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UNSTABLE AND STABLE CLASSIFICATIONS OF SCOMBROID FISHES

Kent E. Carpenter, Bruce B. Collette and Joseph L. Russo

ABSTRACT

Many cladists believe that a classification should strictly reflect a cladistic hypothesis. Consequently, they propose classifications that often differ markedly from existing ones and are potentially unstable due to phylogenetic uncertainty. This is problematic for economically or ecologically important organisms since changing classifications can cause confusion in their management as resources. The classification of the 44 genera of scombroid fishes (the mackerels, tunas, billfishes, and their relatives) illustrates this problem of instability. Previous cladistic analyses and analyses presented in this paper, using different data sets, result in many different cladistic hypotheses. In addition, the inferred cladograms are unstable because of different plausible interpretations of character coding. A slight change in coding of a single character, the presence of splint-like gill rakers, changes cladistic relationships substantially. These many alternative cladistic hypotheses for scombroids can be converted into various cladistic classifications, all of which are substantially different from the classification currently in use. In contrast, a quantitative evolutionary systematic method produces a classification that is unchanged despite variations in the cladistic hypothesis. The evolutionary classification has the advantage of being consistent with the classification currently in use, it summarizes anagenetic information, and it can be considered a new form of cladistic classification since a cladistic hypothesis can be unequivocally retrieved from an annotated form of the classification.

Scombroids are among the best-known fishes anatomically. This should present an opportunity to produce a well-corroborated phylogeny using current cladistic methodology. Instead however, there has been disagreement regarding hypothesized sister group relationships, based on different phylogenetic analyses (Collette et al., 1984; Johnson, 1986). If strict cladistic classification is followed, the results of this phylogenetic uncertainty are several plausible classifications that differ markedly from long standing classifications. We examine the competing phylogenetic hypotheses of scombroid fishes by re-analyzing the data of Johnson (1986), by presenting a new phylogenetic analysis based on a revised character analysis with expanded taxonomic coverage, and by examining yet another hypothesis based on a different interpretation of coding of a single character. Next, we demonstrate a quantitative evolutionary systematic method that appears promising as a basis for producing classifications because of its stability across opposing cladistic hypotheses. Finally, we compare the various potential cladistic classifications, and introduce a classification with minimal changes to the long accepted classification, based on the quantitative evolutionary systematic results.

A Brief History of Scombroid Systematics.—The scombroid fishes as currently defined comprise six families, 44 genera, and about 100 species. All species are primarily marine and either epipelagic, mesopelagic, or benthopelagic. Many are important food fishes. Regan (1909) proposed the first modern definition of scombroid fishes. He clearly separated the scombroids from such percoid families as the Carangidae and Rachycentridae. Within the suborder Scombroidei, Regan recognized four divisions: I. Trichiuriformes (Gempylidae, snake mackerels and Trichiuridae, cutlassfishes); II. Scombriformes (Scombridae, mackerels and tunas); III. Luvariformes (Luvaridae, monotypic louvar); and IV. Xiphiiformes (Istiophoridae, sailfish and marlins, and Xiphiidae, the swordfish, plus three families

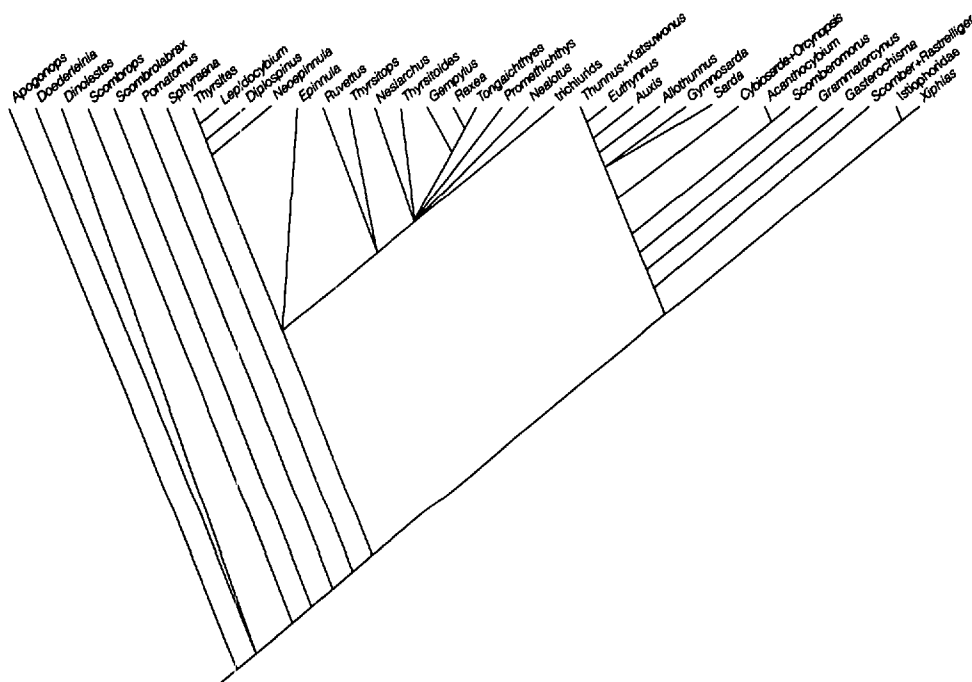


Figure 1. Cladistic hypothesis of the Scombroidei and immediate outgroups as proposed by Collette and Russo (1984, 1986).

known only as fossils). Regan's Scombroidei was defined by three primary characters: premaxillae beaklike, gill membranes free from the isthmus, and epiotics separated by the supraoccipital. To include *Luvarus* in the Scombroidei, reversals must be postulated in these three defining characters. Regan was over influenced by hypurostegy-extension of caudal fin rays over the hypural plate to strengthen caudal propulsion. This condition is present in billfishes, scombrids, and the louvar. However, the louvar has been shown to be a sister group of the Acanthuridae plus Zanclidae (Tyler et al., 1989) and not a member of the Scombroidei.

Collette et al. (1984) summarized available data on the classification of the scombrid fishes and presented a hypothesis of relationships. Scombrid characters were subsequently reevaluated and a revised Wagner tree (Fig. 1) produced for a symposium on the ecology and evolution of large pelagic fishes in Tokyo in July 1985 (Collette and Russo, 1986).

Johnson (1986) presented an alternative phylogenetic analysis of the scombrids. He added primitive outgroups, extended the limits of the Scombroidei to include the Sphyrnidae (barracudas), pointed out errors in the analysis of Collette et al. (1984), proposed novel character interpretations, and suggested a modified cladistic hypothesis (Fig. 2). The major groupings of his cladogram are similar to those proposed by Collette et al. (1984) with respect to the general placement of the Gempylidae, Trichiuridae, and the higher scombrids. One major difference between the Collette and Russo (1984, 1986) and Johnson (1986) hypotheses is in the cladistic position of the wahoo, *Acanthocybium*. The former hypothesized it to be the sister group of the Spanish mackerels (*Scomberomorus*) within the family Scombridae (Fig. 1). Johnson (1986) believes *Acanthocybium* is the sister group of the billfishes (Xiphiidae and Istiophoridae). He bases this

inference largely on the striking similarities in cartilaginous connection of the gill filament blades in *Acanthocybium* and the billfishes. For both hypotheses, numerous reversals and independent acquisitions must have occurred no matter where billfishes are placed. Our concern here is not whether the Collette and Russo (1986) hypothesis or Johnson (1986) is correct; rather, we examine the different classifications that result from opposing phylogenetic hypotheses.

Sources of Instability in Scombroid Systematics.—There are many possible causes of instability and uncertainty for cladistic hypotheses. The present paper focuses on five specific sources of cladistic instability that were encountered while attempting to infer a phylogeny of scombroid fishes. These are: addition of taxa, addition of characters, incorrect assumptions of holophyly of taxa treated in cladistic analysis, different methods in choosing among multiple most parsimonious trees, and alternate interpretations of character coding. Other possible causes of cladistic instability that are not addressed in this paper include alternative character weighting schemes, various criteria for inferring phylogenies besides parsimony, and different ordering (or unordering) schemes for transformation series.

Cladistic hypotheses can vary substantially for the same group of organisms when inference is made from slightly different sets of data. Revised character sets are often the result of new discoveries or the emphasis on data collection of a different suite of characters. The data set used in this study, however, differs from the one used in Johnson's (1986) analysis partly because of a different assumption regarding which data should be initially included in the analysis. We assume that phylogenetic inference is most logically defensible when based on the "Principle of Total Evidence" (Kluge, 1989). That is, all available evidence is potentially relevant and, at least at first, should be included in a cladistic analysis. A potential source of phylogenetic instability results from the uneven application of this principle. The selective disregard for available information is difficult to justify unless it can be demonstrated that the information is unlikely to accurately reflect cladistic branching pattern in the phylogenetic reconstruction method being used and the taxa under study.

Another potential source of cladistic instability can result when an incorrect assumption is made about the holophyly of a taxonomic entity included in the analysis. For example, if a presumed holophyletic supraspecific taxon is included in an analysis and later shown to be para- or polyphyletic, the resulting cladistic classification can change dramatically.

A major source of uncertainty in phylogenetic inference results when multiple most parsimonious trees occur. How to choose a cladistic hypothesis when faced with multiple most parsimonious trees remains an issue of debate. The most common objective methods for resolving this dilemma are using consensus trees (Adams, 1972; Margush and McMorris, 1981; Nelson, 1979; Bremer, 1990) and character weighting (Farris, 1969; Penny and Hendy, 1986), although other objective optimality criteria have also recently been suggested (Rodrigo, 1992). There are many methods for creating consensus trees and for character weighting and there is little agreement on if or how these methods should be applied (Bryant, 1989; Barrett et al., 1991). In this paper, we present the results of both strict consensus trees and successive character weighting (Farris, 1988), because it is not clear which is the best method to resolve this issue (Carpenter, 1988; Anderberg and Tehler, 1990). Besides objective methods of choosing among most parsimonious trees there are also subjective methods that are usually based on informed assumptions concerning which characters are more reliable. We do not believe the evidence is sufficient to warrant post hoc character weighting at this time.

