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SCOMBROID PHYLOGENY: AN ALTERNATIVE HYPOTHESIS

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ABSTRACT

A new hypothesis of the cladistic intrarelationships of the perciform suborder Scombroidei and immediate outgroups is proposed, based on 49 characters, most of them osteological. This hypothesis differs from the one proposed recently by Collette et al. (1984) in several respects. An hypothesis of precise outgroup relationships is presented. Outgroup taxa are, in phyletic sequence: *Dinolestes* plus several genera previously placed in the Acropomatidae; *Scombrops*; *Scombrolabrax*; and *Pomatomus* (first outgroup). *Sphyraena* is included in the Scombroidei as the sister group of all other scombroids. The Gempylidae, rediagnosed, is the sister group of the scombrids plus billfishes; within the Gempylidae, *Lepidocybium* is the sister group of the Gempylinae plus Trichiurinae. The billfishes (Istiophoridae plus *Xiphias*) are the sister group of *Acanthocybium* and, in a cladistic classification, must be treated as a subgroup of the Scombridae. The precise affinities of *Gasterochisma* remain unresolved; data on larval morphology and developmental osteology, currently unavailable, should help resolve the placement of this enigmatic genus, which exhibits a perplexing combination of primitive and derived character states.

The suborder Scombroidei is among the most extensively studied and best known taxonomically of the perciform suborders. Despite continuing disagreement over its limits, the generally accepted concept of the Scombroidei is essentially that of Regan (1909), who included six families: Gempylidae, Trichiuridae, Scombridae, Istiophoridae, Xiphiidae and Luvaridae. Recently Tyler et al. (MS)[1] have shown that the monotypic Luvaridae is not a scombroid but an acanthuroid. Placement of the billfishes, Istiophoridae and Xiphiidae, remains controversial. Although most classifications (Regan, 1909; Berg, 1940; Greenwood et al., 1966; Collette et al., 1984) have included the billfishes in the Scombroidei, some authors (Gosline, 1968; Nakamura, 1983; Potthoff et al., 1980) have disagreed and suggested that billfishes probably originated within the percoids. The extensive classificatory history of the Scombridae was reviewed briefly by Cressey et al. (1983), that of gempylids by Russo (1983) and of billfishes by Nakamura (1983) and will not be recounted here.

At the 1979 meetings of the American Society of Ichthyologists and Herpetologists, I presented a paper in which I described several distinctive specializations of the gill arches and upper jaw development of scombroids. Certain of these features have been cited subsequently (Potthoff et al., 1980; Potthoff and Kelley, 1982; Cressey et al., 1983; Russo, 1983; Collette et al., 1984), but, until now, none have been illustrated or fully described. A primary purpose of this paper is to describe and illustrate these specializations and emphasize their significance. I concluded, in 1979, that these specializations indicate not only that billfishes are scombroids but that their relationships lie within the Scombridae, specifically with the genus *Acanthocybium*.

Recently, Collette et al. (1984) incorporated most of these characters, along with many others, into a phylogenetic hypothesis for the Scombroidei (initially prepared for and presented at the 1981 meetings of the ASIH by Collette and

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[1] J. C. Tyler, G. D. Johnson, I. Nakamura and B. B. Collette. Osteology and relationships of the oceanic fish *Luvarus imperialis* (Luvaridae): an oceanic acanthuroid. Manuscript.

Russo). Collette et al. (1984) agreed that the billfishes are scombroids, but rejected the *Acanthocybium* connection and placed the billfishes as the sister group of the Scombridae. Their analysis, published in the Ahlstrom Memorial Volume, Ontogeny and Systematics of Fishes, was necessarily abbreviated and consisted of only a cladogram (their fig. 312) generated by the Wagner 78 computer program, and an appendix legend listing states of the "40 characters considered significant in assessing scombroid relationships." A full description of characters and discussion of character analysis would undoubtedly have identified and allowed resolution of some of the shortcomings that seem to have resulted from the abbreviated treatment. Problems that I encountered with the Collette et al. (1984) analysis are noted below:

1. Information provided in the appendix legend about symbols and the way in which they apply to reversals and independent acquisitions on the cladogram is insufficient, particularly for multistate characters. Directionality for multistate characters is not clearly indicated, and it is thus impossible to identify from the symbols which state is present at a particular node.
2. Polarity designation, based on *Scombrolabrax* as the outgroup, is confusing and, for some characters, wrong. In the appendix legend, polarity is not indicated by the 0 or 1 code given after each state, as implied at the beginning of the legend, but apparently by the order in which the states are listed.
3. For a few characters, states were not known for some taxa (particularly *Gasterochisma* and the billfishes), but this was not indicated in reference to their distribution as indicated on the cladogram. Thus, as they note in the text, the larva of *Gasterochisma* is unknown, but character states shown on the cladogram imply that *Gasterochisma* lacks the beak of most scombrid larvae and shares with them a precocious spinous dorsal. The confusion results from the fact that character states for larvae were assumed so that developmental characters could be used in the analysis (Collette, pers. comm.).
4. The distributions of a number of known character states (e.g., vertebral number, sequence of dorsal fin development, several caudal fusions) are incorrectly indicated on the cladogram, although in some cases correctly reported in one of the tables. Specific errors are discussed in the character analysis below.
5. Homology of several character states (e.g., articulation and expansion of infraorbitals, subocular shelf, compressed teeth) seems questionable and, in at least one instance (gill filament cross-connections), was incorrectly interpreted.
6. Treatment of the Gempylidae is confusing. Although the question of its monophyly is not specifically addressed, the family is characterized in the discussion, and a separate cladogram of its generic phylogeny (taken from Russo, 1983) implies that it is monophyletic. Nonetheless, the scombroid cladogram indicates paraphyly for the Gempylidae, and one of several unspecified lineages is shown as the sister group of all other scombroids. Additional confusion results from a single listing of all character states that occur at the nodes of the various gempylid clades and another of all homoplasies occurring at various levels within the Gempylidae. Also perplexing is the placement of the highly specialized Trichiuridae as the sister group of all other scombroids; the affinities of trichiurid genera clearly lie with the gempylids.
7. Characters of the caudal skeleton may have been overemphasized. For example, fusions of hypurals 1–2 and 3–4 are treated as two independent characters, even though, as in most perciforms, they never occur independently. Sixteen of 40 characters (11 reductive) involve morphology of the caudal peduncle or skeleton related to increased rigidity (hypurostegy, fusions) and hydrodynamic efficiency (caudal keels). None are unique to scombroids but are seen repeatedly in

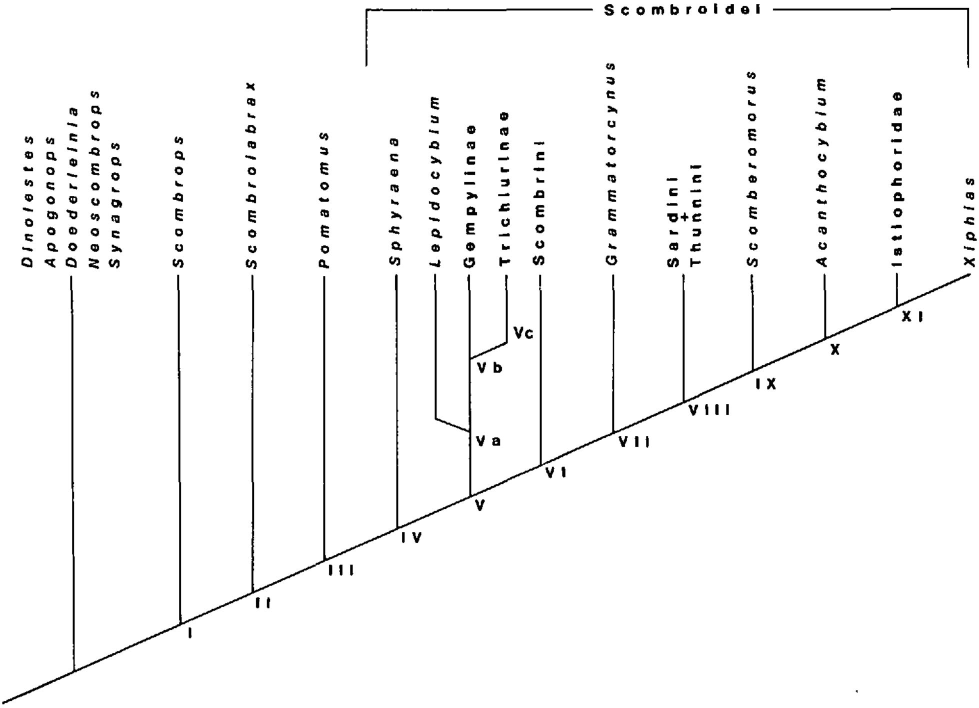

Figure 1. Cladogram representing hypothesized relationships of the Scombroidei and immediate outgroups. Character states (see text for explanation of symbols) are distributed as follows: I—1; II—2; III—$\underline{3}$, 4, 5; IV—$\underline{3'}$, $\underline{6}$, $\underline{7}$, 8, 9, 10; V—11, 12, 13, 14, 15, 16; Va—$\boxed{17}$, $\underline{18}$, $\underline{19}$, $\underline{20}$, $\underline{21}$, $\underline{22}$; Vb—⑭, $\boxed{16'}$, $\underline{23}$, $\underline{24}$, $\underline{25}$; Vc—④, ⑫, 16″, 18′, 26, $\underline{27}$, $\underline{28}$, $\underline{29}$, $\underline{30}$; VI—$\underline{31}$, 32, 33, 34, $\underline{35}$, 36; VII—37, 38, 39; VIII—$\boxed{16'}$, $\boxed{17}$, 40, $\underline{41}$; IX—$\underline{41'}$; X—㉟, $\underline{42}$, $\underline{43}$, 44, 45; XI—⑫, ⑯, 31′, ㊱, ㊲, ㊵, $\underline{46}$, $\underline{47}$, $\underline{48}$, $\underline{49}$.

other pelagic or fast swimming perciform fishes. These specializations certainly represent true synapomorphies at some levels within the Scombroidei, but it seems reasonable to consider them with caution depending on their congruence with other evidence. However, if I interpret their cladogram correctly, Collette et al. (1984) place one line of gempylids as the sister group of scombrids, based on shared caudal fusions achieved independently in scombrids and the highly derived gempylid genera, *Diplospinus* and *Paradiplospinus.* At the same time, caudal fusions are not indicated for the trichiurids, although those with identifiable caudal fins share most of the fusions that characterize the two gempylid genera.

The decision to expand my earlier investigation is founded partly in the difficulties I encountered in interpreting the cladogram of Collette et al. (1984) and in attempting to resolve conflicts between their data and my own. Comparison of my initial cladistic hypothesis with that proposed by Collette et al. (1984) led me to investigate additional morphological features of scombroid fishes and their probable closest relatives. The result, presented here, is a new cladistic hypothesis of the interrelationships of the Scombroidei and immediate outgroups (Fig. 1).

Unless otherwise indicated, the following terminology applies: scombroids refers to *Sphyraena* plus the Scombroidei of Collette et al. (1984), excluding *Gasterochisma*; gempylids refers to *Lepidocybium* plus gempylines (Gempylidae of Collette et al., 1984, excluding *Lepidocybium*) plus trichiurines (Trichiuridae of

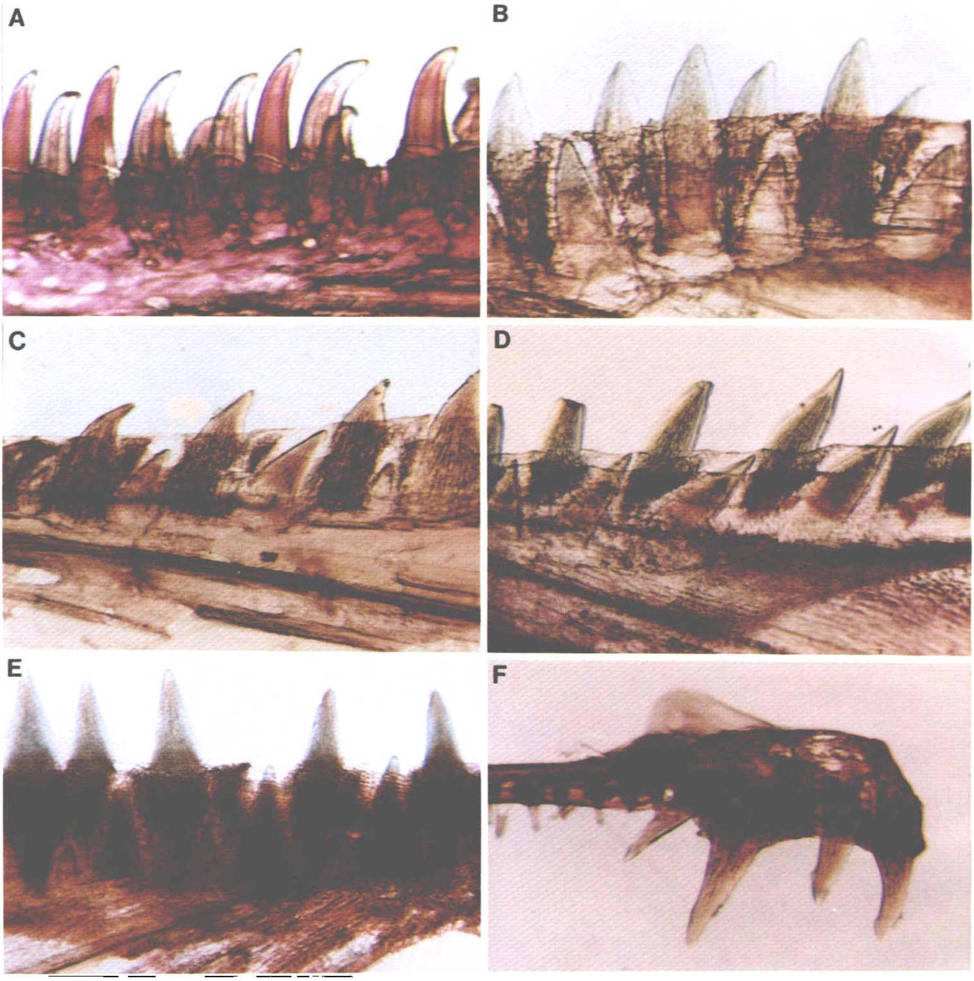

Figure 2. Dentary teeth of: A, *Morone saxatilis,* uncat., 155 mm SL, lateral view; B, *Pomatomus saltatrix,* USNM 236806, 71 mm SL, medial view; C, *Sphyraena barracuda,* USNM 148649, 80 mm SL, medial view; D, *Diplospinus multistriatus,* USNM 215398, 203 mm SL, medial view; E, *Scomberomorus tritor,* USNM 193839, 143 mm SL, lateral view. F, Premaxillary teeth of *Sphyraena barracuda,* USNM 148649, 80 mm SL.

Collette et al., 1984); scombrids refers to the Scombridae of Collette et al. (1984), excluding *Gasterochisma*; Scombrini, Sardini and Thunnini refer to scombrid tribes as defined by Collette et al. (1984); billfishes refers to istiophorids plus *Xiphias.*

MATERIAL

A complete listing of material examined in this study would be impractical, because comparative observations were made on a broad range of perciforms. Cleared and stained gill arches were examined from representatives of all genera of the Scombroidei, all families of the Percoidei, and all but a few families of the Perciformes. The comparative foundation for other features was less extensive but in general included representatives of all scombroid genera and most percoid families. Most specimens examined are part of the permanent skeletal collection (both dry and cleared and stained preparations) of the U.S. National Museum of Natural History. Specimens from which illustrations were prepared are identified in the figure legends; institutional abbreviations follow Leviton et al. (1985).

CHARACTER ANALYSIS

Character polarity was established by outgroup comparison following the methodology of Maddison et al. (1984). The outgroup for the Scombroidei was identified as a small group of monotypic percoid genera (usually placed in separate families) plus several genera currently allocated to the Acropomatidae, which, as defined by Johnson (1984), is apparently paraphyletic. These genera, *Doederleinia, Synagrops, Neoscombrops, Apogonops, Dinolestes, Scombrops, Scombrolabrax, Pomatomus,* and *Sphyraena* share with primitive scombroids (gempylids and trichiurids) an isolated cluster of two or three enlarged, fang-like teeth (smaller and more numerous in *Pomatomus*) located near the symphysis, just medial to the primary row of teeth on each premaxilla (Fig. 2F). These teeth are ankylosed in all but *Pomatomus* and *Doederleinia.* This inner row of premaxillary teeth was described for *Scombrops, Scombrolabrax,* and gempylids by Russo (1983), and its presence in the latter two was noted by Collette et al. (1984). To my knowledge, this specialized premaxillary dentition is unique among perciforms to gempylids and the outgroup taxa. The outgroup taxa share with scombroids at least two additional derived features: cycloid scales, derived but not unique among percoids (Johnson, 1984); and uniquely configured, ankylosed, primary jaw teeth (see character 1 below). There is no compelling morphological evidence that suggests that any of these genera are more closely related to another group in the Percoidei or that refutes their close relationship to the Scombroidei. On the contrary, successively less inclusive groups of them share additional apomorphies with the scombroids (Fig. 1).

