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Osteology, phylogeny, and biogeography of the marine fish family Ephippidae (Perciformes, Acanthuroidei), with comments on sister group relationships

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OSTEOLOGY, PHYLOGENY, AND BIOGEOGRAPHY OF THE MARINE FISH FAMILY EPHIPPIDAE (PERCIFORMES, ACANTHUROIDEI),WITH COMMENTS ON SISTER GROUP RELATIONSHIPS.

A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of The Requirements for the Degree of

DOCTOR OF PHILOSOPHY

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by

Martin R. Cavalluzzi

2000

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This dissertation is submitted in partial fulfillment of

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ABSTRACT

The marine fish family Ephippidae comprises eight genera and 15 species of extant fishes. Spadefishes or batfishes inhabit nearshore tropical to temperate waters. They are almost circumglobal in distribution, with the highest diversity in the Indo-west Pacific and the lowest diversity in the east Pacific and west Atlantic.

Fifty-nine potentially informative morphological characters , 10 outgroup taxa, and eight ingroup taxa (i.e., genera) were used to explore sister group hypotheses to the Ephippidae, as well as generate a phylogeny of the Ephippidae. Seven constraint tree analyses were utilized to examine various sister group hypotheses based on previous morphological and molecular analyses by other researchers. These analyses resulted in maximally parsimonious trees ranging from 184 to 197 steps. As in previous analyses, both the suborder Acanthuroidei and the family Ephippidae were found to be monophyletic. Similar to the results from previous molecular and total evidence analyses, the exact placement of Scatophagidae within the Acanthuroidei could not be determined with this data set. However, in contrast to those results, Drepaneidae was found not to be the sister taxon to Scatophagidae.

A single most-parsimonious tree of 187 steps (CI = 0.412) was chosen as the best hypothesis of relationships utilizing all taxa. However, few additional steps are needed to produce very different topologies. The phylogeny of the Ephippidae was invariant for all constraint tree analyses. Homoplastic evolution is prevalent within the family (CI = 0.687; Bremer Total Support Index = 0.22). The phylogenetic hypothesis depicts two distinct clades: (*Chaetodipterus* (*Ephippus* (*Tripterodon* (*Platax*, *Zabidius*)))) + (*Proteracanthus* (*Parapsettus*, *Rhinoprenes*)). One new synapomorphy is proposed for the Ephippidae: posterior processes of the pelvic-fin girdle elongate, pointed, separate from one another, and parallel to the long axis of the body. Another new synapomorphy, the possession of an elongate fourth pharyngobranchial that completely overlays the dorsal surface of the upper toothplate of the fourth branchial arch, is homoplastically shared with Zanclidae. Ancestral area analysis determined that the ancestor to the Ephippidae most likely had an east Indian/west Pacific distribution. Omnivory is plesiomorphic within the Ephippidae and confirmed to be plesiomorphic for the Acanthuroidei.

OSTEOLOGY, PHYLOGENY, AND BIOGEOGRAPHY OF THE MARINE FISH FAMILY EPHIPPIDAE (PERCIFORMES, ACANTHUROIDEI), WITH COMMENTS ON SISTER GROUP RELATIONSHIPS.

INTRODUCTION

Ephippids, commonly known as spadefishes and batfishes, comprise a small family of marine fishes. They primarily inhabit nearshore tropical to temperate waters of the Indian, Atlantic, and Pacific oceans, but some species enter estuaries and river mouths (Fritzsche and Fuiman 1982, Nelson 1994).

Adults are generally characterized by: deep, laterally compressed bodies ("slab-sided"); the spinous portion of the dorsal fin continuous with, but distinct from soft-rayed portion (except in *Platax*, *Zabidius* and *Parapsettus*); small, nonprotrusive mouths, with rows of compressed tricuspid or setiform teeth; and, gill membranes broadly united to the isthmus (Herre and Montalban 1927, Marshall 1965, Weber and De Beaufort 1936). Maximum length is approximately 80 cm, although most are much smaller. Most species are harvested commercially (small fisheries) or recreationally (e.g., *Chaetodipterus* sp., *Platax* sp., *Parapsettus*). Some, such as *Platax* species, are highly sought after by the aquarium trade. Two species, however, *Proteracanthus sarissophorus* and *Rhinoprenes pentanemus* are very rare and little is known of their habits.

Ephippids typically form schools in relatively shallow water and are usually loosely associated with coral and rocky reefs, mangrove swamps, grass beds, or manmade structures, although some species prefer bays with sand or rubble bottoms (Marshall 1965, Randall 1967). Primary foods include plant material, sponges, gorgonians, zooplankton, and benthic invertebrates such as molluscs and polychaete worms (Hayse 1990, Randall 1967).