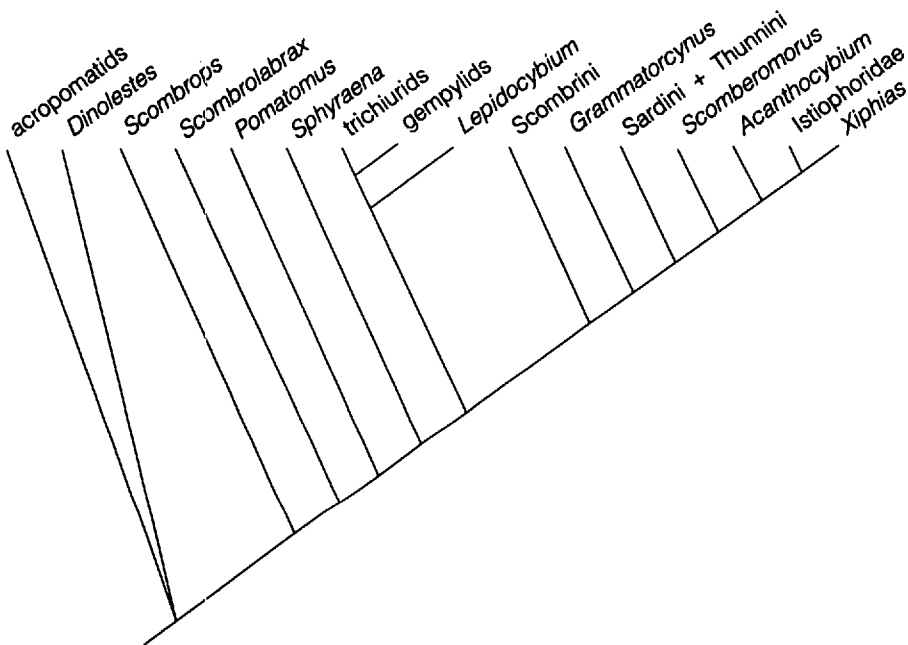


Figure 2. Cladistic hypothesis of the Scombroidei and immediate outgroups as proposed by Johnson (1986).

There are often different plausible interpretations of how a character should be coded. During this study we had difficulty agreeing on how to code two characters, the beak character of the larvae (character 41 presented below), and the absence of splint-like gill rakers (character 44) and therefore analyzed the data several times using the different interpretations. We present the phylogenetic uncertainty encountered because of different interpretations in coding of the gill raker character.

MATERIALS AND METHODS

The material examined are listed either directly or indirectly in papers by Collette and Chao (1975), Collette and Russo (1984, 1986), Collette et al. (1984), and Collette and Gillis (1992). Cladistic analyses were computed under the assumption of parsimony using the computer program Hennig86 (version 1.5; Farris, 1988). Each analysis used the branch-swapping options to generate all possible most parsimonious trees ('mhennig*'; 'bb*'; commands). Strict consensus trees were generated from all trees retained (the 'nelsen' option) and successive weighting was carried out by weighting characters according to their fit on the tree until the weights did not change (series of 'xsteps w' commands). The results of each tree are presented with its length (number of character state changes on the tree) and consistency index (ci). We follow Johnson (1986) in making the biological distinction between "not applicable" and "missing" data in the discussion of characters but note that these are both treated the same (coded as missing) for analyses using Hennig86. Mostly, we also follow Johnson's (1986) polarity of character states as established by outgroup comparison (outgroups the same as in Johnson, [1986] that is, the basal groups below trichiurids listed in Figs. 1-7) with exceptions listed in the discussion on characters. We do not present the result of a cladistic analysis with all characters assumed unordered because this method is controversial (Hauser, 1992; Wilkinson, 1992) and because it only serves to demonstrate yet another source of potential instability for cladistic classification. However, our unpublished cladistic result of this analysis is similar to that presented under the 'Revised Character Analysis' (with corresponding unchanged quantitative evolutionary systematic results).

Quantitative evolutionary systematic analyses were carried out under a criterion to prevent poly-

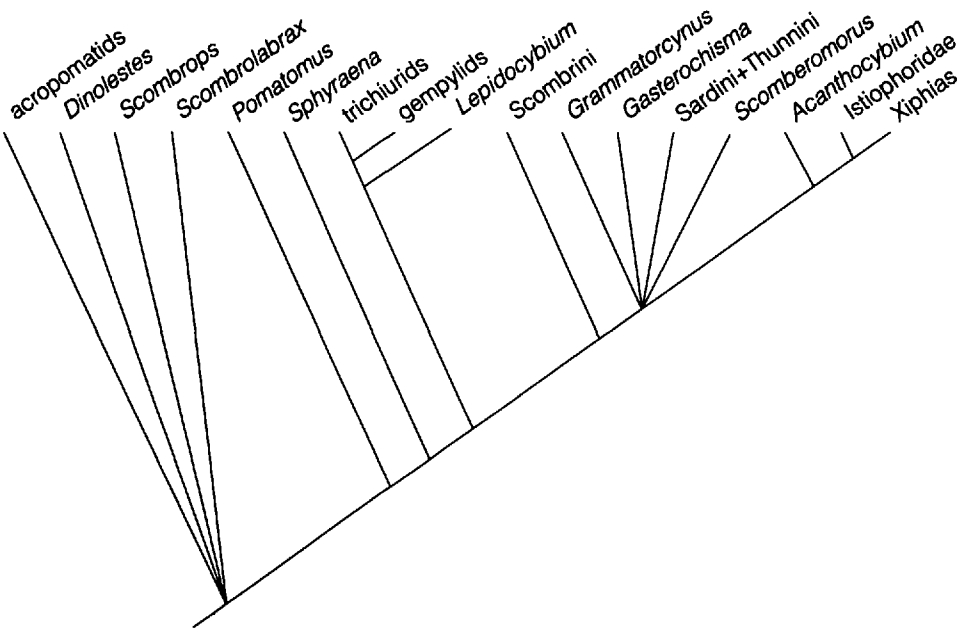


Figure 3. The cladistic hypothesis of the Scombroidei and immediate outgroups resulting from a strict consensus of 20 most parsimonious trees from an analysis of Johnson's (1986) corrected data matrix including *Gasterochisma*.

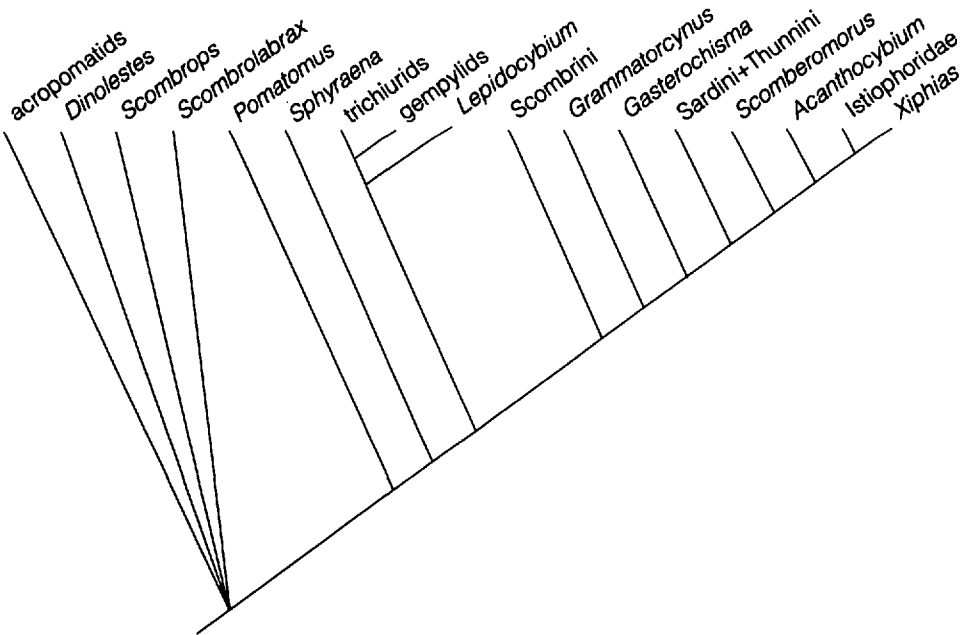


Figure 4. The cladistic hypothesis of the Scombroidei and immediate outgroups resulting from a strict consensus of five most parsimonious trees after successive character weighting from an analysis of Johnson's (1986) corrected data matrix including *Gasterochisma*.

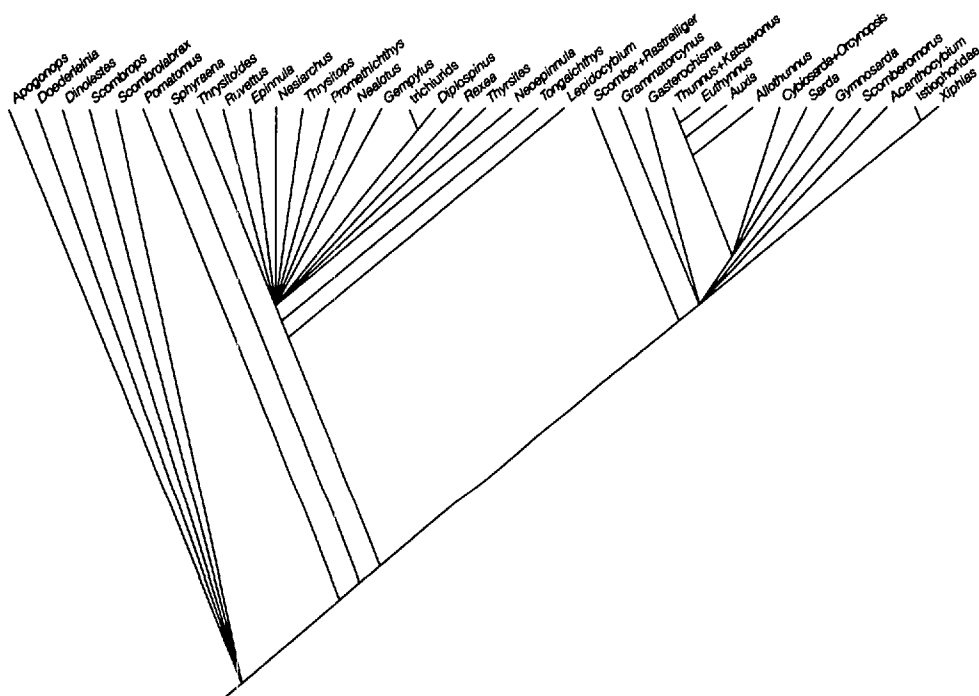


Figure 5. The cladistic hypothesis of the Scombroidei and immediate outgroups resulting from a strict consensus of 1,682 most parsimonious trees from an analysis of the data matrix listed in Table 1.

phyletic taxa (Estabrook, 1986) using George Estabrook's 'CONPHEN5' computer program. A simple matching coefficient was used to generate a matrix of dissimilarity values from the matrix of multistate characters. A dendrogram was generated with CONPHEN5 using UPGMA, the agglomerative unweighted pair group method (Sokal and Michener, 1958), but with clusters restricted to groups of nonpolyphyletic (holophyletic or paraphyletic) taxa. We call the dendrograms produced from this restricted clustering "patrigrams" because the similarity reflected is an approximation of patristic similarity. Phenetic similarity is composed of both patristic (synapomorphic and symplesiomorphic) similarity and homoplastic (parallels and convergences) similarity. Since polyphyletic groups are excluded, we assume that the similarity among groups clustered is due to common descent, that is, both synapomorphic and symplesiomorphic similarity and not phenetic similarity.