For those several characters that vary within the outgroup, the primitive state was hypothesized to be that which characterizes most lower percoids and acropomatids, allowing formulation of an hypothesis of specific outgroup relationships. For the majority of characters, the primitive state was hypothesized to be that shared by all members of the outgroup. *Sphyraena* shares numerous apomorphies with the Scombroidei and is treated as the cladistically most primitive member of the suborder.

The cladogram (Fig. 1) was constructed on the basis of parsimony argumentation using a total of 49 characters (64 synapomorphies, including reversals and independent acquisitions). Reductive (loss) and innovative specializations were treated as equally likely to occur, as were reversals and independent acquisitions. Reversals and independent acquisitions were hypothesized based on the most parsimonious distribution of all character states.

A character matrix (Table 1) was prepared for independent analysis of the data using D. Swofford's PAUP (Phylogenetic Analysis Using Parsimony); this analysis was performed by W.L. Fink on the University of Michigan MTS mainframe system. PAUP produced a cladogram that is identical to the one constructed by hand above *Scombrolabrax,* but identified ambiguity in the sequence of three outgroup taxa, *Dinolestes, Scombrops* and *Scombrolabrax.* Changes in the phyletic sequence of these three taxa does not affect hypotheses of character polarity for the scombroid analysis; my reasons for selecting the specific sequence shown in the cladogram (Fig. 1) are considered in the Discussion.

In the character analysis that follows, characters are numbered and discussed in the order in which they occur as synapomorphies on the cladogram (Fig. 1) and are grouped according to their occurrence at each node (roman numerals).

Table 1. Character matrix for Scombroidei. 0, primitive state; 1–3, derived states; ?, state unknown; N, character not applicable

1				5					10					15					20					25				
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	2	1	1	1	1	1	1	1	0[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
1	1	2	1	1	1	1	1	1	1	1[b]	1[b]	1[b]	0	1	2	1	1	1	1	1	1	1	1	1[b]	0	0	0	0
1	1	2	0	1	1	1	1	1	1	1	0	1	0	1	3	1	2	1	1	1	1	1	1	1	1	1	1	1
1	1	2	1	1	2	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0
1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0
1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0
N	N	2	1	1	1	1	1	1	1	1	0	1	1	1	0	N	0	N	0	0	0	0	0	0	0	0	0	0
N	N	2	0	1	1	1	1	1	1	1	0	1	0	1	0	N	0	N	0	0	0	0	0	0	0	0	0	0
1	1	0	1	1	0	0	0	1	1	0	1	1	0	1	2	?[d]	?[d]	0	0	0	0	0	0	0	0	0	0	0

[a] Questionable, see discussion of character 11.

[b] Some reversal within this group.

[c] Derived state acquired independently within this group.

[d] Larva unknown.

[e] Homology with scombrid condition uncertain without examination of smaller specimens; urostyle, uroneural and all hypurals fused.

[f] Two epurals in adults, but initial number unknown.

Discussion of each character is preceded by a brief italicized description of the derived state. Numbers not enclosed by a square or circle indicate a derived state that occurs as a synapomorphy only once on the cladogram. Numbers followed by ′ or ″ indicate successively more advanced states in a single transformation series. Numbers enclosed in circles indicate hypothesized reversals to the primitive state; numbers enclosed in squares indicate hypothesized independent acquisitions, derived states that appear more than once on the cladogram. Underlined numbers denote apomorphies for which I believe stronger weighting could be argued based on their complexity and/or uniqueness among perciform fishes; character weight was not considered in constructing the cladogram. The number of each character used by Collette et al. (1984) is enclosed in parentheses immediately following the character numbers assigned here.

I. *SCOMBROPS* + *SCOMBROLABRAX* + *POMATOMUS* + SCOMBROIDEI

1. *Distinctive Development, Replacement Mode and Adult Configuration of Primary Jaw Dentition.*—Fink (1981) reported that the typical tooth attachment mode for perciforms is his Type 2, in which there is an intervening layer of collagen between the tooth base and the bone of the jaw (Fig. 2A). Among perciforms, he reported ankylosed (Type 1) teeth in *Sphyraena* and the gempylid *Nesiarchus*; they also occur in some acropomatids, *Dinolestes, Scombrops, Scombrolabrax, Pomatomus,* and all scombroids. In *Doederleinia, Synagrops, Neoscombrops,* and *Dinolestes,* several enlarged ankylosed teeth are found only on the dentary amidst the usual bands of Type 2 teeth. These ankylosed teeth may represent precursors of the unique dentition that characterizes the remainder of the outgroup and all scombroids, which is exceptional in several ways. In this latter condition (Fig. 2B–E), all functional teeth in both jaws are ankylosed and stand in a single row (a few smaller Type 2 teeth are present posteriorly on the premaxilla of *Scombrops* and *Pomatomus*). The bases of these functional teeth

Table 1. Continued

30					35					40					45				49	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	"Acropomatids"
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Dinolestes*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Scombrops*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Scombrolabrax*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Pomatomus*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Sphyraena*
0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	*Lepidocybium*
0	0	0	0	0	0	0	0	0	0[c]	0	0	0	0	0	0	0	0	0	0	Gempylinae
1	0	0	0	?	0	?	0	0	0[c]	0	0	0	0	0	0	0	0	0	0	Trichiurinae
0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	Scombrini
0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	*Grammatorcynus*
0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0[c]	0	0	0	0	Sardini + Thunnini
0	1	1	1	1	1	1	1	1	1	1	2	0	0	0	0	0	0	0	0	*Scomberomorus*
0	1	1	1	1	0	1	1	1	1	1	2	1	1	1	1	0	0	0	0	*Acanthocybium*
0	1	1	1	1	N	0	0	1	1	0	2	1	1	1	1	1	1	1	1	Istiophoridae
0	1	1	1	1	0	0	0	0	1	0	2	1	1	1	0	1	1	1	1	*Xiphias*
0	0	1	1	?[e]	?[e]	?[f]	0	0	1	1	?[d]	0	0	0	0	0	0	0	0	*Gasterochisma*

are situated between, and peripherally ankylosed to, the internal walls of a deep, continuous, longitudinal crypt; the teeth extend only part way into this crypt, so that their unsupported bases are suspended within it.[2] Replacement teeth develop within the crypt on each side of the mature ankylosed teeth, which are apparently shed or resorbed rapidly after the new teeth move into position and become fixed. As a consequence, the teeth appear widely spaced, because, with occasional exceptions, only alternate teeth are fully ankylosed and functional at any given time. An additional unusual feature of these teeth is their reticulate or cancellous appearance internally when viewed in glycerin, not characteristic of most perciform teeth. This reticulate internal structure probably represents the coarse, irregular trabeculae of osteodentine described by Tomes (1923) and Orvig (1967), but confirmation will require histological study.

The pattern of dentition described above has several distinctive features and is considered here to represent a complex synapomorphy uniting *Scombrops, Scombrolabrax, Pomatomus,* and the Scombroidei (including *Sphyraena*) as a monophyletic group (see character 47 for a discussion of dentition in the billfishes). Although treated here as a single complex character, it could justifiably be interpreted as several.

II. *SCOMBROLABRAX* + *POMATOMUS* + SCOMBROIDEI

2. *Single Supernumerary Spine on First Spinous Dorsal Pterygiophore; No Chain Link Articulation.*—Like most generalized percoids, acropomatids and *Scombrops* have two supernumerary spines on the first dorsal pterygiophore, both with the primitive "chain-link articulation" of Bridge (1896) (see Johnson, 1983, fig. 4).

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[2] Tomes (1923) illustrated and briefly described this condition in "the mackerel." In a separate chapter, he described the teeth of *Sphyraena* as being implanted in distinct sockets, but they differ from the condition described above only in having a thin lamina of bone separating the tooth base from the crypt in some areas.

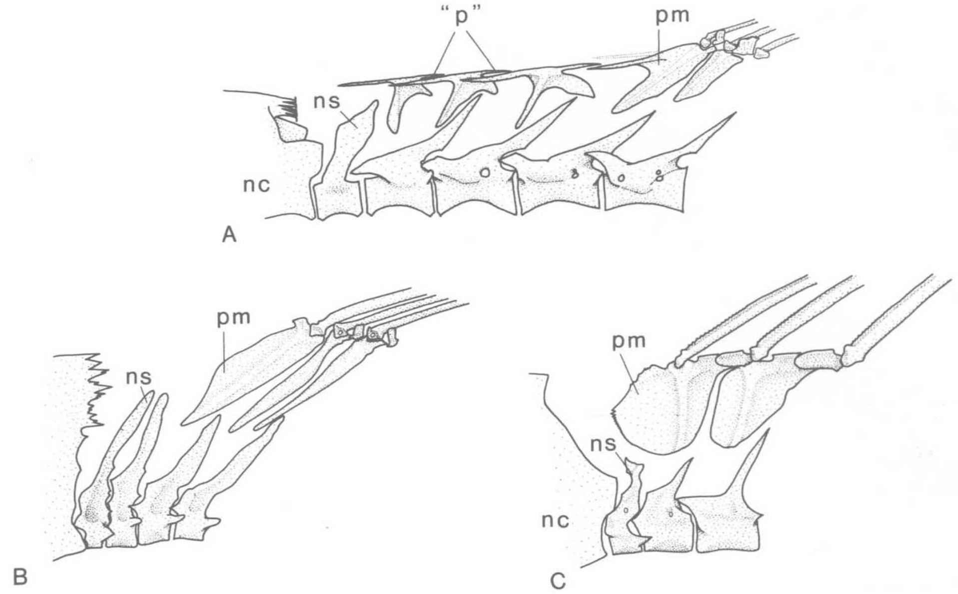

Figure 3. Predorsals and/or anteriormost dorsal pterygiophores in: A, *Sphyraena barracuda,* USNM 226399, 78.5 mm SL; B, *Scomberomorus tritor,* USNM 193839, 143 mm SL; C, *Promethichthys prometheus,* USNM 236797, 133 mm SL.

A single supernumerary spine without the chain-link attachment (Fig. 3A–C) is a synapomorphy of *Scombrolabrax, Pomatomus* and the scombroids. Billfishes are exceptional among scombroids in having additional unattached supernumerary rays on the first dorsal pterygiophore (two in istiophorids, one, occasionally two in *Xiphias*; Potthoff and Kelley, 1982; Collette et al., 1984), but this does not represent a reversion to the primitive percoid state. Billfishes lack a spinous dorsal fin (see character 48), and thus the first pterygiophore is not the strict homologue of that element in other scombroids and the outgroup. A single supernumerary spine in *Dinolestes* is considered an independent acquisition.

III. *POMATOMUS* + SCOMBROIDEI

3. *Enlarged and Reoriented Fronto-sphenotic Shelf Forms Floor of Large Fossa; Infraorbital–Supraorbital Sensory Canal Junction Medially and Somewhat Anteriorly Displaced.*—In most percoids and all outgroup taxa, except *Pomatomus,* the junction of the infraorbital and supraorbital sensory canals is at the posterior margin of the orbit. The uppermost infraorbital rests in (and is frequently bound to) an expanded, trough-like area or notch on the more-or-less vertically oriented, lateral margin of the sphenotic, and the two canals communicate directly at this point (Fig. 4A). A marked modification of this region is shared by *Pomatomus* and all scombroids and represents a complex synapomorphy (conceivably divisible into several characters) of these taxa. In scombroids (3′, Figs. 4B–C and 5A–B), the supraorbital canal is separated from the dorsolateral margin of the orbit by a large fossa (dilatator groove of Allis, 1903, figs. 4, 5, 7, 11, and 54) that houses the relatively enlarged dilatator operculi (DO). The floor of this fossa is formed by a nearly horizontal fronto-sphenotic shelf, the lateral margin of which is thin and not modified to accommodate the dorsalmost infraorbital. Instead, the infraorbital canal passes over the edge of this shelf to join the effectively

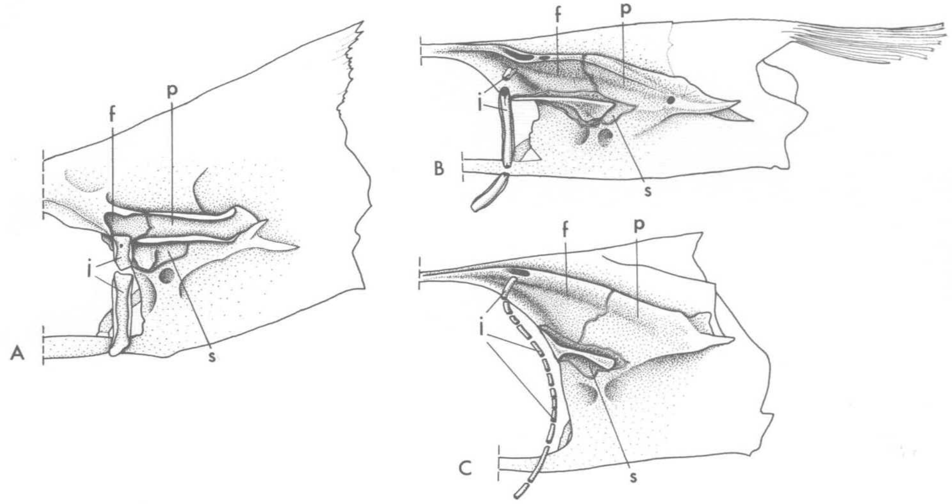

Figure 4. Posterodorsal portion of neurocranium and infraorbital series, left lateral view: A, *Morone mississippiensis*, USNM 218819, 77 mm SL; B, *Sphyraena barracuda*, USNM 226399, 78 mm SL; C, *Promethichthys prometheus*, USNM 236797, 135 mm SL. i, infraorbital; f, frontal; s, sphenotic; p, pterotic.

medially displaced supraorbital canal, and the dorsalmost one to several infraorbitals lie free in the skin covering the DO. The adductor mandibulae usually extends dorsally to cover part or all of the DO. A similar, but probably more primitive condition (3) characterizes *Pomatomus*; the infraorbital–supraorbital junction is identical to that of scombroids, but the lateral margin of the sphenotic shelf is thick and rounded rather than thin, and much of the anterior portion of the fossa is occupied by an enlarged levator arcus palatini (LAP). In scombroids the LAP originates below the DO and thus is not associated with the frontosphenotic fossa.

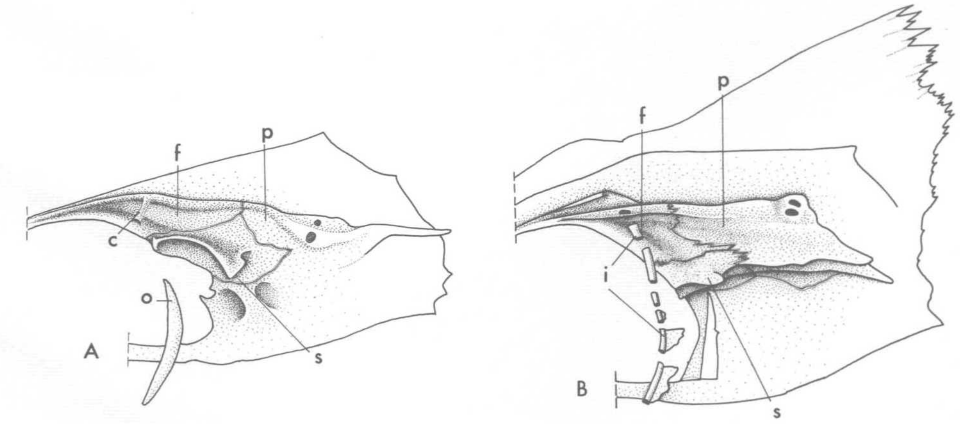

Figure 5. Posterodorsal portion of neurocranium and infraorbital series, left lateral view: A, *Lepturacanthus* sp., USNM uncat., 272 mm SL; B, *Scomberomorus tritor*, USNM 193839, 143 mm SL. c, lateral extension of supraorbital sensory canal; o, ossification with no sensory canal; i, infraorbital; f, frontal; s, sphenotic; p, pterotic.

