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CONTRIBUTIONS TO THE SYSTEMATICS OF COTTOID FISHES (TELEOSTEI: SCORPAENIFORMES)

by

Keith L. Jackson ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial
fulfillment of the requirements for the degree of
Doctor of Philosophy

Department of Biological Sciences

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ABSTRACT

Our current understanding of the systematics of Cottoidei is critically reviewed and a new study is presented on this group's phylogeny and classification. Two views have been widely held: i) the earlier and predominant view that the suborder's type family, Cottidae, is paraphyletic with other specialized cottoid families derived from it, and ii) a recent view, put forth by Mamoru Yabe in his published doctoral dissertation (1985), that Cottidae are monophyletic exclusive of other specialized families that are basal to them within Cottoidei. Upon critical reanalysis of Yabe's own data, little support was found for the view he put forth. A new study was undertaken using sixty-eight morphological characters with 111 steps of evolution that were examined cladistically in 34 cottoid genera with the goal of determining the most parsimonious tree topology. The resulting tree shows that some species of Cottidae (*Scorpaenichthys marmoratus, Jordania zonope,* and *Hemilepidotus hemilepidotus*) are basal to a clade of all remaining Cottoidei including other Cottidae and the specialized families Agonidae, Comephoridae, Cyclopteridae, Hemitripteridae, and Psychrolutidae. Characters mapped onto this tree support the monophyly of Cottoidei with at least 14 characters of which 9 are consistent with respect to their sister taxon, Hexagrammidae. The crown clade within Cottoidei (above the three basal genera) is well supported with at least 13 characters leading up to it from the cottoid root. Strong support is found for the specialized families and moderate support is found for a number of other relations. The hemitripterid examined, *Blepsias cirrhosus,* was found to be sister to Agonidae, and Rhamphocottidae were found to be sister to this clade. A sister taxon, *Artediellus,* is possibly found for Psychrolutidae. The historical basis of our current classification is discussed and changes are proposed, including: the dissolution of Cottoidea and Cyclopteroidea; acknowledgment that Cottidae are a problem taxon; placement of Liparidae into Cyclopteridae; and placement of Rhamphocottidae and Hemitripteridae into Agonidae.

TABLE OF CONTENTS

LIST OF TABLES AND APPENDICES

LIST OF FIGURES

INTRODUCTION

This dissertation addresses some current ideas on the basic systematic biology of a large taxon of fishes, the Cottoidei, and presents some new hypotheses. The systematics of cottoids was last treated with rigor almost 20 years ago by Yabe (1985) in his published doctoral dissertation. Yabe examined 60 morphological characters in a cladistic manner and devised a phylogenetic tree that he used to classify the families of Cottoidei. Prior to Yabe's major work, few large-scale studies had examined Cottoidei as a whole and in any depth. Taranets (1941) was first to examine this taxon in detail, although he concentrated on one of its families, Cottidae. Bolin (1947) discussed the interrelations of Californian Cottidae, and drew a phylogenetic tree for that assemblage, although his work was somewhat limited in scope. Washington *et al.* (1984), like Yabe, devised a phylogeny of Cottoidei based on morphological characters, although their phylogeny was based on only a few characters, and those characters were not discussed in detail. Prior to these studies, work on the basic systematic biology of Cottoidei was mostly about classification, with little explicit emphasis given to underlying interrelations.

In this dissertation I revisit the basic systematic biology of Cottoidei to: i) critically review previous work on this taxon, ii) describe new morphological characters in members of this taxon useable for phylogenetic inference, and iii) treat these characters rigorously with modern phylogenetic methodology. These goals are achieved in three chapters. The first chapter reviews the history of the systematic biology of Cottoidei with particular emphasis on what earlier authors thought about its interrelations (evolution) and how these views grew into our current perspective on the group. The second chapter is a critical examination of Yabe's (1985) phylogeny of Cottoidei. Yabe's work was the most comprehensive systematic treatment of this taxon to date and his phylogeny has been influential in later classifications, and because of this, needs independent review. The third, and main, chapter is a major research paper on the phylogeny of Cottoidei based on known and new morphological characters. This phylogeny is used to amend current classification. This main chapter represents the latest thinking in the field of cottoid systematics.

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1. CURRENT COTTOID SYSTEMATICS

ABSTRACT

Our current understanding of the systematics of Cottoidei is outlined and the historical concepts of the group are reviewed. The taxon now recognized as Scorpaeniformes, that includes Cottoidei, was first recognized in 1820 by Cuvier. The monophyly of Scorpaeniformes has been questioned by some authors, although it is supported by two synapomorphies: 1) a suborbital bar originating off the third infraorbital (including the lachrymal) that articulates with the anterior margin of the preopercle, and 2) the parietal extrascapular fused with the parietal and often bearing a spine. The position of Cottoidei within Scorpaeniformes has been elucidated only recently, although independently by several authors, as near or within Hexagrammoidei. The basal relations within Cottoidei are poorly resolved, but most authors infer that several genera (*Scorpaenichthys, Jordania,* and *Hemilepidotus*) are generalized in form and likely primitive. Recent work by Mamoru Yabe extensively cottoid anatomy examined and came to a conclusion that differs from earlier ideas on the group. Yabe found several cottoid groups, that were previously thought to be specialized cottoid derivatives, to be basal to other more generalized taxa. Yabe's findings have been incorporated into current classifications, although probably prematurely.

Introduction

Cottoidei are a large and diverse suborder of scorpaeniform teleostean fish, represented by 11 families, 141 recognized genera, and 671 valid species (Table 1–1) (Nelson, 1994; Eschmeyer, 2002). Cottoid fishes include sculpins, poachers, lump suckers, and snailfishes. Their species live in marine, brackish, and freshwater, and occur from abyssal trenches (>7000 m; Andriashev, 1975) to mountain streams.

Cottoid fishes are found in cool to cold waters of all oceans, although the group's greatest diversity is in the North Pacific. The family Liparidae has the widest distribution amongst the group, being found in all oceans, including some tropical regions at bathyal depths. The family Psychrolutidae also has a wide antitropical distribution in cool waters of all continents and near some sub-Antarctic islands (Nelson, 1982). Other cottoids are essentially Northern Hemisphere fishes, with the exception of one genus (*Antipodocottus*) of four deep water species of Cottidae from Australia, Kai Islands west New Guinea, and New Zealand; a single species of Agonidae (*Agonopsis chiloensis*) from Chile, Argentina, and the Falkland Islands (Nelson, 1994); and the very aberrant monotypic Bathylutichthyidae from South Georgia Island (Balushkin and Voskoboynikova, 1990). Cottoids are represented in freshwaters of North America and Eurasia by *Cottus* and *Myoxocephalus* and in Lake Baikal, Russia, by 10 endemic genera with 28 species (Sideleva, 1982; Eschmeyer, 2002).

The current state of cottoid systematics is outlined below, including the placement of cottoids amongst other spiny finned fishes (Acanthopterygii), the bounds of the group, and the systematic arrangement of constituent taxa. For consistency in this paper dealing with changing classification schemes, "current classification" above the genus level follows Nelson (1994) (Table 1–1), and at the genus and species level, including statistics on numbers of genera and species, follows Eschmeyer (2002). Taxonomic names that lack direct correspondence to this

Table 1–1. Classification of Scorpaeniformes and Cottoidei after Nelson (1994). Orders end in -iformes; suborders, -oidei; superfamilies, -oidea; families, -idae; subfamilies, -inae. Statistics on the number of recognized genera and valid species of Cottoidei determined from Eschmeyer (2002).

Scorpaeniformes		
Dactylopteroidei		
Dactylopteridae		
Scorpaenoidei		
Scorpaenidae		
Caracanthidae		
Aploactinidae		
Pataecidae		
Gnathacanthidae		
Congiopodidae		
Triglidae		
Platycephaloidei		
Bembridae		
Platycephalidae		
Hoplicthyidae		
Anoplopomatoidei		
Anoplopomatidae		
Hexagrammoidei		
Hexagrammidae		
Normanichthyoidei		
Normanichthyidae		
Cottoidei		**144 / 671**
Cottoidea		***111 / 366***
Rhamphocottidae	grunt sculpin	1 / 1
Ereuniidae		2 / 3
Cottidae	sculpins	64 / 234
incl. Cottocomephorinae		3 / 7
Comephoridae	Baikal oilfish	1 / 2
Abyssocottidae		6 / 19
Hemitripteridae		4 / 8
Agonidae	poachers	20 / 49
Psychrolutidae	fathead sculpins	9 / 42
Bathylutichthyidae		1 / 1
Cyclopteroidea		***33 / 305***
Cyclopteridae	lump suckers	8 / 28
Liparidae	snailfishes	25 / 277

current classification are placed in quotation marks (*e.g.*, "Cataphracti") in the text and are explicitly referred to as such in the tables and figures.

Systematic Position and Monophyly of Scorpaeniformes

Cuvier (1820) was the first to recognize a taxon comparable to Scorpaeniformes (his "mail-cheeked fishes" or "Joues cuirassées") amongst acanthopterygian (spiny-finned) fishes (Table 1–2). The character defining this group is "the suborbital bone being more or less extended over the cheek, and articulated with the operculum." Subsequently (*e.g.*, Gill, 1888), this character has been refined as the posterior extension of the third infraorbital (including the lachrymal as the first

Table 1–2. Cuvier's (1820) classification of "Joues cuirassées" and placement of cyclopteroids on left. Current familial classification for listed genera on right; asterisks denote families no longer included in the Scorpaeniformes.

Division Animalia vertebrata	
Class Pisces	
Order Acanthopterygii	
Family "Jones cuirassées"	
Trigla	Triglidae
Prionotus	Scorpaenidae
Peristedion	Triglidae
Dactylopterus	Dactylopteridae
Cephalacanthus	Dactylopteridae
Cottus	Cottidae
Aspidophorus	Agonidae
Hemitripterus	Hemitripteridae
Hemilepidotus	Cottidae
Platycephalus	Platycephalidae
Scorpaena	Scorpaenidae
Pterois	Scorpaenidae
Blepsias	Hemitripteridae
Apistes	Scorpaenidae
Agriopus	Congiopodidae
Pelor	Scorpaenidae
Synanceia	Scorpaenidae
Monocentris	Monocentridae*
Gasterosteus	Gasterosteidae*
Oreosoma	Oreosomatidae*
Order Malacopterygii sub-brachiati	
Family Discoboli	
Cyclopterus	Cyclopteridae
Liparis	Liparidae

infraorbital) to and articulating with the preoperculum, and is referred to as the presence of a suborbital stay. In his grouping, Cuvier included most of the scorpaeniform fishes recognized at the time in his classification. He did not recognize the suborbital stay in Cyclopteroidea, the genera of which he considered to be in a different order, the "Malacopterygii sub-brachiati." He also included three genera now considered distant from the Scorpaeniformes: the stickleback, *Gasterosteus*; the oreo, *Oreosoma*; and the pinecone fish, *Monocentris.*

Gill (1888) provided a thorough summary on "mail-cheeked fishes." He removed three taxa (*Gasterosteus, Oreosoma,* and *Monocentris*) from Cuvier's (1820) grouping. He included cyclopterid taxa with it, as did Jordan and Gilbert (1882) who were the first to recognize that they also possess a suborbital stay. Gill concluded with a "genealogical tree" of the group's families based on osteological characteristics (Figure 1–1), although the relations of Cyclopteroidea were not discussed and its two families were not placed on his tree. Of interest in Gill's hypothesized relationships, he placed Hexagrammidae and Anoplopomatidae together based on both having relatively little head armament, placed those two taxa near Scorpaenidae because of the generalized condition of the two groups (although he did note that in two characters of cranial osteology the Hexagrammidae "deviate from scorpaenids and approach the cottids"), and placed Rhamphocottidae and Agonidae close to Triglidae. Later workers (*e.g.*, Boulenger, 1904; Regan, 1913; Jordan 1923; Berg, 1940) generally followed Gill, and this grouping has largely remained to date, under various names, but corresponding with current Scorpaeniformes.

Since Gill's (1888) work, two problems on the systematics of scorpaeniform fish have been periodically raised, and are still at issue. The first is on the placement of the order amongst other acanthopterygian fishes. The second is on the monophyly of the order.

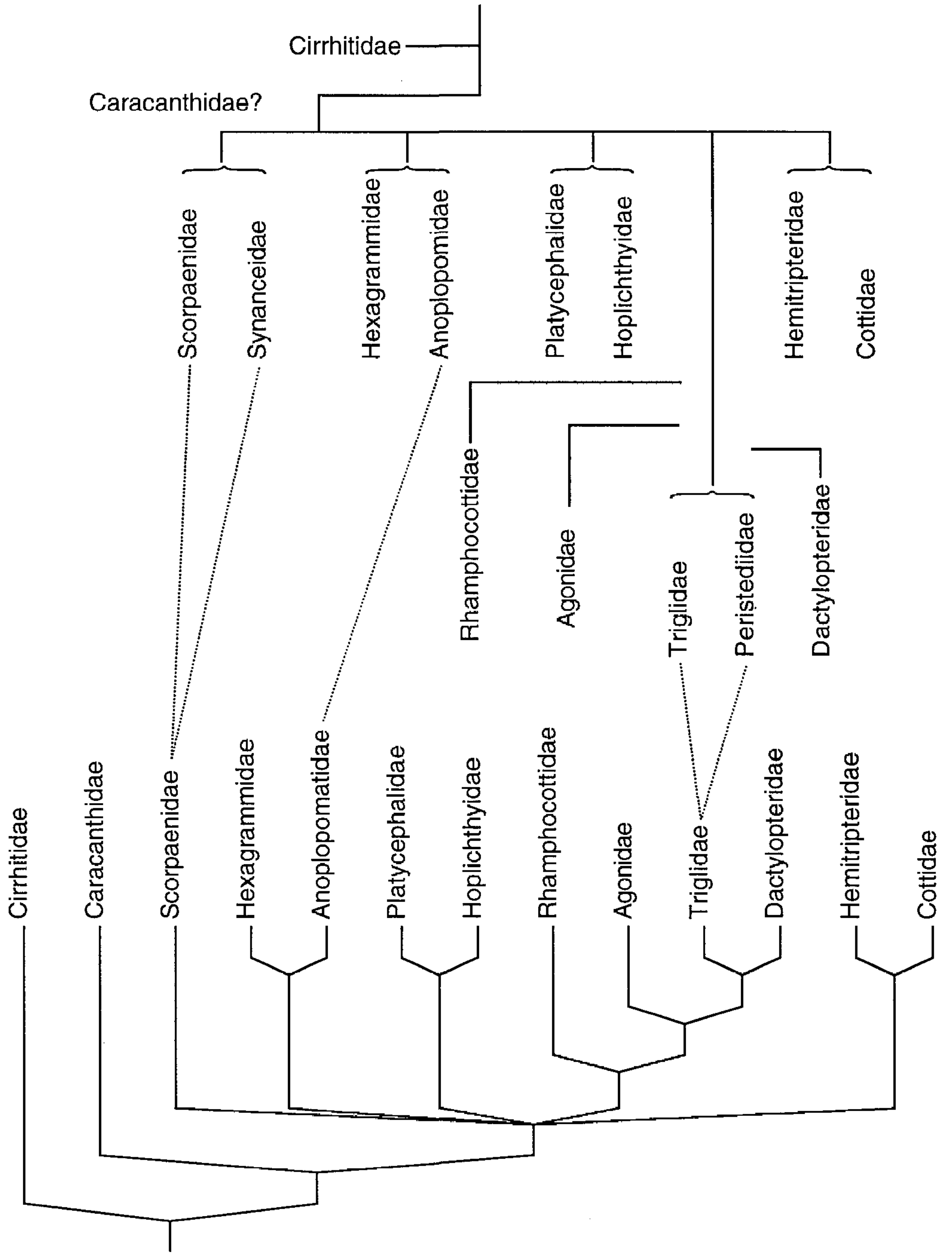

Figure 1–1. Gill's (1888) genealogical tree of "mail-cheeked fishes" with "more generalized types" on the left (top diagram). Gill was uncertain about the placement of Caracanthidae, but provisionally placed it with the other mail-cheeked fishes. Cladistic interpretation shown in bottom diagram with differences in current classification highlighted.

Cuvier (1820) placed his "Joues cuirassées" between Percidae and Sciaenidae. Gill (1888) described his "mail-cheeked fishes" as being generalized in form, as are serranids, sparids, and "numerous others," and considered the group to be derived from a cirrhitid-like ancestor. Most other early classifications (*e.g.*, Boulenger, 1904; Regan 1909; Jordan, 1923) had Scorpaeniformes placed amongst other acanthopterygian families now placed in Perciformes. In contrast, Regan (1913) stated that the "group is a natural one, and so large and varied that it may be accorded ordinal rank, whilst recognizing that the most generalized family, Scorpaenidae, is not very remote from generalized percoids, such as the Serranidae."

This is where the contention lies that exists to date: phylogenetically, Scorpaeniformes join the ranks of other unsorted perciforms, yet their classification is changed with each author. Some authors (*e.g.*, Robins *et al.*, 1991; Nelson, 1994; Eschmeyer 2002) followed Regan's (1909) lead by separating Scorpaeniformes from Perciformes and giving them equal rank, while others (*e.g.*, Robins *et al.*, 1980; Lauder and Liem, 1983; Johnson and Patterson, 1993) placed the Scorpaeniformes within the Perciformes as a suborder. The latter authors reasoned this placement because there is no synapomorphic character uniting Perciformes to the exclusion of Scorpaeniformes, and that the two orders together share many synapomorphic characters not seen elsewhere. Furthermore, recent work (*e.g.*, Mooi and Gill, 1995; Mooi and Johnson, 1997) has uncovered new characters that unite Scorpaeniformes and Perciformes, and has even suggested possible relationships between Scorpaeniformes and specific Perciformes. Mooi and Gill examined the condition of epaxial musculature amongst acanthomorph fishes, and found that Scorpaeniformes share a synapomorphic condition that is also observed in some Perciformes; they posited that the sister relations of Scorpaeniformes might be found in that subset (19 families) of Perciformes. Mooi and Johnson speculated that Champsodontidae (a perciform family) is allied with Scorpaeniformes. This might illuminate the relations of Champsodontidae, but does not necessarily help in illuminating the placement of the combined taxon. These recent findings are preliminary and the sister relations of Scorpaeniformes remain elusive. Yet, there appears to be little reason for excluding Scorpaeniformes from Perciformes.

Three questions concerning the monophyly of Scorpaeniformes are raised: 1) Is the suborbital stay homologous throughout the group? 2) Are there any other characters supporting its monophyly? 2) Do certain included taxa have relationships outside the order?

Quast (1965) speculated that the suborbital stay in Anoplopomatidae may have evolved independently from that of Scorpaeniformes. This speculation has often been cited as a controversy on the monophyly of Scorpaeniformes, but it has not been further substantiated. Shinohara (1994) found the Anoplopomatidae to be the sister-group of Hexagrammoidei and Cottoidei, and the three together to be sister to Scorpaenoidei and Platycephaloidei, although the goal of his study was on the interrelations of Hexagrammoidei and not on clarifying the relations of Anoplopomatidae. A definitive study on the relations of Anoplopomatidae is needed.

Other authors (*e.g.*, Greenwood *et al.*, 1966) questioned the use of only a single synapomorphic character, the suborbital stay, to tie the diverse Scorpaeniformes together. It should be noted, however, that this character is not a simple structure, but is well defined. The first three infraorbitals (including the lachrymal) are large, plate-like, and are well articulated with each other (suborbital bar); the suborbital stay is borne upon the third infraorbital and extends to and articulates with the preopercle; and infraorbitals posterior to the "suborbital" series are comparatively small simple tubular structures ("postorbitals"). To this character complex, I will add that the first three infraorbitals bear two or more arches with pores exiting between them (excepting Agonidae, in which the second infraorbital bears only a single arch) while successive infraorbitals are tubular. The suborbital stay character as described here is present in all Scorpaeniformes (excluding Pataecidae, and in Comephoridae the suborbital stay is variously developed or lacking, although the typical arrangement of a suborbital bar and small postorbitals is present) and is the key diagnostic character of the group.

Four characters other than the suborbital stay have recently been put forth as synapomorphic characters of the Scorpaeniformes: two plate-like hypurals sutured to the preural centrum, the "swim bladder muscle," supratemporal canal (lateralis system) borne upon the parietal with an arch, and cranial spines.

Lauder and Liem (1983) gave two synapomorphic characters for Scorpaeniformes, the suborbital stay and "in the caudal skeleton two plate-like hypurals are sutured to the centrum" (no citation given). This character is frequently encountered amongst Scorpaeniformes, but is not universal. Normanichthyidae (Fujita, 1990), certain Scorpaenoidei (Ishida, 1994), Platycephalidae (Imamura, 1996), and certain Hexagrammoidei (Shinohara, 1994) have more than two hypurals. A wider survey of the caudal skeleton in Scorpaeniformes and Perciformes is required to either refine or refute Lauder and Liem's caudal skeleton character.

Yabe (1985) discussed the evolution of the swim bladder musculature amongst Scorpaeniformes. Shinohara (1994) (and cited in Imamura and Shinohara, 1998) recognized the presence of a "swim bladder muscle" as a synapomorphic character of the order. Shinohara cited Yabe on this character but did not discuss it in detail. According to Yabe, the swim bladder musculature is highly varied amongst Scorpaeniformes, and the primitive condition in this group is similar to that of "generalized percoid fishes." Yabe did not explicitly put forth any characters of the swim bladder musculature as being synapomorphic for the entire order. While it is plausibly a new character uniting the Scorpaeniformes to the exclusion of "generalized percoids," a more thorough study including all relevant taxa is required.

Johnson (1993) gave two synapomorphic characters for Scorpaeniformes: the supratemporal canal partly enclosed on the parietal under a bony arch (first noted by Berg, 1940), and, in larvae of many Scorpaeniformes, spines borne upon this arch. The parietal arch is unique to Scorpaeniformes and one family of Perciformes, Champsodontidae, suggesting a possible relationship of the latter with Scorpaeniformes (Mooi and Johnson, 1997). Other Perciformes typically have a bony element that is separate from the parietal supporting the supratemporal canal, a medial extrascapular. A similar condition to this is observed in the psychrolutid taxa Psychrolutinae and Malacocottinae (Jackson and Nelson, 1998), that have a reduced cranium and a separate bony element associated with the supratemporal canal. This belies the true nature of this arch in other Scorpaeniformes as an extrascapular fused with the parietal (as was first surmised by Berg). Cyclopteroidea lack the supratemporal canal altogether, but the suborbital stay and general anatomy of this taxon leave little question on its placement in Scorpaeniformes. Cranial spines occur frequently but not universally amongst Scorpaeniformes. Johnson pointed out that many larval Scorpaeniformes possess a spine associated with the parietal arch, and that the spine is retained in adults of some species. Cranial spines are present seemingly as a result of independent origins amongst adult Scorpaeniformes, but with little phylogenetic basis (*e.g.*, in Psychrolutidae, two genera that have independently acquired cranial spines, Jackson and Nelson), suggesting that the genetic basis for such structures is present, but variously expressed, amongst Scorpaeniformes. Parietal spines are unique to Scorpaeniformes and the unrelated Beryciformes (Johnson). These two characters are compelling evidence in support of a monophyletic Scorpaeniformes.

Dactylopteridae have been variously included (*e.g.*, Washington *et al.*, 1984;

Nelson, 1994) or excluded (*e.g.*, Berg, 1940; Nelson, 1986; Johnson and Patterson, 1993) from Scorpaeniformes. Washington *et al.* suggested that Dactylopteridae and Triglidae share a common ancestry (an idea first proposed by Gill, 1888), although more recent workers have shown that Scorpaeniformes less Dactylopteridae form a monophyletic group. Johnson (1993) suggested that the presence of a bone-enclosed supratemporal canal on the parietal is a synapomorphic character of Scorpaeniformes that Dactylopteridae lack. Mooi and Gill (1995) described the association of the epaxial musculature with the dorsal pterygiophores in which various Perciformes and Scorpaeniformes share a unique myology not present in Dactylopteridae. Recently, Imamura (2000) concluded that the suborbital stay of Dactylopteridae is not homologous with that of Scorpaeniformes. Imamura went further in suggesting that Dactylopteridae and Malacanthidae may be synonymized as a single perciform family. Accepting this new taxon may be premature until its synapomorphies (which Imamura simply noted as being "uncommon" amongst percoids, with no further discussion on homoplasy) are assessed critically amongst other Scorpaeniformes and Perciformes. Nonetheless, current consensus points to a monophyletic Scorpaeniformes (less Dactylopteridae) and doubts have been raised on whether Dactylopteridae is at all related to Scorpaeniformes.

Three other taxa have had their membership in Scorpaeniformes questioned. Mandrytsa (2001) found Pataecidae (with three genera and five species; Nelson, 1994) to not belong in the Scorpaeniformes and placed it as unsorted in Perciformes. Mandrytsa did not give characters relating Pataecidae with any particular perciform taxon, and he apparently based his decision solely on the family's lack of a suborbital stay connected with the preopercle. Mandrytsa did note that Pataecidae have a sensory canal and bony arch on the parietal, but he did not consider this character as relating the family to other Scorpaeniformes. For these reasons, Mandrytsa's placement of Pataecidae should be followed with caution and further elaborated on or refuted. Normanichthyoidei are represented by a single species, *Normanichthys crockeri,* of questionable relationships, but usually associated with Cottoidei (*e.g.*, Clark, 1936, Washington *et al.*, 1984; Nelson, 1994). Yabe and Uyeno (1996) studied the anatomy of this enigmatic group, and concluded that it is not cottoid in morphology, and consequently left it unplaced in Scorpaeniformes. The aberrant monotypic Bathylutichthyidae (*Bathylutichthys taranetzi*) was recently described as being unusual amongst cottoids, but close to Psychrolutidae or Liparidae (Balushkin and Voskoboynikova, 1990). Mooi and Gill (1995) have subsequently shown its epaxial musculature to be inconsistent with other Scorpaeniformes. These three families represent minor components of scorpaeniform diversity and their questioned phylogenetic placement does greatly not upset the Scorpaeniformes (less Dactylopteridae), an otherwise well-defined and natural grouping of acanthopterygian fishes.

Systematic Position and Monophyly of Cottoidei

Gill (1888) did not recognize a monophyletic taxon comparable with current Cottoidei (Figure 1–1). He placed Rhamphocottidae and Agonidae near to Triglidae and Dactylopteridae, and Cottidae and Hemitripteridae (containing only *Hemitripterus* at the time) together. Gill had these two groupings unresolved amongst other Scorpaeniformes, and he did not consider the relationships of Cyclopteroidea to these two groupings or to other Scorpaeniformes. Gill did note the absence of the basisphenoid in Cottidae, currently a diagnostic character of Cottoidei, but did not note its absence in Rhamphocottidae, Agonidae, or Cyclopteroidea.

Boulenger (1904) clarified the situation slightly by stating that Cottidae "merge insensibly into the still more aberrant Cyclopteridae" and noted that the two groups have large plate-like actinosts, of which some are in contact with the cleithrum. Boulenger placed Rhamphocottidae, Cottidae, and Cyclopteridae together in his key to his "Scleroparei" (Scorpaeniformes), and followed Gill (1888) in placing Agonidae near Triglidae and Dactylopteridae based on these three families having a "completely cuirassed" (armored) skull.

Regan (1913) was the first author to recognize a taxon directly comparable with current Cottoidei (Table 1–3). Regan's diagnostic characters for this taxon included: opisthotic small, basisphenoid absent, one or two pairs of dentigerous upper pharyngeals (three in other Scorpaeniformes), pectoral radials plate-like with foramina small or absent, and (pleural) ribs absent or only on a few posterior precaudal vertebrae. Absence of the basisphenoid was also noted in Anoplopomatidae, a group he (and subsequent authors) did not closely associate with Cottoidei. Yabe (1985) added three further characters unique to Cottoidei amongst Scorpaeniformes: shallow posttemporal fossa, small or absent basihyal, and extrinsic swimbladder muscle inserting on cleithrum. Regan's taxon, currently Cottoidei, has remained largely unchallenged.

Matsubara (1943) was the first to put a monophyletic Cottoidei on a phylogenetic tree amongst other Scorpaeniformes (Figure 1–2). Matsubara did not sug-

Table 1–3. Regan's (1913) classification of "Cottiformes" on left. Current classification on right.

Order Scleroparei	Scorpaeniformes
Division Cottiformes	Cottoidei
Family Cottidae	Rhamphocottidae
	Hemitripteridae
	Cottidae
	Cottocomephorinae
Family Cottunculidae	Psychrolutidae
Family Psychrolutinae	Psychrolutidae
Family Comephoridae	Comephoridae
Family Agonidae	Agonidae
Family Cyclopteridae	Cyclopteroidea

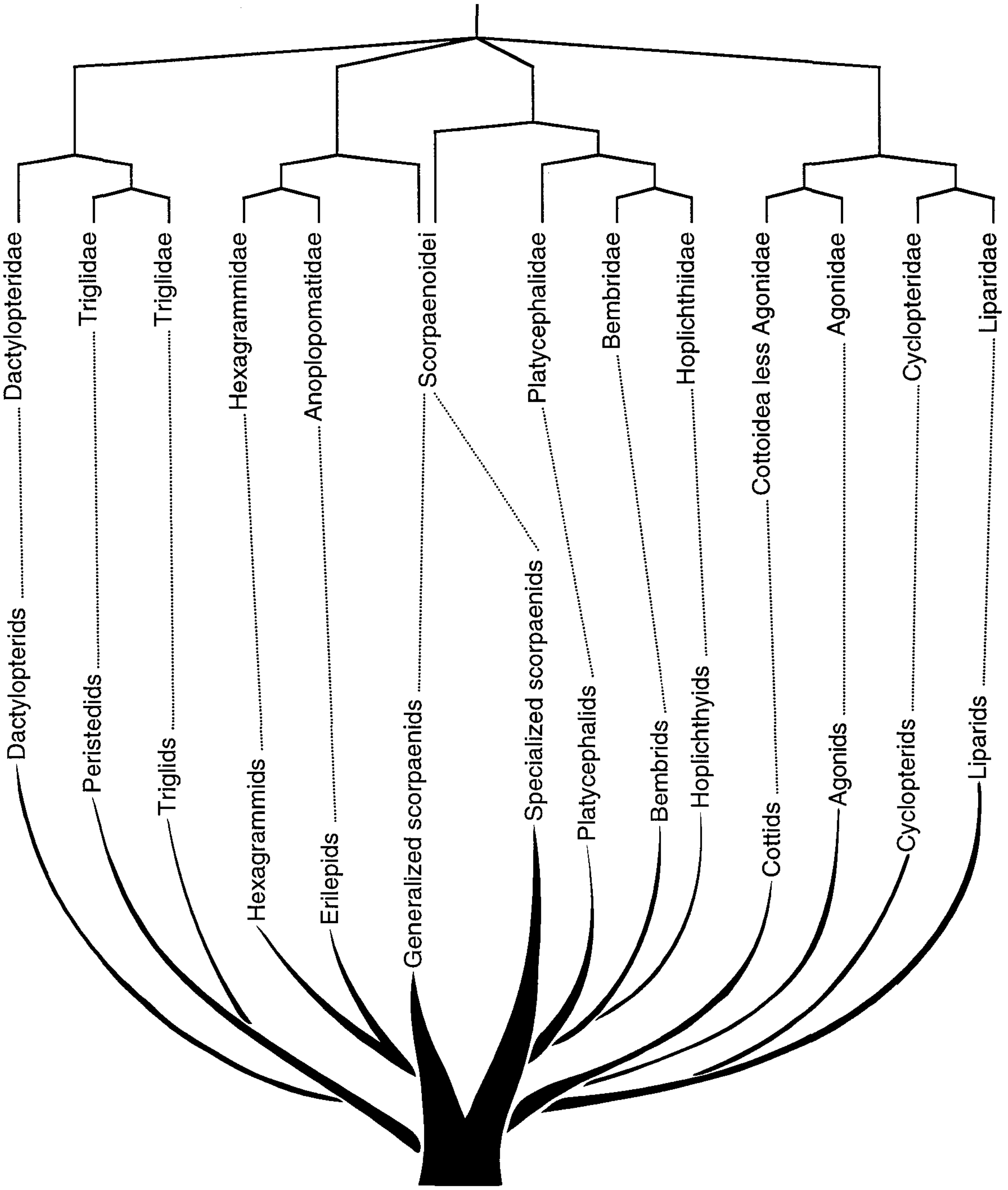

Figure 1–2. Matsubara's (1943) phylogeny of Scorpaeniformes. Current classification and a cladistic interpretation of Matsubara's hypothesized relationships are shown above.

gest a sister group for Cottoidei, and simply has it branching off from some unknown scorpaeniform ancestor. Matsubara's tree was not much progress over that of Gill (1888) (Figure 1–1) other than in grouping Cottoidei together, as Regan (1913) had done already. Matsubara (1955) "refined" his phylogenetic hypothesis of scorpaeniform interrelationships with a classification (Table 1–4) even less resolved than his previous (1943) tree. As a step forward, Dactylopteridae was recognized as separate from Triglidae and other Scorpaeniformes. As a step backwards from his previous tree, Agonidae, Cottoidei (less Agonidae and Cyclopteroidea), Hexagrammoidei, Platycephaloidei, Scorpaenoidei (less Triglidae), and Triglidae are all given equal rank and, curiously, Cyclopteroidea are placed outside of Cot-

Table 1–4. Matsubara's (1955) classification of "Cottida" on left. Current classification on right.

Cottida				Scorpaeniformes
	Cottina			
		Scorpaenicae		Scorpaenoidei
			Scorpaenidae, Synanceiidae	Scorpaenidae
			Congiopodidae	Congiopodidae
		Hexagrammicae		
			Hexagrammidae	Hexagrammidae
			Anoplopomatidae	Anoplopomatidae
		Platycephalicae		Platycephaloidei
			Parabembridae, Bembridae	Bembridae
			Platycephalidae	Platycephalidae
			Hoplichthyidae	Hoplichthyidae
		Cotticae		
			Cottidae	Cottidae
			Psychrolutidae	Psychrolutidae
		Agonicae		
			Agonidae, Aspidophoridae	Agonidae
		Triglicae		
			Triglidae, Peristediidae	Triglidae
	Dactylopterina			
		Cephalicanthidae		Dactylopteridae
	Cyclopteridae			
		Cyclopteridae		Cyclopteridae
		Lipariididae		Liparidae

toidei and other Scorpaeniformes.

Quast (1965) was the first to suggest a sister-group relation for Cottoidei, the Hexagrammoidei; and that *Zaniolepis* (currently included in Hexagrammidae) is intermediate between other Hexagrammoidei and Cottoidei. Quast's conclusions were anticipated by Gill (1888), who noted that some cranial osteology of Hexagrammidae approaches the condition observed in Cottidae. Jordan (1905) also noted similarities between some primitive Cottidae and Hexagrammidae. Hallacher (1974) found similarities in the swim bladder muscle between *Zaniolepis* and Cottoidei, further substantiating Quast. Yabe (1985) described this extrinsic muscle of the swim bladder amongst Scorpaeniformes and found that the condition observed in *Zaniolepis* is also present in Anoplopomatoidei, and suggested that it is intermediate between the condition observed in generalized Scorpaenoidei and Cottoidei.

Shinohara (1994) studied the interrelationships of Hexagrammoidei in detail and found hexagrammoids to be paraphyletic with Cottoidei phylogenetically nested in it (Figure 1–3). Shinohara found the opposite of what Quast (1965) originally suggested, that hexagrammoids other than *Zaniolepis* (together with *Oxylebius*) are closer to Cottoidei. Shinohara gave six synapomorphic characters (two of which were not homoplastic) for Cottoidei and its sister clade within Hexagrammoidei and two further characters supporting these two taxa's relationships to other Hexagrammoidei. Although Shinohara's anatomical description and scope of survey was exemplary, his treatment of homoplasy is wanting.

Systematics and Interrelationships of Cottoidei

Since Regan (1913), Cottoidei have been considered a well-defined group, although often divided into two taxa: Cottoidea and Cyclopteroidea. The monophyly of Cyclopteroidea is in little question because its two constituent families

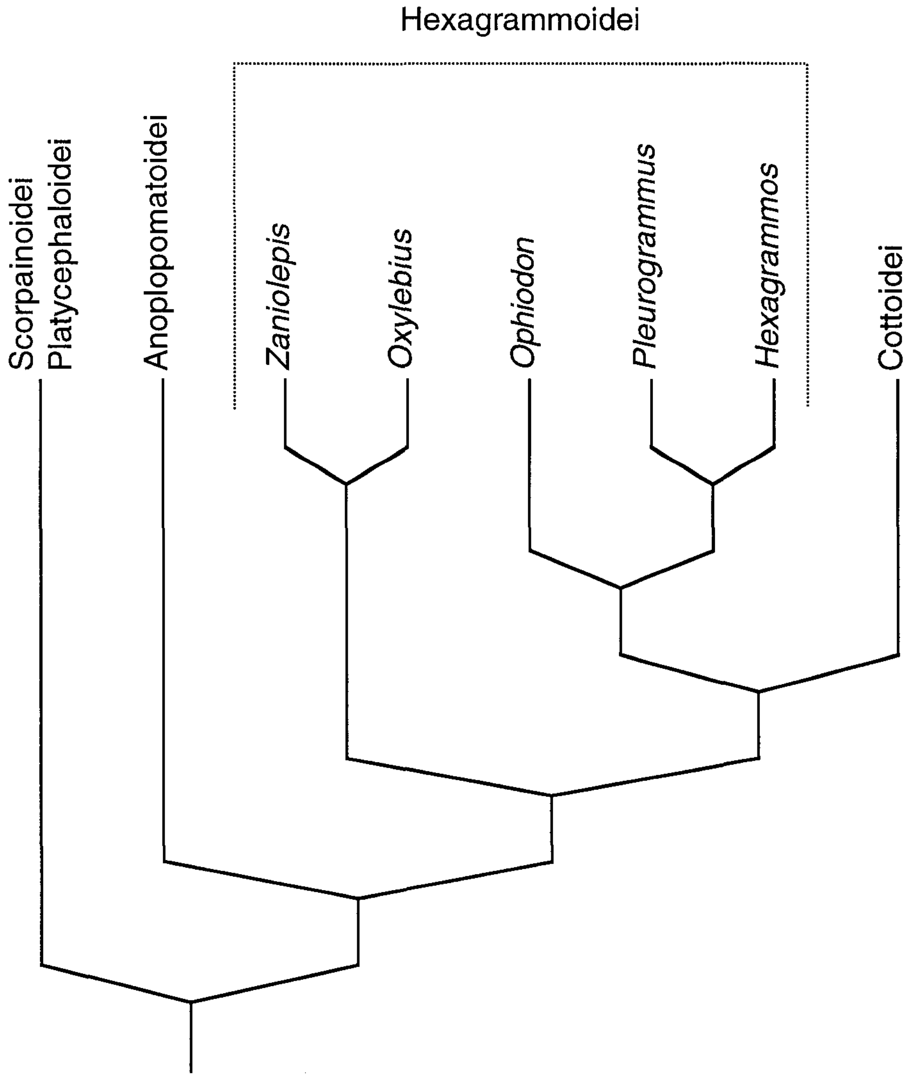

Figure 1–3. Shinohara's (1994) phylogeny of 41 scorpaeniform genera simplified to show the relations of hexagrammoid genera to other Scorpaeniformes. Scorpaenoidei and Platycephaloidei are represented by 23 genera, Anoplopomatoidei by 2 genera, and Cottoidei by 11 genera. The classification is current.

possess a highly derived pelvic girdle modified into a sucking disk. While usually considered a well-defined group, the monophyly of Cottoidea is less certain. Some authors (*e.g.*, Taranets, 1941; Balushkin and Voskoboynikova, 1990) consider Cyclopteroidea to be close to Psychrolutidae and Bathylutichthyidae based on these taxa possessing flaccid skin and a lightly ossified skeleton; although this conclusion has not been supported with other anatomy. It is possible that Cyclopteroidea have their placement amongst extant Cottoidea, although most recent works consider these two taxa as separate and of equal rank (*e.g.*, Yabe, 1985; Nelson, 1994). A study of the relations of Cyclopteroidea to other Cottoidei and Scorpaeniformes is needed.

Although Regan (1913) was first to systematically recognize a taxon corresponding with current Cottoidei, he did not explicitly discuss the interrelationships of the group, other than in lumping certain taxa together based on lack of distinguishability (Table 1–3). Jordan (1923) tackled the interrelationships of Cottoidei by splitting their constituent families into an array of presumed related taxa (Table 1–5), and suggested that his "Icelidae" were derived from a *Jordania*-like ancestor and his "Cottidae" from a *Scorpaenichthys*-like ancestor. Other families were left as "aberrant forms" listed in order of increasing specialization.

Berg (1940) presented a classification (Table 1–6) much less divided than that of Jordan (1923) and not too dissimilar from what is currently accepted. Other than listing some anatomical characters for his groups, Berg's reason for lumping is unclear and his classification is little differentiated from that of Regan (1913) (Table 1–3). Taranets (1941), a contemporary of Berg, devised a much more ambitious and subdivided classification of "Cottidae and related families" (Table 1–7). Curiously, Taranets considered *Scorpaenichthys* not to be related to cottid-like fishes, but allied with Antarctic icefishes (Perciformes, Notothenioidei) based on it having three, as opposed to four pectoral radials. Taranets considered his "Jordaninae" (monotypic, *Jordania zonope*) to be the most primitive member of the group and described the rest as having varying degrees of specialization in comparison to the ancestral generalized form exhibited by "Jordaninae." Taranets thought that two "morphological lines" exist in the group: 1) "Jordaninae" to his

Table 1–5. Jordan's (1923) classification of "Cottiformes" and "Cyclopteriformes" on left. Current classification on right. Generic composition of Jordan's (1923) families of "Cottiformes" given in Appendix 1–1.

Series Cottiformes	Cottoidea
Jordaniidae	Cottidae
Icelidae	Cottidae
Blepsiidae	Hemitripteridae
Scorpaenichthyidae	Cottidae
Cottidae	Cottidae + Psychrolutidae
Abyssocottidae	Abyssocottidae
Ascelichthyidae	Cottidae
Psychrolutidae	Psychrolutidae
Neophrynichthyidae	Psychrolutidae
Synchiridae	Cottidae
Ereuniidae	Ereuniidae
Rhamphocottidae	Rhamphocottidae
Hemitripteridae	Hemitripteridae
Cottocomephoridae	Cottidae (Cottocomephorinae)
Comephoridae	Comephoridae
Agonidae	Agonidae
Aspidophoridae	Agonidae
Series Cyclopteriformes	Cyclopteroidea
Cyclopteridae	Cyclopteridae
Liparopidae	Liparidae
Liparidae	Liparidae

Table 1–6. Berg's (1940) classification of his superfamily "Cottidae" on left. Current classification on right.

Cottidae	Cottoidei
Icelidae	Cottidae (*Icelus*), Ereuniidae
Cottidae	Cottidae, Hemitripteridae (*Blepsias, Nautichthys*), Rhamphocottidae
Cottocomephoridae	Cottidae (Cottocomephorinae)
Comephoridae	Comephoridae
Normanichthyidae	Normanichthyoidei
Cottunculidae	Psychrolutidae
Psychrolutidae	Psychrolutidae
Agonidae	Agonidae
Cyclopteridae	Cyclopteroidei

Table 1–7. Taranets' (1941) classification of Cottidae, its subfamilies, and tribes, and "related families" on left. Current classification on right. The monotypic Scorpaenichthyidae was not considered to be related to other cottid-like fishes, but with the distant Notothenioidei (Perciformes). Generic composition of Taranets' (1941) Cottidae and Psychrolutidae given in Appendix 1–2.

Scorpaenichthyidae*	Cottidae
Ascelichthyidae	Cottidae
Cottidae	
Jordaniinae	Cottidae
Triglopinae	Cottidae
Icelinae	Cottidae
Hemilepidotinae	Cottidae
Pseudoblenniinae	Cottidae
Oligocottinae	Cottidae
Oligocottini	
Artedini	
Gymnocanthinae	Cottidae
Ricuzeniinae	Cottidae
Myoxocephalinae	Cottidae
Myoxocephalini	
Enophryini	
Taurocottini	
Artediellini	
Radulinae	Cottidae
Stlenginae	Cottidae
Nautichthyinae	Hemitripteridae
Cottinae	Cottidae
Cottocomephoridae	Cottidae (Cottocomephorinae)
Comephoridae	Comephoridae
Hemitripteridae	Hemitripteridae
Blepsiidae	Hemitripteridae
Psychrolutidae	Psychrolutidae
Ereuniidae	Ereuniidae
Marukawichthyidae	Ereuniidae
Rhamphocottidae	Rhamphocottidae
Synchiridae	Cottidae
Agonidae	Agonidae

"Icelinae," to more specialized Cottidae and Lake Baikal derivatives, and 2) his "Myoxocephalinae" and Psychrolutidae, to Cyclopteridae and Liparidae. The utility of Taranets' subfamilies of Cottidae is limited because his diagnostic characters for these taxa have much overlap, and no decisive key was provided for them.

Taranets considered that the most derived cottoids are highly specialized for benthic life and that most character evolution in the entire group could be explained by this trend, including: reduction in body armor, reduced lateral line system, gill membranes separate from the isthmus, and an expanded pectoral girdle and fins. Taranets' work is a classic on cottoid systematics as it was the most detailed examination of these fishes at the time, it provided the first descriptions of possible character evolution in the group, and was the first work to acknowledge the distinctiveness of Psychrolutidae and provide a concise diagnosis of that family.

Bolin (1947) discussed the evolution of Californian cottids and provided a phylogenetic tree for that assemblage (Figure 1–4). Of interest, Bolin thought: *Scorpaenichthys* to be the most generalized cottid; *Jordania* and *Paricelinus* to also be generalized and possibly close to *Scorpaenichthys*; *Blepsias* and *Nautichthys* to be closely related (as had Jordan, 1923) and an early cottoid offshoot, although now more specialized in form than the presumed ancestor; and *Hemilepidotus* to be generalized in form, although he nested it somewhat higher in his tree. Bolin did not consider other specialized cottoid families.

Watanabe (1960) examined Japanese cottids and provided a classification (Table 1–8), although most of his work dealt with species accounts and not classification. Watanabe placed Psychrolutidae in two subfamilies of Cottidae,

Table 1–8. Watanabe's (1960) classification of "Cottidae" ("Dasycottinae" and "Gilbertidinae" currently in Psychrolutidae) on left. Generic composition of Watanabe's (1960) subfamilies given in Appendix 1–3.

- Cottidae
  - Ereuninae
  - Triglopsinae
  - Hemilepidotinae
  - Gymnocanthinae
  - Myoxocephalinae
  - Hemitripterinae
- Cottidae (continued)
  - Ceratocottinae
  - Cottinae
  - Pseudoblenninae
  - Cottiusculinae
  - Dasycottinae
  - Gilbertidinae

Figure 1–4. Bolin's (1947) phylogeny of Californian Cottidae simplified to genera. Genera are valid as per Eschmeyer (2000). Cladistic interpretation of Bolin's hypothesised relationships shown above.

"Dasycottinae" and "Gilbertidinae." Of interest in his classification is his grouping of *Blepsias* (and *Histiocottus*, a junior synonym of *Blepsias*) and *Hemitripterus* together in "Hemitripterinae," apparently the first such grouping of these genera. Although "Hemitripterinae" were recognized and accounted for in the Watanabe's key to Japanese Cottidae, the characters given in his systematic treatment are not diagnostic for this taxon, and its relationships were not explicitly stated.

Richardson (1981) examined the larvae of 25 genera of Northeast Pacific Cottoidei. Richardson found six distinct morphotypes (Table 1–9) amongst these 25 genera and postulated that these morphotypes might indicate phylogenetic relationship. Of these morphotypes, the groupings of "Oligocottinae," "Icelinae," "Cottinae," and Psychrolutidae of Taranets (1941) and "Blepsiidae" of Jordan (1923) are supported in part. Current Hemitripteridae (that includes *Blepsias, Hemitripterus,* and *Nautichthys*) were not further substantiated by Richardson's findings.

Yabe (1981) reassessed Berg's (1940) "Icelidae," that included *Icelus, Ereunias,* and *Marukawichthys,* he found *Icelus* to belong to Cottidae, leaving the other two genera as Ereuniidae. Jordan (1923) had also recognized the taxon "Ereuniidae," but with only one included genus, *Ereunias.* Yabe concluded that Ereuniidae are the sister group to the Cottidae of Taranets (1941).

Table 1–9. Richardson's (1981) morphotypes of Cottoidei larvae. U indicates unsortable morphotypes. *Malacocottus* was tentatively identified and one other specimen of group 3 could not be identified with any known adult species.

1)	*Artedius, Clinocottus, Oligocottus, Orthonopias*
2)	*Chitonotus, Icelinus, Icelus, Paricelinus, Triglops*
3)	*Dasycottus* , *Gilbertidia, Malacocottus*, Psychrolutes,* "Cottoid type A"
4)	*Hemilepidotus, Scorpaenichthys*
5)	*Blepsias, Nautichthys*
6)	*Cottus, Leptocottus*
U)	*Enophrys, Gymnocanthus, Hemitripterus, Myoxocephalus, Radulinus, Rhamphocottus*

Washington *et al.* (1984) presented a phylogeny of Cottoidei based on adult and some larval characters (Figure 1–5). They considered Cyclopteroidea to be the sister-group of all other Cottoidei. Of the remaining Cottoidei, they thought: Rhamphocottidae to be most primitive, followed by a clade including *Scorpaenichthys* and *Hemilepidotus*, followed by a mostly unresolved clade that includes the specialized families Agonidae, Hemitripteridae, and Psychrolutidae. Washington *et al.* also thought Agonidae and Hemitripteridae to form a monophyletic group. To my knowledge, this was the first published cladogram on cottoid interrelationships based on shared derived characters and it was the first time that Cyclopteroidea

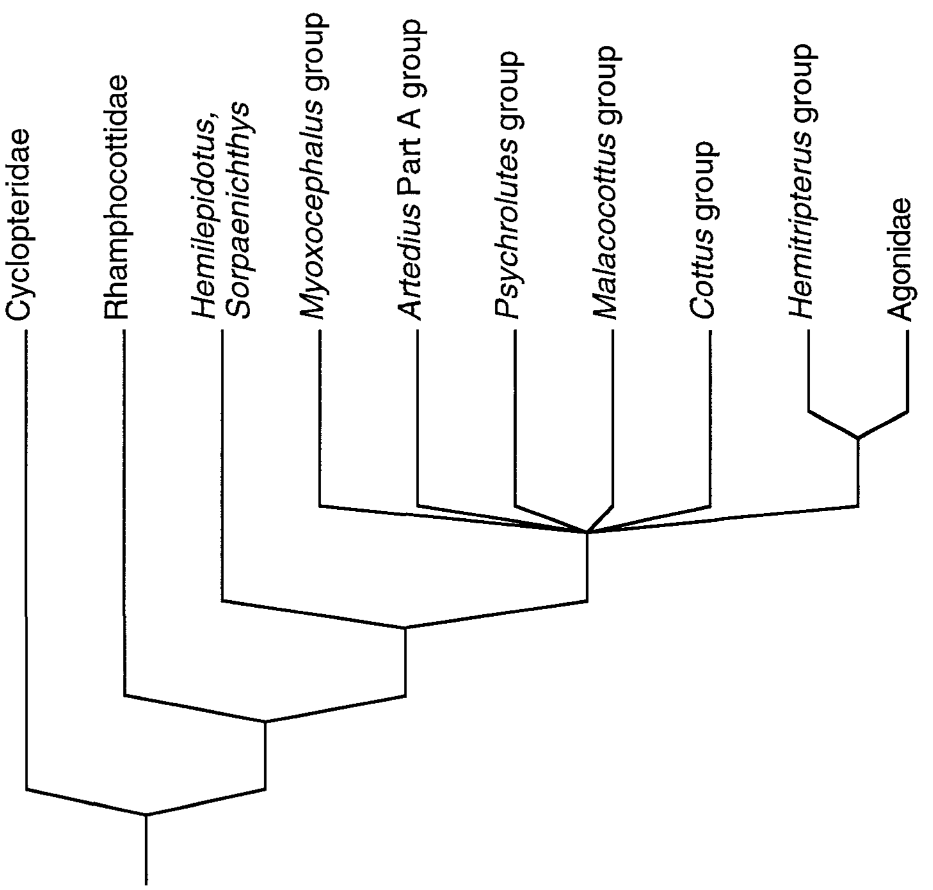

Figure 1–5. Washington *et al.*'s (1984) phylogeny of Cottoidei. Classification is current, except for Cyclopteridae that includes Liparidae.

were explicitly split from other Cottoidei based on phylogenetic relationship. In spite of this achievement, the characters Washington *et al.* used were only cursorily described, homoplasy was little discussed, and other authors have not since independently arrived at this same basal placement of Cyclopteridae.