The term monophyly is defined differently by different schools of systematics. Since we present results representative of both the cladistic and evolutionary schools of systematics we will avoid the use of the term monophyly and instead use the term nonpolyphyletic to refer to groups that are both holophyletic and paraphyletic. We assign the term holophyletic the definition applied by Farris (1974) for monophyletic. Therefore, a holophyletic group of terminal taxa includes the most recent common ancestor of all terminal taxa in the group and all known descendants. A paraphyletic group of terminal taxa contains the common ancestor of all terminal taxa, but not all known descendants of the ancestor. Polyphyletic groups do not contain the most recent common ancestor for all terminal taxa.

RESULTS

Revised Analysis of Johnson's Data Set.—Johnson (1986) presented a cladistic hypothesis (Fig. 2) based on extensive reexamination of 41 osteological characters, six discrete external morphological features, one dental character, and one internal soft anatomy character. Many of his characters were based on developmental information from larvae. He included the enigmatic *Gasterochisma* in his character state matrix, but he did not include it in his primary cladistic analysis because of the lack of data from larvae and because of his doubts about the affinity

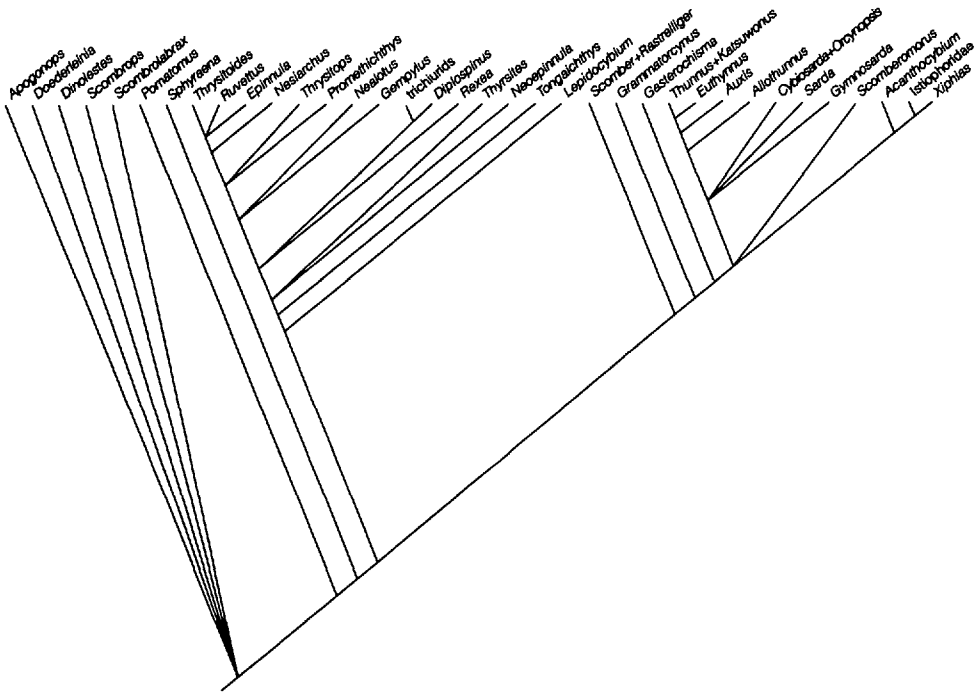


Figure 6. The cladistic hypothesis of the Scombroidei and immediate outgroups resulting from a strict consensus of 142 most parsimonious trees after successive character weighting resulting from an analysis of the data matrix listed in Table 1.

of *Gasterochisma* based on its possession of certain primitive character states. We apply a more rigorous application of the "Principle of Total Evidence" and present the results of a cladistic analysis that includes *Gasterochisma* using Johnson's (1986) data. We note, however, that there are several mistakes in the matrix published by him. As discussed in more detail below, his character 14 (paired fleshy caudal keels present) should be state 1 for *Gasterochisma*, his character 31 (triangular stay position on pharyngeal toothplate) should be state 0 for *Grammatocynus*, and character 38 (fleshy midlateral caudal keel presence) should be state 1 for *Xiphias* and state 0 for istiophorids. In addition, Johnson (1986) (personal communication) now believes that character 37 (subocular shelf configuration) should be coded as "not applicable" for *Sphyraena*, Scombrini, istiophorids, and *Xiphias* based on the discussion he presented. A cladistic analysis of Johnson's (1986) revised character matrix without *Gasterochisma* results in the same cladistic hypothesis as he presented.

A cladistic analysis of Johnson's (1986) corrected character matrix, with *Gasterochisma* included, results in 20 most parsimonious trees (length 85, ci 0.64); the strict consensus tree is presented in Figure 3. The lack of resolution within the Scombridae results from the various placement of *Gasterochisma* either between the nodes connecting the Sardini plus Thunnini and *Scomberomorus* (based on Fig. 2) or between the nodes connecting *Scomberomorus* and *Acanthocybium*, and the various placement of the Sardini plus Thunnini as in Figure 2, or as a holophyletic sister group of *Acanthocybium* plus the billfishes. Successive character weighting results in five most parsimonious trees with the lack of resolution

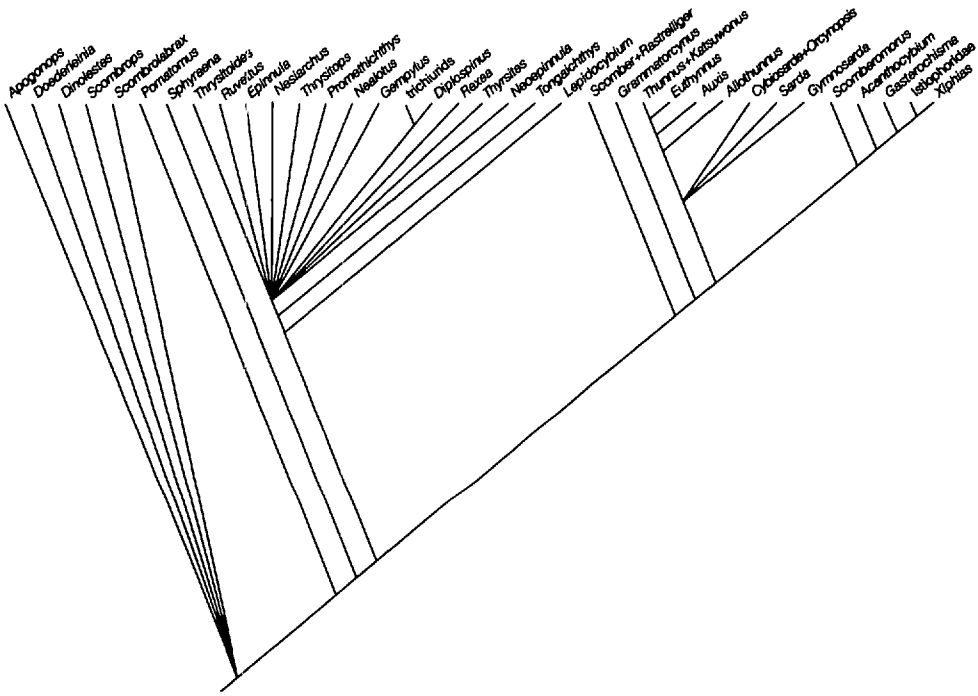


Figure 7. The cladistic hypothesis of the Scombroidei and immediate outgroups resulting from a strict consensus of 2,575 most parsimonious trees resulting from an analysis of the data matrix listed in Table 1 except that character 44 (presence of splint-like gill rakers) is coded using an alternative interpretation.

restricted to the basal groups, and *Gasterochisma* placed between *Grammatocystus* and the Sardini plus Thunnini (Fig. 4).

Hypotheses Based on a Revised Character Analysis.—We assembled a character matrix after reexamining all characters and taxa used in both Johnson's (1986) and Collette et al.'s (1984) cladistic analyses (Table 1). This resulted in 62 binary and multistate characters distributed among 36 presumed holophyletic groups including *Gasterochisma*. The first 49 characters in this matrix are the same characters and number designations as in Johnson's (1986) analysis. Characters 50–56 were used by Collette et al. (1984) and omitted by Johnson (1986) because they “apply only to the monophyly of the Sardini plus Thunnini.” We reinstate these characters because of their presumed relevance in a data set with expanded taxonomic coverage. Additional characters (57–61) are introduced based on new evidence and one character (34) is divided into two binary characters (34 and 62) based on a revised character analysis. In general, if two patterns of character states are easily discernible in what may be considered a character complex (for example, characters 13 and 54, fusion of hypurals), we treat the characters as independent, because of the difficulty in assessing the degree of dependence among character states in a character complex. Johnson (1986) used 16 taxa in his analysis, omitting *Gasterochisma* and utilizing presumed monophyletic groups such as the gempylids, trichiurids, and Thunnini plus Sardini. We expand the coverage of gempylids, Thunnini, and Sardini to include component genera, to avoid making assumptions of independent acquisitions or reversals within grouped taxa.

All characters are ordered, coded, and numbered as in Johnson (1986) with the following exceptions listed according to their respective character number:

13. *Hypurals 1–2 and 3–4 Fuse Ontogenetically*.—Johnson (1986) coded this character as state 1 (hypurals fuse ontogenetically) for trichiurines, but we assume it is not applicable for them because the caudal fin is either greatly reduced or absent in trichiurines and the hypurals of those with identifiable caudal fins have undergone varying degrees of fusion. Because of the lack of caudal fins in some trichiurines, we question the wisdom of coding a character for a group in which it may not be strictly homologous for all members of the group.
14. *Paired Fleshy Caudal Keels Present*.—Johnson (1986) coded this as absent (state 0) for trichiurines, but we code it as not applicable for them because of the lack of a caudal fin in many trichiurines. For *Gasterochisma*, Johnson (1986) incorrectly listed this character in his matrix as state 0, without paired fleshy keels, but it does possess paired fleshy keels (state 1).
16. *Vertebra Number*.—Johnson (1986) arbitrarily coded vertebra number of 24–26 as few (state 0), 30–31 as moderate (state 1), 32–67 as many (state 2) and 98–192 as very many (state 3). We observed that the distribution of vertebra number is relatively continuous across many genera (Collette et al., 1984) except at certain gaps in this distribution. Therefore, we used these gaps to code vertebra number as follows: 24–26 vertebrae as state 0, 30 to 55 vertebrae as state 1, 58–67 vertebrae as state 2, and 98–192 vertebrae as state 3.
17. *Spinous Dorsal Fin Develops before Soft Dorsal Fin*.—We adopt Johnson's (1986) interpretation and coding for this character and note that since larvae for *Cybiosarda* and *Orcynopsis* were not available for examination we code this character as missing for these taxa instead of assuming the spinous dorsal develops first as Johnson (1986) did.
18. *Distinctive Larval Form*.—We adopt Johnson's (1986) interpretation and coding for this character and note that since no larvae for *Cybiosarda* and *Orcynopsis* were examined we code this character as missing for these taxa.
20. *First Dorsal Pterygiophore Expanded*.—Johnson (1986) recognized two character states but because of our expanded taxonomic coverage we recognize three. *Lepidocybium* and *Ruvettus* both have a moderately expanded shaft of the first dorsal pterygiophore (state 1), while the other trichiuroids (i.e., gempylids and trichiurids) have an extremely expanded first dorsal pterygiophore (state 2) and non-trichiuroids do not have an expanded first dorsal pterygiophore (state 0). Johnson (1986) coded this character as state 0 for billfishes, but we code billfishes as not applicable since they do not have a true spinous dorsal fin and their first dorsal pterygiophore is not strictly homologous with that of other scombroids because of a unique developmental sequence (Johnson, 1986).
31. *Triangular Stay Extends Forward from Anteromedial Corner of Fourth Pharyngeal Toothplate*.—Johnson (1986) indicated that the absence of this stay in *Grammatorcynus* was a reversal but he incorrectly listed this as present for *Grammatorcynus* in his matrix. In addition he describes the stay and toothplate as noticeably enlarged in billfishes but did not reflect this in his coding. We code this character as three states: missing (0), present (1), present and greatly expanded (2).
34. *Single Uroneural Pair Develops*.—We adopt Johnson's (1986) coding of this character but create an additional character (62) that reflects the fusion of two uroneurals into a single uroneural within the Gempylidae.