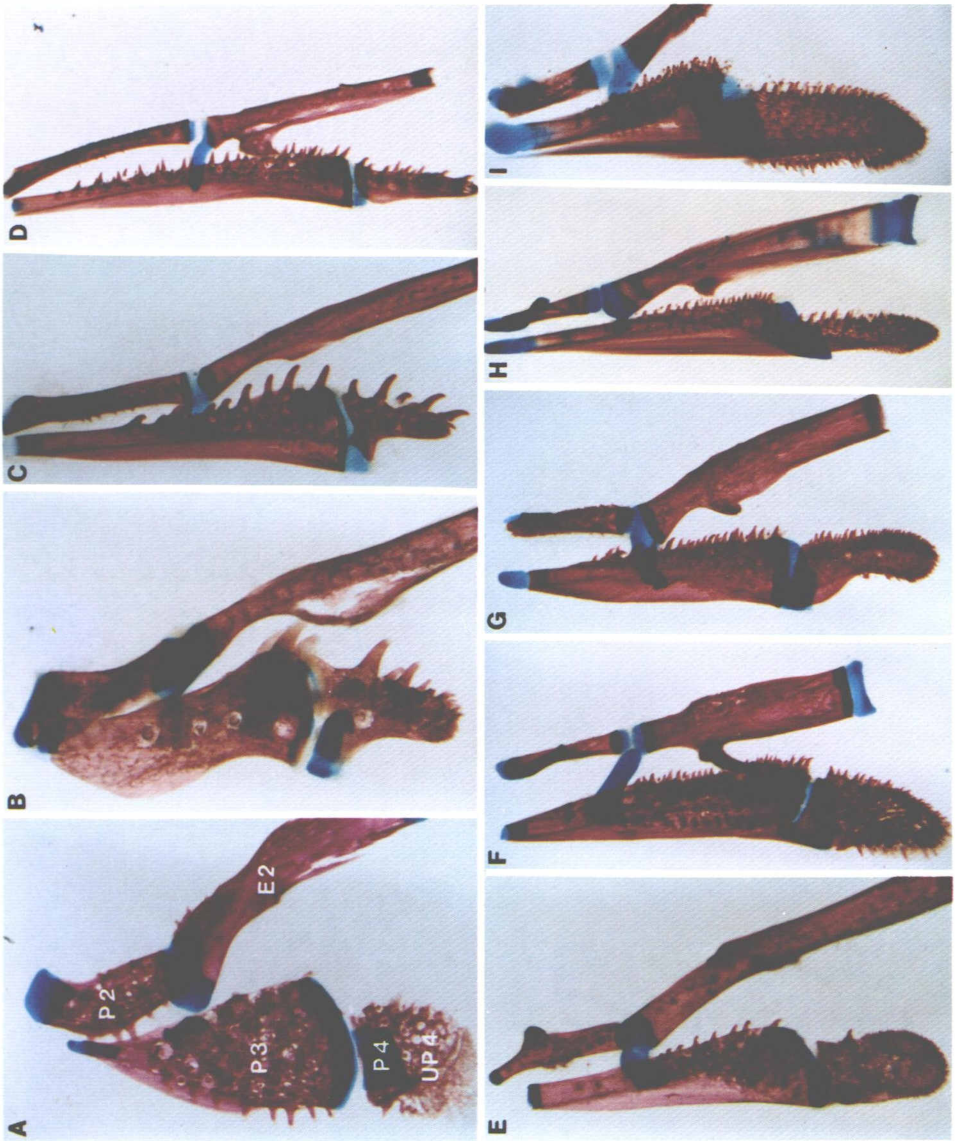

Figure 6. Dorsal gill arches, right side in dorsal view: A, *Morone mississippiensis,* USNM 218819, 77 mm SL; B, *Scombrolabrax heterolepis,* uncat., 140 mm SL; C, *Nealotus tripes,* MCZ 41516; D, *Evoxymetopon taeniatus,* USNM 64490; E, *Sphyraena obtusata,* USNM 198851, 152 mm SL; F, *Euthynnus alleteratus,* uncat. 250 mm SL; G, *Scomberomorus maculatus,* GMBL 71-199, 105 mm SL; H, *Istiophorus albicans,* USNM 188295, 269 mm SL; I, *Xiphias gladius,* USNM 251937, 338 mm SL. P2, pharyngobranchial 2; P3, pharyngobranchial 3; P4, pharyngobranchial 4; UP4, fourth upper pharyngeal toothplate; E2, epibranchial 2; other elements removed.

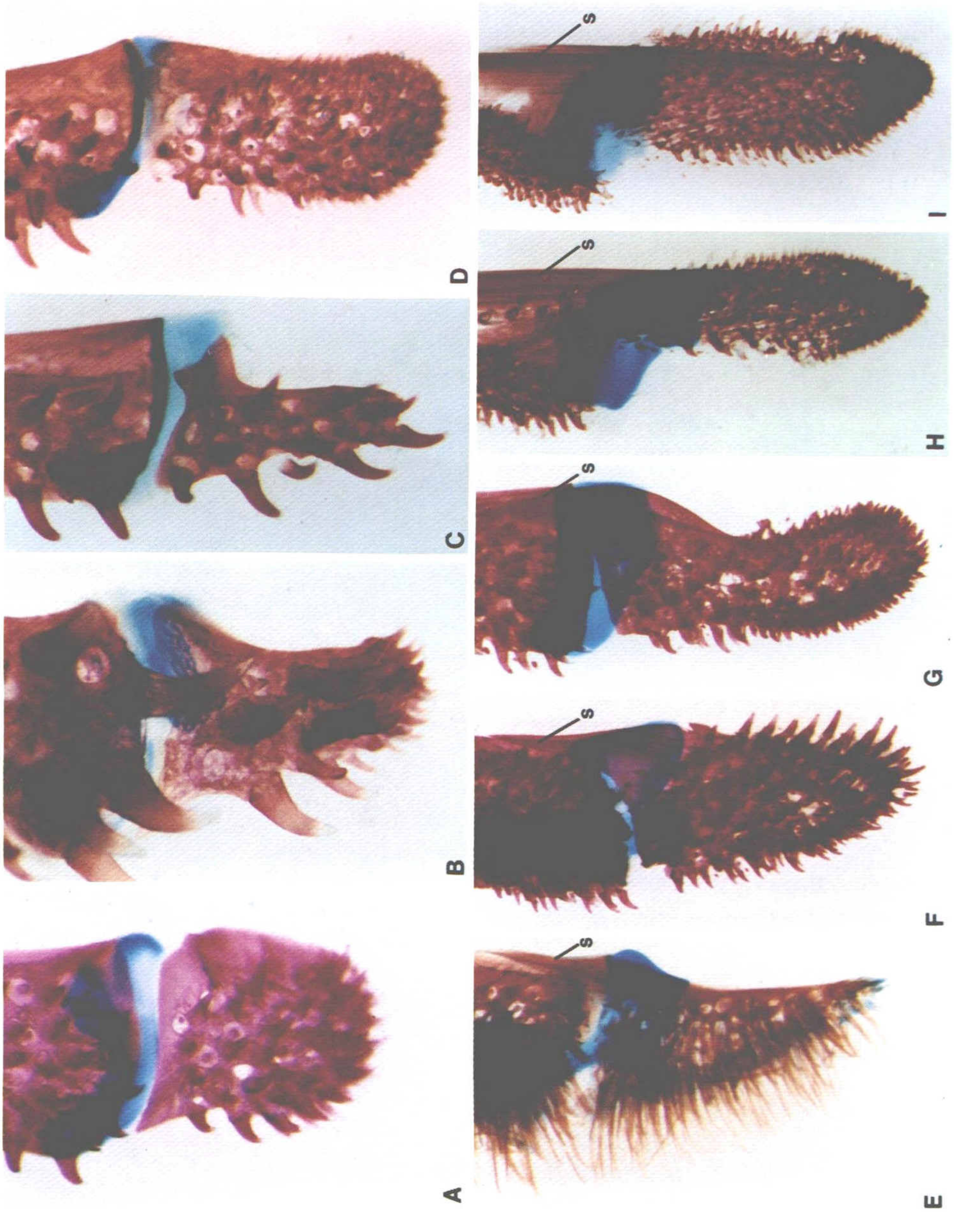

Figure 7. Fourth pharyngeal toothplate showing presence or absence of stay (s) at articulation with pharyngobranchial 3, right side in ventral view: A, *Mycteroperca phenax*, uncat., 61 mm SL; B, *Scombrolabrax heterolepis*, uncat., 140 mm SL; C, *Evoxymetopon taeniatus*, USNM 64490; D, *Sphyraena obtusata*, USNM 198851, 152 mm SL; E, *Scomber scombrus*, uncat., 120 mm SL; F, *Euthynnus alleteratus*, uncat., 250 mm SL; G, *Scomberomorus maculatus*, GMBL 71-199, 105 mm SL; H, *Istiophorus albicans*, USNM 188295, 269 mm SL; I, *Xiphias gladius*, USNM 251937, 338 mm SL.

4. *Dorsal- and Anal-fin Stay Bifurcated Posteriorly.*—In almost all perciform fishes, there is a small, separate bony element associated with the posterior end of the proximal–middle radial of the ultimate dorsal and anal pterygiophores, the vestigial radial of Bridge (1896) or stay of Weitzman (1962, figs. 16B and 17B). Johnson (1984) reported the distribution of this element among percoids. According to Potthoff (1975, 1980) and Potthoff et al. (1980), this stay develops directly from the ultimate proximal–middle radial cartilage, but Kohno and Taki (1983) argue that it is initially separate and thus represents the vestige of a separate pterygiophore. More recent observations by Potthoff (pers. comm.) and me support those of Kohno and Taki.

In most percoids and all outgroup taxa, except *Pomatomus,* the stay is a simple, relatively flat, vertical plate of variable shape. In *Pomatomus* and all scombroids (including *Sphyraena*), except trichiurines, the posterior end of the stay is bilaterally bifurcated, each bifurcation being associated with the supracarinalis posterior of its respective side. Collette et al. (1984, table 161) recorded a bifurcate stay in gempylids, trichiurids (reported incorrectly, based on the gempylid *Diplospinus*), Thunnini, Scombrini, and istiophorids. Potthoff and Kelley (1982) described and illustrated a non-bifurcate stay in *Xiphias.* A bilaterally bifurcate stay is a synapomorphy of *Pomatomus* and scombroids; non-bifurcate stays in trichiurines and *Xiphias* are most parsimoniously interpreted as reversals.

5. *Thick Crescent of Adipose Tissue along Posterior Margin of Eye.*—A thick crescent of adipose tissue along the posterior margin of the orbit is a synapomorphy of *Pomatomus* and all scombroids. This tissue is lacking in all other outgroup taxa and most percoids.

IV. SCOMBROIDEI

3'. *Horizontal Fronto-sphenotic Shelf has Sharp Edge; Fossa Occupied Mainly by Enlarged DO.*

6. (1) *Second Epibranchial–Third Pharyngobranchial Articulation Uniquely Modified.*—The dorsal gill arches of primitive perciforms comprise four pairs of epibranchials, four pairs of pharyngobranchials and an interarcual cartilage between the uncinate process of epibranchial 1 and pharyngobranchial 2. The first (suspensory) pharyngobranchial is rod-like and edentulous. The second, third, and fourth pharyngobranchials bear well-developed toothplates, the second usually notably larger than the other two. The fourth pharyngobranchial is cartilaginous.

In most percoids and all outgroup taxa, the slightly expanded cartilaginous anterior tip of the second epibranchial articulates with the second and third pharyngobranchials as shown in Figure 6A–B. Anterolaterally, it contacts the posterior cartilaginous tip of the second pharyngobranchial, and medially it abuts a large, usually laterally directed cartilaginous condyle on the dorsolateral margin of the third pharyngobranchial.

A unique, specialized articulation of these elements characterizes the Scombroidei (Fig. 6C–I). Here, contact with the second pharyngobranchial is unmodified, but articulation with the third pharyngobranchial is by a curved cartilaginous extension that extends medially well beyond the lateral margin of the third pharyngobranchial to articulate with a small cartilaginous condyle (occasionally absent, Fig. 6D, H) located at the anterior tip of a longitudinally oriented bony column on the mid-dorsal surface of the third pharyngobranchial.

Functionally, this specialized second epibranchial–third pharyngobranchial articulation of scombroids allows greater mobility of the pharyngobranchials with respect to the epibranchials. This is borne out by the anterodorsal extension in many scombroids of the posterior cartilaginous portion of the third pharyngobranchial to form an elongate condyle along which the articular tip of the third epibranchial rides as the pharyngobranchials move back and forth (Fig. 6F). Pharyngobranchial mobility is emphasized within two subgroups of the Scombridae, where it is achieved by two different mechanisms. In *Scomber* (see Allis, 1903, fig. 29) and *Rastrelliger* (the Scombrini), for example, the epibranchials lie at almost right angles to the elongate third and fourth pharyngobranchials. The anterior articular portion of the second epibranchial is greatly expanded and thus replaces the usually narrow cartilaginous extension while still articulating with the dorsal surface of the third pharyngobranchial as in other scombroids. This is a unique apomorphy of the Scombrini.

Pharyngobranchial mobility is achieved differently in the tunas (Thunnini). In four of the five genera (the exception is *Thunnus*) the cartilaginous extension at the anterior tip of the second epibranchial is autogenous, and forms a hinge-like connection that allows extensive anteroposterior movement of the third pharyngobranchial (Fig. 6F). The "prootic pits" characteristic of the Thunnini are probably related to this increased mobility; they serve as fossae for the origin of enlarged levator internus muscles that insert on the third pharyngobranchials. I have observed an autogenous second epibranchial cartilage elsewhere only in the percoid *Mene*, where it differs in being triangular and in articulating with both the second and third pharyngobranchials. *Mene* shares no other scombrid or scombroid specializations of the gill arches, and the separate cartilage there is obviously of independent origin.

7. *Fourth Pharyngobranchial Cartilage Absent.*—In most perciforms and all outgroup taxa, a small, usually block-shaped fourth pharyngobranchial cartilage is present (Figs. 6A–B and 7B), abutting the posterior cartilaginous margin of the third pharyngobranchial and providing the main surface of articulation for the fourth epibranchial. In the Scombroidei, a separate fourth pharyngobranchial is lacking (Figs. 6C–I and 7C–I) (a very small, crescent-shaped element remains in some specimens of *Sphyraena*), and the fourth epibranchial articulates directly with the relatively extensive posterior cartilaginous portion of the third pharyngobranchial, which fills the concave dorsal surface of the fourth pharyngeal toothplate usually occupied by the fourth pharyngobranchial. The medial half of the cartilaginous posterior end of the third pharyngobranchial is conspicuously larger (extends farther posteriorly) than the lateral half, suggesting that it could be the product of a fusion with the cartilaginous fourth pharyngobranchial, which does appear to be separate very early in ontogeny.

The fourth pharyngobranchial is also absent among those perciforms that lack an autogenous fourth pharyngeal toothplate or have it intimately associated with the third toothplate (e.g., Labroidei, sensu Kaufman and Liem, 1982), but this condition differs markedly from that of the Scombroidei. A few percoids with fully autogenous fourth pharyngeal toothplates (e.g., Cepolidae, Opistognathidae, Plesiopidae, and some apogonids and epinepheline serranids) lack a separate fourth pharyngobranchial, but in those that I have examined, the configuration of the remaining elements is distinguishable from that of scombroids, and suggests loss, rather than fusion, of the fourth pharyngobranchial; the lateral half of the cartilaginous posterior end of the third pharyngobranchial does not extend posteriorly to fill the space usually occupied by the fourth pharyngobranchial, and I have found no evidence of ontogenetic fusion. In epinephelines, this space is occupied by the cartilaginous tip of the fourth epibranchial, which articulates directly with the dorsal surface of the fourth pharyngeal toothplate; in the other groups there is no concave dorsal surface on the fourth pharyngeal toothplate, and instead, the anterior margin of this element forms a vertical surface that directly abuts the posterior cartilaginous portion of the third pharyngobranchial.

8. *Third Pharyngobranchial and Fourth Pharyngeal Toothplate Elongate and "Streamlined."*—Although difficult to quantify, there is a visible difference in shape between the third pharyngobranchial/fourth pharyngeal toothplate complex of scombroids and that of the outgroup taxa. In most percoids and all outgroup taxa, these bones are shorter, and there is a relatively broad, rounded shelf along the anteromedial margin of the third pharyngobranchial (Fig. 6A, B). In all scombroids, the third pharyngobranchial and fourth pharyngeal toothplate are notably elongate, and the lateral shelf on the third pharyngobranchial is reduced, so that the medial margin of that bone is relatively straight (Fig. 6C–I).

9. (19) *Upper Jaw Complex Tightly Bound, Non-protrusible.*—In most percoids and all outgroup taxa, the maxillae and premaxillae are free to move independently of one another and of the snout. There is a narrow frenum on the snout of *Scombrops,* but the maxillae and premaxillae function independently and some protrusion is possible. In all scombroids, the premaxillae are tightly bound to the maxillae and to the snout anteriorly, so that the upper jaws are not protrusible. The rostral cartilage does not slide along the ethmoid but instead provides a pivot point for dorsoventral rotation of the premaxillae.

10. *Fifth Branchiostegal Borne Posterior to Anterior Ceratohyal.*—In most percoids with seven branchiostegal rays and all outgroup taxa, except *Dinolestes,* the fifth branchiostegal ray has a spatulate head like the sixth and seventh and inserts on the posteroventral corner of the anterior ceratohyal (McAllister, 1968, pls. 16–17). In all scombroids, the fifth branchiostegal ray has a relatively narrow head and is displaced posteriorly so that it inserts on the anteroventral corner of the posterior ceratohyal or, in some scombrids, at the junction between the two ceratohyal segments (Collette and Chao, 1975, fig. 42). A similar condition in *Dinolestes* (Fraser, 1971, fig. 2) is most parsimoniously interpreted as an independent acquisition.