Yabe (1985) provided the most recent and exhaustive treatise on the relationships of cottoid fishes. Although Yabe found three new synapomorphic characters supporting a monophyletic Cottoidei, he focussed his efforts on resolving the interrelationships of Cottoidea, that he assumed to be monophyletic, with Cyclopteroidea as their sister taxon. Yabe's phylogenetic hypothesis is summarized in Figure 1–6. Yabe thought Rhamphocottidae (monotypic with *Rhamphocottus richardsoni*) to be the most primitive cottoid. Gill (1888) had Rhamphocottidae separate from Cottidae and near Agonidae (Figure 1–1). Regan (1913) and Berg (1940) included *Rhamphocottus* in Cottidae, whereas Jordan (1923) and Taranets (1941) excluded it based on its unique morphology, although neither speculated on its phylogenetic position. Yabe continued his view (from Yabe, 1981) that Ereuniidae are sister to other cottoids, although in an unresolved trichotomy with Taranets' Psychrolutidae. Yabe (1985) placed *Blepsias* and *Nautichthys* near *Hemitripterus,* and considered that clade to be sister to Agonidae, and the two to be sister to the remaining Cottidae. Yabe concluded that all other Cottoidea he examined (with the same composition as Taranets' Cottidae) form a monophyletic taxon, of which *Jordania, Scorpaenichthys,* and *Hemilepidotus* are the most basal. The basal relations and major clades of Yabe's work were largely incorporated into current classification (Nelson, 1994) (Table 1–1 and Figure 1–6). Although Yabe's work was large in scope, and and in my opinion, exemplary in anatomy, as with Shinohara (1994), his work is lacking in its treatment of homoplasy and does not adhere to modern (even at the time) practice in basing conclusions on cladistic methodology.

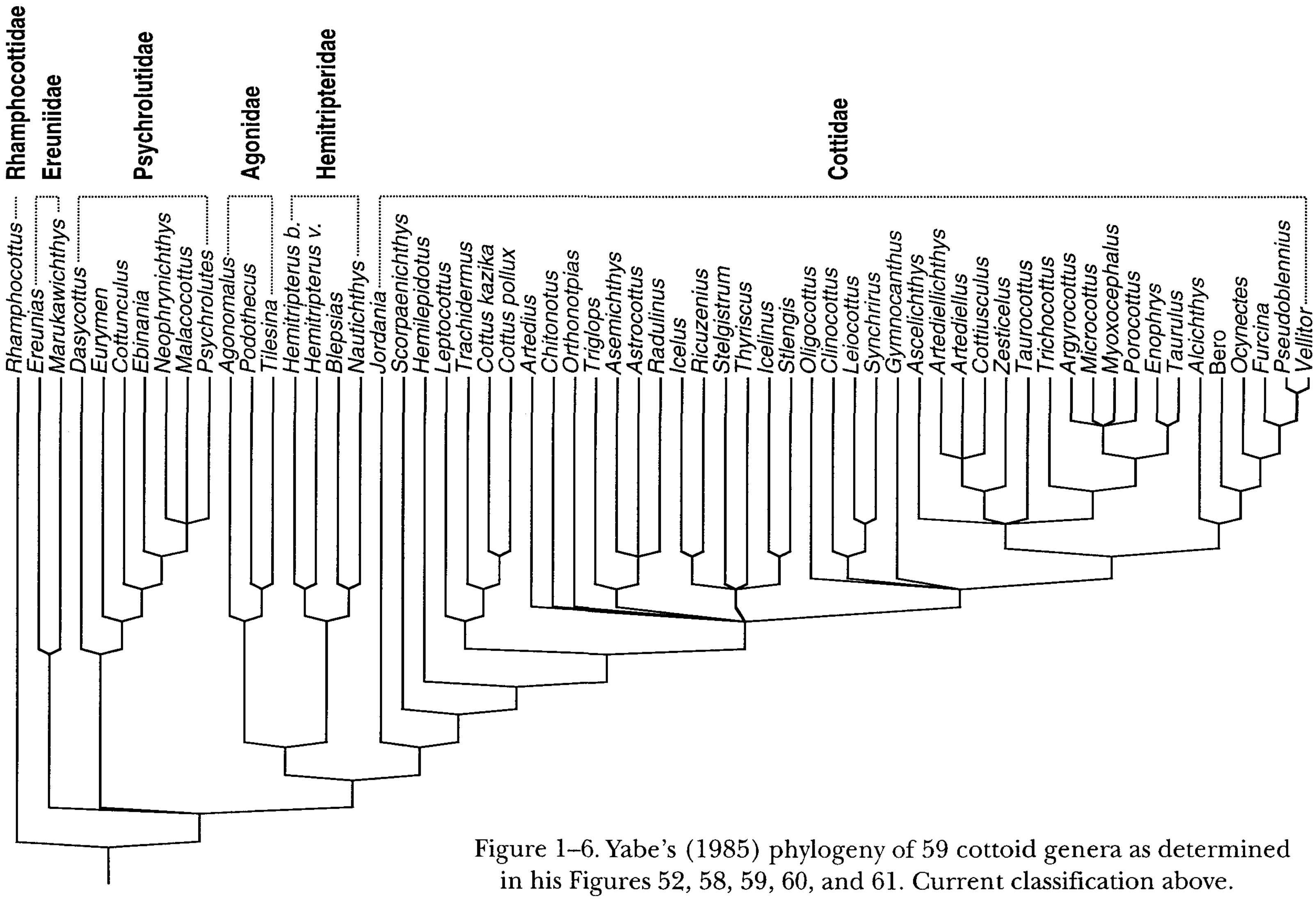

Figure 1–6. Yabe's (1985) phylogeny of 59 cottoid genera as determined in his Figures 52, 58, 59, 60, and 61. Current classification above.

Many workers have contributed to the systematics of cottoid fishes at the family level and below. Bolin (1936) revised the cottid genus *Icelinus* and presented a phylogenetic tree of its species. Cowan (1971, 1972) examined the morphology and meristics of the cottid genus *Myoxocephalus* and concluded that three evolutionary lineages are present that reflect the group's geographic distribution: Holarctic-Atlantic, Bering Sea-trans-Pacific, and Asiatic. Peden (1978) revised the cottid genus *Hemilepidotus* and presented a phylogenetic tree showing the monophyly of the genus as uncertain. Sideleva (1982) revised the endemic sculpins of Lake Baikal, described their lateralis system in detail, and presented a phylogenetic tree for the group. Nelson (1977, 1982) provided much taxonomic work on Psychrolutidae; Nelson and Jackson (1998) cladistically inferred a phylogeny for that group. Kanayama (1991) presented a phylogeny for Agonidae and discussed its classification. Andriashev and Stein have written much on liparids; some important works include: a review of deepwater forms from the North Pacific (Stein, 1978), biogeography of the group suggesting a non-Arctic route of dispersal from the Pacific to Atlantic Ocean (Andriashev, 1990), and a revision of *Careproctus* (Andriashev and Stein, 1998).

Conclusions

Current systematic work on cottoid fishes is alive and well with about five new species being described each year (Figure 1–7). Research on Cyclopteroidea is particularly active due to recently described Southern Ocean forms. The extensive use of cladistic methodology in the past 30 or so years has also influenced cottoid systematics as is seen in recent more rigorous and ambitious papers outlined above (particularly Yabe, 1985 and Shinohara, 1994). Nevertheless, much work remains to be done on this group. At the alpha taxonomic level, many cottoid species have been described from few specimens and may be of questionable valid-

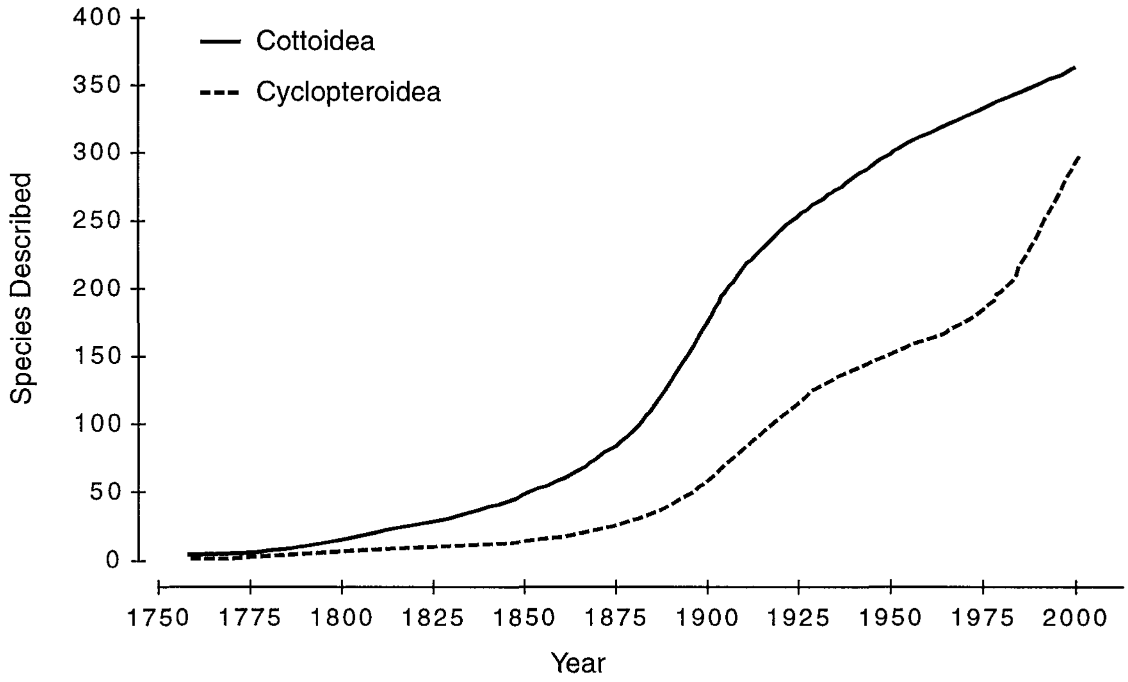

Figure 1–7. Cumulative number of cottoid fishes described and currently valid as per Eschmeyer (2002). Cottoidea and Cyclopteroidea are as recognized by Nelson (1994).

ity. With the exception of some recent comprehensive works (*e.g.*, Peden, 1977), most genera need revision.

Many questions remain about the interrelationships of cottoid taxa. Although the sister relations of Cottoidei seem well founded amongst Hexagrammoidei, the basal relationships in the group are unresolved. Most early authors (*e.g.*, Jordan, 1923; Taranets, 1940; Bolin, 1947) thought that *Scorpaenichthys*, *Jordania*, and *Hemilepidotus* represent the most generalized and primitive extant cottoids while other forms are variously specialized derivatives. Yabe (1985) upset this when he inferred that several specialized groups, Rhamphocottidae, Hemitripteridae, Agonidae, and Psychrolutidae, to be basal groups. Yabe's conclusions are apparently not based on cladistic methodology and it is not certain if current classification has been drawn from a sound phylogeny.

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Appendix 1–1. Generic composition of Jordan's (1923) families of "Cottiformes." Jordan (1923) originally listed genera of each family in order of first description; here, alphabetical order is used. The genera listed here have not been checked for validity in Eschmeyer (2002); many have since been synonymized or otherwise invalidated.

Jordaniidae: *Alcidea, Jordania, Paricelinus*
Icelidae: *Agonocottus, Archaulus, Archistes, Artediellus, Artedius, Aspicottus, Astrolytes, Axyrias, Calycilepidotus, Ceratocottus, Chitonotus, Clypeocottus, Daruma, Enophrys, Hemilepidotus, Icelinus, Icelus, Melletes, Orthonopias, Paraperca, Prionistius, Pterygiocottus, Radulinus, Rastrinus, Ricuzenius, Ruscarius, Schmidtia, Schmidtina, Stelgidonotus, Stelgistrum, Sternias, Stlengis, Tarandichthys, Taurulus, Temnistia, Thyriscus, Triglops*
Blepsiidae: *Blepsias, Histiocottus, Nautichthys, Nautiscus, Peropus*
Scorpaenichthyidae: *Scorpaenichthys*
Cottidae: *Acanthocottus, Ainocottus, Alcichthys, Aphobus, Argyrocottus, Bero, Blennicottus, Boreocottus, Bunocottus, Centridermichthys, Cephalocottus, Clinocottus, Cottiusculus, Cottopsis, Cottunculus, Cottus, Crossias, Dasycottus, Dialarchus, Elaphichthys, Elaphocottus, Eximia, Furcina, Greeleya, Gymnocanthus, Hayia, Hoplocottus, Leiocottus, Leptocottus, Malacocottus, Megalocottus, Mesocottus, Myoxocephalus, Ocynectes, Oligocottus, Oncocottus, Oxycottus, Pegedictis, Phobetor, Podabrus, Porocottus, Potamocottus, Pseudoblennius, Ptyonotus, Rheopresbe, Rusciculus, Rusulus, Sigmistes, Tauridea, Taurocottus, Thecopterus, Trachydermus, Trichocottus, Triglopsis, Uranidea, Vellitor, Zesticelus*
Abyssocottidae: *Abbysocottus, Asprocottus, Batrachocottus, Cottinella, Linnocottus, Procottus*
Ascelichthyidae: *Ascelichthys*
Psychrolutidae: *Gilbertidia, Gilbertina, Eurymen, Psychrolutes*
Neophrynichthyidae: *Besnardia, Neophrynichthys*
Synchiridae: *Synchirus*
Ereuniidae: *Ereunias*
Rhamphocottidae: *Rhamphocottus*
Hemitripteridae: *Hemitripterus, Ulca*
Cottocomephoridae: *Baicalocottus, Cottecomephorus*
Comephoridae: *Comephorus, Elaeorhoüs*
Agonidae: *Agonopsis, Agonus, Aspidophorus, Asterotheca, Averruncus, Bathyagonus, Bothragonus, Brachyopsis, Cataphractus, Cheiragonus, Draciscus, Hippocephalus, Hypsagonus, Leptagonus, Occa, Odontopyxis, Pallasina, Paragonus, Paragonus, Percis, Phalangistes, Podothecus, Ribeiroa, Sarritor, Siphagonus, Stelgis, Stellerina, Tilesina, Xeneretmus, Xenochirus, Xystes*
Aspidophoroididae: *Aspidophoroides, Anoplagonus, Canthirhynchus, Ulcina*

Appendix 1–2. Generic composition of Taranets' (1941) Cottidae and Psychrolutidae. Taranets did not explicitly state the generic composition of other "related families." The genera listed here have not been checked for validity in Eschmeyer (2002); many have since been synonymized or otherwise invalidated.

- Cottidae
  - Jordaniinae: *Jordania, Paricelinus, Alcidea*
  - Triglopinae: *Triglops, Sternias*
  - Icelinae: *Chitonotus, Icelinus, Ruscarius, Ruscariops, Icelus, Thyriscus, Archistes, Stelgistrum*
  - Hemilepidotinae: *Hemilepidotus, Melletes*
  - Pseudoblenniinae: *Alcichthys, Furcina, Ocynectes, Pseudoblennius, Bero, Vellitor*
  - Oligocottinae
    - Oligocottini: *Clinocottus, Oligocottus, Dialarchus, Sigmistes, Oxycottus, Blennicottus, Rusciculus*
    - Artedini: *Axyrias, Allartedius, Astrolytes, Parastrolytes, Artedius, Orthonopias*
  - Gymnocanthinae: *Gymnocanthus*
  - Ricuzeniinae: *Daruma, Ricuzenias*
  - Myoxocephalinae
    - Myoxocephalini: *Myoxocephalus, Triglopsis, Porocottus, Argyrocottus*
    - Enophryini: *Enophrys, Aspicottus, Parenophrys*
    - Taurocottini: Taurocottus
    - Artediellini: *Evermania, Artediellus, Cottiusculus, Artediellina, Zesticelus, Stlegiocottus*
  - Radulinae: *Radulinus, Radulinopsis*
  - Stlenginae: *Stlengis*
  - Nautichthyinae: *Nautichthys*
  - Cottinae: *Cottus, Mesocottus, Trachydermus, Leptocottus, Leiocottus*
- Psychrolutidae: *Cottunculus, Cottunculoides, Ebinania, Dasycottus, Malacocottus, Thecopterus, Neophrynichthys, Eurymen, Gilbertidia, Psychrolutes*

Appendix 1–3. Generic composition of Watanabe's (1960) subfamilies of "Cottidae." The genera listed here have not been checked for validity in Eschmeyer (2002); many have since been synonymized or otherwise invalidated.

Cottidae
- Ereuninae: *Marukawichthys, Ereunias*
- Triglopsinae: *Triglops*
- Hemilepidotinae: *Ricuzenius, Astrocottus, Daruma, Stelgistrum, Stlengis, Icelus, Neohemilepidotus, Hemilepidotus*
- Gymnocanthinae: *Gymnocanthus*
- Myoxocephalinae: *Myoxocephalus, Ainocottus, Porocottus*
- Hemitripterinae: *Histiocottus, Blepsias, Hemitripterus*
- Ceratocottidae: *Ceratocottus*
- Cottinae: *Trachidermus, Cottus*
- Pseudoblenninae: *Argyrocottus, Alcichthys, Bero, Furcina, Ocynectes, Pseudoblennius, Crossias, Vellitor*
- Cottiusculinae: *Cottiusculus*
- Dasycottinae: *Dasycottus, Malacocottus*
- Gilbertidinae: *Eurymen, Gilbertidia, Cottunculus, Ebinania*

2. A REASSESSMENT OF YABE'S PHYLOGENY OF COTTOIDEA

ABSTRACT

Mamoru Yabe's published doctoral dissertation (1985) is the most recent and broadest systematic treatment of cottoid fishes. Yabe proposed that five specialized cottoid families are basal to a monophyletic Cottidae. This is unlike previous workers. who simply considered Cottidae to be a group of generalized cottoids. Here, Yabe's data are reassessed using the maximum parsimony criterion and compared with the tree that Yabe presented. I found that Cottidae is not monophyletic and show that Yabe's own data suggest that some members of Cottidae are basal in the assemblage's phylogeny. Assumptions on character evolution and individual characters are assessed as to whether they support or refute a monophyletic Cottidae. Six characters support Yabe's basal placement of the specialized families, and nine characters conflict the monophyly of Cottidae. Yabe's phylogeny and suggested classification are not supported by formal cladistic analysis. A follow-up study will be pursued to rectify this situation.

Introduction

Yabe (1985) presented the most recent and comprehensive treatment of cottoid systematics. He examined 60 osteological and myological characters amongst 61 Cottoidea (Cottoidei less Cyclopteridae and Liparidae) in an apparently cladistic manner, and presented a largely resolved phylogenetic hypothesis of the interrelationships within the group (Figure 2–1). Yabe (pages 122-123) incorporated his phylogenetic findings into a classification that more recent works (e.g., Nelson, 1994) have made use of.

Yabe's anatomical work was very detailed, although problems can be easily identified with his phylogenetic hypothesis. Using fewer characters than taxa is problematic. This inevitably results in many equally short trees. Furthermore, although Yabe explicitly followed a "cladistic" methodology that he outlined in detail, his method of determining the shortest, or preferred tree is unclear. With such a huge matrix, the possible number of shortest trees is staggering and would be impossible to sort out without a computer program. Below, I reinterpret Yabe's data set and character assumptions using modern cladistic techniques and critically discuss the validity and utility of his findings.

Methods

Yabe's (1985) data matrix (his pages 104-106 and reproduced here in Appendix 2–1) was analyzed with PAUP 4.0b10 (Swofford, 2002). Yabe encoded his characters as being primitive (P or –) or in various derived states (D, D1, D2, *etc.*). The primitive state was determined by out-group comparison. Almost all of the characters were considered ordered (D1, D2, etc.) with the exception of characters 32 and 45. Character 32 was considered to have one primitive state and two ordered series of derived states (D1a, D2a, D1b, D2b). Character 45 was consid-

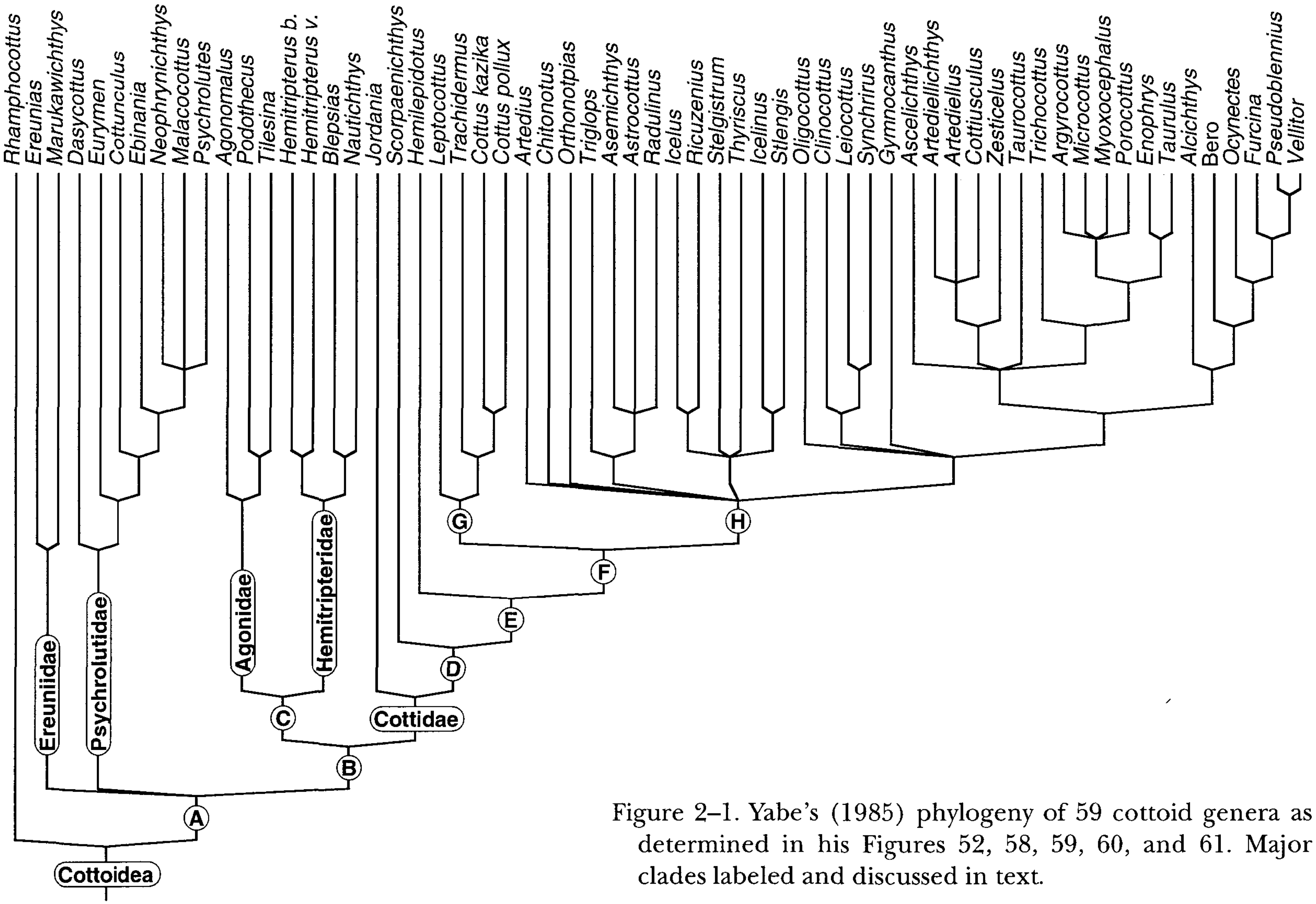


Figure 2–1. Yabe's (1985) phylogeny of 59 cottoid genera as determined in his Figures 52, 58, 59, 60, and 61. Major clades labeled and discussed in text.

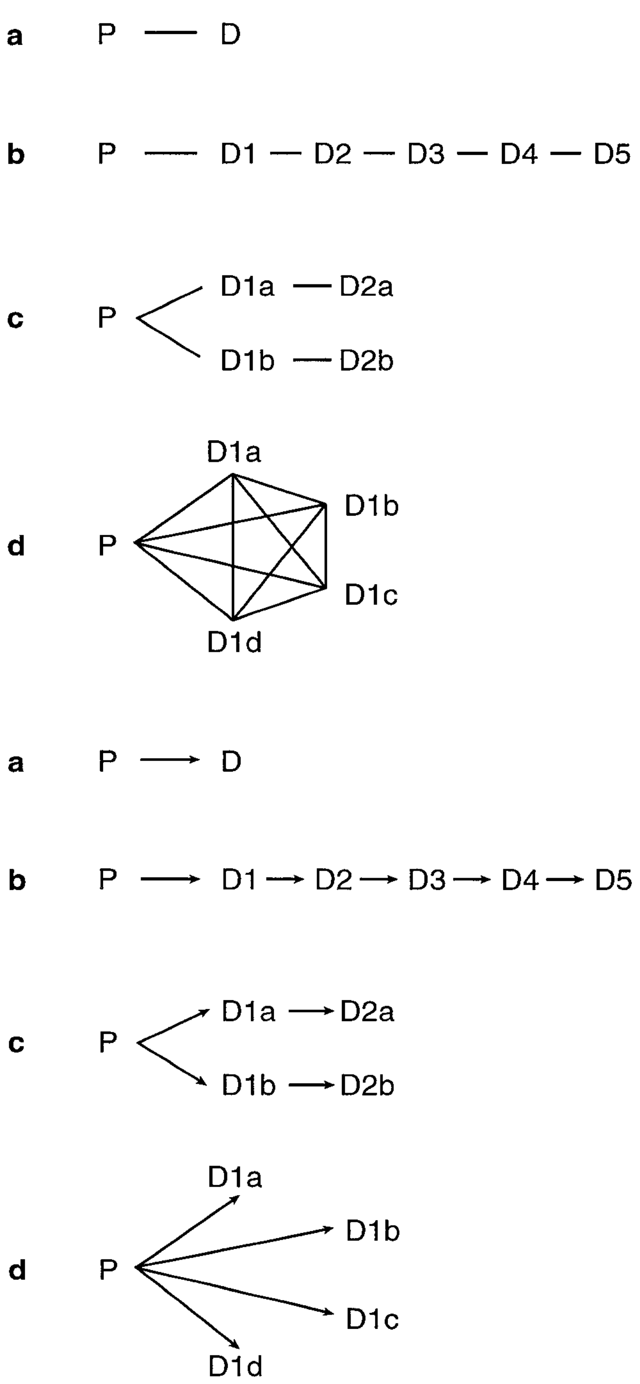
ered to have one primitive state and four possibly independently derived states (D1a, D1b, D1c, D1d).

Of Yabe's 60 characters, six occur only in one taxon and thus are not phylogenetically informative and 18 are Yabe's "synapomorphies" for Cottoidea and are thus also not informative in resolving clades within Cottoidea. The remaining 36 characters are informative and are considered here.

Yabe was unclear on whether reversal was possible once his characters were polarized. In his discussion on character evolution at the beginning of his treatise, he stated that the primitive state was determined by its condition observed in several out-groups. Thus, his initial assumption was that the evolution of characters may occur in any direction. But, his diagrams of character evolution (his Figures 1 and 2) do not indicate reversibility and his lack of discussion on homoplasy, and on reversals in particular, suggests that he considered taxon synapomorphies as uniquely derived. Both assumptions on reversibility are considered here: either characters are reversible or irreversible. These assumptions on character evolution are outlined graphically in Figure 2–2, with the accompanying step-matrices used in parsimony analysis.

Although Yabe acknowledged that some of his characters had derived states present among the various out-group taxa that he examined, he determined character polarity by a technique described at the beginning of his treatise and thereafter did not discuss homoplasy between the in-group and out-groups. Yabe created a hypothetical out-group in which all states were assumed primitive. This was duplicated in PAUP by using the ANCSTATES directive to polarize characters and create rooted trees without an actual out-group.

Two heuristic searches were performed on Yabe's 36 informative characters using the two assumptions on character evolution. With 61 taxa, the possible number of shortest trees is enormous, so the heuristic search was capped at



	P	D1	D2	D3	D4	D5
P	0	1	2	3	4	5
D1	1	0	1	2	3	4
D2	2	1	0	1	2	3
D3	3	2	1	0	1	2
D4	4	3	2	1	0	1
D5	5	4	3	2	1	0

	P	D1a	D2a	D1b	D2b
P	0	1	2	1	2
D1a	1	0	1	2	3
D2a	1	2	0	3	4
D1b	2	1	3	0	1
D2b	2	3	1	4	0

	P	D1a	D1b	D1c	D1d
P	0	1	1	1	1
D1a	1	0	1	1	1
D2a	1	1	0	1	1
D1b	1	1	1	0	1
D2b	1	1	1	1	0

	P	D1	D2	D3	D4	D5
P	0	1	2	3	4	5
D1	∞	0	1	2	3	4
D2	∞	∞	0	1	2	3
D3	∞	∞	∞	0	1	2
D4	∞	∞	∞	∞	0	1
D5	∞	∞	∞	∞	∞	0

	P	D1a	D2a	D1b	D2b
P	0	1	2	1	2
D1a	∞	0	1	∞	∞
D2a	∞	∞	0	∞	∞
D1b	∞	∞	∞	0	1
D2b	∞	∞	∞	∞	0

	P	D1a	D1b	D1c	D1d
P	0	1	1	1	1
D1a	∞	0	∞	∞	∞
D2a	∞	∞	0	∞	∞
D1b	∞	∞	∞	0	∞
D2b	∞	∞	∞	∞	0

Figure 2–2. Character types assumed in reexamining Yabe's (1985) character matrix; a, binary; b, ordered multistate; c, double-ordered multistate (character 32 only); d, multistate unordered (character 45 only). Top series assumes reversibility, bottom series assumes irreversibility. P, primitive state; D*x*, derived states.

100,000 trees (search allowed to complete after MAXTREES was reached). Shortest trees were rooted for tree statistics and consensus.

Results

More than 100,000 equally short trees resulted when character evolution was considered reversible, and 3,456 when irreversible. Tree lengths and consistency indices for Yabe's (1985) tree and the shortest found trees using the two character evolution assumptions are shown in Table 2–1. Reversible character evolution (the least strict assumption) not surprisingly results in the best tree statistics. Consensus trees of the shortest trees from each analysis are plotted in Figure 2–3.

Discussion

Yabe (1985) identified several cottoid clades, labeled in Figure 2–1. Cottoidea are the encompassing clade that Yabe "supported" with 22 synapomorphic characters. Although this number of characters is impressive, no summary was given on which of these characters are homoplastic amongst out-group taxa and which characters informatively support this clade. This is particularly important with Hexagrammoidei, that are probably sister to or encompassing Cottoidei (*e.g.*, Quast, 1965; Shinohara 1994), and Cyclopteroidea, that are certainly sister to or nested within Cottoidea. It remains an open question as to whether Yabe's Cottoidea were discovered or assumed.

Table 2–1. Tree statistics for Yabe's (1985) single tree (Figure 2–1) and the shortest found trees assuming reversible and irreversible character evolution (consensus trees shown in Figure 2–3).

	Yabe's		**Shortest 10,000+**	
	TL	**CI**	**TL**	**CI**
Reversible	176	0.347	159	0.384
Irreversible	211	0.251	189	0.280

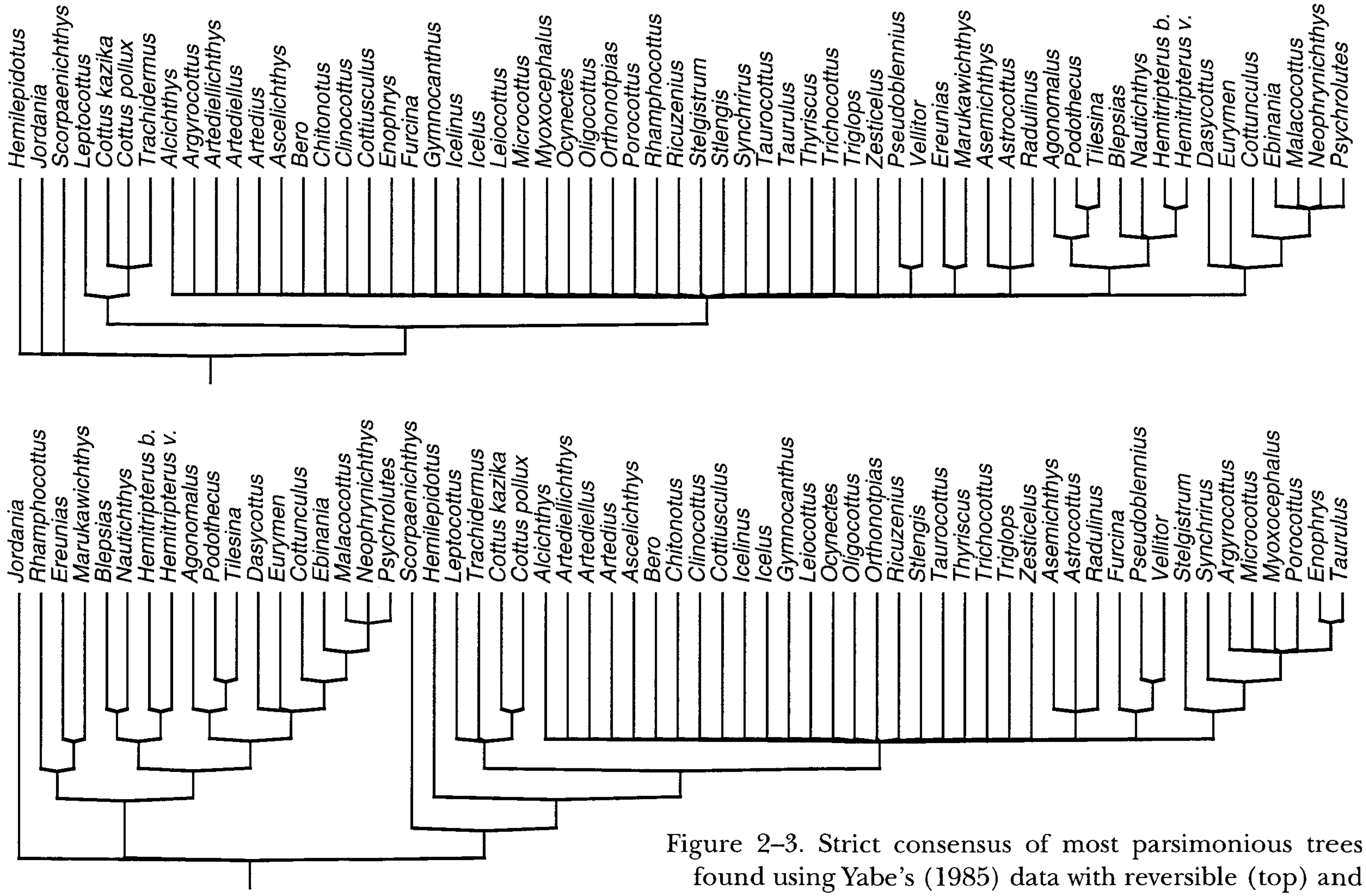


Figure 2–3. Strict consensus of most parsimonious trees found using Yabe's (1985) data with reversible (top) and irreversible (bottom) character evolution assumptions.

Five families are supported on Yabe's tree (Figure 2–1) as monophyletic taxa. Agonidae and Psychrolutidae are well established families (*e.g.*, Taranets, 1941; Kanayama, 1991). Ereuniidae have existed in name since Jordan (1923) with a single genus, *Ereunias*; the genus *Marukawichthys* was described later (Sakamoto, 1931), and the two genera were subsequently lumped with a third, *Icelus*, by Berg (1940) into Icelidae. Ereuniidae was split from *Icelus* by Yabe (1981), who thought that Ereuniidae are a primitive taxon sister to Cottidae and that *Icelus* is a member of Cottidae. Hemitripteridae have existed in name since Gill (1888), with a single genus, *Hemitripterus*. Watanabe (1960) placed *Blepsias* in Hemitripteridae with little justification, although this grouping is supported by Yabe's phylogeny (with *Nautichthys*). Rhamphocottidae, monotypic with *Rhamphocottus*, was either lumped in Cottidae (*e.g.*, Regan, 1913; Berg, 1940) or split as an aberrant family in highly divided classifications of Cottoidei (*e.g.*, Jordan, 1923; Taranets, 1941). Cottidae have been changed in composition by virtually all authors cited here. The Cottidae of Taranets (1941), including *Scorpaenichthys*, are supported by Yabe's phylogeny. Major clades representing Yabe's hypothesized relationships of these families are labeled A, B, and C in Figure 2–1 and basal relationships of Cottidae are shown by clades through H. These clades (families and A through H) will be discussed here.

When character evolution is assumed to be reversible, the resulting consensus of most parsimonious trees (Figure 2–3) is markedly different from and less resolved than what Yabe presented. This tree is contrary to Yabe's, in placing his basal cottoid families nested amongst his Cottidae. Yabe's families other than Cottidae remain monophyletic, as does his proposed sister relationship of Agonidae and Hemitripteridae (clade C). Ignoring the paraphyly of Cottidae, the basal relations of Cottidae are similar to Yabe's phylogeny, with *Hemilepidotus*, *Jordania*, and *Scorpaenichthys* as most basal, followed by clade G, that is sister to clade H.

When character evolution is considered irreversible, the resulting consensus of most parsimonious trees (Figure 2–3) is a little more like what Yabe presented. His Cottidae are nearly monophyletic, with only *Jordania* at a basal position on the tree and otherwise unresolved as to its placement. Yabe's other families remain monophyletic, although their interrelations are not at all comparable with his phylogeny. Agonidae are sister to Psychrolutidae, not to Hemitripteridae. Rhamphocottidae are sister to Ereuniidae. These families (excluding Cottidae) together form a clade that is unresolved at the base of the tree. Yabe's clade G and H are found.

As a consequence of the low number of characters, tree topology is thus volatile depending on character evolution assumptions. With at least 17 steps between Yabe's tree and the shortest tree and only 36 characters to work with, it is unlikely that any mixed set of assumptions would result in a consensus tree agreeing with Yabe's. Character weighting could yield Yabe's phylogeny, but no such assumptions were explicitly stated by Yabe. Certain assumed primitive characters seem to be weighted heavily by Yabe and result in taxa bearing such characters being nested basally on his tree (*e.g.*, Psychrolutidae placed outside of Cottidae might be explained by its having 7 branchiostegal rays and in having an extra element of the hyohyoides muscle complex, characters considered by Yabe to be primitive amongst Cottoidea).

Below are comments on Yabe's 36 informative characters concerning their fit or homoplasy on his tree and possible assumptions about their evolution that support or refute Yabe's tree (see Yabe's manuscript for actual states and detailed descriptions):

1. Infraorbitals. Widely homoplastic between and within families, second derived state (D2) characteristic of Agonidae, but homoplastic in *Cottunculus*.
2. Infraorbital sensory canal. Derived condition of Psychrolutidae.

5. Teeth on prevomer. Primitively present, lost in some Psychrolutidae, some Agonidae and in one of the Cottidae (*Gymnocanthus*). Not informative concerning basal cottoid relations.

6. Palatocranial articulation. Primitive in Hemitripteridae and Cottidae excepting clade H, derived in all members of clade H and remaining families. Does not support a monophyletic Cottidae.

7. Pterosphenoid-parasphenoid junction. Primitive in Ereuniidae, Psychrolutidae, and some Hemitripteridae (*Blepsias* and *Hemitripterus*), derived in all others. Polarity of this character may be in error. Supports Yabe's phylogeny if irreversible.

8. Trigeminofascialis chamber. Unique primitive condition in *Rhamphocottus*, derived (D1) in others, further derived (D2) in Psychrolutidae, some Hemitripteridae (*Blepsias* and *Hemitripterus*), and in *Agonomalus*. Supports Yabe's tree if irreversible, though the polarity of this character should be examined more closely to see if the condition in *Rhamphocottus* is uniquely primitive or uniquely derived.

10. Baudelot's ligament. Derived condition of clade C, but homoplastic in *Pseudoblennius* and *Vellitor*.

11. Supratemporal commissure. Primitive in *Rhamphocottus*, Agonidae, and *Hemitripterus bolini*, derived (D1) in all others, and further derived with four informative states (D2, D3, D4, D5) amongst Psychrolutidae. Supports Yabe's phylogeny if irreversible.

15. Entopterygoid. Primitive in most, derived homoplastically in *Tilesina*, and six clades (with 14 species) within Cottidae. Not informative for basal relations.

16. Palatine teeth. Primitive in Ereuniidae, Hemitripteridae and two Agonidae, derived in *Rhamphocottus*, Psychrolutidae, and *Podothecus*, homoplastic amongst Cottidae in six clades (with 17 species). Not informative for basal relations.

17. Lateral process of the hyomandibular. Derived condition of Cottidae. Supports Yabe's phylogeny concerning the monophyly of Cottidae.

19. First pharyngobranchial. Primitive in *Rhamphocottus*, Ereuniidae, and *Jordania*, derived in all others. Does not support a monophyletic Cottidae.

20. Pharyngobranchials and tooth plates. Primitive in *Rhamphocottus*, Ereuniidae, and various Cottidae, derived in various states amongst Psychrolutidae, Agonidae, Hemitripteridae, and in four clades (with 18 species) of Cottidae. Not informative concerning basal relations.

21. Third epibranchial. Derived in all but *Hemitripterus villosus*. Single uninformative reversal.

22. Basihyal. Two derived states, one (D1) in *Rhamphocottus* and the other (D2) in *Jordania*, further derived (D3) in all others. Does not support a monophyletic Cottidae.

23. Branchiostegal rays. Primitively seven in Psychrolutidae and *Hemitripterus villosus*, derived as six in all others. Polarity of this character is questionable, likely a derived condition of Psychrolutidae and homoplastic in *H. villosus*.

24. Scapular foramen. Two derived states, one (D1) in *Rhamphocottus* and *Jordania*, derived further (D2) in all others. Does not support a monophyletic Cottidae.

27. Pores between each actinost. Derived condition of Psychrolutidae.

28. Free pectoral rays. Derived condition of Ereuniidae.

31. Pelvic fin rays. Primitive in *Jordania* and *Scorpaenichthys*, in Ereuniidae (but absent, D4, in *Ereunias*), derived (D1) in Cottidae below clade H, further derived (D2, D3, D4) in *Rhamphocottus*, Psychrolutidae, Agonidae, Hemitripteridae, and clade H. Does not support a monophyletic Cottidae.

32. Anterior proximal pterygiophore of the dorsal series. Primitive in most, homoplastically derived amongst Ereuniidae, three Agonidae, and four clades (9 species) in Cottidae. Not informative concerning basal relations.

33. Stay. Primitive in *Rhamphocottus* and Ereuniidae, derived in all others. Supports Yabe's phylogeny if irreversible.

34. Fin rays on last proximal pterygiophore. Primitive in *Jordania, Scorpaenichthys,* and *Hemilepidotus,* intermediate (D1) in *Rhamphocottus* and some Hemitripteridae, derived (D2) in all others. Does not support a monophyletic Cottidae.

41. Hypural-parahypural complex bone. Primitive in Hemitripteridae, *Jordania, Scorpaenichthys,* and *Hemilepidotus,* derived in all others. Does not support a monophyletic Cottidae.

42. Caudal fin. Primitive in most, derived in *Rhamphocottus* and clade C (except *Nautichthys*).

43. Neural spine of preural centrum II. Primitive in *Marukawichthys, Jordania, Scorpaenichthys, Hemilepidotus,* and *Trachidermus,* derived in all others. Does not support a monophyletic Cottidae.

44. Isthmus. Primitive in most, derived in *Rhamphocottus,* Psychrolutidae (except *Dasycottus*), *Nautichthys,* and clade G. Not informative for basal relations.

45. Body scales. Primitive condition in Ereuniidae, *Jordania, Hemilepidotus,* and five clades in clade H (13 species), derived loss (D1a) in Psychrolutidae, *Scorpaenichthys,* clade G, and 1 clade (24 species) in clade H, uniquely derived and diagnostic of *Rhamphocottus* (D1c), Agonidae (D1d), and Hemitripteridae (D1b).

46. Position of the anus. Primitive in most, derived in Agonidae and two clades (with five species) in clade H.

49. Hyohyoides inferioris. Primitive in three species of Psychrolutidae and in *Hemitripterus bolini,* derived in all others. Polarity of this character is questionable. Not informative for basal relations.

52. Rectus ventralis. Derived condition of Agonidae.

53. Rectus ventralis interconnecting the urohyal and the third hypobranchial. Primitive in *Rhamphocottus* and Ereuniidae, derived in all others. Supports Yabe's phylogeny if irreversible.

55. Obliquus superioris. Primitive in *Jordania,* derived in all others. Does not sup-

port a monophyletic Cottidae.

58. Anterior tendon of the adductor mandibulae section A1. Derived condition of *Tilesina* and *Podothecus*. Not informative for basal relations.

59. Connection between the adductor mandibulae section A2 and the ligamentum primordium. Homoplastic amongst two Psychrolutidae and five Cottidae. Not informative for basal relations.

60. Coracoradialis. Primitive in Psychrolutidae, derived in all others. Polarity of this character is questionable, likely a derived condition of Psychrolutidae.

Of Yabe's 36 phylogenetically informative characters, 26 are useful in resolving basal relationships of Cottoidea. Ten characters (5, 15, 16, 20, 21, 32, 44, 49, 58, 59) are too homoplastic or limited in distribution (*i.e.*, only found in a few close species) to be useful in deducing basal cottoid relations. Nine characters support Yabe's families: Psychrolutidae (2, 23, 27, 60), Agonidae (1, 45, 46, 52), Ereuniidae (28), and Hemitripteridae (45). Two characters support a clade formed by Agonidae and Hemitripteridae (clade C; 10 and 42). Fifteen remaining characters offer insight into the basal relationships of Cottoidea. Six characters, particularly when considered irreversible, support Yabe's phylogeny with a monophyletic Cottidae with other families basal to it (7, 8, 11, 17, 33, 53). Nine characters do not support a monophyletic Cottidae, because these characters have primitive states observed amongst cottid members (particularly *Jordania, Scorpaenichthys,* and *Hemilepidotus*) and derived states observed amongst cottid members and some (19, 22, 24, 31, 41, 43) or all (6, 34, 55) of the remaining families.

Why Yabe preferred his tree is not obvious, but it is possible that he favored some characters over others. Character 17 (the hyomandibular process), that he identifies as a synapomorphy of his monophyletic Cottidae, seems particularly heavily weighted. Although, irreversibility of this character from its derived condition (presence) would need to be assumed in order to exclude other families from the cottid clade. Also, the presence of some primitive characters in *Rhamphocottus* and Ereuniidae seems to influence Yabe's basal placement of them. Character 17 is the only synapomorphy supporting a monophyletic Cottidae.

Curiously, Yabe's "cladistic" methodology was little differentiated from the methods used by Matsubara (1943), that were remarkably advanced for the time. Granted that 1985 was at the beginning of the computerized cladistics age, Yabe's work was on par with the times, and remains a classic and scholarly treatment of cottoid anatomy and systematics. In conclusion, based only on Yabe's data there is little evidence supporting a monophyletic Cottidae. For now, Cottidae are as unresolved as previously held, and the various cottoid families (Psychrolutidae, Agonidae, Hemitripteridae, Ereuniidae, Rhamphocottidae) are distinct, but it is uncertain whether they are specialized cottids or early cottoid offshoots. Further work will be carried out to clarify this situation.

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Appendix 2–1. Yabe's (1985) data matrix. Informative characters grouped first, followed by Yabe's characters "synapomorphic" for Cottoidea, and noninformative characters grouped last. (Continued on following page...)