35. *Fifth Hypural Fuses to Uroneural, but Not to Hypural Plate.*—Johnson (1986) coded this as the primitive state for trichiurines, but many trichiurines lack a caudal fin and they lack a fifth hypural and therefore it should be coded as not applicable for them.
36. *Only Two Epurals Ultimately Develop.*—There is incomplete or conflicting developmental evidence in some taxa and we therefore emphasize the adult condition for coding of this character. We assume that the adult condition found in *Gasterochisma* of two epurals is equivalent to that found in other scombrids and therefore code this taxon as state 1. We assume that *Diplospinus* is also state 1 (two epurals) since adults all have two epurals and some *Diplospinus* originally develop only two epurals.
37. *Subocular Shelf Distinctively Configured.*—We disagree with Johnson's (1986) assumption that absence of the shelf is not an informative character since this implies that the phylogeny infers the character state distribution rather than the opposite. It is contradictory to state that absence of the subocular shelf is derived within scombrids and then code this state as primitive together with presence of non-distinct subocular shelf. Recognizing three states, presence (state 0), absence (state 1), unique presence (state 2), does however, present problems with assumptions of transformation. The series presence → absence → unique presence, presence → unique presence → absence, absence → presence → unique presence, are equally conceivable, particularly since some outgroups lack a subocular shelf. Therefore, we assume three states for this character but leave them unordered in the analysis.
38. *Fleshy Midlateral Caudal Keel Present.*—This keel is clearly present in *Xiphias* and absent in the istiophorids, although Johnson (1986) had this situation reversed in both his narrative and in his matrix.
39. *Upper and Lower Hypural Plates Fuse Ontogenetically.*—Since many trichiurines lack a caudal fin we assume that this character is not applicable for them.
41. *Formation of the Larval Beak.*—We hypothesize that *Gymnosarda* has an exaggerated beak similar to *Acanthocybium* and *Scomberomorus* based on the external morphology of the larvae (attempts at examining internal morphology were not successful although Johnson [1986] notes that the larvae of *Gymnosarda* have an exaggerated beak), rather than assume it is not elongate as Johnson's (1986) coding reflects. Larvae were unavailable for *Cybiosarda* and *Orcynopsis*, and therefore this character is coded as missing for these taxa.
44. *Absence of Splint-like Gill Rakers.*—We disagree with Johnson's (1986) interpretation that initial absence of splint-like gill rakers is clearly non-homologous with ontogenetic reduction and subsequent absence of splint-like rakers. We assume that there are two possible coding schemes for his character: a) complete absence of gill rakers in adults (*Lepidocybium*, *Acanthocybium*, *Gasterochisma*, and the billfishes) as the derived state and presence of gill rakers in some or all species of the taxon as the primitive state (all other taxa), and b) presence (state 0), partial absence (state 1), and complete

←

absent; 1 = present. 39) Fusion of upper and lower hypural plates, 0 = remain separate; 1 = fuse ontogenetically. 40) Preural centra support of caudal fin rays, 0 = second and third preural centra support, 1 = second, third, and fourth preural centra involved. 41) Rostral cartilage of larval beak, 0 = short, nearly vertical; 1 = short, nearly horizontal; elongate, nearly horizontal; ? = larvae unavailable. 42) Extensive interconnection of gill filament blades, 0 = absent; 1 = present. 43) Bony epithelial toothplates on surfaces of gill filament blades, 0 = absent; 1 = present. 44) Absence of splint-like gill rakers (see text). 45) Fusion of parahypural to hypural plate, 0 = not fused; 1 = fused; 46) Elongate premaxillary bill in adults, 0 = absent; 1 = present. 47) Larval teeth replaced with villiform teeth, 0 = no replacement; 1 = replacement. 48) True spinous dorsal fin, 0 = present; 1 = absent. 49) Brain heater, 0 = present; 1 = absent.

- absence (state 2). For our initial analysis, we assume the former coding scheme and will discuss the second option under a separate analysis.
45. *Parahypural Fuses to Hypural Plate*.—Although Johnson (1986) coded this as not fused (state 0) for *Lepidocybium* and all gempylines, our observation indicates that it is fused in *Lepidocybium*, *Diplospinus*, and *Thyrisites* and therefore should be coded as state 1.
 49. *Brain Heater Present*.—Billfishes and *Gasterochisma* have similar thermogenic cells that function in cranial endothermy (Carey, 1982; Block, 1983; Block, 1986). Although billfishes and *Gasterochisma* may derive these cells from different intrinsic eye muscles, it is not clear if this possible difference precludes a homologous relationship. We assume that this notable specialization occurred once in scombroids and therefore code the presence of a brain heater in both billfishes and *Gasterochisma* as the derived state (1).
 50. *Anterior Corselet*.—No anterior corselet (0), well developed anterior corselet (1).
 51. *Subcutaneous Vascular System*.—Absent (0), poorly developed (1), well developed (2).
 52. *Fronto-parietal Fenestra*.—No frontal-parietal fenestra (0), pair of frontal-parietal fenestra present (1).
 53. *Prootic Pits*.—Prootic pits absent (0), prootic pits slightly developed (1), well developed (2).
 54. *Fusion of Hypural 1 and 2*.—Hypurals 1 and 2 separate or partially fused (0) and completely fused (1).
 55. *Bony Caudal Keels*.—No bony caudal keels (0), weakly developed caudal keels (1), well developed caudal keels (2).
 56. *Hypural Notch*.—Large hypural notch (0), small hypural notch (1), hypural notch absent (2).
 57. *Glossohyal Teeth*.—Discrete tooth patches absent from glossohyal (0), pair of tooth plates fused to glossohyal (1).
 58. *Adipose Eyelid*.—Absent (0), present (1).
 59. *Uroneural-urostyle*.—Uroneural free from urostyle (0), uroneural fused to urostyle (1). This character shows extensive homoplasy in the Gempylidae, Scombridae, and billfishes.
 60. *Sagittae*.—Large (0), very small or almost absent (1).
 61. *Caecal Mass*.—Few individual pyloric caeca (0), well developed mass of hundreds of pyloric caeca (1). A synapomorphy of the Scombridae (except Scombrini) and billfishes.
 62. *Fusion of two Uroneurals to Form a Single Uroneural*.—Two uroneurals not fused (0), two uroneurals fuse (1), initially develops only a single uroneural (N), caudal fin not well developed (N). This is a complex character related to but not taken into consideration by character 34 (single uroneural pair develops). It is coded separately from character 34 because a transformation hypothesis can be assumed for development of a single uroneural pair but not also for subsequent fusion. It is made independent from character 34 by treating the character states as “not applicable” (N) for taxa that do not have two uroneurals for potential fusion.

A cladistic analysis of the above data set results in 1,682 most parsimonious trees (length 136, ci 0.55). The strict consensus tree is shown in Figure 5. Sister group relationships are highly unresolved in the trichiuroids (the 14 genera listed on the branch that includes *Thyrisitoides-Lepidocybium* which are the gempylids, and the trichiurids), although evidently the “Gempylinae” as defined by Johnson

(1986) (the Gempylidae of most other authors) are paraphyletic. The relationships among the Scombridae (all taxa above trichiuroids except the billfishes) and billfishes (istiophorids and *Xiphias*) are also highly unresolved and Johnson's (1986) *Acanthocybium*-billfish sister relationship is not supported from this analysis.

Successive weighting of characters produced a subset of 142 most parsimonious trees (ci 0.74) from the original 1,682 trees. The consensus tree for these 142 weighted trees is shown in Figure 6. A higher degree of resolution results within gempylids and scombrids, including the return of Johnson's (1986) *Acanthocybium*-billfish sister group relationship.

An Alternative Interpretation of the Gill Raker Character.—As stated above, the absence of splint-like gill rakers on the first arch (character 44) has at least two plausible coding schemes according to our interpretation. A different coding scheme from one of simple absence or presence is: completely absent (state 2) for *Lepidocybium*, *Acanthocybium*, *Gasterochisma*, and the billfishes; either reduced to as few as one to four rakers at the angle of the first arch in some or all species, or absent in some but not all species (state 1) of *Sphyraena*, *Gempylus*, *Nealotus*, *Neoepinnulus*, *Nesiarchus*, *Promethichthys*, *Rexea*, *Ruvettus*, and *Scomberomorus*, missing information or questionable (?) for *Epinnula*, *Thyrstites*, *Thyrstoides*, and *Tongaichthys*; and clearly present (state 0) for all remaining taxa. A cladistic analysis of our 62 characters using this alternative coding scheme results in over 2,575 (ci 0.53; Hennig86 reached overflow at this point) most parsimonious trees. The strict consensus tree for these 2,575 trees is shown in Figure 7. Gempylids are less resolved in this consensus tree than the one obtained from the previous interpretation of the gill raker character but the scombrids and billfishes are more resolved; *Gasterochisma* replaces *Acanthocybium* as the sister clade of the billfishes. Successive weighting produced 66 most parsimonious trees (length 141, ci 0.76). The consensus of these trees (Fig. 8) shows greater resolution within the gempylids than with the strict consensus tree but no greater resolution within the Scombridae.

Quantitative Evolutionary Systematics of Scombroid Fishes.—The two interpretations of Johnson's (1986) data (with and without *Gasterochisma*) and the two interpretations of our revised data set (from different coding of the gill raker character) results in seven different cladistic topologies (Figs. 2–8) depending on which method is used to reduce the numerous most parsimonious trees. These trees are based on four different data sets. We now present the results of a quantitative evolutionary systematic analysis of each of the four data sets, given their respective tree topologies.