V. GEMPYLIDAE + SCOMBRIDAE + BILLFISHES

11. (2) *Predorsal Bones Absent.*—Three predorsal bones, the primitive and most common complement among percoids, characterize all outgroup taxa, except *Scombrolabrax.* Absence of predorsal bones (Fig. 3B, C) is a synapomorphy of scombroids above *Sphyraena.* Three gempylid genera, *Ruvettus, Thyrsitops,* and *Tongaichthys,* have a single, small predorsal element in the first interneural space (Potthoff et al., MS).[3] This element is lacking in *Lepidocybium,* the sister group of all other gempylids, and its presence in three gempylids is most parsimoniously viewed as due to reversal(s). Likewise, parsimony dictates that absence of predorsals in *Scombrolabrax* was independently acquired, because *Pomatomus* and *Sphyraena* have the primitive complement.

The three predorsals of *Sphyraena* (Fig. 3A) deserve further discussion. Johnson (1984) discussed homology of predorsal elements among percoids. In light of that discussion, two aspects of the configuration of the predorsals of *Sphyraena* suggest that they could be neomorphs derived by loss of spines from the three anterior dorsal pterygiophores of a gempylid-like ancestor: 1) unlike the predorsals of most

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[3] Potthoff, T., S. Kelley and J. C. Javech. Cartilage and bone development in scombroid fishes. MS.

percoids, but like pterygiophores, these three elements interdigitate strongly with one another dorsally, although they do not have separate distal radials; 2) the first element inserts in the second interneural space rather than the first; in most percoids and the outgroup, insertion is in the first, but insertion in the second is a synapomorphy of the Gempylidae. If the predorsals of *Sphyraena* are newly derived from pterygiophores, *Sphyraena* shares the derived first pterygiophore insertion of gempylids, suggesting that it could be the sister group of gempylids, rather than the sister group of gempylids plus scombrids and billfishes. However, several other characters conflict with that placement.

12. *Finlets Present.*—Short, widely-spaced, disjunct fin rays characterize the posterior portion of the dorsal fin of most scombroids. These modified fin rays, termed finlets, are always supported by pterygiophores with elongate, autogenous middle radials (Potthoff, 1974; 1975, fig. 18). All percoids (except some carangids), all outgroup taxa and *Sphyraena* lack finlets; the presence of finlets is derived for scombroids. Finlets have apparently been lost independently in some gempylines, all trichiurines and the billfishes.

13. (32 in part; 35) *Hypurals 1–2 and 3–4 Fuse Ontogenetically.*—In most percoids, all outgroup taxa and *Sphyraena*, hypurals 1–5 remain autogenous. Collette et al. (1984) treated ontogenetic fusion of the upper hypurals in scombroids as a three state character, the two derived states being 3–4 fused and 3–4–5 fused. Fusion of the lower hypurals, 1–2, was treated as a separate character. Because the fusions of hypurals 1–2 and 3–4 always occur together, they are treated here as a single character, a synapomorphy of scombroids above *Sphyraena*, with some reversals within the gempylines. The fifth hypural never actually fuses to the fourth in scombroids. Its fusion to the urostyle is a separate character (my 35), discussed below.

14. (12) *Paired Fleshy Caudal Keels Present.*—A pair of short, longitudinal fleshy keels lie at the base of the caudal fin in *Lepidocybium*, all scombrids and istiophorids. They are lacking in most percoids, the outgroup taxa, *Sphyraena*, gempylines, trichiurines and *Xiphias*. Reversals are hypothesized for gempylids above *Lepidocybium* and *Xiphias*.

15. *Procurrent Spur Absent.*—All outgroup taxa and *Sphyraena* have a well-developed procurrent spur and associated foreshortened preceding ray (Johnson, 1975). Absence of this feature is a synapomorphy of all scombroids above *Sphyraena*. A reduced spur occurs in some gempylines, but the preceding ray is never foreshortened.

16. (29) *Vertebrae 30–31.*—Character analysis of vertebral number by Collette et al. (1984) is confusing and contains several errors. Vertebral number was treated as a three state transformation series: moderate numbers, 30–31; few, 24–26; and many, 35–170. The character appears only twice on their cladogram—a derived state (presumably 35–170) is indicated at the Trichiuridae-and-above node, and a reversal (24–26) is indicated as a synapomorphy of the billfishes. The character should also appear on their cladogram within the Gempylidae (30–31), at the Scombrini-and-above node (30–31), on the *Gasterochisma* line (35–170) and at the Scomberomorini-and-above node (35–170). Vertebral number obviously varies considerably within the Scombroidei; its value as an indicator of phylogenetic affinity is difficult to assess, and I have little confidence in it. Nonetheless Collette et al. (1984) included it in their analysis, and I have no strong objective argument for excluding it here. Categorization of several states of such a variable meristic

character is necessarily arbitrary and merely based on what seem to be reasonably cohesive units of counts. States designated here differ somewhat from those of Collette et al. (1984). They are indicated as follows: 24–26 (primitive); 30–31 (16); 32–67 (16′); 98–192 (16″). The primitive number characterizes most percoids (Johnson, 1984) and all outgroup taxa except *Scombrolabrax*, which is most parsimoniously hypothesized to have achieved 30 vertebrae independently of primitive scombroids. State 16′ (32–67) is independently derived for gempylines plus trichiurines and for all scombrids above *Grammatorcynus*. State 16″ (98–192), not treated separately by Collette et al. (1984), is a synapomorphy of the Trichiurinae. Billfishes show a reversal to the primitive number (24–26) but have a clearly derived vertebral morphology (Gregory and Conrad, 1937, fig. 4).

Va. GEMPYLIDAE (*LEPIDOCYBIUM* + GEMPYLINAE + TRICHIURINAE)

17. (4) *Spinous Dorsal Fin Develops Prior to Soft Dorsal Fin.*—In larvae of all outgroup taxa and *Sphyraena*, the second (soft) dorsal fin develops prior to the first (spinous). A derived condition, development of the spinous dorsal fin prior to the soft dorsal fin characterizes all gempylids, and all scombrids except the Scombrini and *Grammatorcynus*. Based on the most parsimonious cladogram, the derived state is an independent synapomorphy of the Gempylidae and of the Scombridae above *Grammatorcynus*. A true spinous dorsal fin is lacking in billfishes (see character 48). Collette et al. (1984) failed to show a reversal in *Grammatorcynus* and did not indicate that the state is unknown for *Gasterochisma*.

18. *Distinctive Larval Form.*—Larvae of *Lepidocybium* and most gempylines were illustrated and briefly described by Collette et al. (1984, figs. 313 and 315–318). These larvae are similar, distinctive, and share several derived features (treated here as a single character). In addition to the early developing spinous dorsal (see character 17 above), the pelvics are precocious, and spines of both of these fins are serrate, except in *Thyrsitops*. Larvae of all outgroup taxa and *Sphyraena* lack precocious dorsal and pelvic fins, and only some acropomatids have serrate fin spines. Other derived features shared by larvae of *Lepidocybium* and gempylines include a relatively high and steeply graduated spinous dorsal fin and a serrate spine at the angle of the preopercle. Larvae of the Trichiurinae are poorly known. Those illustrated by Collette et al. (1984, fig. 320) indicate that pelvics, if present, are precocious but smaller than those of gempylines; *Benthodesmus* and *Trichiurus* have serrate dorsal spines, but *Lepidopus* has smooth spines, the first elongate with a filamentous tip. Trichiurine larvae appear to represent a further derived modification of the gempyline larval form (18′).

19. *First Dorsal Pterygiophore Inserts in Second Interneural Space.*—In most percoids (Johnson, 1984), all outgroup taxa, and all scombrids (Fig. 3B), the first dorsal pterygiophore inserts in the third interneural space (between the second and third neural spines). All gempylids exhibit a derived condition (Fig. 3C) unique among scombroids—the first dorsal pterygiophore inserts (alone) in the second interneural space (Collette et al., 1984; Potthoff et al., MS[3]). In billfishes, the first dorsal pterygiophore inserts in the first (Istiophoridae) or second (*Xiphias*) interneural space (Potthoff, MS[3]; Potthoff and Kelley, 1982), along with several succeeding pterygiophores. This condition apparently results from the anterior extension of the soft dorsal fin (the spinous dorsal is lacking, see character 48) and is not strictly homologous with the gempylid configuration. *Sphyraena* is unusual in having the first dorsal pterygiophore in the fourth interneural space (Fig. 3A). If the three predorsal elements of *Sphyraena* represent neomorphs (see character

11), insertion of the first pterygiophore in the second interneural space may be a synapomorphy of *Sphyraena* and the gempylids; however, other characters refute the hypothesis that *Sphyraena* and gempylids are sister groups.

20. *First Dorsal Pterygiophore Expanded; Posterior Portion of Proximal–Middle Radial and Distal Radial Elongate.*—When a single supernumerary spine is borne on the first dorsal pterygiophore in most percoids, all outgroup taxa, and most scombroids, the distal portion of the proximal–middle radial and the distal radial of that pterygiophore are relatively short, so that the supernumerary first spine lies in close proximity to the serial second spine, which rests on the anterodorsal corner of the succeeding pterygiophore (Fig. 3B). Among scombroids, this configuration is uniquely modified in gempylids (Fig. 3C). The distal portion of the proximal–middle radial and the distal radial are longitudinally expanded, so that the first spine lies well anterior to the second. Concomitantly, there is a moderate (in *Lepidocybium* and *Ruvettus*) to extreme (all other gempylids) plate-like expansion of the vertical shaft of the first dorsal pterygiophore. Wide spacing of the spines through distal elongation of the pterygiophores characterizes the entire dorsal and anal fins of gempylids and may not be independent of character 21.

21. *Proximal–Middle and Distal Radials of Spinous Dorsal Fin Overlap Extensively.*—In most percoids, all outgroup taxa, and all scombroids except gempylids, distal radials in the spinous dorsal fin articulate anteriorly with their serially corresponding proximal radial by simple abutment or suture-like association (Figs. 8A and 9A, B). In many of these fishes, contact between the proximal–middle and distal radials may be lost in the posterior portion of the fin, and the two elements may become widely displaced. Gempylids share a unique mode of articulation between the proximal–middle and distal radials of the spinous dorsal pterygiophore (Figs. 8B, C and 9C–E). The mid-ventral ridge of the V-shaped posterior end of the proximal–middle radial continues posteriorly as a spine-like or wedge-shaped process that extends below and is tightly bound to the ventral surface of the expanded distal radial along half or more of its length. This specialized articulation characterizes all spinous dorsal pterygiophores in *Lepidocybium* and gempylines and all dorsal pterygiophores in trichiurines (see character 30).

22. *Distal Radials of Spinous Dorsal Pterygiophores Have Condylar Articulation with Serial Spines.*—In most percoids, all outgroup taxa and all scombroids except gempylids, the posteromedial end of the distal radial of each spinous dorsal pterygiophore is truncate or slightly concave (Fig. 9A, B) and does not usually contact its serial spine except in those that exhibit the primitive chain-link arrangement, wherein a small hook-like process projects through the foramen at the base of the spine (Fig. 9A). In gempylids, the posterior end of the elongate distal radial is convexly rounded and provides an articular condyle with which the concave ventral margin of the serial spine articulates (Figs. 8B, C and 9C–E). This is a unique apomorphy of the Gempylidae; the articulation is further modified in trichiurines (see character 30).

Vb. GEMPYLINAE + TRICHIURINAE

⑭. *Paired Fleshy Caudal Keels Absent.*

$\boxed{16'}$. *Vertebrae 32–67.*

23. (15) *Lacrimal with Anterior Tubular Extension.*—As described by Russo (1983, figs. 17 and 19), the anterior portion of the infraorbital sensory canal of all gem-

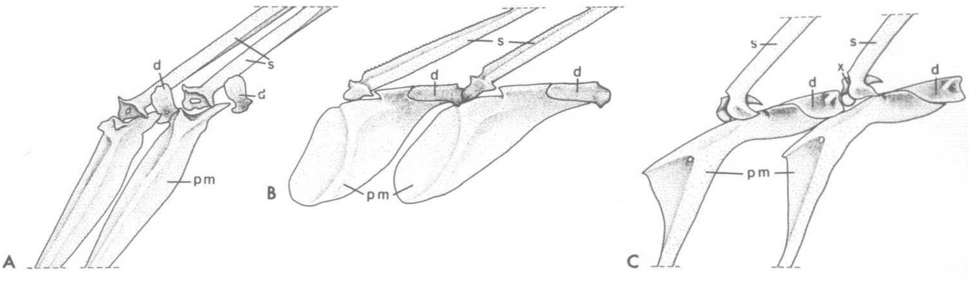

Figure 8. Spinous dorsal pterygiophores and bases of spines, left lateral view: A, *Scomberomorus tritor,* USNM 193839, 143 mm SL; B, *Epinnula orientalis,*USNM 267393, 109 mm SL; C, *Lepturacanthus* sp., USNM uncat., 272 mm SL. s, spine; d, distal radial; p, proximal-middle radial; x, "extra distal radial."

pylids (sensu Russo) except *Lepidocybium,* is carried forward in a bony tubular extension of the dorsal margin of the lacrimal. This lacrimal extension is lacking in most percoids, all outgroup taxa and all other scombroids except trichiurines. It is quite evident in some trichiurines (e.g., *Trichiurus* and *Lepturacanthus*), less so in others, where it appears to have become confluent anteriorly with the dorsal margin of the lacrimal. An anterodorsal lacrimal tube, usually free anteriorly, is a synapomorphy of gempylines and trichiurines.

24. *Dorsal, Usually Stay-like Extension of Posterior Wall of Lacrimal Articular Facet.*—In most percoids, all outgroup taxa and all scombroids except gempylines and trichiurines, the lacrimal bears a large, shallow, cup-like facet dorsally or dorsomedially for articulation with a rounded condyle on the lateral ethmoid.

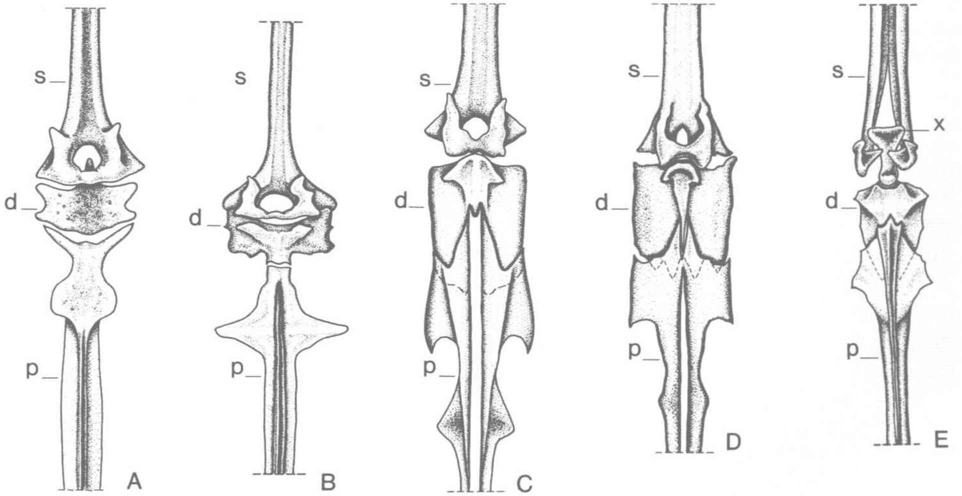

Figure 9. Spinous dorsal pterygiophore and base of serially associated spine, ventral view: A, *Scombrops boops,* USNM 71244, 153 mm SL; B, *Scomberomorus maculatus,* USNM uncat., 154 mm SL; C, *Epinnula orientalis,* USNM 267393, 109 mm SL; D, *Promethichthys prometheus,* USNM 236805, 158 mm SL; E, *Lepturacanthus* sp. USNM uncat., 272 mm SL. s, spine; d, distal radial; p, proximal-middle radial; x, "extra distal radial."

This primitive articular facet characterizes *Lepidocybium,* but in all other gempylids the facet is modified so that its posterior wall is produced dorsally (Russo, 1983, figs. 18 and 20). In a few gempylines (e.g., *Epinnula, Neoepinnula*), a modified articular facet remains and the posterior dorsal extension is relatively short. Most gempylines and all trichiurines lack a true facet (there is no transverse expansion or cup-like depression), and the dorsal extension is a spine-like stay that extends well up the posterior margin of the lateral ethmoid.

25. *Dorsal Postcleithrum Reduced, Not Expanded, Usually Crooked.*—Most percoids, all outgroup taxa, and all scombroids except gempylines and trichiurines have a relatively long and posteriorly expanded, leaf-like dorsal postcleithrum. Gempylines and trichiurines share a considerably reduced and shortened dorsal postcleithrum with no leaf-like posterior expansion, except in *Thyrsitops,* where only the ventral half is expanded, and in *Tongaichthys,* where it is short, but fully expanded (see Nakamura and Fujii, 1983, fig. 12). As noted by Russo (1983, figs. 42–44) for gempylids (his sense), this specialized dorsal postcleithrum is usually somewhat crooked or sigmoid in shape.