	Informative →																			
	1	2	5	6	7	8	10	11	15	16	17	19	20	21	22	23	24	27	28	31
Jordania	–	–	–	–	D	D1	–	D1	–	–	D	–	D1	D	D2	D	D1	–	–	–
Scorpaenichthys	–	–	–	–	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	–
Hemilepidotus	–	–	–	–	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D1
Leptocottus	–	–	–	–	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D1
Trachidermus	–	–	–	–	D	D1	–	D1	D2	–	D	D	D1	D	D3	D	D2	–	–	D1
Cottus kazika	–	–	–	–	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D1
Cottus pollux	–	–	–	–	D	D1	–	D1	–	D	D	D	D1	D	D3	D	D2	–	–	D1
Artedius	–	–	–	D	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D2
Chitonotus	–	–	–	D	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D2
Orthonotpias	–	–	–	D	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D2
Triglops	D1	–	–	D	D	D1	–	D1	–	D	D	D	D1	D	D3	D	D2	–	–	D2
Radulinus	D1	–	–	D	D	D1	–	D1	D2	D	D	D	D1	D	D3	D	D2	–	–	D2
Asemichthys	D1	–	–	D	D	D1	–	D1	D2	D	D	D	D1	D	D3	D	D2	–	–	D2
Astrocottus	D1	–	–	D	D	D1	–	D1	D2	D	D	D	D1	D	D3	D	D2	–	–	D2
Icelus	–	–	–	D	D	D1	–	D1	–	–	D	D	D3	D	D3	D	D2	–	–	D2
Ricuzenius	–	–	–	D	D	D1	–	D1	–	–	D	D	D3	D	D3	D	D2	–	–	D2
Stelgistrum	–	–	–	D	D	D1	–	D1	–	D	D	D	D3	D	D3	D	D2	–	–	D2
Thyriscus	D1	–	–	D	D	D1	–	D1	–	–	D	D	D3	D	D3	D	D2	–	–	D2
Stlengis	–	–	–	D	D	D1	–	D1	D1	–	D	D	D3	D	D3	D	D2	–	–	D3
Icelinus	–	–	–	D	D	D1	–	D1	D1	–	D	D	D3	D	D3	D	D2	–	–	D3
Oligocottus	–	–	–	D	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D2
Clinocottus	–	–	–	D	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D2
Leiocottus	–	–	–	D	D	D1	–	D1	–	D	D	D	D1	D	D3	D	D2	–	–	D2
Synchrirus	–	–	–	D	D	D1	–	D1	D2	D	D	D	D3	D	D3	D	D2	–	–	D2
Gymnocanthus	–	–	D	D	D	D1	–	D1	–	D	D	D	D1	D	D3	D	D2	–	–	D2
Ascelichthys	D1	–	–	D	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D4
Taurocottus	D1	–	–	D	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D2
Trichocottus	D1	–	–	D	D	D1	–	D1	–	D	D	D	D1	D	D3	D	D2	–	–	D2
Myoxocephalus	D1	–	–	D	D	D1	–	D1	–	D	D	D	D3	D	D3	D	D2	–	–	D2
Microcottus	D1	–	–	D	D	D1	–	D1	–	D	D	D	D3	D	D3	D	D2	–	–	D2
Porocottus	D1	–	–	D	D	D1	–	D1	–	D	D	D	D3	D	D3	D	D2	–	–	D2
Argyrocottus	D1	–	–	D	D	D1	–	D1	–	D	D	D	D3	D	D3	D	D2	–	–	D2
Enophrys	D1	–	–	D	D	D1	–	D1	–	D	D	D	D3	D	D3	D	D2	–	–	D2
Taurulus	D1	–	–	D	D	D1	–	D1	–	D	D	D	D3	D	D3	D	D2	–	–	D2
Artediellus	D1	–	–	D	D	D1	–	D1	D1	–	D	D	D1	D	D3	D	D2	–	–	D2
Artediellichthys	D1	–	–	D	D	D1	–	D1	D1	–	D	D	D1	D	D3	D	D2	–	–	D2
Cottiusculus	D1	–	–	D	D	D1	–	D1	D1	–	D	D	D1	D	D3	D	D2	–	–	D2
Zesticelus	D1	–	–	D	D	D1	–	D1	D1	D	D	D	D1	D	D3	D	D2	–	–	D3
Alcichthys	–	–	–	D	D	D1	–	D1	–	–	D	D	D1	D	D3	D	D2	–	–	D3
Bero	–	–	–	D	D	D1	–	D1	–	–	D	D	D2	D	D3	D	D2	–	–	D3
Ocynectes	–	–	–	D	D	D1	–	D1	–	–	D	D	D3	D	D3	D	D2	–	–	D3
Furcina	–	–	–	D	D	D1	–	D1	D1	–	D	D	D3	D	D3	D	D2	–	–	D3
Pseudoblennius	–	–	–	D	D	D1	D	D1	D1	–	D	D	D3	D	D3	D	D2	–	–	D3
Vellitor	–	–	–	D	D	D1	D	D1	D1	–	D	D	D3	D	D3	D	D2	–	–	D3
Hemitripterus v.	–	–	–	–	–	D2	D	D1	–	–	–	D	D3	–	D3	–	D2	–	–	D2
Hemitripterus b.	–	–	–	–	–	D2	D	–	–	–	–	D	D3	D	D3	D	D2	–	–	D2
Blepsias	D1	–	–	–	–	D2	D	D1	–	–	–	D	D2	D	D3	D	D2	–	–	D2
Nautichthys	D1	–	–	–	D	D1	D	D1	–	–	–	D	D3	D	D3	D	D2	–	–	D2
Agonomalus	D2	–	D	D	D	D2	D	–	–	–	–	D	D3	D	D3	D	D2	–	–	D3
Podothecus	D2	–	D	D	D	D1	D	–	–	D	–	D	D3	D	D3	D	D2	–	–	D3
Tilesina	D2	–	–	D	D	D1	D	–	D1	–	–	D	D3	D	D3	D	D2	–	–	D3
Marukawichthys	–	–	–	D	–	D1	–	D1	–	–	–	–	D1	D	D3	D	D2	–	D	D1
Ereunias	–	–	–	D	–	D1	–	D1	–	–	–	–	D1	D	D3	D	D2	–	D	D4
Dasycottus	D1	D	–	D	–	D2	–	D2	–	D	–	D	D3	D	D3	–	D2	D	–	D2
Eurymen	D1	D	–	D	–	D2	–	D2	–	D	–	D	D3	D	D3	–	D2	D	–	D2
Cottunculus	D2	D	–	D	–	D2	–	D3	–	D	–	D	D3	D	D3	–	D2	D	–	D2
Ebinania	D1	D	–	D	–	D2	–	D4	–	D	–	D	D3	D	D3	–	D2	D	–	D2
Neophrynichthys	D1	D	D	D	–	D2	–	D4	–	D	–	D	D3	D	D3	–	D2	D	–	D2
Malacocottus	D1	D	D	D	–	D2	–	D4	–	D	–	D	D3	D	D3	–	D2	D	–	D2
Psychrolutes	D1	D	D	D	–	D2	–	D5	–	D	–	D	D3	D	D3	–	D2	D	–	D2
Rhamphocottus	D1	–	–	D	D	–	–	–	–	D	–	–	D1	D	D1	D	D1	–	–	D2

Appendix 2–1 (...continued).

																“synapomorphies” →			
	32	33	34	41	42	43	44	45	46	49	52	53	55	58	59	60	3	4	12	13
Jordania	–	D	–	D1	–	–	–	–	–	D	–	D	–	–	–	D	D	D	D	D
Scorpaenichthys	D1a	D	–	D1	–	–	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Hemilepidotus	–	D	–	D1	–	–	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Leptocottus	–	D	D2	D2	–	D	D2	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Trachidermus	–	D	D2	D2	–	–	D2	D1a	–	D	–	D	D	–	D	D	D	D	D	D
Cottus kazika	–	D	D2	D2	–	D	D2	D1a	–	D	–	D	D	–	D	D	D	D	D	D
Cottus pollux	–	D	D2	D2	–	D	D2	D1a	–	D	–	D	D	–	D	D	D	D	D	D
Artedius	D1a	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Chitonotus	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Orthonotpias	–	D	D2	D2	–	D	–	–	D2	D	–	D	D	–	–	D	D	D	D	D
Triglops	–	D	D2	D2	–	D	–	–	D1	D	–	D	D	–	D	D	D	D	D	D
Radulinus	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Asemichthys	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Astrocottus	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Icelus	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Ricuzenius	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Stelgistrum	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Thyriscus	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Stlengis	–	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Icelinus	D1a	D	D2	D2	–	D	–	–	–	D	–	D	D	–	–	D	D	D	D	D
Oligocottus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Clinocottus	–	D	D2	D2	–	D	–	D1a	D1	D	–	D	D	–	–	D	D	D	D	D
Leiocottus	–	D	D2	D2	–	D	–	D1a	D1	D	–	D	D	–	–	D	D	D	D	D
Synchrirus	–	D	D2	D2	–	D	–	D1a	D2	D	–	D	D	–	–	D	D	D	D	D
Gymnocanthus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Ascelichthys	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	D	D	D	D	D	D
Taurocottus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Trichocottus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Myoxocephalus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Microcottus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Porocottus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Argyrocottus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Enophrys	–	D	D2	D2	–	D	D2	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Taurulus	–	D	D2	D2	–	D	D2	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Artediellus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Artediellichthys	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Cottiusculus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Zesticelus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Alcichthys	D1a	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Bero	D1a	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Ocynectes	D1a	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Furcina	D1a	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Pseudoblennius	D1a	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Vellitor	D1a	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	D	D	D	D	D
Hemitripterus v.	D2a	D	D1	D1	D	D	–	D1b	–	D	–	D	D	–	–	D	D	D	D	D
Hemitripterus b.	–	D	D1	D1	D	D	–	D1b	–	–	–	D	D	–	–	D	D	D	D	D
Blepsias	–	D	D2	D1	D	D	–	D1b	–	D	–	D	D	–	–	D	D	D	D	D
Nautichthys	–	D	D1	D1	–	D	D2	D1b	–	D	–	D	D	–	–	D	D	D	D	D
Agonomalus	–	D	D2	D2	D	D	–	D1d	D2	D	D	D	D	–	–	D	D	D	D	D
Podothecus	D1b	D	D2	D2	D	D	–	D1d	D2	D	D	D	D	D	–	D	D	D	D	D
Tilesina	D2b	D	D2	D2	D	D	–	D1d	D2	D	D	D	D	D	–	D	D	D	D	D
Marukawichthys	D1a	–	D2	D2	–	–	–	–	–	D	–	–	D	–	–	D	D	D	D	D
Ereunias	D1a	–	D2	D2	–	D	–	–	–	D	–	–	D	–	–	–	D	D	D	D
Dasycottus	–	D	D2	D2	–	D	–	D1a	–	D	–	D	D	–	–	–	D	D	D	D
Eurymen	–	D	D2	D2	–	D	D1	D1a	–	D	–	D	D	–	D	–	D	D	D	D
Cottunculus	–	D	D2	D2	–	D	D2	D1a	–	D	–	D	D	–	–	–	D	D	D	D
Ebinania	–	D	D2	D2	–	D	D2	D1a	–	–	–	D	D	–	–	–	D	D	D	D
Neophrynichthys	–	D	D2	D2	–	D	D2	D1a	–	–	–	D	D	–	–	–	D	D	D	D
Malacocottus	–	D	D2	D2	–	D	D2	D1a	–	D	–	D	D	–	–	–	D	D	D	D
Psychrolutes	–	D	D2	D2	–	D	D2	D1a	–	–	–	D	D	–	D	–	D	D	D	D
Rhamphocottus	–	–	D1	D2	D	D	D2	D1c	–	D	–	–	D	–	–	D	D	D	D	D

Appendix 2–1 (...continued).

															Noninformative →				
	14	18	25	35	36	37	38	39	40	48	51	54	56	57	9	26	29	30	47	50
Jordania	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Scorpaenichthys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	D	–	–	–	–
Hemilepidotus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Leptocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Trachidermus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Cottus kazika	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Cottus pollux	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Artedius	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Chitonotus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Orthonotpias	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Triglops	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Radulinus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Asemichthys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Astrocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Icelus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Ricuzenius	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Stelgistrum	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Thyriscus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Stlengis	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Icelinus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Oligocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Clinocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Leiocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Synchrirus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	D	–	–	–
Gymnocanthus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Ascelichthys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Taurocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Trichocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Myoxocephalus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Microcottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Porocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Argyrocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Enophrys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Taurulus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Artediellus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Artediellichthys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Cottiusculus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Zesticelus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Alcichthys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Bero	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Ocynectes	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Furcina	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Pseudoblennius	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Vellitor	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Hemitripterus v.	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	D
Hemitripterus b.	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Blepsias	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Nautichthys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Agonomalus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Podothecus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Tilesina	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Marukawichthys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Ereunias	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Dasycottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Eurymen	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Cottunculus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Ebinania	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Neophrynichthys	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Malacocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Psychrolutes	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	–	–	–	–
Rhamphocottus	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	–	–	D	–	–

3. PHYLOGENY OF COTTOID FISHES

ABSTRACT

Two contemporary hypotheses of the phylogeny of Cottoidei are considered: i) that Cottidae are not monophyletic exclusive of various specialized cottoid families that were derived from it, and ii) that Cottidae are monophyletic exclusive of other specialized families that are basal to it within Cottoidei. Sixty-eight morphological characters with 111 steps of evolution were cladistically examined in 34 cottoid genera with the goal of determining the most parsimonious tree topology. The resulting tree shows that some species of Cottidae (*Scorpaenichthys marmoratus, Jordania zonope,* and *Hemilepidotus hemilepidotus*) are basal to a crown clade of all remaining Cottoidei, including other Cottidae and the specialized families Agonidae, Comephoridae, Cyclopteridae, Hemitripteridae, and Psychrolutidae. Characters mapped onto this tree find a monophyletic Cottoidei supported with at least 14 characters of which 9 are consistently present with respect to their sister taxon, Hexagrammidae. The crown clade is well supported with at least 13 characters leading up to it from the cottoid root. Strong support is found for the specialized families and moderate support is found for a number of other relations. The hemitripterid examined, *Blepsias cirrhosus,* was found to be sister to Agonidae, and Rhamphocottidae was found to be sister to this clade. A sister taxon, *Artediellus,* is possibly found for Psychrolutidae. The historical basis of our current classification is discussed and changes are proposed, including: the dissolution of Cottoidea and Cyclopteroidea; acknowledgment that Cottidae are a problem taxon; placement of Liparidae into Cyclopteridae; and placement of Rhamphocottidae and Hemitripteridae into Agonidae.

INTRODUCTION

Cottoidei, a suborder of Scorpaeniformes, are a diverse taxon with 671 valid species (Eschmeyer, 2002) currently placed in 11 families (Nelson, 1994). Yabe (1985) divided this suborder into two superfamilies, Cottoidea and Cyclopteroidea, both of which he presumed monophyletic and sister to each other. But, Yabe's reasons for doing so were not made clear and seemingly based on conjecture (his pages 122 and 125). Washington *et al.* (1984) also thought Cyclopteridae to be sister to the remaining Cottoidei, and supported this with three characters. Although that work was not cited by Yabe, it was possibly the reasoning behind his two superfamilies of Cottoidei. Previous authors have either separated Cyclopteridae from Cottoidei (*e.g.*, Jordan, 1923; Matsubara, 1955) or placed Cyclopteridae within Cottoidei as one of their specialized families (*e.g.*, Regan, 1913; Berg, 1940; Taranets, 1941). Washington *et al.*'s basal placement of Cyclopteridae follows the tradition of giving this family special distinction from other Cottoidei, but has not been independently tested. Taranets (1941) followed the other tradition of not giving Cyclopteridae special distinction and even suggested a "morphological line" of "[his] Myoxocephalinae and Psychrolutidae to Liparidae and Cyclopteridae." On the remaining cottoids, the two recent contemporary papers (Washington *et al.*; Yabe) suggested very different possible phylogenies: one with a basal paraphyletic Cottidae and the other with a crown monophyletic Cottidae. Washington *et al.* thought *Rhamphocottus richardsoni* to be the most basal, *Scorpaenichthys marmoratus* and *Hemilepidotus* species to be next most basal, and the remaining cottids and the specialized families Agonidae, what is currently Hemitripteridae, and Psychrolutidae to be a crown clade. Yabe thought that all specialized families are basal, and that his Cottidae (with the same composition as that of Taranets, 1941) are a monophyletic crown clade.

Clearly, the interrelations of the families of Cottoidei are poorly known, and often contradictory between authors. To address this, a rigorous phylogenetic treatment of Cottoidei is sought to: i) acquire novel and known morphological characters, explicitly define them, and set rigorous assumptions about their evolution; ii) do a truly cladistic analysis on these characters with parsimony as the goal, determine character polarity and character evolution based on the postulated tree; iii) acknowledge historical contributions and build on them; and iv) evaluate, and amend if necessary, the current classification within the context of the postulated phylogeny.

MATERIALS AND METHODS

Specimens and Taxa Examined

Valid species names are used following Eschmeyer *et al.* (2002). Institutional abbreviations follow Leviton *et al.* (1985). Data in parentheses include number of specimens available for this study, type of preparation, and standard length in mm when known. Preparations are whole, cleared and stained (cs), or cleared and counter-stained (ccs). Clearing and staining follows Taylor (1967) or Taylor and Van Dyke (1985).

Specimens examined include: *Ambophthalmos angustus* (Nelson 1977): NMNZ P.21416 (1, ccs); *Artediellus uncinatus* (Reinhardt 1835): UAMZ 5640 (8, 4 ccs, 35-45), UAMZ 5639 (13, whole); *Artedius lateralis* (Girard 1854): UAMZ 7909 (5, 3 ccs, 61-76); *Ascelichthys rhodorus* Jordan & Gilbert 1880: UAMZ 1969 (4, cs, 39-74), UAMZ 1970 (6, whole); *Bathyagonus alascanus* (Gilbert 1896): UAMZ 1985 (2, cs, 96-100); *Blepsias cirrhosus* (Pallas 1814): UAMZ 2352 (2, cs, 77-97), UAMZ 3190 (6, cs, 22-33); *Chitonotus pugetensis* (Steindachner 1876): UAMZ 1972 (2, cs, 91-112), UAMZ 7923 (12, whole); *Clinocottus globiceps* (Girard 1858): *Comephorus* *dybowskii* Korotneff 1904: UAMZ 2584 (4, ccs); UAMZ 7901 (4, ccs, 51-71); *Cottunculus thomsonii* (Günther 1882): BMNH 569-570 (2, whole, 130-145), UAMZ 4526 (1; ccs); *Cottus asper* Richardson 1836: UAMZ 2239 (3, cs, 52-59); *Dasycottus setiger* Bean 1890: UAMZ 3181 (1, cs), UAMZ 3196.1 (3, ccs, 73-79); *Ebinania brephocephala* (Jordan & Starks 1903): HUMZ 51823 (1, cs), HUMZ 52187 (1, cs); *Enophrys bison* (Girard 1854): UAMZ 2102 (4, cs, 69-115), UAMZ 2328.1 (1, ccs, 74); *Eumicrotremus orbis* (Günther 1861): UAMZ 2339 (1, ccs); *Eurymen gyrinus* Gilbert & Burke 1912: HUMZ 68060 (1, cs, 130); *Gymnocanthus galeatus* Bean 1881: UAMZ 4684 (1, ccs, 156); *Hemilepidotus hemilepidotus* (Tilesius 1811): UAMZ 1686 (7, 3 cs, 47-126); *Hexagrammos decagrammus* (Pallas 1810): UAMZ 7911 (4, ccs); *Icelinus borealis* Gilbert 1896: UAMZ 1977 (3, cs, 66-77); *Jordania zonope* Starks 1895: UAMZ 1058 (2, cs, 84 and other specimen damaged), UAMZ 1978 (2, whole); *Leiocottus hirundo* Girard 1856: SIO 59-307 (5, 3 ccs, 83-90); *Leptocottus armatus* Girard 1854: UAMZ 7910 (3, ccs, 73-91); *Liparis callyodon* (Pallas 1814): UAMZ 2109 (2, cs); *L. florae* (Jordan & Starks 1895): *L. tunicatus* Reinhardt 1837: UAMZ 6732 (3, ccs); *Malacocottus kincaidi* Gilbert & Thompson 1905: UAMZ 4497 (5, cs, 40-52); *Myoxocephalus polyacanthocephalus* (Pallas 1814): UAMZ 2106 (5, 2 cs), UAMZ 2328.2 (1, ccs; 61-84); *Neophrynichthys heterospilos* Jackson & Nelson 2000: NMNZ 26802 (2, ccs); *Oligocottus maculosus* Girard 1856: UAMZ 7899 (4, ccs, 40-64); *Ophiodon elongatus* Girard 1854: UAMZ 5140 (1, ccs, 184); *Orthonopias triacis* Starks & Mann 1911: UAMZ 7920 (4, ccs, 67-78); *Oxylebius pictus* Gill 1862: UAMZ 5137 (1, ccs, 77); *Psychrolutes paradoxus* Günther 1861: UAMZ 2778 (1, ccs), UAMZ 4618 (2, cs, 30-36); *Radulinus asprellus* Gilbert 1890: UAMZ 3196.7 (22, 4 ccs, 90-99), UAMZ 3939 (1, whole); *Rhamphocottus richardsoni* Günther 1874: UAMZ 3280 (1, cs), UAMZ 7885 (1, whole); *Scorpaenichthys marmoratus* Girard 1854: UAMZ 7906 (2, whole), UAMZ 7915 (4, ccs, 61-80); *Synchirus gilli* Bean 1890: UAMZ 7927 (14, 6 ccs, 34-39); *Xeneretmus latifrons* (Gilbert 1890): UAMZ 3186 (10, cs).

Additional specimens include: *Agonopsis vulsa* (Jordan & Gilbert 1880): UAMZ 1986 (2, cs, 93-109); *Anoplagonus inermis* (Günther 1860): UAMZ 797 (1, whole), UAMZ 2416 (1, cs, 87); *Artedius fenestralis* Jordan & Gilbert 1883: UAMZ 7908 (3, ccs, 67-87); *Bathyagonus infraspinatus* (Gilbert 1904): UAMZ 2774 (1, cs, 95 mm); *Bothragonus swani* (Steindachner 1876): UAMZ 3179 (1, whole); *Clinocottus acuticeps* (Gilbert 1896): UAMZ 2099 (3, cs, 36-44); *Cottus cognatus* Richardson 1836: UAMZ 447 (3, ccs); *Cottunculus microps* Collett 1875: NMC 65-0308, 85-0252, 85-0289, 85-0342 (1 of each lot, whole); *C. sadko* Essipov 1937: NMC 74-0275 (1, whole); *Cyclopterus lumpus* Linnaeus 1758: UAMZ 1391 (1, whole); *Gymnocanthus tricuspis* (Reinhardt 1831): UAMZ 5641 (1, whole), UAMZ 5642 (1, whole); *Hemitripterus americanus* (Gmelin 1789): UAMZ 3653 (1, whole);UAMZ 2110 (2, cs); *Myoxocephalus quadricornis* (Linnaeus 1758): UAMZ 4645 (3, 2 ccs); *Nautichthys oculofasciatus* (Girard 1858): UAMZ 1266 (1, ccs); *Odontopyxis trispinosa* Lockington 1880: UAMZ 4012 (1, whole); *Pallasina barbata* (Steindachner 1876): *Podothecus acipenserinus* (Tilesius 1813): UAMZ 1474 (2, cs); UAMZ 1678 (1, cs, 116); *Psychrolutes sigalutes* (Jordan & Starks 1895): UAMZ 1976 (2, cs).

The in-group comprised 34 genera representing a diversity of Cottoidei. Three genera of the generally accepted sister group of Cottoidei, the Hexagrammidae (*e.g.*, Quast, 1965; Hallacher, 1974; Shinohara, 1994), were selected as the out-group for polarizing characters. Here, all specimens examined are referred to by their species name, except the three anatomically very similar *Liparis* species that are referred to as so. The higher taxa, Hexagrammidae, Agonidae, Cyclopteridae (including Liparidae), and Psychrolutidae, are diverse, well defined, and putatively monophyletic families (although some authors, *e.g.*, Quast, 1965 and Shinohara, 1994, questioned the monophyly of Hexagrammidae without Cottoidei). They are a priori referred to here, although not a priori presumed monophyletic. The families Hemitripteridae (Yabe, 1985, with the genera *Blepsias*, *Hemitripterus*, and *Nautichthys*) and Rhamphocottidae (monotypic with *Rhamphocottus richardsoni*) are not referred to here, because of the nominal status of the former and monotypy of the latter.

Characters Examined

Sixty-eight morphological characters were examined and are outlined numerically below. Characters 1 through 21 are of the lateralis system, osteology associated with it, and of the anatomically close scales; characters 22 through 34 are of non-lateralis related cranial osteology; characters 35 through 42 are of the appendicular skeleton; characters 43 through 53 are of the postcranial axial skeleton; and characters 54 through 60 are of general external anatomy. Eight additional characters derived from the literature on myology are enumerated as characters 61 through 68. Additional characters considered in previous studies but not considered here (and thus not enumerated) follow with discussion on reasons for their exclusion.

The state numbers are generally applied in order of more in number or development to less, present to absent, separate to fused, and in a few cases usual to unusual. Although evolution often involves reduction and simplification, and this coding scheme might largely result in primitive characters being coded as 0, a priori coding of primitive states as 0 and derived states with higher numbers is not followed here. Character polarity is determined at the time of analysis based on out-group rooting. See Appendix 3–1 for a data matrix summarizing character states observed in taxa examined. Character evolution is considered unordered and reversible unless stated otherwise.

1-19. Cranial and postcranial lateralis system and scales.— This anatomical system is given special treatment here because of its extensive development amongst and variety within Cottoidei. Cranial anatomy is outlined in simplified form in Figure

3–1 and osteology of specimens examined here are diagrammed in Figures 3–2a through 3–2g. Cranial characters of particular interest are outlined in Figures 3–3 through 3–7. Postcranial lateral line ossifications and scales of specimens examined are diagrammed in Figures 3–8a through 3–8r and a simplified outline of scale types, distribution, and subsequent characters are given in Figures 3–9 through 3–11.

1. Nasal spine.— Present as a posteriorly oriented spine borne on the arch (state 0) or not developed (state 1). State 0 was observed in most species and state 1 in the hexagrammids *Hexagrammos decagrammus* and *Ophiodon elongatus,* and the cottoids *Artediellus uncinatus, Comephorus dybowskii, Cottus asper, Leptocottus armatus,* Cyclopteridae, and Psychrolutidae. In most species that possess such a spine, it is well-developed and heavy, except in *Ascelichthys rhodorus* where it is not readily seen externally, but is present, elongate, slight in build, and irregular in form.

2, 3. Frontal spines.— The supraorbital canal rims the orbit on the frontal and occasionally has spines associated with it. Two types of frontal spines are observed and presumed not homologous to one another, thus two presence/absence characters are used (with states 0/1 respectively). The first type of spine (hence canal spine, character 2) is usually irregular in form, occasionally bifurcate or in a small cluster, and is borne atop the supraorbital canal or one of its secondary tubules and thus is well in from the rim of the orbit. The second type of spine (hence orbital spine, character 3) is regular in form, not bifurcate or multiple, and is borne on the rim of the orbit lateral to the supraorbital canal (Figure 3–3). In *Chitonotus pugetensis, Icelinus borealis,* and *Myoxocephalus polyacanthocephalus,* several irregular canal spines (character 2, state 0) were observed about two-thirds posteriorly along the supraorbital canal and its secondary tubules. In the psychrolutids *Cottunculus thomsonii* and *Dasycottus setiger,* single large canal spines (character 2, state 0) were observed on most or all arches associated with the supraorbital canal. In *Blepsias*

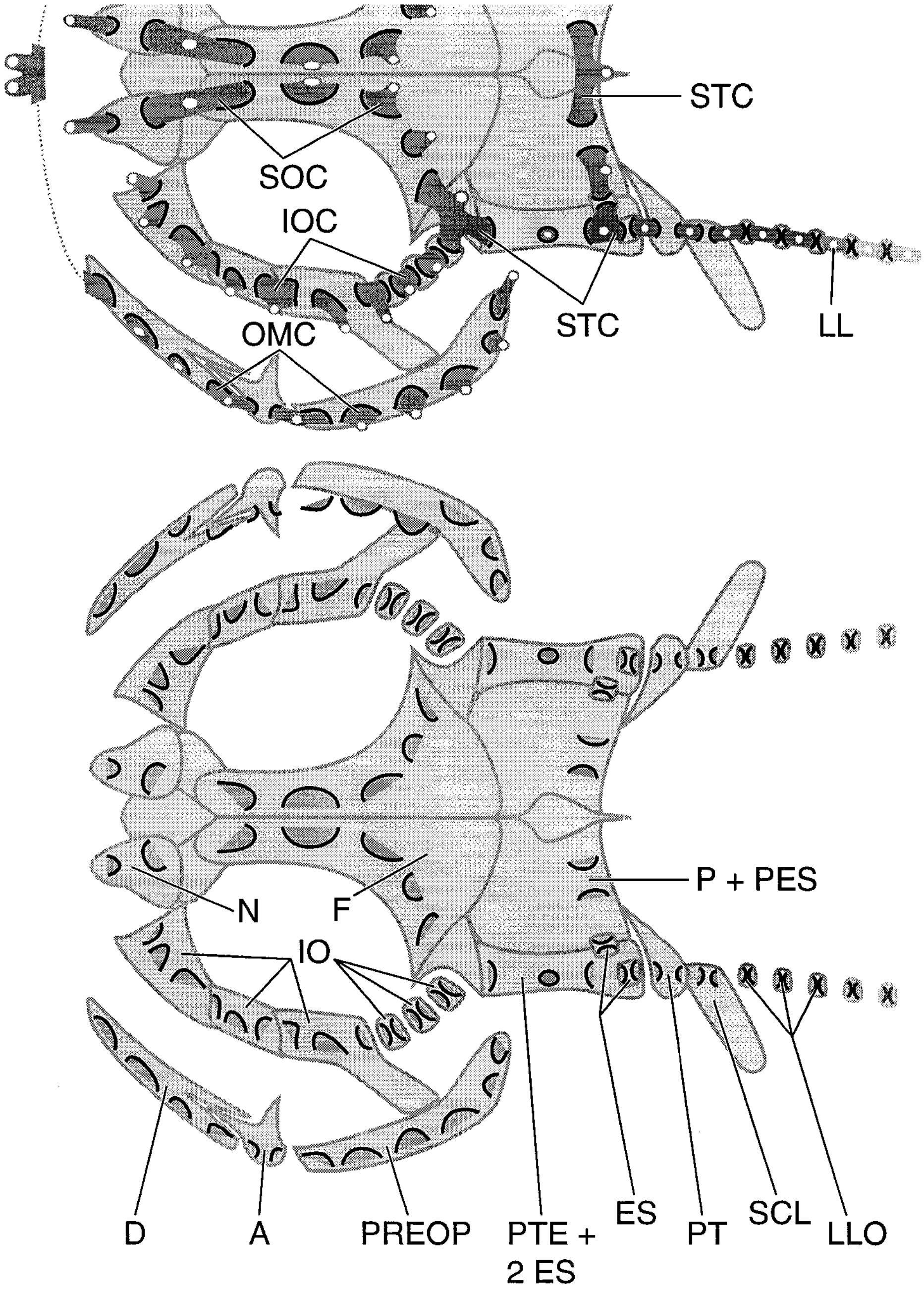


Figure 3–1. Map of the lateralis system (top) and associated osteology (bottom) of a typical cottoid. Dorsal aspect, anterior to the left. IOC, infraorbital canal; LL, lateral line; OMC, operculomandibular canal; SOC, supraorbital canal; STC, supratemporal canal. A, angular; D, dentary; ES, extrascapular; F, frontal; IO, infraorbitals (1-6); LLO, lateral line ossification; N, nasal; P, parietal; PES, parietal extrascapular; PREOP, preopercle; PT, posttemporal; PTE, pterotic; SCL, supracleithrum.

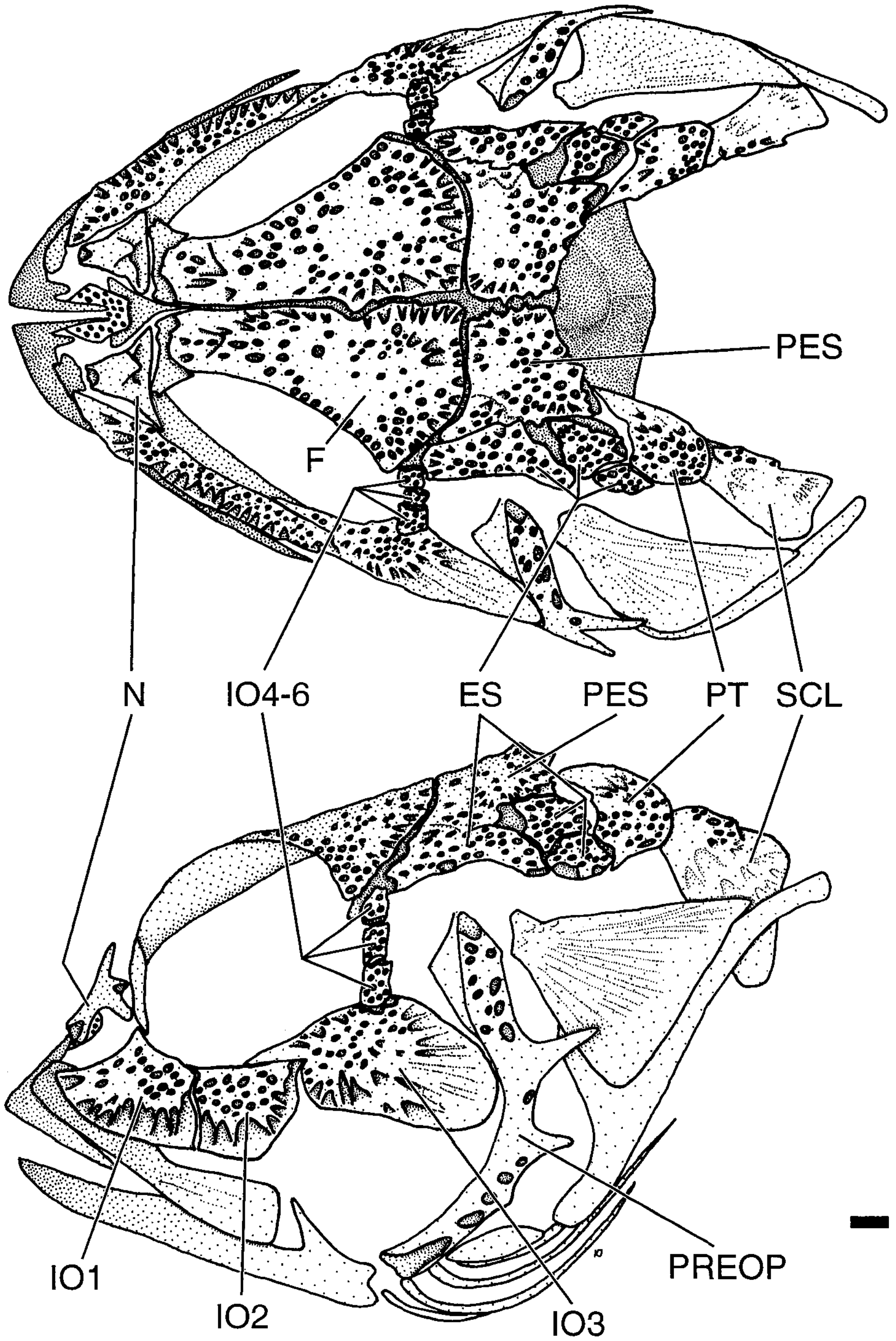


Figure 3–2a. Superficial cranium of *Scorpaenichthys marmoratus*. Top diagram in dorsal aspect, bottom in lateral aspect, scale bar indicates 1 mm. ES, extrascapular; F, frontal; IO1-6, infraorbitals; N, nasal; PES, parietal extrascapular; PREOP, preopercular; PT, posttemporal; SCL, supracleithrum.

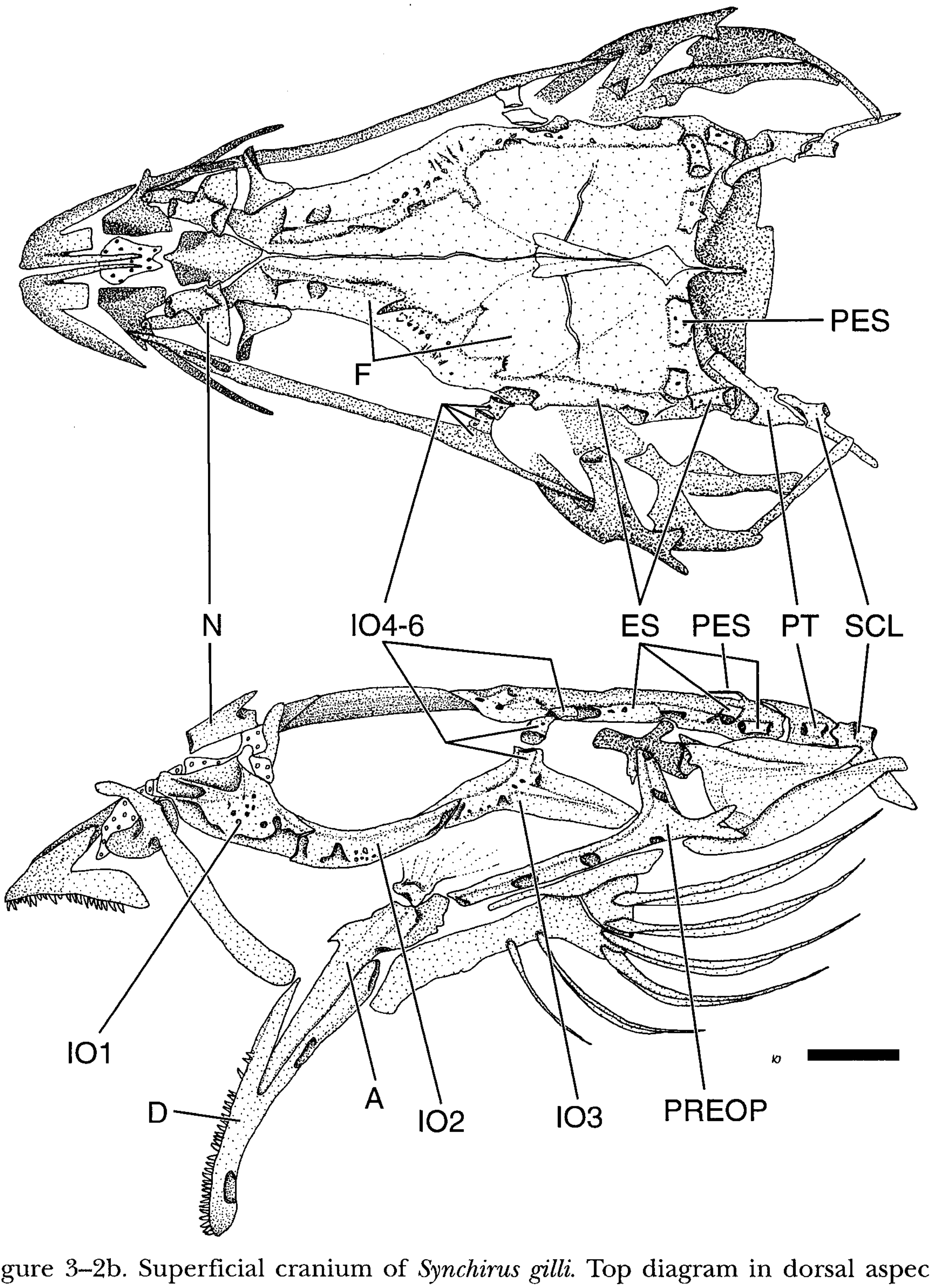


Figure 3–2b. Superficial cranium of *Synchirus gilli.* Top diagram in dorsal aspect, bottom in lateral aspect, scale bar indicates 1 mm. See Figure 3–2a for legend.

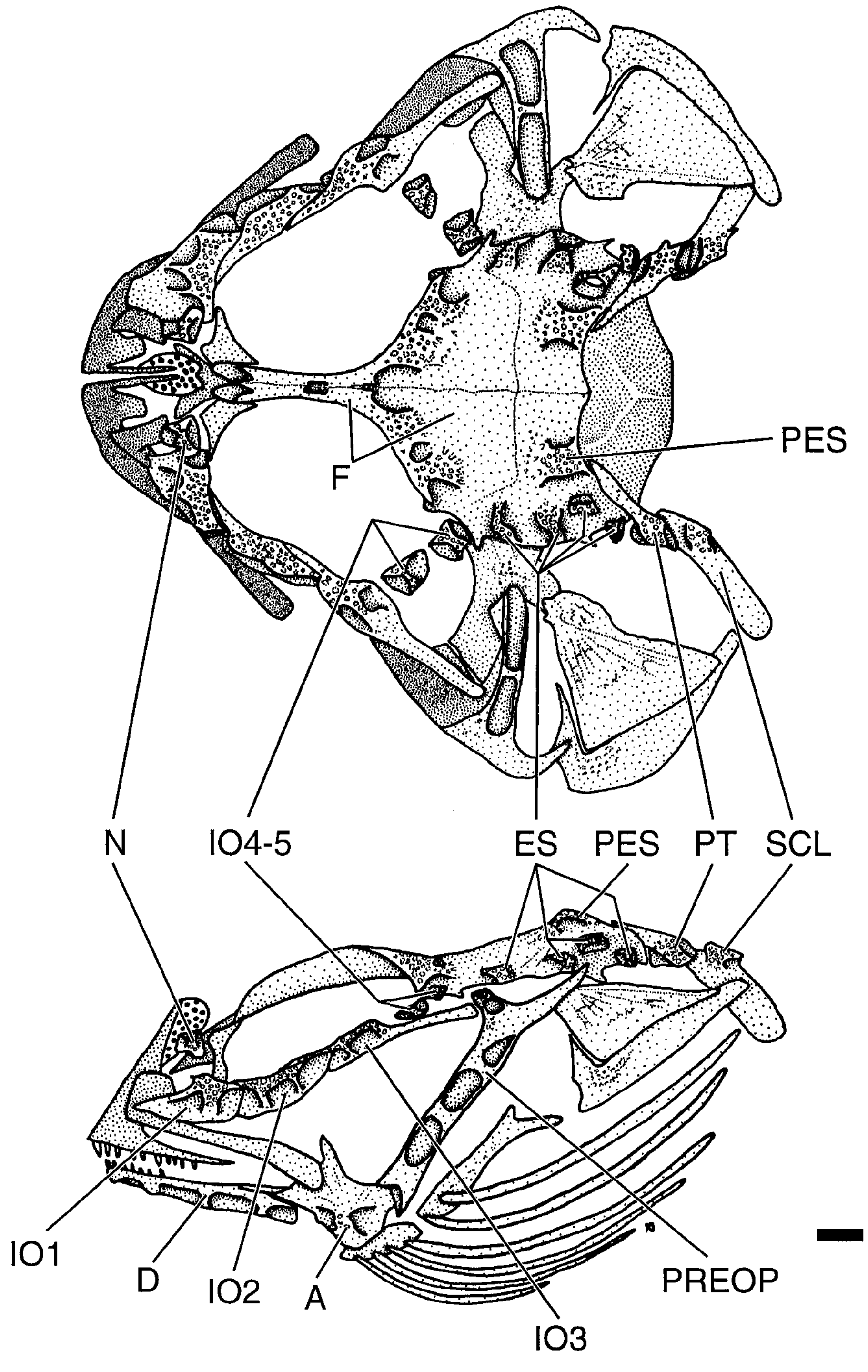


Figure 3–2c. Superficial cranium of *Artediellus uncinatus*. Top diagram in dorsal aspect, bottom in lateral aspect, scale bar indicates 1 mm. See Figure 3–2a for legend.

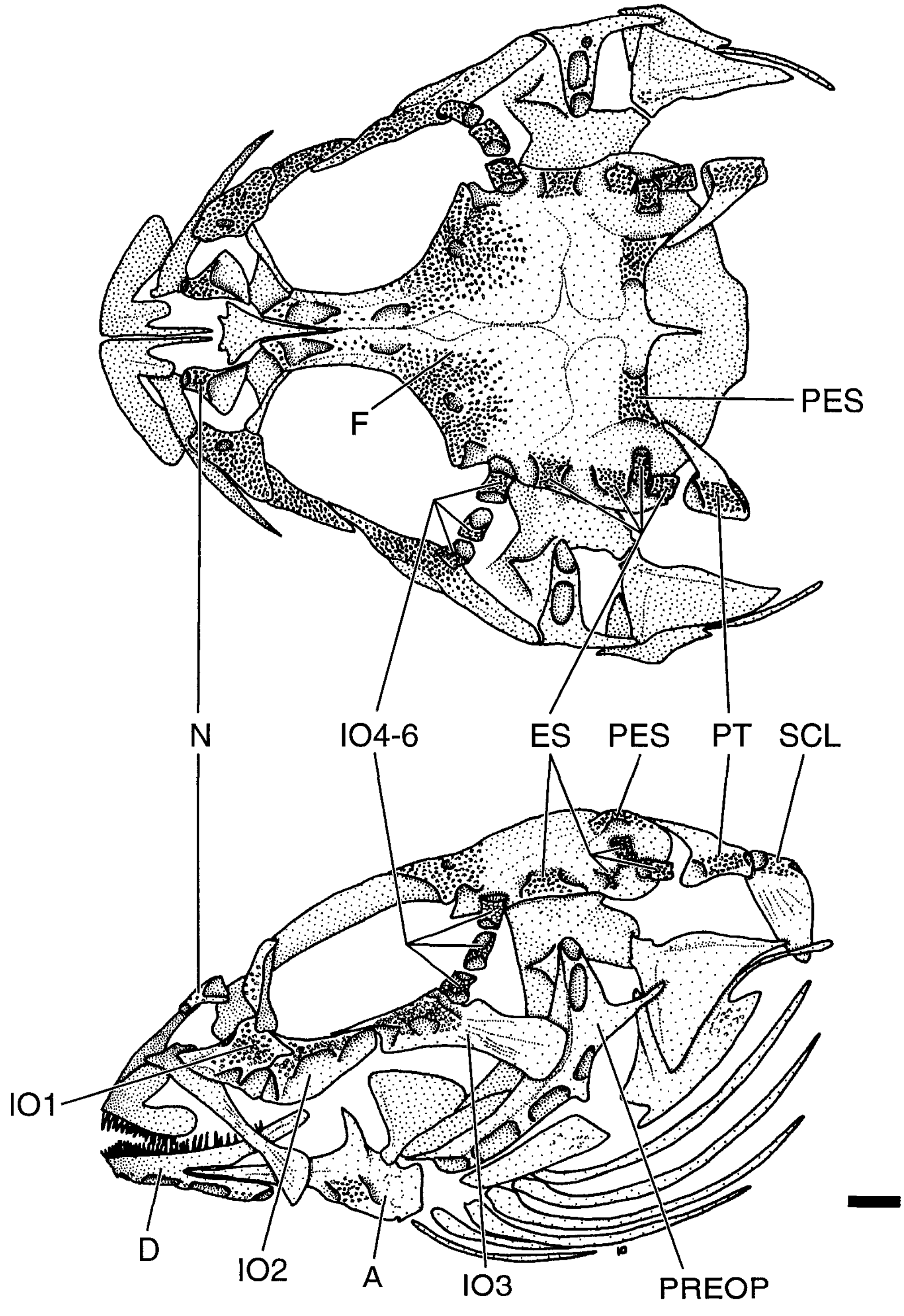


Figure 3–2d. Superficial cranium of *Cottus asper.* Top diagram in dorsal aspect, bottom in lateral aspect, scale bar indicates 1 mm. See Figure 3–2a for legend.

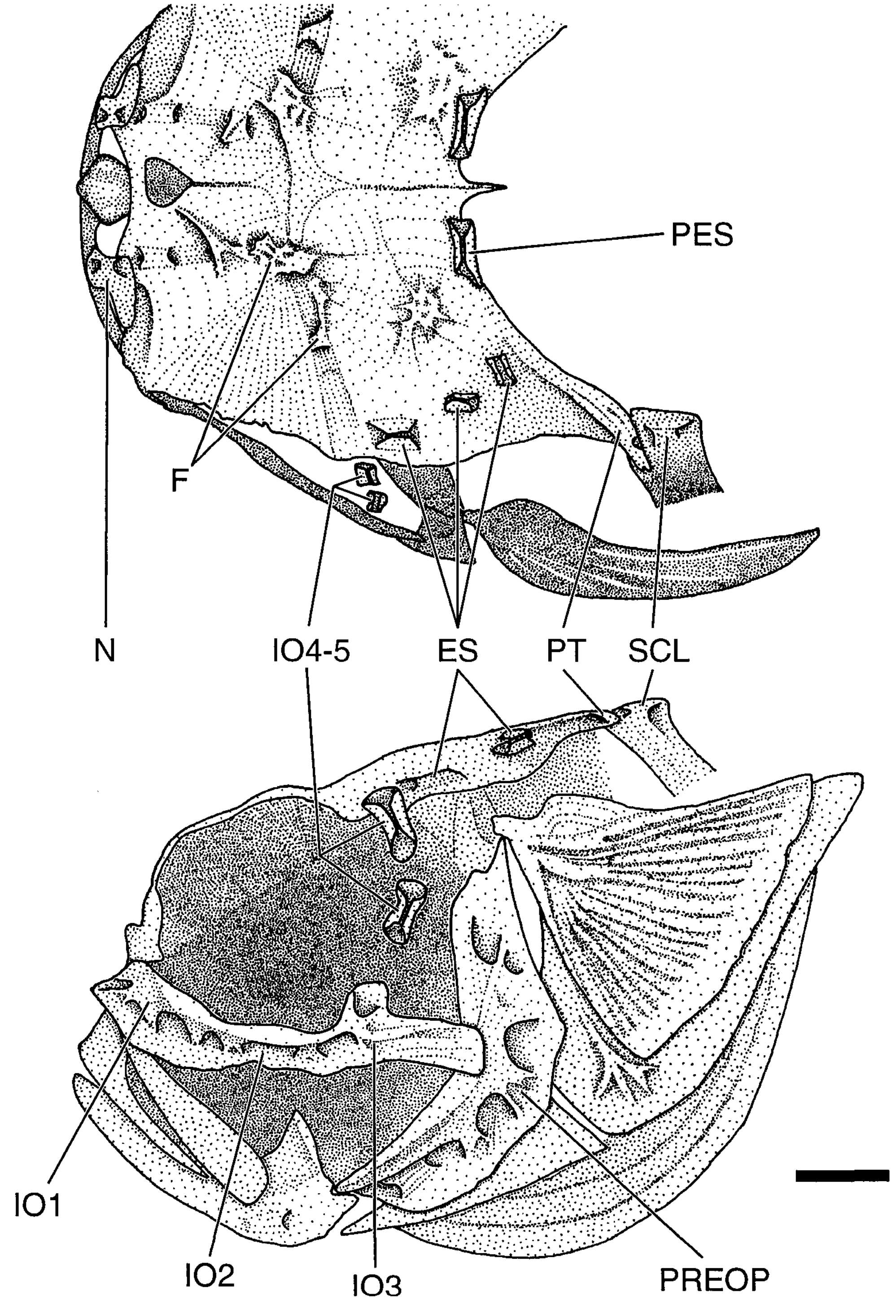


Figure 3–2e. Superficial cranium of *Neophrynichthys heterospilos*. Top diagram in dorsal aspect, bottom in lateral aspect, scale bar indicates 10 mm. See Figure 3–2a for legend.

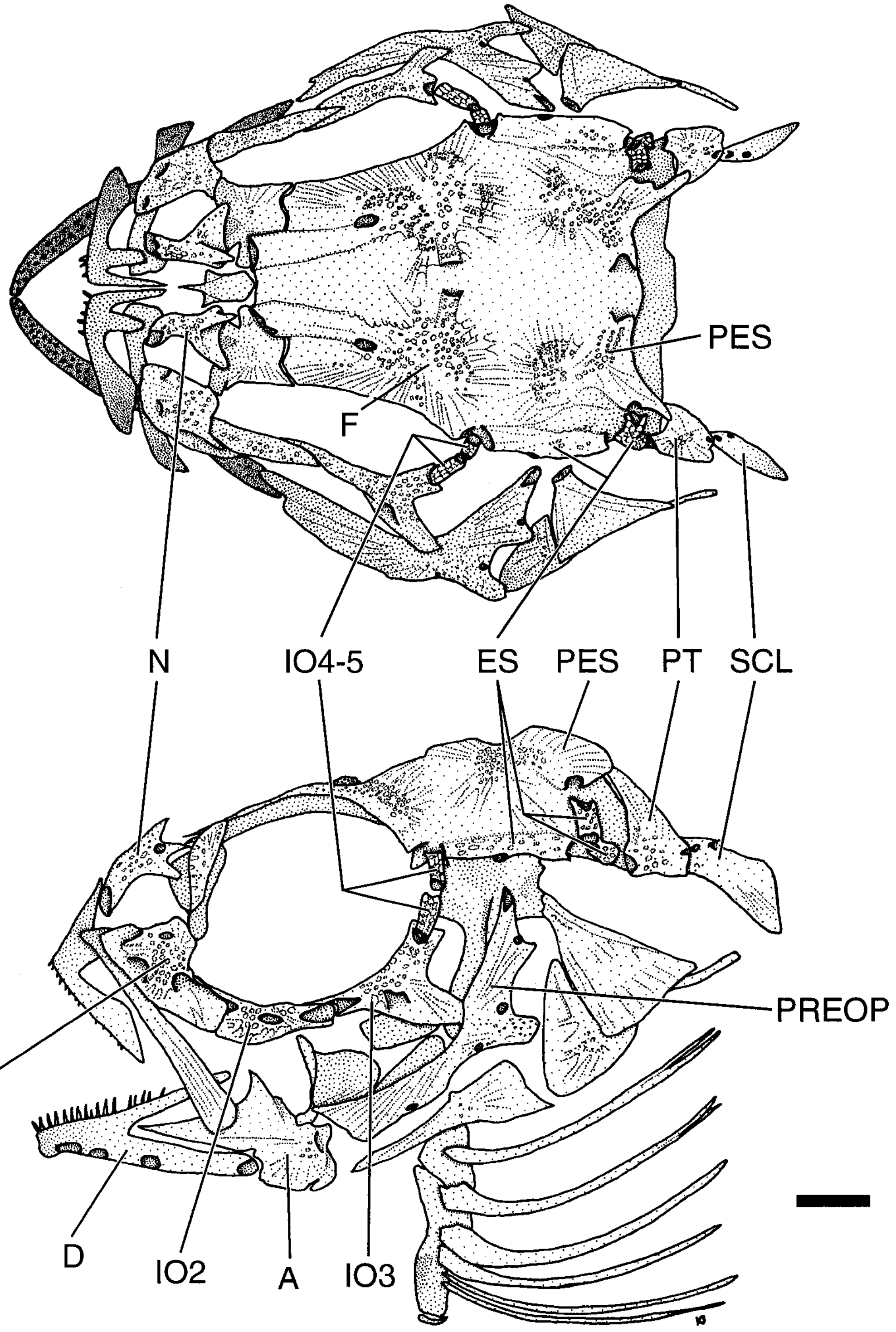


Figure 3–2f. Superficial cranium of *Blepsias cirrhosus*. Top diagram in dorsal aspect, bottom in lateral aspect, scale bar indicates 1 mm. See Figure 3–2a for legend.

