIAN FROM JOFFRE BRIDGE, ALBERTA

INTRODUCTION

In 1984, a mass-death layer of freshwater fish was discovered by a Red Deer resident, Betty Speirs, at the Joffre Bridge roadcut locality near Red Deer, Alberta. This locality is part of the Palaeocene Paskapoo Formation which crops out throughout the Foothills and Central Plains of Alberta. It has been dated as mid-Tiffanian, based on mammal remains (Fox, 1990), which were located 20 metres below the fish layer.

As reported by Wilson and Williams (1991), the teleost fish fauna at this site includes *Speirsaenigma lindoei* (Osmeridae), an amiid and an osteoglossomorph (Li Guo-Qing, pers. comm.), but the vast majority of fish specimens in the mass-death layer are a new species of paracanthopterygian fish. This new species is represented by about 1795 specimens collected by the University of Alberta Laboratory for Vertebrate Paleontology, mostly by technician L.A. Lindoe, during the summers from 1984 until 1993 (Wilson and Williams, 1991; L.A. Lindoe, pers. comm.).

The new species that is the subject of this paper, and the species described in the previous chapter, from Smoky Tower, Alberta, also in the Paskapoo Formation, are, along with †*Mcconichthys* Grande from the Palaeocene of Montana, the oldest freshwater paracanthopterygians known. The only older members of the superorder are in the Cretaceous family †Sphenocephalidae. These are two species of †*Sphenocephalus* Agassiz from marine Campanian deposits in Germany (Rosen and

Patterson, 1969) and a newly described genus, †*Xenyllion*, from marine Cenomanian deposits in Alberta (Wilson and Murray, in press). Other remains from Albian or Cenomanian deposits of the United States, that are similar to †*Xenyllion*, have also been recently described (Stewart, in press).

The new species from Joffre Bridge is of particular phylogenetic interest as it brings to light some character state conflicts that result from the cladogram of paracanthopterygian relationships proposed by Patterson and Rosen (1989). A cladogram may be viewed as a hypothesis of phylogenetic relationships, and as a hypothesis it may be tested by the addition of new species. This new species has different character state combinations from the previously known paracanthoptergyians, and could be aligned with two different proposed lineages based on the character states used by Patterson and Rosen (1989). Placing the species from Joffre Bridge with one or the other of the two lineages would then mean either that the other character state supporting the alternate placement should be interpreted as a homoplasy of the alternate lineage and the species from Joffre Bridge, or that the polarity of some character states of Patterson and Rosen (1989) is incorrect. The new species thus provides information that may result in a new hypothesis of phylogenetic relationships for at least some members of the superorder.

GEOLOGY

The age of the Joffre Bridge Roadcut locality has been determined using three independant approaches: mammalian succession (Fox, 1990); palynostratigraphy

(Demchuck, 1987, 1990); and magnetostraticraphy (Leberkmo *et al.*, 1992). The results of all three dating techniques agree well (Leberkmo *et al.*, 1992) and place the Joffre Bridge Roadcut locality in the middle of the Palaeocene. Mammal ages have become the primary chronological reference for Tertiary nonmarine sediments in North America (Woodburne, 1987), and the mammal remains studied by Fox (1990) indicate a North American Land-Mammal Age of middle Tiffanian, Ti_3 zone, for the Joffre Bridge site. Radiometric dates are not available for Paskapoo strata in the Red Deer area.

The geology of the Joffre Bridge Roadcut locality is currently being studied by Georgia L. Hoffman (Department of Biological Sciences, University of Alberta). Hoffman's research (pers. comm.) indicates that this locality lay near the shifting margin of a freshwater Palaeocene fluvial channel. The active channel moved southwards, gradually abandonning its old channel, which developed into an oxbow lake (Lake Speirs). Later, the lake appears to have become reconnected to the active channel through a breached levee. The layer containing the paracanthopterygian fish described here (the Fish Layer) is thought to have been deposited during the time of breaching.

The Fish Layer (unit 6d of Hoffman) is about 1 cm thick and lies near the top of Hoffman's Upper Lacustrine sequence (unit 6). Hoffman places the Fish Layer at 846 m above sea level. The Mollusc Layer and the Lower Level Vertebrate Bed, which together have produced the mammal remains described by Fox (1990), lie at elevations of 845 and 830 metres respectively. These beds are part of the Lacombe

Member of the Paskapoo Formation as defined by Demchuk and Hills (1991).

ACRONYMS

CAS, California Academy of Sciences; NMC, Canadian Museum of Nature, Ichthyology Collections; SU, Stanford University Collections, at CAS; UALVP, University of Alberta Laboratory for Vertebrate Paleontology; UAMZ, University of Alberta Museum of Zoology.

ABBREVIATIONS

† - denotes fossil taxa

c&s - denotes specimens cleared and stained with Alcian Blue (for cartilage) and Alizarin Red (for bone)

ang, angular; ant, antorbital; boc, basioccipital; brst, branchiostegal ray; ch, ceratohyal; cl, cleithrum; cor, coracoid; den, dentary; ds, dermosphenotic; ect, ectopterygoid; eh, epihyal; end, endopterygoid; ep, epural; epo, epiotic; fr, frontal; hy, hypural; hyo, hyomandibula; ih, interhyal; lac, lacrimal; le, lateral ethmoid; met, metapterygoid; mx, maxilla; na, nasal; nsp, neural spine; op, opercle; pa, parietal; pal, palatine; pcl, postcleithrum; phy, parhypural; pmx, premaxilla; pop, preopercle; ptf, posttemporal fossa; pto, pterotic; ptt, posttemporal; pu, preural centrum; qu, quadrate; ret, retroarticular; sca, scapula; scl, supracleithrum; sn, supraneural; sym, symplectic; u, ural centrum; uh, urohyal; vo, vomer.

MATERIALS AND METHODS

Fossil specimens of the new species were prepared by hand using fine needles. Recent specimens of comparative species were cleared and stained for cartilage and bone following the revised procedure outlined by Taylor and Van Dyke (1985). Drawings were made using a Wild camera lucida attachment on a Wild M5 dissecting microscope.

Material Examined

Amblyopsis spelaea - 3 c&s CAS 78143 (Mitchell, Indiana), *Aphredoderus sayanus* - 3 c&s CAS 57257 (Alachua Co., Florida), *Percopsis omiscomaycus* - 3 c&s UAMZ 3062 (Hay River, NWT), UAMZ 5274, 5275 (no data), †*Amphiplaga brachyptera* - UALVP 13400, 13401 (Eocene, Green River Formation, Fossil Butte, Wyoming), †*Xenyllion zonensis* (Cenomanian, Shaftesbury Formation, Smoky River at Judah, Alberta) - UALVP 32133.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII (*sensu* Nelson, 1994)

Subdivision TELEOSTEI (*sensu* Patterson and Rosen, 1977)

Infradivision EUTELEOSTEI (*sensu* Greenwood *et al.*, 1967)

Sept ACANTHOMORPHA (*sensu* Stiassny, 1986)

Superorder PARACANTHOPTERYGII (*sensu* Patterson and Rosen, 1989)

Order PERCOPSIFORMES (*sensu* Ch. V.)

Family PERCOPSIDAE Regan, 1911

†*Massamorichthys* gen. nov.

Included genera in family - *Percopsis, †Amphiplaga, †Erismatopterus, †Lateopisciculus*

Type and Only Species - *†Massamorichthys wilsoni* gen. et sp. nov.

Diagnosis - As for species.

Etymology - Named for the Mass Death Layer of the type locality, from Latin "massa" abundant, mass, and "mora" death.

†*Massamorichthys wilsoni* sp. nov.

Fig. IV-1

Holotype - UALVP 30842 a and b, part and counterpart.

Topotypic referred specimens - UALVP 21627, 21660, 21758, 23534, 23535, 23538, 23553, 25325, 25417, 25480, 25526, 25614, 25833, 25834, 26528, 27144, 27145, 30842a/b, 30846a, 30878a, 30899a, 31683, 32554, 39089, 39090, 39091, 39092, 39093, 39094.

Locality - Joffre Bridge road cut, on Highway 11, 14 km east of Red Deer, Alberta, Canada. UALVP Locality No. 56 horizon A: the "fish layer"; NE 1/4, S13, T38, R26, W4.

Horizon - Paskapoo Formation, Palaeocene Epoch, Mid-Tiffanian land-mammal age (Fox, 1990).

Diagnosis - Percopsid fish with single arched supraneural dorsal to second and third

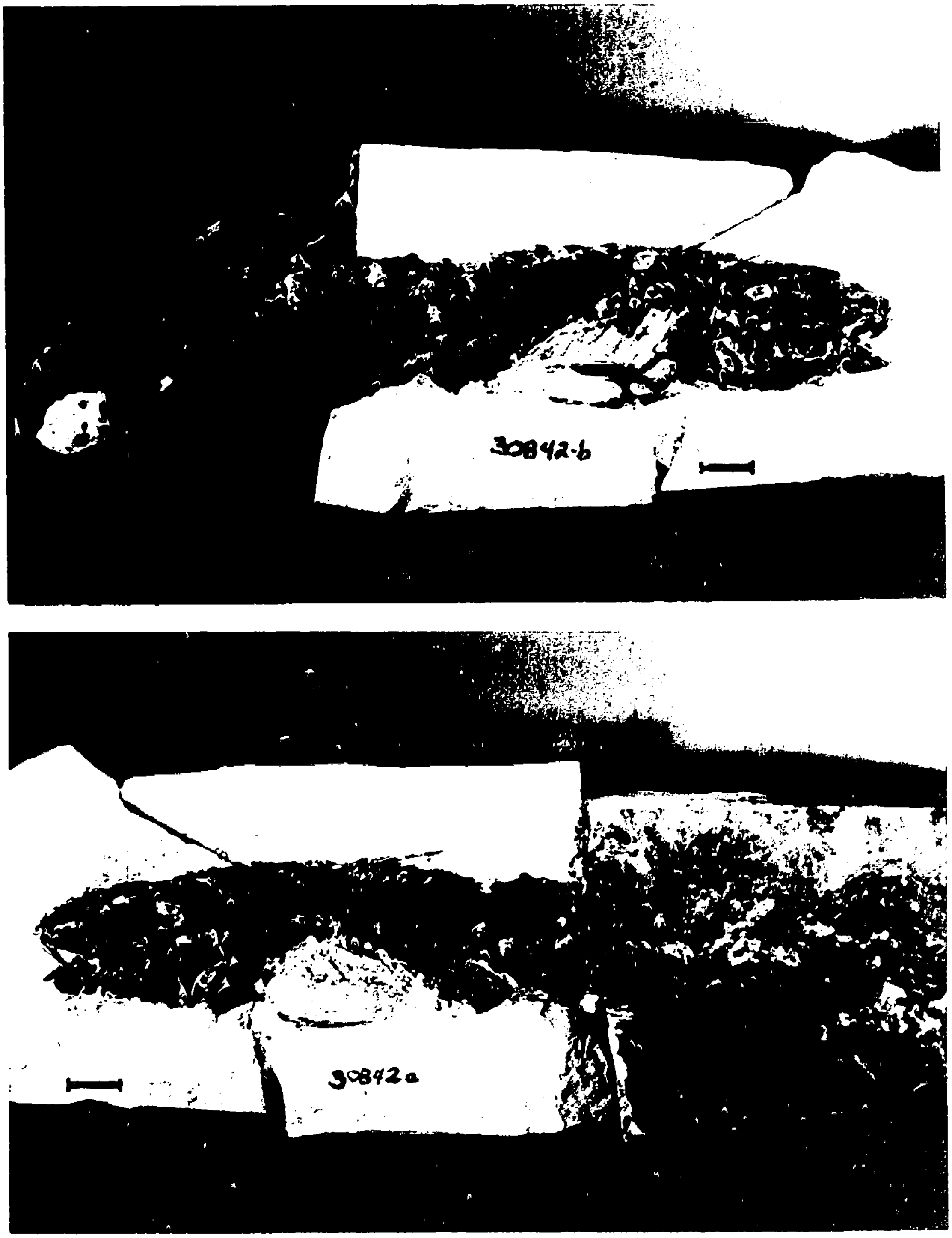

Figure IV-1. †*Massamorichthys wilsoni* gen. et sp. nov., photograph of the holotype UALVP 30842 a and b, part and counterpart. Scale bar = 1 cm.

neural spines; foreshortened second vertebral centrum; "percopsoid projections" (McAllister, 1968) on branchiostegals one through five; and supraoccipital crest extending posteriorly beyond first neural spine; characterized by 42-45 vertebrae.

Etymology - The specific epithet is in honour of Dr. Mark V.H. Wilson, UALVP.

DESCRIPTION

Body form

Because there are a great many specimens from Joffre Bridge, the description that follows is based primarily on a subset of the available specimens selected for their superior preservation. Throughout the description, the number(s) of the specimen(s) which best shows the feature in question is listed. Comparisons to other genera mentioned in the description are based on personal examination of comparative specimens, unless otherwise stated.

The new species from Joffre Bridge (Fig. IV-2) is more similar in its more elongate and slightly depressed body proportions to the Tertiary and Recent percopsiform fishes, such as †*Amphiplaga brachyptera*, than it is to the deeper bodied Cretaceous sphenocephalids. The maximum body depth is about 0.25 SL. The caudal peduncle is narrow and long, also about 0.25 SL. Specimens range from around 5 cm to 15 or 16 cm SL. Meristic counts and measurements of several specimens are given in Tables I and II.

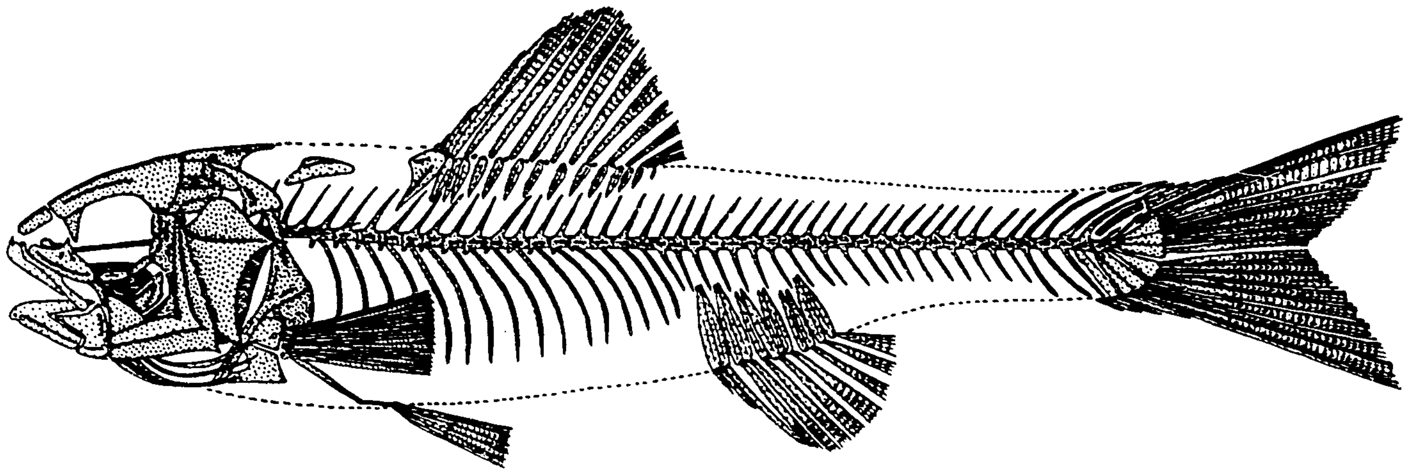

Figure IV-2. Reconstruction of †*Massamorichthys wilsoni* gen. et sp. nov.

Table IV-1. Meristics of †*Massamorichthys wilsoni* gen. et sp. nov.

Specimen	30842	23535	31683	25325	23553	22158	25673	25833	25834
Dorsal fin	IV,13	V,11	IV,8	IV,12	III,12	III,12	IV,12	III,11	IV,8
Dorsal pterygiophore	14	15	13	14	14	14	14?	15	14
Anal fin	III,8	III,8	III,8	III,8	III,8	II,8	III,8	III,8	III,8
Anal pterygiophore	8	10	10	10	7+	10	9	11	9
Pectoral rays	15	17	12+	16	15+	14	17	14	17
Pelvic rays	8	8	8	6+	7	7+	8	8	8
Caudal fin rays	i,8,8,i	i,8,8,i	i,8,8,i	i,8,8,i	i,8,8,i	i,8,8,i	i,8,8,i	-	-
Vertebrae	45	44	43		43	45	45	45	44
* preanal	22	22	20	21	22	22	22	22	21?
* postanal	23	22	23		21	23	23	23	23

*counts are from in front of and behind the first anal pterygiophore

Table IV-2. Measurements of †*Massamorichthys wilsoni* gen. et sp. nov.

Specimen	30842	23535	31683	25325	25624	22158	25673	25833	25834
Standard length	140.8	140.8	142.9	127.2	72.2	81.1	74.8	143.1	139.4
Head length	34.8	33.7	34.0	32.4	18.1	18.5	17.2	32.2	29.1
Body depth	30.4	27.8	30.5	25.4	13.4	14.9	10.8	27.4	24.6
Caudal peduncle depth	13.0	9.1	12.5	10.0	5.5	6.7	4.3	12.4	11.3
Caudal peduncle length	41.9	40.2	44.8	34.8	20.0	21.7	20.5	36.2	35.0

Neurocranium and skull roof

The skull roof (Fig. IV-3 and 4) is well preserved in UALVP 39094, in which the left half is visible in dorsal view although the fish is preserved laterally. The supraoccipital (UALVP 30899a, 39094) is shaped like a battleaxe in lateral view, as in most paracanthopterygians. The crest is long and thickened dorsally. Posteriorly it extends past the first neural spine. The parietals are large, flat and rectangular, very similar to those of †*Mcconichthys* (Grande, 1988: fig. 3), and form the medial wall of the posttemporal fossa. They do not meet in the midline, being separated by the supraoccipital.

The posttemporal fossa (UALVP 39094) is large and oval shaped. It is bordered medially by the parietals, laterally by the pterotics and anteriorly by the frontals. The epiotics form the posteromedial wall of the fossa, as in †*Mcconichthys*. Most specimens have a saccular (= sagitta) otolith preserved in place. The otolith is large, 4.4 mm in length in UALVP 23535 in which the head length measures 30.5 mm, and 2.6 mm in UALVP 39089, which has a head length of 13.0 mm. The right otolith in UALVP 39089 (Fig. IV-5) is the best preserved, showing the external face, beside it, the medial face of the left otolith is visible, but somewhat eroded. The main diagnostic features of an otolith are its outline, the pattern and degree of incision of the sulcus with any associated colliculi, convexity of the inner face, convexity or concavity of the external face and the thickness of the otolith (Nolf, 1985). The only one of these informative characters that is visible on this otolith is its outline. There are more radial lobes present that shown in the figures of otoliths for *Aphredoderus*

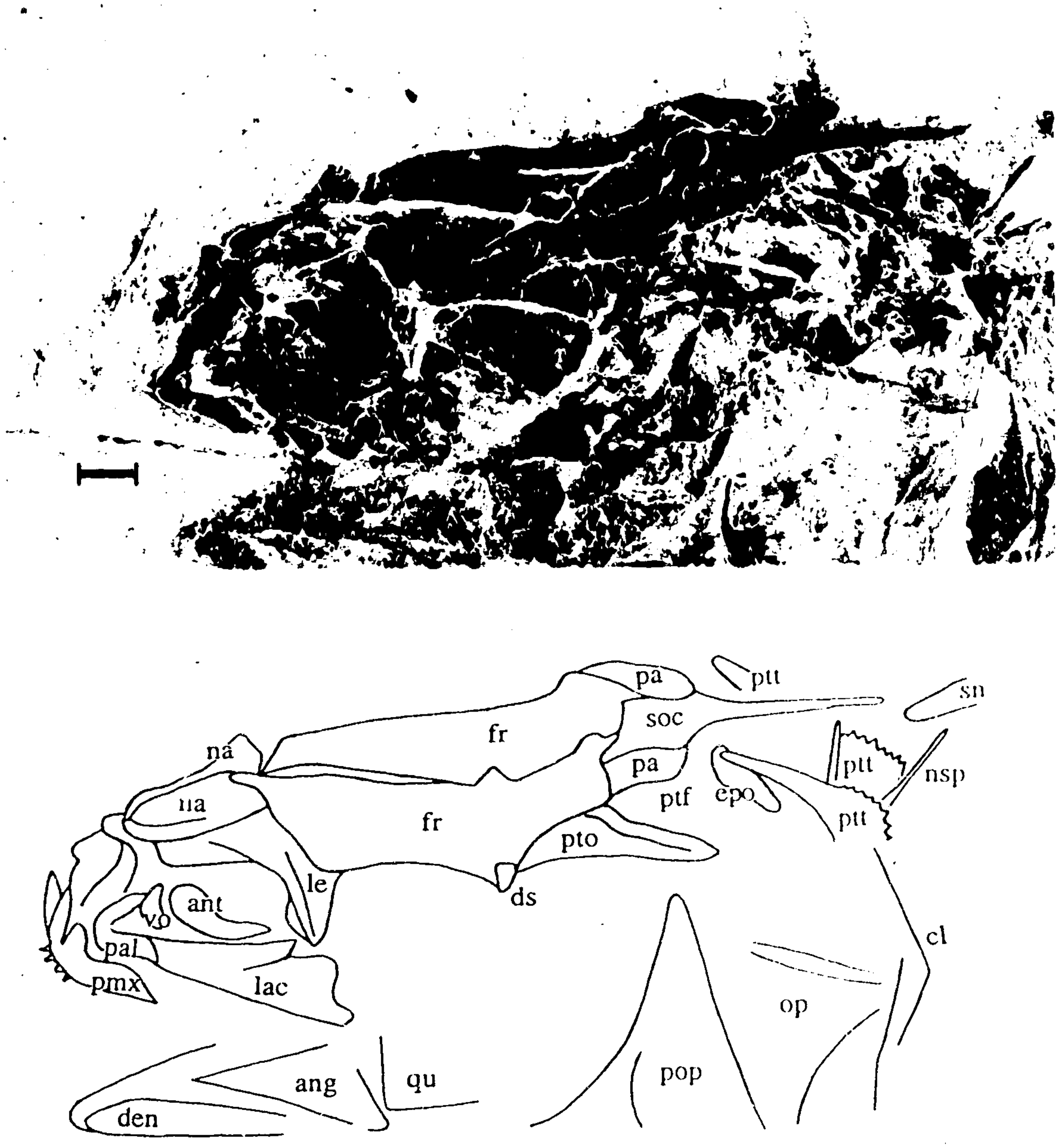

Figure IV-3. †*Massamorichthys wilsoni* gen. et sp. nov., photograph and camera lucida drawing of the skull, UALVP 39094 in dorsolateral view. Anterior to left. Scale bar = 2 mm.

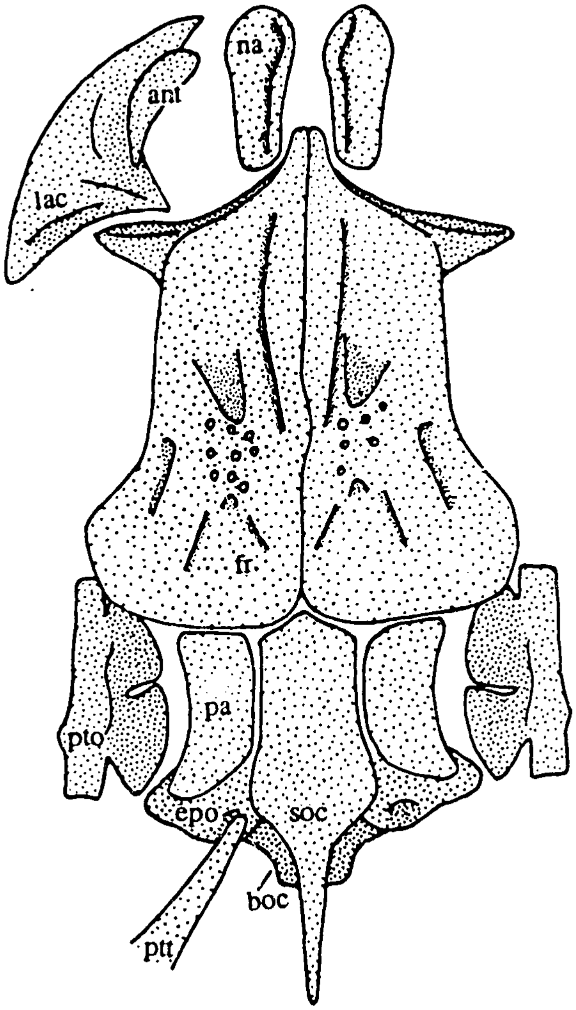

Figure IV-4. †*Massamorichthys wilsoni* gen. et sp. nov., reconstruction of the skull roof in dorsal view, based on UALVP 39094.