Vc. TRICHIURINAE

$\boxed{4}$. *Dorsal- and Anal-fin Stays Not Bifurcated.*
⑫. *Finlets Present.*
16″. *Vertebrae 98–192.*
18′. *Further Derived Gempylid Larval Form.*

26. *Opercle, Subopercle and Lacrimal with Splintered or Fimbriate Margin.*—In most percoids, all outgroup taxa and all scombroids except trichiurines the posterior margin of the opercle and subopercle and ventral margin of the lacrimal are entire. Fimbriate or splintered posterior margins on the opercle, subopercle and lacrimal constitute a synapomorphy of trichiurines; anteriorly, the lateral surface of the opercle and subopercle has the pock-marked or spongy appearance that characterizes the entire lateral surface of these bones in other gempylids.

27. *Infraorbital Sensory Canal Incomplete, All But First Two or Three Infraorbitals Absent.*—In most percoids, all outgroup taxa and all scombroids except the Trichiurinae, the infraorbital sensory canal is complete and housed in a continuous series of bones. In scombroids, the complete infraorbital series comprises as few as six to as many as 30 bones. As described and illustrated by Russo (1983, figs. 17b and 19a), the infraorbital series of the gempylines *Diplospinus* and *Paradiplospinus* is discontinuous; a short gap is present in the middle of the series, but well-developed bony tubes are present on either side of this gap, and it appears that the sensory canal continues across it. In all trichiurines the infraorbital sensory canal does not approach the ventral margin of the orbit but instead turns ventrally (or in *Evoxymetopon,* extends straight back) on the cheek and apparently ends there. Of the original canal-bearing infraorbital bones, only the lacrimal and (in some) the second and/or third infraorbitals remain. In some species, there is also a non-canal-bearing, plate-like ossification lying within the thick adipose tissue at the posterior margin of the orbit. An incomplete infraorbital sensory canal and absence of most of the bones that usually bear it is a synapomorphy of trichiurines.

28. *Nostrils Single.*—Paired nostrils characterize most percoids, all outgroup taxa, and all scombroids except the Trichiurinae. A single nostril on each side of the head is a synapomorphy of trichiurines.

29. *Lateral Bony Tubular Extension of Supraorbital Sensory Canal to Orbital Rim.*—In scombroids and *Pomatomus,* the supraorbital-infraorbital sensory canal junction is separated from the posterodorsal corner of the orbit by the enlarged DO fossa (see character 3). Except in trichiurines, the supraorbital canal communicates with the infraorbital canal through a dorsally or laterally directed pore located directly on the frontal ridge that houses the supraorbital canal. In all trichiurines, a bony tube extends laterally from the supraorbital canal to open near the edge of the frontal. This may be a relatively broad, short tube at the anterior extent of the DO fossa (*Aphanopus, Benthodesmus, Evoxymetopon, Lepturacanthus*) or a longer, narrow tube that lies in the floor of the DO fossa and is covered by the DO (all others, Fig. 5A). Lateral extension of the supraorbital canal to the orbital rim is a synapomorphy of trichiurines.

30. *All Dorsal-fin Rays Supported by Spinous Pterygiophores; Bilaterally Divided Rays Embrace Neomorph(?) Distal Element.*—The spinous dorsal fin of most acanthomorphs is characterized by several features that clearly distinguish it from the soft dorsal fin. True spines are fused bilaterally at their earliest appearance (with the exception, in some groups, of the ultimate dorsal and anal fin spines), unsegmented, and usually have closed bases with a central foramen. Pterygiophores supporting spinous rays consist of a continuous proximal–middle radial and a distal radial (Figs. 8A, B and 9A–D), except in groups such as gobioids, blennioids and others where the distal element has been lost or fused with the succeeding pterygiophore. The middle radial is never separate. The fully developed distal radial is a single median ossification, usually block-shaped (frequently with a posterior median process), flat, or alate, lying just anterior to the base of its serial ray. Typically, it associates with the proximal–middle radial anteriorly by synchondral abuttment or weak suturing, but in gempylids (see character 21) there is an intimate overlapping articulation.

Rays of the soft dorsal fin of most acanthomorphs are divided bilaterally, segmented (at least distally), and have open bases that embrace the serial distal radial. Pterygiophores supporting soft rays consist of a proximal–middle radial (middle radials are frequently separate in the more posterior pterygiophores) and a distal radial. The distal radial comprises separate, initially lens-shaped, bilateral ossifications (each usually with a posterolateral pointed projection) along each side of a median cartilage that lies between the bases of the serial soft ray. Spinous and soft-ray distal radials both appear initially in development as a nodule of cartilage at the distal end of the proximal–middle radial. Potthoff (1975;1980), Potthoff et al. (1980), and Potthoff and Kelley (1982) reported that the distal radial originates from the tip of the proximal–middle radial by pinching off, but Kohno and Taki (1983) and Kohno et al. (1984) reported that it is separate from the time of its initial appearance. Ossification of both spinous and soft-ray distal radials originates from two centers on each side of the dorsal surface of the cartilage; the two ossifications fuse early in the development of spinous distals but usually remain separate in soft-ray distals (they may be fused dorsally or completely in large specimens). Ossification of the cylindrical middle portion of the proximal–middle radial is perichondral and there are never separate centers of ossification; the same is true for autogenous middle radials of the soft dorsal.

Based on the above characterization, most percoids, all outgroup taxa and all scombroids, except trichiurines and billfishes, have distinct spinous and soft dorsal fins. (See character 48 for a discussion of the dorsal fin of billfishes.) The dorsal fin of all Trichiurinae is modified in a way that is unique among acanthomorphs (Figs. 8C and 9E). (The anal fin, not discussed here, is similarly modified.) A variable number of elements (3–46) in the anterior portion of the fin are fused bilaterally and have closed bases; these are true spines. The remaining rays, although apparently lacking segmentation, are divided bilaterally and have open bases embracing additional radial-like elements; these remaining rays, then, appear to be soft rays. The remarkable feature of the trichiurine dorsal fin is that all fin rays are supported by elements with a development and morphology identical to that of spinous pterygiophores of other gempylids (see character 21). Thus it appears that each "soft ray" of the trichiurine dorsal fin is associated with an extra element, the one embraced by the fin-ray bases ("x" in Figs. 8C and 9E). The development and general physiognomy of this additional "distal radial" suggests that it is a neomorph, but further study will be necessary to confirm this. Each extra element appears initially as a distinct egg-shaped cartilage with a median posterodorsal process. Unlike typical distal radials, which have two centers of ossification, ossification appears to commence from a median center on the dorsal surface of the posterior process and proceeds anteriorly. The fully developed structure differs from soft-ray distal radials in being a single median ossification, bifurcate posteriorly, with an anteriorly projecting pedestal that articulates with a concave facet at the end of the spinous distal radial. Although the homology of this additional element is unresolved, it clearly represents, along with the associated modifications, a complex synapomorphy of the trichiurines. Collette et al. (1984) considered a 1:1 relationship of the second dorsal fin pterygiophores to neural spines (their character 21) an autapomorphy of trichiurines. That condition may be related to the more complex modification described above.

VI. SCOMBRIDAE + BILLFISHES

31. (3) *Triangular Stay Extends Forward from Anteromedial Corner of Fourth Pharyngeal Toothplate.*—In all gempylids, *Sphyraena,* all outgroup taxa and other percoids, the anterior margin of the fourth pharyngeal toothplate is relatively truncate and there is no appreciable bony contact between it and the third pharyngobranchial (Fig. 7A–D). In all Scombridae, with the exception of *Grammatorcynus,* and all billfishes, the anteromedial corner of the fourth pharyngeal toothplate gives rise to a large, laminar, approximately triangular, bony stay that extends anteriorly along the ventromedial side of the third pharyngobranchial (Fig. 7E–I). In the billfishes (Figs. 6H, I and 7H, I), the stay and toothplate are notably elongated, so that the overall length of the fourth pharyngeal ossification considerably exceeds that of the third pharyngobranchial (31′). This fourth pharyngeal stay is unique among acanthomorphs to scombrids and billfishes and is compelling evidence in support of the monophyly of this assemblage. Absence of the stay in *Grammatorcynus* is considered a reversal. Placement of *Grammatorcynus* as the sister group of all scombrids, plus billfishes, though one step less parsimonious, would resolve this conflict.

32. (18) *Inner Row of Fang-like Premaxillary Teeth Absent.*—As described in the outgroup discussion, an inner row of two or three enlarged, fang-like teeth near the premaxillary symphysis characterizes the outgroup taxa, *Sphyraena* and the gempylids. Absence of these specialized teeth is a synapomorphy of scombrids and billfishes.

33. (14) *Hypurostegy.*—In most percoids, all outgroup taxa, *Sphyraena* and gempylids, the caudal fin ray bases embrace only the distal margins of the hypurals.

Hypurostegy, the extreme anterior extension of the caudal fin ray bases to cover each side of the hypural plate, is a synapomorphy of scombrids and billfishes.

34. (30) *Single Uroneural Pair Develops.*—Many lower percoids, all outgroup taxa, *Sphyraena,* and most gempylids (some specimens of *Diplospinus* have only one initially; caudal development unknown for trichiurines) have two pairs of uroneurals, at least at their initial development. Development of a single (anterior) uroneural pair is a synapomorphy of scombrids and billfishes.

35. *Fifth Hypural Fuses to Uroneural, But Not to Hypural Plate.*—Collette et al. (1984) indicated fusion of the single uroneural to the urostyle (their 31) as a synapomorphy of all scombrids and billfishes, with a reversal to the primitive autogenous state in *Xiphias* and some independent acquisitions within the Gempylidae. My observations indicate that among scombrids, the uroneural actually remains separate from the urostyle in *Grammatorcynus, Scomberomorus,* and *Acanthocybium.* I did not include this specific fusion as a character in this analysis; it is one of the most common fusions among percoids, highly variable with size and seems to show considerable homoplasy within scombroids. However, a distinctive relationship between the uroneural and the fifth hypural is a synapomorphy at the Scombridae-plus-billfishes node, with a reversal at *Acanthocybium.* In this unique configuration, the distal ends of the uroneural embrace and eventually fuse with the proximal portion of the fifth hypural, forming a single hockey-stick-shaped strut. The ventral margin of the fifth hypural remains separate from the hypural plate, even in those forms in which the uroneural is fused anteriorly with the urostyle. In *Acanthocybium* and *Xiphias,* the uroneural and fifth hypural remain separate. Istiophorids are unique in that they never develop a fifth hypural.

36. (7) *Only Two Epurals Develop.*—Most percoids, all outgroup taxa, *Sphyraena,* and most gempylids have three epurals. The development of only two epurals is a synapomorphy at the Scombridae-plus-billfishes node; a reversion to the primitive state characterizes the billfishes. Collette et al. (1984) indicated two epurals to be a synapomorphy of scombrids and one or all (unclear which) of several gempylid lineages, with a reversal in the billfishes but no reversal indicated within the gempylids. According to their discussion and table 161, only *Diplospinus,* among gempylines, has two epurals, and the table indicates that this genus (except in some specimens) acquires two epurals through ontogenetic fusion of the first and second epurals, whereas scombrids have only two at their earliest appearance. Adult trichiurines have only one epural, but caudal development has not been observed (Potthoff, pers. comm.).

VII. *GRAMMATORCYNUS* + SARDINI-THUNNINI + *SCOMBEROMORUS* + *ACANTHOCYBIUM* + BILLFISHES

37. (10) *Subocular Shelf Distinctively Configured.*—Like most generalized percoids, all outgroup taxa except *Dinolestes,* have a well-developed subocular shelf on the third infraorbital. Absence of this shelf is derived for scombroids and seems to have occurred independently at least four times—in *Sphyraena,* gempylids (present in *Rexea, Thyrsitops, Thyrsitoides* and *Tongaichthys,* absent in all others), Scombrini and the billfishes. Absence of the shelf is not an informative character, but all scombrids above the Scombrini share a derived configuration of the subocular shelf, a synapomorphy at this level. In the outgroup taxa, the shelf originates from, and is limited to, the entire medial margin of the third infraorbital. In scombrids, the shelf originates from the posterior portion of the third infraorbital

and projects posteriorly along the medial side of the adjacent infraorbital(s); the subocular shelf is lacking in billfishes, a reversal. Collette et al. (1984) indicated presence of a subocular shelf as a synapomorphy (reversal) of the Scombridae, including *Scomber* and *Rastrelliger*, but the slightly inrolled margin of the dorsal expansion of the third infraorbital in the Scombrini is not a true subocular shelf and does not exhibit the derived configuration of other scombrids.

38. (11) *Fleshy Midlateral Caudal Keel Present.*—A fleshy mid-lateral keel on the caudal peduncle is a specialization of *Lepidocybium*, all scombrids above the Scombrini, and the Istiophoridae; such a keel is lacking in the Scombrini, Gempylinae, Trichiurinae, *Sphyraena* and all outgroup taxa. The keel in *Lepidocybium* is most parsimoniously hypothesized to have been acquired independently of that of scombrids and lost secondarily in *Xiphias*.

39. (34) *Upper and Lower Hypural Plates Fuse Ontogenetically.*—In most percoids, all outgroup taxa, *Sphyraena* and most gempylids (including *Lepidocybium*), the upper and lower hypural plates remain separate from one another (no fusion between hypurals 2 and 3). Collette et al. (1984) indicated that fusion of the upper and lower hypural plates characterizes all scombrids and billfishes except the Scombrini, *Gasterochisma* and *Grammatorcynus*. My observations indicate that only the Scombrini are exceptional, *Gasterochisma* and *Grammatorcynus* having the dorsal and ventral hypural plate fully fused. Fusion of the upper and lower hypural plates is a synapomorphy of scombrids (above Scombrini) and billfishes. It occurs independently in a few gempylines and trichiurines.

VIII. SARDINI-THUNNINI + *SCOMBEROMORUS* + *ACANTHOCYBIUM* + BILLFISHES

$\boxed{16'}$. *Vertebrae 32–67.*

$\boxed{17}$. *Spinous Dorsal Fin Develops Prior to Soft Dorsal.*

40. (8) *Neural and Haemal Spines of Fourth or Fourth and Fifth Preural Centra Involved in Support of Caudal-fin Rays.*—In most percoids, all outgroup taxa, *Sphyraena* and most scombroids, the neural and haemal spines of only the second and third preural centra are involved in support of caudal fin rays. In scombrids, above *Grammatorcynus*, neural and haemal spines of the third and fourth preural centra are elongate and sharply inclined backward so that they also provide support for some procurrent caudal rays. Reversion to the primitive state characterizes the billfishes.

41. (5) *Larval Beak Forms by Restructuring of Premaxillae-Rostral Cartilage-Ethmoid Complex.*—As described above (character 9), the premaxillae of all scombroids are tightly bound to the snout, so that the upper jaws are not protrusible. Non-protrusible premaxillae have evolved in many unrelated pelagic or fast-swimming fishes in which speed may be more important to predation than maneuverable jaws and an expandable orobranchial cavity; there is usually nothing particularly distinctive about the way in which these fixed premaxillae develop in the larvae. Within the Scombridae, however, larvae of all except *Grammatorcynus* and the Scombrini share a distinctive, ostensibly unique configuration of the premaxillae-rostral cartilage-ethmoid complex.

The developing snout of *Rastrelliger* and *Scomber* (Fig. 10A) resembles that of generalized percoids such as *Morone* and all outgroup taxa. The articular processes of the premaxillae are distinct, and the ascending processes and long axis of the oval rostral cartilage are approximately vertically oriented, the posterior margin of the latter abutting the ethmoid cartilage. A specialized, beak-like configuration

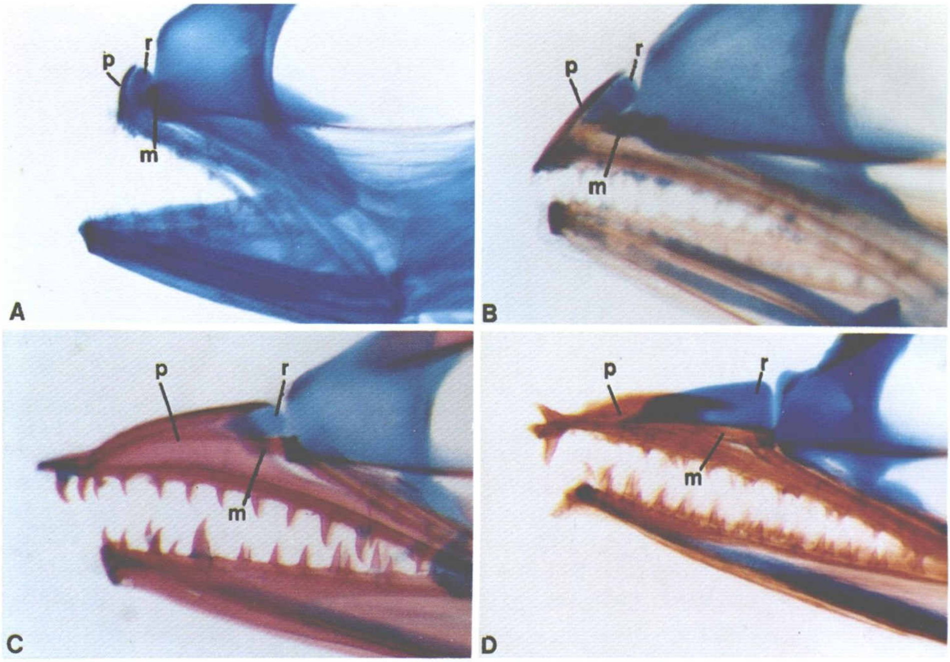

Figure 10. Developing upper jaw in four larval scombroids, left lateral view: A, *Scomber japonicus*, 11.5 mm SL; B, *Auxis* sp., 12.4 mm SL; C, *Scomberomorus maculatus*, 9.0 mm SL; D, *Istiophorus platypterus*, 7.4 mm SL. p, premaxilla; r, rostral cartilage; m, maxilla.