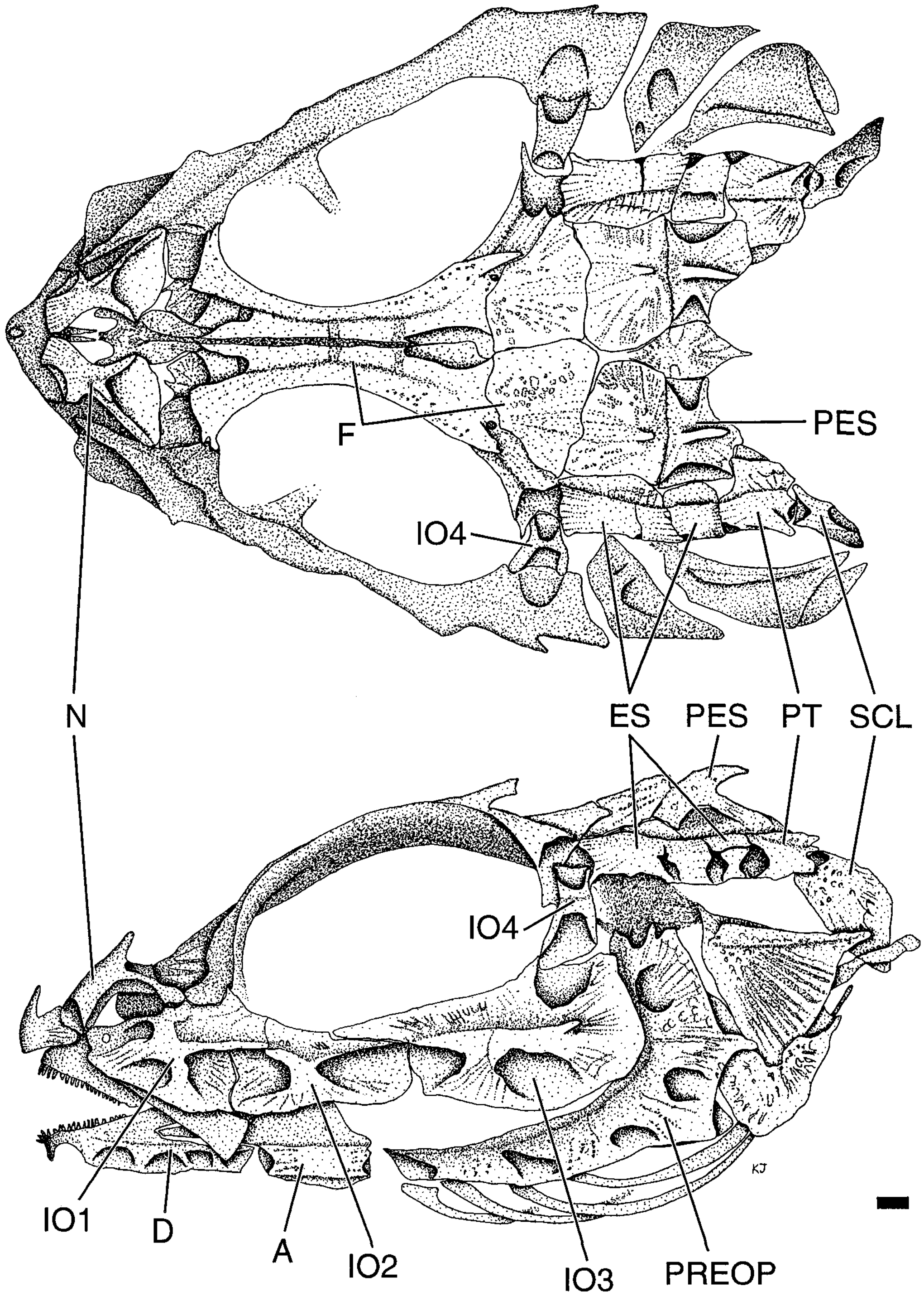
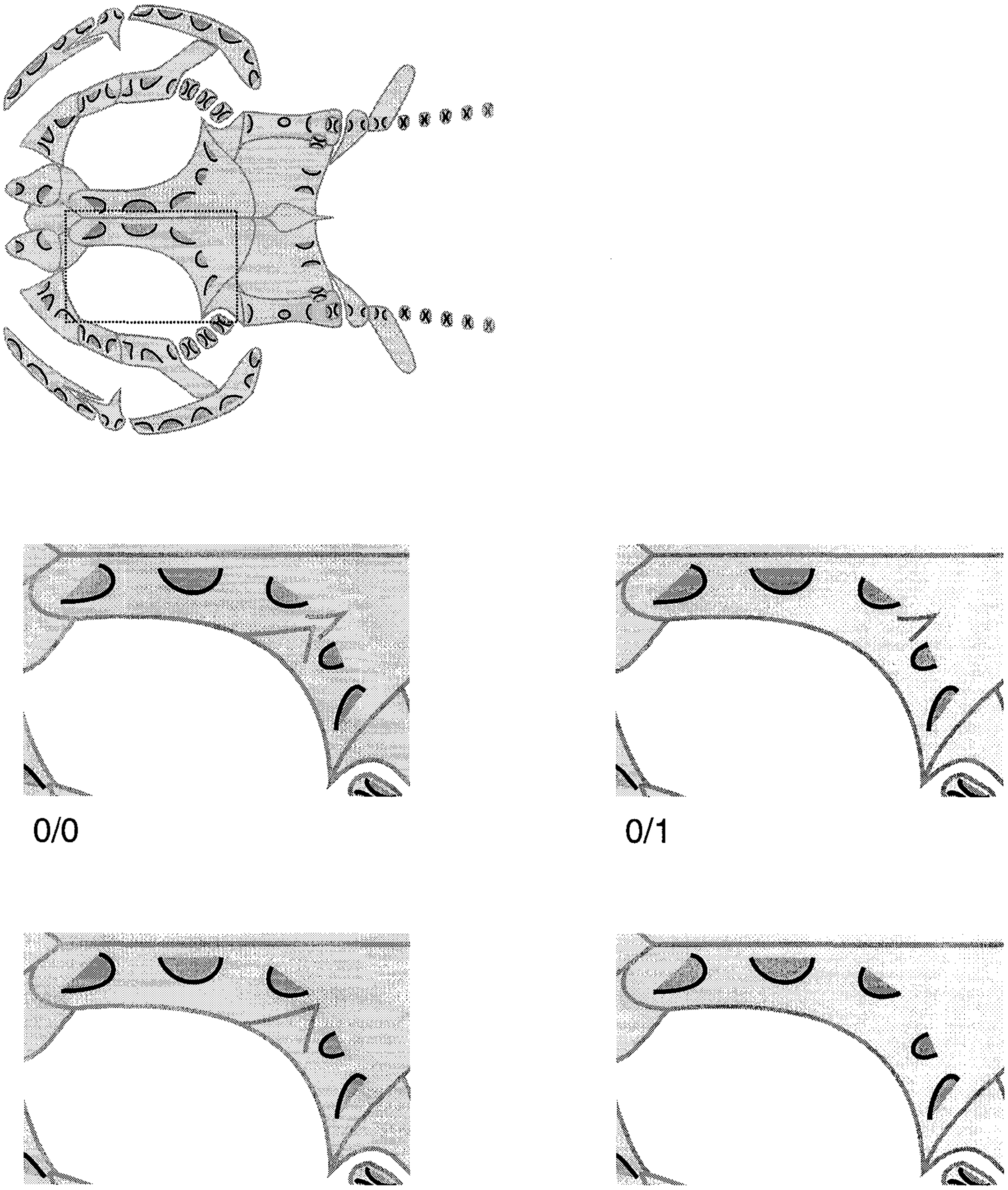


Figure 3–2g. Superficial cranium of *Xeneretmus latifrons*. Top diagram in dorsal aspect, bottom in lateral aspect, scale bar indicates 1 mm. See Figure 3–2a for legend.



0/0

0/1

1/0

1/1

Figure 3–3. Characters and states observed with frontal spines. State 0/0, both canal and orbital spines present; 0/1, orbital spine absent; 1/0, canal spine absent; 1/1, no spines present.

cirrhosus (particularly evident in large specimens), *Rhamphocottus richardsoni,* and Agonidae, a well-developed orbital spine (character 3, state 0) was observed on the rim of the orbit lateral to the supraorbital canal. Both types of spines were observed in *Gymnocanthus galeatus* with the orbital spine being considerably different in form from the canal spine suggesting that the two types are not homologous. Spines were not observed (characters 2 and 3, state 1) in Hexagrammidae and all other Cottoidei.

4. Orbital pores.— Two lateralis sensory canals circle the orbit, one dorsally by the supraorbital canal borne upon the frontal and the other ventrally by the infraorbital canal borne upon the infraorbitals. There are three general conditions of these two canals: with pores exiting from the canals laterally from the supraorbital and dorsally from the infraorbital canals to the orbit (state 0); with pores not exiting to the orbit, canals enlarged and largely exposed, and bony covering reduced to arches (state 1); or with pores not exiting to the orbit, canals reduced (particularly the supraorbital) and largely encased in bone (state 2) (Figure 3–4). State 0 was observed in Hexagrammidae and most Cottoidei; state 1 in *Comephorus dybowskii, Cottus asper, Leptocottus armatus,* Cyclopteridae, and Psychrolutidae; and state 2 in *Blepsias cirrhosus, Rhamphocottus richardsoni,* and Agonidae. In *Artediellus uncinatus* and *Ascelichthys rhodorus,* the supraorbital canal is largely exposed, but typically has one or more pores opening to the orbit as does the infraorbital canal in *A. rhodorus.*

5. Infraorbital number.— The infraorbital series forms the ventral and posterior margin of the orbit. The first three in the series includes the lachrymal and are plate-like bones forming a suborbital bar with a stay arising from the third infraorbital extending to the preopercle (suborbital stay). The additional infraorbitals are simpler tubular bones and vary in number from three to one. The total number of infraorbitals is coded as six (state 0), five (state 1), and four (state 2).

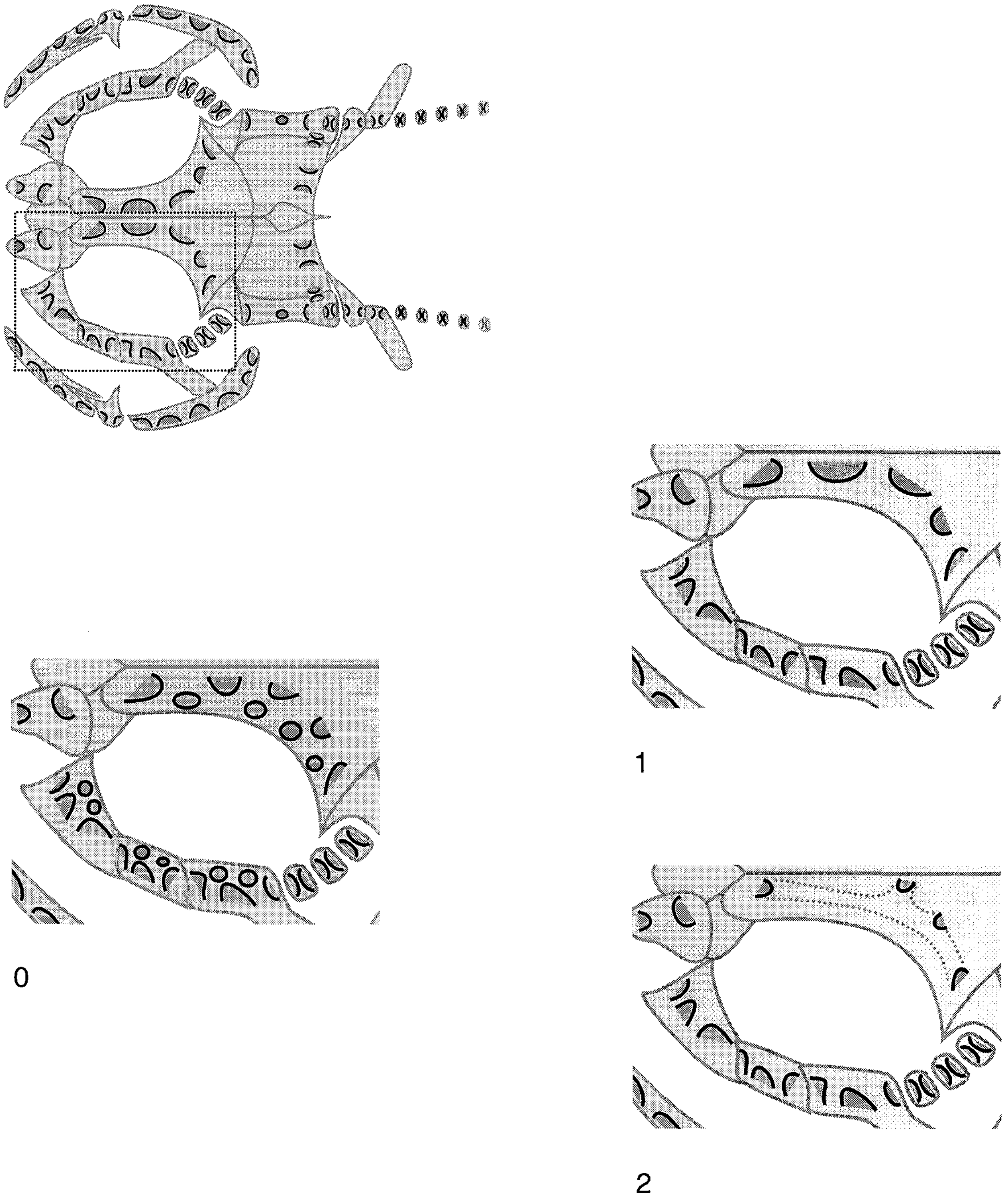


Figure 3–4. Orbital pores. State 0, pores present on the lateral side of supraorbital canal and dorsal side of infraorbital canal, opening on the orbit; 1, enlarged pores present along medial side of supraorbital canal and ventral side of infraorbital canal only, pores not opening on orbit; 2, supraorbital canal pores much reduced, infraorbital canal pores opening ventrally only.

State 0 was observed in Hexagrammidae and most Cottoidei; state 1 in *Artediellus uncinatus, Blepsias cirrhosus, Comephorus dybowskii, Enophrys bison, Myoxocephalus polyacanthocephalus, Radulinus asprellus, Rhamphocottus richardsoni,* and Psychrolutidae excepting *Cottunculus thomsonii*; and state 2 in Cyclopteridae and Agonidae. The psychrolutid *Cottunculus thomsonii* has four infraorbitals, but it is doubtful that this condition is homologous with state 2 because the infraorbital series in Cyclopteridae and Agonidae completely encircle the ventral and posterior margin of the orbit while in *C. thomsonii* it appears as though one infraorbital is simply missing (this is supported by one congener, *C. nudus,* that has the missing infraorbital; Nelson, 1989); and is thus coded as unique (state 3). The evolution of this character is considered ordered from state 0 to 1 to either 2 or 3 (step matrix shown in Table 3–1). Yabe(1985, character 1) considered this character, but noted *Synchirus gilli* as having five infraorbitals. But, amongst the six specimens available, most were observed with six infraorbitals and a few had five due to fusion of the fourth and fifth as evidenced by varying degrees of fusion (fused in the specimen shown in Figure 3–2b).

6. *Infraorbitals 1-3 pores.*— The three suborbital infraorbitals each bear at least one pore for a sensory tubule to exit, as well as tubules exiting between bony arches on adjacent bones (state 0); the second infraorbital lacks a pore and has a single arch (state 1); or the second infraorbital is open with the infraorbital canal occupying a groove (state 2). State 0 was observed in Hexagrammidae and most Cottoidei,

Table 3–1. Step matrix for the infraorbital number character (5) with *from* on the vertical and *to* on the horizontal axes.

	0	**1**	**2**	**3**
0	.	1	2	2
1	1	.	1	1
2	2	1	.	1
3	2	1	1	.

state 1 in *Rhamphocottus richardsoni* and Agonidae, and state 2 in Cyclopteridae. A pore on the second infraorbital of *Blepsias cirrhosus* is present but reduced in size, and is possibly an intermediate between states 0 and 1. The condition of the first three infraorbitals in Cyclopteridae is not easily compared with other Cottoidei examined: the first infraorbital (lachrymal) bears two arches and two pores, the second infraorbital does not enclose the canal although a sensory tubule does arise at that location, and the third infraorbital bears a single arch and a single pore.

7. *Infraorbitals 4-6 pores.*— The posterior tubular infraorbitals (postorbitals) carry the infraorbital canal from which sensory tubules exit between elements. Additionally, sensory tubules may pass through pores on these bones (state 0) or not (state 1). State 0 was observed in Hexagrammidae, and the cottoids *Ascelichthys rhodorus, Chitonotus pugetensis, Enophrys bison, Gymnocanthus galeatus, Hemilepidotus hemilepidotus, Jordania zonope, Myoxocephalus polyacanthocephalus,* and *Scorpaenichthys marmoratus*; and state 1 in all other Cottoidei.

8. *Preopercle pores.*— The preopercle carries the posterior portion of the operculomandibular canal. The preopercle bears more than four pores (state 0), four pores between five arches (state 1), three pores between four arches (state 2), or two pores between three arches (Figure 3–5). The evolution of this character is assumed to be ordered. State 0 was observed in Hexagrammidae (six or more) and the cottoids *Jordania zonope* (five or six) and *Scorpaenichthys marmoratus* (six or more); state 1 in the majority of Cottoidei; state 2 in *Comephorus dybowskii*; and state 3 in Cyclopteridae. Although species with state 0 were observed with variability in pore count, species with the reduced states were remarkably conservative.

9. *Preopercular spines.*— The posterior margin of the preopercle is extruded into one or more spines (state 0) or is smooth and without spines (state 1). State 0 was observed in most Hexagrammidae and Cottoidei; and state 1 in the hexagrammid *Hexagrammos decagrammus* and in the cottoids *Comephorus dybowskii,* Cyclopteridae,

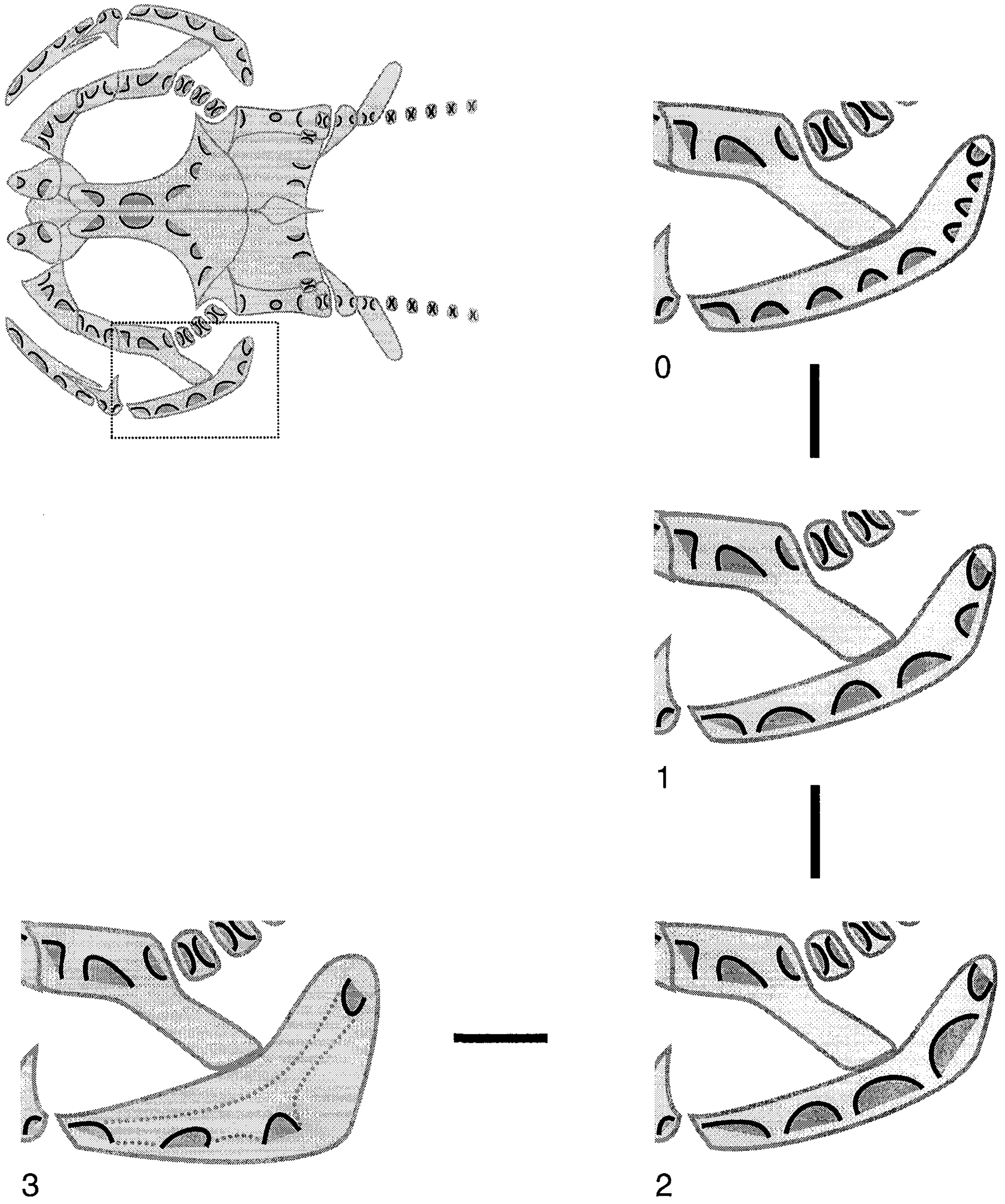
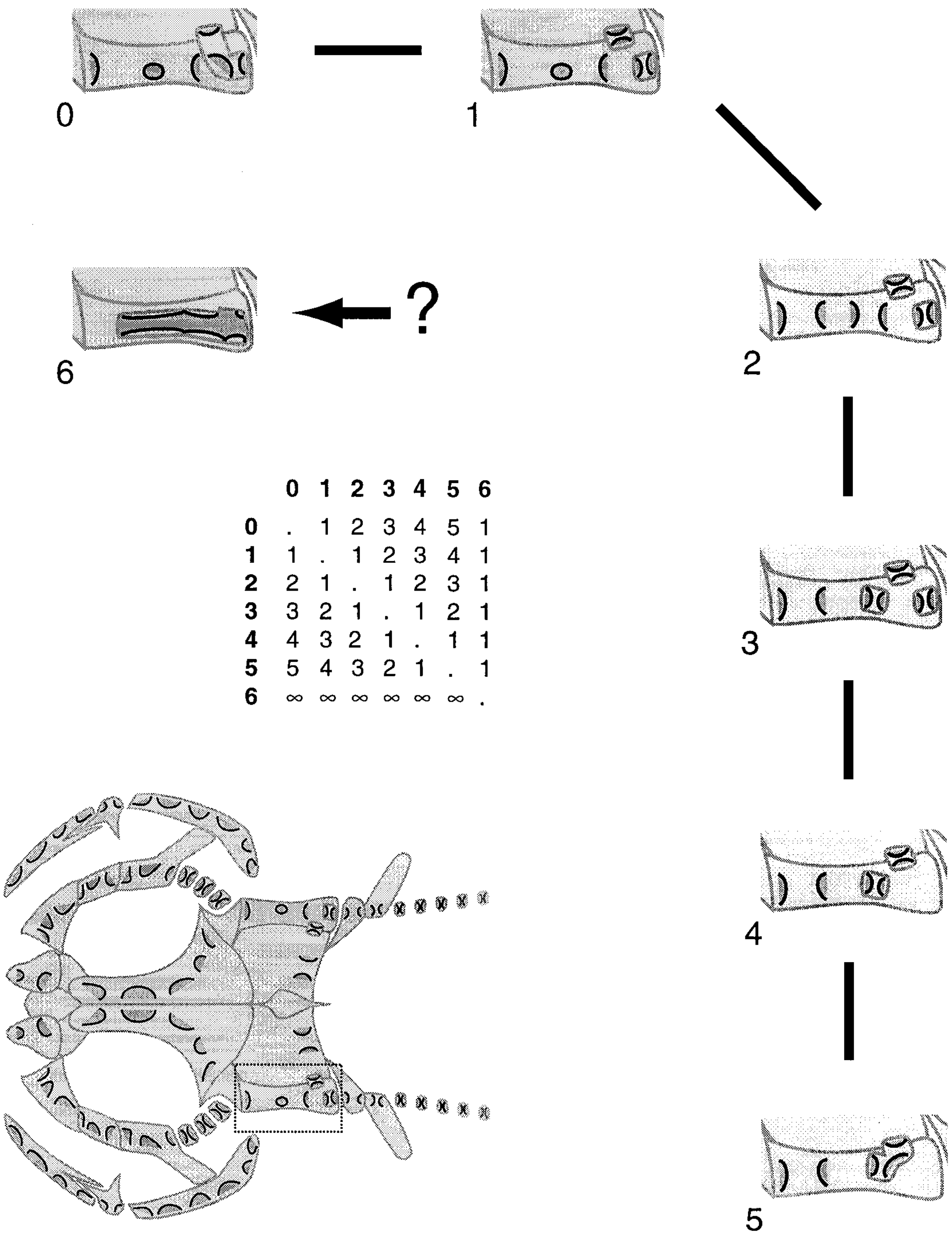


Figure 3–5. Character states observed with the preopercular pores. State 0, more than four pores; 1, four pores; 2, three pores; 3, two pores along length of preopercle (end openings pass the operculomandibular canal proper and are not included in count; number of arches equal to number of pores + 1).

and the psychrolutids *Ambophthalmos angustus, Cottunculus thomsonii, Ebinania brephocephala, Eurymen gyrinus, Neophrynichthys heterospilos,* and *Psychrolutes paradoxus.* Jackson and Nelson (1998) showed that the preopercular spines observed in *Cottunculus* sp. are not homologous to the spines that originate as posterior extensions of the preopercular margin. Bolin (1947) discussed the evolution of preopercular spines amongst his Californian Cottidae and thought that four undifferentiated spines are primitive and that preferential development and elaboration of the dorsalmost spine occurs in various lineages. It is possible that there is much phylogenetic information in the great variety of preopercular spination observed amongst Cottoidei. But, I found a continuous spectrum that does not readily give up discrete characters suitable for cladistic analysis.

10. Operculomandibular and infraorbital canals.— Not connected to each other (state 0) or with the operculomandibular canal connecting to the infraorbital canal between two postorbitals (state 1). State 0 was observed in Hexagrammidae and Cottoidei excepting Psychrolutidae with state 1. The connection of these two canals was first noted as unique to psychrolutids by Taranets (1941) and was also used by Yabe (1985, character 2). But, the connection of these two canals was also observed in *Jordania zonope, Leiocottus hirundo,* and *Orthonopias triacis*; but these species possess well-developed secondary sensory tubules and the connection of the two canals appears to be by secondary tubules, not the main canal. The condition observed in psychrolutids is unique in that the canals broadly connect to each other and do not have secondary tubules.

11. Extrascapulars.— The supratemporal canal is the extension of the lateral line anterior to the supracleithrum. It continues anteriorly through the posttemporal and a variable number of lateral extrascapulars to fork over the sphenotic into the supraorbital and infraorbital canals. The supratemporal canal also has a transverse bridge originating at the location of the lateral extrascapulars and crossing the cranium through two medial extrascapulars (on each side), the lateral one free-floating and the medial one usually fused with the parietal. The condition of the lateral extrascapulars is varied amongst Cottoidei, particularly in Psychrolutidae, and was described and used phylogenetically by Yabe (1985, character 11). It is used here again as an ordered transformation series, but in an elaborated form, without the presumption of an ancestral state: the parietal extrascapular is treated separately (Figure 3–6). One end-point (state 0) on this series has the posteriormost lateral extrascapular present, fused with the medial extrascapular, and the anterior lateral extrascapulars are fused to the pterotic and largely fused with each other into a tube with one or more pores; in state 1, the posteriormost lateral extrascapular and the medial extrascapular are separate elements; in state 2, the anterior lateral extrascapulars do not form a tube, but are clearly separate elements borne on the pterotic; in state 3, the posterior pterotic extrascapular is free; in state 4, the posterior extrascapular is lost; and in state 5, the medial and posterior pterotic extrascapular are fused. State 6 is an unusual condition in which the transverse bridge of the supratemporal canal is lost, and a medially oriented pore arises in that position as a presumed rudiment. In state 6, the lateral extrascapulars are more or less fused to each other forming an open groove for the canal to run along. State 6 is a major modification on the usual cottoid pattern and can not be surely linked with any other state; thus it is assumed to be equally derivable from any other state and irreversible once achieved (step matrix shown in Figure 3–6). State 0 was observed in *Blepsias cirrhosus* (fusion is variable, increasing with specimen size; young specimen shown in Figure 3–2f with intermediate fusion), *Rhamphocottus richardsoni*, and Agonidae; states 1 and 2 in most Cottoidei; states 3 through 5 are unique amongst Psychrolutidae with, state 3 in *Dasycottus setiger* and *Eurymen gyrinus*, state 4 in *Ebinania brephocephala*, *Malacocottus kincaidi*, and *Psychrolutes paradoxus*, and state 5 (first described in Jackson and Nelson,



	0	1	2	3	4	5	6
0	.	1	2	3	4	5	1
1	1	.	1	2	3	4	1
2	2	1	.	1	2	3	1
3	3	2	1	.	1	2	1
4	4	3	2	1	.	1	1
5	5	4	3	2	1	.	1
6	∞	∞	∞	∞	∞	∞	.

Figure 3–6. Transformation series observed with the extrascapulars. States described in text. Evolution assumed ordered as indicated and with state 6 possibly derived irreversibly from any other state. Step matrix inset, with *from* on vertical and *to* on horizontal axes. Minimum possible number of steps is 6.

1998) in *Ambophthalmos angustus* and *Cottunculus thomsonii.* The anterior extrascapular on the pterotic also becomes free (presumably from state 4) in *P. paradoxus* (this is observed in *P. sigalutes* too), but this condition is not informative in the context of this study and is not considered. The unusual state 6 was observed in Cyclopteridae.

12. Parietal extrascapular.— Present (state 0) or obscure (state 1). State 0 was observed in Hexagrammidae and Cottoidei excepting Cyclopteridae with state 1. The transverse bridge of the supratemporal canal is not present in Cyclopteridae and makes it difficult to determine if the extrascapular is present or not (presence is given away by a foramen for the canal to pass through).

13. Parietal extrascapular, autogeny.— Autogenous (state 0) or fused with the parietal (state 1) (Figure 3–7a). State 0 was observed in the psychrolutids *Ebinania brephocephala, Malacocottus kincaidi, Neophrynichthys heterospilos,* and *Psychrolutes paradoxus*; and state 1 in Hexagrammidae and all other Cottoidei. Not observable in Cyclopteridae. Yabe (1985, character 11) considered this condition as part of his "supratemporal commissure" character. Johnson (1993) considered the extrascapular fused with the parietal as synapomorphic for Scorpaeniformes.

14. Parietal extrascapular, spine or blunt protrusion.— A spine is associated with this bone (state 0) or not (state 1) (Figure 3–7b). State 0 was observed in *Blepsias cirrhosus, Chitonotus pugetensis, Enophrys bison, Gymnocanthus galeatus, Icelinus borealis, Myoxocephalus polyacanthocephalus, Rhamphocottus richardsoni,* Agonidae, and in the psychrolutids *Cottunculus thomsonii* and *Dasycottus setiger*; and state 1 in all other Cottoidei. Parietal spines are part of a ridge (extremely developed in *R. richardsoni*) that may be broken into several spines (*e.g., B. cirrhosus, G. galeatus,* and Agonidae). Some larval sculpins are known to possess parietal spines that disappear in adults, including *Hemilepidotus hemilepidotus* (Peden, 1978) amongst species examined here.

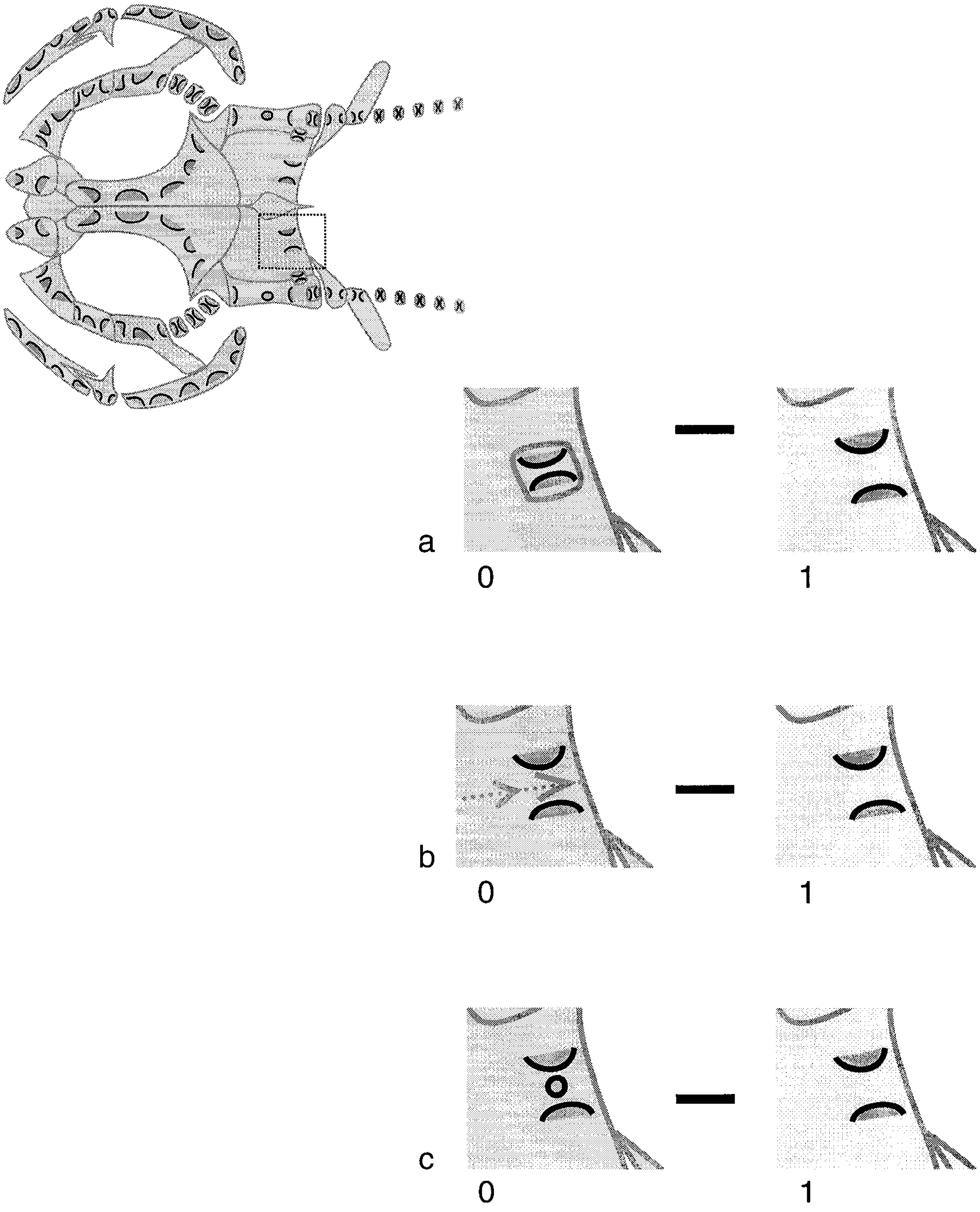


Figure 3–7. Characters and states observed with the parietal extrascapular. A, autogeny: state 0, autogenous, 1, fused with parietal. B, spine(s): state 0, present; 1, absent. C, pores: state 0, present; 1, absent.

15. Parietal extrascapular, pores.— The transverse bridge of the supratemporal canal passes through this bone. This bone has pores for sensory tubules to pass through (state 0) or not (state 1) (Figure 3–7c). State 0 was observed in Hexagrammidae, *Hemilepidotus hemilepidotus, Jordania zonope,* and *Scorpaenichthys marmoratus*; and state 1 in all other Cottoidei. Pores are observed at the edges of the parietal extrascapular in *Enophrys bison,* but not on the main body of the bone, and is thus considered state 1. Although Cyclopteridae lack the transverse bridge of the supratemporal canal altogether, this character is coded as state 1 as it represents a reduction in supratemporal canal pores that state 1 reflects.

16. Lateral line.— Present (state 0) or highly reduced (state 1). State 0 was observed in Hexagrammidae and Cottoidei excepting Cyclopteridae with state 1. In Cyclopteridae, a rudimentary lateral line is present with typically two pores and a single lateral line ossification. Some Cyclopteridae are known to possess a complete lateral line (*e.g.*, Stein, 1978).

17. Lateral line ossifications, number.— The number of ossifications (and sensory tubules that emanate from between ossifications) is comparable with vertebral number (state 1), more numerous (state 0), or less numerous (state 2). The evolution of this character is assumed to be ordered. Most Cottoidei examined have lateral line ossifications tracking the number of vertebrae very closely, within 10%. The ossifications in such specimens were seen to directly correspond with the underlying myomeres, for which vertebrae serve as a surrogate count. State 0 was observed in the hexagrammids *Hexagrammos decagrammus* (~1.92:1), *Ophiodon elongatus* (2.60:1), and *Oxylebius pictus* (1.58:1), and the cottoids *Blepsias cirrhosus* (~1.24:1), *Gymnocanthus galeatus* (1.16:1), *Hemilepidotus hemilepidotus* (~1.67:1), and *Scorpaenichthys marmoratus* (~2.20:1); state 2 in *Artediellus uncinatus* (~1:1.22) and Psychrolutidae (<1:1.80); and state 1 in all other Cottoidei. Unobservable in Cyclopteridae, but apparently state 2 occurs in species that do possess a lateral line (*e.g.*, *Osteodiscus cascadiae* with 51-56 vertebrae and 20 lateral line pores counted on the diagrammed specimen; Stein, 1978).

18. Lateral line ossifications, pores.— A sensory tubule branches off the lateral line canal posterior to each ossification (state 0); or an accessory tubule arises ventrally from a pore on the ossification (state 1); or two accessory tubules arise, one ventrally and the other dorsally, from pores on the ossification (state 2). States 1 and 2 are not considered necessarily linked to each another and the evolution of this character is not assumed to be ordered. State 0 was observed in most Cottoidei; state 1 in *Chitonotus pugetensis* and *Icelinus borealis*; and state 2 in *Enophrys bison* and *Myoxocephalus polyacanthocephalus*. The posterior margin of each ossification is typically concave and raised as a lip around the tubule. An extreme variant on this is seen in *Radulinus asprellus* that has its tubules directed ventrally and wrapped extensively in a groove. Multiple minute pores are observed on the skin surrounding each ossification in *Hemilepidotus hemilepidotus* and *Scorpaenichthys marmoratus*; but these pores do not seem to be connected with the canal when it was injected with stain. Although the lateral line is extremely reduced in Cyclopteridae, they clearly display state 0 in what remains. Taranets (1941) used the condition of the lateral line in diagnosing his subfamilies of his Cottidae: he noted the unusual condition of *Chitonotus*, although he did not notice the similar condition in *Icelinus*, and he noted the triple tubules of his Myoxocephalinae, of which several genera were presumed to have lost one or two tubules. According to Taranets, the single tubules observed in *Artediellus* (part of his Myoxocephalinae) are remnants of the lowermost of the three tubules; but this is doubtful because the tubules in that species arise posterior to each ossification as in other Cottoidei, not from a pore on the ossification.

19. Lateral line ossifications, ctenii.— Ctenii are borne on the posterior and or dorsal margin of lateral line ossifications (state 0) or not (state 1). Ctenii are spine-like ossifications of independent origin from the underlying scale or lateral line ossification. This is best exhibited in *Jordania zonope* (Figure 3–8j), that has some ctenii well fused to the lateral line ossification and other ctenii with suture zones evident. It is inferred that spines and serrated edges on other species' ossifications are similarly ctenii. State 0 was observed in *Artedius lateralis, Chitonotus pugetensis, Hemilepidotus hemilepidotus, Icelinus borealis, J. zonope, Orthonopias triacis, Radulinus asprellus, Synchirus gilli,* and *Rhamphocottus richardsoni*; and state 1 in all other Cottoidei (and in the single ossification observed in Cyclopteridae). The lateral line ossifications of *Enophrys bison* bear spines, but these are not assumed to be homologous; because the entire ossification (as opposed to only the posterior margin) is covered with small spines as are most exposed cranial bones; and it is likely that some other unique phenomenon is occurring.

20. Scales.— Present (state 0) or absent (state 1). State 0 was observed in Hexagrammidae and many Cottoidei (species listed in character 21); and state 1 in *Ascelichthys rhodorus, Clinocottus globiceps, Comephorus dybowskii, Enophrys bison, Oligocottus maculosus, Scorpaenichthys marmoratus,* the *Liparis* spp. cyclopterids, and the psychrolutids *Ambophthalmos angustus, Ebinania brephocephala, Eurymen gyrinus, Neophrynichthys heterospilos,* and *Psychrolutes paradoxus.*

21. Scale, type and distribution.— A transformation series is drawn for this character, although its two component characters are discussed individually first. Species that lack scales are coded with a separate character (20) and are treated as having unknown states in this character. This is done because absence might simply be observed, but the character is still present in juveniles or the potential for the character to be expressed remains.

21.1. Scales, type.— Ctenoid, in which a scale base is present with ctenii on the posterior end (state 0); modified ctenoid, in which a scale base is present with a single row of ctenii borne on its posterior half (state 1); fused ctenii, in which a

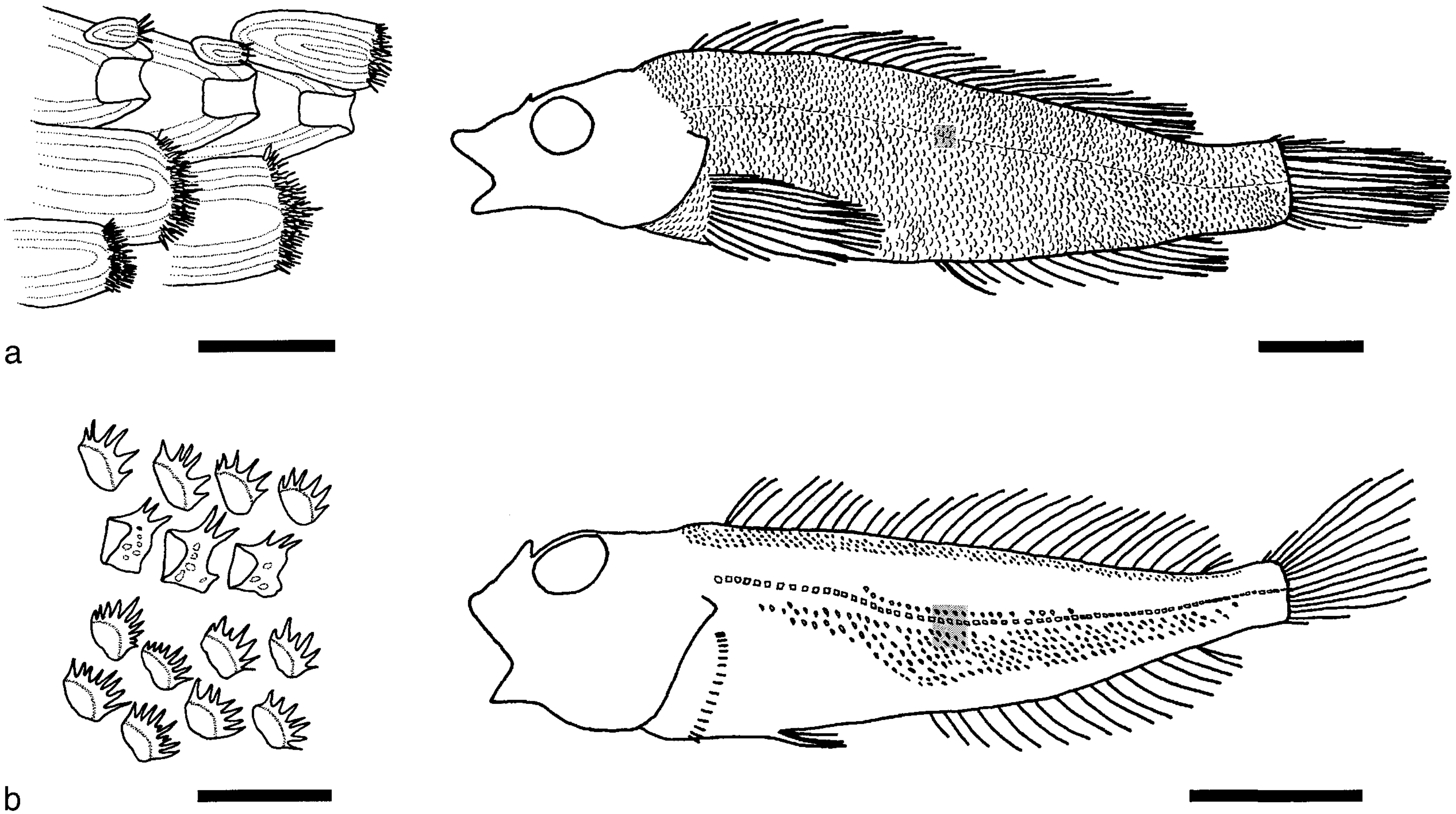


Figure 3–8a-b. Postcranial lepidology and lateral line ossifications of *Oxylebius pictus* (a) and *Hemilepidotus hemilepidotus* (b). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams.

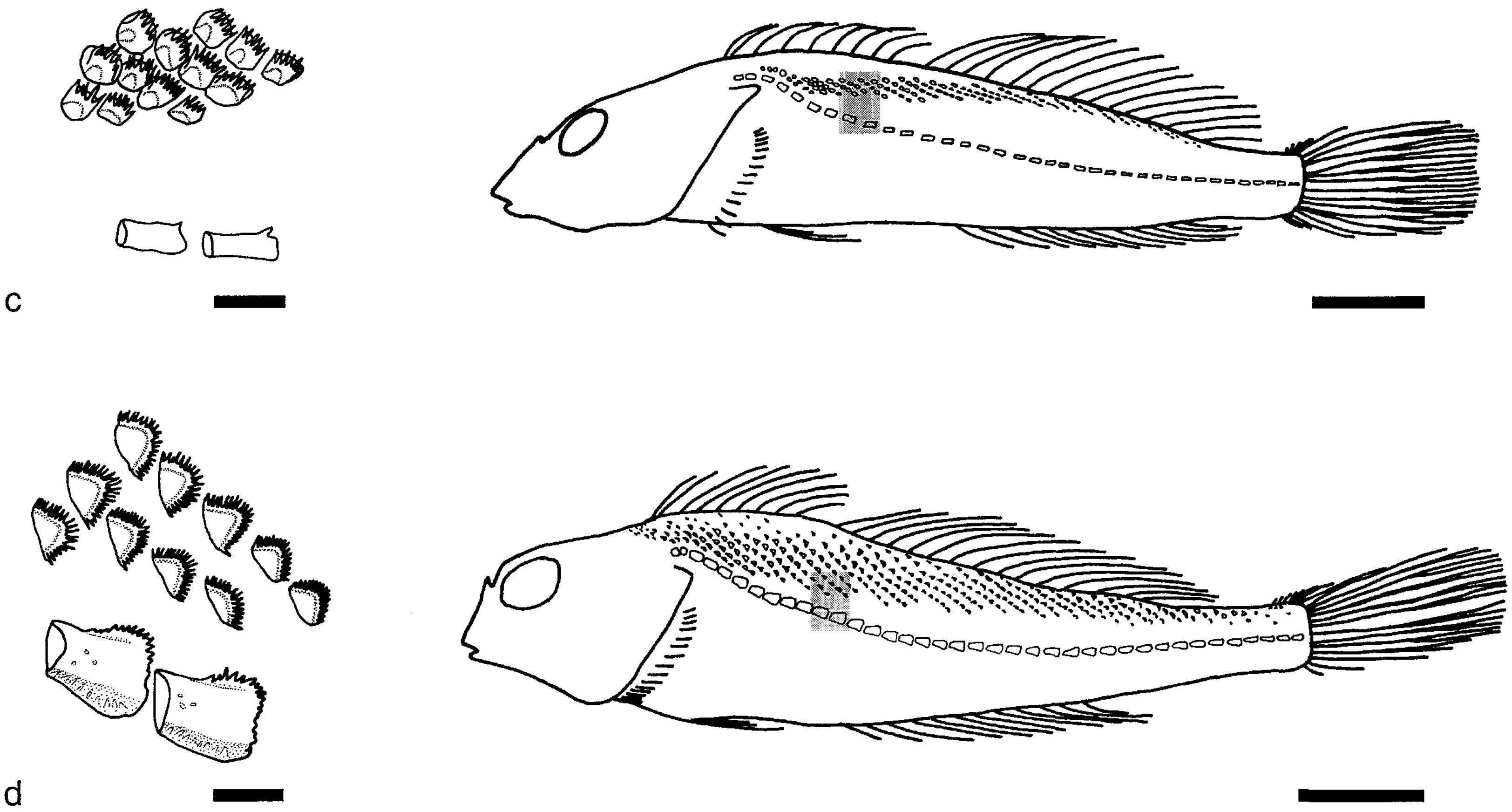


Figure 3–8c-d. Postcranial lepidology and lateral line ossifications of *Artedius lateralis* (c) and *Orthonopias triacis* (d). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams.

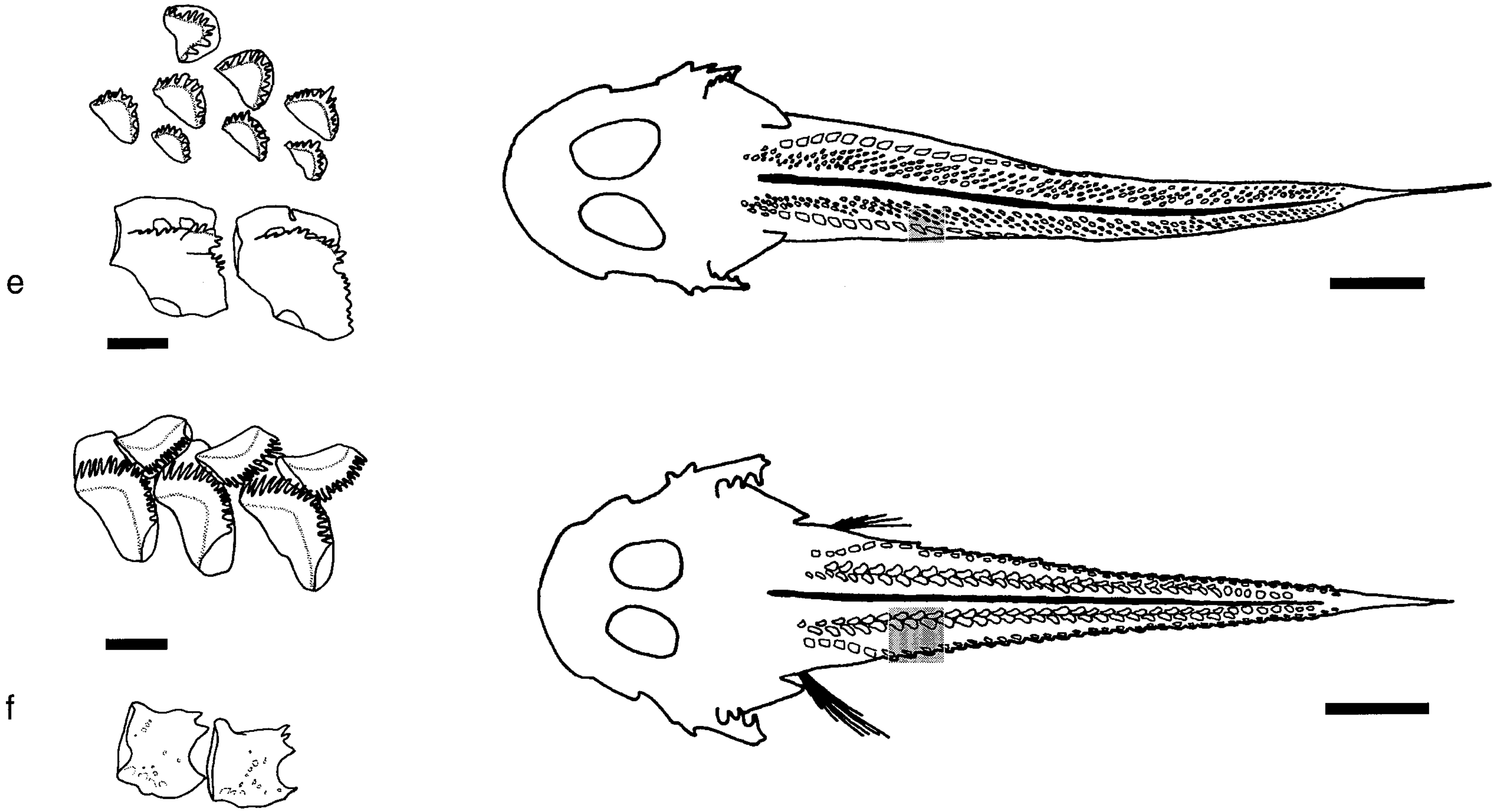


Figure 3–8e-f. Postcranial lepidology and lateral line ossifications of *Chitonotus pugetensis* (e) and *Icelinus borealis* (f). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams. Note this figure does not show the ventral pores on the lateralis elements of *I. borealis* because it is just on the proximal side of the element and not captured in this aspect.