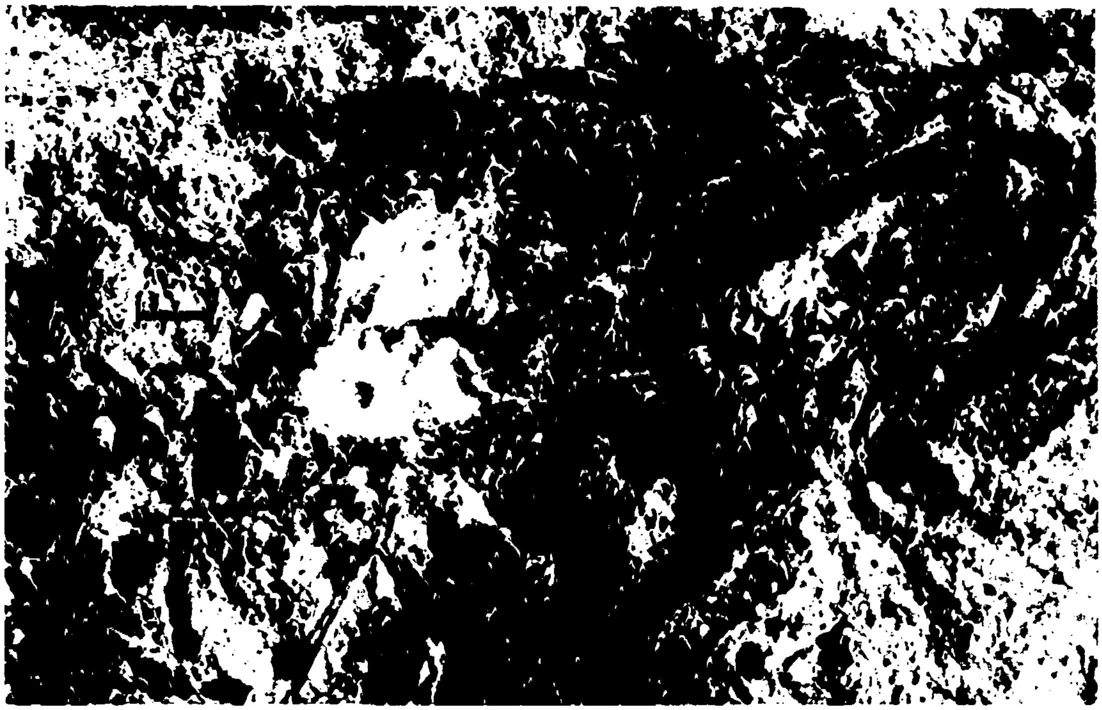

Figure IV-5. †*Massamorichthys wilsoni* gen. et sp. nov., photograph of the otolith, UALVP 39089. Anterior to the upper right. Scale bar = 1 mm.

and *Percopsis*, but in general terms, there is a similarity between the shape of these otoliths and those figured for *Aphredoderus sayanus* and *Percopsis transmontana* by Nolf (1985: fig. 48 b and c), but the new species is slightly more oval in shape than the other two genera.

The frontal (UALVP 39094) is similar to that of *Percopsis*, in that it is truncated anteriorly (Rosen and Patterson, 1969). On the anterior portion is a trough for the supraorbital sensory canal, which is enclosed by bone for a short length above the orbit, with a few "pores" around the anterior opening of the tunnel. There is a medial crest that borders the trough for the canal. There are no spines or tubercles ornamenting the frontals.

The nasals are long rectangular bones, rounded anteriorly. The sensory canal from the frontals continues anteriorly over the nasals (UALVP 39094) in a trough. As in other paracanthopterygians, the nasals are rolled upwards medially to form the trough.

The pterotic (UALVP 25526) has the wingshape common in paracanthopterygians. It has a lateral ridge dorsal to the groove for the sensory canal, and a narrow anterior extension. There is a notch on the posterior portion of the pterotic through which passed the sensory canal to the preopercle.

The lateral ethmoid (UALVP 23535, 39094) is rectangular and lies slightly posterior and medial to the ascending dorsal process of the lacrimal. It is neither sutured to nor fused with either the vomer or the parasphenoid.

Although several specimens are preserved so as to reveal the ventral surface of the braincase, none clearly show an intercalar or prootic bone. The vomer is almost complete in UALVP 30878a and 39089. The anterior end of the bone broadens slightly laterally, and the posterior end appears to taper to a point posterior to the lateral ethmoid. There are no teeth anywhere on the vomer. Overall, the vomer is very similar to that of *Percopsis omiscomaycus*, but the anterior end is relatively broader in the new species.

The parasphenoid (UALVP 21627 and 39089) is straight and narrow as in *Percopsis* rather than broad as in *Aphredoderus*. There is a central ridge down the ventral surface, and large lateral expansions on both sides, just anterior to the prootic.

The basioccipital and traces of the exoccipitals are visible in UALVP 30878a. It appears likely that the exoccipital condyles were separated to the same extent as in *Percopsis*.

Of the infraorbital series, the antorbital, lacrimal and four other bones (infraorbitals 2-5) are present (UALVP 21758, 27145). The antorbital (UALVP 39094), just in front of the ascending process of the lacrimal, is comma-shaped, with the posteroventral edge thickened. It is larger than that of †*Sphenocephalus* (Rosen and Patterson, 1969: fig. 29), †*Mcconichthys* (Grande, 1988: fig. 3), and *Percopsis*.

The lacrimal bears a large dorsal process, slightly posterior to the middle of the bone. A deep lateral shelf on the lacrimal formed a flange over the sensory canal. The edge of the flange is smooth, as is the ventral edge of the lacrimal. The second infraorbital, displaced ventrally in UALVP 27145, also has a flange but it is not as deep as the one on the lacrimal. There is no spiny ornamentation on any of the infraorbitals.

Jaws and Suspensorium

The jaws and suspensorium are illustrated in Figure IV-6. The gape extends back just to the front of the orbit, with the quadrate/angular articulation under the anterior part of the orbit. There are numerous small, fine, sharp teeth on the premaxilla and dentary.

The ascending process of the premaxilla (UALVP 25614) is about 1.5 times the height of the articular process. The two are separated by a deep cleft. The alveolar

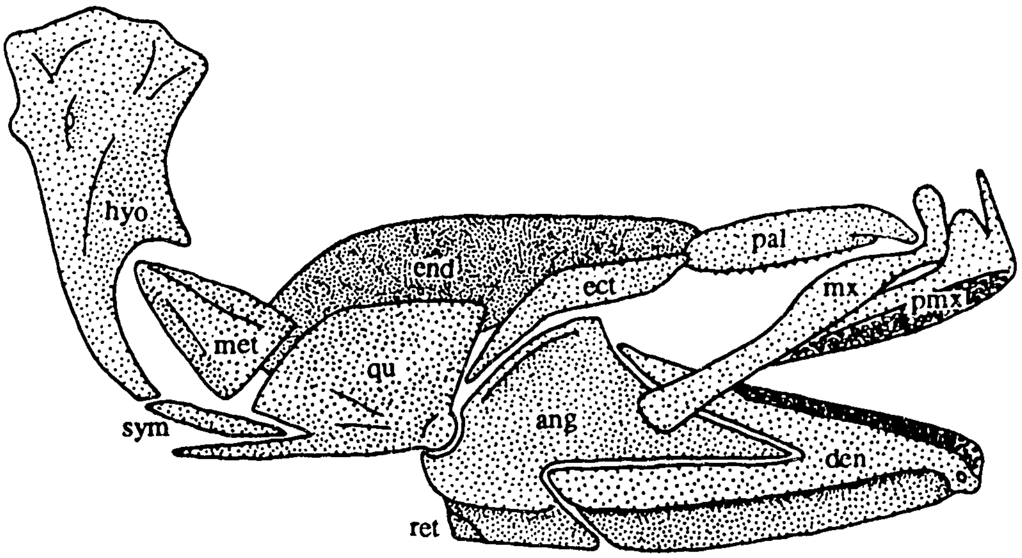

Figure IV-6. †*Massamorichthys wilsoni* gen. et sp. nov., reconstruction of the jaws and suspensorium, based on UALVP 21660, 23535, 30842 a/b and 39094. Anterior to right.

process is not segmented, and there is no postmaxillary process on the premaxilla (UALVP 30846a). A foramen is present in the alveolar process just posterior to the articular process (UALVP 30878a) as in *Percopsis*. The premaxilla is more robust than the maxilla, but, as in *Percopsis*, it is shorter and does not reach the dentary (UALVP 30842b).

The maxilla (UALVP 23535) bears a dorsal process that is long and low, the highest point more anterior to the middle of the maxilla and not higher than the maxillary articular head. The posterior end of the maxilla is slightly expanded. There are no supramaxillaries and no teeth on the maxilla.

A retroarticular (UALVP 27145) is present at the posteroventral corner of the angular. It is small and rounded, fitting into the excavated posterior edge of the angular, and does not contribute to the articulation with the quadrate.

The dentary (UALVP 30842b) has small, fine, sharp teeth similar to those on the premaxilla. Anteriorly, there are two foramina as in *†Mcconichthys* (Grande, 1988: fig. 5), at either end of the short bone-enclosed portion of the groove for the sensory canal. The upper limb in lateral view narrows posteriorly, while the lower limb is deep and the posterior end is vertical. The ventral surface of the dentary near the symphysis is distinctly notched.

The angular (UALVP 27144, 21660) is deeply notched posteriorly to receive the condyle of the quadrate. The dorsal edge of the angular is flat with a postero-dorsal projection, similar to that of *Percopsis*. The flange on the base of the angular is shallower and shorter than that seen in *†Xenyllion*.

The hyomandibula (UALVP 23553, 23538, 25325, 30842b) is vertical as in †*Amphiplaga*, with a single head. There is an anteroventral projection towards the metapterygoid, similar to that of †*Xenyllion*. The length of the ventral shaft that articulates with the symplectic is about half the width of the head and both the ventral shaft and the symplectic incline anteriorly. The foramen for N. VII is visible in the head of the hyomandibula.

The symplectic (UALVP 30842a) is strongly inclined forwards, such that the condyle of the quadrate lies beneath the anterior part of the orbit, below the second infraorbital. The symplectic may articulate in a groove on the quadrate as it does in *Percopsis, Amblyopsis* and †Sphenocephalidae.

There are no teeth seen on the metapterygoid, ectopterygoid or endopterygoid (UALVP 30842b). The metapterygoid seems to be relatively larger than that of percopsiform fishes, and it is roughly rectangular in shape. The ectopterygoid is similar to that of †*Xenyllion*, but lacks a dorsal process. The endopterygoid is not clearly visible.

Fine long teeth, like those in the jaws, are visible in UALVP 25325 in a position which indicates they were probably on the palatine. The anterior portion of the palatine is preserved in lateral view in UALVP 39094 and in dorsal view in UALVP 27144. It has a well-developed maxillary process. No teeth are visible on the head of the vomer (UALVP 39094).

Hyoid arch and opercular region

The preopercle (UALVP 21660, 25480, 27144) (Fig. IV-7) is similar overall to that of other percopsids. The horizontal limb is just slightly longer than the vertical. Behind a flange is an open groove for the sensory canal, which is not enclosed by bone anywhere on the preopercle. The limbs form an angle just greater than 90 degrees. The vertical limb tapers to a point; the horizontal limb is of uniform thickness along its length, and the anterior end is blunt and straight. There are no spines or serrations along the horizontal limb but the posterior edge of the vertical limb has thirteen or more small spines of equal size, and a larger spine at the angle. The flange has a single spine at its angle.

The subopercle (UALVP 25480) is visible but partly hidden under the opercle. It has a blunt anterior process, not a spike or a spine such as that found in *†Mcconichthys* (Grande, 1988: fig. 4). An interopercle is visible in UALVP 21660 and 27144 but details of its morphology are not clear.

The opercle (UALVP 30842a, 27144) has a pronounced horizontal ridge on both medial and lateral sides, that projects posteriorly as a strong spine, as is typical in paracanthopterygians. Above this ridge is a dorsal projection that is excavated anteriorly. Ventral to the ridge, the anterior edge of the opercle is thickened and curves away from the preopercle ventrally, becoming a ventral spine, also typical in paracanthopterygians. The posterior edge ventral to the horizontal ridge is concave, but of less curvature than in *Percopsis*. All the edges of the opercle are smooth, with no serrations.

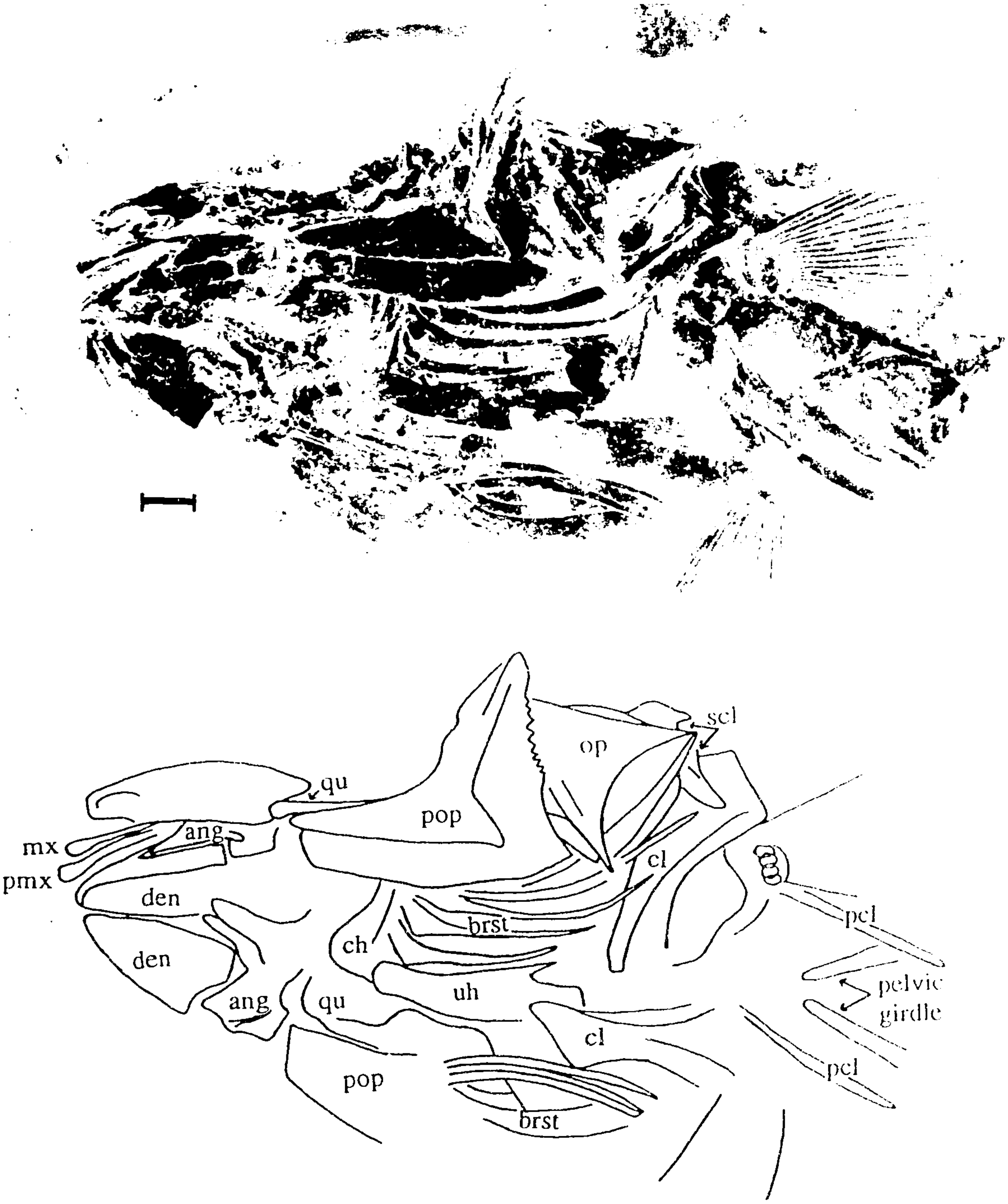

Figure IV-7. †*Massamorichthys wilsoni* gen. et sp. nov., photograph and camera lucida drawing of the skull in lateroventral view, UALVP 21660. Anterior to left. Scale bar = 2 mm.

The urohyal (Fig. IV-8A) (UALVP 31683, 25480), is roughly rectangular in lateral view, and similar to that of *Amblyopsis*. It has a ridge that runs from the anteroventral corner to the posterodorsal edge, where it projects slightly. A second ridge is present along the ventral edge of the urohyal. The anterior articular head is ventral to a thin flange of bone that forms the anterodorsal edge.

The ceratohyal (UALVP 21660, 30842b, 26528, 39094) (Fig. IV-8B) narrows in the centre; the posterior part is much larger than the anterior part. Traces of two hypohyals are visible on UALVP 26528. There are six branchiostegal rays with the "percopsoid projections" of McAllister (1968) on at least the five anterior rays. The head of the sixth ray is not visible in any specimen. The anterior five rays are acinaciform, and the sixth ray is scimitar-shaped, almost twice as broad as the other five. A complete epihyal (posterior ceratohyal) has not been seen.

Vertebral column

The total number of vertebrae, counting PU1+U1 and U2 as one centrum each, is 42-45; there are 18-21 in front of the first anal pterygiophore, and 23-25 behind. The centra are long and slender. The second centrum (UALVP 23535, 30842a) is shorter than centra 1 and 3. Unlike in †*Mcconichthys* (Grande, 1988: fig. 6), there are no zygapophyses overlapping the following centrum on the anterior (or any other) centra, nor are there anterodorsal projecting prezygapophyses as in †*Amphiplaga* (Rosen and Patterson, 1969:fig. 21). The first parapophyses occur on the first centrum (UALVP 23535, 27145) and are present on all the preanal centra, although they

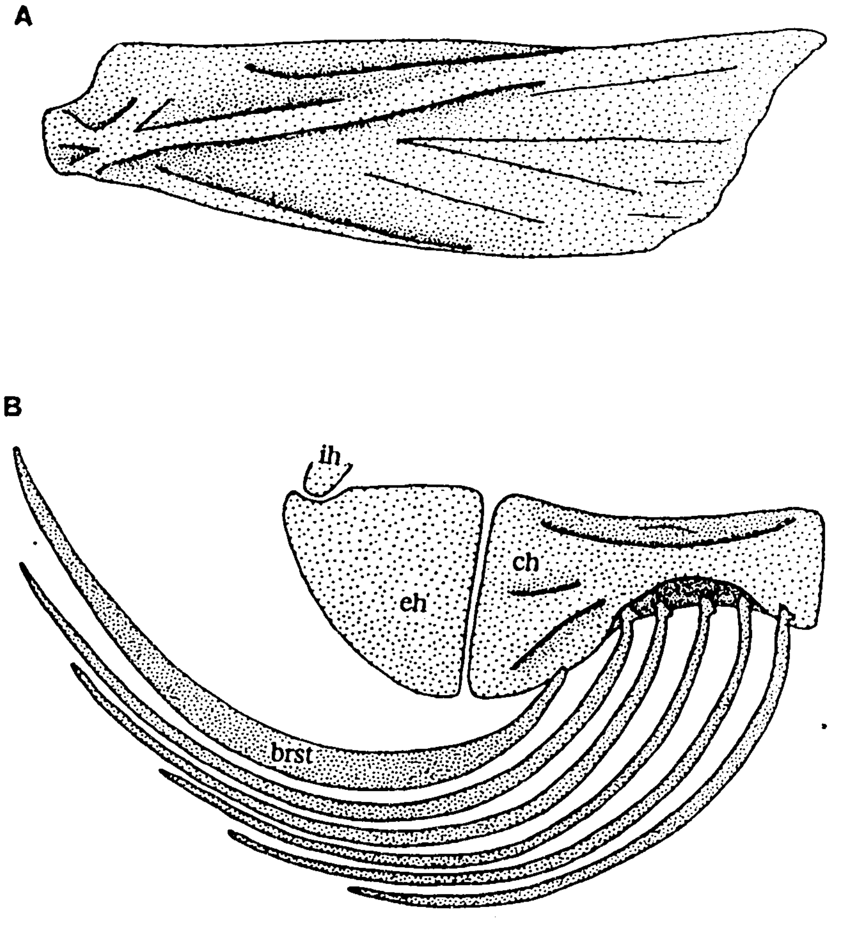

Figure IV-8. †*Massamorichthys wilsoni* gen. et sp. nov., reconstruction of: A) urohyal, anterior to left; based on UALVP 25480 and 31683, and B) ceratohyal, epihyal and branchiostegal rays, anterior to right, based on UALVP 26528.

diminish in size on the last few. The anterior centra have well-developed parapophyses that angle anteriorly from the centra, then project laterally. They are broad and rounded at their tips.

Thick and robust pleural ribs insert behind the parapophyses, with the head of each rib articulating on the posterior surface of its parapophysis. The first pleural rib is on the third centrum and ribs continue on all the following centra up to and including the last preanal centrum, for a total of 15 to 18 pairs of pleural ribs.

The intermuscular bones, called epipleurals by most authors but epineurals following Johnson and Patterson (1993), are present on the first three vertebrae, arising from the neural arch (UALVP 23535). The epineurals are each almost as long as three centra.

The first neural arch is not in close articulation, nor is it fused, with the supraoccipital crest (UALVP 30899a). The first neural spine is similar to the rest, not reduced nor modified as it is in carapids (Markle and Olney, 1990: fig. 278). A single large supraneural lies between the supraoccipital crest and the dorsal fin, dorsal to the second and third neural spines. It is long and slightly curved, with a triangular flange in the middle of the dorsal surface.

Caudal skeleton

The deeply forked caudal fin (Fig. IV-9) has18 principal rays, 16 branched (formula i,8,8,i), and 8-10 dorsal and 7-9 ventral procurrent rays. The caudal skeleton contains six hypurals, none fused together. Hypurals 1 and 2 articulate on the fused

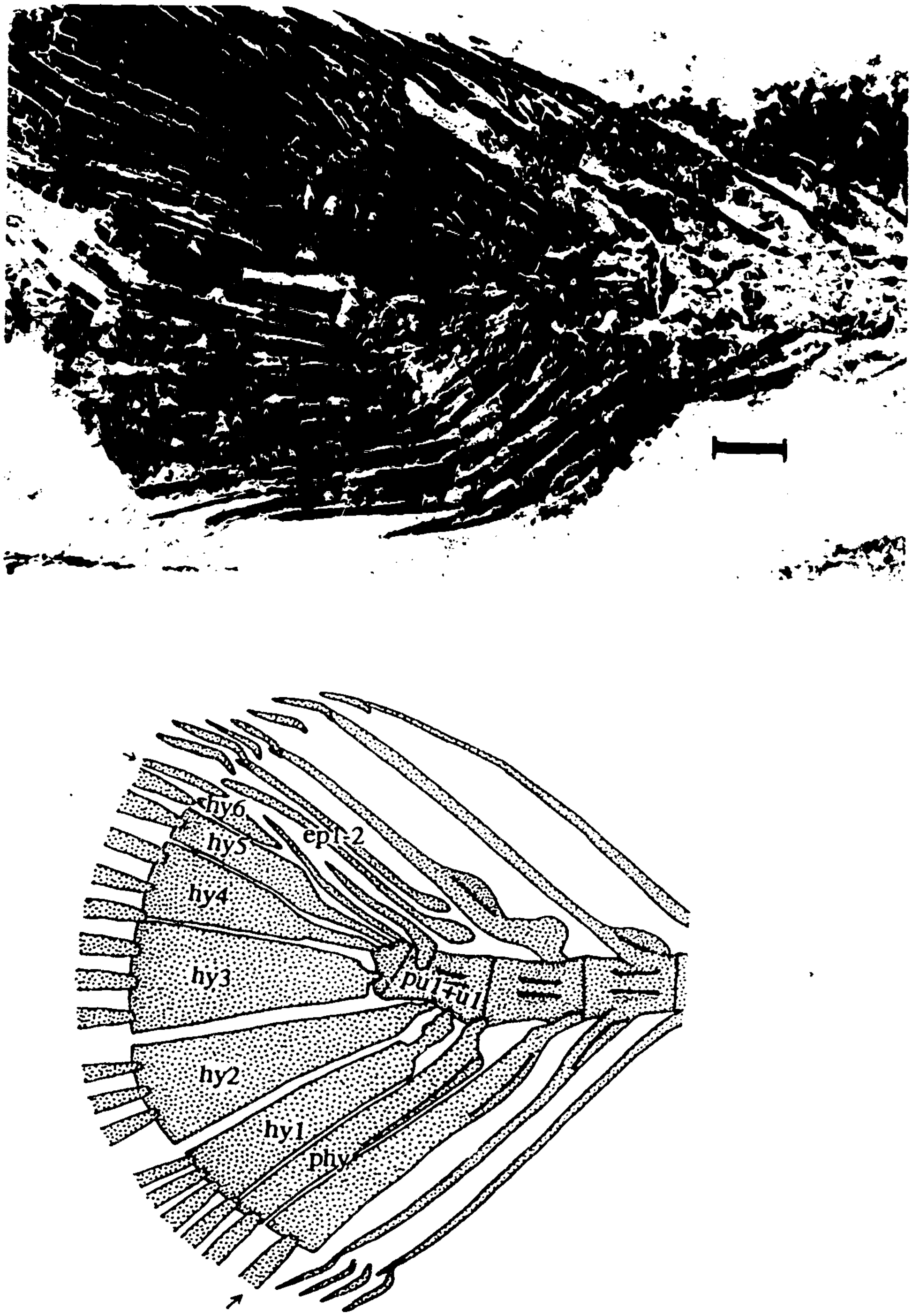

Figure IV-9. †*Massamorichthys wilsoni* gen. et sp. nov., photograph and reconstruction of the caudal skeleton, UALVP 23535. Anterior to right. Scale bar = 2 mm.

first preural and first ural centra (PU1+U1), along with the parhypural. Hypurals 3, 4 and 5 articulate on the second ural centrum (U2), but hypural 6 is free. There are two epurals between the first uroneural (UN1) and the neural spine of the second preural centrum (NPU2). The epurals are as long as the posterior neural spines and have slight expansions at their proximal ends. The second uroneural curves upwards and terminates between hypural 6 and UN1. There is a full neural spine on PU2, with a small anterior midsagittal flange just above its base (UALVP 31683). The neural spine on the third preural centrum (NPU3) also has a small anterior midsagittal flange (UALVP 31683, 23535), and that of the fourth preural centrum may have a similar flange (UALVP 23535).