The patrigrams based on the cladograms inferred from Johnson's (1986) revised data set with and without *Gasterochisma* are shown in Figures 9 through 11. Except for the necessary addition of a cluster with the addition of *Gasterochisma*, the three patrigrams are basically the same. The primary clusters separate the "higher scombroids" (Scombridae plus the billfishes) from the trichiuroids (*Lepidocybium* plus the gempylids plus the trichiurids) and the basal groups. Within the higher scombroids, *Scomberomorus* and the Sardini plus Thunnini cluster closely and are joined next by *Grammatorcynus* and the Scombrini, followed by *Acanthocybium* and, when present in the analysis, joined subsequently by *Gasterochisma*. This paraphyletic group, the Scombridae of most authors, forms a distinct cluster and is joined subsequently at a high dissimilarity level by the billfishes.

Patrigrams resulting from an analysis of the two revised and expanded data sets and their respective four reduced tree topologies share the same basic patristic

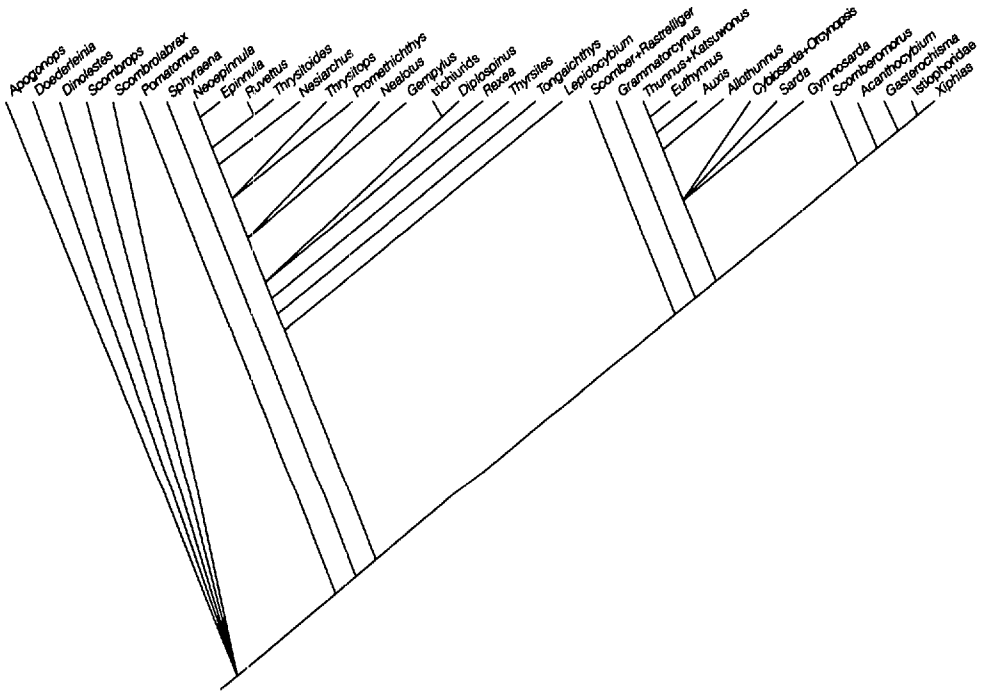


Figure 8. The cladistic hypothesis of the Scombroidei and immediate outgroups resulting from a strict consensus of 66 most parsimonious trees after successive character weighting resulting from an analysis of the data matrix listed in Table 1 except that character 44 (presence of splint-like gill rakers) is coded using an alternative interpretation.

patterns with each other (Figs. 12–15) and with the patrigrams from the revised analysis from Johnson's (1986) data set (Figs. 9–11). Again, the primary clusters separate the higher scombroids from the trichiuroids and the basal groups. Within the higher scombroids the pattern of patristic clusters is always the same for the four reduced cladograms from the two data sets. The Scombridae always form a distinct paraphyletic cluster from the billfishes. In the Scombridae, the holophyletic Thunnini (*Thunnus* plus *Katsuwonus*, *Euthynnus*, and *Auxis*) and the paraphyletic Sardini (*Allothunnus*, *Sarda*, *Cybiosarda* plus *Orcynopsis*, and *Gymnosarda*) each and subsequently together form a distinct cluster. These are then joined by a cluster of *Grammatocypinus* and *Scomberomorus*, followed by *Acanthocybium*, the Scombrini, and *Gasterochisma*.

Within the trichiuroids, there are some differences in position of clusters among the patrigrams based on the strict consensus trees and the consensus trees from successive weighting. This is mostly due to the lack of cladistic resolution in the gempylids on the strict consensus tree. Clusters in the unresolved group of gempylids on the strict consensus tree become polyphyletic when this part of the cladogram is more resolved with successive weighting of characters. The data sets analyzed here were assembled primarily to examine the higher order relationships of scombroid fishes and therefore does not contain enough information to resolve in detail either cladistic or anagenetic pattern within the gempylids. Presumably a data set with more characters that vary within the trichiuroid fishes would be more appropriate for this purpose.

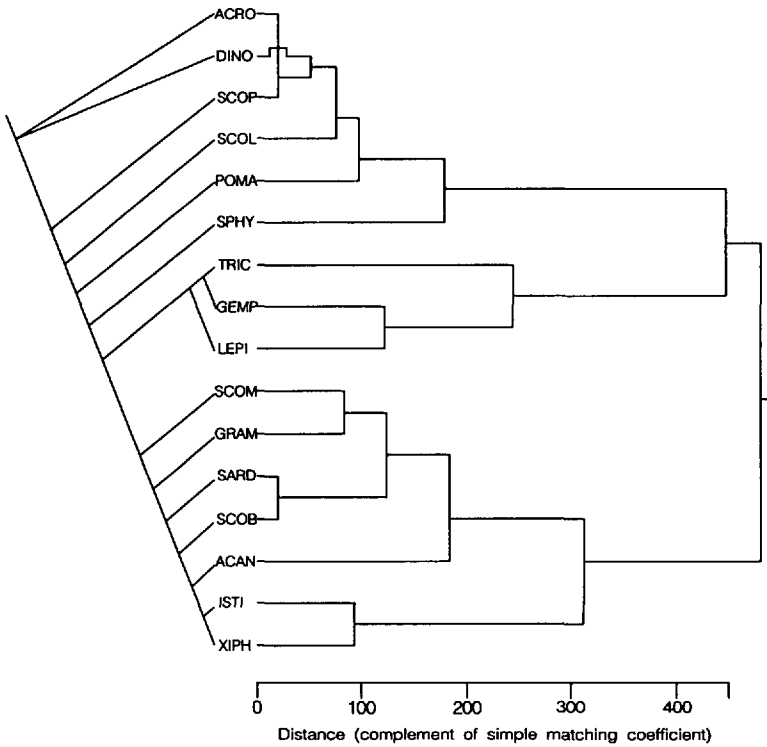


Figure 9. The cladistic hypothesis and patrigram from the quantitative evolutionary analysis of the Scombroidei and immediate outgroups using Johnson's (1986) corrected data matrix excluding *Gasterochisma*. The cladistic hypothesis and taxa abbreviations correspond with Figure 2.

Cladistic and Evolutionary Classifications.—Johnson (1986) presented a cladistic classification (Table 2) that would need to be modified depending on which of the above cladistic reinterpretations one chooses to accept. The cladograms inferred after the addition of *Gasterochisma* in the analysis with Johnson's (1986) corrected data matrix (Figs. 2, 3) suggest two different classifications depending on the use of strict consensus or character weighting. The cladogram inferred from successive weighting of characters is similar to the cladogram originally presented by Johnson (1986) and the subsequent cladistic classification need not change substantially from the classification proposed by him; only the position of *Gasterochisma* and the removal of "incertae sedis" would be necessary. A more conservative approach (and perhaps a more appropriate one considering Johnson's [1986] initial reluctance to include *Gasterochisma* in the analysis) would be to follow the convention of Anderberg and Tehler (1990) by constructing the classification from the consensus tree. To be minimally disruptive to Johnson's (1986) original classification, one tribe could be erected to include *Acanthocybium* plus the billfishes and "incertae sedis" added to all but the tribe Scombrini. However, there are various other cladistic classifications that could be fashioned from the consensus tree.

There are a variety of novel cladistic classifications that could result from the cladograms inferred by the expanded and revised data set (Figs. 5, 6). The cladistic inference most disruptive to Johnson's (1986) classification is the realization of his suspicion that his "Gempylinae" are paraphyletic. To maintain his original

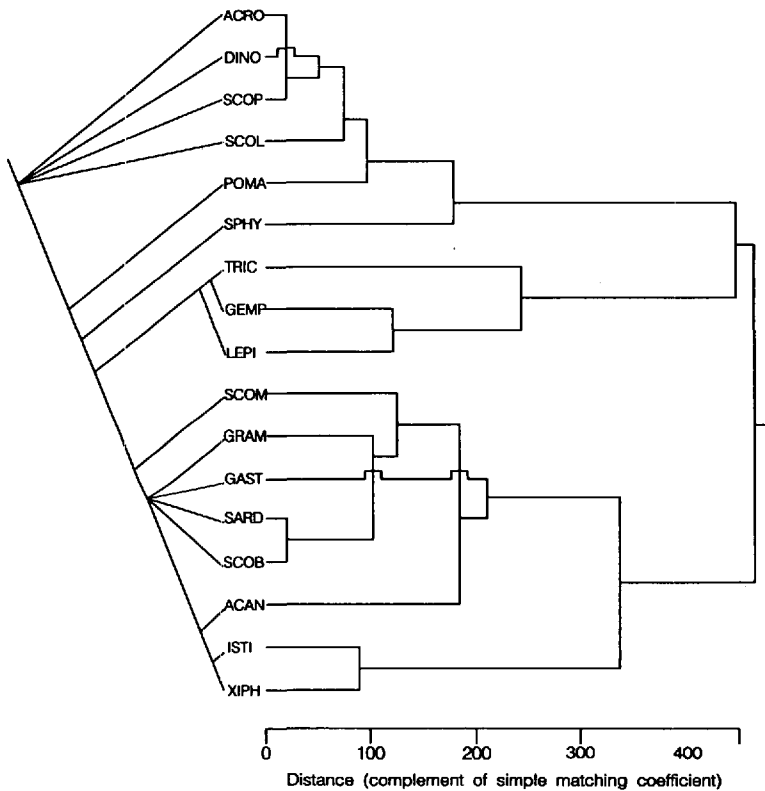


Figure 10. The strict consensus cladistic hypothesis and patrigram from the quantitative evolutionary analysis of the Scombroidei and immediate outgroups using Johnson's (1986) corrected data matrix including *Gasterochisma*. The cladistic hypothesis and taxa abbreviations correspond with Figure 3.

subfamilies, many more subfamilies would need to be erected. Alternatively, the rank structure of his entire classification could be changed. We will not speculate further on the many possibilities of changing Johnson's (1986) cladistic classification to accommodate the paraphyly of the gempylids because more data are needed to resolve cladistic pattern within this group. Any cladistic classification we could suggest would likely change substantially with the addition of this new information.