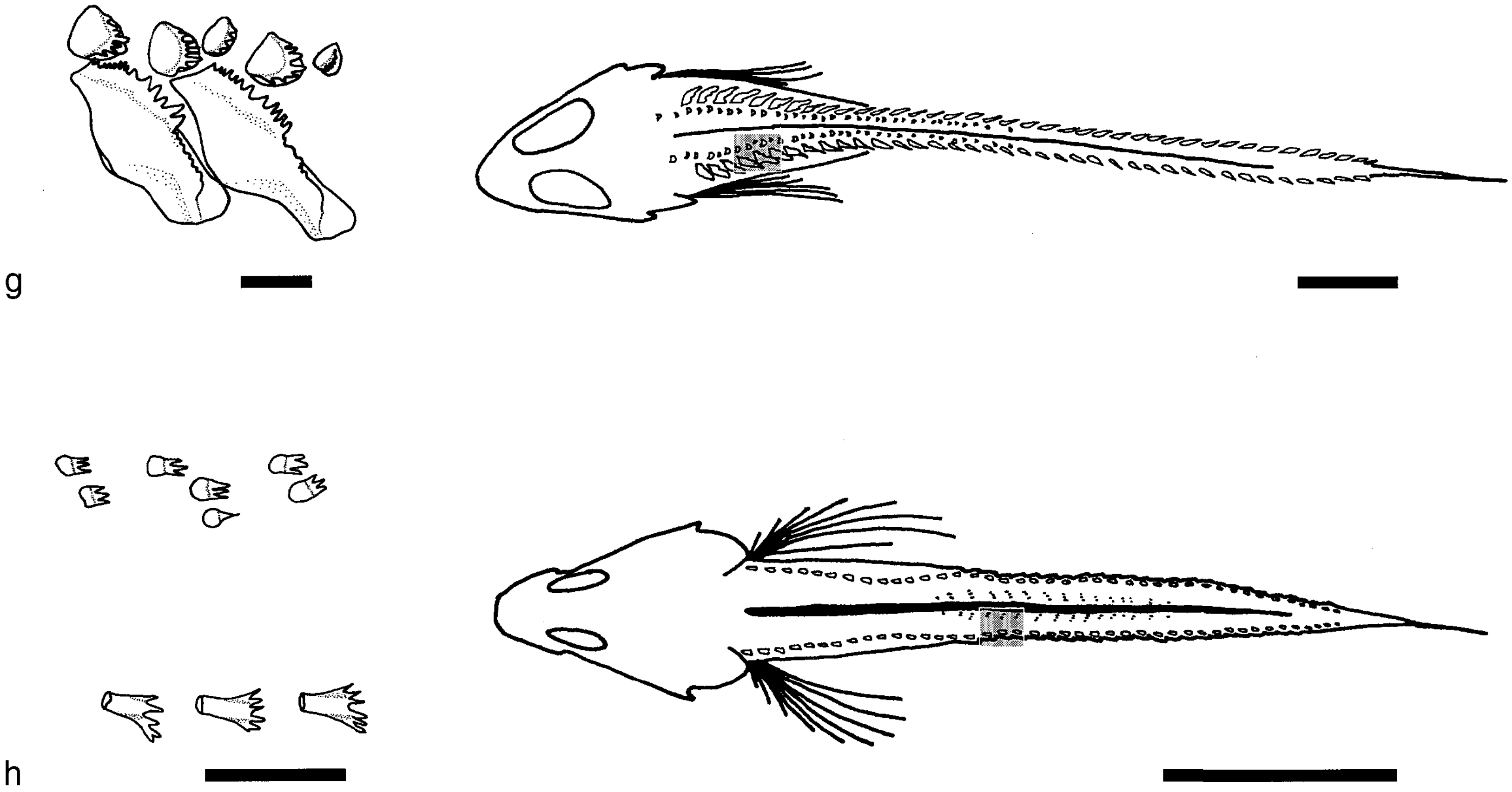


Figure 3–8g-h. Postcranial lepidology and lateral line ossifications of *Radulinus asprellus* (g) and *Synchirus gilli* (h). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams.

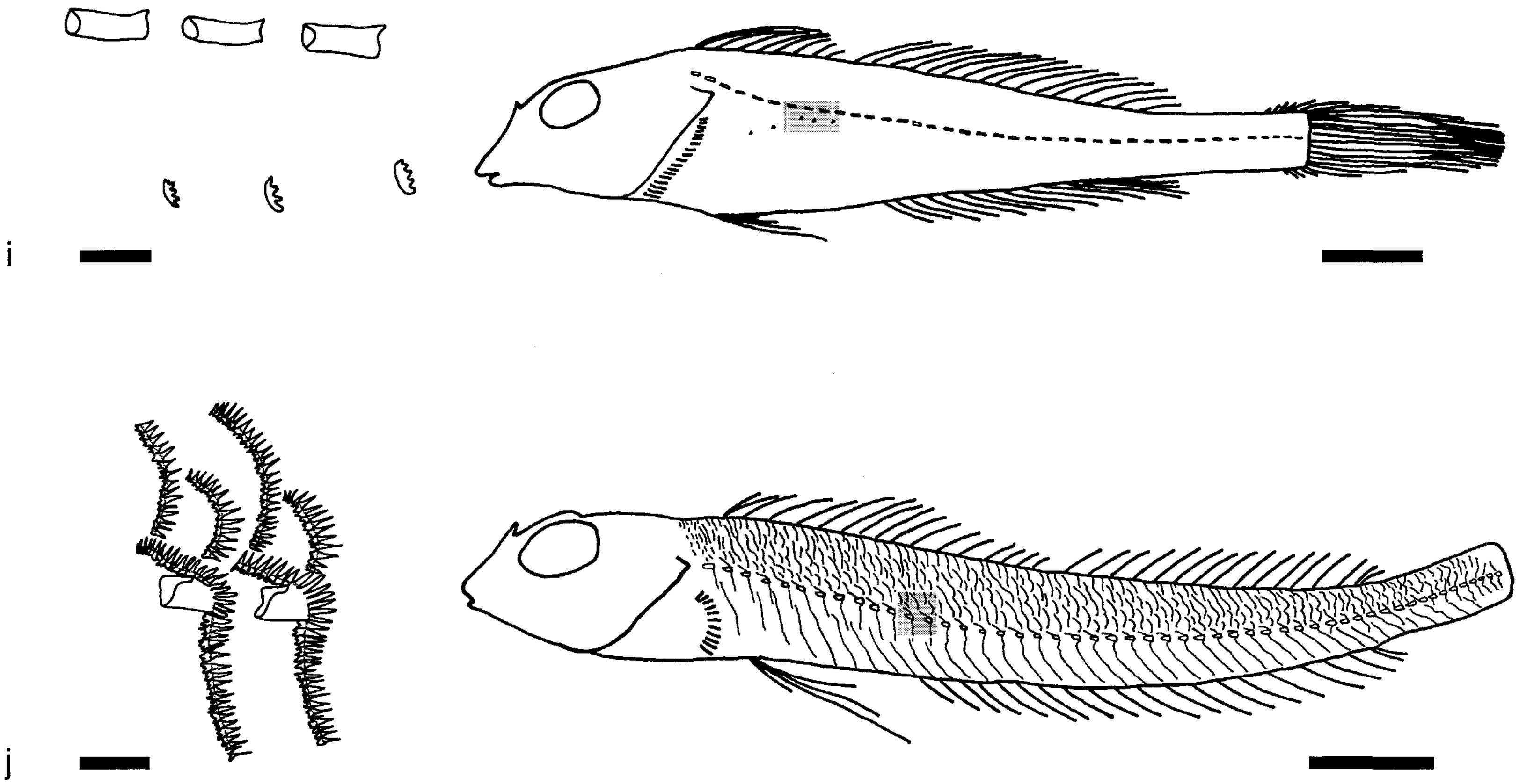


Figure 3–8i-j. Postcranial lepidology and lateral line ossifications of *Leiocottus hirundo* (i) and *Jordania zonope* (j). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams.

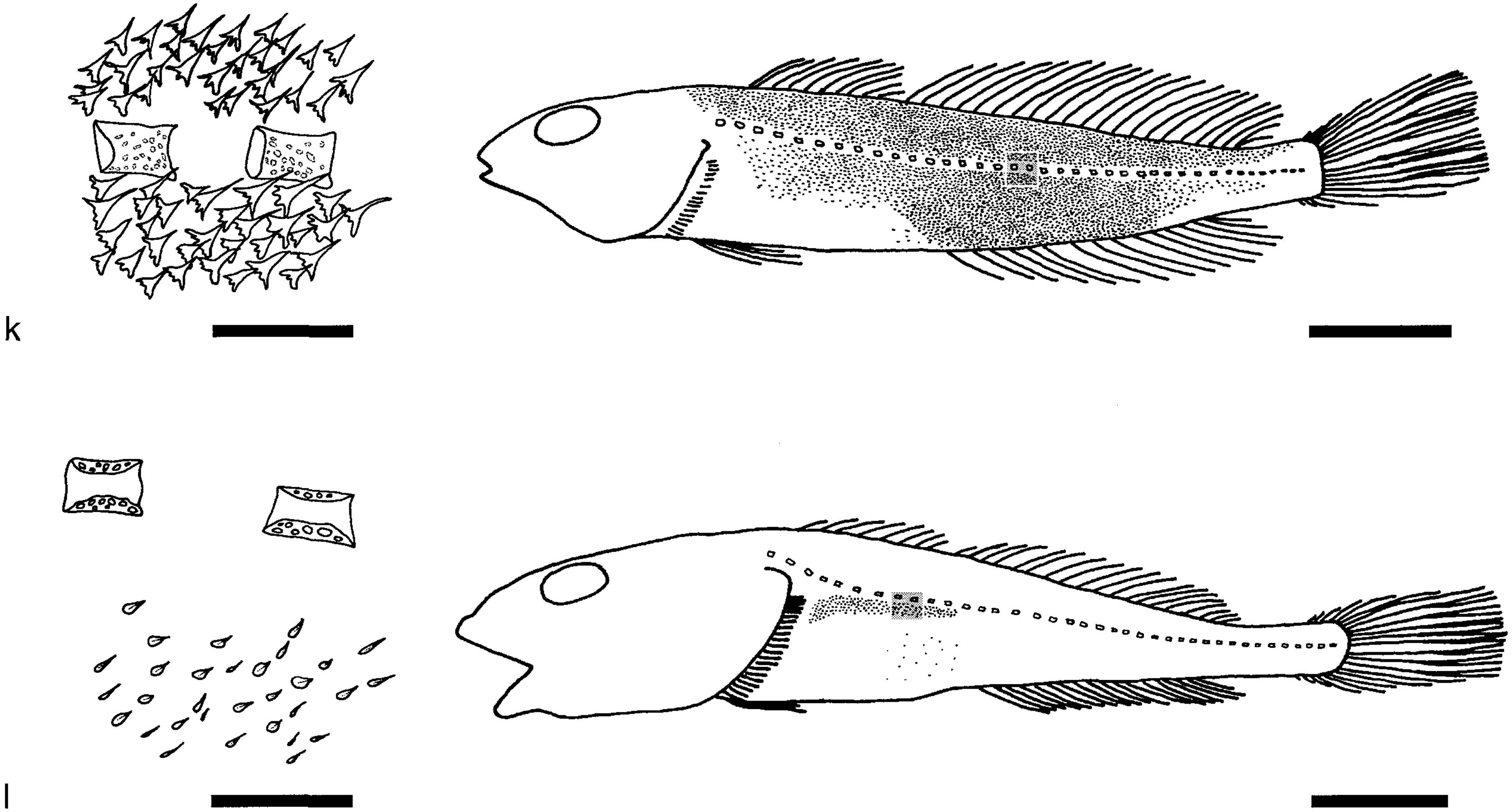


Figure 3–8k-l. Postcranial lepidology and lateral line ossifications of *Cottus asper* (k) and *Leptocottus armatus* (l). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams.

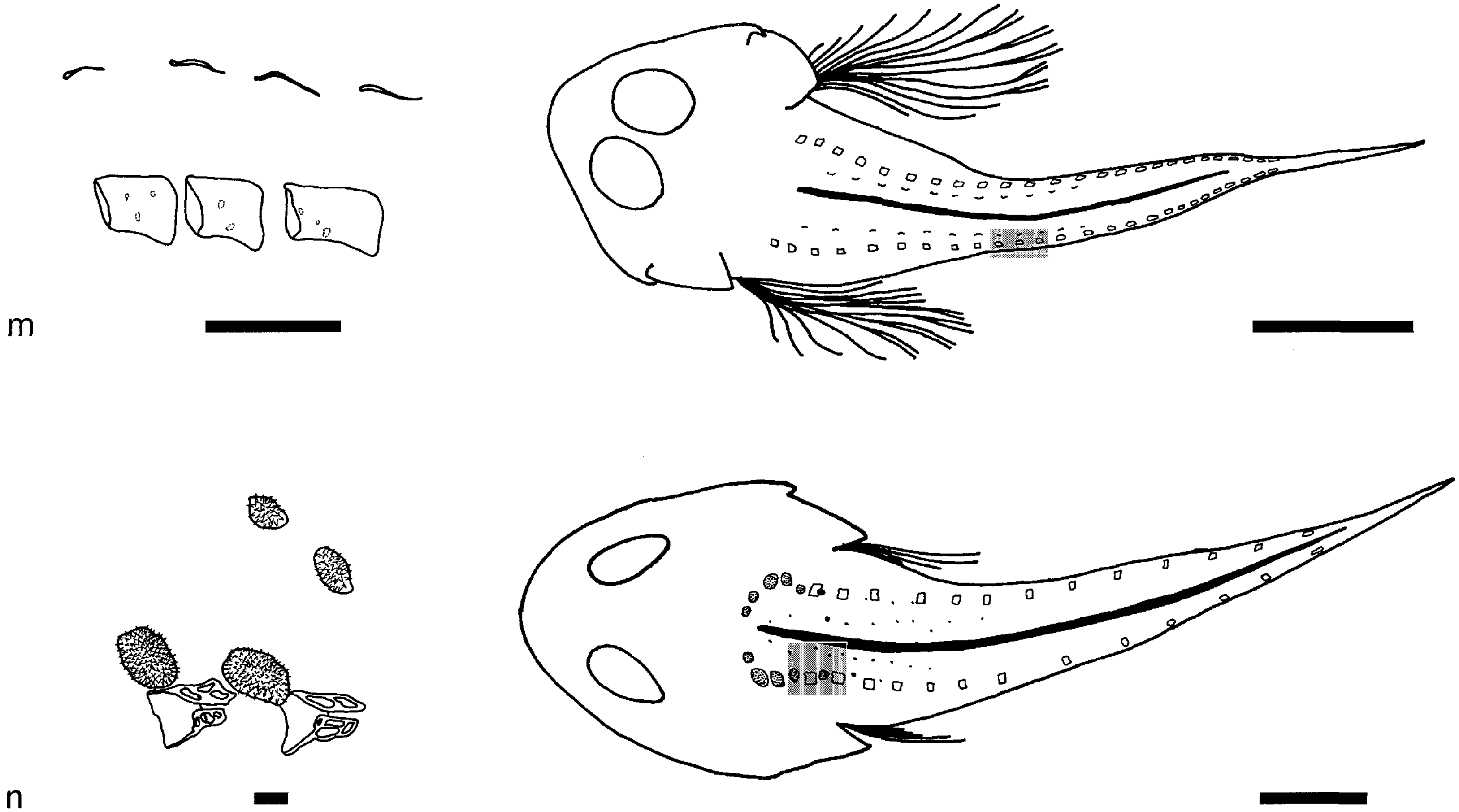


Figure 3–8m-n. Postcranial lepidology and lateral line ossifications of *Artediellus uncinatus* (m) and *Dasycottus setiger* (n). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams. *Dasycottus setiger* represented by two specimens.

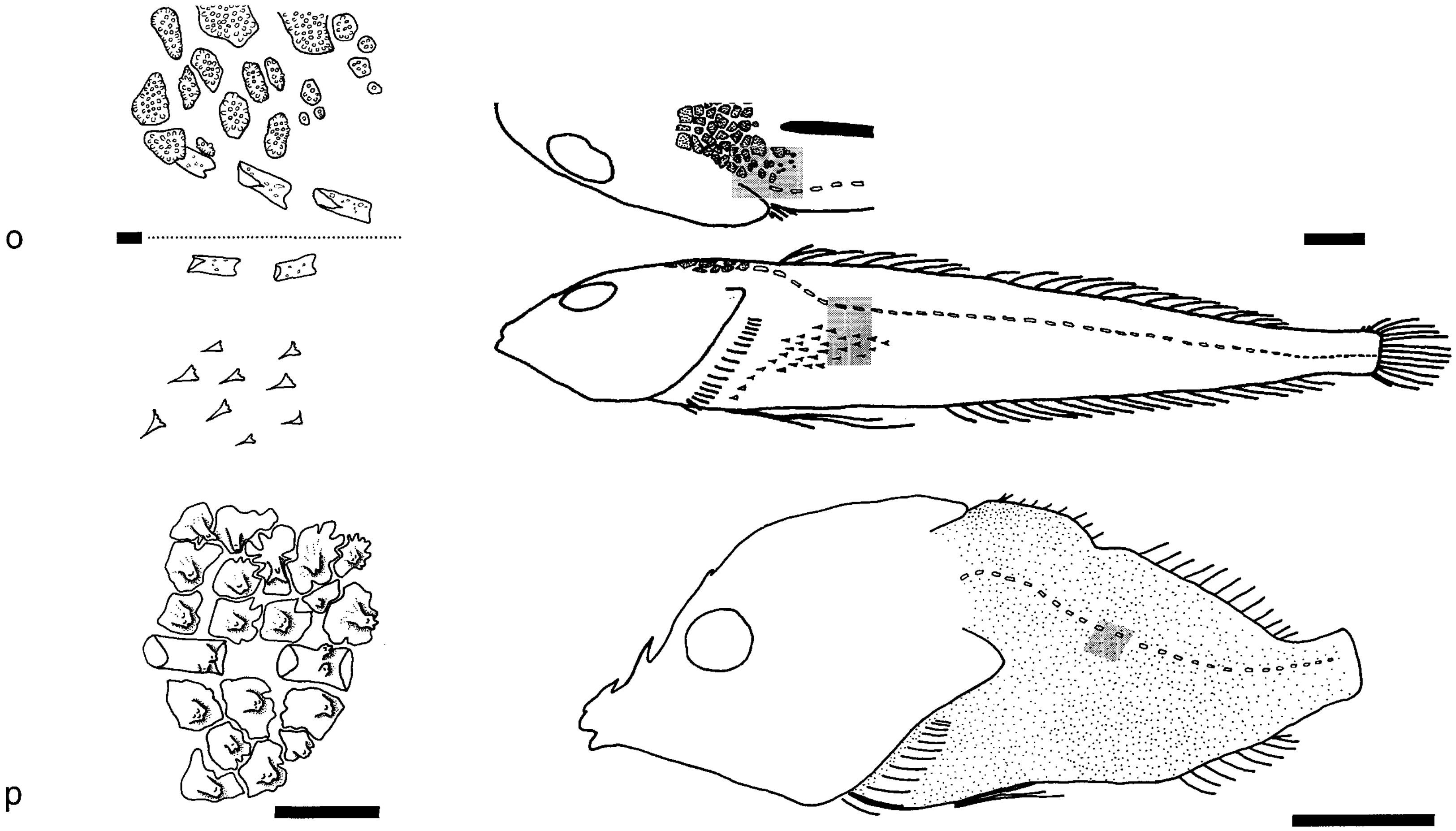


Figure 3–8o-p. Postcranial lepidology and lateral line ossifications of *Gymnocanthus galeatus* (o) and *Rhamphocottus richardsoni* (p). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams.

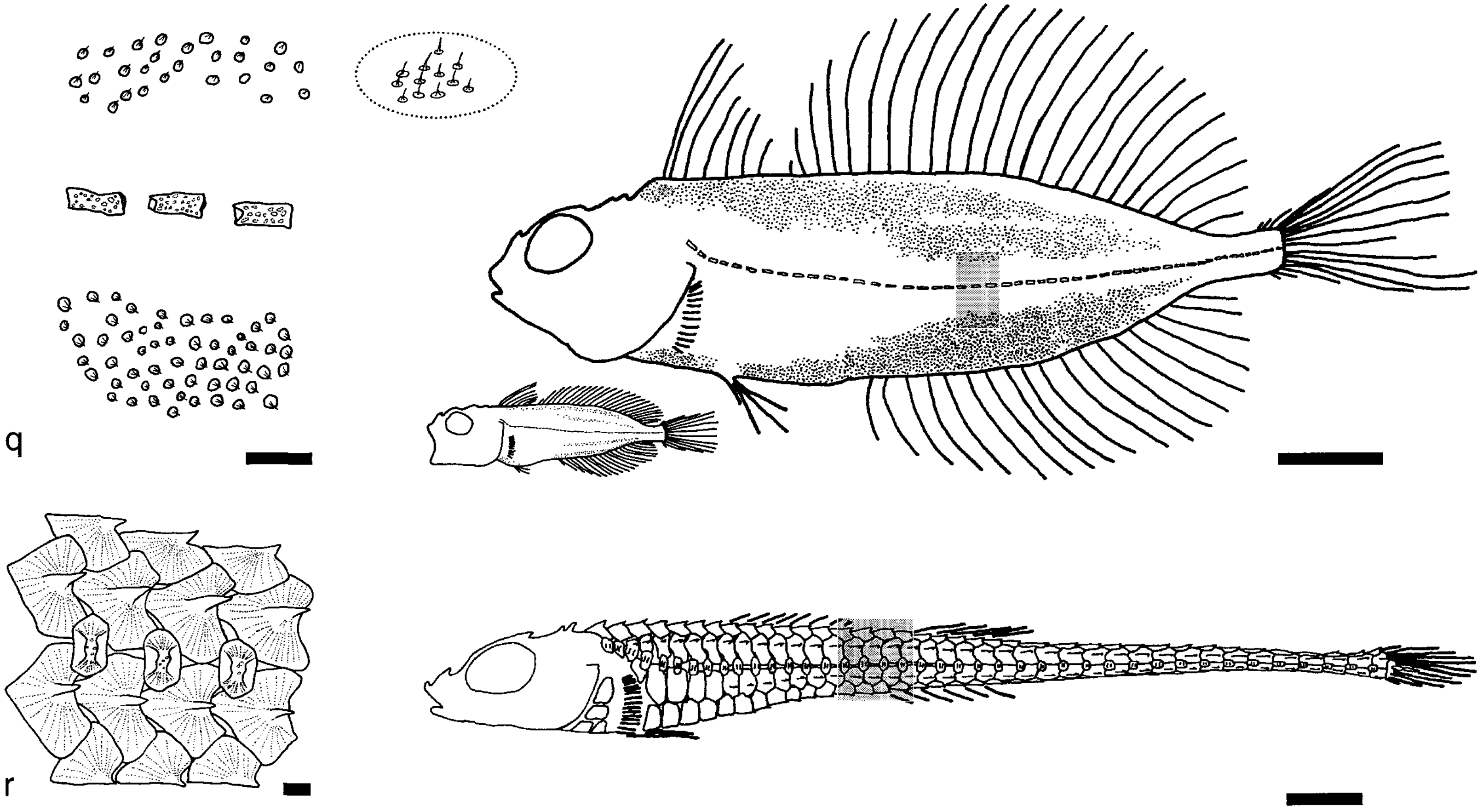


Figure 3–8q-r. Postcranial lepidology and lateral line ossifications of *Blepsias cirrhosus* (q) and *Xeneretmus latifrons* (r). Left diagrams show several enlarged scales and lateral line ossifications; right diagrams show their postcranial distribution and location of enlargements (shaded). Scale bars indicate 1 mm for enlarged diagrams and 10 mm for whole-specimen diagrams. *B. cirrhosis* represented by two whole-specimens, juvenile and adult; enlarged diagram is of adult, inset is in oblique aspect.

scale base is absent or obscure, but ctenii are present in clumps, plates, or lines (state 2), and isolated ctenii (state 3) (Figure 3–9). State 0 was observed in Hexagrammidae; state 1 in *Artedius lateralis, Chitonotus pugetensis, Hemilepidotus hemilepidotus, Icelinus borealis, Leiocottus hirundo, Myoxocephalus polyacanthocephalus, Orthonopias triacis, Radulinus asprellus,* and *Synchirus gilli*; state 2 in *Jordania zonope,* the cyclopterid *Eumicrotremus orbis,* and the psychrolutids *Cottunculus thomsonii, Dasycottus setiger,* and *Malacocottus kincaidi*; and state 3 in *Artediellus uncinatus, Blepsias cirrhosus, Cottus asper, Leptocottus armatus,* and Agonidae. Two states were observed in *Gymnocanthus galeatus* with state 1 expressed posterior to the pectoral fin and ventral to the lateral line, and state 2 expressed dorsal to the lateral line and predominantly on the cranium posterior to the origin of the dorsal fin. Although species with state 2 also exhibit state 3 as the fused ctenii scales reduce in size posteriorly, with the smallest ones often consisting of a single ctenus, these species are coded simply with state 2. These homologies might be debated. In particular, it might be argued that large plate-like scales of Agonidae are not greatly enlarged

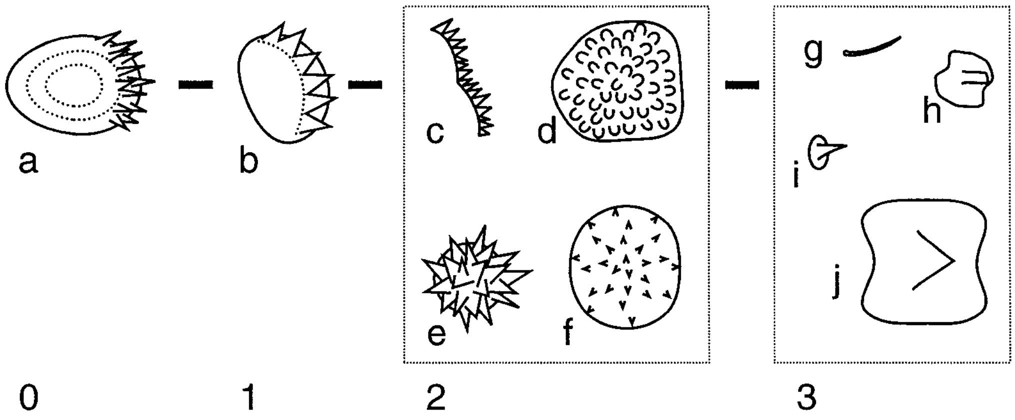


Figure 3–9. Scale types. General states: 0, ctenoid; 1, modified ctenoid; 2, ctenoid plate; 3, isolated ctenii. Specific scale types: a, ctenoid; b, modified ctenoid; c, *Jordania*; d, *Gymnocanthus*; e, Psychrolutidae; f, *Eumicrotremus* (Cyclopteridae); g, *Artediellus*; h, *Rhamphocottus*; i, *Blepsias*; j, Agonidae.

ctenii, but instead some neomorphic feature. My reasoning is based on the smallest scales on the cranium of certain Agonidae being very similar to the isolated scale ctenii of *Blepsias cirrhosus.* Although the variety within states 2 and 3 may represent homoplasy, the transformation from states 0 through 4 as progressive reduction and modification is plausible and is hypothesized here. These homologies are put forth as a starting point to tap into the phylogenetically significant variety observed amongst cottoid scales, and hopefully future studies will consider ontogeny and wider taxonomic diversity to clarify this character. Yabe (1985, character 45) considered scale morphology, but his findings differ considerably from what is presented here. His treatment was very cursory (three text lines on page 103 and no figures) and is not further discussed.

21.2. Scales, postcranial distribution.— Scale distribution can be classified in two manners (Figure 3–10): as widely or diffusely distributed (state 0) or confined to well defined bands, usually above the lateral line (state 1); or by where the scales form, that can not be assuredly determined as described below. State 0 was observed in Hexagrammidae, *Blepsias cirrhosus, Cottus asper, Gymnocanthus galeatus, Jordania zonope, Leptocottus armatus, Leiocottus hirundo, Rhamphocottus richardsoni,* the psychrolutid *Cottunculus thomsonii,* and Agonidae; and state 1 in *Artediellus uncinatus, Artedius lateralis, Chitonotus pugetensis, Hemilepidotus hemilepidotus, Icelinus borealis, Orthonopias triacis, Myoxocephalus polyacanthocephalus, Radulinus asprellus, Synchirus gilli,* and the psychrolutids *Dasycottus setiger* and *Malacocottus kincaidi.* Regarding where the scales form, I hypothesize that at least amongst Cottoidei, there are four potential postcranial scale-forming regions: the dorsal fin series, below that fin and often encircling it anteriorly and posteriorly; the dorsal lateralis series immediately above the lateral line; the ventral lateralis series, below the lateral line; and the anal fin series, above that fin and occasionally encircling it (Figure 3–10a and b). Support for this hypothesis is shown in juvenile *Blepsias cirrhosus*

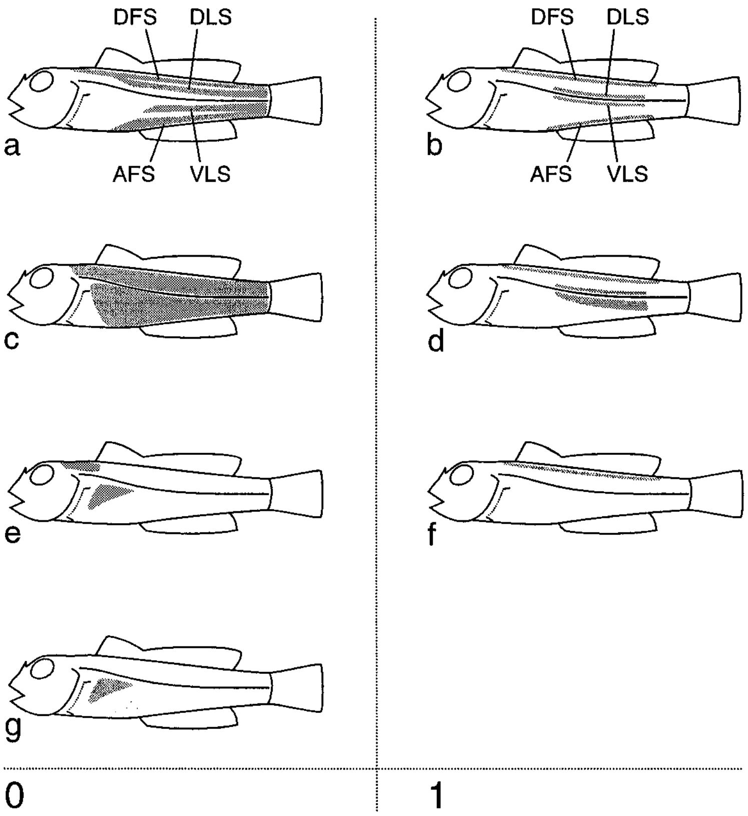
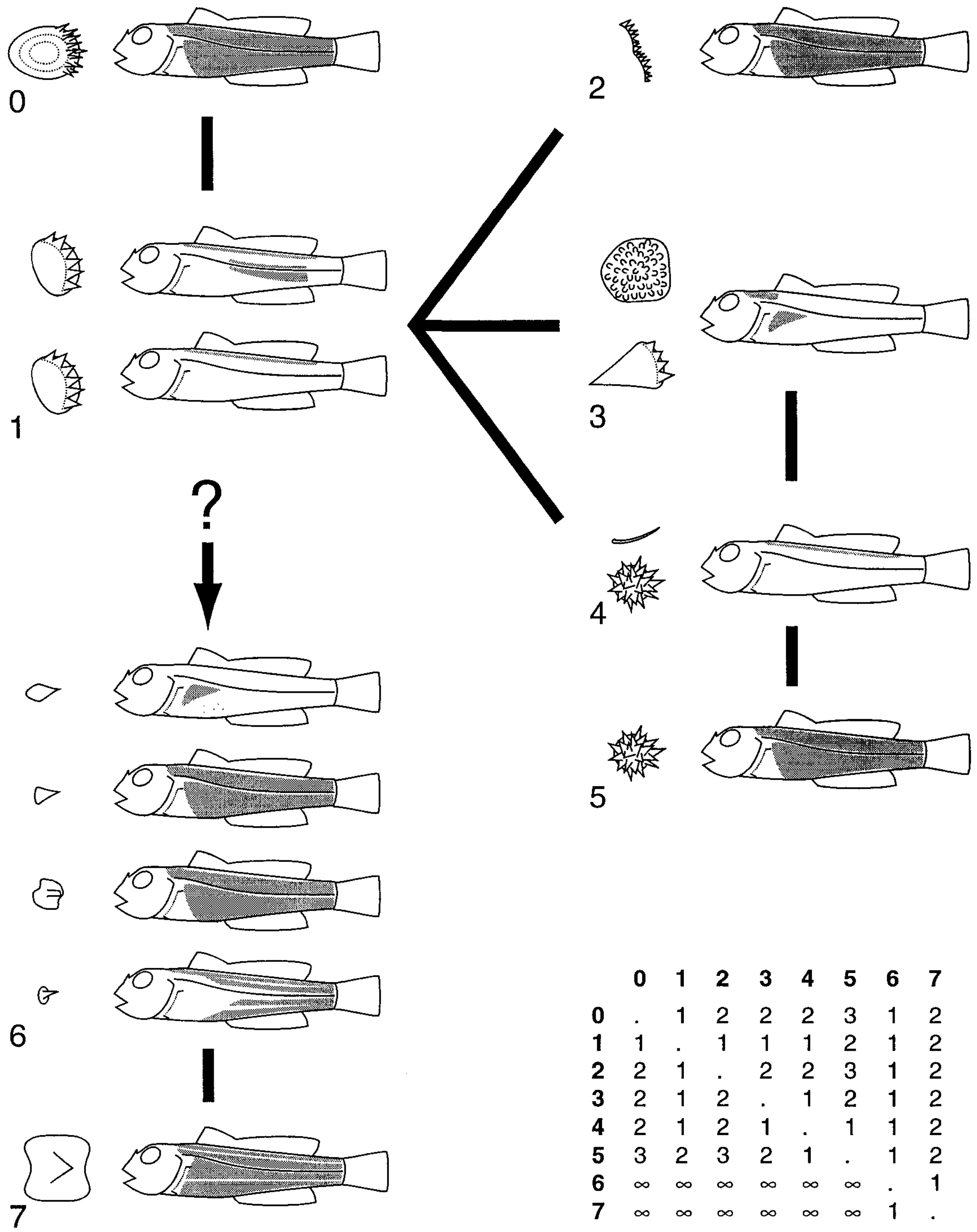


Figure 3–10. Postcranial scale distribution patterns. General states: 0, wide or sparse distribution; 1, restricted to distinct bands. AFS, anal fin series; DFS, dorsal fin series; DLS, dorsal lateralis series; VLS, ventral lateralis series. Labeled distribution patterns referred to in text.

(Figure 3–8q) and juvenile *Hemilepidotus hemilepidotus* (Peden, 1978) (Figure 3–8b). In *B. cirrhosus,* the four series merge with maturity while in *H. hemilepidotus,* the anal fin series is lost in adults that retain the three other series as distinct bands (Figure 3–10b and d). Further support is seen amongst Agonidae (Figure 3–8r) that have four series of postcranial plates (additionally observed in the agonids *Agonopsis vulsa, Anoplagonus inermis, Bathyagonus infraspinatus, Bothragonus swani, Odontopyxis trispinosa, Pallasina barbata,* and *Podothecus acipenserinus*) and in the cyclopterid *Cyclopterus lumpus* that has four primary rows of scales with less developed rows between. A number of Cottoidei retain only the dorsal fin series as adults, usually as distinct bands (Figures 3–8c-h, m-n, and 3–10f). Some Cottoidei are completely scaled without a trace of the hypothesized scale-forming regions (Figures 3–8j-k, p, and 3–10c), and only further detailed ontogenetic work will clarify whether such species possess the regions, a reduced number of regions, or something completely different. Some cottoid species retain scales behind and under the pectoral fin or on the nape (Figures 3–8i, l, o, 3–10e and g) and these are probably remnants of wider scale distribution in juveniles (McAllister and Lindsey, 1959, found that coastal *Cottus asper* retains scales in zones of least wear, primarily behind the pectoral fin). Unfortunately there is insufficient evidence on the ontogeny of well scaled Cottoidei to treat scale distribution on its own under this essentially ontogenetic hypothesis, and diffuse or irregular versus distinct bands observed in adults is the only clear character remaining.

21. Scales, type and distribution (transformation series).— When scale type and their postcranial distribution are combined, and with the hypothesis on scale-forming regions described under character 21.2 considered, a model of scale evolution is proposed (Figure 3–11). In state 0, ctenoid scales are widely distributed. State 1 is linked to state 0 by ctenoid scales modified to the cottoid morphology and scales distributed in distinct bands. State 2 is linked to state 1 by scale bases lost but ctenii remain arranged in a typical cottoid morphology and distinct bands merge. State 3 is linked to state 1 by modification of the dorsal fin series into fused ctenii scales, retention of modified ctenoid scales in the ventral series, and the anterior concentration of the scale distribution. State 4 may be linked with either states 1 or 3 by modification of the dorsal series into fused ctenii scales or isolated ctenii from state 1 or by loss of the the ventral lateralis series from state 3. State 5 is linked with state 4 by expansion and diffusion of the distinct scale bands. In state 6, isolated ctenii are present in a diffuse and usually wide distribution, and may be



	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**
0	.	1	2	2	2	3	1	2
1	1	.	1	1	1	2	1	2
2	2	1	.	2	2	3	1	2
3	2	1	2	.	1	2	1	2
4	2	1	2	1	.	1	1	2
5	3	2	3	2	1	.	1	2
6	∞	∞	∞	∞	∞	∞	.	1
7	∞	∞	∞	∞	∞	∞	1	.

Figure 3–11. Transformation series of scale types and postcranial distribution combined. States described in text. State 6 may be irreversibly derived from any of states 0 through 5. Step matrix inset, with *from* on vertical and *to* on horizontal axes. Minimum possible number of steps is 7.

linked with any of states 0 through 5. The transformation of any state to state 6 must be considered irreversible to avoid triangle inequity violations in constructing the step matrix that models this transformation series (otherwise unlikely paths might result; *e.g.*, states 5 to 6 to 0). It is reasonable to assume that a simplified structure would unlikely give rise to a complex structure indistinguishable from the original complex structure and thus the irreversible constraint on transformation to state 6 is also reasonable. State 7 is linked with state 6 by expansion of the isolated ctenii into large plates. Distances between these linkages are given as a step matrix in Figure 3–11. State 0 was observed in Hexagrammidae; state 1 in *Artedius lateralis, Chitonotus pugetensis, Hemilepidotus hemilepidotus, Icelinus borealis, Leiocottus hirundo, Myoxocephalus polyacanthocephalus, Orthonopias triacis, Radulinus asprellus,* and *Synchirus gilli*; state 2 in *Jordania zonope*; state 3 in *Gymnocanthus galeatus*; state 4 in *Artediellus uncinatus* and the psychrolutids *Dasycottus setiger* and *Malacocottus kincaidi*; state 5 in the cyclopterid *Eumicrotremus orbis* and the psychrolutid *Cottunculus thomsonii* (additionally observed in *C. microps* and *C. sadko* and known in *C. granulosus,* Nelson and Nakamura, 1980); state 6 in *Blepsias cirrhosus, Cottus asper, Leptocottus armatus, Rhamphocottus richardsoni*; and state 7 in Agonidae. It might be desirable to further subdivide state 1 based on which bands develop or state 6 based on the tooth-like morphology observed in *C. asper* and *L. armatus* versus the thumbtack morphology observed in *B. cirrhosus* and *R. richardsoni,* but there is insufficient data on ontogeny for clarifying state 1 and it would be premature to determine homologies of state 6.

22. Frontal, orbital rim.— The lateral margin of the frontal forms the majority of the dorsal rim of the orbit and is thick and distinct (state 0) or produced over the eye as a thin sheet of bone with an irregular edge (state 1). State 0 was observed in Hexagrammidae and the majority of Cottoidei; and state 1 in Cyclopteridae and the psychrolutids *Ebinania brephocephala, Neophrynichthys heterospilos,* and *Psychrolutes* *paradoxus.* This character was described amongst Psychrolutidae by Jackson and Nelson (1998, character 3).

23. Vomer, teeth.— The head of the vomer bears teeth (state 0) or not (state 1). State 0 was observed in Hexagrammidae and Cottoidei excepting *Gymnocanthus galeatus,* Cyclopteridae, and the psychrolutids *Ambophthalmos angustus, Malacocottus kincaidi, Neophrynichthys heterospilos,* and *Psychrolutes paradoxus,* all with state 1. Yabe (1985, character 5) considered this character and noted state 1 additionally in the agonids *Agonomalus jordani* and *Podothecus sachi.*

24. Palatine, teeth.— Teeth present (state 0) or not (state 1). State 0 was observed in Hexagrammidae and most Cottoidei; and state 1 in *Comephorus dybowskii, Enophrys bison, Gymnocanthus galeatus, Leiocottus hirundo, Myoxocephalus polyacanthocephalus, Radulinus asprellus, Rhamphocottus richardsoni,* Cyclopteridae, and Psychrolutidae. Yabe (1985, character 16) considered this character, but missed the few small teeth present somewhat posteriorly along the palatine in *Synchirus gilli.*

25. Palatocranial articulation.— The palatine possesses an articular facet that matches a facet on the prefrontal (state 0) or this articulation is obscure (state 1). State 0 was observed in Hexagrammidae, *Blepsias cirrhosus, Comephorus dybowskii, Cottus asper, Hemilepidotus hemilepidotus, Jordania zonope, Leptocottus armatus,* and *Scorpaenichthys marmoratus.*; and state 1 was observed in all other Cottoidei. Yabe (1985, character 6) examined this character; I have confirmed his observations and added *Comephorus dybowskii* with state 0.

26. Entopterygoid.— This bone lies medial to the palatine when present (state 0) or is absent (state 1). State 0 was observed in Hexagrammidae and most Cottoidei and state 1 in *Comephorus dybowskii, Radulinus asprellus,* and *Synchirus gilli.* Yabe (1985, character 15) examined this character and considered a third state in which the entopterygoid is reduced in size and does not meet the metapterygoid. I found this distinction difficult to assess due to varying degrees of development of this bone, and some genera thought by Yabe to have a normal development of this bone (*e.g.*, the psychrolutid *Malacocottus kincaidi*) I found to closely approach the condition observed in some species he considered to have a reduced version (*e.g.*, *Artediellus*). Taranets (1941, "mesopterygoid" therein) gives a "greatly reduced" entopterygoid as a diagnostic feature of his "Cottidae and related families." Similar development of this bone was observed in Hexagrammidae and thus, Taranets' reduced state is not informative here.

27. Basisphenoid.— Present (state 0) or absent (state 1). State 0 was observed in Hexagrammidae and state 1 in Cottoidei. Absence of the basisphenoid was first noted as a character of Cottoidei by Regan (1913) and has been subsequently used as a diagnostic character of the group by various authors (*e.g.*; Taranets, 1941; Yabe 1985, character 12).

28. Pterosphenoid-parasphenoid.— These two bones meet each other (state 0) or are separated by the intervening prootic (state 1). State 0 was observed in Hexagrammidae and most Cottoidei, and state 1 in *Blepsias cirrhosus* and Psychrolutidae excepting *Dasycottus setiger.* This character was first used by Regan (1913) in his key distinguishing his Cottidae from his Cottunculidae, but he did not elaborate on the condition in his other cottoid families. Taranets (1941) used state 0 in diagnosing his Cottidae, but he did not elaborate on this condition in other cottoids. Yabe (1985, character 7) found state 0 in most Cottoidei and state 1 in *B. cirrhosus* and Psychrolutidae amongst specimens examined here as well as in *Hemitripterus* sp. and his Ereuniidae. Yabe's states were verified here with the exception of the psychrolutid *D. setiger,* that has these two bones in contact. Oddly, Yabe (1985, Figure 7) diagrammed the connection of these two bones in *D. setiger,* but this condition is not reflected in his textual description and data matrix.

29. Trigeminofascialis chamber.— This bowl-shaped depression of the prootic houses the foramina from which cranial nerves III, V, and VII pass, and is covered by a vertical bony bridge dividing the opening into two parts (state 0) or has only the anterior opening and no bridge (state 1). State 0 was observed in Hexagrammidae and most Cottoidei, and state 1 in *Blepsias cirrhosus* and Psychrolutidae. The taxonomic significance of this character was first noted by Taranets (1941) as a distinguishing character of his Cottidae, that have it, and of his Blepsiidae (with *Blepsias* sp.) and his Hemitripteridae (with *Hemitripterus* sp.), that lack it. Yabe (1985, character 8) considered this character, but with a third state in which the bridge is thick and nearly covers the trigeminofascialis chamber. Yabe observed this thick bridge only in *Rhamphocottus richardsoni* and "generalized percoids." In this study, the three species of the out-group Hexagrammidae have a narrow bridge comparable in stature with various Cottoidei, and thus the thick bridge of *R. richardsoni* is a unique specialization and not informative.

30. Intercalar.— Large and extending anteriorly to the prootic (state 0) or small and excluded from the prootic by the intervening pterotic and exoccipital (state 1). State 0 was observed in Hexagrammidae and state 1 in Cottoidei. The hexagrammid *Ophiodon elongatus* has an intercalar that is excluded from meeting the prootic, but it is considerably more developed than in any of the Cottoidei examined. The reduced size of the intercalar was first noted as a diagnostic character of Cottoidei by Regan (1913, opisthotic therein) and was used subsequently by Taranets (1941, opisthotic therein) and Yabe (1985, character 13).

31. Baudelot's ligament.— This ligament connects the cleithrum with the posterior end of the basioccipital (state 0) or the first vertebral centrum (state 1). Yabe (1985) first noted that this condition is varied amongst Cottoidei, with state 0 in most species, and state 1 in his Hemitripteridae, Agonidae, and two other cottoid genera (*Pseudoblennius* and *Vellitor*). These states were verified with state 0 observed in Hexagrammidae and most Cottoidei, and state 1 in *Blepsias cirrhosus* and Agonidae.

32. Basihyal.— Present and well ossified (state 0) or obscure (state 1). State 0 was observed in Hexagrammidae and state 1 in Cottoidei. Shinohara (1994) observed an ossified basihyal in all hexagrammid species he examined (relatively reduced in *Zaniolepis frenata,* but still substantial and ossified). Yabe (1985, character 22) noted a highly reduced basihyal as a synapomorphy for his Cottoidea, but this is true in Cyclopteridae as well. Yabe also observed a very reduced and cartilaginous basihyal in *Jordania zonope* and *Rhamphocottus richardsoni.* He assigned distinct states to these and they figured in his phylogenetically basal placement of these two species. I was able to confirm Yabe's observation in *R. richardsoni,* but not in two reasonably well-prepared *J. zonope* specimens available to me. It is possible that a rudimentary basihyal can develop in some individuals of *J. zonope* and not in others, and if so, possibly in other species where Yabe did not observe it as well. Also, use of rudimentary characters as intermediates between full development and loss may not accurately reflect evolution, as loss is simply what is not observed. Only the two states are used here. Some alcian-blue cartilage stain was taken up just anterior to the hyoid arch in *Synchirus gilli,* possibly indicating a rudimentary basihyal. The general absence of a basihyal in Cottoidei seems correlated with their usually blunt and rounded buccal cavity and hyoid tongue. A rudimentary basihyal might be characteristic of cottoids with a narrow mouth and drawn-out tongue (*R. richardsoni* and *S. gilli* were the only such species available to me).

33. Pharyngobranchial tooth plates.— The second, third, and fourth pharyngobranchials bear tooth plates (state 0); or only the second and third (state 1); or only the third (state 2). The evolution of this character is assumed to be ordered. State 0 was observed in Hexagrammidae; state 1 in most Cottoidei; and state 2 in *Blepsias cirrhosus, Enophrys bison, Hemilepidotus hemilepidotus, Myoxocephalus polyacanthocephalus, Synchirus gilli,* Agonidae, Cyclopteridae, and Psychrolutidae. A reduced number of pharyngobranchial tooth plates was noted as a peculiarity amongst Cottoidei by Regan (1913), who thought that the third and fourth tooth plates are united and that the second plate is variously present or lost. Taranets (1941) correctly recognized that the fourth plate is lost in Cottoidei, and he used further loss of the second plate in diagnosing his subfamilies of his Cottidae. Yabe (1985, character 20) used this character with a fourth state in which the second plate is present but rudimentary and without teeth. Yabe's extra state was observed in *Bero elegans* and *Blepsias cirrhosus,* and is not considered here as it would be autapomorphic in the latter and not informative. Yabe reported two tooth plates in *Hemilepidotus hemilepidotus,* but I found only one plate present in the three specimens available to me and this concurs with Taranets who gave a single tooth plate as a diagnostic character of his Hemilepidotinae.

34. Branchiostegal rays.— Seven (state 0) or six (state 1) rays are present. State 0 was observed in Hexagrammidae and Cottoidei excepting Psychrolutidae with state 1. Taranets (1941) first noted seven branchiostegal rays as being diagnostic of Psychrolutidae. Yabe (1985, character 23) considered this character, but thought that seven rays is the primitive number for his Cottoidea and that six is derived.

35. Scapula-actinost.— The scapula and dorsalmost actinost are separate bones (state 0) or are fused to each other (state 1). State 0 was observed in Hexagrammidae and most Cottoidei, and state 1 in *Scorpaenichthys marmoratus* and Agonidae (Figure 3–12). Taranets (1941) thought that *S. marmoratus* was related to the Antarctic Notothenioidei and not to his Cottidae based on its having its dorsal actinost fused to the scapula. Yabe (1985, character 26) considered this character and observed this unusual condition only in *S. marmoratus,* but did not note it amongst the Agonidae he examined. State 1 was additionally observed in all other agonids available to me (*Agonopsis vulsa, Anoplagonus inermis, Pallasina barbata,* and *Podothecus acipenserinus*).