Although there continues to be great interest in the taxonomy of ephippids (see "Historical Taxonomy"), studies involving the biology of these fishes have increased in the last 20 years, covering a wide spectrum of problems, including: patterns in marine fish feeding (Couto and Filho 1980, Hayse 1990, Kotrschal 1988, Randall 1967); aquaculture (Gaspar 1984, Gaspar and Cervigón 1987; Matus-Nivón et al. 1990, Walker 1991); age and growth (Hayse 1990); egg and larval development (Johnson 1978, Gaspar 1984, Martínez-Pecero et al. 1990, Masanet 1994); hyperostosis (Smith-Vaniz et al. 1995); parasitic infestations (Ramos et al. 1994); growth and diet (Robaina and Salaya 1993); reproduction (Couto and Filho 1980, Gaspar 1984, Hayse 1990, Masanet 1994); community studies (Santos-Martínez and Acero P. 1991, Silgado 1981); and biogeography (Springer 1982). Regarding biogeography, Rosen (1988) observed that understanding the origins of biodiversity in the Indo-west Pacific requires corroborated phylogenies of closely related taxa. As in biogeography, all aspects of biology (listed above) could certainly benefit from a historical perspective.

The Ephippidae comprises eight genera and 15 species of extant fishes; five of the genera are monotypic (Table 1). The largest genus is *Platax*, with five species. In addition, there are two extinct monotypic genera known from fossil deposits dated from the Eocene (56.5-35.5 mya; Patterson 1993). The current classification is based on Johnson (1984) and is amended to include *Zabidius* (Eschmeyer 1998). Although monophyly of the family has been proposed by Johnson (1984), no formal cladistic analysis has been performed to corroborate this hypothesis, and relationships among genera are unclear. The purpose of this study was to elucidate the hypothesized monophyly of the Ephippidae and provide a formal cladistic hypothesis of relationships among the eight ephippid genera (see "Objectives" for detailed goals).

Historical Taxonomy

Cuvier, in Cuvier and Valenciennes (1831; as cited in Burgess 1978), placed those fishes possessing scales on the bases of their dorsal- and anal fins (including ephippids) in the family Squamipinnes (=Squamipennes). This polyphyletic group contained fishes now included in the families Ephippidae, Drepaneidae, Chaetodontidae, Pomacanthidae, Scatophagidae, Zanclidae, Monodactylidae, Pempheridae, Psettidae, and Toxotidae, among others.

Günther (1860) subdivided the Squamipinnes into three groups, one of which, Chaetodontina, contained fishes now included in the families Chaetodontidae, Ephippidae, Pomacanthidae, Scatophagidae and others. Kaup (1860) retained genera of these families in the family Chaetodontidae, which was subdivided into five subfamilies. *Ephippus*, *Drepane*, and *Scatophagus* were placed in the subfamily Drepaninae. *Platax* was placed in Psettinae.

Gill (1862) included genera now allocated to Ephippidae in the family Chaetodontidae. Playfair in Playfair and Günther (1866) described the monotypic *Tripterodon* and allocated it to Sparidae. In 1873, Gill elevated the ephippids, then in the family Chaetodontidae, to family level. This included fishes currently allocated to the genera *Chaetodipterus*, *Ephippus*, and *Platax*.

Klunzinger (1870) placed the ephippid genera in the group Drepanini. In 1884, he allocated these same genera to the subfamily Drepaninae.

Bleeker (1877) considered the following ephippid genera to be in the family Chaetodontidae, which was subdivided into subfamilies: *Platax* (Plataciformes); *Proteracanthus* (Proteracanthiformes); *Ilarches* (=Chaetodipterus; Chaetodipteriformes).

Jordan and Evermann (1898) recognized several suborders within the Squamipinnes. Regan (1913) placed *Platax* with *Ephippus* in the Ephippidae, and placed *Drepane* in the family Drepanidae. Barnard (1927) followed Regan's classification. Fowler (1925) also followed Regan's classification, but later (Fowler 1929, 1934) allocated *Drepane* to subfamilial rank within the Ephippidae and elevated *Platax* to family level. In addition, he placed *Tripterodon* in the Girellidae (Fowler 1925, 1934) and *Proteracanthus* in the Girellidae (Fowler 1938). Matsubara (1955) allocated the families Ephippidae (includes their Platacidae), Drepanidae, Chaetodontidae, Pomacanthidae, Scatophagidae, Zanclidae, Acanthuridae, Scorpididae, Antigoniidae, Toxotidae, and Monodactylidae in the suborder Chaetodontina.

Munro (1964) described the monotypic genus *Rhinoprenes* from the Gulf of Papua New Guinea. He allocated this genus to the suborder Percoidei. Greenwood et al. (1966) included the genera *Drepane*, *Chaetodipterus*, *Platax*, and *Ephippus* in their Ephippidae. They treated *Rhinoprenes* as a separate family (Rhinoprenidae).