The strict consensus trees (Figs. 5, 7) and the consensus trees from the successive weighting of characters (Figs. 6, 8) suggest several different cladistic classifications for the tunas, mackerels, and billfishes. To be minimally disruptive to Johnson's (1986) classification, taxa from the strict consensus could be similar to those suggested for the strict consensus from Johnson's (1986) original data with *Gasterochisma* (Fig. 3), except the tribe with *Acanthocybium* would be separate from a tribe containing the billfishes. With the consensus tree from successive weighting, however (Fig. 6), a separate tribe for *Acanthocybium* is not necessary, and it could be included in a tribe with the billfishes. With the alternative strict consensus tree (Fig. 7), a tribe could be erected that includes *Scomberomorus*, *Acanthocybium*, *Gasterochisma*, and the billfishes.

The consistent patristic pattern inferred from the quantitative evolutionary systematic analysis suggests one classification that is minimally disruptive with the

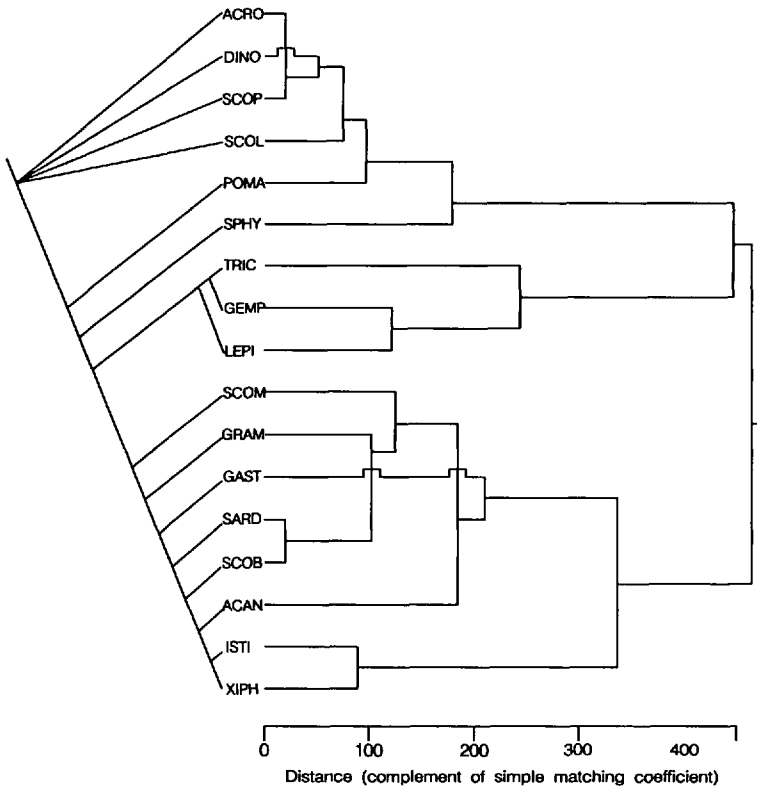


Figure 11. The strict consensus cladistic hypothesis from successive character weighting and patrigram from the quantitative evolutionary analysis of the Scombroidei and immediate outgroups using Johnson's (1986) corrected data matrix including *Gasterochisma*. The cladistic hypothesis and taxa abbreviations correspond with Figure 4.

traditional classification (Table 3, Collette and Nauen, 1983; Nelson, 1984; Eschmeyer, 1990). This classification reflects patristic pattern and is also a form of cladistic classification since the cladogram can be reconstructed from it using a set of symbols (Carpenter, 1987). We defer further comment on this classification to the discussion presented below.

DISCUSSION

We make three general observations from the results presented here: 1) with the total evidence at hand, many cladistic relationships within scombroids in general are not well corroborated, and in particular, certain relationships within the Scombridae proposed by Johnson (1986) are not well supported unless successive weighting of characters is applied, 2) the choice of a cladistic classification is not clear because of the many alternative cladistic hypotheses, and 3) a stable classification that reflects both cladistic and anagenetic pattern and closely resembles the existing classification can be constructed using a quantitative evolutionary systematic method. We discuss each of these observations in turn.

The extensive information available on the osteology and morphology of scombroid fishes is not sufficient to resolve phylogenetic relationships satisfactorily. One of Johnson's (1986) primary conclusions, that *Acanthocybium* is the sister

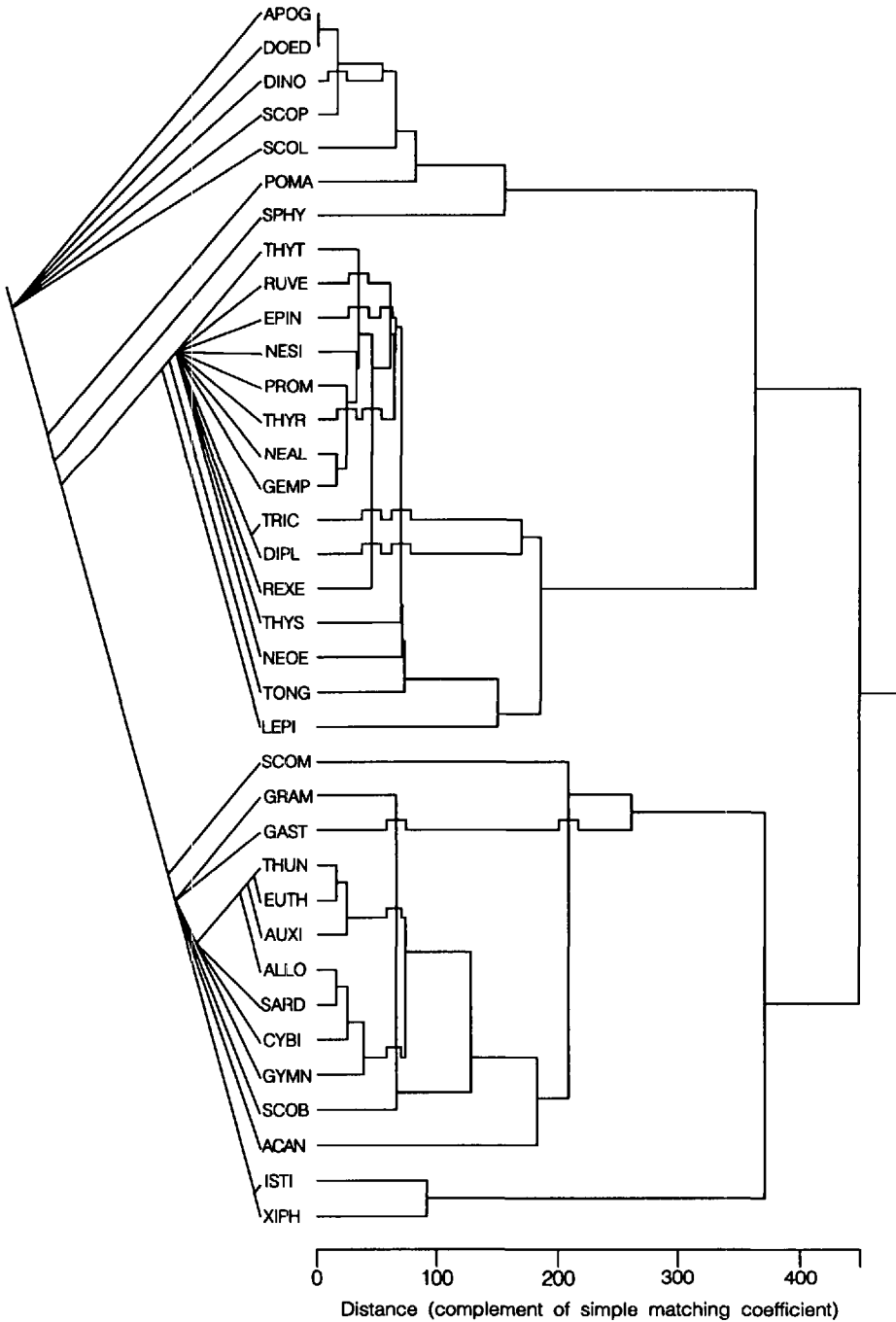


Figure 12. The strict consensus cladistic hypothesis and patrigram from the quantitative evolutionary analysis of the Scombroidei and immediate outgroups using the data matrix listed in Table 1. The cladistic hypothesis and taxa abbreviations correspond with Figure 5.

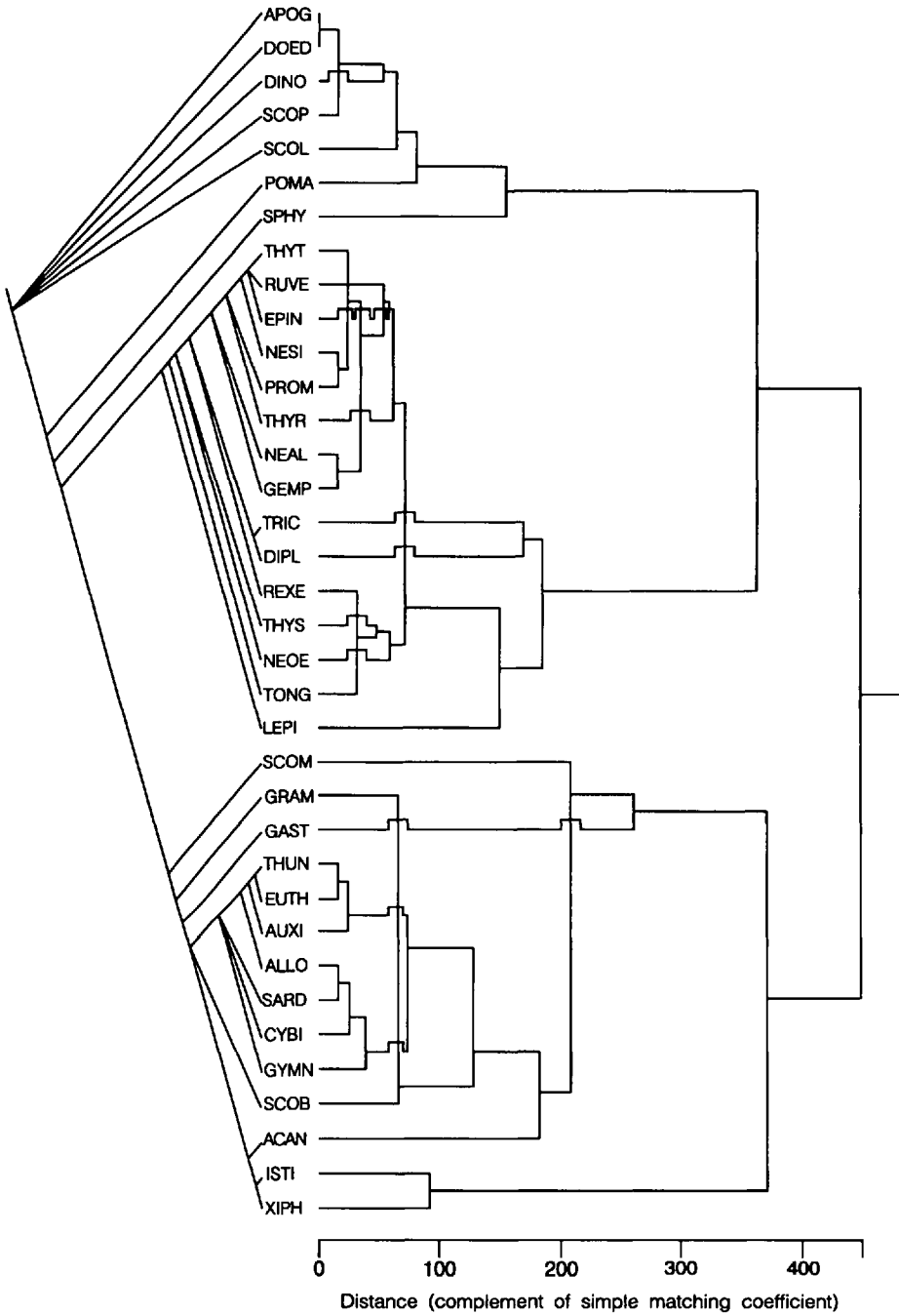


Figure 13. The strict consensus cladistic hypothesis from successive character weighting and patri-gram from the quantitative evolutionary analysis of the Scombroidei and immediate outgroups using the data matrix listed in Table 1. The cladistic hypothesis and taxa abbreviations correspond with Figure 6.