36. Coracoid, base.— The base of the coracoid attaches to the base of the cleithrum

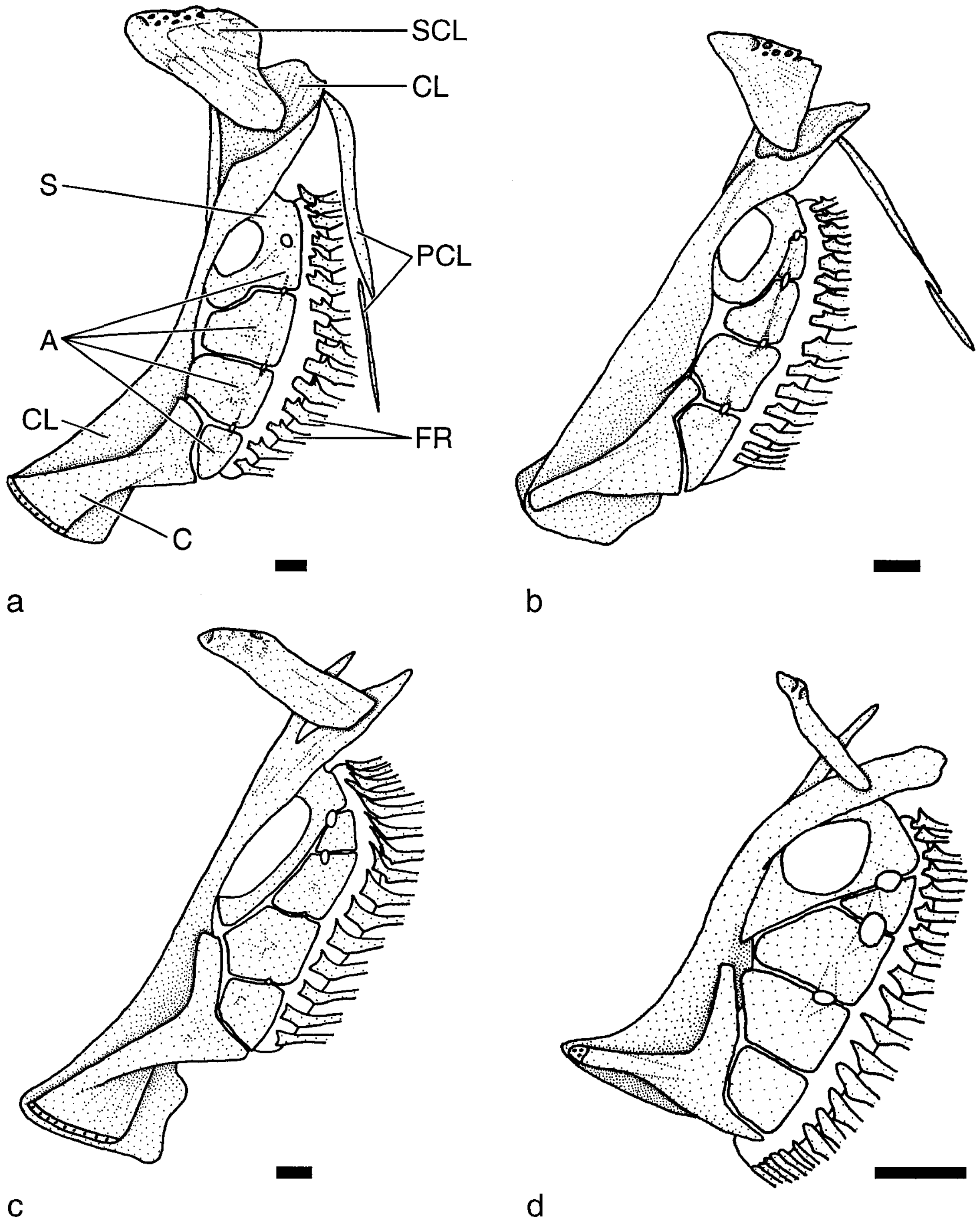


Figure 3–12a-d. Pectoral girdle of *Scorpaenichthys marmoratus* (a), *Hemilepidotus hemilepidotus* (b), *Artedius lateralis* (c), and *Synchirus gilli* (d) in lateral aspect. A, actinost; C, coracoid; CL, cleithrum; FR, fin ray; PCL, postcleithra; S, scapula; SCL supracleithrum. Scale bars indicate 1 mm.

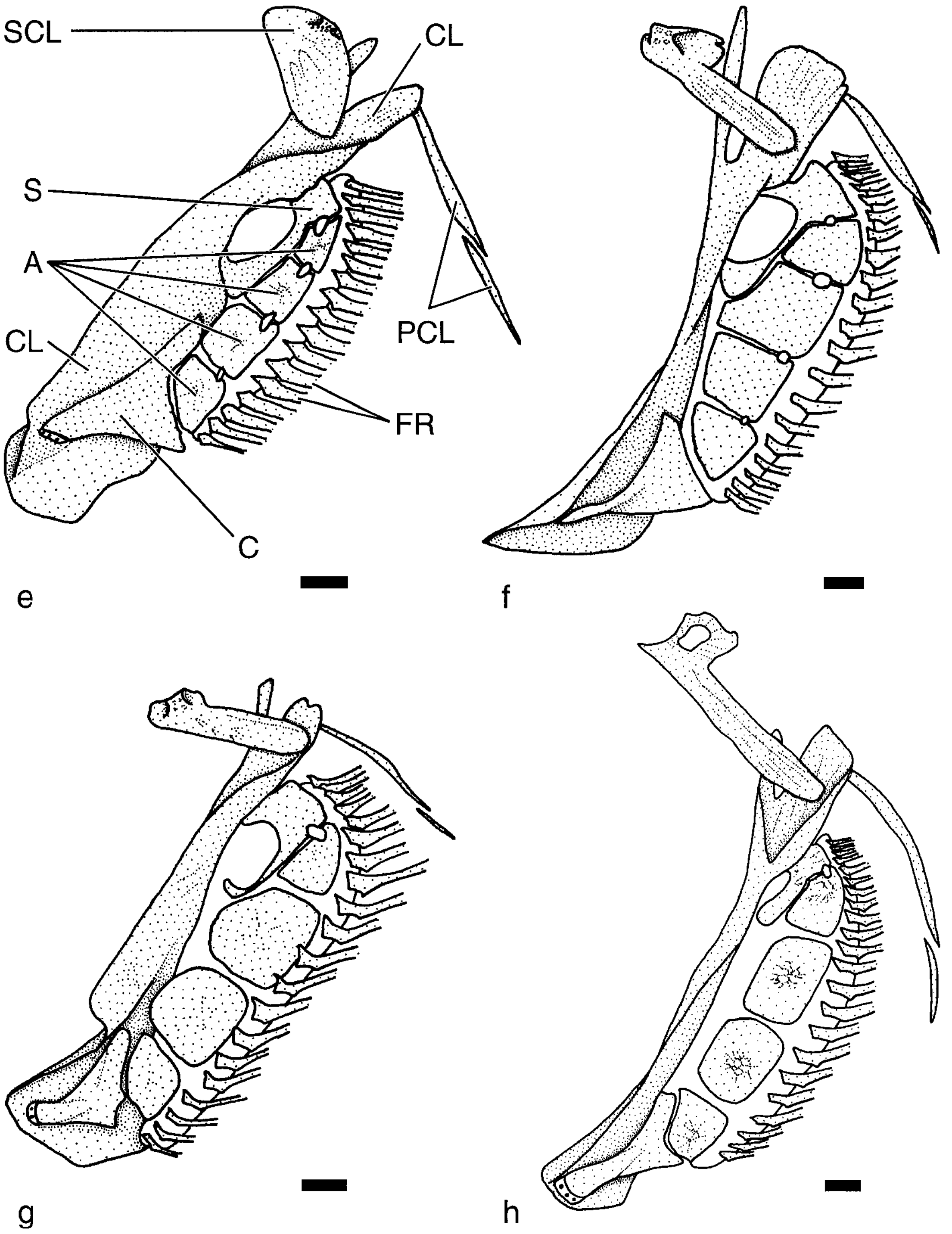


Figure 3–12e-h. Pectoral girdle of *Cottus asper* (e), *Leptocottus armatus* (f), *Artediellus uncinatus* (g), and *Malacocottus kincaidi* (h) in lateral aspect. See Figure 3–12a-d for legend. Scale bars indicate 1 mm.

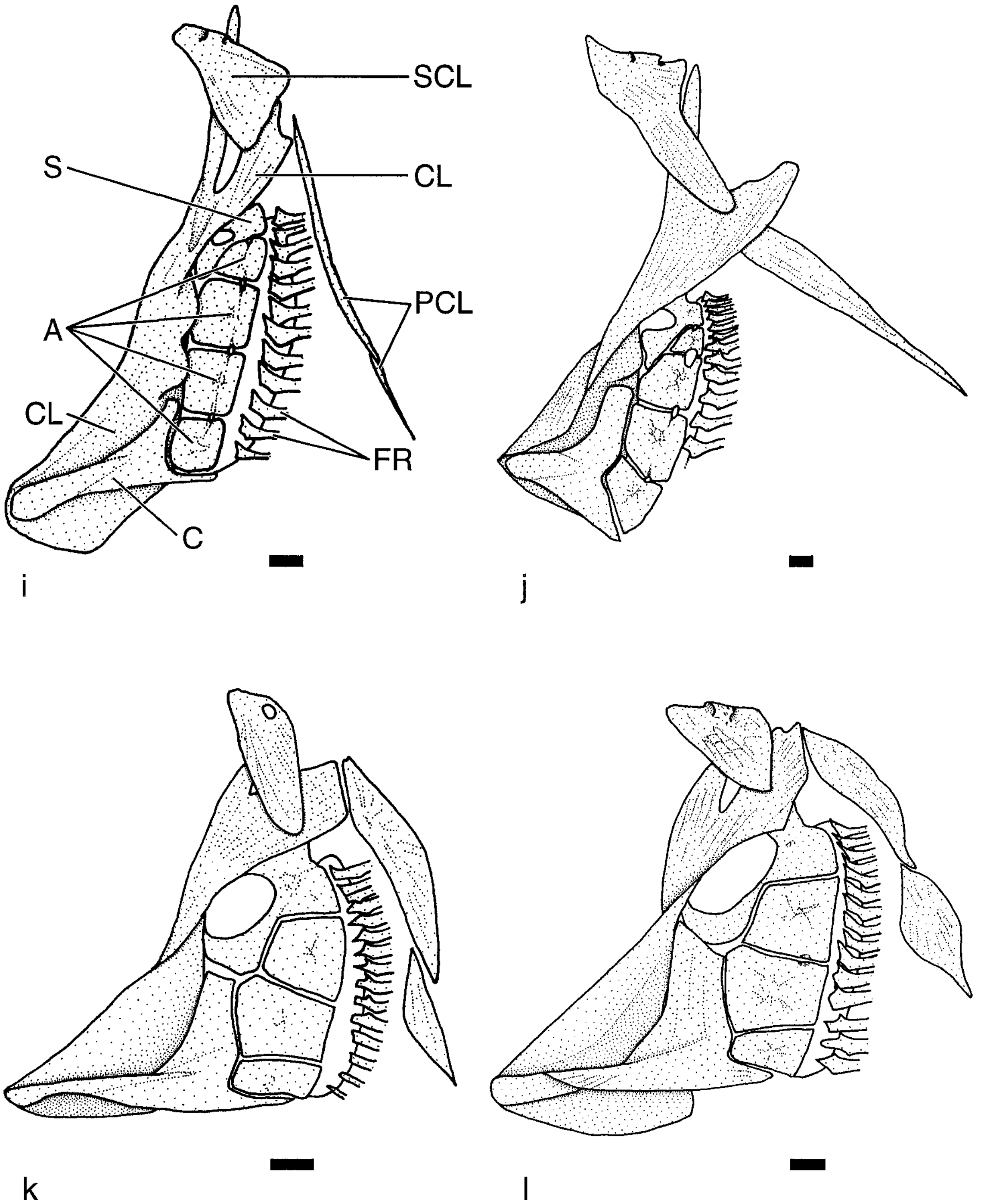


Figure 3–12i-l. Pectoral girdle of *Blepsias cirrhosus* (i), *Rhamphocottus richardsoni* (j) (ventral postcleithrum missing), *Bathyagonus alascanus* (k), and *Xeneretmus latifrons* (l) in lateral aspect. See Figure 3–12a-d for legend. Scale bars indicate 1 mm.

in one of three manners: on the lateral wing of the cleithrum that forms the posterior wall of the opercular cavity (state 0), narrowly and anteriorly on the main shaft of the cleithrum usually near the cleithral symphysis (state 1), or broadly and very close to the cleithral symphysis where the base of the coracoid roughly traces out the base of the cleithrum in width (state 2). The evolution of this character is assumed to be ordered. State 0 was observed in Hexagrammidae, *Comephorus dybowskii, Cottus asper, Leptocottus armatus,* and Agonidae. In *Hexagrammos decagrammus, Oxylebius pictus, Comephorus dybowskii, Cottus asper,* and *L. armatus,* this state is particularly evident with the coracoid base narrow and well lateral on the wing of the cleithrum. In *Ophiodon elongatus,* the cleithral wing is not particularly well-developed near the base of the cleithrum and as a result the coracoid attaches on the wing, but close to the cleithral shaft. In Agonidae, the wing of the cleithrum is well-developed and the coracoid broadly attaches to the full width of the wing. State 1 was observed in most cottoid fishes and state 2 in *Artedius lateralis, Chitonotus pugetensis, Leiocottus hirundo, Oligocottus maculosus, Orthonopias triacis,* and *Scorpaenichthys marmoratus.* (Figure 3–12.)

37. Actinost foramina.— Four foramina are present with three between the four actinosts and one between the dorsalmost actinost and scapula (state 0), the lowermost foramen is obscure (state 1), the lower three foramina are obscure with only the foramen between the dorsal actinost and scapula present (state 2), or all foramina are obsolete (state 3). State 0 was observed in Hexagrammidae and most Cottoidei; state 1 in *Enophrys bison, Gymnocanthus galeatus, Myoxocephalus polyacanthocephalus, Radulinus asprellus,* and *Synchirus gilli*; state 2 in *Artediellus uncinatus* and the psychrolutid *Malacocottus kincaidi*; and state 3 was observed in *Comephorus dybowskii,* Agonidae, and in the remaining Psychrolutidae (Figure 3–12). Often the foramina are larger dorsally and the observation of four, three, one, or no remaining pores is tantalizing evidence to consider the evolution of this character as ordered. But, in *Blepsias cirrhosus* all foramina are very small and in *Xeneretmus latifrons* there are what appears to be the vestiges of a foramen between the middle two actinosts. Therefore, modeling this character's evolution may not be so simple and here it is left unordered. Regan (1913) considered the reduction of these foramina to be characteristic of Cottoidei amongst Scorpaeniformes and diagrammed several species. Taranets (1941) considered the reduction of these foramina as being evolutionarily plastic, and thought that reduction to be characteristic of less mobile species, with well-developed foramina associated with well-developed pectoral musculature. Yabe (1985, character 27) simply considered the presence or absence of foramina in general and found absence to be diagnostic for Psychrolutidae; but this was found to not be the case here, with *M. kincaidi* having a single well-developed foramen present in all five specimens examined.

38. Postcleithra.— Two expanded blade-like postcleithra are present (state 0), or else two (state 1) or one (state 2) rod-like postcleithra are present, or postcleithra are absent (state 3). The evolution of this character is assumed to be unordered because of the rarity of state 2, suggesting that state 3 (complete loss) may arise directly from either state 0 or 1. State 0 was observed in Agonidae; state 1 in Hexagrammidae and most Cottoidei; state 2 in the psychrolutids *Cottunculus thomsonii* and *Eurymen gyrinus*; and state 3 in *Artedius lateralis, Ascelichthys rhodorus, Clinocottus globiceps, Comephorus dybowskii, Synchirus gilli,* and *Psychrolutes paradoxus* (Figure 3–12). Taranets (1941) used this character in his key of "Cottidae and related families," distinguishing his Cottidae with postcleithra usually present from his Cottocomephoridae and Comephoridae with postcleithra rudimentary or absent. Yabe (1985) noted the number of this bone amongst specimens he examined but did not consider its phylogenetic significance.

39. Pelvic girdle.— The paired basipterygia form a kite-shaped pelvic girdle (state 0), a distinct box like morphology (state 1), or are highly modified to support a sucking-disc pelvic fin (state 2). State 0 was observed in Hexagrammidae and most Cottoidei, state 1 in the psychrolutids *Ambophthalmos angustus* and *Cottunculus thomsonii*, and state 2 in Cyclopteridae. State 1 was first reported in the psychrolutid genera *Ambophthalmos* and *Cottunculus* by Jackson and Nelson (1998). In state 2, the pelvic girdle is expanded anteriorly, well articulated with the cleithra, and the posterior margin is twisted anteriorly to support the circular sucking-disc pelvic fin. Unusual morphology was also observed in *Leptocottus armatus*, that has its pelvic girdle greatly expanded anteriorly, and in *Rhamphocottus richardsoni*, that has a highly angled pelvic girdle with a prominent subpelvic process (described by Yabe, 1985, character 30). These two autapomorphic conditions of the pelvic girdle are not phylogenetically informative here and are thus coded as state 0.

40. Subpelvic process.— Present (state 0) or rudimentary (state 1). State 0 was observed in Hexagrammidae and most Cottoidei, and state 1 in *Blepsias cirrhosus* and Agonidae. Yabe (1985) described the subpelvic process and noted that it is rudimentary in his Hemitripteridae and obscure in Agonidae, but he did not further consider its phylogenetic significance.

41. Pelvic fin.— The pelvic fin is present (state 0) or absent (basipterygia are developed) (state 1). State 0 was observed in Hexagrammidae and Cottoidei, excepting *Ascelichthys rhodorus* and *Comephorus dybowskii* both with state 1.

42. Pelvic fin, spine and rays.— The counts are: I,5; I,4; I,3; or I,2 (states 0-3 respectively). The evolution of this character is assumed to be ordered. State 0 was observed in Hexagrammidae, *Jordania zonope, Scorpaenichthys marmoratus,* and Cyclopteridae; state 1 in *Cottus asper, Hemilepidotus hemilepidotus,* and *Leptocottus armatus*; state 2 in the majority of Cottoidei; and state 3 in Agonidae. The condition is not observable in *Ascelichthys rhodorus* and *Comephorus dybowskii.* In Cyclopteridae, the pelvic fin is modified into a sucker with one thin spine and five rays (although these "rays" are unsegmented, and are only differentiated from the "spine" by their number, position, and much larger size). Taranets (1941) used this character in diagnosing his subfamilies of his Cottidae, and Yabe (1985, character 31) considered its phylogenetic significance amongst his Cottoidea.

43. First neural arch.— Complete (state 0) or incomplete (state 1). State 0 was observed in Hexagrammidae, and the cottoids *Comephorus dybowskii, Cottus asper, Hemilepidotus hemilepidotus, Leptocottus armatus, Rhamphocottus richardsoni, Scorpaenichthys marmoratus,* and the *Liparis* spp. cyclopterids; and state 1 in all other Cottoidei (Figure 3–13). In addition to the first neural arch, the second is also incomplete in the cyclopterid *Eumicrotremus orbis.* An incomplete neural arch appears to be an adaptation to allow space for the first, enlarged, double pterygiophore of the dorsal fin (see character 44). But, this is not always apparent as some species (*e.g.*, *Artediellus uncinatus* or the psychrolutid *Psychrolutes paradoxus*) have a very small first pterygiophore that does not intrude into the neural arch; moreover species of Agonidae have no pterygiophore in the first or second interspace, yet such species still have an incomplete first neural arch. Washington *et al.* (1984) considered absence of the neural spine and an incomplete neural arch (in larvae at least) of the first vertebral centrum synapomorphic of their cottoid crown clade. In Yabe's (1985) general description of the cottoid vertebral column, he stated that the first neural arch is incomplete in his Cottoidea.

44. First dorsal pterygiophore.— A large double pterygiophore is present with multiple axes of ossification, almost always bearing two spines, and anterior to the first neural spine (state 0); or it is anterior to the second neural spine (state 1); or a normal pterygiophore bearing a single spine inserts posterior to the second neural spine (state 2) (Figure 3–14). The evolution of this character is assumed to be ordered. State 0 was uniquely observed in the hexagrammid *Ophiodon elongatus,* state 1 in other Hexagrammidae and the majority of Cottoidei, and state 2 in the *Liparis* spp. cyclopterids and Agonidae. Amongst species with state 0, a single spine

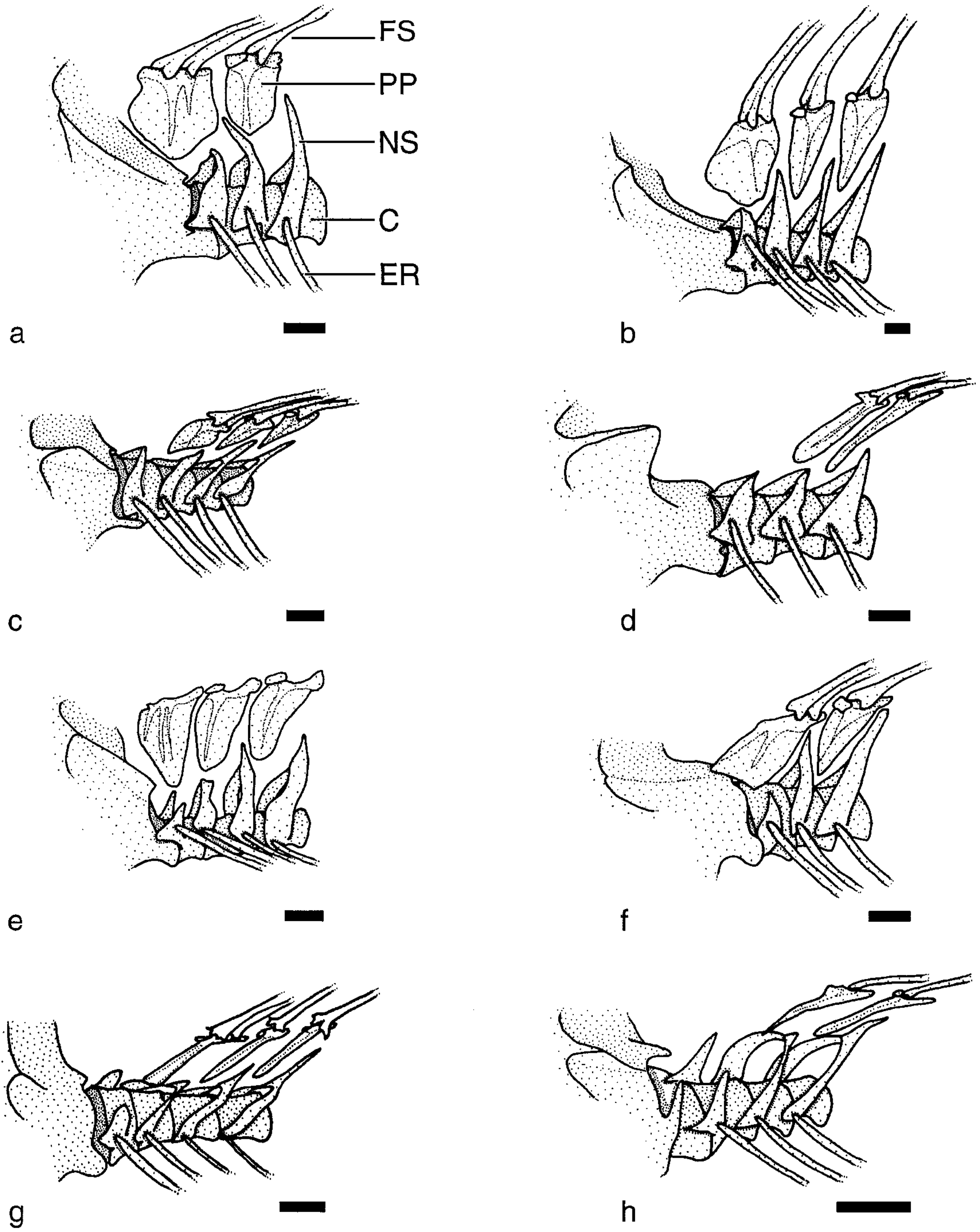


Figure 3–13. Anterior neural arches of *Scorpaenichthys marmoratus* (a), *Hemilepidotus hemilepidotus* (b), *Cottus asper* (c), *Leptocottus armatus* (d), *Jordania zonope* (e, spines missing), *Icelinus borealis* (f), *Artediellus uncinatus* (g), and *Psychrolutes paradoxus* (h) in dorso-lateral aspect. C, centrum; ER, epipleural rib; FS, fin spine; NS, neural spine and arch; PP, proximal pterygiophore. Scale bars indicate 1 mm.

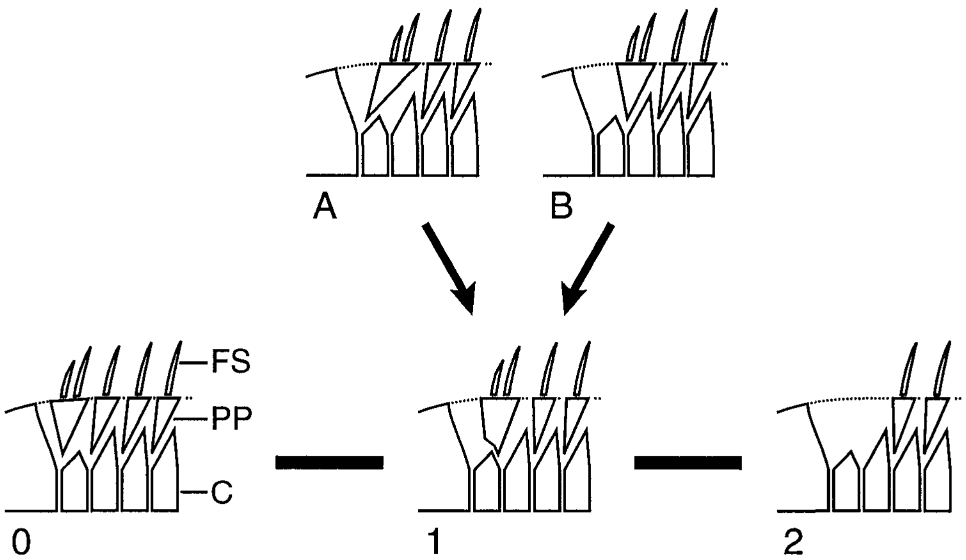


Figure 3–14. First proximal pterygiophore. C, centrum (and neural spine); FS, fin spine; PP, proximal pterygiophore. State 0, double pterygiophore inserts before first neural spine; 1, double pterygiophore inserts before second neural spine; 2, normal pterygiophore inserts after second neural spine. A and B, Yabe's (1985, Figure 31) states presumed to be the same as state 1 here.

was observed on the first pterygiophore in *Leptocottus armatus*, the cyclopterid *Eumicrotremus orbis*, the psychrolutids *Cottunculus thomsonii*, *Ebinania brephocephala*, and some specimens of *Psychrolutes paradoxus*; and no spine in *Comephorus dybowskii*. Yabe (1985, character 32, Figure 31) described the condition of the anterior pterygiophore in Scorpaeniformes, but considered two states (conditions A and B) for what I consider state 1 here. The first pterygiophore when in its "double" form is often large and occupies much of the space between the supraoccipital crest and the second neural spine, and in such a condition it is unclear as to in which interspace it inserts because it clearly rests in both interspaces. Yabe also considered multiple states for what I consider state 2; he considered any particular interspace of first insertion as a unique state. I presume that the position of posteriorly displaced dorsal fins is less stable in evolution as changes in vertebral number and other meristic features would probably affect it, unlike states 0 and 1 that are the leading end of the meristic series. Therefore, I consider state 2 in its various incarnations to be roughly comparable and more homologous with one another than with states 0 or 1. The "double" nature of the first pterygiophore is exemplified by multiple (usually two, but sometimes apparently more) axes of ossification, and in some young specimens of *Blepsias cirrhosus* and *Hemilepidotus hemilepidotus* in which two closely coupled pterygiophores were observed that presumably would fuse later in ontogeny into the single unit seen in adults.

45. Dorsal fin separation.— The dorsal fin usually has a pronounced notch between spinous and rayed portions, but with all pterygiophores bearing a ray or spine (state 0) or with the spinous and rayed portions separated by rayless pterygiophores (states 1, 2, 3, 4 directly corresponding with the number of rayless pterygiophores). The evolution of this character is considered ordered. State 0 was observed in Hexagrammidae and most Cottoidei; state 1 in *Enophrys bison, Gymnocanthus galeatus, Jordania zonope, Myoxocephalus polyacanthocephalus,* and *Oligocottus maculosus*; states 1 or 2 in *Blepsias cirrhosus*; state 2 in the cyclopterid *Eumicrotremus orbis,* states 3 or 4 in *Xeneretmus latifrons*; and state 4 in *Bathyagonus alascanus.*

46. Last dorsal and anal pterygiophore.— The last pterygiophore of the dorsal and anal fin bears two rays (state 0), only the anal pterygiophore has two rays (state 1), or both pterygiophores have a single ray (state 2). Although state 1 is presumably linked with state 0, it is plausible that state 2 could be linked with either states 0 or 1 (both rays lost simultaneously); thus, the evolution of this character is not considered ordered. State 0 was observed in Hexagrammidae and the cottoids *Cottus asper, Hemilepidotus hemilepidotus, Jordania zonope,* and *Scorpaenichthys marmoratus*; state 1 in *Rhamphocottus richardsoni*; and state 2 in all other Cottoidei. Yabe (1985, character 34) considered this character and observed state 1 in *R. richardsoni* as confirmed here, and in *Hemitripterus* species and *Nautichthys* species Yabe observed state 2 in two species of *Cottus* (*C. kazika* and *C. pollux*), a discrepancy with *C. asper* examined here.

47. Anal fin pterygiophores, spines, and rays.— The anteriormost (proximal unless specified otherwise) pterygiophore is enlarged and supports two heavy spines, and the next pterygiophore supports one smaller spine and one ray (state 0); or the anteriormost pterygiophore supports a weak spine and a ray (state 1); anteriormost two pterygiophores insert into one haemal spine interspace, and each supports one ray (state 2); or the anteriormost pterygiophore supports two rays and the posteriormost pterygiophore is rayless (state 3) (Figure 3–15). The evolution of this character appears to be ordered: with state 1 derived from state 0 by loss of the anteriormost pterygiophore, state 2 from state 1 either by conversion of the spine into a ray and division of the compound anteriormost pterygiophore into

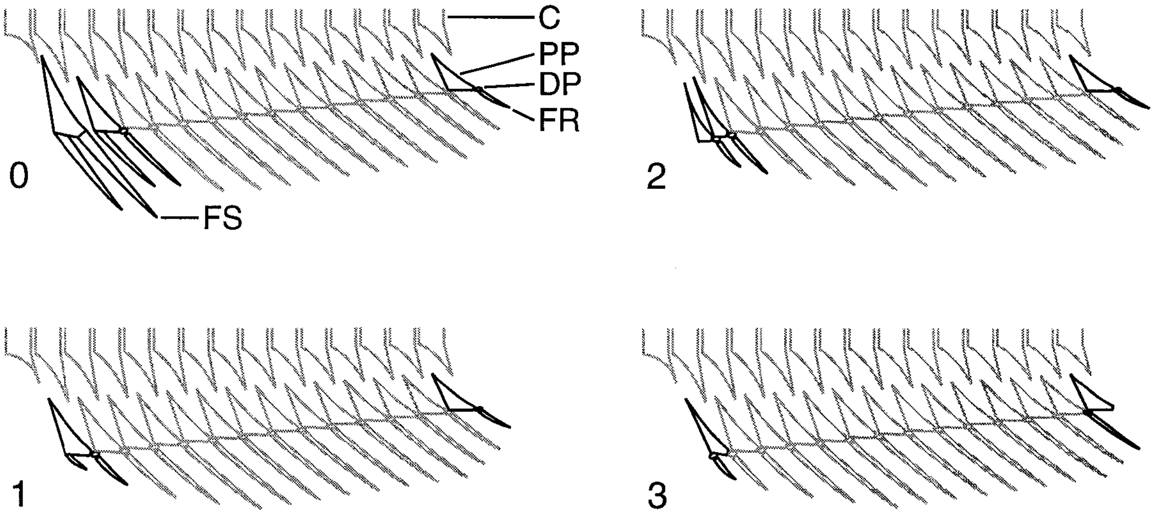


Figure 3–15. Anal pterygiophores and supported fin spines or rays. C, centrum (and haemal sipine); DP, distal pterygiophore; FR, fin ray; FS, fin spine; PP, proximal pterygiophore. State 0, anterior two pterygiophores support three spines and one ray; 1, anterior pterygiophore supports a weak spine and a ray; 2, double anterior pterygiophore supports two rays; 3, single anterior pterygiophore supports two rays and posterior pterygiophore rayless.

two narrow ones or by loss of the spine and displacement of the anteriormost pterygiophore into the interspace of its posterior neighbor, and state 3 from state 2 by loss of the anteriormost proximal pterygiophore but retention of its ray and distal pterygiophore. The evolution of this character is nonetheless considered unordered because it is possible that state 3 is derived directly from state 1 by conversion of the spine on the anteriormost pterygiophore into a ray and loss of the posteriormost ray. In all states, rays sit atop distal pterygiophores that articulate with their proper proximal pterygiophore and partly with a facet on the posterior neighboring proximal pterygiophore. In state 3, this articulation with the posterior neighbor is particularly well-developed and appears to be functionally more important than the articulation with its proper proximal pterygiophore. This is evidenced in species with this state by the posteriormost pterygiophore that lacks its own proper ray but has a well-developed articular facet for the preceding distal pterygiophore and its ray. State 0 was observed in the hexagrammid *Oxylebius pictus*; state 1 in the hexagrammid *Hexagrammos decagrammus* and *Ophiodon elongatus*; and state 2 in all Cottoidei excepting Cyclopteridae with state 3. Taranets (1941) considered the lack of true spines (in all fins presumably) to be diagnostic of his "Cottidae and related families." Cottoidei unquestionably have true, although weak, spines in the anterior dorsal fin. Although the first anal ray is typically segmented in Cottoidei, it can be small and with obscure segmentation (*e.g.*, in *Comephorus dybowskii*, *Myoxocephalus polyacanthocephalus*, and Cyclopteridae). Washington *et al.* (1984) gave a "simple" first anal pterygiophore as a synapomorphy of non-Cyclopteridae Cottoidei. Findings here suggest that the first pterygiophore might not be so simple in that assemblage but simpler (more derived) in Cyclopteridae. Yabe (1985, character 35) considered lack of spines in the anal fin to be a synapomorphy for his Cottoidea. Shinohara (1994) well describes the condition of this character amongst Hexagrammoidei, but simply used presence or absence of robust spines as a character in his phylogenetic analysis.

48. Pleural ribs.— These begin on the third vertebra (state 0), on the sixth vertebra or more posteriorly (state 1), or are entirely absent (state 2). The evolution of this character is considered ordered. State 0 was observed in Hexagrammidae, state 1 in most Cottoidei, and state 2 in *Comephorus dybowskii* and Agonidae. Regan (1913) gives "ribs absent or developed on a few posterior praecaudals only" as a diagnostic character of his Cottiformes (Cottoidei). Yabe (1985, character 36) clarified this character (states 0 and 1 used here), using state 1 as a synapomorphy of his Cottoidea (state 1 is also present in Cyclopteridae examined here).

49. Preural centrum 2: neural spine.— The spine is fully developed (state 0), or truncate (state 1). State 1 was observed in Hexagrammidae, *Cottus asper, Hemilepidotus hemilepidotus, Jordania zonope,* and *Scorpaenichthys marmoratus*; and state 0 in all other Cottoidei. Washington *et al.* (1984) considered development of this spine synapomorphic of their cottoid crown clade, but they did not notice its absence in the crown member *Cottus* species and its presence in the non-crown members *Rhamphocottus richardsoni* and the Cyclopteridae that they studied. Yabe (1985, character 43) examined this character, and curiously similar to character 46 here, *Cottus asper* is discrepant with the two *Cottus* species Yabe found to have state 0.

50. Preural centrum 2 and 3: haemal spine.— Both spines are autogenous (state 0), or only the one on preural centrum 2 is autogenous (state 1), or both are fused to their centrum (state 2). The evolution of this character is considered ordered. State 0 was observed in Hexagrammidae, state 1 in Cyclopteridae, and state 2 in all other Cottoidei. Yabe (1985, character 38) considered state 2 of this character synapomorphic for his Cottoidea (it is also known amongst Cyclopteridae). Shinohara (1994, Figure 35) describes the progressive fusion of the caudal skeleton amongst Scorpaeniformes, and amongst Cyclopteridae found state 1 in *Liparis agassizii* and *Eumicrotremus birulai,* and state 2 in *Careproctus macrodiscus.*

51. Urostyle-hypurals.— Separate elements (state 0) or fused (state 1). State 0 was observed in Hexagrammidae and the *Liparis* spp. cyclopterids and state 1 in all other Cottoidei. Yabe (1985, character 40) considered state 1 of this character to be synapomorphic for his Cottoidea (this is also the case with the cyclopterid *Eumicrotremus orbis*).

52. Hypurals-parahypural.— *The* upper three hypurals and the lower two hypurals+parahypural are fused into two plates (state 0) or these two complex plates are fused into a single plate (state 1). State 0 was observed in Hexagrammidae (the uppermost hypural is also free in *Oxylebius pictus,* the parahypural is also free in *Ophiodon elongatus*), *Blepsias cirrhosus, Hemilepidotus hemilepidotus, Jordania zonope, Rhamphocottus richardsoni, Scorpaenichthys marmoratus,* and Cyclopteridae; and state 1 in all other Cottoidei. Washington *et al.* (1984) considered fusion of these two plates into a single plate synapomorphic of their cottoid crown clade, but they did not note its reversal in the crown member *Blepsias cirrhosus* that they examined. Yabe (1985, character 41) considered this bone in two plates or completely fused to be synapomorphic for his Cottoidea, but, this is also true of the hexagrammid *Hexagrammos decagrammus* and Cyclopteridae. Shinohara (1994 Figure 35) outlined the progressive fusion of these bones amongst Scorpaeniformes.

53. Epurals.— These number three elements (state 0) or two (state 2). State 0 was observed in Hexagrammidae and most Cottoidei; and state 1 in *Comephorus dybowskii,* Agonidae, and the *Liparis* spp. cyclopterids. States 0 and 1 were observed in *Blepsias cirrhosus,* with reduction in number by fusion as evidenced by partial fusion in some specimens. One specimen of *Psychrolutes paradoxus* was observed to have two epurals, but it showed abnormal formation of its caudal skeleton with irregular bones throughout. Two methods of reduction might have occurred, fusion as previously described, or loss as seems to be the case in *Liparis* species, that have two thin epurals well spaced from each other. Yabe (1985) briefly mentioned the variety of epurals of his Cottoidea, and amongst specimens examined here, he observed two epurals in *Ascelichthys rhodorus* and *Leptocottus armatus,* and two or three in *Artediellus dydymovi* (*A. uncinatus* examined here) and *Dasycottus setiger*; three epurals were consistently observed in the specimens available to me (three specimens of *L. armatus* and at least four specimens of each of the other species).

54-57. Fin ray branching.— Pelvic (54), pectoral (55), dorsal and anal (56), and caudal fins (57) may have branched (state 0) or simple rays (state 1). Pelvic fin with state 0 was observed in the hexagrammids *Ophiodon elongatus* and *Oxylebius pictus* and the cottoids *Jordania zonope* and *Scorpaenichthys marmoratus*; and state 1 in the hexagrammid *Hexagrammos decagrammus* and all other Cottoidei (not observable in *Ascelichthys rhodorus* and *Comephorus dybowskii*). Pectoral fins with state 0 was observed in the hexagrammids *Ophiodon elongatus* and *Oxylebius pictus* and the cottoids *Artediellus uncinatus, Ascelichthys rhodorus, Jordania zonope, Scorpaenichthys marmoratus,* and Psychrolutidae; and state 1 in the hexagrammid *Hexagrammos decagrammus* and all other Cottoidei. State distribution of dorsal and anal fins was observed to match that of the pectoral fin with the exception of *Jordania zonope,* with state 1. A caudal fin was observed with state 0 in Hexagrammidae and most Cottoidei excepting *Blepsias cirrhosus, Rhamphocottus richardsoni,* and Agonidae with state 1. These four characters generally form a transformation series from all fins with branched rays to all fins with simple rays; with simplification of the pelvic fin rays first, the pectoral, dorsal, and anal fin rays next, and finally the caudal fin rays. This series is not considered because *J. zonope* presents a unique case and two species lack pelvic fins altogether. Yabe (1985, character 42) considered unbranched rays in the caudal fin and found it to be a peculiarity of *Rhamphocottus richardsoni*; his Hemitripteridae (excepting *Nautichthys*), and Agonidae.

58. Nostrils.— Anterior and posterior nostrils are both present (state 0) or the posterior nostril is obsolete (state 1). State 0 was observed in Cottoidei and state 1 in Hexagrammidae. Regan (1913) noted a single nostril as characteristic of Hexagrammidae. Obsolete posterior nostrils are known amongst some Cyclopteridae (*e.g.*, Stein, 1978).

59. Branchiostegal membranes.— These are free from each other (state 0), connected to each other but free from the isthmus (state 1), connected to each other and partially to the isthmus (state 2), or completely connected to the isthmus (state 3). The evolution of this character is assumed to be ordered. State 0 was observed in the hexagrammid *Ophiodon elongatus* and the cottoid *Comephorus dybowskii*; state 1 in the hexagrammids *Hexagrammos decagrammus* and *Oxylebius pictus* and the majority of Cottoidei; state 2 in *Artediellus uncinatus, Cottus asper, Enophrys bison, Myoxocephalus polyacanthocephalus,* Agonidae, and the psychrolutids *Dasycottus setiger* and *Eurymen gyrinus*; and state 3 in *Leptocottus armatus, Rhamphocottus richardsoni,* Cyclopteridae, and the remaining Psychrolutidae. Yabe (1985, character 44) considered this character but my findings differ from his. Yabe found his *Cottus* species and *Enophrys bison* to have branchiostegal membranes completely fused to the isthmus where I could detect a fold, and he distinguished different states between *Eurymen gyrinus* and *D. setiger* that I found unjustified.

60. Anus position.— The anus is immediately in advance of the anal fin and at the posterior end of the abdominal cavity (state 0) or advanced anteriorly (state 1). State 0 was observed in Hexagrammidae and most Cottoidei; and state 1 in *Blepsias cirrhosus, Leiocottus hirundo, Orthonopias triacis, Synchirus gilli,* Agonidae, and Cyclopteridae. An unusual condition was observed in *B. cirrhosus,* in which the anus in juvenile specimens is located posteriorly, but in adults the anus is advanced far anteriorly to just posterior of the pelvic girdle. The anus in *Clinocottus globiceps* externally appears slightly advanced anteriorly, but this is due to a large, retracted urogenital papilla; the entire structure viewed in cleared specimens is at the posterior end of the abdominal cavity and thus is state 0. Yabe (1985, character 46) considered this character with two states of anteriorly advanced anus: one with it advanced midway between the anal and pelvic fins and the other with it far advanced to just posterior of the pelvic girdle. I find this distinction unjustifiable, because in some species (*e.g., Synchirus gilli*) the anus is advanced only midway, but is also just posterior to an elongated pelvic girdle. Yabe's findings also differ slightly from mine on *C. globiceps*, that he thought to have an advanced anus.

61-68. Myology.— Eight of fourteen myological characters reported on by Yabe (1985) are considered here. It is presumed that the states Yabe observed are consistent with the species of the same genera considered here. All genera considered here, excepting two agonid genera, *Ambophthalmos*, and *Comephorus*, were reported on by Yabe. These characters were consistent within all Agonidae Yabe examined, and are presumed to be consistent with the two agonid species considered here. The other two genera do not have data ascribed to them.

61. Hyohyoides inferioris.— This is present (state 0) or absent (state 1). Yabe (1985, character 49) observed state 0 well-developed in Cyclopteridae and less developed in the psychrolutids *Ebinania, Neophrynichthys*, and *Psychrolutes*; and state 1 in other Cottoidei and Hexagrammidae (Hexagrammidae confirmed by Shinohara, 1994). Yabe considered state 0 as primitive amongst Cottoidei despite describing it in Hexagrammidae as well. State 1 was additionally observed in *Ambophthalmos angustus.*

62. Levator externus III.— This is present (state 0) or absent (state 1). Yabe (1985, character 51) observed state 0 in Hexagrammidae (confirmed by Shinohara, 1994, character 45) and state 1 in Cottoidei.

63. Rectus ventralis first series.— Rectus ventralis I, II, and III are present (state 0); II and III are present (state 1); or only III is present (state 2). The evolution of this character is not considered to be ordered, as state 1 appears to be a unique specialization and not intermediate between 0 and 2. Yabe (1985, character 52) observed state 0 in Cyclopteridae (well-developed in *Liparis* and ligamentous in *Eumicrotremus*), state 1 in Agonidae, and state 2 in Hexagrammidae (confirmed by Shinohara, 1994) and all other Cottoidei.

64. Rectus ventralis second series.— This is present and interconnecting the the third hypobranchial and urohyal (state 0) or absent (state 1). Yabe (1985, character 53, RVu) observed state 0 in most Cottoidei and state 1 in *Rhamphocottus richardsoni,* his Ereuniidae, the cyclopterid *Eumicrotremus,* and other Scorpaeniformes (including Hexagrammidae). Shinohara (1994) did not report on this muscle in Hexagrammidae, that presumably supports Yabe.

65. Obliquus superioris.— This muscle anteriorly extends to the cranium (state 0) or only to the cleithrum (state 1). Yabe (1985, character 55) observed state 0 in Hexagrammidae and the cottoid *Jordania zonope,* and state 1 in all other Cottoidei. Shinohara (1994) described this muscle in Hexagrammidae as anteriorly attaching to the cleithrum and postcleithrum, and although he dd not mention its attachment to the cranium, he diagramed it attaching to the cranium in *Hexagrammos octogrammus* (his Figure 47).

66. Extrinsic muscle of the swimbladder.— This inserts on vertebrae (state 0) or on the cleithrum (state 1). Hallacher (1974) examined the swim bladder musculature amongst Scorpaeniformes and described many of the states used by Yabe (1985, character 57). Yabe observed state 0 in Hexagrammidae (Yabe had an additional state intermediate between 0 and 1 that he observed in the hexagrammid *Zaniolepis* that was not examined here) and state 1 in Cottoidei. Shinohara (1994) confirmed Yabe's states in Hexagrammidae.

67. Coracoradialis.— It is present (state 0) or absent (state 1). Yabe (1985, character 60) observed state 0 in Hexagrammidae (confirmed and described by Shinohara, 1994) and the Psychrolutidae among cottoids, and state 1 in the remaining

Cottoidei.

68. Lateral head of the epaxialis.— This has some fibers inserting into the posttemporal fossa (state 0) or not (state 1). Yabe (1985, no character) observed state 0 in Hexagrammidae and the cottoids *Cottus, Jordania, Scorpaenichthys,* and his Ereuniidae; and state 1 in all other Cottoidei. Yabe (1985, character 14) described a reduced posttemporal fossa as synapomorphic for his Cottoidea (he also observed this in Cyclopteridae) compared to other "generalized percoids" that have a well-developed posttemporal fossa. I could not distinguish this character between Cottoidei and Hexagrammidae. It seems that a more informative and precise character is as used here (*i.e.*, no insertion of the muscle equals fossa not developed). It is unusual that Yabe described this character, but did not consider it in his phylogenetic treatment.

Characters not considered.— As far as possible, previous morphological characters used in the systematics of Cottoidei were considered in this study, particularly those of Taranets (1941), Washington *et al.* (1984), and Yabe (1985). These, and other, authors' contributions are referred to in the preceding character descriptions. These authors also put forth characters that are ambiguous or otherwise not informative here. Some of these excluded characters are outlined below. Six of Yabe's characters are not informative within Cottoidei (his characters 9, 26, 29, 30, 47 and 50). Of Yabe's 36 characters informative within Cottoidei, five (his characters 17, 19, 24, 33, and 59) were found to be ambiguous, and were not used. Of Yabe's 22 proposed synapomorphies for Cottoidei, 11 (his characters 3, 4, 14, 18, 24, 25, 37, 39, 48, 54, and 56) were observed in or are known to be present in Hexagrammidae (*e.g.*, Shinohara, 1994), and were not used.

Myodome.— The myodome is variously developed in Cottoidei, from being developed in *Scorpaenichthys marmoratus* (to a similar degree as in Hexagrammidae) to obscure in Cyclopteridae, and with a complete spectrum between. A potentially useful character in quantifying the development of the myodome is whether the prootic meets its antimere on the dorsal roof of the myodome chamber. The prootics were observed to meet each other for some length in Hexagrammidae, *Enophrys bison, Hemilepidotus hemilepidotus, Rhamphocottus richardsoni,* and *Scorpaenichthys marmoratus.*; and to be significantly separated from each other in *Clinocottus globiceps, Cottus asper, Comephorus dybowskii,* Psychrolutidae, and Cyclopteridae. Other Cottoidei were observed with the prootics meeting at point contact or with the medial "points" just slightly separated from each other, making discrete character states difficult to assign. Gill (1888) separated his Cyclopteroidea from other "mail-cheeked fishes" based on the "myodome completely wanting" versus "more or less developed." Taranets (1941) used the condition of the myodome in his key of "Cottidae and related forms" and in diagnosing a few of the subfamilies of his Cottidae. It was not considered by Yabe (1985).

Posttemporal fossa.—Yabe (1985, character 14). See character 68.

Hyoid process.—Yabe (1985, character 17) described a pointed lateral process on the hyomandibular as a synapomorphy for his Cottidae. This feature is often well-developed and easily observed amongst most of Yabe's Cottidae. But, I found ambiguity in assigning discrete states to this character. Distinctly developed and pointed processes were observed in some of Yabe's Cottidae (*e.g., Artediellus uncinatus*), but not pointed and little extended in others (*e.g., Hemilepidotus hemilepidotus*). I found species thought by Yabe to not express this character (*e.g., Blepsias cirrhosus, Rhamphocottus richardsoni,* Agonidae, and the cyclopterid *Eumicrotremus orbis*) to have it similarly developed as in some of his Cottidae. Even the hexagrammids *Hexagrammos decagrammus* and *Oxylebius pictus* were observed with slight development of this character. This process is an extension of an attachment surface on the hyomandibular to which adductor mandibulae section A1 inserts. This attachment surface, with varying development, is common to all Hexagrammidae and

Cottoidei.

Pharyngobranchial I.— Yabe (1985, character 19) noted a small, rod-like pharyngobranchial I in *Jordania zonope*, *Rhamphocottus richardsoni*, and his Ereuniidae. Additionally here, a very small cartilaginous pharyngobranchial I was observed in *Scorpaenichthys marmoratus.* Shinohara (1994) observed pharyngobranchial I only in the two hexagrammids *Ophiodon elongatus* and *Zaniolepis frenata.* This rudimentary character is probably not phylogenetically informative as its absence is only observed, and unobserved rudiments might persist.

Scapular foramen.— Yabe (1985, character 24) described three states of the scapular foramen: closed, closed but with a crack, and open. The synapomorphy for his Cottoidea was the foramen not closed, and amongst his Cottoidea the state "closed with a crack" was observed only in *Jordania zonope* and was thought to be a primitive intermediate condition. An open scapular foramen was observed in Hexagrammidae, making the closed-foramen state not informative. Moreover, close inspection and dissarticulation of the scapula from the cleithrum in *J. zonope* revealed that the scapular foramen is indeed open, even to a similar extent as observed in some other Cottoidei.

Scapula-coracoid.— Yabe (1985, character 25) put forth the connection of these two bones as primitive and their separation as a synapomorphy of his Cottoidea. These two bones meet in many Cottoidei (*e.g.*, Agonidae), but never intimately suture with each other, and this is probably what Yabe meant. This same condition is observed in all Hexagrammidae and is thus not informative.