Johnson (1984) proposed a monophyletic Ephippidae comprising seven genera: *Chaetodipterus*, *Ephippus*, *Parapsettus*, *Platax*, *Proteracanthus*, *Rhinoprenes*, and *Tripterodon*. He included the genera *Parapsettus*, *Rhinoprenes*, and *Proteracanthus*, previously of the families Scorpididae, Rhinoprenidae, and Girellidae, respectively, and removed *Drepane*, formerly placed in the Ephippidae in the subfamily Drepaneinae (Nelson 1984). Citing Johnson (1984), Nelson (1994) elevated *Drepane* to familial status, Drepanidae (=Drepaneidae), and proposed a close relationship between this family and the Coracinidae. The family Ephippidae was expanded to include *Zabidius* by Eschemeyer (1990).

Monophyly of the Ephippidae

Johnson (1984) hypothesized the monophyly of the Ephippididae (= Ephippidae) based on four shared specializations involving the gill arches: (1) absence of the interarcual cartilage; (2) possession of a relatively large first pharyngobranchial; (3) reduction or absence of the basihyal; and, (4) possession of a comblike series of large blunt rakers associated with the anterior margin of the first epibranchial. Of these four specializations, two can no longer be considered diagnostic of the Ephippidae. The first, absence of the interarcual cartilage, was found by Tyler et al. (1989) to be a synapomorphy of the Acanthuroidei, of which the Ephippidae is the basalmost member (see "Intrafamilial Relationships" and "Sister-group relationships").

The second specialization, possession of a large first pharyngobranchial, will be shown herein to be present in all ephippids except *Proteracanthus*. Therefore, this character does not diagnose the Ephippidae without considering an independent loss within *Proteracanthus*. The reduction to only two shared specializations that unambiguously unite the Ephippidae, combined with the fact that Johnson (1984) was not able to examine all species, justifies further exploration for additional synapomorphies.

Intrafamilial Relationships

Intrafamilial relationships of the Ephippidae have only been examined in a cursory fashion. Mok and Shen (1983) attempted to examine the relationship between *Platax* (their Platacidae), *Ephippus* (Ephippidae), and other squamipinnian fishes. Although they hypothesized a sister-group relationship between *Platax* and *Ephippus* (Fig. 1a), their overall results were questioned by Tyler et al. (1989), who cited numerous problems with the analysis, interpretation, and conclusions. There were four primary criticisms: (1) an inadequate number of taxa within each family was examined (e.g., three of a possible seven species representing *Platax* and *Ephippus*, using six specimens total); (2) nodes on their cladogram were supported by no more than two characters; (3) numerous characters were misinterpreted; and (4) parsimony was cited as the criterion for favoring one hypothesis over another, although it was not evident how parsimony was used in cladogram construction.

In a study of tetraodontiform fishes and their allies, Rosen (1984) examined the ephippids *Platax* and *Chaetodipterus*. He found that these genera could be differentiated from *Drepane* (Drepaneidae; then part of Ephippidae) based on similarities in upper jaw morphology and caudal skeleton anatomy. However, in one character involving the structure of dorsal- and anal-fin radials, Rosen found similarities between *Platax* and *Drepane*, to the exclusion of *Chaetodipterus*.

In a study of acanthuroid fishes and their allies, Tang et al. (1999), included two ephippids, *Platax* and *Chaetodipterus*. In two separate analyses, one utilizing molecular evidence, the other total evidence (both morphological and molecular evidence), they found support for a sister group relationship between these genera, but found two equally-parsimonious hypotheses regarding the sister group to the Ephippidae (see "Sister-group relationships").

The only other formal analysis involving intrafamilial relationships of the Ephippidae is that of Blum (1988, unpubl. Ph.D. diss.). His analysis, using three ephippid genera, *Chaetodipterus*, *Rhinoprenes*, and *Platax*, hypothesized a sister-group relationship between *Rhinoprenes* and *Platax*, and a sister-group relationship between these two taxa and *Chaetodipterus* (Fig. 1b). However, these relationships as depicted in his figure are not supported by his data. An examination of the character matrix (cf. Blum 1988: 57, table 1) reveals that it is more parsimonious (by one step) to hypothesize a sister-group relationship between *Platax* and *Chaetodipterus*, and a sister-group relationship between these two genera and *Rhinoprenes*. To my knowledge, only one portion of Blum's dissertation was published (Blum 1989); this publication focused on current and historical biogeography of chaetodontids, and presented the cladogram of chaetodontid relationships: it did not include discussion of outgroups or descriptions of osteological characters. In summary, there exists no formal cladistic hypothesis of relationships among ephippid genera.