(Fig. 10B) characterizes the developing snout of all other scombrids (*Grammatorcynus* appears somewhat intermediate). The ascending and articular processes are not separate and together form a broad, pointed beak. Concomitantly, the triangular (in dorsal view) rostral cartilage has rotated from its usual vertical axis to an oblique to horizontal one. The usual dorsal end of the rostral cartilage is directed posteriorly and abuts the truncated ethmoid cartilage to provide the rotational pivot point for the premaxillary beak. The usual posterior margin of the rostral cartilage is ventral and is supported by spatulate anterior extensions of the medial portions of the maxillary heads.

The culmination (41′) of this larval beak in scombrids occurs in larval *Scomberomorus* (Fig. 10C) and *Acanthocybium*, where the beak and maxillary processes are substantially longer and fully horizontal. (The larvae of *Gymnosarda* also have an exaggerated beak, but I have been unable to examine its internal structure.) The bill of istiophorids and *Xiphias* is formed in exactly the same way as the beak of *Scomberomorus* and *Acanthocybium*. In istiophorids the bill develops initially as a short premaxillary beak, embracing an enlarged, horizontally oriented, rostral cartilage that tightly abuts the ethmoid cartilage posteriorly and is supported ventrally by spatulate extensions of the maxillary heads (Fig. 10D). The relative length of this beak increases with growth. Larval *Xiphias* exhibit the same basic configuration, but the beak becomes much longer at early stages, so that the rostral cartilage is greatly enlarged, more tightly associated with the ethmoid cartilage, and supported ventrally by much longer extensions of the maxillary heads. *Xiphias* also has narrow, finger-like extensions of the premaxillary ascending processes extending along each side of the dorsal midline of the bill; these processes were mistakenly identified by Gregory (1933) and Gregory and Conrad (1937) as the nasal bones, which are actually quite reduced and form at the base of the bill as in istiophorids (Conrad, 1938; pers. obs.).

Summarizing, the ontogenetic restructuring of the upper jaw-snout complex in the Scombridae (above Scombrini), Istiophoridae and *Xiphias* represents a synapomorphy unique to these three groups. A further derived state (41′) is a synapomorphy of *Scomberomorus, Acanthocybium* and the billfishes.

In larvae of *Sphyraena* and many gempylids (but not the more primitive *Lepidocybium, Epinnula, Neoepinnula,* and *Thyrsitops*) the premaxillae have a short, beak-like configuration that superficially resembles the scombrid larval beak. If this condition is homologous with that of scombrids (i.e., represents an earlier stage in a transformation series) it would represent an additional synapomorphy of the Scombroidei, and independent reversals must be hypothesized for the Scombrini and within the Gempylidae. In larval *Sphyraena,* the premaxillary ascending and articular processes are separate, and the rostral cartilage, although rotated outward and supported anteriorly by the maxillary heads, rests on top of the ethmoid cartilage rather than abutting it. In larval gempylids, the premaxillary ascending and articular processes may be coalesced, but as in *Sphyraena,* the rostral cartilage does not have an intimate pivotal abuttment with the ethmoid. Thus, it is unclear whether the modified upper jaws of larval *Sphyraena* and most gempylids were acquired independently of that of scombrids or represent the first stage in transformation to the scombrid condition.

IX. *SCOMBEROMORUS* + *ACANTHOCYBIUM* + BILLFISHES

41′. *Larval Beak Notably Longer and Fully Horizontal.*

X. *ACANTHOCYBIUM* + BILLFISHES

㉟. *Fifth Hypural Does Not Fuse to Uroneural Anteriorly.*

42. (6, in part) *Gill Filament Blades Interconnected by Extensive Latticework of Cartilaginous Bridges.*—It has been known for some time that the gill filaments of some scombrids and billfishes exhibit extensive reticulate connections along their margins. Lutken (1880) cited "the peculiar modification of the branchiae" as evidence of a possible close affinity between *Acanthocybium* and *Xiphias*; it was also referred to by Trois (1883), Kishinouye (1923), and Conrad (1938). Bevlander (1934) noted that a similar modification occurs in istiophorids. Despite these references to gill filament fusion, no detailed descriptions were provided until the work of Muir and Kendall (1968). They reported that similar reticulate connections characterize the gill filaments of *Thunnus,* and suggested that the apparent independent acquisition of this condition within the Thunnini casts doubt on its phylogenetic significance.

In addition to gross examination, Muir and Kendall (1968) studied thick sections and variously stained thin sections of gill filaments from several scombrids and billfishes, including *Scomber, Katsuwonus, Euthynnus, Thunnus* (two species), *Acanthocybium, Tetrapturus,* and *Xiphias.* No modifications were found in the gill filaments of *Scomber,* but Muir and Kendall observed what they called filamentar fusion in *Acanthocybium, Tetrapturus, Xiphias,* and *Thunnus* and attributed it in all four genera to "an extensive elaboration of the mucosal epithelium of the leading and following edges of the filaments with fusions between adjacent filaments;" they noted that differences among these taxa are mainly quantitative. They also reported that *Katsuwonus* and *Euthynnus* lack this filamentar fusion

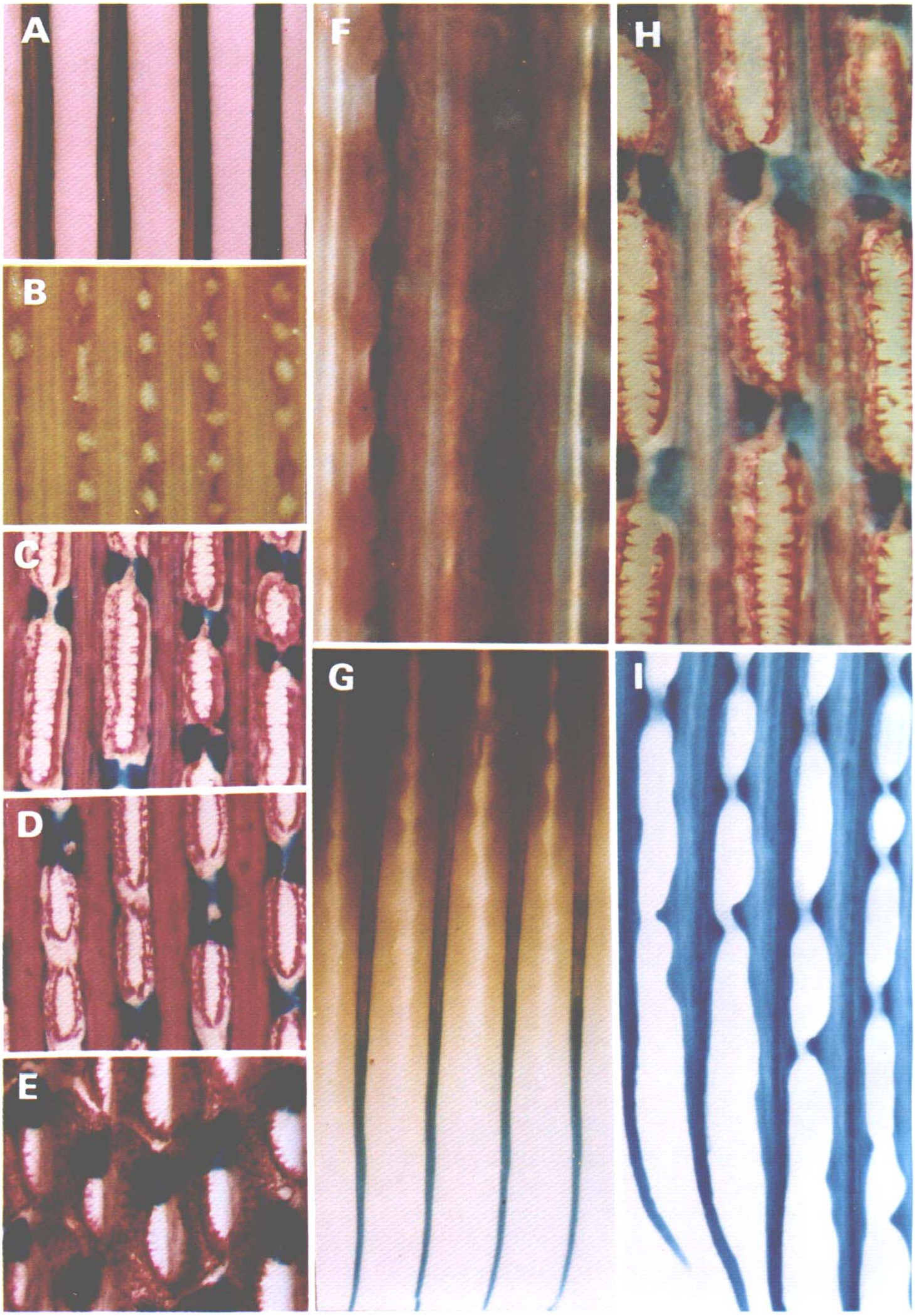

Figure 11. Adjacent gill filaments, cleared and stained, all views looking across filament blades from outflow side. Midway along length: A, *Scomberomorus maculatus,* 355 mm SL; B, Thunnus albacares, 525 mm SL; C, *Acanthocybium solandri,* 460 mm SL; D, *Tetrapterus albidus,* 780 mm SL; E, *Xiphias gladius,* 950 mm SL. F, *Thunnus atlanticus,* 535 mm SL, near growing distal tips; G, same, close-up midway along length. H, *Acanthocybium solandri,* 460 mm SL, near growing distal tips; I, same, close-up midway along length.

but share with *Thunnus* a fusion of the opposing edges of the secondary lamellae of adjacent filaments; they considered this lamellar fusion evidence that these three genera "are in a group distinct from the other genera examined," a conclusion supported by Collette et al. (1984), and with which I concur.

Concerning the taxonomic distribution of filamentar fusion, Muir and Kendall (1968) reached a different conclusion: "The similarity of the filamentar fusion or 'reticulate gill' of *Thunnus* with that found in *Acanthocybium solandri, Tetrapturus audax,* and *Xiphias gladius* (and presumably other billfishes) is evidently a matter of convergence. The filamentar fusion therefore, is of questionable taxonomic significance, for we cannot be certain that convergence has not occurred among the non-*Thunnus* possessors as well."

One might accept the logic of this argument if the structural basis for filamentar fusion is indeed identical in *Thunnus, Acanthocybium* and the billfishes, as Muir and Kendall (1968) believed and Collette et al. (1984) apparently accepted. On the contrary, my examination of cleared and stained gill filaments of these taxa (and other genera of scombrids and billfishes) indicates that the resemblance between interfilamentar connections in *Thunnus* on the one hand and *Acanthocybium* and the billfishes on the other, is superficial.

A view across the outflow edges of several cleared and stained adjacent gill filaments from *Scomberomorus* (Fig. 11A) shows the lack of interfilamentar connections, a condition characteristic of most scombroids and all other perciforms. A similar view of the cleared and stained gill filaments in *Thunnus* (Fig. 11B) illustrates the heavy investment of mucosal epithelium that forms the network of cross connections between the filament blades. The resultant pores are lined by short mucous tubes (whitish in Fig. 11B, bluish in Fig. 11F) through which water exits from the interfilamentar spaces. This is the "filamentar fusion" described by Muir and Kendall (1968) for *Thunnus* and incorrectly attributed by them to *Acanthocybium* and the billfishes. In this condition, a unique apomorphy of *Thunnus,* there is no true fusion of the filament blades, but merely a connective latticework of the thickened, overlying, mucosal epithelium. A view (11G) across the growing tips of these blades (beyond the yellowish mucous) shows that the blades themselves lack interconnecting outgrowths.

In *Acanthocybium* (Fig. 11C, H–I), the structural basis for filamentar interconnection is entirely different. There is no heavy investment of mucosal epithelium at the outflow edge of the filament blades. Interfilamentar connections are the result of a network of cartilaginous bridges formed by the coalition of actual outgrowths of the broadened edges of the cartilaginous filament blades. A view (Fig. 11I, compare with 11G) across the growing tips of these blades shows the initial formation of the cartilaginous outgrowths. This is true gill filament fusion. An identical condition is shared by all istiophorids (Fig. 11D) and *Xiphias* (Fig. 11E). So far as is known, a comparable structural modification of the gill filaments does not occur elsewhere among fishes; it is a unique synapomorphy of *Acanthocybium* and the billfishes.

43. *Bony Epithelial Toothplates Invest Inflow and Outflow Surfaces of Gill Filament Blades.—Acanthocybium,* istiophorids and *Xiphias* share an additional unique specialization of the gill filaments. Bony epithelial toothplates cover both the inflow and outflow surfaces of the filament blades. These resemble the toothplates that are found on various parts of the gill arches (e.g., basibranchials) in many other fishes, although they were mistakenly referred to by Muir and Kendall (1968) as "horny spines." On the outflow surface (Fig. 11C–E, H), these toothplates are discontinuous and arranged around the openings of the oblong pores created by the cartilaginous fusion latticework. On the inflow surface, they are more or less

continuous along the entire length of each filament blade with occasional small outgrowths that join similar outgrowths from the toothplates of adjacent filaments, providing additional support to the cartilaginous latticework of the outflow side. The arrangement of toothplates on the inflow and outflow edges of the filament blades is remarkably similar in *Acanthocybium* and istiophorids, and differs in *Xiphias* only in having the outflow toothplates more uniform in size and less obviously associated with the oblong pores. I know of no other fishes in which toothplates extensively invest the gill filaments.

44. *Gill Rakers Absent.*—The gill arches of most percoids, all outgroup taxa, and most scombroids bear two distinct types of gill rakers. Typically, the first arch is straddled by a graduated series of variously elongate, splint-like bones that bear small tooth-like spinules along most of their length (Potthoff, 1980, fig. 12D); these rakers are bifurcated at their bases and sit astride the hypo-, cerato-, and epibranchials. Rakers of the other three arches consist of flat upright plates (covered with spinules of various lengths) that are applied to each side of the arches; these rakers are not elongate and do not straddle the arches.

In many scombrids, flat, spinulose plates lie between the splint-like rakers on the first arch; in some species of *Scomberomorus*, several (all but one in *S. maculatus*) of the anterior splint-like rakers are absent, so that only the flat plates remain along the anterior part of the first arch. In *Acanthocybium* and the billfishes, the first gill arch lacks all splint-like rakers, and (except in *Xiphias*) is tightly and fully covered by variously coalesced, finely spinulose, bony plates; in *Xiphias* the bony plates are also lacking. Because there is no reason to question the monophyly of *Scomberomorus* as presently diagnosed (Collette and Russo, 1984) loss of some rakers within that genus has apparently occurred independently. Complete absence of splint-like gill rakers is here interpreted as a synapomorphy of *Acanthocybium* and the billfishes. Splint-like rakers are also absent from the first arch (except at the angle) in most gempylids, but unlike the condition described above, this occurs through ontogenetic reduction; long, splint-like rakers are present initially and gradually transform to resemble the upright, plate-like rakers typical of the other three arches (Matsubara and Iwai, 1952).

45. (36) *Parhypural Fuses to Hypural Plate.*—In most percoids, all outgroup taxa and most scombroids, the parhypural is autogenous. Collette et al. (1984) indicated fusion of the parhypural with the hypural plate as a synapomorphy of the Scomberomorini, Sardini and Thunnini with an independent acquisition in istiophorids (and within the gempylids). My observations indicate a different distribution of this fusion among scombrids. It characterizes istiophorids, *Acanthocybium* (but not *Scomberomorus*), and among the Sardini and Thunnini only *Gymnosarda* and some specimens of *Katsuwonus*. Because the monophyly of the Sardini-Thunnini is well-corroborated (Collette and Russo, 1984), fusion of the parhypural with the hypural plate in *Gymnosarda* and *Katsuwonus* is most parsimoniously hypothesized to be independent of that in *Acanthocybium* and istiophorids. I have interpreted this fusion as a synapomorphy of *Acanthocybium* and the billfishes with a reversal in *Xiphias*. Equally parsimonious is the possibility that it was acquired independently in *Acanthocybium* and istiophorids.