Dorsal fin stay.— Yabe (1985, character 33) observed a stay posterior to the last dorsal pterygiophore in *Rhamphocottus richardsoni* and his Ereuniidae. I was unable to confirm this in my specimens of *R. richardsoni.*

Supernumerary anal elements.— Washington *et al.* (1984) gave absence of supernumerary anal elements as a synapomorphy of non-Cyclopteridae Cottoidei. An extra rayless pterygiophore was observed at the posterior end of the dorsal and anal fins in only one *Liparis* species (*L. florae*). This character is not informative here. Also, the first two pterygiophores of the anal fin in non-Cyclopteridae Cottoidei are supernumerary (see character 47).

Haemal spine on second preural centrum.— Washington *et al.* (1984) gave presence of an enlarged haemal spine on the second preural centrum as a synapomorphy of non-Cyclopteridae Cottoidei. This spine was observed to be slight in build in the *Liparis* spp. cyclopterids, but not in the cyclopterid *Eumicrotremus orbis,* that has this spine developed to a similar degree as other non-Cyclopteridae Cottoidei.

Hypurapophysis.— Yabe (1985, character 39) put forth the absence of a hypurapophysis as a synapomorphy for his Cottoidea. Amongst specimens examined here, a hypurapophysis was only observed in *Oxylebius pictus* (also in *Zaniolepis* sp. amongst Hexagrammidae; Shinohara, 1994) and is thus not informative here.

Uroneural.— A uroneural is observed in some Cottoidei and often variably so within such species (*e.g., Scorpaenichthys marmoratus*). It is not considered phylogenetically reliable here because Fujita (1990) showed that this bone often fuses with the urostyle making actual loss difficult to determine. It was discussed briefly by Yabe (1985), but not considered in his phylogeny.

RESULTS

Phylogenetic Analysis

Sixty four characters with a total of 111 minimum steps were used to find the most parsimonious tree describing the interrelations of the 34 in-group taxa. A heuristic search of 100 replicates starting from random trees consistently found the same batch of 96 equally shortest trees of 234 steps (using PAUP* 4.0b10, Swofford, 2002). These trees were rooted with Hexagrammidae as a paraphyletic out-group. This was done because several authors (*e.g.*, Quast, 1965 and Shinohara, 1994) independently suggested that Hexagrammidae might not be monophyletic without inclusion of Cottoidei and characters were not examined with the intent of resolving Hexagrammidae. The strict consensus of the 96 rooted trees is shown in Figure 3–16.

The evolution of two characters (11 and 21) were modeled as asymmetric step-matrices (shown in Figures 3–6 and 3–11) that impose rooting prior to determining tree length; and by extension, in searching for the most parsimonious (shortest) tree. Without ancestral states a priori assumed, a single tree may be rooted at several nodes without affecting tree length. This results in searched trees being multiply rooted and treated as separate trees. In the search conducted here, 6181 different rootings were found that reduced to 96 unique trees when rerooted with Hexagrammidae as the out-group. Internal states of the basal node of these trees were reconstructed with PAUP* (accelerated and delayed transformation assumptions yielded the same reconstructed states on this node) and were used to set ancestral states to limit superfluous rootings in further analysis.

Character fit on the 96 shortest trees is 0.47 consistent (111 minimum steps out of 234 most parsimonious tree steps). Character evolution over the consensus tree is summarized in Appendix 3–2 and ambiguous character evolution modeled with delayed and accelerated transformation in Appendix 3–3. Phylogenetic signal of these data in constructing the presented consensus phylogeny was tested by permutation tail probability (PTP, Faith and Cranston, 1991). One thousand replicates of random data were generated for the 68 characters in the in-group only and searched heuristically from 10 replicates of random-addition-sequence starting trees to find the shortest tree consistent with the consensus tree from the actual data. The shortest tree found from these replicates was 400 steps, and most

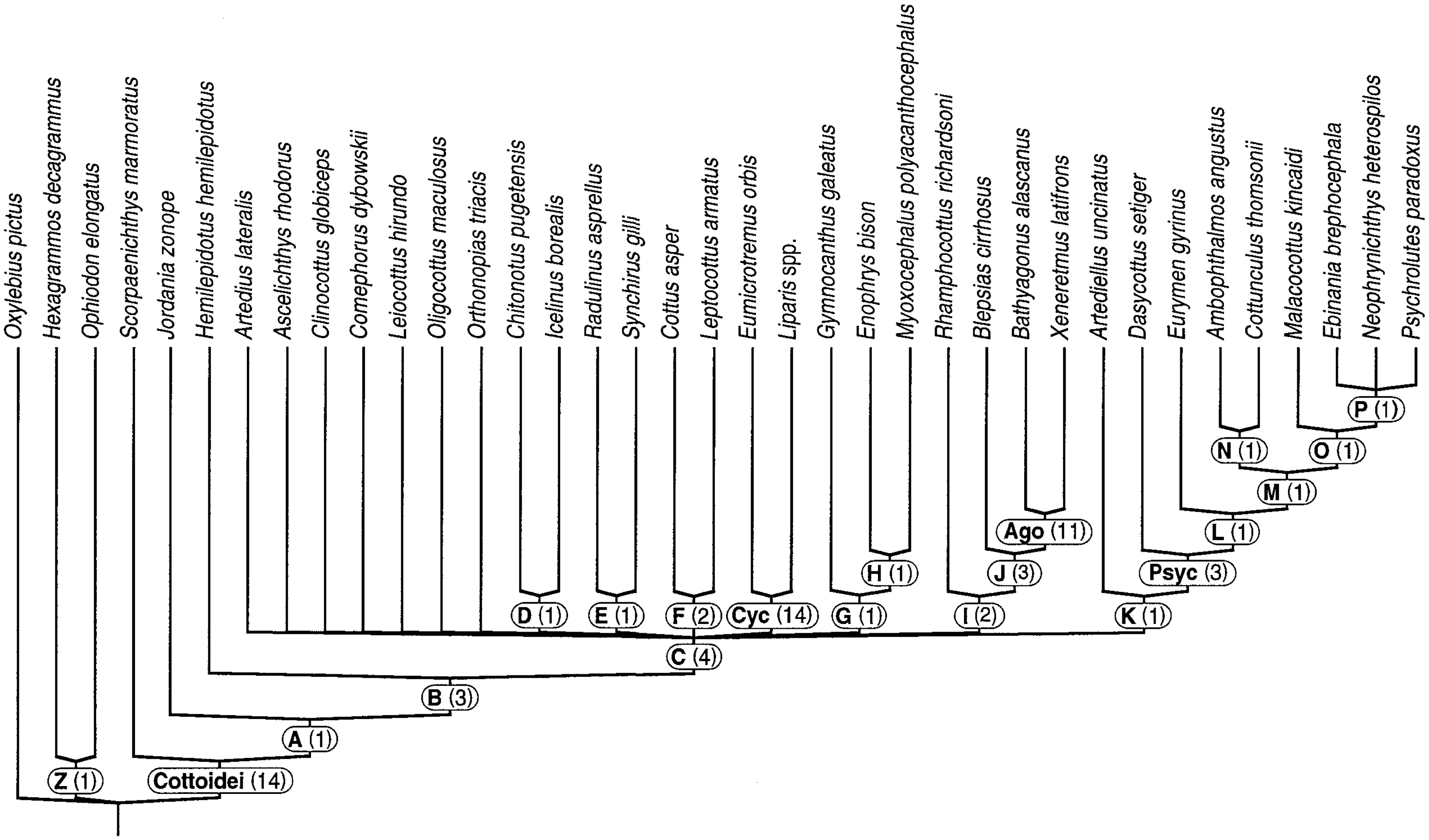


Figure 3–16. Strict consensus of 96 equally most parsimonious trees based on 68 characters with 111 minimum steps of evolution. Clades labeled for reference in text and decay indices (Bremer, 1988) given in parentheses. Ago, Agonidae; Cyc, Cyclopteridae; Psyc, Psychrolutidae.

were about 412 steps. The probability that random data could generate the tree plotted in Figure 3–16 is p=0.001.

Relative support of individual clades of the consensus tree was measured with Bremer (1988) decay indices. The program TreeRot.v2 (Sorenson, 1999) was used to generate constraint clades of the 21 internal nodes of the consensus tree. For each constraining clade, a heuristic search from 100 random addition sequence replicates was used to find the shortest tree that did not support the constraining clade. These decay values indicate how much longer the overall tree can be before a given clade is no longer strictly supported, and are plotted on the corresponding branches of Figure 3–16.

DISCUSSION

Character Evolution

1. *Nasal spine.*— Primitively present; lost in the hexagrammid clade Z and the cottoids *Comephorus dybowskii*, clade F, Cyclopteridae, and clade K. When evaluating equivalent state changes on two or more branches of an unresolved clade (*i.e.*, clade C), it is important to note that those changes may or may not be homoplastic depending on how the true phylogenetic tree is resolved. For example, the loss of this character is unequivocally homoplastic between clade Z and Cyclopteridae, but it may or may not be homoplastic between Cyclopteridae and *C. dybowskii*, clade F, or K. This is expanded on for some of the characters discussed below.

2. *Frontal spines (on supraorbital canal).*— Primitively absent; developed in clade D, *Gymnocanthus galeatus*, *Myoxocephalus polyacanthocephalus*, and the psychrolutids *Dasycottus setiger* and *Cottunculus thomsonii*. Development of these spines might be independently acquired by *G. galeatus* and *M. polyacanthocephalus*, or a character of

clade G with loss in *E. bison* (Appendix 3–3). The spines in psychrolutids that form on most or all cranial arches are not homologous with such spines in other Cottoidei that form predominantly on the third arch (or equivalent location).

3. Frontal spine (orbital rim).— Primitively absent; developed in *Gymnocanthus galeatus* and clade I. This spine in *G. galeatus* is similar to that of *Blepsias cirrhosus* (member of clade I), but its homology is cast in doubt.

4. Orbital pores.— Primitively present; lost in *Comephorus dybowskii,* clade F, Cyclopteridae, and Psychrolutidae; lost also, but in a unique manner with mostly bone enclosed reduced canals, in clade I.

5. Infraorbital number.— Primitively six; reduced to five in *Comephorus dybowskii, Radulinus asprellus,* clades H, I, and K; further reduced to four in Cyclopteridae, Agonidae, and the psychrolutid *Cottunculus thomsonii.* The mode of reduction in *C. thomsonii* is anatomically distinct and, not surprisingly, evolutionarily distinct.

6. Infraorbitals 1-3 pores.— Primitively with at least one pore on each infraorbital; pore on second infraorbital lost in *Rhamphocottus richardsoni* and Agonidae; unique condition developed in Cyclopteridae. A weakly developed pore on the second infraorbital in *Blepsias cirrhosus* suggests that loss or reduction of this pore is a synapomorphy of clade I (this is equally parsimonious and modeled with accelerated transformation, Appendix 3–3).

7. Infraorbitals 4-6 (postorbitals) pores.— Primitively present; lost in clade C excepting *Ascelichthys rhodorus, Chitonotus pugetensis,* and clade G. Loss of these pores maps as a character of clade C, because most of its unresolved clades lack them. Although, if the true phylogeny has *A. rhodorus, C. pugetensis,* or clade G, or some combination thereof at the base of clade C, loss of these pores would be a character of the superseding sister clade and not of clade C. This applies to some other characters of clade C (25, 42, 43, 46, 49, 52) discussed below.

8. Preopercle pores.— Primitively more than four; reduced to four in clade B; further reduced to three in *Comephorus dybowskii*; and two in Cyclopteridae. Whether the condition in *C. dybowskii* is intermediate to the more reduced state in Cyclopteridae is not resolved. As mapped on the unresolved clade C, this character jumps two steps in Cyclopteridae.

9. Preopercular spines.— Primitively present; lost in the hexagrammid *Hexagrammos decagrammus* and the cottoids *Comephorus dybowskii*, Cyclopteridae, and clade L; redeveloped in *Malacocottus kincaidi.*

10. Operculomandibular and infraorbital canals.— A broad connection of these two canals between infraorbitals four and five is unique to Psychrolutidae.

11. Extrascapulars.— State 0 in this transformation series with fusion of the posterior lateral and medial extrascapulars is a synapomorphy of clade I and homoplastic in the hexagrammid *Hexagrammos decagrammus.* State 1 with the pterotic extrascapulars continuous is primitive for Cottoidei and state 2 with them separate arose in *Ascelichthys rhodorus, Comephorus dybowskii, Icelinus borealis, Radulinus asprellus,* and in clades F and K. State 3 with the posterior pterotic extrascapular autogenous is unique to Psychrolutidae and states 4 with loss of the posterior lateral extrascapular and 5 with fusion of the posterior pterotic and medial extrascapulars are unique to the psychrolutid clades M and N respectively. State 6 is unique to Cyclopteridae and its ancestral state is undetermined but is state 0, 1, or 2 depending on how clade C resolves.

12. Parietal extrascapular.— Lost or obscured uniquely in Cyclopteridae.

13. Parietal extrascapular, autogeny.— Autogeny unique to clade O.

14. Parietal extrascapular, spine or blunt protrusion.— Primitively absent; developed in clades D, G, I, and the psychrolutids *Dasycottus setiger* and *Cottunculus thomsonii.* Like frontal canal spines (character 2), these spines in Psychrolutidae are not homologous with such spines in other Cottoidei.

15. Parietal extrascapular, pores.— Loss of pores is a character of clade C.

16. Lateral line.— Marked reduction unique to Cyclopteridae.

17. Lateral line ossifications, number.— Primitively large in number, greatly outnumbering the vertebrae by at least 1.5:1; reduced to correspond with the number of underlying vertebrae in *Jordania zonope* and most of clade C excepting *Gymnocanthus galeatus* and *Blepsias cirrhosus* with a ratio less than 1.25:1. Depending on delayed or accelerated transformation, this reduction may be homoplastic between *J. zonope* and clade C, or a character of clade B with reversal in *Hemilepidotus hemilepidotus* (Appendix 3–3). The aberrant counts in *G. galeatus* and *B. cirrhosus* are likely reversals due to the disparity in number compared with the basal taxa, and in *B. cirrhosus* by its resolved nested position above the base of clade C. Further reduction to less than the number of vertebrae is unique to clade K.

18. Lateral line ossifications, pores.— Ventral accessory tubule unique to clade D and both dorsal and ventral accessory tubules unique to clade H. These two instances of accessory tubules are not related.

19. Lateral line ossifications, ctenii.— Primitively absent; developed in *Jordania zonope, Hemilepidotus hemilepidotus, Artedius lateralis, Orthonopias triacis,* clades D, E, and *Rhamphocottus richardsoni.* Depending on delayed or accelerated transformation, this character was independently gained in *J. zonope* and *H. hemilepidotus,* or gained in clade A and subsequently lost in clade C (Appendix 3–3). Because these ctenii occur in several of clade C's unresolved branches, it is likely a character of clade A with loss in branches of clade C.

20. Scales.— Primitively present; lost in *Scorpaenichthys marmoratus, Ascelichthys rhodorus, Clinocottus globiceps, Comephorus dybowskii, Oligocottus maculosus, Liparis* species, *Enophrys bison, Eurymen gyrinus, Ambophthalmos angustus,* and clade P. Evolution of this character is ambiguous within Psychrolutidae (Appendix 3–3).

21 Scales, type and distribution (transformation series).— Primitively ctenoid scales (state 0 in transformation series) in the out-group and modified in Cottoidei.

Modification of ctenoid scale to the cottoid morphology (state 1) is either a character of Cottoidei or clade A, because absence of scales in *S. marmoratus* leaves ambiguity on when this transformation occurred (Appendix 3–3). Specialized states are unique to *Jordania zonope* and *Gymnocanthus galeatus* (states 2 and 3 respectively). Ctenoid plate scales in dorsal bands (state 4) is a character of clade K, although possibly homoplastic with the widely distributed ctenoid plate scales (state 5) of Cyclopteridae that presumably arose from a similar intermediate (state 4). Ctenoid plate scales of the cyclopterid *Eumicrotremus orbis* (state 5) are ambiguous as to whether they are unique to that species or a character of Cyclopteridae that is not expressed in *Liparis* species (Appendix 3–3). Widely distributed isolated ctenii scales (state 6) possibly arose twice, in clades F and I, both determined to be from ancestral modified ctenoid scales (state 1). Large ctenii modified into armor plates (state 7) are unique to Agonidae and are derived from isolated ctenii scales (state 6).

22. Frontal, orbital rim.— Lateral expansion in Cyclopteridae and clade P.

23. Vomer, teeth.— Primitively present; lost in Cyclopteridae, *Gymnocanthus galeatus, Ambophthalmos angustus,* and clade O excepting *Ebinania brephocephala.* The evolution of this character in Psychrolutidae is ambiguous (Appendix 3–3).

24. Palatine, teeth.— Primitively present; lost in *Comephorus dybowskii, Leiocottus hirundo, Radulinus asprellus,* Cyclopteridae, clade G, *Rhamphocottus richardsoni,* and Psychrolutidae.

25. Palatocranial articulation.— Primitively developed, lost in clade C excepting *Comephorus dybowskii,* clade F, and *Blepsias cirrhosus.* See character 7 for a discussion on characters of clade C with reversals in unresolved branches.

26. Entopterygoid.— Primitively present; lost in *Comephorus dybowskii* and clade E.

27. Basisphenoid.— Primitively present; loss is a character of Cottoidei.

28. Pterosphenoid-parasphenoid.— Primitively these two bones meet; excluded from each other by the intervening prootic in *Blepsias cirrhosus* and clade L.

29. Trigeminofascialis chamber.— Primitively with two openings; reduced to a single opening in *Blepsias cirrhosus* and Psychrolutidae. This and the previous character (28) are curious homoplasies between apparently distant taxa.

30. Intercalar.— Primitively large and meeting the prootic; marked reduction and exclusion from the prootic is a character of Cottoidei.

31. Baudelot's ligament.— This ligament primitively attaches to the basioccipital and attaches to first vertebral centrum uniquely in clade J.

32. Basihyal.— Primitively developed and ossified, and rudimentary or unobserved is a uniquely derived character of Cottoidei.

33. Pharyngobranchial tooth plates.— Primitively the second, third, and fourth plates are present; loss of the fourth plate is a character of Cottoidei; and loss of the second plate occurs in *Hemilepidotus hemilepidotus, Synchirus gilli,* Cyclopteridae, clades H, J, and Psychrolutidae.

34. Branchiostegal rays.— Primitively six rays; seven rays is unique to Psychrolutidae.

35. Scapula-actinost.— Primitively separate elements; scapula and dorsalmost actinost fused in *Scorpaenichthys marmoratus* and Agonidae.

36. Coracoid, base.— Primitively articulates with lateral wing of the cleithrum in the out-group; articulation relocated onto main shaft of the cleithrum in Cottoidei, reversed in *Comephorus dybowskii,* clade F, and Agonidae; specialized enlarged coracoid base in *Scorpaenichthys marmoratus, Artedius lateralis, Clinocottus globiceps, Leiocottus hirundo, Oligocottus maculosus,* and *Orthonopias triacis.* Informativeness of the specialized state is undetermined with clade C unresolved.

37. Actinost foramina.— Primitively all four foramina present; lowermost foramen lost in clades E and G; all but the dorsalmost foramen lost in *Artediellus uncinatus* and *Malacocottus kincaidi*; all foramina lost in *Comephorus dybowskii,* Agonidae, and Psychrolutidae excepting *M. kincaidi.* Possibly two modes of loss occurred: loss of all at once and loss of ventral foramina first. The former route appears to be the case in Agonidae with its sister taxa, *Blepsias cirrhosus* and *Rhamphocottus richardsoni,* showing all four foramina present but poorly developed (Figure 3–12i-l). The latter route appears to be the case in Psychrolutidae with its sister taxon, *Artediellus uncinatus,* showing a well-developed dorsalmost foramen and a similar reversal in one psychrolutid, *M. kincaidi* (Figure 3–12g-h). Although the evolution of this character is ambiguous between clade K and Psychrolutidae (Appendix 3–3), the accelerated transformation model is preferred as it predicts the above mentioned hypothesis about this character's evolution in this clade.

38. Postcleithra.— Primitively two present; one lost in *Eurymen gyrinus* and *Cottunculus thomsonii*; both lost in *Artedius lateralis, Ascelichthys rhodorus, Clinocottus globiceps, Comephorus dybowskii, Synchirus gilli,* and *Psychrolutes paradoxus*; blade-like specialization of both postcleithra unique to Agonidae.

39. Pelvic girdle.— Primitively kite-shaped; sucker and box-like specializations unique to Cyclopteridae and clade N, respectively.

40. Subpelvic process.— Primitively well-developed; rudimentary process unique to clade J.

41. Pelvic fin.— Lost in *Ascelichthys rhodorus* and *Comephorus dybowskii.*

42. Pelvic fin, spine and rays.— Primitively I,5 in out-group and basal Cottoidei, I,4 in clade B, I,3 in clade C, and I,2 in Agonidae. Reversal to I,5 from I,3 in Cyclopteridae is certainly homoplastic and its unique "rays" are so specialized they could be considered a unique state. Reversal to I,4 from I,3 in clade F is dependent on where it resolves in the true phylogeny of clade C (see character 7 for a discussion on characters of clade C with reversals in unresolved branches).

43. First neural arch.— Primitively complete; incomplete in *Jordania zonope* and clade C excepting *Comephorus dybowskii,* clade F, *Liparis* spp. cyclopterids, and *Rhamphocottus richardsoni.* Evolution of this character in basal Cottoidei is unresolved, with either homoplastic incompletion in both *J. zonope* and clade C, or an incompletion in clade A and a reversal in *Hemilepidotus hemilepidotus* (Appendix 3–3). See character 7 for a discussion on characters of clade C with reversals in unresolved branches. Washington *et al.* (1984) considered an incomplete first neural in larvae (at least) synapomorphic of their cottoid crown clade that is roughly comparable with clade C here.

44. First pterygiophore.— Primitively a double pterygiophore in advance of the second neural spine; unique anterior displacement in *Ophiodon elongatus;* posterior displacement in *Liparis* spp. cyclopterids and Agonidae.

45. Dorsal fin separation.— Rayed and soft portions of the dorsal fin primitively continuous; separated by one unrayed pterygiophore in *Jordania zonope, Oligocottus maculosus,* and clade G; further separated by one or two unrayed pterygiophores in clade J; and separated by three or four unrayed pterygiophores in Agonidae. The internal node assignments for this character are ambiguous within clade J (Appendix 3–3), but dorsal fin separation greater than seen in other Cottoidei is a character of clade J and further separation a character of Agonidae.

46. Last dorsal and anal pterygiophore.— Primitively each bearing two rays; reduced to each bearing a single ray in clade C excepting *Cottus asper* and *Rhamphocottus richardsoni* (lost on the last dorsal pterygiophore only in this species). See character 7 for a discussion on characters of clade C with reversals in unresolved branches.

47. Anal fin pterygiophores, spines, and rays.— Primitive state undetermined as the three basal taxa (*Oxylebius pictus,* clade Z, and Cottoidei) each have a different state and ordered evolution was not assumed. Considering that non-cottoid Scorpaeniformes typically have anal fin spines and that Hexagrammidae are generally thought be sister to or to include Cottoidei (*e.g.*, Quast, 1965 and Shinohara, 1994), it is likely that one of the states of the hexagrammids *O. pictus* or clade Z is primitive on this tree (Appendix 3–3). Shinohara (1994) suggested that *O. pictus* (with *Zaniolepis* spp.) is sister to a clade including clade Z (and *Pleurogrammus* spp.) and Cottoidei. This would support ordered evolution of this character: with the heavy first pterygiophore of *O. pictus* lost, leaving a first pterygiophore with a single weak spine as evidenced in clade Z, then this remaining spine lost as a character of Cottoidei, and the articulation of fin rays with the posterior next pterygiophore a specialized character of Cyclopteridae.

48. Pleural ribs.— Primitively beginning on third vertebra; beginning on sixth or more posterior vertebrae a character of Cottoidei; completely lost in *Comephorus dybowskii* and Agonidae.

49. Preural centrum 2: neural spine.— Primitively truncate; developed in clade C excepting *Cottus asper.* See character 7 for a discussion on characters of clade C with reversals in unresolved branches.

50. Preural centrum 2 and 3: haemal spine.— Primitively both autogenous; fusion of both to their centra a character of Cottoidei; autogeny of the haemal spine on the second preural centrum only reacquired as a character of Cyclopteridae.

51. Urostyle-hypurals.— Primitively autogenous; fused together a character of Cottoidei; autogeny reacquired in the *Liparis* spp. cyclopterids.

52 Hypurals-parahypural.— Primitively in two or more plates; fused in clade C excepting Cyclopteridae, *Rhamphocottus richardsoni,* and *Blepsias cirrhosus.* See character 7 for a discussion on characters of clade C with reversals in unresolved branches. Within clade I, this character has ambiguous evolution: with independent autogeny in *R. richardsoni* and *B. cirrhosus,* or autogeny in clade I and fusion reacquired in Agonidae (Appendix 3–3).

53. Epurals.— Primitively three; two or three in *Blepsias cirrhosus*; and two in *Comephorus dybowskii, Liparis* spp. cyclopterids, and Agonidae. The internal node assignments of this character within clade J are ambiguous (Appendix 3–3), but it appears that fusion of epurals occasionally observed in *B. cirrhosus* is the mode of reduction to two epurals seen in Agonidae.

49-53. Caudal skeleton (transformation series).— Shinohara (1994, Figure 35) outlines a transformation series of caudal skeleton fusion amongst Scorpaeniformes that seems geared toward progressive fusion rather than based on phylogeny. Here a similar transformation series is drawn (Figure 3–17), but based on the overall phylogenetic tree and including two other characters: the condition of the neural spine on the second preural centrum and the number of epurals. Amongst specimens examined here, nine states are observed in the caudal skeleton with clear transformations between each. In Hexagrammidae the haemal spines on both the third and second preural centra are autogenous, the neural spine on the second preural centrum is not developed, the urostyle is not fused with the hypurals, and the hypurals and parahypural show varying degrees of, but not complete fusion (states 0, a, and b, in Figure 3–17). The less fused forms of the hypurals-parahypural plates of Hexagrammidae are not exhibited within Cottoidei and not phylogenetically informative within the scope of this study; therefore, those three states are considered state 0. State 1 is linked to state 0 by at least two steps: the haemal spines are fused with the preural centra and the urostyle is fused with the upper hypurals plate. State 2 is linked to state 1 by one step: the hypurals and parahypural are fused into one complete bone. State 3 is linked to state 1 by one step: the development of the neural spine on the second preural centrum. State 4 is linked to states 2 or 3 by one step: development of the neural spine on the second preural centrum or fusion of the hypurals-parahypural plates. State 5 is linked to and not very differentiated from state 3 by one step: the partial fusion of two epurals. State 6 is linked to states 4 and 5 by one step: loss of an epural or the fusion of the hypurals-parahypural plates. State 7 is linked with state 3 by one step: the haemal spine on the second preural centrum autogenous. State 8 is linked to

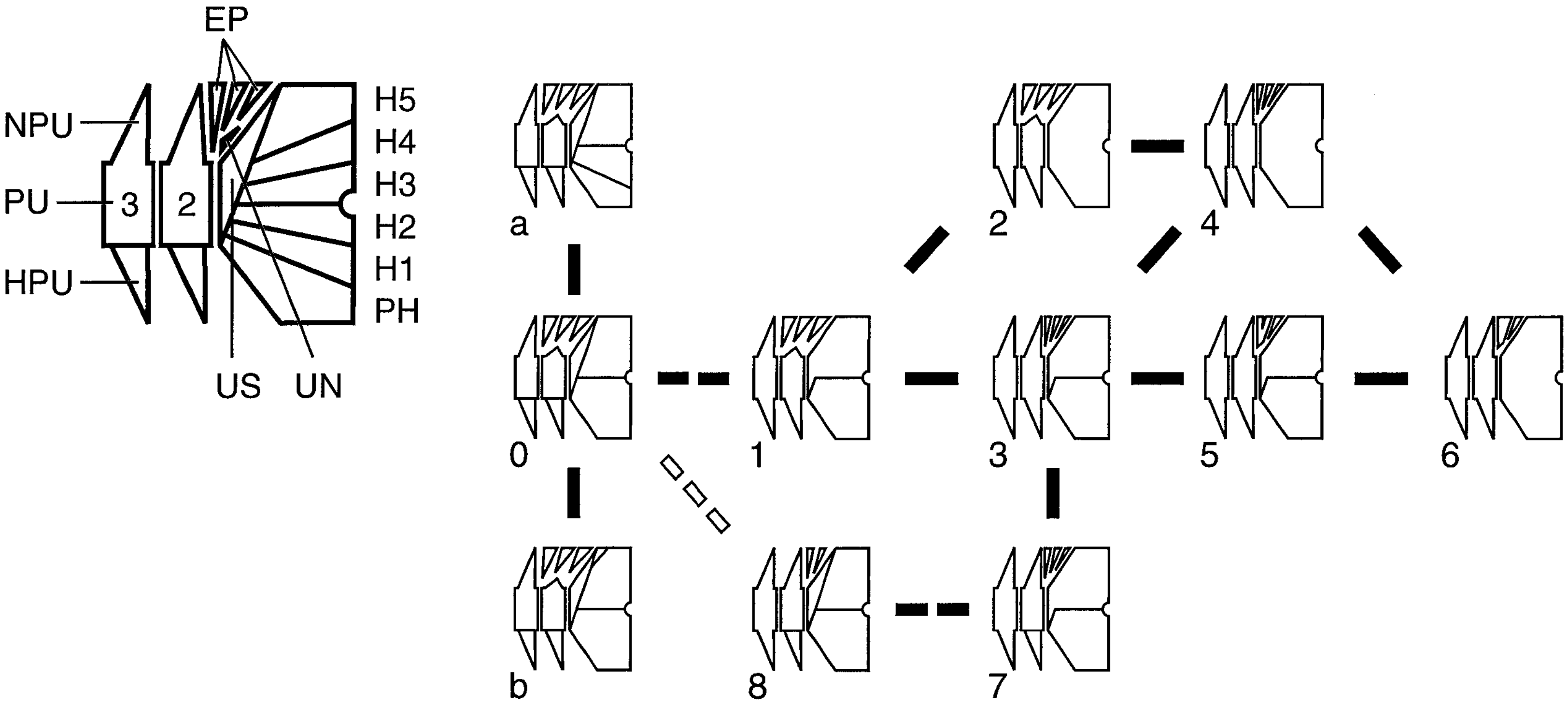


Figure 3–17. Caudal skeleton and transformation series. EP, epural; H1-5, hypural; HPU, haemal spine (of preural centrum); NPU, neural spine (of preural centrum); PH, parahypural; PU, preural centrum (2 and 3); UN, uroneural; US, urostyle. States described in text. Links count number of evolutionary steps between states. Outlined links are hypothetical and not supported by the overall phylogeny (Figure 16). Unfused elements of the caudal skeleton at left.

state 7 by two steps: the urostyle becoming free from the hypurals-parahypural plates and the loss of one epural. State 0 can also be linked to state 8 by three steps: fusion of the haemal spine on the third preural centrum, development of the neural spine on the second preural centrum, and loss of one epural. State 0 is in the out-groups; state 1 is primitive for Cottoidei; higher than state 1 amongst clade C; state 2 in *Cottus asper*; state 3 in *Rhamphocottus richardsoni*; state 4 in the majority of clade C; state 5 in *Blepsias cirrhosus*; state 6 in *Comephorus dybowskii* and Agonidae; and states 7 and 8 in the cyclopterids *Eumicrotremus orbis* and *Liparis* species, respectively. The ancestral states of state 2 in *C. asper* and state 3 in *R. richardsoni* are not resolved and are either directly from state 1 or a reversal from state 4. State 3 in *R. richardsoni* was ancestral to state 5 in *Blepsias cirrhosus* that was ancestral to state 6 in Agonidae. State 6 in *Comephorus dybowskii* was derived from state 4. The ancestral state for Cyclopteridae was state 3 that is only present in *R. richardsoni* on this tree, but state 3 is also known amongst other Cyclopteridae not examined here (Shinohara, 1994), further suggesting that state 8 in *Liparis* species is not phylogenetically linked with state 0 in the hexagrammid out-groups.

54-57. Fin ray branching.— Primitively rays in all fins branched; dorsal and anal rays simplified in *Hexagrammos decagrammus* and clade A; pelvic and pectoral rays simplified in *H. decagrammus* and clade B; caudal rays simplified in Cyclopteridae and Agonidae; reversal to branched rays in the pectoral, dorsal, and anal fins in *Ascelichthys rhodorus*, and clade K.

58. Nostrils.— Posterior nostril obsolete in Hexagrammidae but developed in Cottoidei. With the majority of percomorph and other scorpaeniform fishes having both nostrils developed, it is difficult to believe that the posterior nostril of Cottoidei is neomorphic, but with recent work suggesting that Hexagrammidae are paraphyletic without inclusion of Cottoidei (*e.g.*, Quast, 1965, Shinohara, 1994), this might very well be the case. Further work on hexagrammid nasal anatomy is needed to investigate just how obsolete the group's posterior nostril really is.

59. Branchiostegal membranes.— Primitively connected to each other but not to the isthmus; freed from each other in the hexagrammid *Ophiodon elongatus* and *Comephorus dybowskii*; connected to each other and partly to the isthmus in clades F and H, Agonidae, and clade K; connected broadly to the isthmus in *Leptocottus armatus*, Cyclopteridae, *Rhamphocottus richardsoni*, and clade M. The internal state assignments of this character within clade I are ambiguous (Appendix 3–3).

60. Anus position.— Primitively at the posterior end of the abdominal cavity and immediately in advance of the anal fin; anteriorly advanced in *Leiocottus hirundo*, *Orthonopias triacis*, *Synchirus gilli*, Cyclopteridae, and clade J.

61. Hyohyoides inferioris.— Primitively not developed; developed in Cyclopteridae and developed to a lesser degree in clade P.

62. Levator externus III.— Primitively developed; loss is a character of Cottoidei.

63. Rectus ventralis first series.— Primitively only section III developed; II and III developed in Agonidae; and I, II, and III developed in Cyclopteridae. The condition of this muscle in Agonidae is not intermediate to that in Cyclopteridae.

64. Rectus ventralis second series.— Primitively absent; development of this muscle is a character of Cottoidei; reversed in the cyclopterid *Eumicrotremus orbis* and *Rhamphocottus richardsoni*.

65. Obliquus superioris.— Primitively extending to the cranium; extending only to the cleithrum in Cottoidei excepting *Jordania zonope*. The evolution of this character is ambiguous as either a homoplasy between *Scorpaenichthys marmoratus* and clade B, or a character of Cottoidei but reversed in *J. zonope* (Appendix 3–3).

66. Extrinsic muscle of the swimbladder.— Primitively inserting on vertebrae; inserting only on the cleithrum is a character of Cottoidei.

67. Coracoradialis.— Primitively developed; loss a character of Cottoidei; redeveloped as a character of Psychrolutidae.

68. Lateral head of the epaxialis.— Primitively inserting into the posttemporal fossa; loss of this insertion a character of clade B; reversed in *Cottus asper.*

Clade Support

Cottoidei are strongly supported with at least 14 unambiguous steps of evolution with respect to the Hexagrammidae out-group; of the 14 characters nine are valid in all 34 Cottoidei examined (Figure 3–18). A decay value of 14 steps indicates that these state changes are nearly incontrovertible (within the data set used here) in supporting this clade. The eight unique state changes (autapomorphies) include: loss of the basisphenoid (character 27), marked reduction of the intercalar (30), reduction and lack of ossification or complete loss of the basihyal (32), loss of the fourth pharyngobranchial tooth plate (33), first anal fin pterygiophore double with each supporting one ray (47, ancestral state ambiguous, Figure 3–19 and Appendix 3–3; first pterygiophore lost but its ray retained in Cyclopteridae), pleural ribs not anterior of the sixth vertebra (48), possession of two nostrils (58), absence of the levator externus III (62), and external muscle of the swimbladder inserting only on the cleithrum and not on vertebrae (66). Homoplastic state changes supporting this clade include: coracoid attaching to the shaft of the cleithrum, not on its lateral wing (36, reversed in *Comephorus dybowskii,* clade F, and Agonidae), fusion of the haemal spines with the second and third preural centra (50, two steps, autogeny reacquired on the second preural centrum only in Cyclopteridae), fusion of the hypural plate to the urostyle (51, reversed in *Liparis* species), development of the rectus ventralis second series (64, lost in the cyclopterid *Eumicrotremus orbis* and *Rhamphocottus richardsoni*), and loss of the coracoradialis (67, redeveloped in Psychrolutidae). Additionally, two ambiguous state changes might support Cottoidei (Figure 3–19; see the *Character Evolution* section for discussion on ambiguous characters): modification of ctenoid

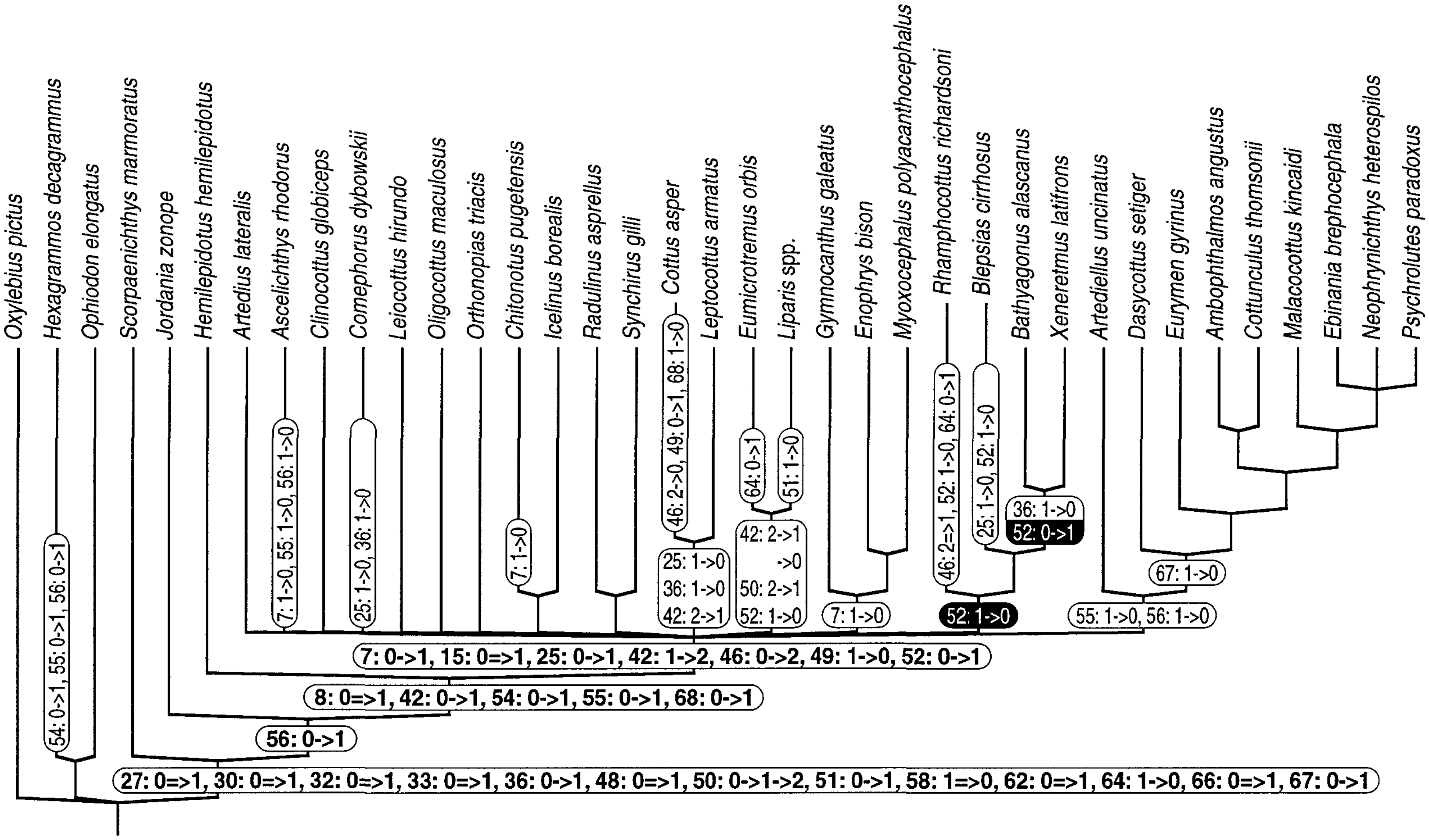


Figure 3–18. Unambiguous state changes in the basal interrelations of Cottoidei (branches Cottoidei, A, B, and C of Figure 3–16). Unique changes (=>) distinguished from homoplastic (->) and all homoplastic changes mapped. Character 52 ambiguous in clade I and modeled with delayed (normal print) and accelerated transformation (inverse).

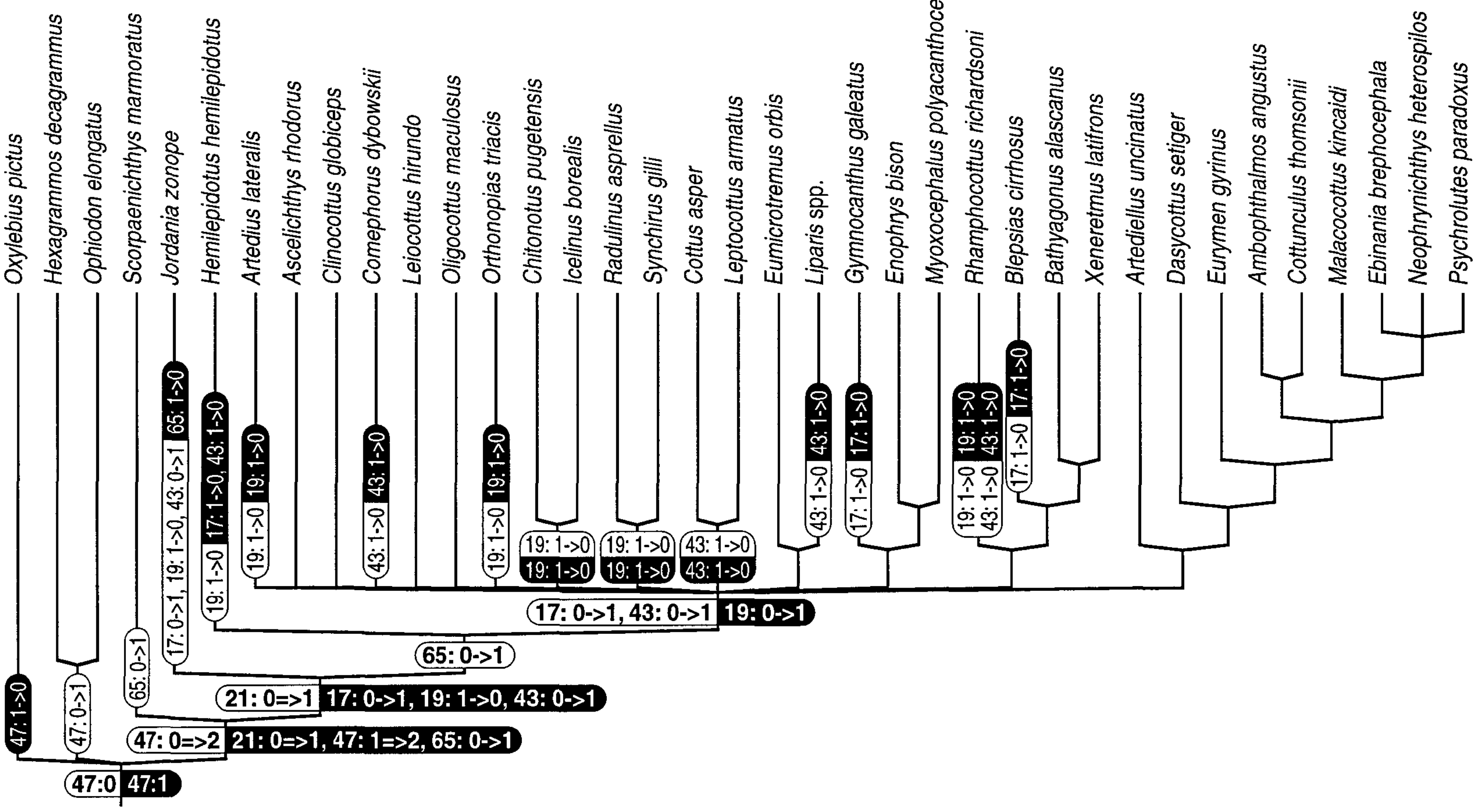


Figure 3–19. Ambiguous state changes in the basal interrelations of Cottoidei (branches Cottoidei, A, B, and C of Figure 3–16) modeled with delayed (normal print) and accelerated transformation (inverse). Unique changes (=>) distinguished from homoplastic (->) and all homoplastic changes mapped.

scales (21, scales absent in *Scorpaenichthys marmoratus*) and obliquus superioris not extending to the cranium (65, reversed in *Jordania zonope*).

The basal interrelationships of Cottoidei are a nested set of primitive taxa and a large crown clade: (*Scorpaenichthys marmoratus*, clade A: (*Jordania zonope*, clade B: (*Hemilepidotus hemilepidotus*, clade C))). Support for *S. marmoratus* as the most basal cottoid as opposed to *J. zonope* (clade A) is weak with only one homoplastic step of evolution (Figure 3–18) and a decay index of one step: simplification of dorsal and anal fin rays (56, homoplastic in *Hexagrammos decagrammus* and reversed in *Ascelichthys rhodorus* and clade K). Four additional ambiguous state changes might support clade A (Figure 3–19): reduction of lateral line ossifications to correspond with underlaying myomeres (17, reversed in *H. hemilepidotus*, *Gymnocanthus galeatus*, and *Blepsias cirrhosus*), development of ctenii on lateral line ossifications (19, lost in most branches of clade C), modification of ctenoid scales (21), and incompletion of the first neural arch (43, reversed in *H. hemilepidotus*, *Comephorus dybowskii*, clade F, *Liparis* spp. cyclopterids, and *Rhamphocottus richardsoni*).

In contrast, the sister relationship of *Scorpaenichthys marmoratus* and *Jordania zonope* to the remaining Cottoidei (clade B) is more strongly supported with five steps of evolution (Figure 3–18) and a decay index of three steps. Clade B is supported by one unique state change: reduction to four preopercular pores (8, further reduced to three pores in *Comephorus dybowskii* and two pores in Cyclopteridae); and four homoplastic state changes: reduction of pelvic fin rays from I,5 to I,4 (42, reversed in Cyclopteridae and further reduced in other taxa), pelvic and pectoral fin ray simplification (54 and 55, both homoplastic in *Hexagrammos decagrammus* and reversed for the pectoral fin in *Ascelichthys rhodorus* and clade K), and lateral head of the epaxialis not inserting in the posttemporal fossa (68, reversed in *Cottus asper*). One additional ambiguous state change might support this clade

(Figure 3–19): obliquus superioris not extending to the cranium but only to the cleithrum (65, homoplastic in *S. marmoratus*)

Clade C is a large and poorly resolved crown clade, but is well supported with seven steps of evolution (Figure 3–18) and a decay index of four steps. One unique state change supports this clade: loss of sensory pores arising from the parietal (15). Six homoplastic state changes also support this clade: loss of pores on postorbitals (7, reversed in *Ascelichthys rhodorus, Chitonotus pugetensis,* and clade G), obsolete palatocranial articulation (25, reversed in *Comephorus dybowskii,* clade F, and *Blepsias cirrhosus*), reduction of pelvic fin rays from I,4 to I,3 (42, reversed to I,5 in Cyclopteridae and to I,4 in clade F), and reduction to a single ray supported on the posteriormost dorsal and anal pterygiophore (46, reversed in *Cottus asper* and reversed on the anal pterygiophore only in *Rhamphocottus richardsoni*), development of the neural spine on the second preural centrum (49, reversed in *C. asper*), and fusion of the hypurals-parahypural into a single plate (52, reversed in Cyclopteridae, *R. richardsoni,* and *B. cirrhosus*). Three additional ambiguous state changes might support this clade (Figure 3–19): reduction in number of lateral line ossifications to closely correspond with underlying myomeres (17, homoplastic in *Jordania zonope,* reversed in *Gymnocanthus galeatus* and *B. cirrhosus,* and further reduced in clade K), loss of ctenii on lateral line ossifications (19, regained in *Artedius lateralis, Orthonopias triacis,* clades D, E, and *R. richardsoni*), and incomplete first neural arch (43, homoplastic in *J. zonope* and reversed in *C. dybowskii,* clade F, *Liparis* spp. cyclopterids, and *R. richardsoni*).

Clades D, E, and F are resolved sister pairs of cottoid taxa, there is weak support for D and E with a decay index of one step and moderate support for F with a decay index of two steps. Clade D is supported by one unique state change: development of ventral accessory sensory tubules from pores on lateral line ossifications (18), and three homoplastic state changes: development of spines on the bony covering of the supraorbital canal (2, homoplastic in *Gymnocanthus galeatus, Myoxocephalus polyacanthocephalus,* and the psychrolutids *Dasycottus setiger* and *Cottunculus thomsonii*), on the parietal extrascapular (14, homoplastic in clades G, I, and the psychrolutids *D. setiger* and *C. thomsonii*), and development of ctenii on lateral line ossifications (19, homoplastic in *Jordania zonope, Hemilepidotus hemilepidotus, Artedius lateralis, Orthonopias triacis,* clade E, and *Rhamphocottus richardsoni*) (Appendix 3–2). Clade E is supported by three homoplastic state changes: development of ctenii on lateral line ossifications (19, homoplastic in taxa listed immediately above), loss of the entopterygoid (26, homoplastic in *Comephorus dybowskii*), and loss of the ventralmost actinost foramen (37, homoplastic in clade G and further reduced in *C. dybowskii,* Agonidae, and clade K) (Appendix 3–2). Clade F is supported by nine homoplastic state changes: loss of the spine on the nasal (1, homoplastic in the hexagrammid clade Z and the cottoids *C. dybowskii,* Cyclopteridae, and clade K), loss of orbital sensory pores (4, homoplastic in *C. dybowskii,* Cyclopteridae, and Psychrolutidae), pterotic extrascapulars separated by a space (11, homoplastic in *Ascelichthys rhodorus, C. dybowskii, Icelinus borealis, Radulinus asprellus,* and clade K), scales reduced to widely scattered prickles (21, homoplastic in clade I), palatocranial articulation present (25, reversed from its loss in parent clade C and homoplastic in *C. dybowskii* and *Blepsias cirrhosus*), coracoid base attaching to the lateral wing of the cleithrum (36, reversed from attaching to main shaft of cleithrum in parent clade Cottoidei and homoplastic in *C. dybowskii* and Agonidae), pelvic formula I,4 (42, extra ray acquired from reduction to I,3 in parent clade C), completion of the first neural arch (43, reversed from its incompletion in parent clade C and homoplastic in *J. zonope, C. dybowskii, Liparis* species, and *R. richardsoni*), and branchiostegal membranes connected to each other and partly to the isthmus (59, homoplastic or further developed in Cyclopteridae, clade H, *R. richardsoni,* Agonidae, and clade K) (Appendix 3–2).