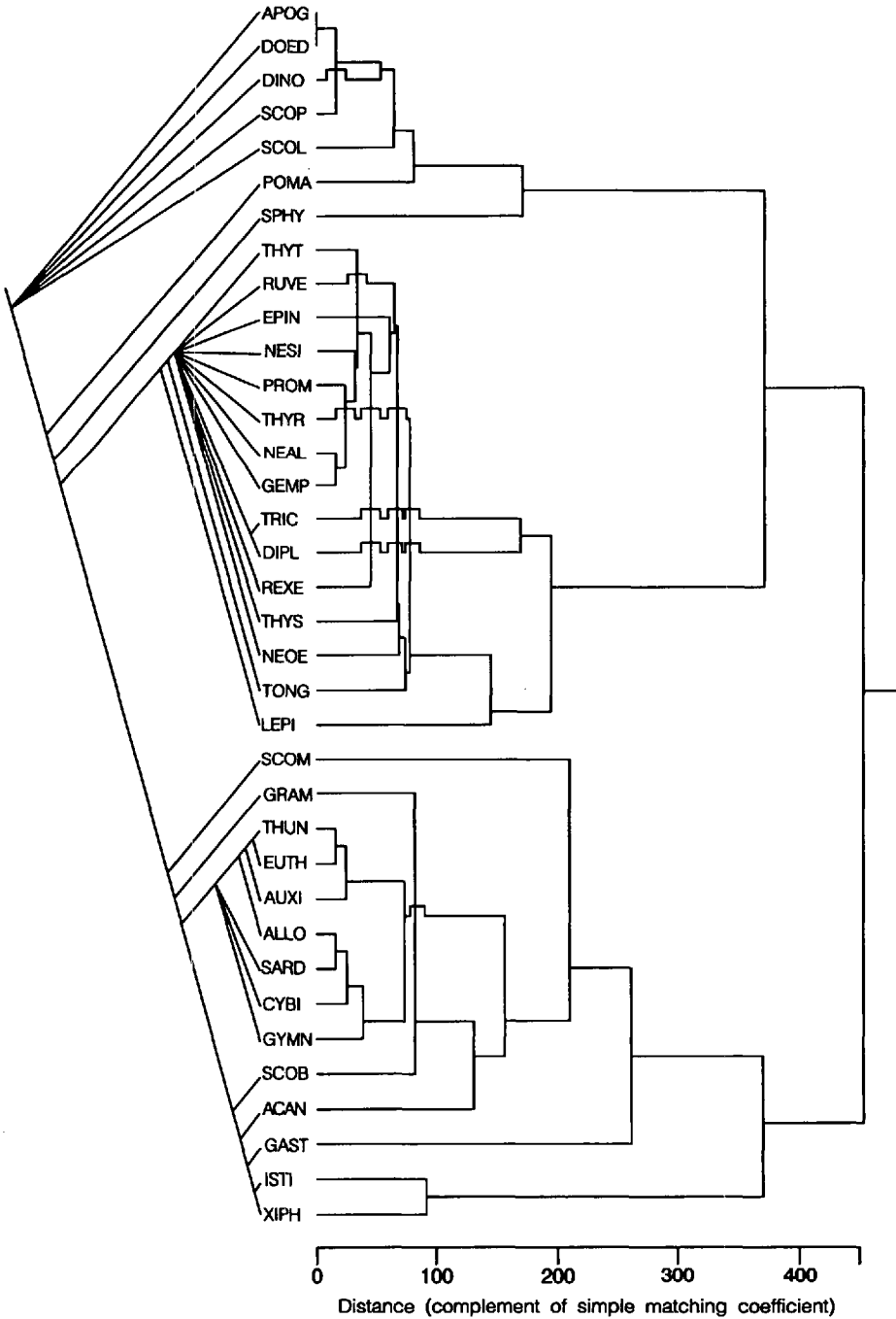


Figure 14. The strict consensus cladistic hypothesis and patrigram from the quantitative evolutionary analysis of the Scombroidei and immediate outgroups using the data matrix listed in Table 1 except that character 44 (presence of splint-like gill rakers) is coded using an alternative interpretation. The cladistic hypothesis and taxa abbreviations correspond with Figure 7.

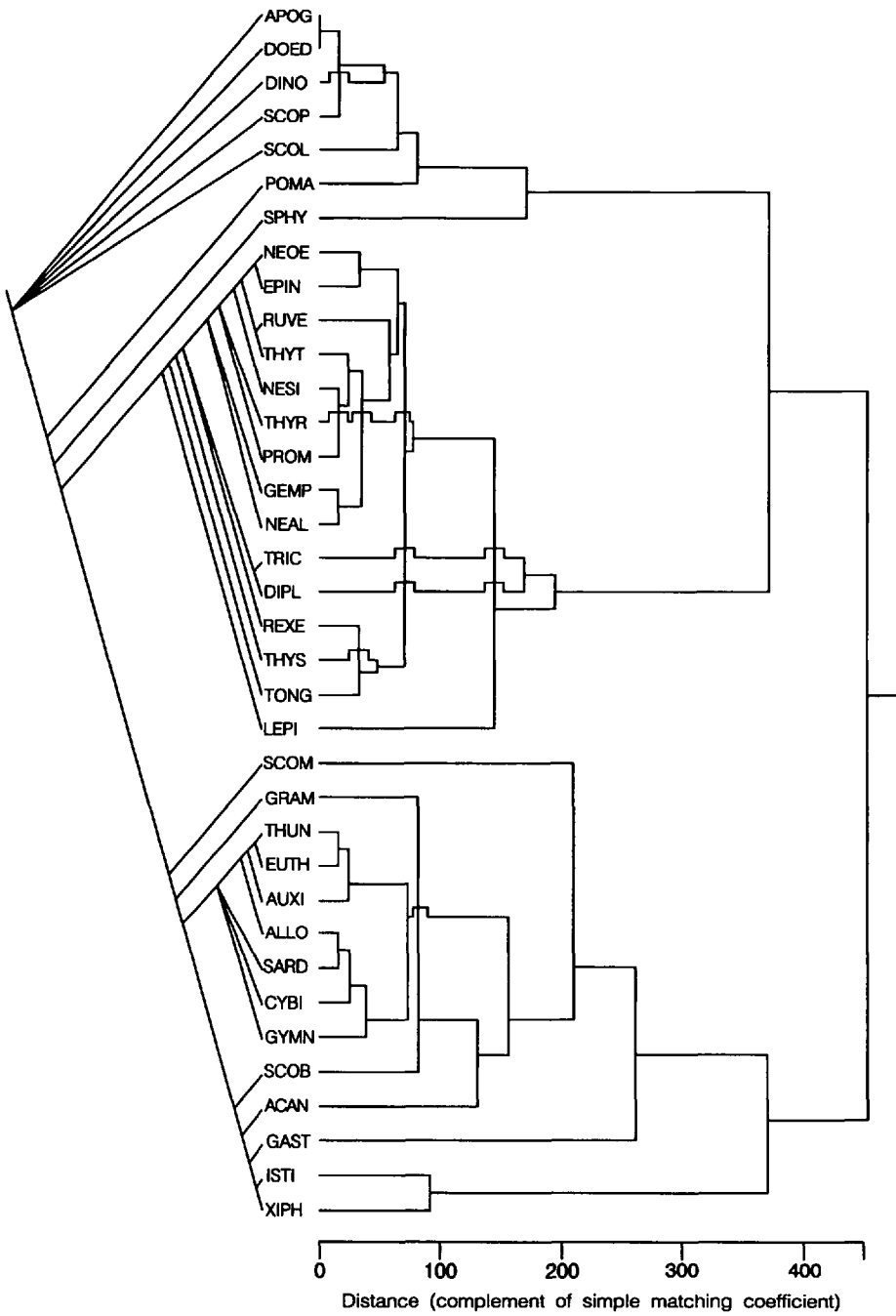


Figure 15. The strict consensus cladistic hypothesis from successive character weighting and patrigram from the quantitative evolutionary analysis of the Scombroidei and immediate outgroups using the data matrix listed in Table 1 except that character 44 (presence of splint-like gill rakers) is coded using an alternative interpretation. The cladistic hypothesis and taxa abbreviations correspond with Figure 8.

Table 2. Johnson's (1986) classification of the Scombroidei. The phyletic sequencing convention was used.

Suborder Scombroidei
Family Sphyraenidae
Family Gempylidae
Subfamily Lepidocybiinae
Subfamily "Gempylinae"
Subfamily Trichiurinae
Family Scombridae
Incertae sedis: Tribe Gasterochismatini
Tribe Scombrini
Tribe Grammatorcynini
Tribe Sardini
Tribe Scomberomorini
Tribe Acanthocybiini
Tribe Istiophorini
Tribe Xiphiini

Table 3. A cladistic and quantitative evolutionary classification of the Scombroidei. The cladistic hypothesis that we wish to reflect in this classification is shown in Figure 5 (with trichiuroid fishes simplified), which should be referred to for easy reference to the genealogical relationships. However, the cladogram can also be retrieved from the classification by following these rules: 1) taxa are listed in phyletic sequence; 2) taxa without brackets or parentheses listed on the same line are ignored while reconstructing the cladogram; 3) sets of open and closed parentheses are nested sets representing holophyletic groups that include the taxon from the line they are listed on; 4) an open parenthesis listed with a dash indicates that the branch is a multifurcation with the next nested taxon.