The parhypural is broad, almost as wide at its distal end as hypural 1, and has a flange on the anterior edge that is broad proximally and narrows to a point that almost reaches the distal end of the parhypural. The haemal spine on PU2 is as wide distally as the parhypural and also has an anterior flange, but this flange is smaller and confined to the base of the spine. The haemal spine of the third and fourth preural centra also bear small anterior midsagittal flanges proximally.

Dorsal fin

The dorsal fin is situated midway along the back, its origin slightly closer to the head than the caudal fin. It is quite large and triangular. There are four (UALVP 31683) or five (UALVP 23535, 25325) spines and ten rays, the last ray doubled. The first spine is very short and may not have protruded all the way through the skin. The second spine is slightly longer, about one-sixth the length of the longest ray. The third spine is just under half the length of the longest ray, and the fourth spine is five-sixths the length of the longest ray. The fifth spine is the longest, just slightly shorter than the longest ray.

The dorsal fin is supported by 14-15 pterygiophores (13 in UALVP 39094) in total, the first four supported the five spines. The first pterygiophore has an anterior projecting flange, thickened dorsally similar to that of †*Mcconichthys* (Grande, 1988:figs. 1 and 2). The rest of the pterygiophores have a normal triangular shape. Some of the middle pterygiophores are also preserved.

Anal fin

The anal fin has its origin slightly posterior relative to the dorsal fin insertion. The anal fin is slightly smaller than the dorsal fin, but it is also triangular. There are three spines and seven (UALVP 23535) or eight (UALVP 25834) rays in the anal fin. All three spines articulate with the first two pterygiophores. In most specimens there are 11 or 12 pterygiophores supporting the fin (only 10 in UALVP 25834). Rod-shaped middle pterygiophores are visible above and between some of the proximal pterygiophores.

Pectoral girdle and fins

A reconstruction of the pectoral girdle is shown in Figure IV-10. The pectoral is composed of 15-17 rays. It inserts low on the body, almost at the ventral edge

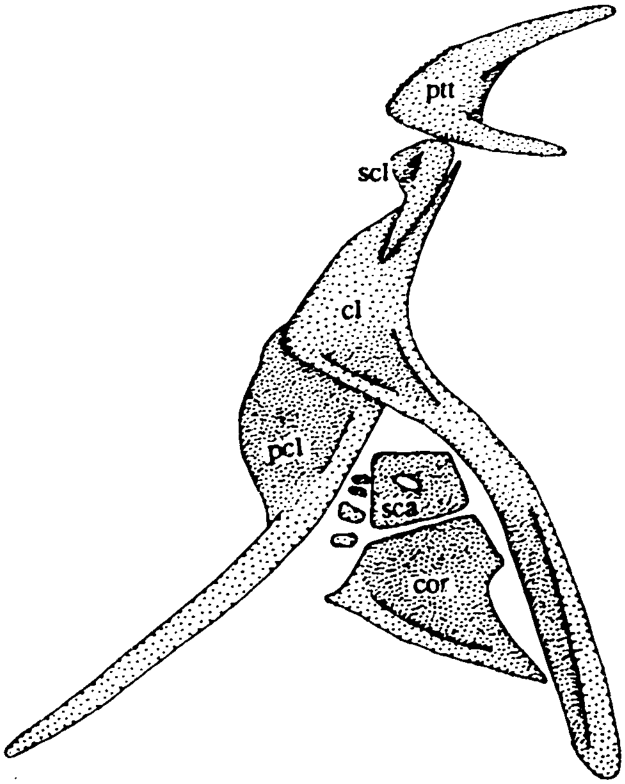

Figure IV-10. †*Massamorichthys wilsoni* gen. et sp. nov., reconstruction of the pectoral girdle and postcleithrum, based on UALVP 21660, 23535 and 39091. Anterior to right.

of the body, anterior and dorsal to the pelvic fin. There are four hourglass-shaped ossified radials (UALVP 23534, 23535). The scapular foramen is in the centre of the square scapula (UALVP 23535). The anterior process of the coracoid (UALVP 23535, 25325) arches deeply to meet the cleithrum, as in other percopsids. The coracoid and scapula are not sutured together; their placement indicates they would have been joined by cartilage.

The cleithrum (UALVP 27144, 31683, 39094) has a long ventral projection similar to that of *Percopsis*. Posterodorsally it is plate-like and triangular (like that of percopsids), just below the vertebral column. There is a tapered dorsal projection running alongside the supracleithrum (UALVP 27144, 31683, 39094) as in *Percopsis*. The supracleithrum (UALVP 39091) is a rod-like structure, extending ventrally to the middle of the dorsal plate of the cleithrum. Below the point of articulation with the posttemporal is a thin triangular flange projecting posteriorly from the supracleithrum. The posttemporal (UALVP 30842b) is ornamented with 14 or more spines on the posterior half of the dorsal edge.

The postcleithrum (UALVP 23535, 25833, 27144) has a large dorsal plate (postcleithrum 2 of Gottfried, 1989), which is fused to the long ventral rod-like portion (postcleithrum 3 of Gottfried, 1989). It crosses the pelvic girdle but may not have been attached to it.

Pelvic girdle and fins

The pelvic fins are subthoracic (UALVP 25417, 30842b, 23535) with no contact to the pectoral girdle. The left and right halves of the pelvic girdle overlap in the midline (Fig. IV-11A and B), and are similar to those of *P. omiscomaycus*. There are seven rays, the first unbranched. A pelvic splint is visible in UALVP 32554, 25833 and 27145. The anterior projections of the pelvic girdle cross the postcleithra, but may not attach to them.

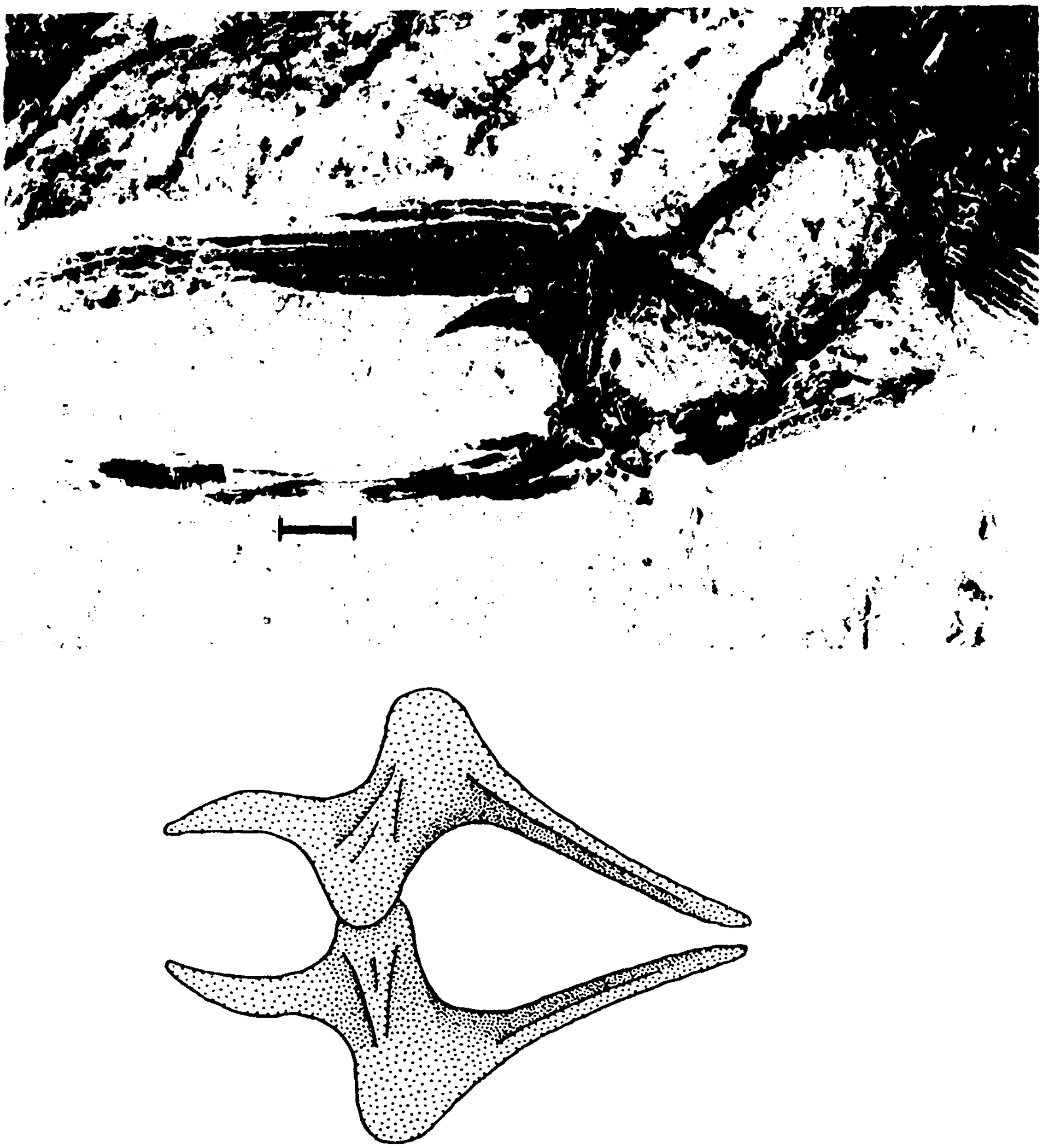

Figure IV-11. †*Massamorichthys wilsoni* gen. et sp. nov., pelvic girdle. A. photograph of UALVP 30842 b; B. reconstruction. Anterior to right. Scale bar = 2 mm.

Scales

Scales cover the whole body (UALVP 30842b) and extend anteriorly to cover the opercle (UALVP 30846a). The scales are almost circular, and small, (about 1.3 by 1.2 mm on UALVP 30842 and about 0.65 mm on UALVP 39090). The scales on the body are ctenoid, and those on the opercle appear to be cycloid. The body scales have about 18-21 strong long ctenii, which appear to be of the peripheral ctenoid type as described by Roberts (1993) that are also found in *Aphredoderus sayanus*. The ctenoid scales have about 18-24 closely spaced circuli, and the focus is extremely close to the posterior edge of the scale. No radii are visible. Based on the small size of the scales, there were probably more than 100 scales along the length of the body. The scales on the opercle (UALVP 39090) are also circular, but slightly larger than those on the body (about 0.8-0.96 mm diam in UALVP 39090). These cycloid scales also have about 18-20 closely spaced circuli and no radii are visible.

RELATIONSHIPS OF THE NEW SPECIES FROM JOFFRE BRIDGE

The new species from Joffre Bridge is classified in the Superorder Paracanthopterygii based on the presence of a single supraneural bone, a full neural spine on the second preural centrum, and presence of two epurals in the caudal skeleton. The most recent cladistic analysis of the paracanthopterygian fishes, that of Patterson and Rosen (1989), included a cladogram of relationships that had the Order Percopsiformes disbanded into three lineages (Percopsidae, Aphredoderoidei, and †*Libotonius*) which formed a trichotomy in the basal position of the superorder.

†Sphenocephalus, a Cretaceous marine fish which, until recently, was the oldest known member of the superorder, was previously classified in the Order Percopsiformes, but in the revised cladogram of Patterson and Rosen (1989:fig. 16) it was considered closer to the higher paracanthopterygians than the Percopsidae, *†Libotonius* and the Aphredoderoidei (Aphredoderidae plus Amblyopsidae). The rest of the groups in the superorder are placed in more derived positions on this cladogram, with the Ophidiidae and Carapidae forming another polytomy above *†Sphenocephalus*, followed by the Bythitoidei, and finally the Order Gadiformes forming the sister group to the Pediculati (Lophiiformes plus Batrachoidiformes).

Recently, a new species of paracanthopterygian, *†Xenyllion zonensis*, has been described and classified in the Family †Sphenocephalidae, based on the unique recurved posterodorsal edge of the opercle and the preopercular spines (Wilson and Murray, in press). *†Xenyllion* was found in Alberta, in deposits dated as Cenomanian, making it the oldest known paracanthopterygian.

The cladogram presented by Patterson and Rosen (1989) is based on twenty presumed synapomorphies, the first thirteen of which apply to the groups below the gadiforms and pediculates. Characters fourteen through twenty either cannot be determined or are not present in the new species from Joffre Bridge; therefore, this fish is not classified with either the gadiforms or pediculates.

Of the thirteen applicable characters, the first four have derived states that are considered synapomorphies of the Superorder Paracanthopterygii. These are: 1) presence of a full neural spine on the second preural centrum; 2) reduction from three to two epurals in the caudal skeleton; 3) a single supraneural above the first or second neural spine; and 4) an enlarged intercalar. The first three are present in the new species from Joffre Bridge, and the fourth cannot be determined.

Characters eight through thirteen have states that distinguish the group named Anacanthini, composed of the ophidiids, carapids, gadiforms and pediculates (Patterson and Rosen, 1989: fig.16) from the lower paracanthopterygians. Derived states of characters eight, ten, eleven, and twelve (loss of myodome, loss of interarcual cartilage, exoccipital condyles cartilage filled and tube-like, and pattern of the third pharyngobranchial respectively) cannot be assessed on specimens of the new species from Joffre Bridge, because of the preservation of the fossil material. This leaves four characters (numbers five, six, seven, and nine) which might determine the placement of the new species relative to the percopsids, aphredoderoids, †*Libotonius* and sphenocephalids.

The derived state of character five of Patterson and Rosen (1989: fig.16) is the second or second and third centra being shorter than the first, or first and second, and fourth centra. This state is evident in the new species (UALVP 23535, 30842a). Character six, with the derived state having the exoccipital condyles displaced forwards from the plane of the basioccipital condyle, and corresponding modification of the "prezygapophyes" on the first centrum, is considered by Grande (1988) to be uninformative, and present in diverse lineages. I agree with Grande's assessment, but in any case, this derived state is not present in the new species.

Character seven, the postmaxillary process of the premaxilla, has the derived state of a "gadoid notch" being present behind the process. The new species from Joffre Bridge does not have a postmaxillary process on the premaxilla, and so has no "gadoid notch". The derived state of the ninth character (loss of parapophyses on the first three to seven vertebrae with ribs inserting into ventrolateral cavities on the centra) is also not possessed by the new species from Joffre Bridge, in which well-developed parapophyses with ribs are evident on the anterior vertebrae (UALVP 23535, 27145).

The new species from Joffre Bridge, based on the above possession or lack or derived character states used by Patterson and Rosen (1989: fig.16), would be classified between the polytomy of the basal groups (Percopsidae, Aphredoderoidei, and †*Libotonius*) and †*Sphenocephalus*; however, there is a character state conflict when a synapomorphy of the Percopsidae is taken into consideration. The percopsid synapomorphy, the presence of a dorsal process on the maxilla, is found in no other paracanthopterygian lineage, but it is present in the new species from Joffre Bridge. Because of this, the new species could be classified either within the Percopsidae or closer to †*Sphenocephalus*. This character state conflict suggests the scheme of relationships proposed by Patterson and Rosen (1989) may not be correct. For this reason a new phylogenetic analysis was done (Chapter V) in which new characters of osteology were used, and fossil species were included in the analyses. From this new analysis, the character of the dorsal process on the maxilla was deemed to be indicative of relationship, and the foreshortened centrum was reinterpreted to be primitively present, rather than its presence being derived. The new species from

Joffre Bridge is therefore classified in the Family Percopsidae based on the presence of the maxillary dorsal process, a synapomorphy for that family.

DEPOSITIONAL ENVIRONMENT

The reconstruction of the habitat of the Joffre Bridge locality based on the geology of the area (Hoffman, pers. comm.) is supported by the fish fossils found at this site. The presence of the percopsid, osteoglossomorph, amiid and smelt indicate that the habitat may have been a shallow lake, probably heavily vegetated based on the habitats frequented by extant members of these groups.

The aggregation of the paracanthopterygian specimens may be related to several aspects of their biology, if these fish had a similar life style to that of *Percopsis omiscomaycus*. *Percopsis omiscomaycus* aggregates to spawn in streams and shallow in-shore waters of lakes, and these fish also aggregate inshore at night to feed (Scott and Crossman, 1973). A crevasse splay is often formed by flood waters (M.V.H. Wilson, pers. comm.), which indicates that this deposit may have been formed during the late spring when flooding likely occurred. Spawning occurs from May to August in Alberta (Nelson and Paetz, 1992). It may be that during these aggregations either to feed or spawn, these fish were buried, forming the mass death layer.

A more probable explanation is that a crevasse splay enabled the fish to enter the shallow waters of an oxbow lake from the main stream or river. After entering the shallow area the fish died before being buried by sediments. Occasional mortalities of

P. omiscomaycus have been documented. The mortalities have been the result of temperature stress (Grande, 1984), death after spawning, and from parasitic infection (Scott and Crossman, 1973). If this was the case with the Palaeocene paracanthopterygians at Joffre Bridge, burial must have occurred shortly after the mortality, as specimens show little or no sign of disturbance or predation.

Taphonomy of the fish in the mass death layer is being studied by Wilson (1992). His studies indicate the fish were oriented by waves rather than currents and the paracanthopterygians are distributed in clusters rather than uniformly spaced. This information supports the idea that these fish aggregated in shallow in-shore waters to spawn or feed.

The new percopsid from Joffre Bridge is the second percopsid described from the Palaeocene of Alberta. The two Palaeocene percopsids extend the age and distribution of the family from the Eocene Green River Formation of the northcentral United States to the middle of the Palaeocene of central Alberta.

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V. GENERAL DISCUSSION: PHYLOGENETIC RELATIONSHIPS OF THE BASAL PARACANTHOPTERYGIANS

INTRODUCTION

The Superorder Paracanthopterygii, first created by Greenwood *et al.* (1966) as the sister group to the Acanthopterygii, was shown to be monophyletic by Patterson and Rosen (1989). Subgroups within the superorder, in contrast, have undergone much revision (*e.g.* Rosen, 1962, 1985). The most recent cladistic analysis (Patterson and Rosen, 1989) resulted in several groups (Ophidiidae, Carapidae and Bythitoidei) being removed from the Order Gadiformes and the basal Order Percopsiformes being disbanded into four separate lineages, †*Sphenocephalus*, †*Libotonius*, Percopsidae and Aphredoderoidei, the latter three in an unresolved polytomy.

Since Patterson and Rosen presented this cladogram, four new species of fossil paracanthopterygians have been described. The first of these was †*Mcconichthys longipinnis* Grande, from early Palaeocene freshwater deposits in Montana. When Grande (1988) described this fish, he used the characters of Patterson and Rosen (1989) to place †*Mcconichthys* in their cladogram with the higher paracanthopterygians, in a trichotomy with the Pediculati and the Gadiformes.

More recently, †*Xenyllion zonensis*, from marine Cenomanian deposits in Alberta has been described (Wilson and Murray, in press). †*Xenyllion* has been classified in the Family †Sphenocephalidae based on the unique preopercular spines and recurved posterodorsal edge of the opercle. Similar fossils have been found in late Albian or early Cenomanian deposits in Utah (Stewart, in press), which seem to be at least congeneric, if not conspecific, with the Alberta sphenocephalid.

The two other new paracanthopterygians (Ch. III and IV) are both from Palaeocene deposits in Alberta. These two new species provided new information with which to perform a reanalysis of the basal paracanthopterygians. Presumed derived character states possessed by one of these new species (the one from Joffre Bridge, Ch. IV) contradicted the relationships hypothesized by Patterson and Rosen (1989:fig. 16). Accordingly, a new cladistic analysis of basal paracanthopterygians was done, using osteological characters and including many fossil genera.

PHYLOGENETIC RECONSTRUCTION

A new hypotheses of paracanthopterygian relationships based on thirty-seven osteological characters is shown in the cladogram in Fig. V-1. A list of characters, character states, weights of characters, and states for all the species included in the analysis can be found in Appendix I. Three of the characters were given half the weight of the rest of the characters. These three are the antrobital, retroarticular, and percopsoid projections being present or absent. These characters are lost in several lineages, and had individual consistency indices of 0.25 or less in MacClade, when the unweighted character matrix was run using P.A.U.P. The individual consistency indices indicate these three characters are more prone to homoplasy than the other characters. The characters are discussed below. Methods for the analyses are outlined in Chapter II.

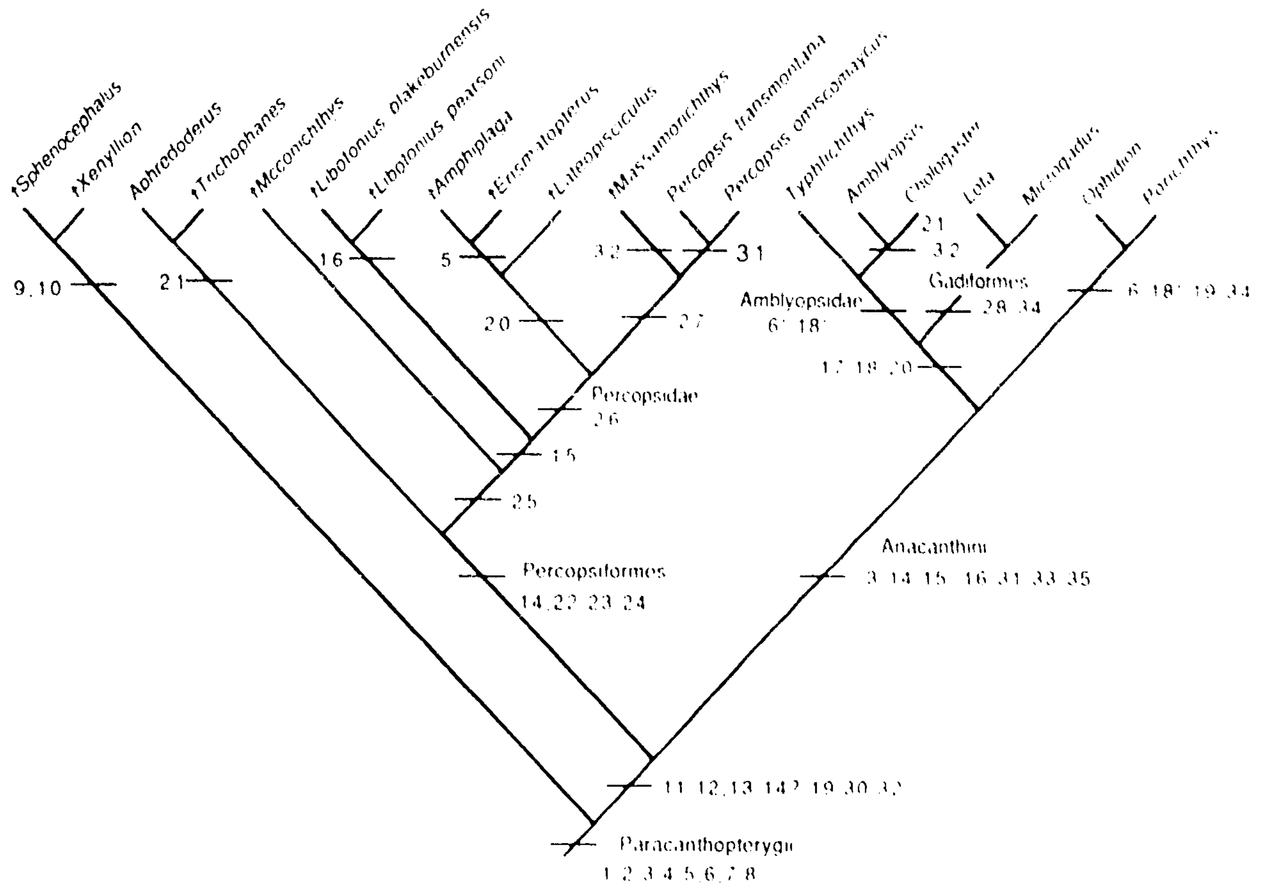

Figure V-1. Cladogram of the new proposed phylogenetic relationships of the Superorder Paracanthopterygii.