Cyclopteridae are strongly supported with at least 23 steps of evolution (Appendix 3–2) and a decay index of 14 steps. Eight unique state changes support this clade: an exposed infraorbital canal on the second infraorbital (6), reduction to two preopercular pores (8, by two steps of evolution, of which the first step is homoplastic in *C. dybowskii* and the second step is unique), extrascapulars largely fused to each other and forming an open groove (11), parietal extrascapular obscure (12), highly reduced lateral line (16, but developed in other cyclopterids not examined here), pelvic girdle modified into a sucking disc (39), loss of the anteriormost anal fin pterygiophore but retention of its ray and loss of the ray on the posteriormost pterygiophore (47), and rectus ventrali series I, II, and III developed (63). Fifteen homoplastic state changes also support this clade: loss of the spine on the nasal (1, homoplastic in the hexagrammid clade Z and the cottoids *Comephorus dybowskii,* clades F, and K), loss of orbital sensory pores (4, homoplastic in *C. dybowskii,* clade F, and Psychrolutidae), reduction to four infraorbitals (5, homoplastic in Agonidae), loss of preopercular spines (9, homoplastic in the hexagrammid *Hexagrammos decagrammus* and the cottoids *C. dybowskii* and clade L), lateral expansion of the frontal over the orbit (22, homoplastic in clade P), loss of teeth on the vomer (23, homoplastic in *Gymnocanthus galeatus, Ambophthalmos angustus,* and clade O), loss of teeth on the palatine (24, homoplastic in *C. dybowskii, Leiocottus hirundo, Radulinus asprellus,* clade G, *Rhamphocottus richardsoni,* and Psychrolutidae), loss of the second pharyngobranchial toothplate (33, homoplastic in *Hemilepidotus hemilepidotus, Synchirus gilli,* clades H, J, and Psychrolutidae), pelvic formula I,5 (42, two extra rays reacquired from reduction to I,3 in parent clade C and homoplastic in clade F, that reacquired one extra ray to I,4), autogenous haemal spine on second preural centrum (50, reversed from its fusion to the centrum in parent clade Cottoidei), separation of the hypurals-parahypural plate into two plates (52, reversed from parent clade C and homoplastic in

R. richardsoni and *Blepsias cirrhosus*), caudal fin rays simplified (57, homoplastic in clade I), branchiostegal membranes fused with isthmus (59, homoplastic in *Leptocottus armatus*, *R. richardsoni*, and clade M), anus anteriorly advanced (60, homoplastic in *L. hirundo*, *Orthonopias triacis*, *S. gilli*, and clade J), and development of the hyohyoides inferioris (61, homoplastic, but less developed, in clade P).

Clades G and H are a nested series of three cottoid taxa (*Gymnocanthus galeatus*, (*Enophrys bison*, *Myoxocephalus polyacanthocephalus*)), both clades with weak support of 1 decay step. Clade G is supported by five homoplastic state changes: pores developed on the postorbitals (7, reacquired from loss in parent clade C and homoplastic in *Ascelichthys rhodorus* and *Chitonotus pugetensis*), parietal extrascapular spines developed (14, homoplastic in clades D, I, and the psychrolutids *Dasycottus setiger* and *Cottunculus thomsonii*), loss of teeth on the palatine (24, homoplastic in *Comephorus dybowskii*, *Leiocottus hirundo*, *Radulinus asprellus*, Cyclopteridae, *Rhamphocottus richardsoni*, and Psychrolutidae), loss of the lowermost actinost foramen (37, homoplastic in clade E and further reduced in *C. dybowskii*, Agonidae, and clade K), and loss of one fin ray between spiny and rayed portions of the dorsal fin (45, homoplastic in *Jordania zonope*, *Oligocottus maculosus*, and clade J and further loss in the cyclopterid *Eumicrotremus orbis* and clade J) (Appendix 3–2). One additional ambiguous state change might support clade G (Appendix 3–3): development of spines on the bony covering of the supraorbital canal (2, with reversal in *E. bison*, and homoplastic in clade D and the psychrolutids *D. setiger* and *C. thomsonii*). Clade H is supported by one unique state change: development of ventral and dorsal accessory sensory tubules from pores on lateral line ossifications (18), and three homoplastic state changes: reduction to five infraorbitals (5, homoplastic in *C. dybowskii*, *R. asprellus*, clades I, and K, and reduced further to four in Cyclopteridae and Agonidae), loss of the second pharyngobranchial toothplate (33, homoplastic in *Hemilepidotus hemilepidotus*, *Synchirus gilli*, Cyclopteridae, clade J, and Psychrolutidae), and branchiostegal membranes connected to each other and partly to the isthmus (59, homoplastic or further developed in clade F, Cyclopteridae, *R. richardsoni*, Agonidae, and clade K) (Appendix 3–2).

Clade I is supported with seven steps of evolution (Appendix 3–2) and a decay index of two steps. One unique state change supports this clade: loss of orbital pores and reduction of the size of pores on the supraorbital canal (4). Six homoplastic state changes also support this clade: development of orbital rim spines on the frontal (3, homoplastic in *Gymnocanthus galeatus*), reduction to five infraorbitals (5, homoplastic in *Comephorus dybowskii, Radulinus asprellus,* clades H, and K, and reduced further to four in Cyclopteridae and Agonidae), fusion of the posteriormost lateral extrascapular with the medial extrascapular (11, homoplastic in the hexagrammid *Hexagrammos decagrammus*), parietal extrascapular spines developed (14, homoplastic in clades D, G, and the psychrolutids *Dasycottus setiger* and *Cottunculus thomsonii*), scales reduced to widely scattered prickles (21, homoplastic in clade F), and caudal fin rays simplified (57, homoplastic in Cyclopteridae). Three additional ambiguous state changes might support this clade (Appendix 3–3): loss of sensory pore on second infraorbital (6, with reversal in *Blepsias cirrhosus*), separation of the hypurals-parahypural plate into two plates (52, reversed from parent clade C and further reversed in Agonidae; homoplastic in Cyclopteridae), and branchiostegal membranes fused with each other and to the isthmus (59, further fused in *Rhamphocottus richardsoni,* and freed from isthmus in *B. cirrhosus*).

Clade J is well supported with four steps of evolution (Appendix 3–2) and a decay index of three steps. Two unique state changes support this clade: Baudelot's ligament attaching to the first vertebral centrum (31) and obsolete subpelvic process (40). Two homoplastic state changes also support this clade: loss of the second pharyngobranchial toothplate (33, homoplastic in *Hemilepidotus hemilepi-*

dotus, Synchirus gilli, Cyclopteridae, clade H, and Psychrolutidae) and anus advanced anteriorly in adults (60, homoplastic in *Leiocottus hirundo, Orthonopias triacis, Synchirus gilli,* and Cyclopteridae). Two additional ambiguous state changes might support this clade (Appendix 3–3): loss of two fin rays between spiny and rayed portions of the dorsal fin (45, occasionally only one ray lost in *Blepsias cirrhosus* and homoplastic in the cyclopterid *Eumicrotremus orbis*) and reduction to two epurals (53, occasionally three present in *B. cirrhosus,* homoplastic in *Comephorus dybowskii* and *Liparis* spp. cyclopterids).

Agonidae are strongly supported with at least 11 steps of evolution (Appendix 3–2 and 3–3) and a decay index of 11 steps. Five unique state changes support this clade: scales modified into large plates (21), postcleithra plate-like (38), pelvic formula I,2 (42), spinous and soft portions of dorsal fin separated by more than 2 rayless pterygiophores (45, ancestral state ambiguous, Appendix 3–3), and first series of rectus ventralis II and III present (63, I, II, and II present in Cyclopteridae but apparently not homologous, Yabe, 1985). Six homoplastic state changes also support this clade: reduction to four infraorbitals (5, homoplastic in Cyclopteridae), fusion of the dorsalmost actinost with the scapula (35, homoplastic in *Scorpaenichthys marmoratus*), coracoid base attaching to the lateral wing of the cleithrum (36, reversed from attaching to main shaft of cleithrum in parent Cottoidei and homoplastic in *Comephorus dybowskii* and clade F), all actinost foramina obsolete (37, homoplastic in *C. dybowskii* and Psychrolutidae), first dorsal pterygiophore displaced posterior of the second vertebra (44, homoplastic in *Liparis* species), and complete loss of pleural ribs (48, homoplastic in *Liparis* species). Four additional ambiguous state changes might support this clade (Appendix 3–3): loss of sensory pore on second infraorbital (6, homoplastic in *Rhamphocottus richardsoni*), fusion of the hypurals-parahypural plate (52, reversed from parent clade I), reduction to two epurals (53, occasionally three present in

Blepsias cirrhosus, homoplastic in *C. dybowskii* and *Liparis* spp. cyclopterids), and branchiostegal membranes connected to each other and partly to the isthmus (59, homoplastic or further developed in clade F, Cyclopteridae, clade H, *R. richardsoni,* and clade K).

Clade K is supported with a decay index of one step and eight steps of evolution (Appendix 3–2). One unique state change supports this clade: reduction in the number of lateral line ossifications to less than the number of vertebrae (17, 1:1.22 in *Artediellus uncinatus* and 1:1.80 or less in Psychrolutidae). Seven homoplastic state changes also support this clade: loss of the spine on the nasal (1, homoplastic in the hexagrammid clade Z and the cottoids *Comephorus dybowskii,* clade F, and Cyclopteridae), reduction to five infraorbitals (5, homoplastic in *C. dybowskii, Radulinus asprellus,* clades H, and I, and reduced further to four in Cyclopteridae, Agonidae, and the psychrolutid *Cottunculus thomsonii*), pterotic extrascapulars separated by a space (11, homoplastic in *Ascelichthys rhodorus, C. dybowskii, Icelinus borealis, R. asprellus,* and clade F), isolated ctenii or ctenii plate scales present in a dorsal scale band (21, further modified in *C. thomsonii* to widespread ctenoid plate scales, that are homoplastic in the cyclopterid *Eumicrotremus orbis*), rays branched in pectoral, dorsal, and anal fins (55 and 56, reversed from simplification in parent clade A and homoplastic in *A. rhodorus*), and branchiostegal membranes connected to each other and partly to the isthmus (59, homoplastic or further developed in clade F, Cyclopteridae, clade H, *Rhamphocottus richardsoni,* and Agonidae). One additional ambiguous state change might support this clade (Appendix 3–3): loss of the ventral three actinost foramina (37, dorsalmost foramen lost in Psychrolutidae excepting *Malacocottus kincaidi*). For reasons given in the "Character Evolution" section above, this ambiguous character change (37) is probably unique to this clade.

Psychrolutidae are well supported with nine steps of evolution (Appendix

3–2 and 3) and a decay index of three steps. Three unique state changes support this clade: broad connection of the operculomandibular and preopercular canals (10), autogeny of posterior extrascapular on pterotic (11), and seven branchiostegal rays (34). Six homoplastic state changes also support this clade: loss of orbital sensory pores (4, homoplastic in *Comephorus dybowskii,* clade F, and Cyclopteridae), loss of teeth on the palatine (24, homoplastic in *C. dybowskii, Leiocottus hirundo, Radulinus asprellus,* Cyclopteridae, clade G, and *Rhamphocottus richardsoni*), reduction to a single opening of the trigeminofascialis chamber (29, homoplastic in *Blepsias cirrhosus*), loss of the second pharyngobranchial toothplate (33, homoplastic in *Hemilepidotus hemilepidotus, Synchirus gilli,* Cyclopteridae, clade H, and J), all actinost foramina obsolete (37, ancestral state is ambiguous, Appendix 3–3; homoplastic in *C. dybowskii* and Agonidae), and presence of the coracoradialis (67, reacquired from its loss in parent clade Cottoidei).

Psychrolutidae are mostly resolved with clades L, M, N, O, and P supported by one decay step each. Clade L is supported by two homoplastic state changes: loss of preopercular spines (9, homoplastic in the hexagrammid *Hexagrammos decagrammus* and the cottoids *Comephorus dybowskii* and Cyclopteridae, and reversed in *Malacocottus kincaidi*) and separation of the pterosphenoid and parasphenoid by the intervening prootic (28, homoplastic in *Blepsias cirrhosus*) (Appendix 3–2). Clade M is supported by one unique state change: loss of the posteriormost lateral extrascapular (11), and one homoplastic state change: branchiostegal membranes fused with isthmus (59, homoplastic in *Leptocottus armatus,* Cyclopteridae, and *Rhamphocottus richardsoni*) (Appendix 3–2). Clade N is supported by two unique state changes: fusion of the posterior extrascapular of the pterotic with the medial extrascapular (11) and box-like pelvic girdle (39) (Appendix 3–2). Clade O is supported by one unique state change: autogenous parietal extrascapular (13) (Appendix 3–2). Clade P is supported by two homoplastic state changes: lateral expansion of the frontal over the orbit (22, homoplastic in Cyclopteridae), and development of the hyohyoides inferioris (61, homoplastic, but more developed, in Cyclopteridae) (Appendix 3–2). Three additional characters are phylogenetically significant within Psychrolutidae but have ambiguous evolution (Appendix 3–3): absence of scales (20), widespread distribution of ctenoid plate scales (21), and loss of teeth on the vomer (23).

Comparison with Other Works

Yabe (1985) presented an extensive treatment on the systematics of Cottoidei. He developed an unorthodox phylogenetic hypothesis in which previously considered specialized cottoids were placed basally and the generalized family Cottidae was slightly restricted in scope compared with some previous authors and placed as a monophyletic crown clade. In Yabe's hypothesis, 36 characters informative within his in-group (Cottoidea, a subset of Cottoidei excluding Cyclopteridae) with 61 steps of evolution were used to resolve 43 clades. Homoplasy and alternative equally or more parsimonious trees were little discussed. Yabe paid little attention to Cyclopteridae (pages 122 and 125), but thought it to be sister to all other Cottoidei, his Cottoidea. Although Yabe's phylogenetic hypothesis seems based largely on conjecture, it stands as the most comprehensive evolutionary study of Cottoidei to its date and is considerably more sophisticated than any work before it. Its clade hypotheses need to be weighed carefully.

The shortest tree consistent with Yabe's (1985) tree using the data and character evolution assumptions here, is presented in Figure 3–20. This was done in PAUP under same methods used here but with Yabe's tree as a constraint tree and omitting two genera not examined by Yabe. This tree is considerably less parsimonious than the tree postulated here with 272 versus 242 steps. Four of Yabe's clades are in particular need of scrutiny: Cottoidea, clades X, Y, and Cottidae.

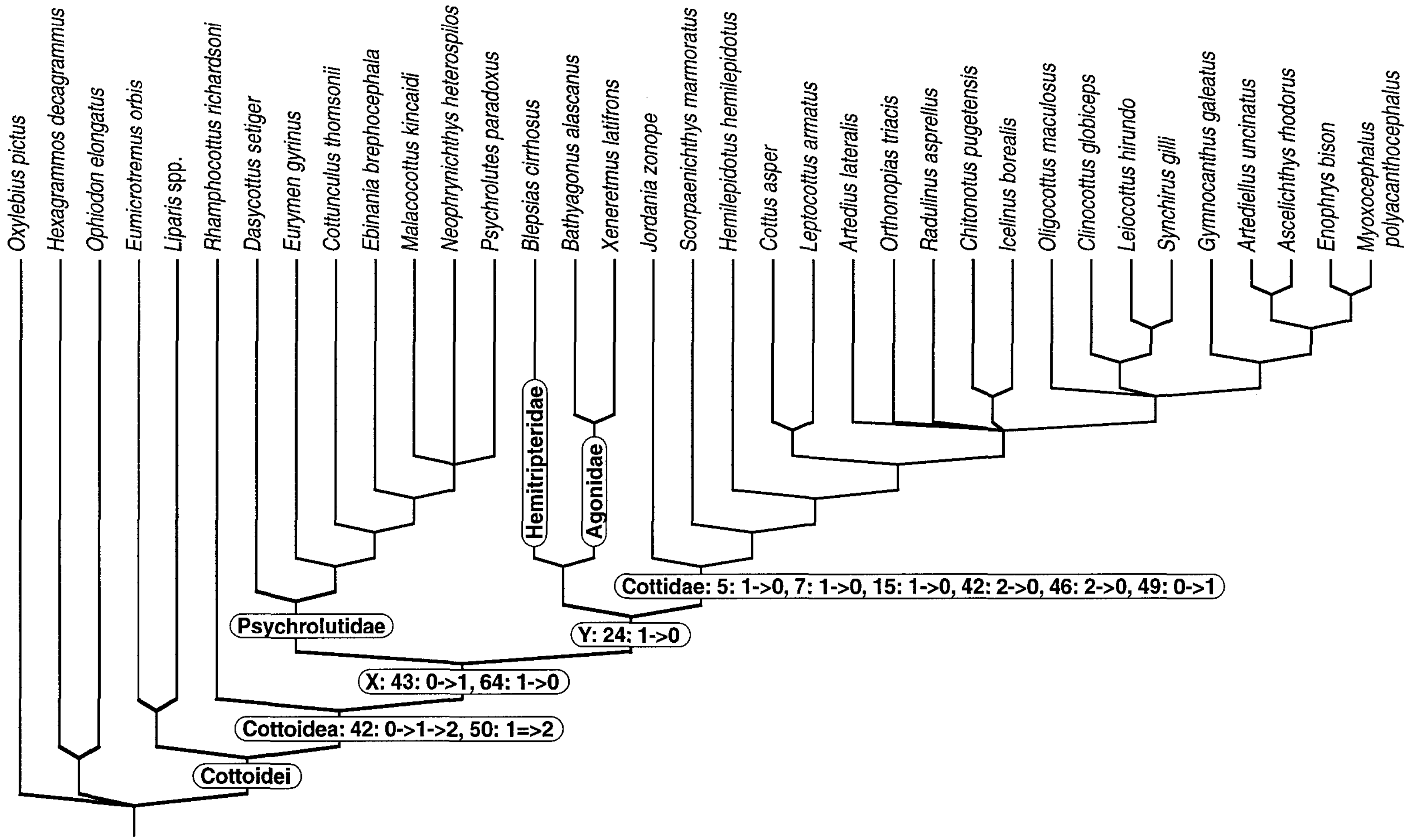


Figure 3–20. Shortest tree compatible with Yabe's (1985) phylogeny of Cottoidea with key basal clades labeled (for reference in text) and unambiguous state changes supporting four key clades given. Unique changes (=>) distinguished from homoplastic (–>).

Yabe (1985) gives 22 "synapomorphies" for his Cottoidea, of which many are true in some or all Scorpaeniformes and most of the remainder were also found in Cyclopteridae. Only two unambiguous state changes remain to support his Cottoidea (Figure 3–20): pelvic count reduced from I,5 to I,3 (character 42 here, reversed to I,5 in basal Cottidae) and fusion of the haemal spines with the second preural centra (50, unique state change). Clade X is supported by two unambiguous homoplastic state changes: neural arch on first centrum complete (43, reversed in basal and other Cottidae) and presence of the rectus ventralis second series (64, homoplastic in *Liparis* spp. cyclopterids). Clade Y is supported by only one unambiguous homoplastic state change: reacquisition of palatine teeth (24, from loss in parent clade Cottoidei, and lost again in various Cottidae). Cottidae are supported by six unambiguous homoplastic state changes: infraorbital number increase from four to five (5, reversed from reduction to four in Cottoidei and further reduced again in higher Cottidae), redevelopment of pores on the postorbitals (7, from loss in parent clade Cottoidei and lost again in higher Cottidae), redevelopment of pores on the parietal (15, from loss in parent clade Cottoidei and lost again in higher Cottidae), redevelopment of pelvic rays to I,5 (42, from reduction to I,3 in parent clade Cottoidei and reduced again in higher Cottidae), redevelopment of an extra ray on the last dorsal and anal pterygiophores (46, from loss in parent clade Cottoidei and lost again in higher Cottidae), and truncation of the neural spine on the second preural centrum (49, from its development in parent clade Cottoidei, and subsequently redeveloped in higher Cottidae).

Few characters support Yabe's (1985) key clades and almost all are widely homoplastic. Only one unique state change supports Cyclopteridae as sister to his Cottoidea and all six state changes supporting his Cottidae are reversals that are homoplastic in the out-group. The only derived character given by Yabe in supporting his Cottidae is the lateral process of the hyomandibular, and I do not recognize it as valid. One notable exception to the lack of support for Yabe's phylogeny is the clade formed by Agonidae and Hemitripteridae, that I find strongly supported. Also, within Yabe's Cottidae are two relations supported here: (*Cottus, Leptocottus*) and (*Gymnocanthus,* (*Enophrys, Myoxocephalus*)). Further, Yabe finds the *Cottus-Leptocottus* clade to be basal on what might be transposed to my unresolved clade C (Figure 3–16). Yabe supposed this because two primitive characters in this clade are derived in his higher Cottidae: palatocranial articulation developed (character 25 here) and pelvic count I,4 (42). Other primitive features were observed here in this clade: first neural arch complete (43) and in *C. asper*: two rays on last dorsal and anal pterygiophores (46) and truncate neural spine on second preural centrum (49). But, the basal placement of this clade ignores characters that might align it with other cottoids and the fact that two characters that are advanced in *Leptocottus* imply homoplasy one way or the other (*i.e.*, either the advanced characters in *Leptocottus* were developed independently of other Cottoidei or the primitive characters of *C. asper* were reacquired).

Like Yabe (1985), some authors considered Cyclopteridae as an aberrant clade within but separate from other Cottoidei, presumably based on the group's highly specialized nature (*e.g.*, Boulenger, 1904; Jordan, 1923; Matsubara, 1955; and Washington *et al.*, 1984). Other authors considered Cyclopteridae as unplaced but not of special status within Cottoidei (*e.g.*, Regan, 1913 and Berg, 1940). Taranets (1941) went further in suggesting a "morphological line" between "Myoxocephalinae and Psychrolutidae to Liparidae and Cyclopteridae." I too strongly feel that Cyclopteridae are nested within Cottoidei and should be treated as other taxa of this clade. A variety of characters (characters of clades A, B, and often C described in previous sections) support its nested position, but no single strong neomorphic feature ties it within clade C. My guess at the phylogenetic position of Cyclopteridae is near to clade F (*Cottus asper, Leptocottus armatus*) with the higher number of pelvic rays in this group and the vaguely similar, unusual pelvic girdle morphology (not considered here) of *L. armatus*, and near to *Comephorus dybowskii* with its reduced number of preopercular pores, and near to both groups in being somewhat degenerate.

Gill (1888) presented a detailed review of as then current knowledge on "mail-cheeked fishes" (current Scorpaeniformes) and drew a "genealogy" that placed *Rhamphocottus richardsoni* sister to Agonidae and Triglidae, vaguely predicting what is clade I here. Regan (1913) was first to recognize a taxon directly comparable with Cottoidei considered here. Regan lumped *R. richardsoni* into Cottidae as he "could not recognize even [it] as the type of a distinct family; the example I have examined... ... the whole skeleton is Cottid." Although Regan laid the foundation for the modern classification of Cottoidei, he did little else in elaborating its phylogeny.

Jordan (1923) presumed two basal lineages in Cottoidei: one with *Jordania* leading to his Icelidae (including *Artediellus, Artedius, Enophrys, Chitonotus, Hemilepidotus, Icelinus, Orthonopias,* and *Radulinus* amongst genera considered here) and the other with *Scorpaenichthys* leading to his Cottidae (including *Clinocottus, Cottus, Cottunculus, Gymnocanthus, Leiocottus, Leptocottus, Myoxocephalus,* and *Oligocottus* amongst genera considered here). While it is possible that clade C here is polyphyletic, Jordan's two lineages split some taxa that are reasonably well resolved (*e.g.*, *Enophrys* and *Myoxocephalus*) and are apparently only based on "true scales" present in his Icelidae versus prickles or "imbedded dermal plates" in his Cottidae. Jordan did not elaborate on the interrelations of his other cottoid families.

Taranets (1941) is next to Yabe (1985) in providing the most detailed examination of many Cottoidei in an evolutionary context. Taranets' Cottidae were divided into 13 subfamilies and he also considered 13 other specialized families related to his Cottidae. Within Taranets' Cottidae, his subfamilies Icelinae with *Chito-*

notus and *Icelinus,* Myoxocephalinae with *Enophrys* and *Myoxocephalus,* and Cottinae with *Cottus* and *Leptocottus,* amongst genera considered here, support the relations hypothesized here. Taranets' Myoxocephalinae includes *Artediellus,* a grouping that is not supported here, but he proposes a "morphological line" between this subfamily and Psychrolutidae that possibly predicted clade K found here. Taranets' suggested that his Radulininae (with *Radulinus* considered here) to be related to his Myoxocephalinae, a relationship not supported here. Taranets' Cottinae also include the genus *Leiocottus* that is neither supported nor refuted here. Taranets was first to recognize Psychrolutidae in a composition similar to today's.

Bolin (1947) drew up a phylogenetic tree of Californian Cottidae that included many genera examined here but did not include more specialized cottoids such as Agonidae, Cyclopteridae, Psychrolutidae, or *Rhamphocottus richardsoni.* Bolin thought that *Jordania* and *Scorpaenichthys* were basal cottids, as supported here; but he has them sister to each other with a long independent evolution. Bolin thought *Blepsias* to be a basal cottid too, to a similar degree as but independent of *Jordania* and *Scorpaenichthys,* an idea that is not supported here. Bolin noted the primitive morphology of *Hemilepidotus,* but he nested it higher in his Cottidae as sister to a large crown clade vaguely comparable to much of clade C here, excepting *Ascelichthys, Enophrys,* and *Leptocottus,* that he thought to be earlier offshoots. Bolin thought *Chitonotus* to be sister to *Icelinus,* as supported here. Bolin also postulated relationships between *Artedius, Clinocottus, Leiocottus, Oligocottus, Orthonopias,* and *Radulinus,* these were examined here but their interrelations were not resolved.

Richardson (1981) examined 25 genera of larval cottoids, that she divided into six morphotypes that she thought likely to reflect relationship. Of Richardson's morphotypes, types 2, 3, 4, and 6 are supported by findings here. Type 1 with *Artedius, Clinocottus, Oligocottus,* and *Orthonopias* is neither supported nor refuted.

Type 2 with *Chitonotus* and *Icelinus* (and *Icelus, Paricelinus,* and *Triglops*) is supported. Type 3 with the psychrolutids *Dasycottus, Malacocottus,* and *Psychrolutes* (and "Cottoid type A") is supported. Type 4 with *Scorpaenichthys* and *Hemilepidotus* is supported if that morphotype is ancestral for Cottoidei. Support for type 5 with *Blepsias* (and *Nautichthys*) is not determined here. Type 6 with *Cottus* and *Leptocottus* is supported. Richardson could not place larvae for *Enophrys, Gymnocanthus, Myoxocephalus, Radulinus,* or *Rhamphocottus* (and *Hemitripterus*) into any morphotype, but these larval types might be revisited under the phylogeny presented here.

Washington *et al.* (1984) examined 28 genera of adult and larval cottoids and developed a phylogeny of the group. They found Cyclopteridae to be sister to all remaining Cottoidei based on the remaining cottoids having: the first anal pterygiophore simple, no supernumerary anal elements, and the haemal spine on the second preural centrum enlarged. But Cyclopteridae also have the first anal pterygiophore simple, they often lack supernumerary anal elements (occasional presence is autapomorphic within some members of the group), and the haemal spine of the second preural centrum is not universally enlarged amongst non-cyclopterid Cottoidei and is enlarged in some Cyclopteridae. Next on their tree is *Rhamphocottus richardsoni* sister to remaining Cottoidei (predicting Yabe's, 1985, conclusions). Curiously, five slash marks on their tree (their Figure 241) presumably indicating five synapomorphies are given for the clade above *R. richardsoni,* but are not labeled or elaborated on at all in the text. They found *Scorpaenichthys* and *Hemilepidotus* next up the tree, sister to remaining cottoids; that is supported here. They found these two genera sister to each other as well; that is not supported here. They did not examine *Jordania* or other possible primitive Cottoidei and under the phylogenetic hypothesis presented here, their synapomorphies for *Scorpaenichthys* and *Hemilepidotus* might prove to be primitive states for Cottoidei and not indicative of relationship to each other that they postulate. Sister to those two genera, they found a large crown clade comparable to clade C here, with Agonidae, Hemitripteridae, and Psychrolutidae embedded amongst other Cottidae, supporting findings here. They found a *Hemitripterus* group (with *Blepsias* examined here) sister to Agonidae, supporting clade J here. Another interesting finding of theirs was that of the first neural arch being incomplete in larva of this crown clade (that includes *Cottus* and *Leptocottus*, examined); this substantiates possible reversal of this character in adults of some species in clade C here.

Classification

The partly resolved phylogeny put forth here presents a challenge to classification. Two of three basal taxa (*Scorpaenichthys* and *Jordania*) are only weakly resolved with respect to each another, and the reasonably well supported large clade C (Figure 3–16) is poorly resolved internally. These issues need to be addressed before a reasonable cladistic classification can be applied to the group. Key to resolving this is consideration of additional taxa, particularly ones believed to be primitive cottids: *Paricelinus* (thought primitive by Jordan, 1923), other members of Taranets' (1941) Triglopinae and Icelinae, *Zesticelus* (thought primitive by Bolin, 1947), and Yabe's (1981) Ereuniidae. Also, Yabe and Ueno (1996) examined the osteology of *Normanichthys crockeri* and determined it not to be a cottoid, but they did not refute it as the primitive sister taxon of Cottoidei. The aberrant monotypic family Bathylutichthyidae (Balushkin and Voskoboynikova, 1990) might also be a primitive form or a missing link to Cyclopteridae. Much could be done simply with the characters presented here by evaluating them in other cottoids. Additional taxa found to be primitive might bolster the basal relationships determined here, while widely homoplastic characters (*e.g.*, states 1 and 2 of character 11) might aid in sorting out smaller clades within clade C.

For now, a critical reexamination of the current classification of Cottoidei (*e.g.*, Nelson, 1994) can be done. Nelson followed Yabe (1985) in recognizing two superfamilies of Cottoidei: Cottoidea and Cyclopteroidea. This implies monophyly of each taxon and sister relationship of the two taxa, but this is clearly not supported here. Nelson also followed Yabe in listing Rhamphocottidae and Ereuniidae before Cottidae implying an earlier evolutionary position of these taxa; again this is not supported here. Rhamphocottidae are not the most basal cottoids; that distinction clearly belongs to *Scorpaenichthys*, *Jordania*, or some other cottoid taxon not examined here. Possibly Ereuniidae are the most basal cottoid taxon, but they have a number of characters that are derived in the phylogeny presented here: obscure palatocranial articulation, pelvic formula I,4, single ray on last dorsal and anal pterygiophore, neural spine developed on the second preural centrum (in *Ereunias*), and obliquus superioris not extending to the cranium (from Yabe, 1985). Listing Ereuniidae before Cottidae is premature. Cottidae are clearly polyphyletic without all other cottoid families. Cladistically, Cottidae should be dissolved and those members not placed in specialized families should be left in Cottoidei as *incertae sedis* (although few systematists would appreciate so many genera without families). A less perfect cladistic classification would retain Cottidae, despite its known paraphyly, and list it first amongst Cottoidei to indicate its status of generating subsequent taxa (a paraphyletic "wastebasket taxon"). Of subsequent taxa, only Rhamphocottidae, Hemitripteridae, and Agonidae can be sequenced or grouped to reflect their interrelationships. The monophyly of Hemitripteridae should be independently reexamined, because Yabe lists only one character to support this taxon: scales reduced to prickles. Under my hypothesis of scale evolution, the plates in Agonidae are directly derived from the prickles in Hemitripteridae, and thus this character is not informative about monophyly of Hemitripteridae exclusive of Agonidae. The sister relationship of Psychrolutidae and *Artediellus* is an exciting find, but too weakly supported for what would be a major change in classification.

Following the guidelines given above and using Nelson's (1994) style of sequencing taxa to best match relations and, in the absence of knowledge on relationships, sequencing from generalized to specialized, a classification of Cottoidei is presented in Table 3–2. In this classification: Cottidae are listed first indicating their basal, paraphyletic, and generalized status (in composition, Cottidae remain unchanged from the concept of Yabe, 1985, that is the same as that of Taranets, 1941, with the inclusion of *Scorpaenichthys*); Ereuniidae, Comephoridae, and Abyssocottidae follow as not particularly modified cottid derivatives; Agonidae follow containing Rhamphocottinae, Hemitripterinae, and Agoninae sequenced in order of their interrelationships; and Psychrolutidae, Bathylutichthyidae, and Cyclopteridae follow in order of increasing specialization. Cyclopteroidea are reduced to familial status and Cyclopteridae and Liparidae become subfamilies of this unquestionably monophyletic group. Other than the special status of Cottidae, the

Table 3–2. Classification of Cottoidei that is compatible with the phylogeny presented here (Figure 16). Paraphyletic taxon is marked with an asterisk. Authority for the composition of taxa given on right. Placement of species examined within this classification given in Appendix 3-4.

Cottoidei	Composition:
Cottidae*	Taranets, 1941; Yabe, 1985
Ereuniidae	Yabe, 1981
Comephoridae	Sideleva, 1982
Abyssocottidae	Sideleva, 1982
Agonidae	*novo*
Rhamphocottinae	monotypic
Hemitripterinae	Yabe, 1981
Agoninae	Kanayama, 1991
Psychrolutidae	Taranets, 1941; Jackson and Nelson, 1998
Bathylutichthyidae	monotypic
Cyclopteridae	*novo*
Cyclopterinae	Eschmeyer, 2002
Liparinae	Eschmeyer, 2002

sequencing of the specialized families is arbitrary and could be done alphabetically.

These conclusions might seem to be a step backwards to Boulenger's (1904) "[Cottidae] merge insensibly into the still more aberrant Cyclopteridae" and it might appear that classification has not greatly progressed since Regan (1913). But, major new findings are postulated: i) Cottidae are a basal polyphyletic assemblage within Cottoidei from which all specialized families were derived; ii) Cyclopteridae are nested well within the group and not sister to it; iii) *Rhamphocottus richardsoni,* Hemitripteridae, and Agonidae form a nested clade; and iv) a sister group, *Artediellus,* is possibly found for Psychrolutidae.

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Appendix 3-1. Data matrix of 68 characters (enumerated) by 37 taxa. Unknown states are indicated with a question mark. (Continued on following page...)

	1-5	6-10	11-15	16-20	21-25
Hexagrammidae					
Hexagrammos decagrammus	11100	00010	00110	00010	00000
Ophiodon elongatatus	11100	00000	10110	00010	00000
Oxylebius pictus	01100	00000	10110	00010	00000
Cottoidei					
Artediellus uncinatus	11101	01100	20111	02010	40001
Artedius lateralis	01100	01100	10111	01000	10001
Ascelichthys rhodorus	01100	00100	20111	01011	?0001
Blepsias cirrhosus	01021	01100	00101	00010	60000
Chitonotus pugetensis	00100	00100	10101	01100	10001
Clinocottus globiceps	01100	01100	10111	01011	?0001
Comephorus dybowskii	11111	01210	20111	01011	?0010
Cottus asper	11110	01100	20111	01010	60000
Enophrys bison	01101	00100	10101	01211	?0011
Gymnocanthus galeatus	00000	00100	10101	00010	30111
Hemilepidotus hemilepidotus	01100	00100	10110	00000	10000
Icelinus borealis	00100	01100	20101	01100	10001
Jordania zonope	01100	00001	10110	01000	20000
Leiocottus hirundo	01100	01101	10111	01010	10011
Leptocottus armatus	11110	01100	20111	01010	60000
Myoxocephalus polyacanthocephalus	00101	00100	10101	01210	10011
Oligocottus maculosus	01100	01100	10111	01011	?0001
Orthonopias triacis	01100	01101	10111	01000	10001
Radulinus asprellus	01101	01100	20111	01000	10011
Rhamphocottus richardsoni	01021	11100	00101	01000	60011
Scorpaenichthys marmoratus	01100	00000	10110	00011	?0000
Synchirus gilli	01100	01100	10111	01000	10001
Agonidae					
Bathyagonus alascanus	01022	11100	00101	01010	70001
Xeneretmus latifrons	01022	11100	00101	01010	70001
Cyclopteridae					
Eumicrotremus orbis	11112	21310	61?11	1?010	51111
Liparis spp.	11112	21310	61?11	1?011	?1111
Psychrolutidae					
Ambophthalmos angustus	11111	01111	50111	02011	?0111
Cottunculus thomsonii	10113	01111	50101	02010	50011
Dasycottus setiger	10111	01101	30101	02010	40011
Ebinania brephocephala	11111	01111	40011	02011	?1011
Eurymen gyrinus	11111	01111	30111	02011	?0011
Malacocottus kincaidi	11111	01101	40011	02010	40111
Neophrynichthys heterospilos	11111	01111	40011	02011	?1111
Psychrolutes paradoxus	11111	01111	40011	02011	?1111

Appendix 3-1 (...continued). Polymorphism observed with characters 45 and 54 in some taxa: a indicating states 0 and 1; b, 1 and 2; and c, 3 and 4.

	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-
H. decagrammus	00000	00010	00100	00010	01010	00011	10110	10210	000
O. elongatatus	00000	00010	00100	00000	01010	00000	00100	10210	000
O. pictus	00000	00010	00100	00010	00010	00000	00110	10210	000
A. uncinatus	01001	01110	12100	02110	22102	11010	00020	11201	111
A. lateralis	01001	01110	20300	02110	22102	11011	10010	11201	111
A. rhodorus	01001	01110	10300	1?110	22102	110?0	00010	11201	111
B. cirrhosus	01111	11210	10101	0211b	22102	10a11	11011	11201	111
C. pugetensis	01001	01110	10100	02110	22102	11011	10010	11201	111
C. globiceps	01001	01110	20300	02110	22102	11011	10010	11201	111
C. dybowskii	11001	01110	03300	1?010	22202	111?1	10000	?????	???
C. asper	01001	01110	00100	01010	02112	11011	10020	11201	110
E. bison	01001	01210	11100	02111	22102	11011	10020	11201	111
G. galeatus	01001	01110	11100	02111	22102	11011	10010	11201	111
H. hemilepidotus	01001	01210	10100	01010	02112	10011	10010	11201	111
I. borealis	01001	01110	10100	02110	22102	11011	10010	11201	111
J. zonope	01001	01110	10100	00111	02112	10000	10010	11200	110
L. hirundo	01001	01110	20100	02110	22102	11011	10011	11201	111
L. armatus	01001	01110	00100	01010	22102	11011	10030	11201	111
M. polyacanthocephalus	01001	01210	11100	02111	22102	11011	10020	11201	111
O. maculosus	01001	01110	20100	02111	22102	11011	10010	11201	111
O. triacis	01001	01110	20100	02110	22102	11011	10011	11201	111
R. asprellus	11001	01110	11100	02110	22102	11011	10010	11201	111
R. richardsoni	01001	01110	10100	02010	12102	10011	11030	11211	111
S. marmoratus	01001	01111	20100	00010	02112	10000	00010	11201	110
S. gilli	11001	01210	11300	02110	22102	11011	10011	11201	111
B. alascanus	01001	11211	03001	0312c	22202	11111	11021	11101	111
X. latifrons	01001	11211	03001	03124	22202	11111	11021	11101	111
E. orbis	01?01	01210	10120	00112	23101	10011	11031	01011	11?
Liparis spp.	01001	01210	10120	00020	23101	00111	11031	01001	111
A. angustus	01111	01200	13110	02110	22102	11010	00030	1????	???
C. thomsonii	01111	01200	13210	02110	22102	11010	00030	11201	101
D. setiger	01011	01200	13100	02110	22102	11010	00020	11201	101
E. brephocephala	01111	01200	13100	02110	22102	11010	00030	01201	101
E. gyrinus	01111	01200	13200	02110	22102	11010	00020	11201	101
M. kincaidi	01111	01200	12100	02110	22102	11010	00030	11201	101
N. heterospilos	01111	01200	13100	02110	22102	11010	00030	01201	101
P. paradoxus	01111	01200	13300	02110	22102	11010	00030	01201	101

Appendix 3–2. Unambiguous state changes along branches of the strict consensus tree presented in Figure 3–16. Unique changes (=>) are distinguished from homoplastic (->). (Continued on following page...)

Z
1: 0->1

Cottoidei
27: 0=>1
30: 0=>1
32: 0=>1
33: 0=>1
36: 0->1
48: 0=>1
50: 0->1
->2
51: 0->1
58: 1=>0
62: 0=>1
64: 1->0
66: 0=>1
67: 0->1

A
56: 0->1

B
8: 0=>1
42: 0->1
54: 0->1
55: 0->1
68: 0->1

C
7: 0->1
15: 0=>1
25: 0->1
42: 1->2
46: 0->2
49: 1->0
52: 0->1

D
2: 1->0
14: 1->0
18: 0=>1
19: 1->0

E
19: 1->0
26: 0->1
37: 0->1

F
1: 0->1
4: 0->1
11: 1->2
21: 1->6
25: 1->0
36: 1->0
42: 2->1
43: 1->0
59: 1->2

Cyclopteridae
1: 0->1
4: 0->1
5: 0->1
->2
6: 0=>2
8: 1->2
=>3
9: 0->1
11: 1=>6
12: 0=>1
16: 0=>1
22: 0->1
23: 0->1
24: 0->1
33: 1->2
39: 0=>2
42: 2->1
->0
47: 2=>3
50: 2->1
52: 1->0
57: 0->1
59: 1->2
->3
60: 0->1
61: 1->0
63: 2=>0

G
7: 1->0
14: 1->0
24: 0->1
37: 0->1
45: 0->1

H
5: 0->1
18: 0=>2
33: 1->2
59: 1->2

I
3: 1->0
4: 0=>2
5: 0->1
11: 1->0
14: 1->0
21: 1->6
57: 0->1

J
31: 0=>1
33: 1->2
40: 0=>1
60: 0->1

Agonidae
5: 1->2
21: 6=>7
35: 0->1
36: 1->0
37: 0->3
38: 1=>0
42: 2=>3
44: 1->2
48: 1->2
63: 2=>1

K
1: 0->1
5: 0->1
11: 1->2
17: 1=>2
21: 1->4
55: 1->0
56: 1->0
59: 1->2

Psychrolutidae
4: 0->1
10: 0=>1
11: 2=>3
24: 0->1
29: 0->1
33: 1->2
34: 1=>0
67: 1->0

L
9: 0->1
28: 0->1

M
11: 3=>4
59: 2->3

N
11: 4=>5
39: 0=>1

O
13: 1=>0

P
22: 0->1
61: 1->0

Appendix 3–2 (...continued).

Hexagrammos decagrammus
9: 0–>1 55: 0–>1
11: 1–>0 56: 0–>1
54: 0–>1
Ophiodon elongatus
44: 1=>0 59: 1–>0
Scorpaenichthys marmoratus
20: 0–>1 36: 1–>2
35: 0–>1
Jordania zonope
21: 1=>2 45: 0–>1
Hemilepidotus hemilepidotus
33: 1–>2
Artedius lateralis
19: 1–>0 38: 1–>3
36: 1–>2
Ascelichthys rhodorus
7: 1–>0 41: 0–>1
11: 1–>2 55: 1–>0
20: 0–>1 56: 1–>0
38: 1–>3
Clinocottus globceps
20: 0–>1 38: 1–>3
36: 1–>2
Comephorus dybowskii
1: 0–>1 26: 0–>1
4: 0–>1 36: 1–>0
5: 0–>1 37: 0–>3
8: 1–>2 38: 1–>3
9: 0–>1 41: 0–>1
11: 1–>2 43: 1–>0
20: 0–>1 48: 1–>2
24: 0–>1 53: 0–>1
25: 1–>0 59: 1–>0

Leiocottus hirundo
24: 0–>1 60: 0–>1
36: 1–>2
Oligocottus maculosus
20: 0–>1 45: 0–>1
36: 1–>2
Orthonopias triacis
19: 1–>0 60: 0–>1
36: 1–>2
Chitonotus pugetensis
7: 1–>0
Icelinus borealis
11: 1–>2
Radulinus asprellus
5: 0–>1 24: 0–>1
11: 1–>2
Synchirus gilli
33: 1–>2 60: 0–>1
38: 1–>3
Cottus asper
46: 2–>0 68: 1–>0
49: 0–>1
Leptocottus armatus
59: 2–>3
Eumicrotremus orbis
45: 0–>1 64: 0–>1
–>2
Liparis spp.
20: 0–>1 51: 1–>0
43: 1–>0 53: 0–>1
44: 1–>2
Gymnocanthus galeatus
3: 1–>0 21: 1=>3
17: 1–>0 23: 0–>1
Enophrys bison
20: 0–>1

Rhamphocottus richardsoni
19: 1–>0 46: 2=>1
24: 0–>1 64: 0–>1
43: 1–>0
Blepsias cirrhosus
17: 1–>0 28: 0–>1
25: 1–>0 29: 0–>1
Dasycottus setiger
2: 1–>0 14: 1–>0
Eurymen gyrinus
38: 1–>2
Cottunculus thomsonii
2: 1–>0 14: 1–>0
5: 1=>3 38: 1–>2
Malacocottus kincaidi
9: 1–>0 37: 3–>2
Ebinania brephocephala
23: 1–>0
Psychrolutes paradoxus
38: 1–>3

Appendix 3-3. Characters with ambiguous evolution along branches of the strict consensus tree presented in Figure 16, showing equally parsimonious manners in which the character changes may be mapped with either delayed or accelerated transformation assumed. Character number in first column. Unique changes (=>) are distinguished from homoplastic (–>).

	Delayed		Accelerated	
2:	1->0	*Gymnocanthus galeatus*	1->0	G
	1->0	*Myoxocephalus polyacanthocephalus*	0->1	*Enophrys bison*
6:	0->1	*Rhamphocottus richardsoni*	0->1	I
	0->1	Agonidae	1->0	*Blepsias cirrhosus*
17:	0->1	*Jordania zonope*	0->1	A
	0->1	C	1->0	*Hemilepidotus hemilepidotus*
19:	1->0	*Jordania zonope*	1->0	A
	1->0	*Hemilepidotus hemilepidotus*	0->1	C
20:	0->1	*Eurymen gyrinus*	0->1	L
	0->1	*Ambophthalmos angustus*	1->0	*Cottunculus thomsonii*
	0->1	P	1->0	*Malacocottus kincaidi*
21:	0=>1	A	0=>1	Cottoidei
	1->4->5	*Eumicrotremus orbis*	1->4->5	Cyclopteridae
	4->5	*Cottunculus thomsoni*	4->5	N
23:	0->1	*Ambophthalmos angustus*	0->1	M
	0->1	O	1->0	*Cottunculus thomsonii*
37:	0->2	*Artediellus uncinatus*	0->2	K
	0->3	Pychrolutidae	2->3	Pychrolutidae
43:	0->1	*Jordania zonope*	0->1	A
	0->1	C	1->0	*Hemilepidotus hemilepidotus*
45:	0->1	J	0->1->2	J
	1->1,2	*Blepsias cirrhosus*	2->1,2	*Blepsias cirrhosus*
	1->2->3	Agonidae	2->3->4	Agonidae
	3->3,4	*Bathyagonus alascanus*	4->3,4	*Bathyagonus alascanus*
	3->4	*Xeneretmus latifrons*		
47:	0=>1	Z	1=>0	*Oxylebius pictus*
	0=>2	Cottoidei	1=>2	Cottoidei
52:	1->0	*Rhamphocottus richardsoni*	1->0	I
	1->0	*Blepsias cirrhosus*	0->1	Agonidae
53:	0->1	Agonidae	0->1	J
	0->0,1	*Blepsias cirrhosus*	1->0,1	*Blepsias cirrhosus*
59:			1->2	I
	1->2->3	*Rhamphocottus richardsoni*	2->3	*Rhamphocottus richardsoni*
	1->2	Agonidae	2->1	*Blepsias cirrhosus*
65:	0->1	*Scorpaenichthys marmoratus*	0->1	Cottoidei
	0->1	B	1->0	*Jordania zonope*

Appendix 3-4. A classification of species examined that is compatible with Table 3-2. Paraphyletic taxon is marked with an asterisk.

- Cottoidei
  - Cottidae*
    - *Artediellus uncinatus, Artedius lateralis, Ascelichthys rhodorus, Chitonotus pugetensis, Clinocottus globiceps, Cottus asper, Enophrys bison, Gymnocanthus galeatus, Hemilepidotus hemilepidotus, Icelinus borealis, Jordania zonope, Leiocottus hirundo, Leptocottus armatus, Myoxocephalus polyacanthocephalus, Oligocottus maculosus, Orthonopias triacis, Radulinus asprellus, Scorpaenichthys marmoratus, Synchirus gilli*
  - Ereuniidae
    - none examined
  - Comephoridae
    - *Comephorus dybowskii*
  - Abyssocottidae
    - none examined
  - Agonidae
    - Rhamphocottinae
      - *Rhamphocottus richardsoni*
    - Hemitripterinae
      - *Blepsias cirrhosus*
    - Agoninae
      - *Bathyagonus alascanus, Xeneretmus latifrons*
  - Psychrolutidae
    - *Ambophthalmos angustus, Cottunculus thomsonii, Dasycottus setiger, Ebinania brephocephala, Eurymen gyrinus, Malacocottus kincaidi, Neophrynichthys heterospilos, Psychrolutes paradoxus*
  - Bathylutichthyidae
    - none examined
  - Cyclopteridae
    - Cyclopterinae
      - *Eumicrotremus orbis*
    - Liparinae
      - *Liparis* spp.

CONCLUSIONS

Three chapters have critically examined our current knowledge of the systematic biology of Cottoidei, examined one seminal paper on this subject in particular depth, and have furthered our knowledge with new anatomical descriptions, interpretations of character evolution, and rigorous cladistic methodology.

Most early works on cottoid fishes were broad in scope but cursory in description of anatomy and phylogenetic inference. Such works typically presented a classification that presumably reflected the author's concepts of evolution within the group, although rarely was this explicitly stated or characters given to back up their assertions. To the best of my ability, in the first chapter I attempted to interpret all previous systematic works on Cottoidei in a modern light that would be more accessible to current researchers in this field. This modern interpretation also serves to introduce my thinking on this group, and this will help in understanding my logic (or biases as the case may be) in the subsequent chapters where I more directly examined the evolution of Cottoidei.

Yabe (1985) presented a phylogeny and classification of Cottoidei. Yabe differed from previous workers in finding a monophyletic Cottidae with the other cottoid families basal to Cottidae. Previous workers (*e.g.*, Regan, 1913; Jordan, 1923; Taranets, 1941) listed Cottidae first in their classifications and other cottoid families subsequently as specialized derivatives. Washington *et al.* (1984) presented a (purportedly) cladistic phylogenetic tree of the Cottoidei that was largely compatible with the classifications of previous workers in having a paraphyletic Cottidae. Nevertheless without independent support, Yabe's paper became influential and has remained the seminal treatise on the subject. In the second chapter, I directly challenged Yabe's phylogenetic hypothesis by examining his assumptions (and lack thereof) and methodology, and found that his work does not stand up to my scrutiny. I reanalyzed his data cladistically and carefully considered homoplasy. I found that his data do not support his phylogeny and, in particular, his monophyletic Cottidae.

In the third chapter I presented a new phylogenetic study that is readily testable, where characters, evolutionary assumptions, and phylogenetic methods are explicitly and clearly described. This clarity will allow future researchers to interpret and use these findings easily and critically. The phylogeny I found supports early classifications of Cottoidei that have Cottidae listed first as the generalized and paraphyletic family of the suborder and subsequent listed families as specialized derivatives: three cottid genera (*Scorpaenichthys marmoratus*, *Jordania zonope*, and *Hemilepidotus hemilepidotus*) are basal to a large crown clade that includes all specialized cottoid families examined. One cottoid taxon, Cyclopteridae, has often been given special status presumably based on its highly specialized morphology, but phylogenetically it is shown not to warrant such special treatment: Cyclopteridae are cottoid derivatives and members of the crown clade. A major cottoid taxon is identified for the first time: Agonidae with Rhamphocottinae, Hemitripterinae, and Agoninae. A sister taxon is possibly found for one cottoid family: *Artediellus* for Psychrolutidae.

The results presented here firm some ideas on the systematics of Cottoidei and open new questions to be resolved, such as: i) what other genera are basal cottoids? ii) how does the crown clade resolve? and iii) are Hemitripterinae (with *Blepsias*, *Hemitripterus*, and *Nautichthys*) monophyletic exclusive of Agoninae? Moreover, the new relationships I postulate here should be independently tested. These questions will require much further work to resolve. Some thoughts on future work include addition of taxa, in particular those that are presumed primitive within Cottoidei. Further anatomical systems should be examined, including the osteology of the inside of the cranium, histology, and neurology. Ontogeny and variation in the lateralis system, particularly on the cranium, must be evaluated and closer examination of scale morphology and ontogeny will yield a wealth of phylogenetic information that will surely make my assumptions seem pioneering. I also look forward to genetic work on Cottoidei to resolve shortcomings in my phylogeny and ideas on complex character evolution. Much has been resolved here, yet even more questions are opened.

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