XI. BILLFISHES (ISTIOPHORIDAE + *XIPHIAS*)

⑫. *Finlets Absent.*

⑯. *Vertebrae 24–26.*

31′. *Length of Fourth Pharyngeal Toothplate with Stay Considerably Exceeds Length of Third Pharyngobranchial.*

㊱. *Three Epurals Develop.*
㊲. *Subocular Shelf Absent.*
㊵. *Neural and Haemal Spines of Fourth and Fifth Preural Centra Not Involved in support of Caudal-fin Rays.*

46. (13) *Elongate Premaxillary Bill in Adults.*—As described in character 41, larvae of *Scomberomorus, Acanthocybium* and the billfishes develop a fully horizontal premaxillary beak, supported internally by an enlarged triangular or conical rostral cartilage (Fig. 10C, D). Extension and retention of this larval beak as an elongate bill in the adults is a synapomorphy of billfishes. Nakamura's (1980) contention that "the extremely large and flat bill of *X. gladius* (has) no relation with the bill of Istiophoridae from the phylogenetic point of view" is unfounded. Aside from differences in general shape, homology of the bill of all billfishes is confirmed in every respect by its developmental and terminal morphology.

47. *Larval "Scombroid" Dentition Replaced Ontogenetically by Broad Band of Villiform Teeth.*—The distinctive primary jaw dentition shared by *Scombrops, Pomatomus* and all other scombroids (character 1) is lacking in adult billfishes, although larvae have jaw teeth similar to those of other larval scombroids (Fig. 10D). In scombroid larvae, replacement teeth initially lie in epithelium superficial to the bone of the jaws and only later come to develop within a longitudinal crypt. The latter stage is never reached by billfishes. Instead, during development, additional rows of non-ankylosed teeth developing in the epithelium are successively added until the apposing surfaces of the premaxillae and dentaries are entirely covered by a broad band of villiform teeth. The latter teeth are retained in istiophorids, but become gradually reduced in *Xiphias.* Ontogenetic replacement of larval teeth with villiform teeth is a synapomorphy of billfishes.

48. *True Spinous Dorsal Fin Lacking; Spine-like Rays Develop Secondarily from Soft Rays.*—A spinous dorsal fin, as defined in character 30, is found in most percoids, all outgroup taxa and all scombroids except the billfishes. In the dorsal fin of larval and juvenile billfishes, all rays are divided bilaterally and have open bases that embrace bilateral ossifications of the distal radial cartilages. In *Xiphias,* the two halves of each unsegmented ray never fuse along the midline, but, in adults, may become very tightly attached or sutured. The bases remain open and embrace the fully developed distal radial, a cuboidal ossification typical of pterygiophores of the soft dorsal of most percoids and other scombroids. In adult istiophorids, the dorsal-fin rays may fuse bilaterally but usually along only part of their length. The ray bases resemble those of spinous rays in having closed bases with a central foramen, but I do not believe this condition is homologous with that of true spines. The distal radials, although present and separate in larvae and juveniles, are absent in the adult fin, and I conclude that it is their fusion to the open ray bases that creates the closure. In a specimen 260 mm SL, the basal closure is clearly formed from the still cartilaginous distal radial that is just beginning to ossify.

Thus, although billfishes are frequently reported to have spinous dorsal-fin rays anteriorly, the development and adult configuration of all dorsal-fin rays and pterygiophores suggests that these "spines" are secondarily derived through modification of soft rays. This is further borne out by the fact that, unlike other scombrids (except trichiurines, which apparently have no true soft dorsal fin), developing pterygiophores of the entire dorsal fin are added anteriorly and posteriorly, and the anterior and posterior portions of the fin are never separate during development. Absence of a true spinous dorsal fin and concomitant modification of the existing soft rays constitute a complex synapomorphy of billfishes. Fusion of the distal radials to the ray bases is an autapomorphy of istiophorids.

49. *Brain Heater Present, Derived from Superior Rectus Muscle of Eye.*—As described by Carey (1982) and Block (1983), *Xiphias* and the istiophorids have a mitochondria-rich organ located just below the brain and posterior to the eyes, receiving blood from the carotid arteries through a well-developed counter-current heat exchanger. The function of this heat producing and conserving complex is to provide warm blood to the brain and eyes, so that their temperature can be maintained well above the ambient water temperature. This organ is derived from the superior rectus muscle of the eye and represents a unique synapomorphy of the billfishes (see discussion of *Gasterochisma*).

Excluded Characters.—Several characters included in the Collette et al. (1984) analysis were omitted from this analysis because of excessive homoplasy or questionable homology. They are discussed below.

(9) The cladogram of Collette et al. (1984) indicates that plate-like expansions on the infraorbital bones are a derived feature characterizing the Istiophoridae, Xiphiidae and Scombrini, with a reversal indicated for all other scombrids. The infraorbitals of *Xiphias* are actually very small simple tubes, and the strict homology of the extensively expanded infraorbitals of istiophorids and the Scombrini seems dubious. Infraorbital configuration among scombrids is more complex than this simple characterization would indicate. In fact, at least two of the posterior infraorbitals of all scombrids except members of the Sardini and Thunnini bear laminar expansions (Fig. 5B, and Collette and Russo, 1984, fig. 21). These are most extensive in *Scomber* and *Rastrelliger*, where all elements (about ten total) posterior to the second bear anterior and posterior plates, the posterior ones forming a cohesive laminar shield that completely covers the cheek. In istiophorids (about eight total elements), infraorbitals 4–7 are expanded posteriorly to cover about one-third of the cheek; these expansions are thick and somewhat rugose, and there is some indication that they may form through fusion with cheek scales, but only further study of ontogenetic series could verify this. In *Grammatorcynus* (about 13 total elements), all infraorbitals posterior to the third bear small thin plates posteriorly that cover about one-fifth of the cheek (Collette and Russo, 1984, fig. 21). In *Scomberomorus* (11–13 total) and *Acanthocybium* (7–8 total), expansions similar in appearance but smaller than those in istiophorids are borne on two adjacent posterior infraorbitals.

It appears then, that absence of infraorbital expansions could be a synapomorphy of the Sardini plus Thunnini, which seem (all taxa not examined) also to be characterized by elongate cheek scales that flex medially at their junction with the posterior infraorbitals.

It is evident that further work is needed to establish clear homologies and transformation series for this aspect of infraorbital morphology. Accordingly, I did not include this character in the analysis.

(20) "Number of ossifications in last dorsal and anal pterygiophore" in the Collette et al. (1984) analysis apparently refers to the number of ossifications in the dorsal- and anal-fin stays (see character 4 above). This character provides no information for the present analysis, because the derived state, two ossifications, occurs only within the Gempylinae (in 10 of 15 genera, Potthoff, pers. comm.).

(25) Collette et al. (1984) treated jaw tooth shape as a two state character, conical as primitive, compressed as derived. Their cladogram indicates that compressed teeth are a synapomorphy of *Scomberomorus* and *Acanthocybium* and do not occur elsewhere among scombroids. In fact, compressed teeth are primitive

for scombroids; flattened teeth with sharp edges characterize *Scombrops, Scombrolabrax, Pomatomus, Sphyraena,* and all gempylids except *Lepidocybium.* The subjectivity associated with distinctions between conical teeth and various types of compressed teeth led me to avoid this character; relatively conical teeth might be considered a synapomorphy of the Scombridae, with a reversal to the primitive compressed form hypothesized for *Scomberomorus* and *Acanthocybium,* however the teeth of the latter two are notably different in shape. The sharply pointed, blade-like teeth of *Scomberomorus* resemble those of gempylids, being relatively elongate with a gradual dorsal compression. Those of *Acanthocybium* are relatively shorter and broader and taper more abruptly near their rounded or blunt tips. This character is not relevant to billfishes because their adult teeth are not strict homologues of those of scombrids (see character 47).

(28) Collette et al. (1984) interpreted simple contact between the first and second infraorbitals as primitive for scombroids, the derived state being a tightly bound joint. Their polarity assessment for this character was reversed; *Scombrolabrax* (and the other outgroup taxa, except *Dinolestes*) have the tightly bound condition. They also incorrectly indicated that the latter condition characterizes billfishes and the Scombrini. Billfishes lack contact between the first and second infraorbitals altogether, and, although the two bones overlap in the Scombrini, the second lies medial to the first (unlike the outgroup taxa and other scombrids) and the two are not tightly bound. I excluded this character because of ambiguities in its characterization and apparent excessive homoplasy.

(33) Collette et al. (1984) treated size of the posterior notch in the hypural plate as a three state character—large, small and absent. Subjectivity in distinguishing between the first two states, concern about the significance of slight differences in size of this notch, and substantial variation with size (Potthoff, pers. comm.) led me to avoid this character, although complete absence of the notch may be a valid synapomorphy of the Sardini plus Thunnini.

(37) The number of autogenous haemal spines is an uninformative character. The derived state, one, is an autapomorphy of *Xiphias.*

(38) Distribution of flattened tips on the neural and/or haemal spines of the fourth preural vertebrae, as reported in the Collette et al. (1984), cladogram offers little information, and I found its characterization too subjective to be useful.

(39) Collette et al. (1984) incorporated pectoral-ray number into their analysis using two presumably independent transformation series, one of two and the other of three states. As with vertebral number, I question the validity of using continuous meristic variables in this type of analysis. Because they gave no justification for the two transformation series or what seem to be arbitrary and sometimes overlapping ranges of counts for each state, I was unable to interpret this character and did not include it.

Other characters considered by Collette et al. (1984) but omitted here (16, 17, 22, 23, 24, 26, 27, 40) apply only to the monophyly of the Sardini plus Thunnini as defined by Collette et al. (1984) or the relationships within that assemblage, neither of which was challenged by the present analysis. See the cladogram of Collette et al. (1984) for the distribution of those characters.

DISCUSSION

The hypothesis of scombroid phylogeny presented here differs from that of Collette et al. (1984) in several respects:

1. An hypothesis of specific outgroup relationships is proposed. *Pomatomus* is the first outgroup, *Scombrolabrax* the second, *Scombrops* the third and *Dinolestes*

plus some acropomatids (sensu Johnson, 1984) the fourth. Collette et al. (1984) used *Scombrolabrax* as the only outgroup and did not consider the relationship of scombroids to other perciforms.

2. *Sphyraena* is included in the Scombroidei as the sister group of all other scombroids, a position occupied by *Scombrolabrax* in the Collette et al. (1984) hypothesis.

3. The Gempylidae, rediagnosed, is the sister group of scombrids plus billfishes. Within the gempylids, *Lepidocybium* is the sister group of gempylines plus trichiurines. Collette et al. (1984) placed the Trichiurinae (their Trichiuridae) as the sister group of all other scombroids with one of several unspecified gempylid lineages as the sister group of billfishes plus scombrids.

4. The billfishes are the sister group of *Acanthocybium*. Collette et al. (1984) placed them as the sister group of the Scombridae.

5. The placement of *Gasterochisma* is unresolved. Collette et al. (1984) placed it within the Scombridae as the sister group of all scombrids except the Scombrini.

These points are discussed in order below.

Outgroup.—The expanded outgroup hypothesis is discussed at the beginning of the character analysis section. As noted there, the PAUP analysis demonstrated ambiguity in the sequence of the outgroup taxa, *Dinolestes, Scombrops* and *Scombrolabrax*; however, my cladogram (Fig. 1) shows the following resolved sequence: "acropomatids" and *Dinolestes* (interrelationships of these taxa unresolved)–*Scombrops–Scombrolabrax*. The ambiguity detected by PAUP results from the distribution of the derived states of characters 1 and 2. *Scombrops* and *Scombrolabrax* share the derived state of character 1 (modified primary jaw dentition), which *Dinolestes* lacks, and *Dinolestes* and *Scombrolabrax* share the derived state of character 2 (single supernumerary spine on first dorsal pterygiophore), which *Scombrops* lacks. Because the modified dentition represents a complex synapomorphy that could justifiably be treated as several (see discussion of character 1), I consider the sequence shown in Fig. 1 as the most parsimonious. This is the only instance in which I considered character weight (beyond the initial delineation of characters) in resolving the cladogram.

Sphyraena.—The classificatory history of the Sphyraenidae was most recently reviewed by deSylva (1984). Most classifications (Greenwood et al., 1966; Nelson, 1984; deSylva, 1984) have placed the Sphyraenidae in a separate suborder, with suggestions that they may be related to the Mugilidae and Polynemidae. Others have included all three families in an order (Berg, 1940) or suborder (Gosline, 1968, 1971), and some (Myers, 1928; Hubbs, 1944; Gosline, 1962) have proposed that these families are closely related to the Atherinidae and Phallostethidae. The latter hypothesis has been convincingly discounted (Rosen, 1964; Rosen and Parenti, 1981; Parenti, 1984). The evidence most frequently cited in support of a close relationship among sphyraenids, mugilids and polynemids is the somewhat posterior placement of the pelvic fins and corresponding lack of contact with the cleithra. Whether this character is primitive or secondarily derived for any or all of these families has never been resolved. Another shared feature (emphasized by Hubbs, 1944) is the distinct separation of the spinous and soft dorsal fins, but this occurs commonly among perciform fishes. The only other notable feature shared by the three families is the brush-like extension of the epioccipitals. In other aspects of neurocranial morphology as well as the configuration of the jaw apparatus, pectoral fins, gill arches and dentition, there are trenchant differences between *Sphyraena* and the mugilids and polynemids. Similarities in some of these complexes noted by Rosen (1964) represent symplesiomorphies with respect to atherinomorphs, not synapomorphies.

Differences between *Sphyraena* and mugilids and polynemids do not, per se, refute the hypothesis of a close relationship between those taxa; that hypothesis is refuted by several distinctive synapomorphies that support the relationship of *Sphyraena* to the scombroids. *Sphyraena* shares an inner row of ankylosed, fang-like teeth and unique primary jaw dentition with the Scombroidei and immediate outgroups. With *Pomatomus* and the Scombroidei, *Sphyraena* shares an enlarged and reoriented fronto-sphenotic shelf and associated modifications of the infraorbital–supraorbital sensory canal junction, bifurcate dorsal and anal fin stays, and thick adipose tissue along the posterior margin of the orbit. Evidence that *Sphyraena* is the sister group of all other scombroids is manifest in the dorsal gill arches which share the elongate pharyngobranchials and modified second epibranchial–third pharyngobranchial articulation of scombroids and lack (or have an extremely reduced) fourth pharyngobranchial cartilage. *Sphyraena* and other scombroids also share a derived pattern of branchiostegal articulation and nonprotrusible premaxillae with reduced articular and ascending processes. Furthermore, if the three predorsal bones of *Sphyraena* are neomorphs, as their configuration suggests they may be, absence of true predorsals is a synapomorphy of *Sphyraena* and other scombroids. Other derived features, including a cartilaginous projection on the lower jaw, reduction and posterior placement of pelvic fins, similar gill raker morphology, and pronounced internal pigment on the snout of larvae, are shared with some gempylids, but the present synapomorphy scheme indicates that they have probably developed in parallel.

Gempylidae.—Treatment of the Gempylidae is the most troublesome aspect of the analysis of Collette et al. (1984). Those authors noted that the gempylids were grouped together in the cladogram because data were not available for all characters. They presented a separate cladogram for the Gempylidae (fig. 314) from Russo (1983) that purportedly resolves the unresolved lower portion of the scombroid cladogram; they did not discuss how this resolution is effected. In fact, Russo's analysis cannot resolve the lower portion of the scombroid cladogram, because it does not address all taxa pertinent to that problem; instead, it hypothesizes cladistic relationships among a group of gempylid genera that do not form a monophyletic assemblage. Collette et al. (1984) considered *Scombrolabrax* the sister group of all other scombroids and thus the outgroup for their character polarization; Russo (1983) also used *Scombrolabrax* (along with *Scombrops* and *Pomatomus*) as the outgroup for the Gempylidae (his sense) alone, with no consideration of character states in the more closely related trichiurids or scombrids. Consequently, the Gempylidae, as defined and analyzed by Russo (1983), is paraphyletic, and many characters considered synapomorphies within his Gempylidae are actually shared by the trichiurids as well. Russo apparently recognized the limitations of his analysis and avoided any reference to the monophyly of his Gempylidae, although he did state that it is divisible into six monophyletic subgroups.

My analysis indicates that the Gempylidae (rediagnosed to include the gempylids of Russo and the trichiurids of Collette et al.) constitute a monophyletic group that is the sister group of the scombrids plus billfishes. Gempylids share several unique features of the dorsal- and anal-fin pterygiophores and a specialized larval form. *Lepidocybium* is the sister group of all other gempylids, which share a high vertebral number, bony tubular extension of the lacrimal, reduced and usually crooked dorsal postcleithrum and modified articular facet on the lacrimal.