Several indices generated by MacClade give an indication of the parsimony of a cladogram. These are the consistency, retention and rescaled consistency indices (C.I., R.I. and R.C. respectively). The indices for the cladogram in Figure V-1 are: C.I. = 0.62, R.I. = 0.81, and R.C. = 0.50. If the Amblyopsidae is placed as the sister group to the Aphredoderidae, as previously classified, the same indices for the resulting cladogram are: C.I. = 0.53, R.I. = 0.72, and R.C. = 0.38. Another measure of parsimony is the tree length of the cladogram. The cladogram in Figure V-1 has a tree length of 123, with weights of characters scaled at 1 and 2. If the Amblyopsidae is moved to a position as the sister to the Aphredoderidae within the Percopsiformes the resulting cladogram has a tree length of 143, with the same character weights. These measures of parsimony show that the new hypothesis of relationships accounts for the distribution of character states with less instances of convergent evolution (homoplasies) than the previous classification.

The new cladogram (Fig. V-1) shows the Family †Sphenocephalidae to be the sister group to the rest of the superorder. The families Percopsidae (*Percopsis, †Amphiplaga, †Erismatopterus*), Aphredoderidae (Aphredoderus, *†Trichophanes*), and †Libotoniidae (*†Libotonius*), are united with the two new Palaeocene percopsids from Alberta and *†Mcconichthys* to establish a monophyletic Order Percopsiformes.

Notably absent from the order is the Family Amblyopsidae (*Amblyopsis, Chologaster, Typhlichthys*, and *Speoplatyrhinus*). This family was previously classified with the Cyprinodontoidei (*e.g.* Regan, 1911; Woods and Inger, 1957). Rosen (1985) later united the Amblyopsidae with the Aphredoderidae (in the Order

Percopsiformes), together forming the Suborder Aphredoderoidei of Patterson and Rosen (1989). In the new scheme of relationships, the Amblyopsidae are removed from the Suborder Aphredoderoidei and placed with the higher paracanthopterygians in the Anacanthini. The analyses resulted in the Amblyopsidae and the Order Gadiformes in a sister group relationship. However, if the amblyopsids are placed as the sister group to all the rest of the Anacanthini, the resulting cladogram has a tree length only four steps longer than if the amblyopsids are the sister group to the Gadiformes; therefore, the placement of the amblyopsids as the sister group to the gadiforms is considered tentative. Although this new placement of the amblyopsids results in viewing two characters previously used to unite the amblyopsids and aphredoderids as homoplasies (segmented premaxilla and jugular vent), there are several characters shared by the gadiforms and amblyopsids, and other anacanthines to support the new placement of the amblyopsids.

Speoplatyrhinus poulsoni was described by Cooper and Kuehne (1974) within the Amblyopsidae. No material was available to me for examination, and Cooper and Kuehne (1974) included no osteology in their original description. Although this species has not been included in any of the analyses in this study, it is accepted as an amblyopsid based on the analyses of Cooper and Kuehne (1974) and therefore it is kept with the Amblyopsidae in the family's new placement in the Anacanthini. The revised classification (to genus for the main groups under study) using the sequencing convention is as follows:

Superorder Paracanthopterygii

Order †Sphenocephaliformes

Family †Sphenocephalidae
    †Xenyllion
    †Sphenocephalus

Order Percopsiformes

Family Aphredoderidae
    †Trichophanes
    Aphredoderus
Family †Mcconichthyidae
    †Mcconichthys
Family †Libotoniidae
    †Libotonius
Family Percopsidae
    †Amphiplaga
    †Erismatopterus
    †Lateopisciculus
    †Massamorichthys
    Percopsis

Order Amblyopsiformes (may be a suborder of the Order Gadiformes)

Family Amblyopsidae (sistergroups not resolved)
    Amblyopsis
    Chologaster
    Speoplatyrhinus
    Typhlichthys

Order Gadiformes

Ophidiidae (position is tentative)

Order Batrachoidiformes

Order Lophiiformes

DISCUSSION OF CHARACTERS FOR THE NEW CLADOGRAM

Superorder Paracanthopterygii

The Superorder Paracanthopterygii was considered monophyletic by Patterson and Rosen (1989:fig. 16) on the basis of four synapomorphies which are included in the new cladogram (characters 1-4 in figure V-1). The first, a full neural spine on the second preural centrum, is found in most members of the superorder, except those with greatly reduced caudal skeletons (*e.g.*, carapids). The second synapomorphy, reduction from three epurals to two, occurs in all paracanthopterygians, and the epurals are further reduced in the Amblyopsidae (one full epural and one very small epural in *Typhlichthys*, and a single epural in *Amblyopsis* and *Chologaster*) (Fig. V-2).

A single supraneural, behind the first or second neural spine, is the third synapomorphy for the superorder. The question of terminology for supraneurals and predorsals is discussed by Mabee (1988), who suggested the term "supraneural" is appropriate except for the bones in front of the dorsal fin formed from rayless pterygiophores, which should be called "rayless pterygiophores." Markle and Olney (1990:279) consider both "predorsals" (or rayless pterygiophores) and "supraneurals" to be present in the carapids. The term supraneural is used here, following Rosen and Patterson (1969) and Patterson and Rosen (1989). Whatever the homology of the supraneurals, the character state changes from three upright bones situated between the neural spines in the outgroups, to a single irregularly shaped bone lying above the neural spines in the basal paracanthopterygians. This single supraneural is lost in many of the paracanthopterygians (*e.g.*, gadiforms, *Porichthys*), and in some carapids

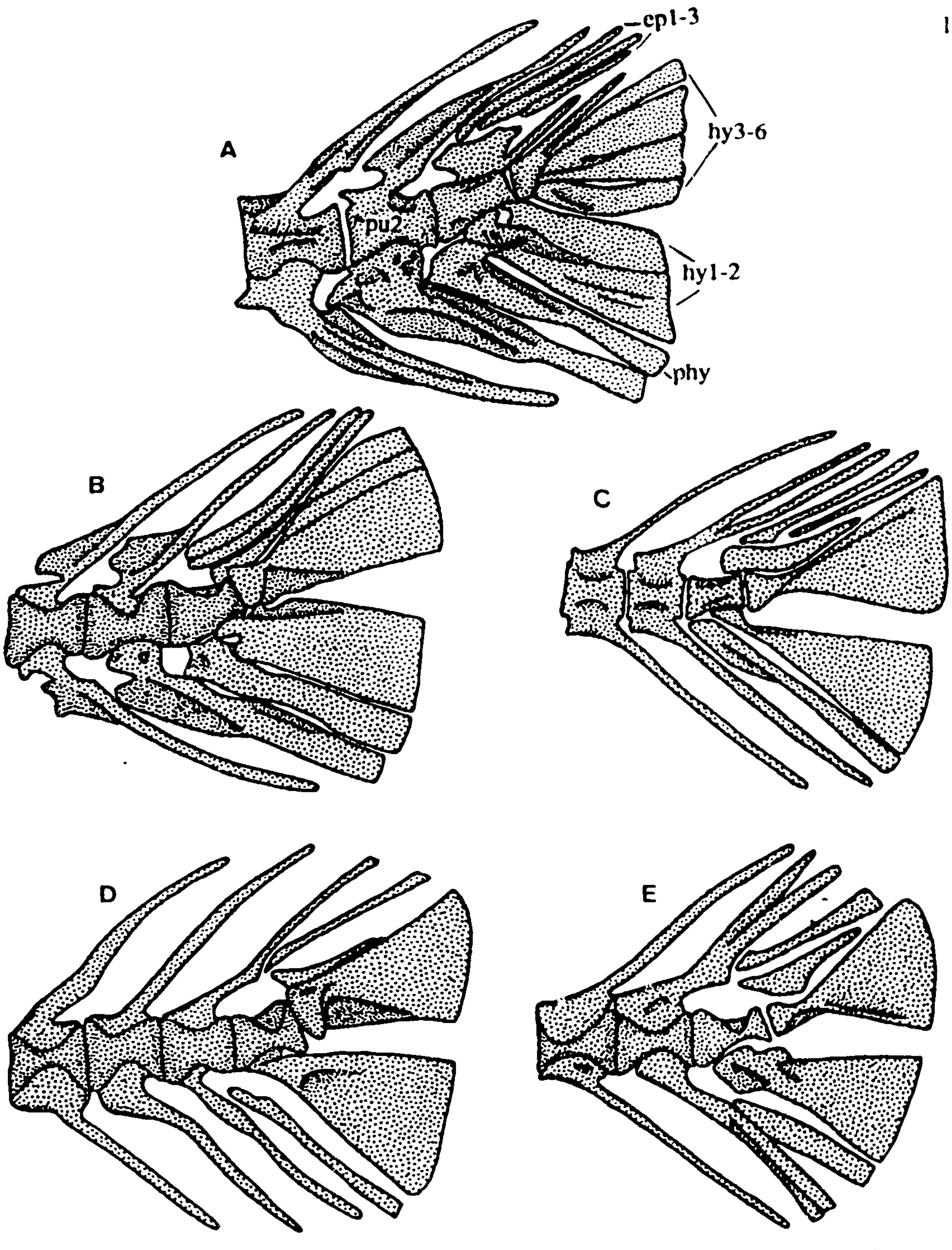

Figure V-2. Camera lucida drawings of the caudal skeletons of *Polymixia* and representative paracanthopterygians. A. *Polymixia japonica*, NMC 79-0001; B. *Percopsis omiscomaycus*, UAMZ 3062; C. *Aphredoderus sayanus*, CAS 57257; D. *Amblyopsis spelaea*, CAS 78143; E. *Chologaster agassizi*, CAS 57170;

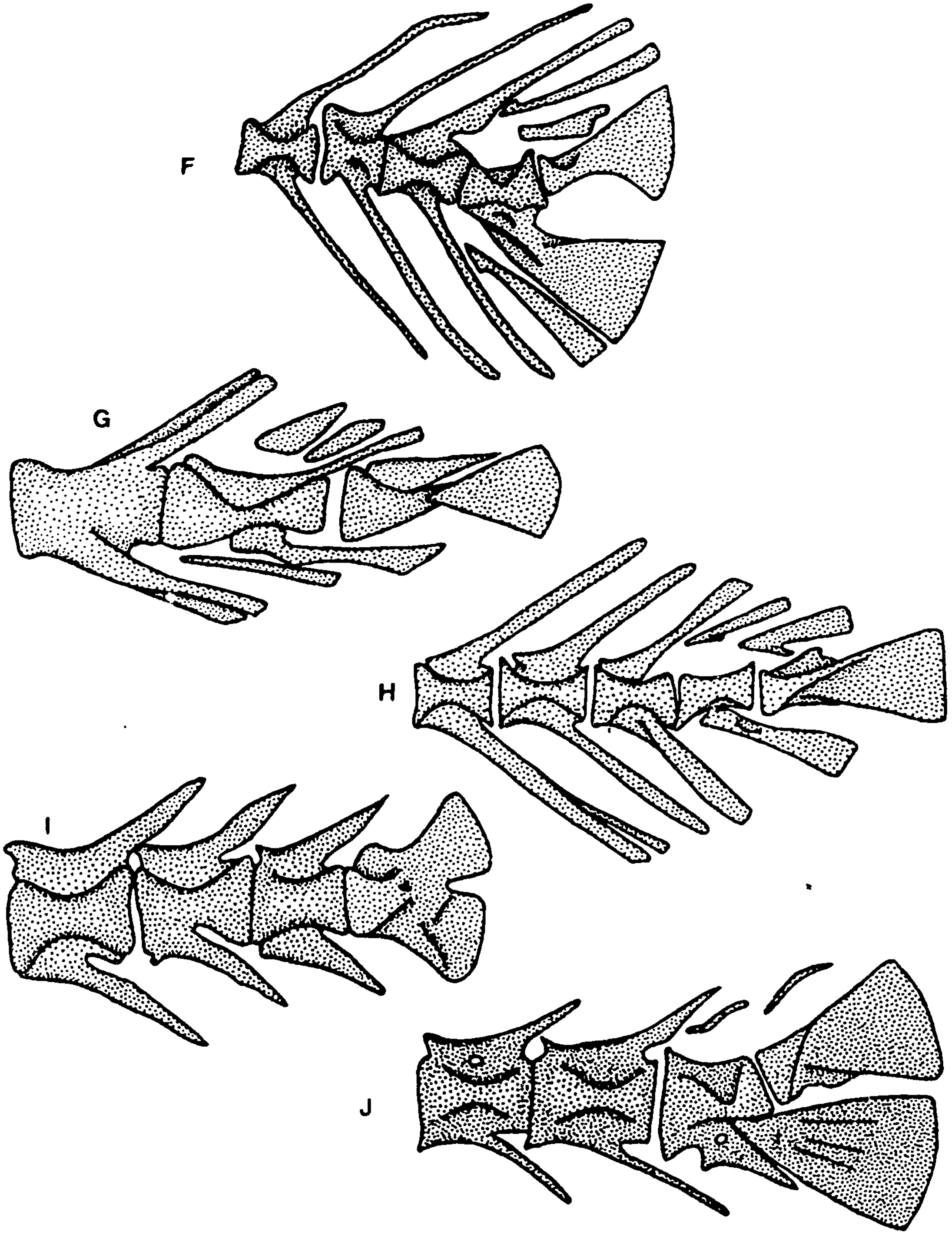

Figure V-2 continued. F. *Typhlichthys subterraneus*, SU 1310; G. *Lota lota*, UAMZ 7595; H. *Microgadus proximus*, UAMZ 7594; I. *Ophidion welshi*, UAMZ 6597; J. *Porichthys notatus*, UAMZ 2011.

there is a series of several bones or cartilages anterior to the dorsal fin. The carapid condition was secondarily derived according to Patterson and Rosen (1989), an interpretation that is followed here.

The fourth synapomorphy for this superorder given by Patterson and Rosen (1989) is the enlarged intercalar (= opisthotic) containing the glossopharyngeal foramen and forming part of the cranial wall. Although the state of this character could not be determined for the two new species, the synapomorphy is accepted in this study.

Four additional derived character states for the superorder from this study can be added (Fig. V-1). These are: 5) "percopsoid projections" (McAllister, 1968) present on the heads of some branchiostegal rays, 6) a prominent dorsal ascending process on the lacrimal, 7) a strong horizontal ridge on the opercle from the hyomandibular suspension which extends posteriorly as a spine, and 8) a strong ventral ridge on the opercle extending as a spine. Of these four characters, number 5 is lost in five genera (*Amblyopsis, †Amphiplaga, †Erismatopterus, †Mcconichthys, Porichthys*), and 6 is lost in the Pediculati and *Opidion*. The monophyly of the Superorder Paracanthopterygii is however supported in this study.

Order †Sphenocephaliformes

The Family †Sphenocephalidae is monophyletic based on the unique preopercular spines and opercular posterodorsal recurved edge (Wilson and Murray, in press). This family is the sister group to the rest of the Superorder Paracanthopterygii, and is given ordinal status following Wilson and Murray (in press). The rest of the superorder share derived states of two characters, loss of the beryciform foramen, and shortening of the premaxilla. The number of postcleithra also changes, from two present in sphenocephalids to a single one in the rest of the superorder; however, the single postcleithra may have been acquired more than once, as the postcleithrum of percopsiforms has a large dorsal plate, unlike that of the anacanthines.

Unranked subgroup Anacanthini

The Anacanthini, as defined by Patterson and Rosen (1989) contains the Pediculati (Lophiiformes and Batrachoidiformes) and the Gadiformes, and includes the Ophidiidae, Carapidae and Bythitoidei. Members of the Carapidae and Bythitoidei were not included in the analyses of this study as no specimens were available. The Ophidiidae representative (*Ophidion welshi*) used in this study was placed as the sister group to the pediculate representative (*Porichthys notatus*) based on derived states of characters 18 and 19, and the loss of character 6. These are: the fusion of the parhypural to the lower hypural plate (Fig. V-2); the rod-shaped cleithrum (which may be explained by the loss of the expanded dorsal plate) which also occurs in the Amblyopsidae (Fig. V-3); and the loss of the dorsal process on the lacrimal. I agree with Patterson and Rosen (1989) that the Ophidiidae do not belong with the Gadiformes, as previously classified (*e.g.* Greenwood *et al.*, 1966); however, because some groups were not well represented in this study, the placement of the Ophidiidae in Figure V-1, relative to the other members of the Anacanthini, is not well supported

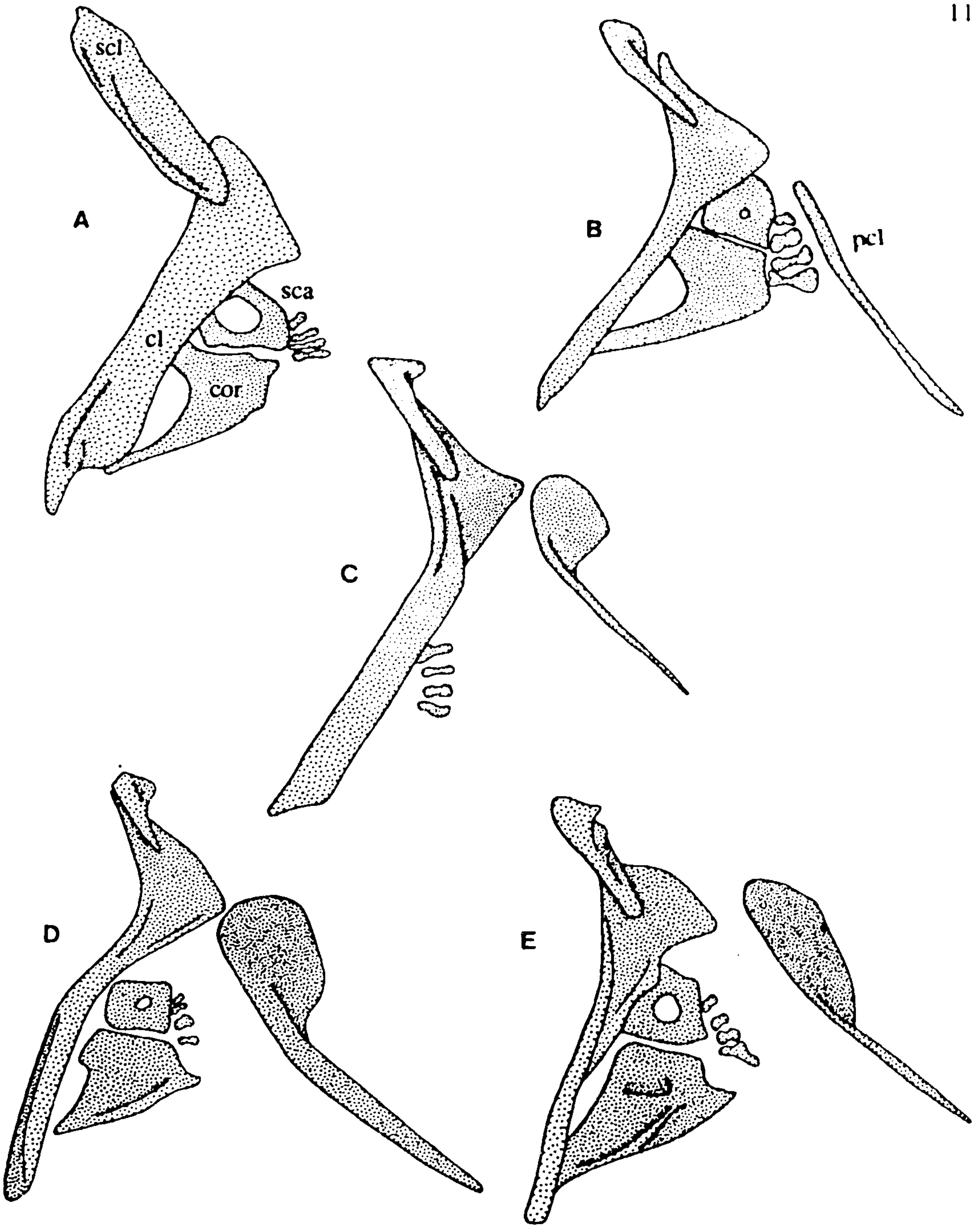

Figure V-3. Camera lucida drawings of the pectoral girdles of *Polymixia* and representative paracanthopterygians. A. *Polymixia japonica*, NMC 79-0001; B. *Aphredoderus sayanus*, CAS 57257; C. †*Trichophanes foliarum*, UALVP 17741; D. †*Massamorichthys wilsoni*, based on UALVP 23535, 27144 and 39094; E. *Percopsis omiscomaycus*, UAMZ 3062;

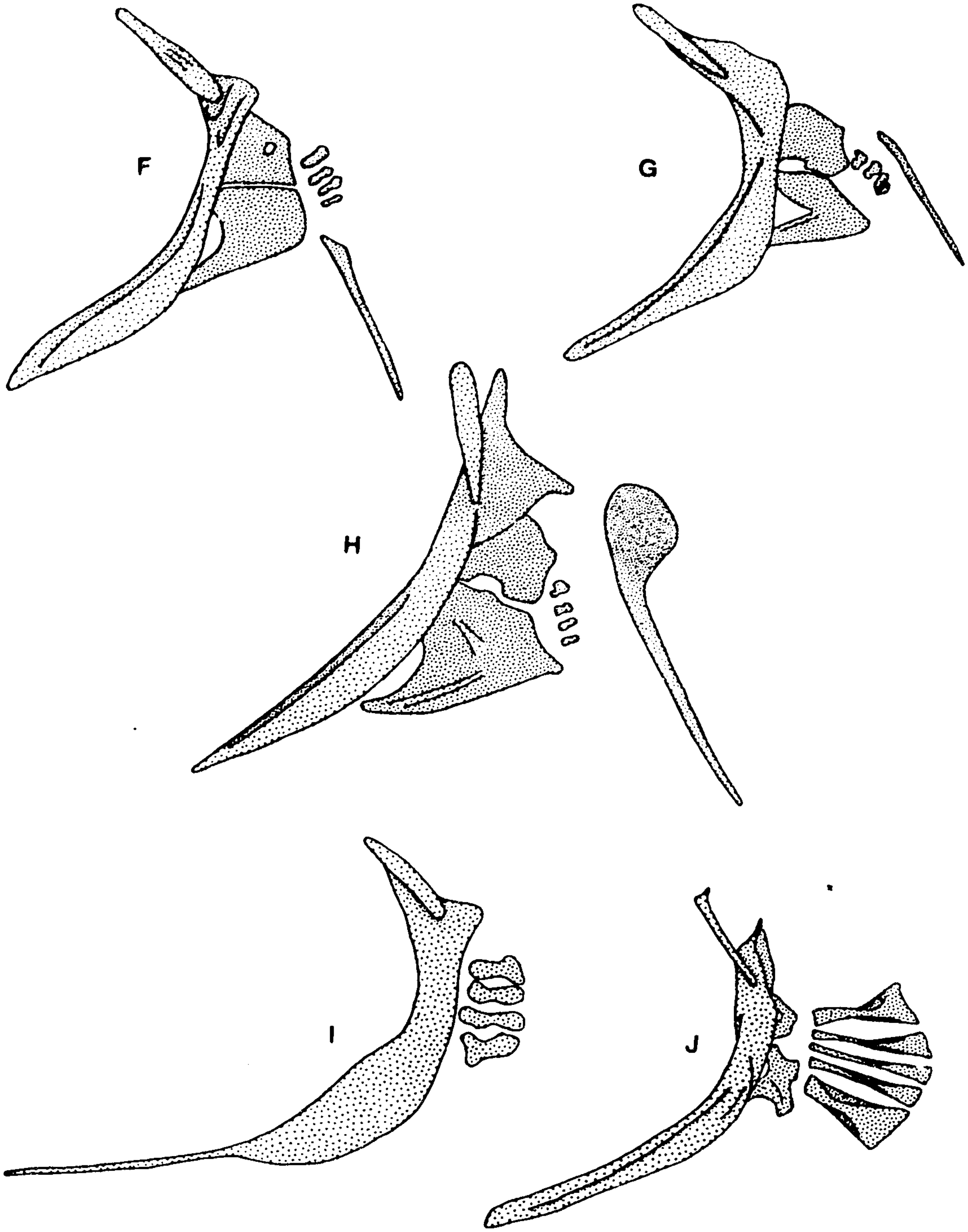

Figure V-3 continued. F. *Amblyopsis spelaea*, CAS 78143; G. *Lota lota*, UAMZ 7595; H. *Microgadus proximus*, UAMZ 7594; I. *Ophidion welshi*, UAMZ 6597; J. *Porichthys notatus*, UAMZ 2011.

and should be considered tentative. A sister group relationship may exist between the Pediculati and the Ophidiidae, but such a relationship has not been well tested in this study.