Suborder SCOMBROIDEI	
Superfamily Sphyraenoidea	()
Superfamily Trichiuroidea	()
Superfamily Scombroidea	
Family Scombridae	
Subfamily Scombrinae	
Tribe Scombrini	()
<i>Scomber</i>	
<i>Rastrelliger</i>	
Tribe Sardini	
<i>Sarda</i>	((—(—
<i>Gymnosarda</i>	(—
<i>Cybiosarda</i>	(—
<i>Orycnopsis</i>	(—
<i>Allothunnus</i>	(
Tribe Thunnini	
<i>Auxis</i>	(
<i>Thunnus</i>	(—
<i>Katsuwonus</i>	(—
<i>Euthynnus</i>	()))))))
Tribe Scomberomorini	
<i>Grammatorcynus</i>	(—
<i>Acanthocybium</i>	(—
<i>Scomberomorus</i>	(—
Subfamily Gasterochismatinae	
<i>Gasterochisma</i>	(—
Superfamily Xiphioidei	
Family Xiphiidae	(
Family Istiophoridae	()))))))

clade of the billfishes, is supported by some results presented here (Figs. 3, 4). We suspect this conclusion however, because in a revised data set this relationship is supported only in an analysis with successive weighting of characters (Fig. 6). Also, this cladistic relationship varies with the slight change in coding of the gill-raker character (Figs. 7, 8). This variation in coding did not change the relative character states of the billfishes, *Acanthocybium*, or *Gasterochisma* and yet the cladistic position of these shifted with the alternative coding. Instability due to different interpretations of the gill raker character is similar to the instability that we found in a preliminary analysis with the upper jaw character. The upper jaw of juveniles can be coded as a three-state character (not elongate, 0; elongate, 1; very elongate, 2) or as a two-state character in two different ways (not elongate, 0; elongate 1; or, not elongate or slightly elongate, 0; very elongate, 1). One set of coding resulted in cladograms like Johnson's (1986) hypothesis, another like that of Collette et al. (1984) and these results were presented at several conferences. After we reevaluated and revised the states of all characters for the analysis that we present here, this difference in coding no longer made such dramatic shifts in the cladograms but instability appeared instead with alternate hypothesized codings of the gill raker character. Because of this instability from different character coding, variations in cladistic inference would also be expected if certain additional characters were considered. For example, if morphometric data (that includes many similarities between *Scomberomorus* and *Acanthocybium*) or the biochemical information that suggests billfishes and tunas (including *Acanthocybium*) are cladistically distant (Block et al., 1993; Finnerty and Block, 1994) were included in an analysis with the data presented here, it is possible that Johnson's (1986) *Acanthocybium*-billfish relationship would not be supported.

The choice of a cladistic classification for scombroids is not clear because of the instability of cladistic inference within this group. Our results suggest that a cladistic classification could be based on one of the most parsimonious trees, the strict consensus trees, or the trees based on successive weighting of characters. Furthermore, the inconsistent cladistic inference due to addition of taxa and characters (our revised analyses), inclusion of component genera of presumed holophyletic groups (e.g., the gempylids), and uncertainty in coding of characters, indicates that more information is necessary to substantiate cladistic pattern in this group. Therefore, it is premature to recognize a novel cladistic classification because likely future changes in the cladistic hypothesis would require additional changes in the classification.

Evolutionary systematists (Mayr and Ashlock, 1991) and cladists (Kluge, 1989) recognize the frequent instability of cladistic hypotheses and the undeniable importance of a conservative system of classification for storage and retrieval of information. Because of this, we question how or if strict cladistic classification (sensu Wiley, 1981a) should be used. If it is, it may be advisable to change existing classifications in favor of cladistic classification only after a single hypothesis has been very well corroborated or has existed long enough to stand a "test of time." However, this raises questions that do not appear to have explicit answers: How well corroborated is well corroborated enough? How long must a cladistic hypothesis be around until it has passed the test of time?

This is not to assert that classifications should never be changed based on a phylogenetic analysis. Classifications should and will change when our understanding of evolutionary relationships changes. For example, a comparative study clearly showed that the louvar had a more recent common ancestor with acanthuroid fishes than with scombroids (Tyler et al., 1989). This demonstrated that the association of the louvar with scombroids was polyphyletic. Consequently,

the classification of acanthuroid and scombroid fishes changed. However, in the interest of stability, it is best to maintain the status quo in a classification unless cladistic evidence clearly shows the polyphyly of a recognized taxon or anagenetic evidence clearly indicates the distinctness of a formerly unrecognized group. For example, we do not believe that the cladistic or anagenetic patterns inferred within the trichiroid fishes were well supported and therefore we tentatively adopt the previously accepted classification that includes the paraphyletic Gempylidae and the apparently holophyletic Trichiuridae. In contrast, although Johnson (1986) suspected that his presumed holophyletic "Gempylinae" may be paraphyletic, he nevertheless presented a new cladistic classification that must now be modified.

Besides the problem of cladistic instability, a strict cladistic classification for scombroid fishes is inconsistent with the classification currently in use (Table 2; Collette and Nauen, 1983; Nelson, 1984; Eschmeyer, 1990). These types of questions are apparently the cause of a general reluctance to follow cladistic classifications (Nelson, 1984; Eschmeyer, 1990). Fink (1985) proposed a cladistic classification of stomiiform fishes that is not being widely used because it differs substantially from previously used classifications (Eschmeyer, 1990). Richards and Robins (1990) point out that the many different cladistic hypotheses proposed for gadiform fishes (Cohen, 1989) is another source of "nomenclatural chaos" if cladistic classification is followed. The use of unstable classifications will complicate the retrieval of information from the literature. Presenting new, equivocal cladistic classifications will cause confusion for biologists, and resource and environmental managers using the classifications, and serve to reinforce the negative suspicions that many biologists harbor toward systematists. Therefore, ideally, a system of classification would not contradict cladistic and anagenetic evidence, be stable, and be minimally disruptive to existing classifications.

The results of the quantitative evolutionary analyses of scombroid fishes are promising in the search for an ideal system of classification. These results are stable despite differing cladistic hypotheses and data sets, and are congruent with the traditional classification of scombroid fishes, anagenetic pattern, and cladistic pattern. For example, the tunas and mackerels have long been considered a distinct group and although paraphyletic according to our analyses, they are consistently distinct in a patristic sense and are maintained as a separate family from the billfishes. This suggests that traditional classifications, although not necessarily constructed using explicit methods, need not be evolutionarily inconsistent with phylogenetic reconstructions based on recent evidence and methods. It also raises our hopes that an explicit methodology can be used to confirm, and where necessary, modify existing classifications without seriously disrupting them. Similar to the scombroid classification presented here, a quantitative evolutionary systematic analysis of caesionid fishes also did not require major changes in an existing classification (Carpenter, 1990, 1993) and is consistent with both cladistic and anagenetic pattern.

In the past, cladists have defended the use of cladistic classification and rejected the use of evolutionary classification because of the explicit methods associated with the former and the perceived lack of explicit methodology of the later (Brooks and Wiley, 1985). However, it should be clear from the many possible interpretations of cladistic conventions and methods presented in this paper that there is a great deal of subjectivity involved in cladistic taxonomy. Besides the quantitative evolutionary method used here, there are explicit methods for directly choosing classifications from inferred cladistic and patristic hypotheses (Carpenter, 1993). Some of these methods are newly proposed, however, and could not be included in this paper because of computational difficulties.

There has also been an attempt to reject evolutionary classification because of a supposed logical inconsistency of paraphyletic groups with a phylogeny (Wiley, 1981b). However, Meacham and Duncan (1987) rejected this assertion and have shown that a system using both holophyletic and paraphyletic groups forms a valid and useful consistency criterion.

Cladists often justify the use of cladistic classification because of the primacy of cladistic pattern for comparative biology (Wiley, 1981a). We agree that cladistic pattern is the most important pattern in evolution to infer because it is the basis for formulating and testing hypotheses of homology. However, initially it is degree of divergence (similarity of structure of characters) that allows the first step to be taken in hypotheses of homology and suggests likelihood of homoplasy. Cladistic methodology therefore implicitly and explicitly weights decisions of homology based on presumed degree of divergence. For example, Johnson (1986: 25) entertained the possibility of homology in the larval beak morphology between *Sphyræna*, certain gempylids, and higher scombrids because of a resemblance in the structure of their beaks. But, he ultimately did not recognize this as an example of homologous similarity, presumably because of the unique divergence of structures associated with the larval beak between the groups involved, although the groups are closely related cladistically. It is therefore important to study degree of divergence, including consistent enumeration of uniquely derived features, to make informed decisions about homology.

Cladistic pattern is also very important in providing the framework for understanding the other evident pattern and process of evolution, anagenetic divergence. With an inferred cladistic pattern the anagenetic divergence that clearly distinguishes certain groups of taxa can be interpreted meaningfully, and it is useful to have this information summarized in the classification. For example, a comparison of a biological system (which may functionally involve many characters in a phylogenetic study) between istiophorids with *Xiphias* and a biological comparison of *Acanthocybium* with *Xiphias* should be treated differently although a hypothesis indicates that the cladistic relationship may be similar (Fig. 2). Billfishes and scombrids are distinct groups because of anagenetic divergence and comparisons within each of these groups should be treated differently than comparisons between groups. As Johnson (1986: 34) states "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." However, in following the conventions of cladistic classification Johnson (1986) failed to summarize this obvious and important observation of the evolution of scombroid fishes. He placed the two billfish groups each as one of eight separate tribes within the family Scombridae. This allows retrieval of his cladistic hypothesis (if one knows that the sequencing convention was used) but gives no information about the "extensive modification" part of evolution that he admits is obvious. In contrast, the rank structure of our classification (Table 3) reflects the degree of divergence between billfishes and scombrids, while annotation (or reference to a figure of the cladogram) allows explicit statements to be made about genealogical relationships. Strict cladistic classification allows only retrieval of cladistic information.

The scombroid classification resulting from the quantitative evolutionary systematic analysis (Table 3) has the advantages of stability, avoiding polyphyletic taxa, and reflecting important anagenetic pattern while allowing unequivocal reconstruction of a cladistic hypothesis. Because of competing cladistic inferences, we choose to recognize the strict consensus cladogram in our classification since it does not contradict the different possibilities. However, our classification can

be rearranged and re-annotated to reflect any of the cladistic hypotheses presented, without changing the classification currently in use. The strategy of annotation or reference to a figure to present the cladogram is perhaps the most practical in terms of usefulness of the classification for all biologists, at least until the phylogenetic uncertainty is overcome with respect to scombroid fishes. We caution that this phylogenetic uncertainty may never be resolved however, since synapomorphies are both created and obliterated in the evolutionary process. However, it is essential to use cladistic analysis to understand anagenetic pattern, provide a better framework for comparative biologists, and to construct meaningful classifications.

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