Monophyly of the Trichiurinae is corroborated by numerous synapomorphies: further increased vertebral number, further derived larval form, splintered opercular and subopercular margin, incomplete infraorbital sensory canal, single nostrils, lateral tubular extension of the supraorbital sensory canal to the orbital rim and a complex modification of the dorsal fin. Resolution of the precise relationship between gempylines and trichiurines will require further work. To date, I have found no apomorphies that define the Gempylinae, and they may be paraphyletic, with some smaller subgroup being the sister group of the Trichiurinae.

Billfishes.—The idea that the affinities of the billfishes lie within the Scombridae, specifically with *Acanthocybium,* was proposed as early as 1880 by Lutken but seemingly put to rest by Conrad's (1938) comparative osteological study of *Acanthocybium* and a similar study of the billfishes by Gregory and Conrad (1937). Conrad pointed out that in most respects *Acanthocybium* is more similar to other scombrids than to the billfishes and concluded that it "is an aberrant but true member of the Scombridae with no genetic relation or even parallelism to the Xiphiiformes." He was particularly impressed, as others have been, by substantial differences between the vertebral column of scombrids and billfishes, which led him to postulate that descendants of an *Acanthocybium*-like ancestor might "be found among the primitive cutlass-fishes, such as *Ruvettus,* which are characterized by many segmented columns."

The effectiveness of Conrad's "overall similarity" argument is evident in the subsequent literature. The only more recent proponent of Lutken's (1880) hypothesis seems to have been Fraser-Brunner (1950, fig. 2), who indicated a connection between *Acanthocybium* and the billfishes in his diagram of the relationships of scombrid fishes, but did not discuss it. Indeed, the numerous osteological differences between scombrids and billfishes have made even those authors who include billfishes in the Scombroidei (including Collette et al., 1984) uncomfortable with the idea of an *Acanthocybium*–billfish connection. There can be no argument that to hypothesize derivation of the present-day billfishes from an *Acanthocybium*-like ancestor requires that extensive morphological restructuring (particularly in the vertebral column and median fins) has occurred. Whatever their origin, it is a fact that the billfishes have undergone extensive modification during their evolutionary history—this is what makes them billfishes, unique among perciforms. Continued enumeration of uniquely derived features in which billfishes differ from *Acanthocybium,* or some other hypothesized sister group, serves no phylogenetic purpose.

Despite their distinctiveness, we can only postulate the genealogical relationships of the billfishes based on the uniquely derived features that remain as synapomorphies with other taxa. The scombroid and scombrid affinities of the billfishes are corroborated by a number of such features, the most compelling of which include the fronto-sphenotic fossa and associated modifications, bifurcate fin stays and uniquely modified dorsal gill arches. My analysis indicates that the most parsimonious placement of the billfishes within the Scombroidei is as the sister group of *Acanthocybium.* This hypothesis is slightly more parsimonious than that of Collette et al. (1984), who placed the billfishes as the sister group of the Scombridae, but discovery of a few additional characters could conceivably reverse the parsimony situation. So long as the parsimony argument remains close, I believe it is important to emphasize the following. Three characters that corroborate the *Acanthocybium*–billfish hypothesis (ontogenetic restructuring of the snout and upper jaw, fusion of the gill filaments, and extensive investment of the latter with toothplates) are distinctive, complex specializations, unique among perciforms. A hypothesis that does not treat *Acanthocybium* and the billfishes as sister groups would require that these unique innovations, along with the uncommon complete loss of gill rakers, have arisen twice independently in the evolution of scombroid fishes.

The *Acanthocybium*–billfish hypothesis requires three hypothetical reversals not required by the billfish–Scombridae hypothesis: loss of the subocular shelf, loss of association of the fourth and fifth neural and haemal spines with the caudal fin rays, and reemergence of a third epural. Loss of the subocular shelf is common among perciforms and has clearly occurred several times in scombroid evolution. Reversion of the caudal skeleton to an apparently more primitive morphology is not a common occurrence, but may be related to overall restructuring of the postcranial skeleton.

The major morphological differences between adult billfishes and scombrids are found in the configuration of the median fins and fin supports, the number and configuration of the vertebrae and some aspects of the caudal skeleton. I have demonstrated that the median fins of billfishes are restructured, so that the anterior portion of the dorsal fin is not the strict homologue of that in scombrids (see character 48); thus the differences in that area of the fin are due to an autapomorphy of billfishes, not to reversals that would represent character conflicts in the proposed phylogeny. If billfishes are scombroids, then at some point in their evolution the vertebral column must have undergone major structural modification involving reduction in vertebral number and alteration of vertebral configuration; I suspect that loss of the spinous dorsal fin in billfishes is related to this. Loss of posterior caudal vertebrae could also explain the secondary "primitiveness" of the billfish caudal skeleton, particularly if that loss actually resulted from consolidation of vertebrae. One could envision a dissociation of the neural and haemal spines from the third through fifth preural centra as these were consolidated; likewise, a dissociated neural spine could become a neomorph "first epural," resulting in the secondary total of three epurals in billfishes. There is, however, no ontogenetic evidence to support non-homology between the first epural of scombrids and that of billfishes or between the posteriormost preural vertebrae of these two groups. Furthermore, the second and third preural centra bear autogenous haemal spines in istiophorids (only the second in *Xiphias*), as they do in scombrids, suggesting that these centra are indeed homologous. Fossil billfishes could also prove useful in establishing the homology of the first epural. Although most fossil billfishes have a vertebral number similar to that of extant billfishes, those of the family Paleorhynchidae have 45–60 (Danil'chenko, 1960). If the third epural of extant billfishes represents a neural spine dissociated during consolidation and/or loss of vertebrae, the caudal skeleton of paleorhynchids should have only two epurals, like that of scombrids. Further study of paleorhynchids is needed to determine the structure of the caudal skeleton and also to establish the true relationships of these fossil fishes; some authors (Gosline, 1968; Fierstine and Appelgate, 1974) have questioned their classification as billfishes.

Additional support for the *Acanthocybium*–billfish connection is evident in the occurrence of the five known species of the parasitic copepod *Gloiopotes*. In a study of host–parasite relationships and their bearing on scombrid phylogeny, Cressey et al. (1983) reported that *G. hyomanius* is common on (infestation rate 42–54%) and restricted to *Acanthocybium* and that the other four species of *Gloiopotes* are found only on various species of istiophorids. Unlike most of the other similar associations they reported, Cressey et al. (1983) dismissed this one, suggesting that it is "best interpreted as evidence of ecological similarity between the groups (fast swimming, high-seas species) rather than as evidence of phylogenetic relationships." The only justification given for their conclusion "that the presence of *Gloiopotes* on *Acanthocybium* and istiophorids is an ecological relationship, but that occurrence of three species of *Tuxophorus* on *Acanthocybium* and *Scomberomorus* reflects shared phylogeny" is the following unsubstantiated surmise: "The morphological similarities between *Acanthocybium* and the Istiophoridae seem best explained as convergences; those between *Acanthocybium* and *Scomberomorus* indicate that *Acanthocybium* is the specialized sister group of *Scomberomorus* (fig. 4)."

The figure referred to is a cladogram expressing the relationships of *Grammatorcynus, Acanthocybium* and the species of *Scomberomorus,* subsequently published with a list of characters in Collette and Russo (1984, fig. 70) and slightly modified in Collette and Russo (1985, fig. 3). I am not convinced that the analysis of Collette and Russo supports the hypothesized *Acanthocybium–Scomberomorus* sister-group relationship to the exclusion of the billfishes, as they indicate. Many of the characters in their analysis involve only relative sizes or shapes of bones, features perhaps useful and even necessary for the analysis of interspecific relationships, but probably less reliable at the intergeneric level in scombroids. At least one character reported as a synapomorphy of *Scomberomorus* and *Acanthocybium,* fusion of the fourth and fifth hypural, is incorrect. As noted above (see character 35), the fifth hypural is fully autogenous in *Acanthocybium* (and *Xiphias*) and fused with the uroneural anteriorly (not the fourth hypural) in *Scomberomorus.* Finally, there is a methodological problem similar to that in Russo's (1983) gempylid study. According to the cladogram in Collette et al. (1984, fig. 312), the first outgroup for *Scomberomorus* plus *Acanthocybium* should be Sardini plus Thunnini, the sister group of those two genera; *Grammatorcynus,* the sister group of all these, should be the second outgroup. Instead, Collette and Russo (1984; 1985) used the monotypic *Grammatorcynus* as the first outgroup, and did not consider character states in the Sardini and Thunnini. As a result, many (most?) character states interpreted as synapomorphies of *Scomberomorus* and *Acanthocybium* are actually synapomorphies of these two genera plus the Sardini and Thunnini (e.g., hyomandibular spine, narrow palatine tooth patch, vertebrae 40–56, 4–5 vertebrae supporting caudal fin, third actinost articulating at junction between scapula and coracoid). This problem is explicitly demonstrated in Collette and Russo (1985) wherein certain of these character states (e.g., vertebrae 40–56, 4–5 vertebrae supporting caudal fin) are cited in the introduction as synapomorphies of a monophyletic group comprising *Scomberomorus, Acanthocybium,* Sardini and Thunnini and are then used in the subsequent phylogenetic analysis to corroborate a sister-group relationship between *Scomberomorus* and *Acanthocybium.*

Furthermore, and fundamental to the argument of Cressey et al. (1983), none of these character states were considered for the billfishes; thus the Collette and Russo (1984 and 1985) analysis provides no refutation of a sister group relationship between *Acanthocybium* and the billfishes. There is no more reason to reject the *Gloiopotes* evidence (or dismiss it as an ecological coincidence) than any of the other associations that Cressey et al. (1983) considered phylogenetically significant. Moreover, there is no other specific parasite association of billfishes that supports the Collette et al. (1984) placement or conflicts with the *Acanthocybium* connection. On the contrary, the occurrence of three closely related species of *Tuxophorus* on *Acanthocybium* and *Scomberomorus,* which Cressey et al. (1983) stated "reflects shared phylogeny" may actually further corroborate a *Scomberomorus–Acanthocybium*–billfish phyletic sequence (R. Cressey, pers. comm.). Further investigation by Cressey has shown that these three *Tuxophorus* species actually "represent a new genus closely related to *Gloiopotes* or are possibly members of *Gloiopotes*" (Cressey et al., 1983).

Gasterochisma.—With some exceptions (Starks, 1910; Kishinouye, 1923; Gosline, 1968; 1971), the monotypic *Gasterochisma* has been included in the Scombridae since its original description (Richardson, 1845; Regan, 1909; Berg, 1940; Fraser-Brunner, 1950; Greenwood et al., 1966; Collette and Chao, 1975; Nelson, 1984; Collette et al., 1984; Kohno, 1984). Often referred to as an aberrant or primitive member of the family, *Gasterochisma* has a perplexing combination of character states primitive with respect to scombroids, derived and shared with some scombrids, and uniquely derived among scombroids. The latter features include greatly enlarged pelvic fins in the juveniles, a well-developed otophysic connection, an extreme supraoccipital crest and lack of other cranial crests, a series of laterally directed, vertical laminae on the prootic, large thick scales, and a brain heater apparently derived from a different intrinsic eye muscle than that of billfishes (Block, 1983). As with the billfishes, these notable autapomorphies do not preclude the possibility that the ancestry of *Gasterochisma* lies within the Scombridae, but would require that its morphology has been considerably modified since its initial divergence from a scombrid-like predecessor.

More troublesome to the hypothesis of a scombrid ancestry for *Gasterochisma* is the absence of several trenchant synapomorphies of the Scombroidei, which would require that several exceptional reversals have occurred. *Gasterochisma* has three well-developed predorsal bones. The fronto-sphenotic DO trough is lacking; instead, the sphenotic is covered dorsally by a fronto-pterotic roof (Kohno, 1984, fig. 3). There is an autogenous fourth pharyngobranchial cartilage, the third pharyngobranchial and fourth pharyngeal toothplate are robust, the second epibranchial–third pharyngobranchial articulation is unmodified, and there is no stay on the fourth pharyngeal toothplate.

Recently, Kohno (1984) described the osteology of *Gasterochisma,* based on four dissected and cleaned and one alcoholic specimen (smallest, 203 mm SL), and compared it to that of scombroids, stromateoids, and a few percoid families. Kohno concluded that *Gasterochisma* should remain in the Scombridae because it possesses 12 of 13 characters that he recognized as osteological characteristics of the Scombridae. These include some rather general features (such as bones generally sturdy and greasy, neurocranial sutures strong and rigid, canine teeth never developed, and cleithrum not much developed above pectoral fin, placed more obliquely, sloping forward), most of which I believe lack validity as diagnostic characters of the Scombridae. Only one of these characters, hypurostegy, was considered by Collette et al. (1984) or herein as a synapomorphy of the Scombridae, and this condition is known to characterize other unrelated, large fast-swimming perciform fishes such as *Luvarus* and some carangids. Kohno's study provides a sound description of many aspects of the osteology of *Gasterochisma,* particularly the neurocranium, but does not offer a satisfying answer to the question of its relationships.

To date, small specimens of *Gasterochisma* have not been available for clearing and staining, and the larvae remain undescribed; thus, certain aspects of the osteology have not been adequately examined, and nothing is known of the larval morphology or developmental osteology. Because states for a number of characters important to this analysis remain unknown, inclusion of *Gasterochisma* in the overall parsimony analysis is premature and would require assumptions that I am unable to justify. It seems preferable, given our present state of knowledge of *Gasterochisma,* to simply discuss alternate hypotheses of its affinities.

Excluding those characters for which states are unknown, and assuming that the caudal fusions seen in *Gasterochisma* develop as in scombrids, we can enumerate the additional character state transformations required with placement of *Gasterochisma* between each successive node on the cladogram. These are as follows: between nodes I–II, 17 transformations; II–III, 16; III–IV, 15; IV–V, 14; V–VI, 10; VI–VII, 10; VII–VIII, 10; VIII–IX, 10; IX–X, 9; X–XI, 12. In this scheme, parsimony would dictate that *Gasterochisma* is either the sister group of the Scombridae plus billfishes or of some scombrid clade but would not resolve its precise placement (unless one accepts the 9 vs. 10 transformation argument that would place it in an unlikely position between *Scomberomorus* and *Acanthocybium*).

The relationships of *Gasterochisma* were also analyzed using PAUP. In this analysis, no assumptions were made about the development of the caudal skeleton; unknown character states were coded as missing (Table 1). PAUP consistently placed *Gasterochisma* between nodes V and VI, i.e., as the sister group of scombrids plus billfishes. Inclusion of *Gasterochisma* in the PAUP analysis resulted in ambiguity in the sequence of the Scombrini and *Grammatorcynus*; this is not surprising in view of the fact that the parsimony argument resolving that sequence in the original analysis involves a single transformation difference (see character 31).

If *Gasterochisma* is a scombrid, it has apparently reacquired the predorsal bones, gill arches and at least some aspects of the neurocranium of a generalized percoid. Alternately, its origin lies among the percoids, and it has independently acquired the dentition, bifurcate fin stays, finlets and many of the caudal specializations of scombrids. Additional osteological and ontogenetic information will hopefully corroborate one or the other of these hypotheses. Identification and study of the larvae of *Gasterochisma* is critical. This would not only provide the missing information about character states involving larval morphology, but could potentially resolve questions about the homology of those characters that have ostensibly undergone reversal or been acquired independently.

CLASSIFICATION

The phylogeny proposed here will undoubtedly undergo modification as additional information about the morphology and ontogeny of scombroid fishes becomes available. As well as these fishes are known, much detailed anatomical work on both larvae and adults remains to be done. The primary purpose of this paper was to describe and emphasize the importance of certain previously unrecognized or misinterpreted morphological specializations and to demonstrate that their distribution within the Scombroidei supports a hypothesis of relationships different in several respects from that recently proposed by Collette et al. (1984).

Although a formal cladistic classification may be premature at our current level of knowledge, it seems appropriate to indicate the classification dictated by the hypothesis proposed here. In order that this classification be minimally disruptive, I have used the phyletic sequencing convention proposed by Wiley (1979). Within the Scombridae, tribal subgroups are more consistent with previous classifications, and the subfamilial category is thus omitted. The composition of each terminal taxon, as shown on the cladogram (based on the terminology set forth in the beginning of this paper), is given in parentheses.

Suborder Scombroidei
  Family Sphyraenidae (*Sphyraena*)
  Family Gempylidae

Subfamily Lepidocybiinae (*Lepidocybium*)
Subfamily "Gempylinae" (Gempylinae)
Subfamily Trichiurinae (Trichiurinae)
Family Scombridae
incertae sedis: Tribe Gasterochismatini
Tribe Scombrini (Scombrini)
Tribe Grammatorcynini (*Grammatorcynus*)
Tribe Sardini (Sardini + Thunnini)
Tribe Scomberomorini (*Scomberomorus*)
Tribe Acanthocybiini (*Acanthocybium*)
Tribe Istiophorini (Istiophoridae)
Tribe Xiphiini (*Xiphias*)

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