The Family Amblyopsidae is placed within the Anacanthini (Figure V-1). Its placement as the sister group to the Order Gadiformes is considered tentative as only two species of gadiforms were included in the analysis, and, as mentioned previously, the tree length of the cladogram is only four steps longer if the amblyopsids are placed as the sister group to all the anacanthines, rather than just the gadiforms.

This is not a completely new placement for the Amblyopsidae. Previous authors (*e.g.*, Gosline, 1963; Lauder and Liem, 1983:fig. 37) have placed the percopsiform fishes, including the amblyopsids, as the most closely related group to the gadiform fishes. Patterson and Rosen (1989) disputed this relationship, considering the gadiforms as much more derived than the percopsiform fishes. In their 1989 paper, Patterson and Rosen suggested that if the sister group to the gadiforms were within the percopsiform lineage, it could be one of several different groups, the percopsids, aphredoderoids (including amblyopsids), or the fossil genus *†Libotonius*. The separation of the amblyopsids and aphredoderids was not suggested, and the two families have been associated since Rosen (1962) first removed the amblyopsids from their association with the cyprinodontoids and reclassified them as the sister group to the percopsids plus aphredoderids, then later suggested uniting them with the Aphredoderidae (Rosen, 1985) as a single lineage (Aphredoderoidei of Patterson and Rosen, 1989). The separation of the amblyopsids from the aphredoderids in this study resulted in a monophyletic Order Percopsiformes (without Amblyopsidae), and removes much character conflict seen as homoplastic between the gadiforms and percopsiforms including amblyopsids (Patterson and Rosen, 1989:fig. 16).

The redefined Anacanthini, now including the Family Amblyopsidae, has two characters to support it (Fig. V-1). These characters are: 14) the postcleithrum being a single rod, without a dorsal plate (Fig. V-3), and 15) the loss of the subopercle anterior projection (Fig. V-4).

Several other characters are included at this level as well, although there is some homoplasy with other lineages. Character 16, the loss of ornament (small spines or serrations) on the preopercle (Fig. V-5), may have occurred separately in several groups. *Microgadus proximus* has a few rounded spines on the preopercle. If the condition in *Microgadus* is secondarily derived, then loss of ornament would be another anacanthine character, homoplastically present in *†Libotonius*. The loss of the single supraneural, the presence of which is a paracanthopterygian synapomorphy, is interpreted as a derived character state of the Anacanthini, with secondarily derived cartilages present in the carapids and bythitoids (Patterson and Rosen, 1989). As mentioned above, the representatives of the Ophidiidae (*Ophidion welshi*) and Pediculati (*Porichthys notatus*) are in a sister group relationship based on the characters used in this study, although this relationship needs more research.

The Order Gadiformes and Family Amblyopsidae are placed as sister groups on the basis of having the derived states of two characters, number 17) the preopercle

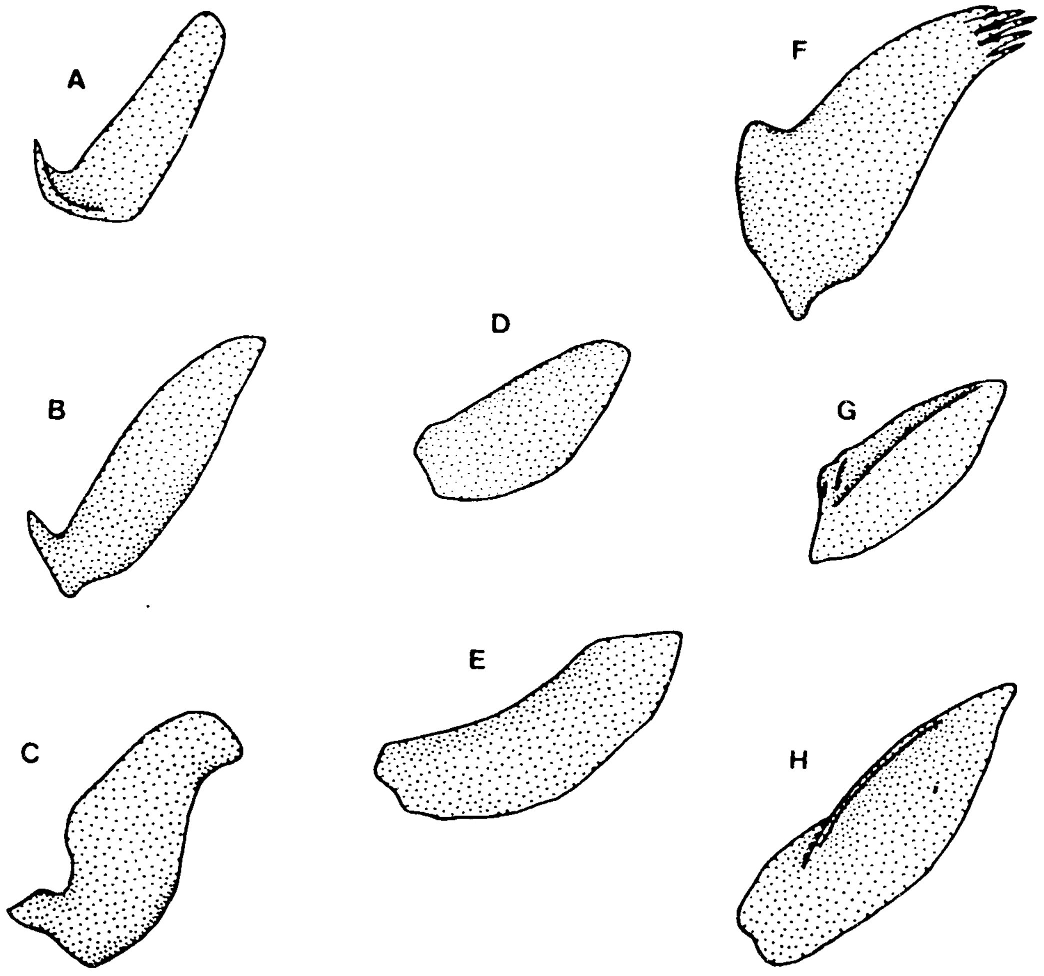

Figure V-4. Camera lucida drawings of the subopercles of *Polymixia* and representative paracanthopterygians. A. *Polymixia japonica*, NMC 79-0001; B. *Aphredoderus sayanus*, CAS 57257; C. *Percopsis omiscomaycus*, UAMZ 3062; D. *Amblyopsis spelaea*, CAS 78143; E. *Chologaster cornutus*, UAMZ 1635; F. *Ophidion welshi*, UAMZ 6597; G. *Lota lota*, UAMZ 7595; H. *Microgadus proximus*, UAMZ 7594.

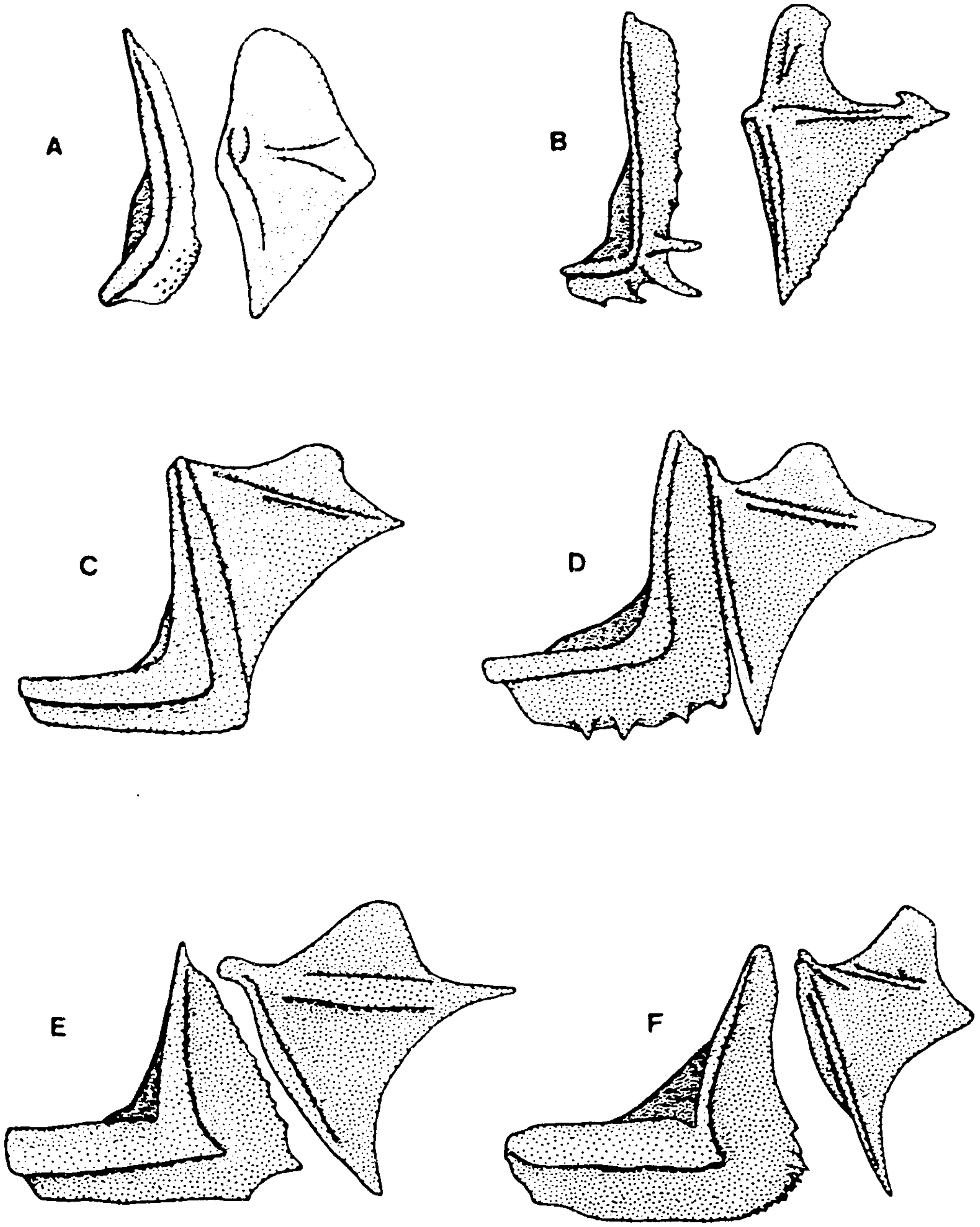

Figure V-5. Camera lucida drawings of the opercles and preopercles of *Polymixia* and representative paracanthopterygians. A. *Polymixia japonica*, NMC 79-0001; B. *†Xenyllion zonensis*, redrawn from Wilson and Murray, in press; C. *Aphredoderus sayanus*, CAS 57257; D. *†Lateopisciculus turrisfumosus*, UALVP 22870; E. *†Massamorichthys wilsoni*, UALVP 21660; F. *Percopsis omiscomaycus*, UAMZ 3062;

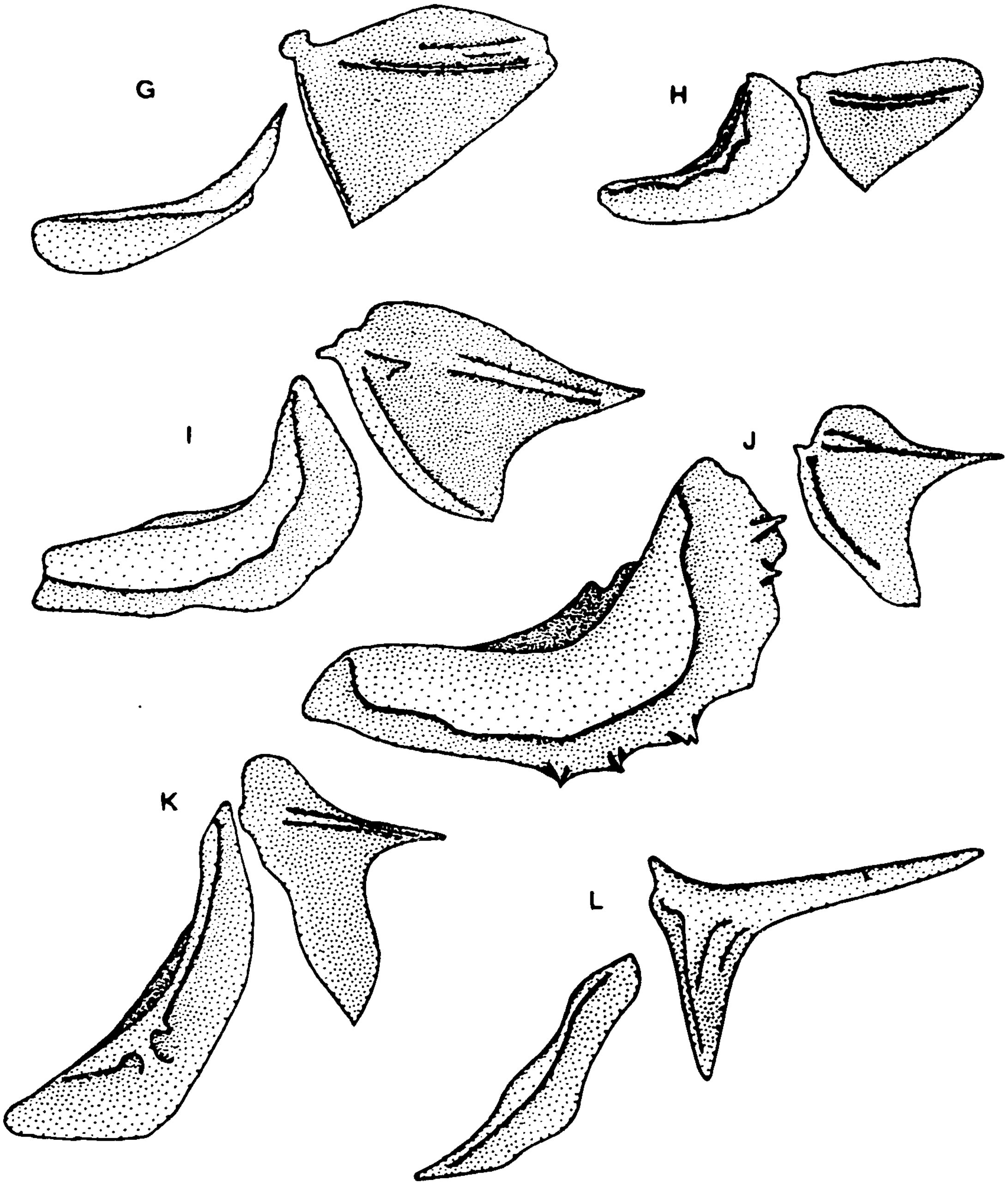

Figure V-5 continued. G. *Amblyopsis spelaea*, CAS 78143; H. *Chologaster cornutus*, UAMZ 1635; I. *Lota lota*, UAMZ 7595; J. *Microgadus proximus*, UAMZ 7594; K. *Ophidion welshi*, UAMZ 6597; L. *Porichthys notatus*, UAMZ 2011.

orientation and shape, with the horizontal limb being longer than the vertical and the whole bone being rounded, rather than with sharp angles as in the percopsids (Fig. V-5); and 18) the parhypural being free from the fused second preural and first ural centrum (Fig. V-2). These two lineages also share loss of the antorbital, present in *Ophidion* and *Porichthys*, although the antorbital is also lost in some of the percopsids.

Family Amblyopsidae

Within the Family Amblyopsidae, relationships are uncertain. Poulson (1963) indicated that *Chologaster* is the most primitive genus of the family based on the degree of cave adaptation. The trends presented by Poulson (1963) would indicate that *Typhlichthys* and *Amblyopsis* are sister groups, although Poulson was not presenting a cladistic analysis, and did not group any of the genera within the family. Woods and Inger (1957) suggested that either the three known genera (*Speoplatyrhinus* had not yet been described) either split from an ancestor at the same time, or *Chologaster* and *Typhlichthys* were more closely related to each other than either was to *Amblyopsis*. Woods and Inger (1957) based these relationships on two osteological characters: presence or absence of the postcleithrum and presence or absence of the scleral cartilages.

In this study, *Amblyopsis* and *Chologaster* resulted in a sistergroup relationship, sharing the character state of the segmented alveolar process of the premaxilla, that is absent in *Typhlichthys*, based on x-rays of specimens. *Speoplatyrhinus* was not included in this analysis. The relationships within the Amblyopsidae are not considered to have been resolved.

Order Percopsiformes

The Order Percopsiformes, consisting of the families Aphredoderidae, †Mcconichthyidae, †Libotoniidae and Percopsidae, shares derived states of three characters: 14) fused upper plate-like and lower rod-like postcleithra (Fig. V-3); 22) the dorsal process of the opercle above the posterior ridge being excavated or truncated anteriorly (Rosen and Patterson, 1969) (Fig. V-5); 23) strongly ctenoid or peripheral ctenoid scales with a posterior focus; and 24) the loss of the postmaxillary process of the premaxilla (Fig. V-6). The postmaxillary process of the premaxilla was shown and described as "present low" (Rosen and Patterson, 1969:fig. 15, tab. 1) in *Percopsis omiscomaycus*. The specimens of *Percopsis* that I examined do not have this process (Fig. V-6), and in the analyses, this character state was coded as absent. If the process is present in some specimens of *P. omiscomaycus*, I suggest it is at least under reduction in this group, if not lost completely. In either case, *P. omiscomaycus* does not have a well-developed and distinct postmaxillary process as is found in other paracanthopterygians.

The Aphredoderidae is the sister group to the other percopsiforms. The Aphredoderidae retain the small spines on the lacrimal and infraorbital bones as in †*Sphenocephalus* and the rest of the order has smooth infraorbital bones.

The Percopsidae and †Libotoniidae are separated from the †Mcconichthyidae

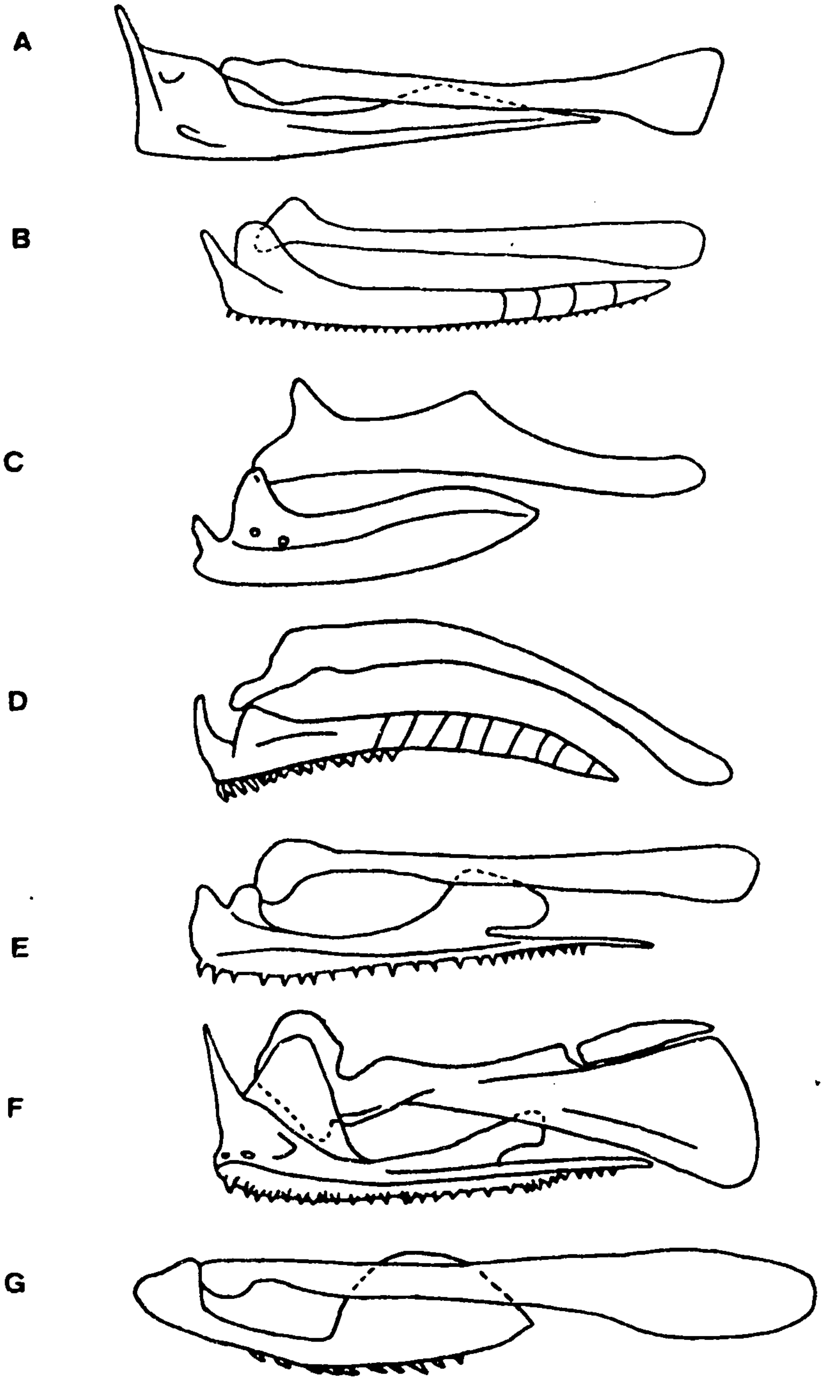

Figure V-6. Premaxillae and maxillae of *Polymixia* and representative paracanthopterygians. A. *Polymixia japonica*, NMC 79-0001; B. *Aphredoderus sayanus*, CAS 57257; C. *Percopsis omiscomaycus*, UAMZ 3062; D. *Amblyopsis spelaea*, CAS 78143; E. *Microgadus proximus*, UAMZ 7594; F. *Ophidion welshi*, UAMZ 6597; G. *Porichthys notatus*, UAMZ 2011.

by the two former groups having lost the spiked anterior projection of the subopercle, instead having a blunt anterior projection (character 15) (Fig. V-4). The family †Libotoniidae is placed as the sister group to the Percopsidae. The Percopsidae, which includes the two new species of Palaeocene paracanthopterygian fishes described in Chapters III and IV, is considered monophyletic based on the presence of the dorsal process on the maxilla (# 26). Within the Percopsidae, *†Amphiplaga* and *†Erismatopterus* are sister groups, both having lost the percopsoid projections (McAllister, 1968), and the new species from Smoky Tower is the sister to these two Eocene percopsids, all three of which have lost the antorbital bone (# 20). The new species from Joffre Bridge forms the sister group to the genus *Percopsis*, both genera having a supraoccipital crest which extends past the first neural spine (# 27).

This revised phylogeny and classification establish a monophyletic Order Percopsiformes, after the removal of the Family Amblyopsidae, which is placed in the Anacanthini, tentatively as the sister group to the Order Gadiformes. Within the Order Percopsiformes are two of the three families (Percopsidae and Aphredoderidae) previously placed in that order (Rosen and Patterson, 1969), together with the †Libotoniidae and †Mcconichthyidae. The two new Palaeocene species from Alberta are members of the Family Percopsidae. The Family †Sphenocephalidae is the sister to the rest of the Superorder Paracanthopterygii.

COMMENTS ON THE CHARACTERS OF PATTERSON AND ROSEN (1989)

The scheme of relationships proposed by Patterson and Rosen (1989) is shown in Figure V-7. They defined the superorder with four characters. As discussed above, these are accepted as paracanthopterygian synapomorphies and were included in the new cladogram. The remaining characters used by Patterson and Rosen to support their hypothesis of relationships need some discussion.

Characters 5, 6, and 7 of Patterson and Rosen (1989:fig. 16) were used to unite *†Sphenocephalus* with the Anacanthinii (carapids, ophidiids, Gadiformes, Lophiiformes and Batrachoidiformes). If the new scheme is correct, the sphenocephalids would not have these characters and the Amblyopsidae would have them. Character 5, the second or second and third vertebral centra being shorter than the first and third or fourth, is present in *†Sphenocephalus* and *Porichthys*, as stated by Patterson and Rosen; however, in the specimens of *Lota* and *Microgadus* I examined, this state is absent as the first centrum is shorter than the second. In the specimens of the outgroup *Vellifer* (Lampriformes), the second centrum is shorter than the first and third; therefore, *Vellifer* possesses the character state. This is also the case in the new species from Joffre Bridge. I suggest that the foreshortened centrum is in fact primitive, and tends to be lost in many separate lineages. Conversely, this character may be advanced, but subject to much homoplasy.

The sixth character of Patterson and Rosen, is the exoccipital condyles being widely separated and displaced forwards from the plane of the basioccipital condyle, with corresponding modification of the "prezygapophyses" on the first centrum. This character could actually be broken down into three component parts. Gosline (1963, 1971) used the widely separated exoccipital condyles to unite the gadiforms and

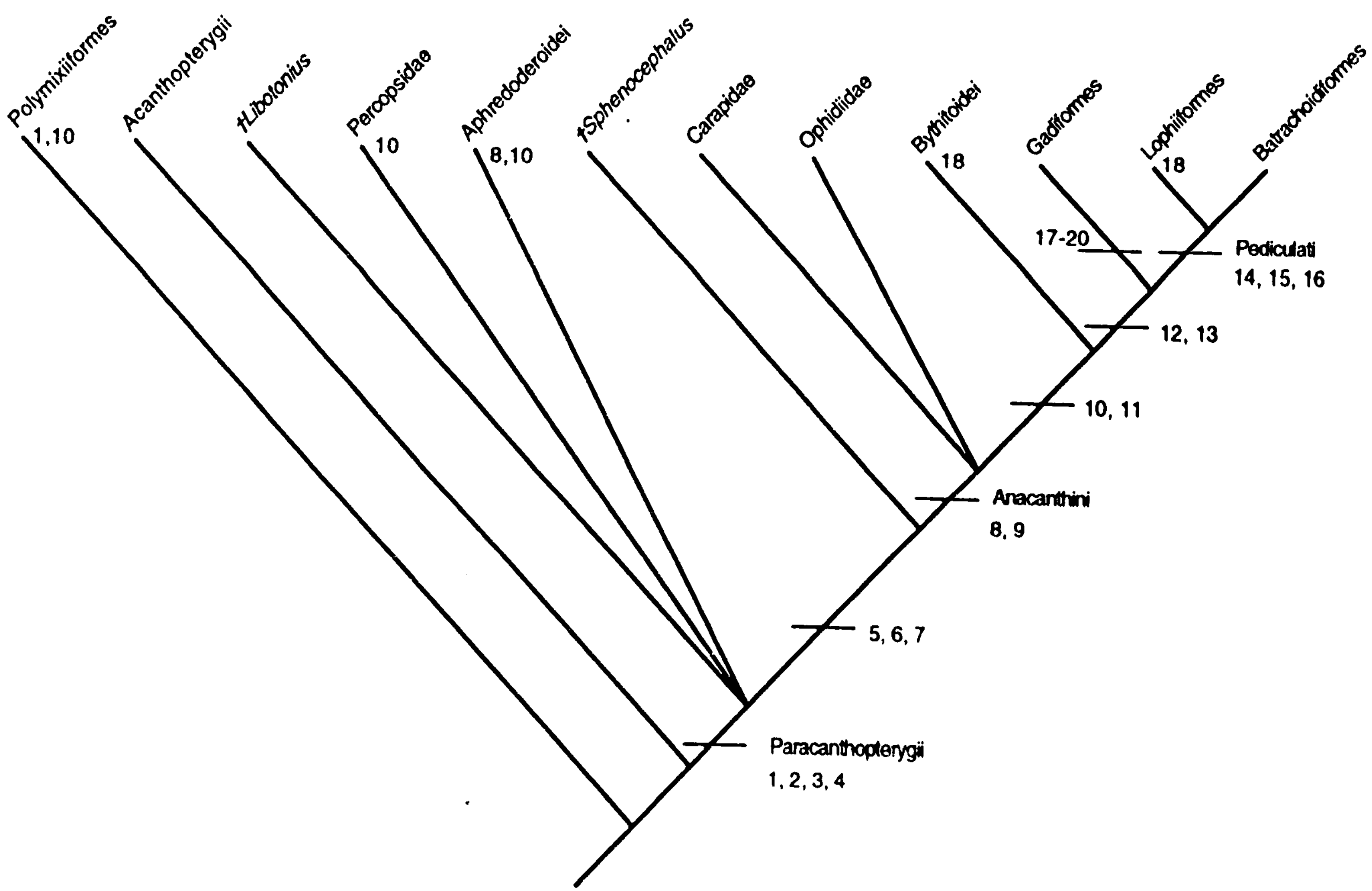

Figure V-7. Cladogram of proposed paracanthopterygian relationships redrawn from Patterson and Rosen (1989:fig. 16) percopsiform fishes, including the amblyopsids. The specimens I examined also have widely separated exoccipital condyles which agrees with the information of Rosen and Patterson (1969:379, figs. 10A, B, C). The displacement forward of the exoccipital condyles from the plane of the basioccipital condyle is present in examined specimens of *Percopsis omiscomaycus*, but is absent in examined specimens of *Lota* and *Amblyopsis*, and is also absent in *†Sphenocephalus* (Rosen and Patterson, 1969, fig. 33). The exoccipital condyles are not displaced forwards in the lophiiforms and batrachoidiformes, constituting a reversal that is character sixteen of Patterson and Rosen (1989, fig. 16, exoccipital condyles secondarily elongated, extending to or beyond the basioccipital) used to unite these two orders in the group Pediculati. The first two components of this character, therefore, do not seem to be useful to form the relationships suggested. The third part, modification of the "prezygapophyses" on the first centrum, is present in *†Sphenocephalus* (Rosen and Patterson, 1969:403), bythitoids (Rosen, 1985:fig. 36B), and the gadiforms *Gadus* (Rosen, 1985:fig. 38A) and *Lota* (Fig. V-8). The lophiiform *Tetrabrachium ocellatum* (Peitsch, 1981:fig. 4) and a lophiid (UAMZ 1572) do not have this feature. The specimens of *Amblyopsis* examined do have modified "prezygapophyses" on the first centrum, simiiar to those of *Lota* (Fig. V-8). From this distribution of the modified "prezygapophyses", this feature could be interpreted as primitively present and lost in percopsiforms and lophiiforms independently, or primitively absent with its presence derived homoplastically in gadiforms/amblyopsids/ophidiids and in *†Sphenocephalus*. This character does not effect the placement of the amblyopsids.

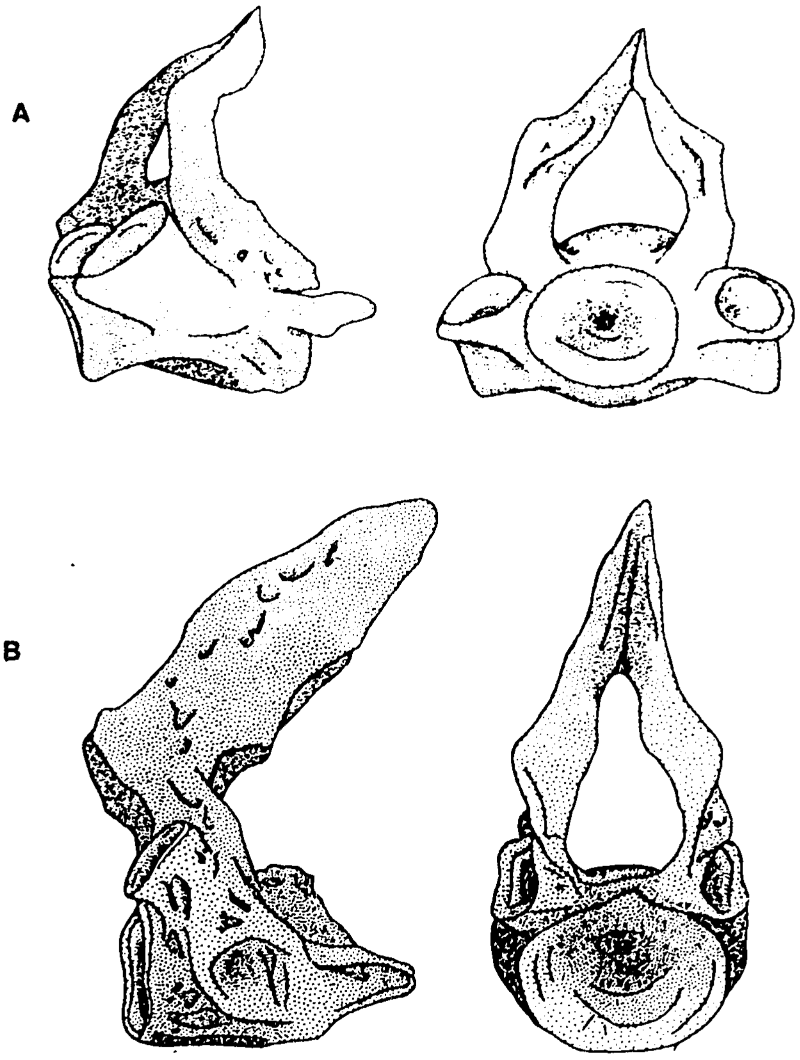

Figure V-8. Camera lucida drawings of the first vertebra in lateral and anterior view. A. *Amblyopsis spelaea* CAS 78143, B. *Lota lota* UAMZ 7596.

A "gadoid notch" behind the postmaxillary process of the premaxilla in *†Sphenocephalus* and higher paracanthopterygians is the seventh of the characters listed by Patterson and Rosen (1989:fig. 16). The presence of the postmaxillary process of the premaxilla is considered primitive by most authors (*e.g.* Greenwood *et al.*, 1966; Rosen and Patterson, 1969), and also by comparison to the outgroups in this study. The "gadoid notch" is present in *†Sphenocephalus, Ophidion, Lota* and *Microgadus*, and possibly in *†Xenyllion*; however, the notch is absent in *Porichthys*, in which the alveolar process appears to have been truncated at the posterior end of the postmaxillary process (Fig. V-6). I suggest that the presence of a postmaxillary process of the premaxilla is primitive for the Paracanthopterygii, and that the "gadoid notch" is a synapomorphy of the superorder, later lost in some lineages. The total loss of the postmaxillary process in the Percopsiformes (*sensu lato*) (based on examined material, with the possible reduction of the process in *Percopsis omiscomaycus* based on Rosen and Patterson (1969: fig. 15), as mentioned above) is seen as an advanced character state, homoplastically present in the Amblyopsidae. The presence of the postmaxillary process without the "gadoid notch" in *Porichthys* was explained by the alveolar process of the premaxilla being truncated at the posterior end of the postmaxillary process in the Batrachoidifomes and Lophiiformes (Patterson and Rosen, 1989). This explanation could still be acceptable, or conversely, the batrachoidiform and lophiiform fishes could have retained the primitive state, and the "gadoid notch" could be homoplastically present in *†Sphenocephalus*, ophidiids and gadiforms.

Character eight of Patterson and Rosen (1989), loss of the myodome, united the ophidiids, carapids, gadiforms, lophiiforms and batrachoidiforms, and was interpreted as homoplastically present in the Amblyopsidae. In the new cladogram, the placement of the amblyopsids with the higher paracanthopterygians is supported by this character.

Character nine of Patterson and Rosen (1989: fig.16) is the loss of parapophyses on the first three to seven vertebrae, and ribs inserting instead in ventrolateral cavities on the centra. *Microgadus* has enlarged, overlapping pre- and postzygapophyses and no parapophyses on the first four vertebrae. The first and second ribs are in a cavity on the prezygapophysis of the second and third vertebra, and the third rib, on the fifth centrum, originates from a transverse parapophysis. The situation in *Lota* is similar, although the number of ribs in cavities is three. The Batrachoidiformes and Lophiiformes have no pleural ribs (charcter 14 of Patterson and Rosen, 1989:fig. 16). The condition in various ophidiids and carapids differs among authors (*e.g.*, Markle and Olney, 1990; Patterson and Rosen, 1989).

The condition in *Percopsis omiscomaycus* corresponds to *Microgadus* (Figs. V-9, V-10). There are no parapophyses on the first three vertebrae, and the ribs on those vertebrae (the first pleural rib is on the third vertebra) articulate on the prezygapophysis at the base of the neural arch. The first distinct parapophysis is found on the fourth vertebra. In *Amblyopsis*, the first rib is on the third centrum and it originates off a well-developed parapophysis (Fig. V-9). This character is therefore absent in *Amblyopsis*, but may be present in *Percopsis*. A more complete study of this feature in many more representative gadiforms and other paracanthopterygians than were available for this study may clarify this character.

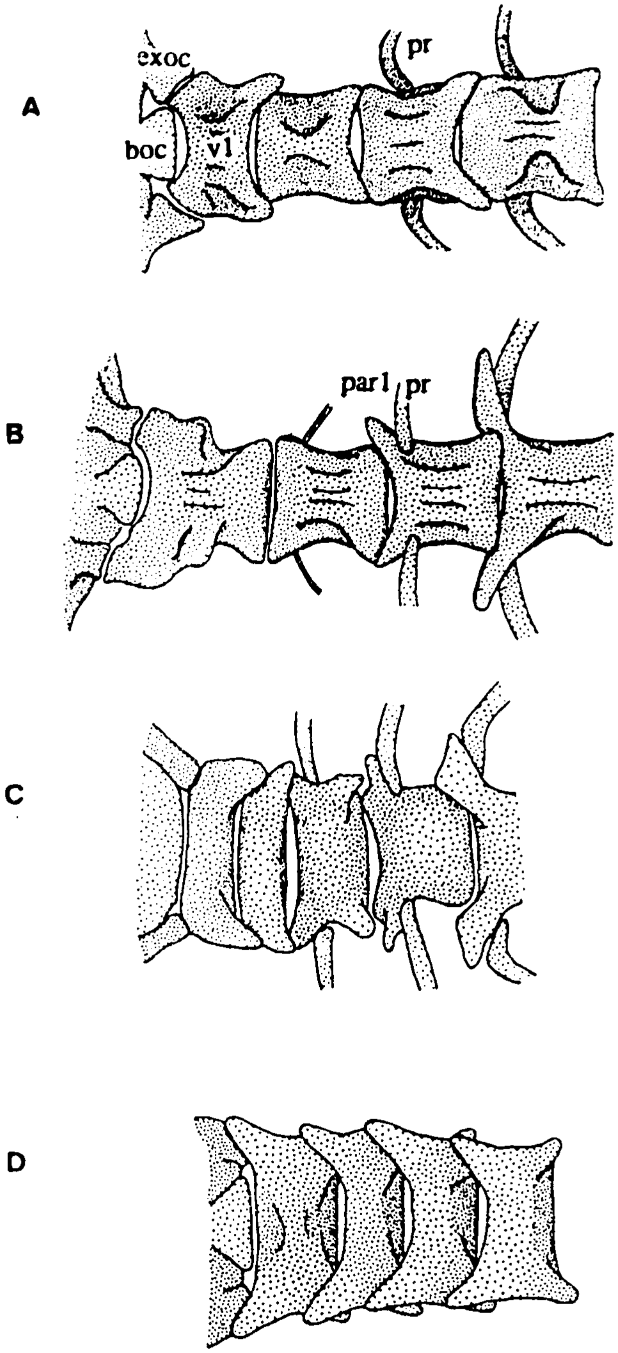

Figure V-9. Camera lucida drawings of the basioccipital, exoccipitals and first four vertebrae in ventral view. A. *Percopsis omiscomaycus*, UAMZ 3062; B. *Amblyopsis spelaea*, CAS 78143; C. *Microgadus proximus*, UAMZ 7594; D. *Porichthys notatus*, UAMZ 2011.

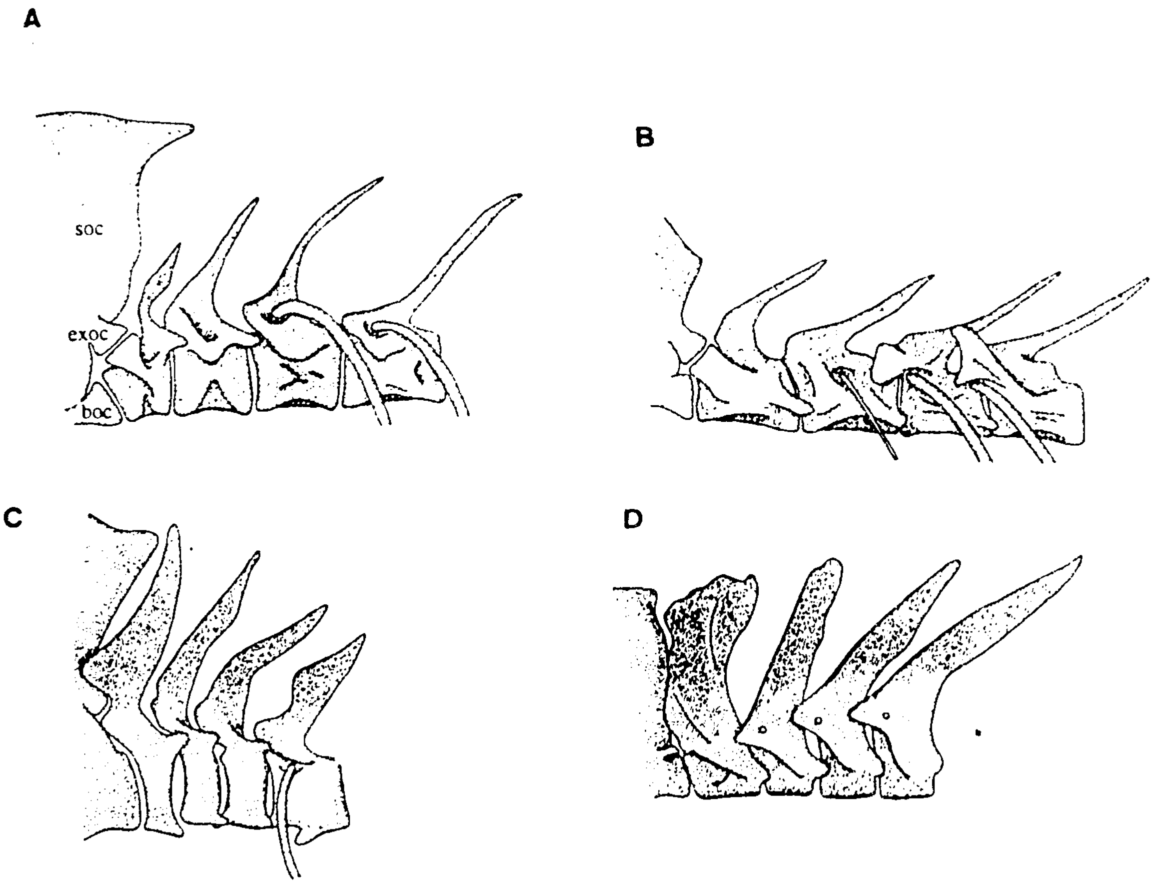

Figure V-10. Camera lucida drawings of the supraoccipital crest, basioccipital, exoccipitals and first four vertebrae in lateral view. A. *Percopsis omiscomaycus*, UAMZ 3062; B. *Amblyopsis spelaea*, CAS 78143; C. *Microgadus proximus*, UAMZ 7594; D. *Porichthys notatus*, UAMZ 2011.

Characters ten, eleven, twelve and thirteen of Patterson and Rosen (1989: fig.16) united the gadiform, lophiiform and batrachoidiform fishes in an unnamed group. Character ten is loss of the interarcual cartilage, which, when present, is found between the second epibranchial and the third pharyngeobranchial. The interarcual cartilage is absent in the specimens of *Percopsis, Amblyopsis, Aphredoderus,* and *Porichthys* examined. This observation is the same as noted by Patterson and Rosen (1989), who considered the interarcual cartilage to be under reduction in gadiforms (with complete loss in some groups), and interpreted the state in *Percopsis, Aphredoderus* and *Amblyopsis* as a homoplastic loss of the cartilage in those lineages. The new placement of the amblyopsids would not be contradicted by this interpretation. Of the two lineages in which the interarcual cartilage is retained, it is rod-like in the ophidiids and ossified in the carapids (Travers, 1981). Patterson and Rosen (1989:fig. 16) interpret the rod-like interarcual cartilage of ophidioids as derived relative to the small interarcual cartilage of the Myctophiformes. An alternate interpretation of this character could be that the absence of the interarcual cartilage is the primitive state within the paracanthopterygians, with its presence being secondarily derived in the ophidiids and carapids, and in the process of being regained in the gadiforms. Neither interpretation contradicts the new placement of the Amblyopsidae.

Character eleven of Patterson and Rosen (1989) involved the exoccipital condyles being "cod-like", widely separated, tube-like and cartilage filled. A comparison of *Amblyopsis* (Fig. V-11) to the figures of the occipital region of *Percopsis, Aphredoderus* and *Porichthys*, (Rosen and Patterson, 1969:figs. 10A, B, C)

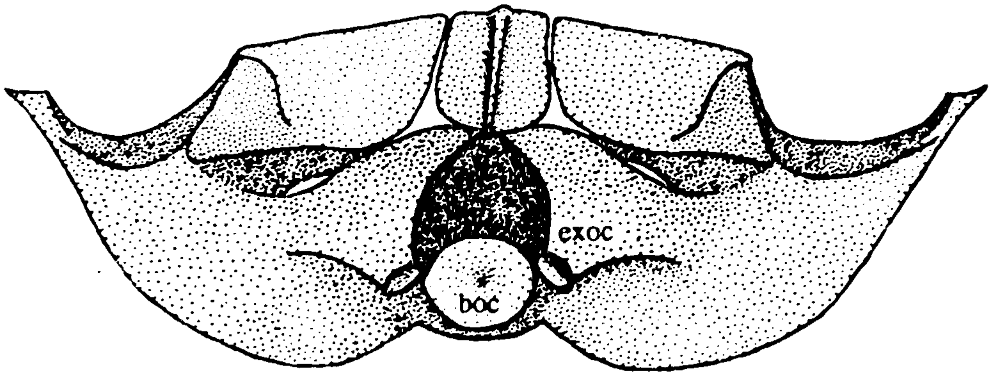

Figure V-11. Camera lucida drawing of the skull of *Amblyopsis spelaea*, CAS 78143, posterior view.

shows that *Amblyopsis* is more similar in appearance to *Porichthys*. Although it is difficult to see whether the exoccipital condyles of *Amblyopsis* are in fact cartilage filled, this genus appears to have the character state.

The twelth character for this group is the third pharyngeobranchial having three processes for articulation with epibranchials 2, 3, and 4 that give it the appearance of a "bear's paw". This character state is clearly present in the gadiforms (Patterson and Rosen, 1989:fig. 12). It is not present in the ophidioids, carapids and bythitoids, which have a long, simple third pharyngobranchial (Patterson and Rosen, 1989: figs. 13F, G, H, K). The same is true in the Lophiiformes, and was considered a secondary loss by Patterson and Rosen (1989:25, figs. 10D, E1, E2). The batrachoidiform condition is considered similar to that of the gadiforms by Patterson and Rosen (1989); however, from their drawings (figs. 10A, B and C) and the specimens of *Porichthys* I examined, the third pharyngeobranchial in batrachoidiforms is broad anteromedially, much as that of the amblyopsids is anteriorly (figs. 12G, H). If the batrachoidiform and gadiform patterns are the same, the new cladogram forces the conclusion that this is a homoplastic similarity. I suggest that the pattern seen in the batrachoidiforms is different, and that the "bear's paw" shape of the third pharyngobranchial is a synapomorphy for the gadiforms.

From the drawings and discussion of Patterson and Rosen (1989) another character may be mentioned: the loss the the first pharyngeobranchial. This loss occurs in the bythitoids, some gadiforms and the Amblyopsidae. It may prove to be indicative of a relationship among these groups.

Character thirteen is the close articulation or suturing of the first neural spine and the supraoccipital crest. I agree with Patterson and Rosen (1989) that this character state is present in both the gadiforms and pediculates (batrachoidiforms and lophiiforms) (Fig. V-10). If the placement of the amblyopsids with the gadiforms is correct, there may be two interpretations of the lack of this character in the amblyopsids; either the condition in the gadiforms and pediculates is a result of homoplasy or the character has been secondarily lost in the amblyopsids.

Characters 14, 15 and 16 define the pediculates, and characters 17, 18, 19 and 20 are synapomorphies of the gadiforms, and none of these characters would contradict the placement of the amblyopsids. Of the thirteen applicable characters used by Patterson and Rosen (1989:fig. 16) (excluding character 9 which remains unclear), seven of them (numbers 1, 2, 3, 4, 8, 10 and 11) are not contradicted in the new scheme, two (numbers 5 and 7) are reinterpreted with a reversed polarity, and only two (numbers 6 and 13) must be explained as homoplasies. The remaining character (number 12) may be reinterpreted as a synapomorphy for the Order Gadiformes, or homoplastic between gadiforms and pediculates, depending on the interpretation of the pattern of the third pharyngobranchial in these lineages.

COMMENTS ON THE PLACEMENT OF †*MCCONICHTHYS* BY GRANDE, 1988

Grande (1988), when describing the Palaeocene paracanthopterygian fish †*Mcconichthys*, followed the scheme of relationships proposed by Patterson and Rosen (1989) to place the new species in a trichotomy with the pediculates (lophiiforms and batrachoidiforms) and gadiforms, based on the characters of the latter authors (Fig. II-1; Grande, 1988: fig.7). In the new scheme of relationships (Fig. V-1), †*Mcconichthys* is placed within the Order Percopsiformes.

Grande's discussion of the character states in †*Mcconichthys* is considered here, and the alternate placement explained. The first four synapomorphies serve to define the superorder and have no bearing on the internal relationships of the paracanthopterygians. Character five (foreshortening of the second centrum) is discussed above, and its presence in †*Mcconichthys* is considered to be primitive, as is the case with the new species from Joffre Bridge. Character six (displacement of the exoccipital condyles) was considered uninformative by Grande (1988:128), and is not present in †*Mcconichthys*. The postmaxillary process of the premaxilla (character seven) is absent in †*Mcconichthys*, and therefore supports the placement of this fish within the Order Percopsiformes.

The absence of the myodome in †*Mcconichthys*, if it is truly absent, must be considered a homoplasy if †*Mcconichthys* is a percopsiform. There is some question about this character state, as it is noted by Grande that radiographs of the appropriate area of the skull in the fossil "indicate an apparent absence of the myodome" (Grande, 1988:128). Character nine, the absence of parapophyses, is present in †*Mcconichthys*, which Grande (1988:fig. 6) shows as lacking the parapophyses on the first seven centra. This is interpreted as a homoplasy in the new cladogram of relationships.

Grande (1988) was unable to assess the states of characters ten, twelve and fifteen (dealing with the pharyngeobranchials) as they are not preserved in the fossil.

Character eleven, the cod-like exoccipital condyles, is recorded as present by Grande. I disagree with this interpretation based on the photographs and figures included in the description (Grande, 1988:figs. 3, 6) in which it appears that the exoccipital condyles are more similar to those of the percopsiforms; however, perhaps on the original material, which I have not examined, this character is present. As mentioned, there is no information for character twelve.

Character thirteen, the close articulation between the first neural spine and the supraoccipital crest, is considered present by Grande (1988). A reexamination of this character, using the figure of *†Sphenocephalus* (Rosen and Patterson, 1969:fig. 32), shows that the condition in *†Mcconichthys* (Grande, 1988:fig. 3) is more similar to that of *†Sphenocephalus*, in which the first neural spine comes in contact with the base of the supraoccipital just above the first centrum, but the neural spine contacts neither the rest of the supraoccipital nor the actual crest of the supraoccipital. It seems that Patterson and Rosen also did not consider the condition of *†Sphenocephalus* to be the same as that in the gadiforms and batrachoidiforms, as *†Sphenocephalus* is not listed as having this character (1989:fig. 16). I consider the condition in both *†Mcconichthys* and *†Sphenocephalus* to be different from that of gadiforms and pediculates.

The rest of the characters of Patterson and Rosen (1989) for which there were data were considered absent for *†Mcconichthys* by Grande (1988). Therefore, the placement of *†Mcconichthys* in the Order Percopsiforms based on the presence of the ctenoid scales and within the order based on the loss of the postmaxillary process of the premaxilla, is contradicted by only one character, number nine, the parapophyses absent on the first seven centra.

COMMENTS ON PARACANTHOPTERYGIAN CHARACTERS OF OTHER AUTHORS

A review of some of the other literature on the percopsiform, gadiform, and amblyopsid fishes provides no characters to contradict the placement of the amblyopsids as the sister group to the gadiforms. Gosline (1963) uses the lack of a true pelvic spine, presence of an intervertebral articulation between the second ural centrum and one of the upper hypurals, loss of the basisphenoid and orbitosphenoid, an enlarged intercalar and the exoccipital condyles separated from one another, to show relationships among all three of these groups. Gosline (1963) also comments on the contact between the pleurosphenoids and the prootics in *Percopsis* and *Aphredoderus*, versus the contact between the pleurosphenoid and anterolateral expansions of the parasphenoid in *Chologaster* (Amblyopsidae). The gadiform pattern is the same as that of *Percopsis* and *Aphredoderus* (Mujib, 1967), suggesting that the pattern in *Chologaster* may be a synapomorphy for the Amblyopsidae.

Gosline (1971) notes that the exoccipital condyles are distinct from the basioccipital condyle (which is commented on above) and that epineural bones are absent from both the percopsiforms (which included the amblyopsids and aphredoderids) and the gadiforms. Johnson and Patterson (1993) described the intermuscular bones in *Polymixia* and *Aphredoderus* as epineurals. In any case, the Amblyopsidae are not effected by this, as it relates this family to both the gadiforms and percopsiforms.

Freihofer (1970) used nerve patterns to discern relationships in the paracanthopterygians. His conclusions were that the amblyopsids were closer to the percopsids than the aphredoderids in the ramus lateralis accessorius (RLA) nerve pattern; however, it is the apredoderids which were considered to have the derived state.

Lauder and Liem (1983) suggested a relationship between the gadiform and batrachoidiform lineage (the latter consisting of batrachoidiforms, lophiiforms, and gobiesociforms) based on the reduced or lost scales, and the reduced opercle and enlarged subopercle. The amblyopsids have the small cycloid scales as in the gadiform and batrachoidiform-lineage. The cycloid scales were considered to be secondarily derived in *Chologaster* (Rosen, 1962:30); however, the presence of cycloid scales in the sphenocephalid *†Xenyllion*, contrasting to the ctenoid scales of *†Sphenocephalus* (Rosen and Patterson, 1969), indicates that cycloid scales could be primitive for the superorder. The "strongly ctenoid" scales of fossil percopsiforms may well be the same as the "periferal ctenoid" scales found in *Aphredoderus* (Roberts, 1993). The most parsimonious distribution of scale characters within the superorder is to view ctenoid scales as a synapomorphy for the redefined Order Percopsiformes, rather than the superorder as a whole gaining ctenoid scales with later reversals to cycloid scales in many lineages.

The enlarged subopercle mentioned by Lauder and Liem (1983) is also present in the Amblyopsidae, and *Typhlichthys* has the same loss of the dorsal process on the opercle as found in *Porichthys*. *Amblyopsis* and *Chologaster* both have a reduced and somewhat flattened dorsal process on the opercle, which, although not the same as that found in *Lota* and *Microgadus*, does seem to be a reduction in size. These trends may well be associated with the flattening of the head, as suggested by Lauder and Liem (1983), which also occurs in the amblyopsids.

Other characters mentioned for paracanthopterygian groups by Lauder and Liem (1983) are the long and many rayed median fins confluent with the caudal fin, anterior vertebrae joined via overlapping pre- and postzygapophyses, and accessory upper pectoral radial. The latter is not present in the gadiforms (Patterson and Rosen, 1989:14). The overlapping pre- and postzygapophyses are present in *Amblyopsis*, and to some extent also in *Percopsis*. The many-rayed median fins confluent with the caudal fin are not present in lophiiforms nor amblyopsids. The presence of this type of median fin in gadiforms and batrachoidiforms could be homoplastic, or it could indicate that the amblyopsids would be more correctly placed as the sister to the rest of the Anacanthini, and the lophiiform condition is a reversal.

Rosen (1962), in comparing the Cyprinodontoidei, Amblyopsidae and Aphredoderidae, commented on the muscles of the jaw. His comparison in fact related the amblyopsids not only to the aphredoderids, but also to the percopsids and the gadiforms.

Other authors have looked at different aspects of anatomy to provide evidence of relationship within the Paracanthopterygii. Mattei (1991) examined sperm structure, only to conclude that it was not useful for phylogenetic analysis of the paracanthopterygians because of the great number of autapomorphies within the superorder. Jamieson (1992) also looked at sperm structure, but not that of the percopsiforms or gadiforms. He suggested a relationship between the Batrachoidiformes and Lophiiformes, along with the Gobiesociformes.

None of the previous studies contradicts the new proposed hypothesis of paracanthopterygian relationships. Although further studies are needed for many of the paracanthopterygians, I suggest that the Amblyopsidae be removed from the Percopsiformes.

BIOGEOGRAPHY

Biogeography is the description of distribution patterns, both temporal and spatial, of related organisms, and the explanation of the distribution patterns observed (Cox and Moore, 1980). A biogeographic analysis relies on a sound phylogeny of the group of organisms to be studied, in order for the distribution patterns of organisms to be understood in context with their relationships to one another (Humphries and Parenti, 1986). However, study of the biogeography of a group of organisms may in turn bring to light inconsistencies in a phylogeny or even incorrect identification of specimens (*e.g.* Nolf, 1985) based on prior knowledge of general distribution patterns from other organisms or geological history of an area.

Two explanations used by biogeographers to account for the observed distribution patterns of organisms are vicariance and dispersal. Vicariance events, resulting from geological causes such as plate tectonics, can be used to explain disjunct ranges of related taxa. The earlier distribution of a group of organisms is hypothesized to have been continuous over a larger area that included the two or more disjunct known locations, and this continuous distribution was later disrupted by a geographic barrier (*e.g.* continental drift) followed by the organisms in parts of the original range becoming extinct, leaving isolated populations in which allopatric speciation could occur (Briggs, 1987). An alternate explanation, dispersal, is that the distribution of a group of organisms is a result of active or passive movement from a centre of origin to a new area.

In the past, biogeographers tended to favour one of these two theories over the other as an explanation of observed distribution patterns; however, many authors now use both vicariant and dispersal events to explain the observed patterns of distribution (Nelson, 1994). When deciding which of these events is more likely to explain the modern distribution of related organisms, knowlege of the geological age of the group can be helpful. Vicariant events that took place in the Mesozoic should not be used to explain the modern distribution pattern of a group of organisms that probably arose in the Tertiary (Briggs, 1987). The fossil record of the group under study is therefore important for an understanding of the biogeography of the group.

The modern distribution of the freshwater fishes of North America is well documented (*e.g.* Lee *et al.*, 1984), and much of the biogeography of these fishes has been published based on the distribution patterns (*e.g.* Hocutt and Wiley, 1986). The object of this section is not to present a new study on the biogeography of the Recent percopsiforms, but rather to synthesize the prior knowledge that relates to these extant fish in order to test the hypothesis of relationships presented in the cladogram (Fig. V-1) and suggest additional information based on the fossil record.

Distribution

The Superorder Paracanthopterygii contains both freshwater and marine groups. Of the 1212 species included in the superorder only about 20 species are restricted to fresh water (Nelson, 1994). The Family †Sphenocephalidae is marine, but all the fossil and recent members of the Percopsiformes and the Amblyopsidae are found in fresh water. Two gadiforms are also found in fresh water (*Lota* and *Microgadus*), and the remaining fresh water paracanthopterygians are members of the Bythitidae (Ophidiiformes).

Figure V-12 shows the distribution of the extant percopsiforms and amblyopsids, and known localities of the North American fossil percopsiforms and sphenocephalids. The geological history of the Paracanthopterygii, based on the fossil record, indicates the group probably evolved in the Early to middle Cretaceous, as representatives were present by the Late Cretaceous, and there are no known acanthomorphs older than latest Albian or early Cenomanian (Stewart, in press). The oldest known paracanthopterygians are the marine sphenocephalids. *†Sphenocephalus fissicaudus* is from Campanian deposits in Germany, and *†Xenyllion zonensis* is from the older Cenomanian deposits of the interior of North America. The Utah fossils closely related to *†Xenyllion zonensis* are either early Cenomanian or late Albian (Stewart, in press), making them possibly the oldest paracanthopterygian (and

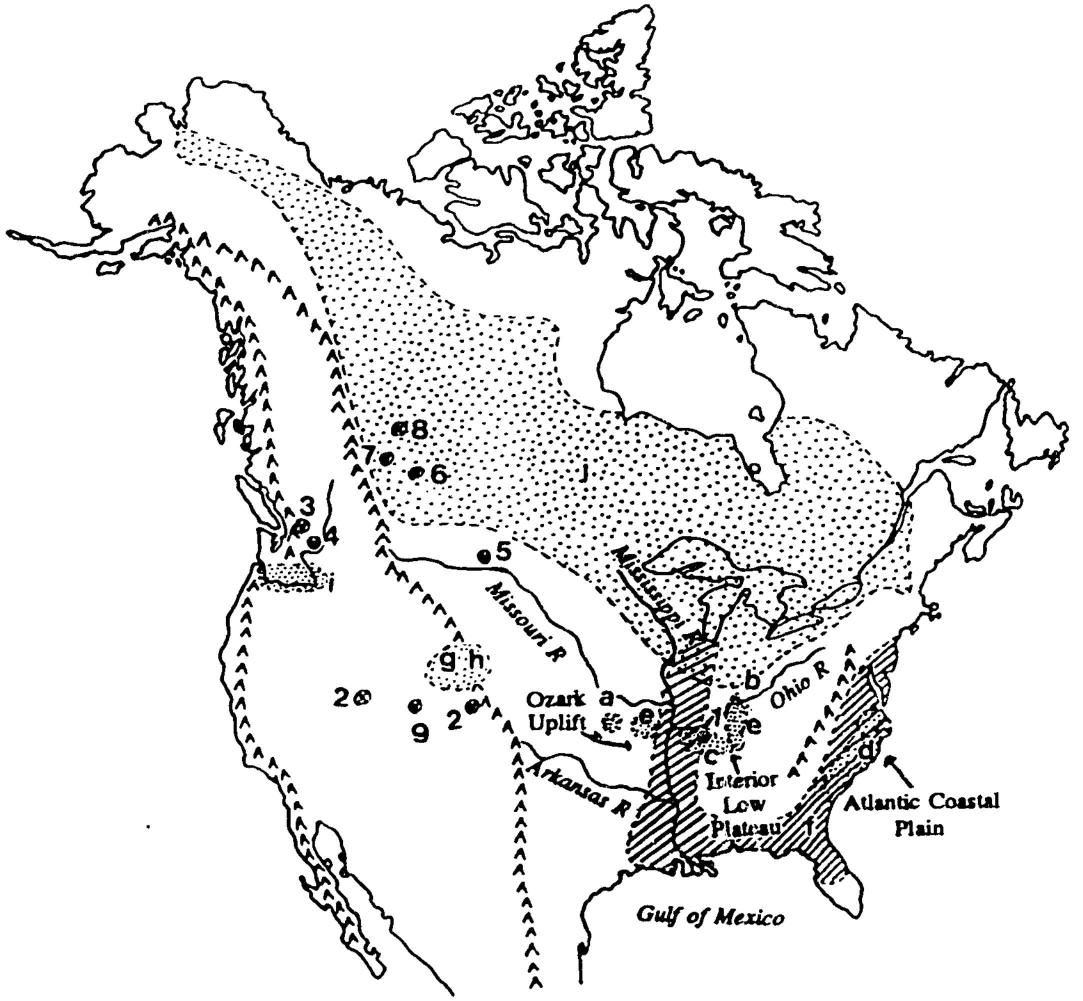

Figure V-12. Distribution of †*Xenyllion*, the percopsiforms and amblyopsids.

Ranges: ░ or ▨		Single localities: ●	
Amblyopsis rosae	a	*Speoplatyrhinus poulsoni*	1
A. spelaea	b	†*Trichophanes*	2
Chologaster agassizi	c	†*Libotonius blakeburnensis*	3
C. cornutus	d	†*L. pearsoni*	4
Typhlichthys subterraneus	e	†*Mcconichthys longipinnus*	5
Aphredoderus sayanus	f	†*Massamorichthys wilsoni*	6
†*Amphiplaga brachyptera*	g	†*Lateopisiculus turrisfumosus*	7
†*Erismatopterus levatus*	h	†*Xenyllion zonensis*	8
Percopsis transmontana	i	†*Xenyllion* sp.	9
P. omiscomaycus	j		

acanthomorph) fossils known.

The earliest known freshwater paracanthopterygians are the fossil percopsiforms from lower Palaeocene deposits in Montana (*†Mcconichthys*) and the two middle Palaeocene species *†Massamorichthys* and *†Lateopisiculus* from Alberta. Thus, in the Palaeocene, percopsiform fishes were established and diverse in fresh waters. The localities of these fossil fishes are all in the western-central region of North America.

In the Eocene and Oligocene, a greater diversity (based on known fossil records) of percopsiforms existed, represented by six species in four genera (*†Amphiplaga, †Erismatopterus, †Libotonius* and *†Trichophanes*) and three families. Percopsiform fishes were still distributed in the same area as they were during the Palaeocene, but some members are known to have occurred farther west and south, with *†Libotonius* in Washington and British Columbia, and *†Trichophanes* in Colorado and Nevada.

The Recent percopsiforms (excluding the Amblyopsidae based on the new cladogram) have become less diverse, with only three extant species, *Percopsis omiscomaycus*, *P. transmontana* and *Aphredoderus sayanus*; however, they have a much larger known distribution. *Percopsis omiscomaycus* is found in the Atlantic slope and Missouri River basin of the United States and throughout Canada, with the exception of most of British Columbia, west of the continental divide (Gilbert and Lee, 1980). The congeneric species, *P. transmontana*, is endemic to the middle and lower Columbia River drainage in the state of Washington (McPhail and Lindsey, 1986). *Aphredoderus sayanus* is found in the south-central and eastern United States, in the lowlands of the Atlantic and Gulf slope, and the Mississippi Valley (Lee, 1980). Of these three species, the only overlap of ranges occurs south of the Great Lakes between *A. sayanus*, in the northern part of its range, and *P. omiscomaycus*, in the southeastern part of its range.

Members of the Recent Family Amblyopsidae are adapted, to varying degrees, to low light or cave habitats. This family has a limited distribution in east-central and southeastern United States. The two species of the genus *Chologaster* are found in disjunct areas, with *C. cornutus* on the Atlantic coastal plain in southeast Virginia and eastcentral Georgia (Cooper and Rohde, 1980) and *C. agassizi* in southcentral Tennessee and southcentral and western Kentucky (Cooper, 1980b).

The two recognized species of *Amblyopsis* also have disjunct distributions. *A. rosae* is found only in the Ozark Plateau of southwestern Montana, northwestern Arkansas and northeastern Oklahoma, and *A. spelaea* is limited to the Pennyroyal and Mitchell Plateaus of Kentucky and southern Indiana (Cooper, 1980a).

Typhlichthys subterraneus is found in two disjunct populations, one on the Ozark Plateau of southern Montana and the other in the Interior Plateau of northern Alabama, northwestern Georgia, central Tennessee and Kentucky and southern Indiana (Cooper, 1980c). The most recently described amblyopsid, *Speoplatyrhinus poulsoni*, is the one with the most limited known distribution, having been found only in the type locality, a cave on the Tennessee River west of Florence, Alabama (Cooper and Kuehne, 1974). Among the species of the Family Amblyopsidae, the only area of range overlap occurs in Mammoth Cave, Kentucky, among the species *T. subterraneus, C. agassizi* and *A. spelaea* (Cooper, 1980).

Interpretation

The centre of origin that I propose for the Superorder Paracanthopterygii is the North American epicontinental sea, which formed during the mid-Cretaceous (Briggs, 1987). The epicontinental sea in the middle to Late Cretaceous covered most of the central part of the North American continent (Laporte, 1968). The area covered includes the Albertan locality of *†Xenyllion zonensis* and the locality of the congeneric or possibly conspecific remains from Utah (Stewart, in press). The locations of the specimens of *†Xenyllion* indicate that this genus had a range of at least 1800 km along the western part of the seaway (Stewart, in press). The other known Cretaceous genus, *†Sphenocephalus*, from localitites in what is present day Germany, extends the range of the Family †Sphenocephalidae north through the shallow seaway, which would not have been a barrier to movement. Although the epicontinental seaway is suggested as the area where the superorder arose, these fish may have had a much larger distribution. There is no evidence to suggest that the range of the earliest paracanthopterygians were restricted to this area.

Order Percopsiformes

From a Cretaceous North American epicontinental sea centre of origin, the ancestor of the percopsiform lineage moved from the marine environment into fresh water. This event presumably occurred before the end of the Cretaceous, because the epicontinental sea had begun to recede in the Late Cretaceous, and the order is already diverse (three fossil genera and two families) in the Palaeocene. During the Late Cretaceous when the seaway covered the central part of North America, the eastern part of the continent was connected to Europe and the western part was connected to Asia. If the percopsiforms invaded fresh water when these connections existed, members of the order may also have been present in Europe or Asia. No fossil percopsiforms are known from Asia, but some remains that may belong to a percopsiform have been found in Italy (M.V.H. Wilson, pers. comm.). If these Italian fossils do belong to a percopsiform it would suggest that either percopsiforms invaded the fresh waters of eastern North America first and then spread to Europe, or they invaded Europe first then spread to eastern North America, followed by an extinction of the group in Europe.

By the Eocene, another family of percopsiforms, the †Libotoniidae, was in evidence, along with the persisting Percopsidae. The sister group relationship of the Percopsidae and †Libotoniidae (Fig. V-1) indicate the two families diverged before the Early Palaeocene. The two species of *†Libotonius* may have dispersed westwards into what is now British Columbia and Washington State, or have been isolated in the western area by a vicariant event, probably in the Late Cretaceous to early Palaeocene.

The aphredoderid lineage, based on known fossils, was present at latest by the Oligocene, with two species of the genus *†Trichophanes*. *†Trichophanes foliarum* is from the late Eocene (or possibly Oligocene) Florissant lake beds of Colorado and *†T. hians* is from the Osino beds of Nevada. The Osino beds are also thought to be late Eocene or Oligocene (van Houten, 1956). Based on the cladistic relationships of the aphredoderids (Fig. V-1), the aphredoderid lineage diverged from the †Mcconichthyidae/†Libotoniidae/ Percopsidae lineage even earlier than the †Libotoniidae diverged from the Percopsidae. The genus *†Trichophanes* may have dispersed separately into the two areas, or a continuous range may have been split into two isolated areas where speciation occurred.

Members of the Percopsidae have stayed closest to the order's proposed ancestral home in west-central North America. This family appears to have dominated the central area while members of related families have been pushed to the periphery. The Eocene percopsids, *†Amphiplaga* and *†Erismatopterus*, are found in this area (Green River Formation of Wyoming, Colorado and Utah), and it is probable that the ancestral *Percopsis* originally had a continuous range over much of this area. The present disjunct distribution of the two species of *Percopsis* could be the result of a vicariant event. Several possible causes for such events have occurred in this area: the orogenic events of the Miocene to Pliocene that formed the Coastal and Cascade Mountains; the volcanism of the mid-Pliocene to Recent; and the several ice ages which have occurred in the last 100,000 years (McPhail and Lindsey, 1986).

The present widespread distribution of *Percopsis omiscomaycus* in eastern and northern Canada is considered to be a reinvasion of that area by the species after the last, Wisconsonian, ice age during which this species was confined to two or more refugia to the south and north of the ice sheet (McAllister, *et al.*, 1986). Pflieger (1971) suggested that *P. omiscomaycus* could have been present preglacially in all the principal drainages of the northern United States and Canada. After the last ice receded, this species returned to its former range.

McPhail and Lindsey (1986) considered *P. transmontana* to be a relict or endemic population, left over from the Cascadian Refugium after the Wisconsonian ice age in the Columbia River, an area that was ice-free during this ice age. Whether *P. transmontana* was distinct from *P. omiscomaycus* before or after the periods of glaciation is unknown.

The modern range of *Aphredoderus sayanus* is the Mississippi River basin and Atlantic coastal regions of the United States. The current range of *Aphredoderus sayanus* could also be a result of dispersal, through estuarine flooding or interconnected drainages, from the central United States eastwards then southwards through the Mississippi River basin to the Atlantic Coastal Plain via the Mississippi River embayment area (Conner and Suttkus, 1986). *Aphredoderus sayanus* may have occupied the lowlands of the Mississippi Valley throughout the Cenozoic, or may have been confined to a refugium in the Atlantic coastal plain during the ice ages (Schmidt, 1986). This fish then invaded the northern Appalachian area around the Gulf of St. Lawrence after the last ice age.

Family Amblyopsidae

The Family Amblyopsidae has no known fossil record; therefore, the biogeography of the family can only be based on the distribution of extant members and closely related groups, such as the gadiforms (Fig. V-1). Extant amblyopsids are mostly found in springs and caves in the east-central United States in two general areas, the Ozark Uplift and the Interior Low Plateau. The Ozark Uplift is west of the Mississippi River, between the Arkansas River to the south and the Missouri River to the north. The Interior Low Plateau, designated by Fenneman (1968), is the area east of the Mississippi River roughly bounded by the Ohio River to the north, the Tennessee River to the west and south, and the Cumberland Plateau to the east. Several authors have proposed explanations for the present distribution of the members of the family.

Woods and Inger (1957) suggested that this family moved into the groundwaters of the Interior Low Plateau during the Tertiary, and then dispersed throughout the area underground, via interconnected groundwater channels in the karst landscape. These authors did not, however, suggest an area from which the lineage leading to the Amblyopsidae dispersed into the Interior Low Plateau. The time frame is further narrowed by the probability that the karst area of eastern and central United States was only established by the mid-Tertiary (White, 1988). Woods and Inger (1957) considered the boundary of the family range to have been no further north in the past than it is at present because of the lack of evidence to show that amblyopsids occurred north of the Interior Low Plateau, and sparse karst habitat in the north. This indicates the Interior Low Plateau as the centre of origin for the Family Amblyopsidae.

Woods and Inger (1957) proposed that members of the Family Amblyopsidae underwent two or more waves of dispersal from the Interior Low Plateau, which were influenced by fluctuations in the water table. They proposed that an ancestral stock of *Chologaster cornutus* migrated from this area, around the Appalachian Mountains, in a ring of swamps that fringed the Mississippi Embayment area, thereby dispersing to the Atlantic Coastal Plain. *Chologaster cornutus*, according to Woods and Inger (1957), formerly had a range that extended westwards at least as far as the Mississippi River, and a later reduction of the range was caused by drought during or after the glacial period. Alternatively, *Chologaster cornutus* may have dispersed from the Interior Low Plateau into the Atlantic Coastal Plain through headwater transfers through the Appalachian Mountains. Natural exchanges of headwater species are known to have occurred between the Tennessee River and the Savannah and Santee rivers of the Atlantic Coastal Plain (Starnes and Etnier, 1986)

Pfleiger (1971) suggested that fluctuations in the water table were caused by the alternate cycle of erosion and sedimentation which occurred in the Mississippi Embayment area during the Pleistocene. The fluctuating water table may then have accounted for the dispersal and present east-west disjunct distribution of *Amblyopsis rosae* (Ozark Uplift) and *A. spelaea* (Interior Low Plateau). These fluctuations of the water table might have created ecological conditions in subterranean waters that would favour alternate periods of dispersal and isolation.

An alternative explanation for the distribution on the two species of *Amblyopsis* is that of Woods and Inger (1957). They suggested that the ancestral *Amblyopsis* spread from the north throughout the limestone plateaus of both the Ozark Uplift and

Tennessee-Cumberland basins (Interior Low Plateau). This range was later split, and *Amblyopsis* forced into two isolated pockets, during the Pleistocene, by the more competitively successful *Typhlichthys subterraneus*. The two species of *Amblyopsis* diverged in these two isolated pockets.

T. subterraneus is found in two disjunct localities, one in the Ozark Uplands, the other in the Interior Low Plateau. Pflieger (1971) suggested that *T. subterraneus* is a recent invader of the Ozark Uplands, and may have dispersed westward, from the Tennessee-Cumberland river drainage basin (Interior Low Plateau), during the erosional cycle that accompanied the advance of the Wisconsonian ice. Pflieger (1971) considered headwater transfers across major divides to have been important in the dispersal of fishes in the Ozark Uplands. Starnes and Etnier (1986) also considered headwater transfers to be important in the Tennessee-Cumberland basins. They suggested that many opportunities to transgress these weak divides have probably occurred for headwater species. However, Starnes and Etnier (1986) suggested that subterranean dispersal routes and dispersal under the Mississippi River were most likely responsible for the distribution of *T. subterraneus*. Both Pfleiger (1971) and Starnes and Etnier (1986) suggested dispersal from the east (Tennessee-Cumberland drainage, Interior Low Plateau) to the west (Ozark Uplift) for *T. subterraneus*.

Headwater transfers may account for the more restricted co-occcurrence of the cave springfish, *C. agassizi* (Starnes and Etnier, 1986) in both the Tennessee and Cumberland drainages. Ground water systems likely connect the headwaters of the

Tennessee drainage (Elk and Duck rivers) and the Cumberland drainage (Stone and Caney Fork rivers). Starnes and Etnier (1986) suggested headwater dispersal from the Elk River system through the upper Duck River and then into the upper Caney Fork system. *Chologaster agassizi*, like *T. subterraneus*, is found in both the Tennessee and Cumberland drainages. Dispersal along the main channels of the Tennessee and Duck rivers was considered much less probable for a spring-adapted form, such as *C. agassizi*, and such a dispersal route would likely have resulted in additional populations along the route rather than the observed dispersal pattern (Starnes and Etnier, 1986).

Speoplatyrhinus poulsoni is a Tennessee River endemic. Starnes and Etnier (1986) proposed that this species most probably dispersed through headwaters also.

The above indicates that *Amblyopsis* and *Typhlichthys* first inhabited the Tennessee River basin, and dispersed from there into the Cumberland River basin and under the Mississippi River to the Ozark Uplift. The fish fauna of the Tennessee-Cumberland basins and Ozark areas suggests that gene flow between the two areas has continued for a long period of time (Starnes and Etnier, 1986). *Chologaster* likely dispersed from the Tennessee-Cumberland drainage basin eastwards, to the Atlantic Coastal Plain.

Phylogenetic implications

The biogeography of the freshwater percopsiform and amblyopsid fishes neither supports nor contradicts the hypothesis of relationships presented in Figure V-1.

Based on the information above, if the Amblyopsidae are the sister group to the Aphredoderidae, as postulated by Patterson and Rosen (1989), the amblyopsid lineage must have diverged from the aphredoderid lineage by the Early Tertiary, possibly in the central United States. If this is the case, a freshwater percopsiform ancestor shared between the aphredoderids and amblyopsids would be expected, prior to the late Eocene or Oligocene, as the genus *†Trichophanes* is an aphredoderid. Based on the assumption of a sister-group relationship between the amblyopsids and the aphredoderids, I would suggest that the ancestral amblyopsid lineage dispersed into the Interior Low Plateau, in the mid-Tertiary, from the northcentral United States, through the Missouri and Mississippi river basins. The populations in the Ozark Uplift may have been left behind during this dispersal, or these populations may have dispersed back to the western side of the Mississippi River as suggested by Pflieger (1971) and Starnes and Etnier (1986).

If the new hypothesis of relationships (Fig. V-1) is correct, the most parsimonious explanation of the observed distribution pattern is that the Amblyopsidae have independently invaded fresh waters. This invasion may have been from the Gulf of Mexico shallow coastal regions into the Tennessee River system. During the Tertiary the upper and middle Tennessee River had a southern outlet to the Gulf of Mexico (Starnes and Etnier, 1986). From the Tennessee River Basin, the genus *Chologaster* might have dispersed to the Atlantic Coastal Plain (*Chologaster cornutus*), either around the Appalachian Mountains to the south or through headwater transfers. The genera *Typhlichthys* and *Amblyopsis* might have dispersed to the Ozark Uplift through subterranean routes and under the Mississippi River.

Although the Superorder Paracanthopterygii is predominantely marine, except for the Order Percopsiformes, Family Amblyopsidae and several bythitids, two gadiforms have also independently invaded the freshwater environment from the marine: *Lota lota* and *Microgadus tomcod. Microgadus tomcod* is usually found in the marine environment or brackish waters, occasionally entering fresh water to spawn. It is a permanent resident in lakes near the Atlantic coast from Labrador to Virginia, where it has become landlocked (Scott and Crossman, 1973).

Lota lota is only found in fresh water. The distribution of this species is circumpolar, in North America and Eurasia. During the ice ages, this species was restricted to several glacial refugia in North America, probably three: the Beringian, Mississippian and Missourian (Crossman and McAllister, 1986). The oldest fossil specimens of *Lota* are from the late Pleistocene, and fossil remains have been found in northern Kansas and southern Nebraska, localities that were south of the ice sheet during glacial periods (Stewart, 1994). After the Wisconsonian ice retreated, *Lota* reinvaded the northern part of North America. Because these two species and several bythitids have independantly adapted to fresh water, the hypothesis that the amblyopsid lineage adapted to fresh water separately from the percopsiform lineage is not unlikely.

The fresh water percopsiforms likely evolved in North America or Europe in the Late Cretaceous and are now endemic to North America. If the undescribed remains from Italy do belong to a percopsiform, they would indicate that the range of the Order Percopsiformes was much greater in the past, including Europe as well as North America. The eastern part of North America was connected to Europe in the northern latitudes in the Late Cretaceous and early part of the Palaeogene (Wilson and Williams, 1991). If the Italian specimens are a percopsiform, the origin of the order may have been in Europe, rather than North America. The land connection between Europe and North America may have allowed the dispersal of the percopsiforms from North America to Europe or from Europe to North America.

SUMMARY

The two Palaeocene percopsids from Alberta have provided new information on which to base a phylogenetic analysis of the Order Percopsiformes. These two new species extend the known age of the Family Percopsidae by about eight million years, from the early and middle Eocene to the middle of the Palaeocene. *†Mcconichthys*, included in the Order Percopsiformes, is the only fresh water paracanthopterygian known that is older than the Albertan percopsids. All the described percopsiforms are endemic to North America.

Although more information and further analyses are needed before all the relationships of the paracanthopterygian fishes are resolved, the results of this study suggest some areas for more attention. The relationship of the amblyopsids with the anacanthines instead of the percopsiforms is suggested here, but is contradicted by the segmented alveolar process of the premaxilla and by the jugular vent, two characters previously thought to unite the aphredoderids and amblyopsids. A study involving other techniques, such as DNA sequencing, might prove useful to examine this suggested relationship among the extant paracanthopterygians, particularly the Anacanthini that have a poor fossil record.

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APPENDIX

LIST OF CHARACTERS

1. Full neural spine on second preural centrum
    - 0: absent
    - 1: present

2. Number of epurals in caudal skeleton
    - 0: three
    - 1: two
    - 2: one or none

3. Number and orientation of supraneural
    - 0: two or three, upright between neural spines
    - 1: one irregular shaped, over neural spines

4. Intercalar bone
    - 0: not enlarged
    - 1: enlarged

5. "Percopsoid" projections on branchiostegal rays
    - 0: absent
    - 1: present on some

6. Dorsal process on lacrimal
    - 0: absent
    - 1: small, rounded
    - 2: strong spike

7. Opercle horizontal ridge extending posteriorly as a spine
    - 0: absent
    - 1: present

8. Opercle vertical ridge on anterior edge extending as a ventral spine
    - 0: absent
    - 1: present

9. Large preopercular spines
    - 0: absent
    - 1: present

10. Opercle posterodorsal edge
    0: not recurved
    1: recurved

11. Beryciform foramen in ceratohyal
    0: present
    1: absent

12. Premaxilla and maxilla lengths
    0: premaxilla equal or longer than maxilla
    1: premaxilla shorter than maxilla

13. Number of supramaxillaries
    0: one or more
    1: none

14. Number of postcleithra
    0: two
    1: one, with an enlarged dorsal plate
    2: single rod-shaped or absent

15. Anterior projection of subopercle
    0: with a spike
    1: blunt
    2: absent (no projection)

16. Ornament (small spines or serrations) on the preopercle
    0: present
    1: absent

17. Preopercle orientation and shape
    0: two distinct limbs (vertical and horizontal) meeting in a pronounced angle with the vertical limb being longer than the horizontal
    1: less angled, overall bone is rounded
    2: bone almost completely vertical

18. Articulation of the parhypural
    0: on fused preural and ural centrum (PU1+U1)
    1: fused to (lower) hypural plate
    2: free from centrum

19. Cleithrum
    - 0: almost uniformly thick along its length
    - 1: with a distinct triangular dorsal plate
    - 2: no distinct plate, not thick

20. Antorbital
    - 0: present
    - 1: absent

21. Alveolar process of premaxilla
    - 0: not segmented
    - 1: segmented

22. Dorsal projection of opercle above horizontal ridge
    - 0: vertical anteriorly
    - 1: anteriorly truncated or excavated

23. Scales
    - 0: cycloid, with a central focus
    - 1: ctenoid, ("peripheral ctenoid" or "strongly ctenoid") with a posterior focus

24. Postmaxillary process of the premaxilla
    - 0: present
    - 1: present, with "gadoid notch"
    - 2: absent

25. Ornament (small spines or serrations) on the lacrimal and infraorbital bones
    - 0: present
    - 1: absent

26. Dorsal process on maxilla
    - 0: absent
    - 1: present

27. Length of supraoccipital crest
    - 0: short, not reaching to or beyond first neural spine
    - 1: long, reaching beyond first neural spine

28. Scapular foramen
    - 0: in centre of scapula
    - 1: between scapula and coracoid

29. Retroarticular
    - 0: present
    - 1: absent

30. Number of branchiostegal rays
    - 0: nine or more
    - 1: eight
    - 2: seven
    - 3: six or less

31. Scale covering
    - 0: on opercle
    - 1: head naked

32. Epihyal and ceratohyal
    - 0: not sutured
    - 1: few sutures
    - 2: fully sutured

33. Pelvic splint
    - 0: present
    - 1: absent

34. Pelvic girdle left and right medial processes
    - 0: do not meet
    - 1: overlap
    - 2: meet in the midline

35. Pelvic girdle and postcleithra
    - 0: do not overlap
    - 1: overlap or attach

MACLADE DATA MATRIX

	1	2	3	4	5	6	7	8	9	10
	nPU2	epural	supnrl	interca	p. proj	lac prj	op hor	op ver	pop sp	op rec
Aulopus	0	0	0	?	0	0	0	0	0	0
Myctophum	0	0	0	?	0	0	0	0	0	0
Lampanyctus	0	0	0	?	0	1	0	0	0	0
Polymixia	1	0	0	?	0	0	0	0	0	0
Melamphaes	0	0	0	?	0	0	0	0	0	0
Vellifer	0	0	0	?	0	1	0	0	0	0
L. pearsoni	?	?	?	?	1	2	1	1	0	0
L. blakeburnensis	1	1	1	?	1	2	1	1	0	0
P. transmontana	1	?	1	1	1	2	1	1	0	0
P. omiscomaycus	1	1	1	1	1	2	1	1	0	0
Amphiplaga	1	1	1	?	0	2	1	1	0	0
Erismatopterus	1	1	1	?	0	2	1	1	0	0
Amblyopsis	1	2	-	1	0	2	1	1	0	0
Aphredoderus	1	1	1	?	1	2	1	1	0	0
Chologaster	1	2	-	?	1	2	1	1	0	0
Trichophanes	1	1	1	?	1	2	1	1	0	0
Typhlichthys	1	2	-	?	1	2	1	1	0	0
Sphenocephalus	1	1	1	?	1	2	1	1	1	1
Xenyllion	1	?	?	?	1	?	1	1	1	1
Joffre Bridge	1	1	1	?	1	2	1	1	0	0
Smoky Tower	1	1	1	?	1	2	1	1	0	0
Ophidion	1	2	-	1	1	0	1	1	0	0
Mcconichthys	1	?	1	?	0	2	1	1	0	0
Lota	1	1	-	1	1	2	1	1	0	0
Microgadus	1	1	-	1	1	2	1	1	0	0
Asineops	1	1	0	?	0	1	1	1	0	0
Porichthys	1	1	-	-	0	0	1	1	0	0
Saurida	0	0	0	?	0	0	0	0	0	0
fossil beryciforms	0	0	0	?	0	1	0	0	0	0

"-" denotes gaps; "?" denotes missing data

	11	12	13	14	15	16	17	18	19	20
	ber for	px,mx	supmx	postcle	sop	pop orr	pop shp	phyp	cleith	antorb
Aulopus	1	0	0	?	2	1	0	0	?	0
Myctophum	1	0	0	0	2	1	0	2	0	1
Lampanyctus	1	0	0	0	2	1	0	2	0	1
Polymixia	0	0	0	0	0	0	0	0	0	1
Melamphaes	0	0	0	0	0	0	0	2	0	1
Vellifer	0	1	0	?	0	?	1	0	0	1
L. pearsoni	1	1	1	?	?	1	0	0	1	0
L. blakeburnensis	1	1	1	1	1	1	0	0	1	0
P. transmontana	1	?	1	?	1	0	1	?	1	0
P. omiscomaycus	1	1	1	1	1	0	1	0	1	0
Amphiplaga	1	1	1	1	1	0	0	0	1	1
Erismatopterus	1	1	1	1	1	?	0	0	1	1
Amblyopsis	1	1	1	2	2	1	2	1	2	1
Aphredoderus	1	1	1	2	0	0	0	1	1	1
Chologaster	1	1	1	2	2	1	2	1	2	1
Trichophanes	1	1	1	1	?	0	0	0	1	1
Typhlichthys	1	1	1	2	?	1	2	1	2	?
Sphenocephalus	0	0	0	0	0	0	0	0	0	0
Xenyllion	0	0	0	?	?	0	0	?	0	?
Joffre Bridge	1	1	1	1	1	0	1	0	1	0
Smoky Tower	1	1	1	1	1	0	0	0	1	1
Ophidion	1	1	0	2	0	1	0	2	2	0
Mcconichthys	1	1	1	1	?	0	0	0	?	0
Lota	1	1	1	2	0	1	2	1	1	1
Microgadus	1	1	1	2	0	0	2	1	1	1
Asineops	1	0	0	0	0	1	0	0	0	1
Porichthys	1	1	1	2	1	1	0	2	2	1
Saurida	1	0	0	0	0	1	0	0	0	1
fossil beryciforms	0	0	0	0	0	0	0	0	0	0

"-" denotes gaps; "?" denotes missing data

	21 alv px	22 op ant	23 scales	24 pmxpx	25 lac orn	26 mx prc	27 soc lng	28 sca for	29 retro	30 brst #
Aulopus	0	0	0	2	-	0	0	0	0	0
Myctophum	0	0	0	2	-	0	0	0	0	0
Lampanyctus	0	0	0	2	1	0	0	0	0	0
Polymixia	0	0	0	0	1	0	0	0	0	2
Melamphaes	0	0	0	2	0	0	0	0	1	1
Vellifer	0	0	0	2	-	0	0	0	0	3
L. pearsoni	0	1	?	2	1	0	?	0	?	?
L. blakeburnensis	0	1	2	2	1	0	0	0	0	3
P. transmontana	0	1	2	2	-	1	1	0	0	3
P. omiscomaycus	0	1	2	2	1	1	1	0	0	3
Amphiplaga	0	1	2	2	1	1	0	0	1	3
Erismatopterus	0	1	2	2	1	1	0	0	1	3
Amblyopsis	1	0	0	2	1	0	0	0	1	3
Aphredoderus	1	1	2	2	0	0	0	0	0	3
Chologaster	1	0	0	2	1	0	0	0	1	3
Trichophanes	1	1	2	2	0	0	0	0	1	3
Typhlichthys	0	-	0	2	1	0	0	0	0	3
Sphenocephalus	0	0	?	1	0	0	0	0	0	?
Xenyllion	0	0	0	1	?	0	?	0	1	1
Joffre Bridge	0	1	2	2	1	1	?	0	0	3
Smoky Tower	0	1	2	2	1	1	0	0	0	3
Ophidion	0	0	0	1	1	0	0	0	1	3
Mcconichthys	0	1	2	2	1	0	0	0	0	3
Lota	0	0	0	1	1	0	0	1	0	2
Microgadus	0	0	0	1	1	0	0	1	0	2
Asineops	0	1	0	0	-	0	0	0	0	2
Porichthys	0	-	0	0	-	0	0	0	0	3
Saurida	0	0	0	2	?	0	0	0	0	0
fossil beryciforms	0	0	?	0	?	0	0	0	0	1

"-" denotes gaps; "?" denotes missing data

	31	32	33	34	35
	scl cov	eh,ch	plv spl	pg med	pg, pcl
Aulopus	0	0	0	?	?
Myctophum	0	0	0	0	0
Lampanyctus	0	0	?	0	0
Polymixia	0	0	1	1	1
Melamphaes	0	0	1	2	1
Vellifer	?	0	1	?	0
L. pearsoni	?	?	?	?	?
L. blakeburnensis	0	?	0	0	1
P. transmontana	1	?	?	?	?
P. omiscomaycus	1	1	0	1	1
Amphiplaga	0	?	0	1	1
Erismatopterus	?	?	0	1	1
Amblyopsis	1	0	-	-	-
Aphredoderus	0	1	0	1	1
Chologaster	1	0	1	1	-
Trichophanes	0	?	0	?	1
Typhlichthys	1	1	-	?	-
Sphenocephalus	0	0	0	1	1
Xenyllion	0	0	?	?	?
Joffre Bridge	0	0	0	1	1
Smoky Tower	?	?	0	1	1
Ophidion	1	1	1	2	0
Mcconichthys	?	?	0	?	1
Lota	1	1	1	0	0
Microgadus	1	1	1	0	0
Asineops	0	?	1	2	0
Porichthys	1	1	1	2	0
Saurida	0	0	1	0	0
fossil beryciforms	0	0	?	1	1

"-" denotes gaps; "?" denotes missing data

CHARACTER TYPES AND WEIGHTS

Character	Type	Weight	States
1. full neural spine on PU2	unordered	1	2
2. epural number	ordered	1	3
3. supraneural	unordered	1	2
4. intercalar	unordered	1	2
5. percopsoid projections	unordered	0.5	2
6. lacrimal process	unordered	1	3
7. opercle horiontal ridge	unordered	1	2
8. opercle vertical ridge	unordered	1	2
9. 3 large preopercular spines	unordered	1	2
10. opercle recurved posterodorsally	unordered	1	2
11. beryciform foramen	unordered	1	2
12. premaxilla/maxiila length	unordered	1	2
13. supramaxillary number	unordered	1	2
14. postcleithra	unordered	1	3
15. subopercle	unordered	1	3
16. preopercle ornament	unordered	1	2
17. preopercle shape/angles	unordered	1	3
18. parhypural	unordered	1	3
19. cleithrum	unordered	1	3
20. antorbital	unordered	0.5	2
21. segmented alveolar process	unordered	1	2
22. opercle anterodorsally	unordered	1	2
23. scales	unordered	1	2
24. postmaxillary process of premaxilla	unordered	1	3
25. lacrimal ornament	unordered	1	2
26. maxilla dorsal process	unordered	1	2
27. supraoccipital length	unordered	1	2
28. scapula foramen	unordered	1	2
29. retroarticular	unordered	0.5	2
30. branchiostegal number	ordered	1	4
31. scale covering	unordered	1	2
32. epihyal and ceratohyal	unordered	1	2
33. pelvic splint	unordered	1	2
34. pelvic girdle medial processes	unordered	1	3
35. pelvic girdle and postcleithra	unordered	1	2