Sister-group Relationships

Currently, there are four data-supported hypotheses regarding sister groups to the Ephippidae. These hypothesized sister groups are as follows: (1) the clade comprising the families Scatophagidae, Siganidae, Luvaridae, Zanclidae, and Acanthuridae (= Acanthuroidei less Ephippidae) (Tyler et al. 1989; Winterbottom 1993); (2) the family Drepaneidae (Blum 1988); (3) the clade comprising the families Siganidae, Luvaridae, Zanclidae, and Acanthuridae (= restricted Acanthuroidei) (Tang et al. 1999); and, (4) the clade comprising the families Scatophagidae and Drepaneidae (Tang et al. 1999). In the following paragraphs, I describe the studies resulting in these sister-group hypotheses.

Tyler et al. (1989) removed Luvaridae from the Scombroidei (Nelson 1984) and allocated it to the Acanthuroidei, then comprising the families Siganidae, Zanclidae and Acanthuridae. Using Scatophagidae and Ephippidae as the first and second outgroups, respectively, Tyler et al. (1989) produced a highly corroborated phylogeny of the Acanthuroidei (Fig. 2a). The sequence Siganidae + Luvaridae + Zanclidae + Acanthuridae was hypothesized utilizing 90 morphological characters of adults and larvae. Tyler et al. (1989) then proposed monophyly of the group containing Ephippidae, Scatophagidae, and the Acanthuroidei based on six synapomorhies (see below). Both Tyler et al. (1989) and Winterbottom (1993) (described below) hypothesized Ephippidae to be the basal member (and therefore, sister taxon) of this group.

The phyletic sequence Ephippidae + Scatophagidae + Siganidae + Luvaridae + Zanclidae + Acanthuridae has been corroborated, in whole or in part, by several independent studies. Leis and Richards (1984) found support for the sequence proposed by Tyler et al. (1989; cited as MS) based on early life history characters. Johnson and Washington (1987), utilizing early life history characters, also corroborated the phyletic sequence proposed by Tyler et al. (1989; cited as MS), and found additional characters supporting the monophyly of the Acanthuroidei.

Winterbottom (1993), utilizing data from myology only, corroborated the sequence hypothesized by Tyler et al. (1989) except that the relationship between Scatophagidae and Ephippidae was left unresolved (Fig. 2b). He then combined data from four additional studies (185 morphological characters in all) (Guiasu and Winterbottom 1993; Johnson and Washington 1987; Mok 1977; Tyler et al. 1989), and produced a highly resolved cladogram (CI = 0.925) of relationships of Drepaneidae + Ephippidae + Scatophagidae + restricted Acanthuroidei. Characters were polarized using Drepaneidae as the sole outgroup. Based on six osteological and morphological characters described by Tyler et al. (1989) and one myological character, Winterbottom removed Ephippidae and Scatophagidae from the Percoidei (Nelson 1984) and allocated them to the Acanthuroidei in the phylogenetic sequence: Ephippidae + Scatophagidae + Siganidae + Luvaridae +

Zanclidae + Acanthuridae. The seven morphological characters used as support for monophyly of the six families are: (1) interarcual cartilage absent; (2) interopercle distinctly shaped with a narrow anteriorly-projecting extension; (3) articular equal to or shorter than the dentary; (4) nonprotrusive premaxillae; (5) gill membranes broadly united to the isthmus; (6) surfaces of the frontal and supraoccipital bones cancellous; and (7) presence of a myocommatum (i.e., septum between two adjacent myotomes) in adductor mandibulae section A2.

Utilizing 37 morphological characters, Blum (1988) hypothesized a sister-group relationship between Ephippidae and Drepaneidae (Fig. 1b). He hypothesized the sister group to this clade to be the clade comprising Siganidae, Acanthuridae, and Scatophagidae. The clade comprising these five families was hypothesized to be the sister group to the clade comprising Pomacanthidae + Chaetodontidae. Tyler et al. (1989) tentatively accepted Blum's hypothesis of an Ephippidae/Drepaneidae sister group relationship because it was based on additional characters than their hypothesis and because the placement of Drepaneidae did not change polarity assessments within the Acanthuroidei.

Recently, Tang et al. (1999) examined acanthuroid relationships utilizing five different approaches: (1) examination of mitochondrial DNA for 14 acanthuroid taxa and seven outgroup taxa; (2) a restricted total evidence analysis utilizing both mitochondrial DNA and morphological data for 15 taxa (14 acanthuroid taxa plus Drepaneidae; Ephippidae, Scatophagidae, and Drepaneidae were designated as the outgroups); (3) a corresponding DNA-only analysis utilizing the same taxa and outgroups as in "2"; (4) a restricted total evidence analysis utilizing both mitochondrial DNA and morphological data for 15 taxa (14 acanthuroid taxa, plus Drepaneidae designated as the sole outgroup); and, (5) a corresponding DNA-only analysis utilizing the same taxa and outgroups as in"4". Two ephippid species, *Chaetodipterus faber* and *Platax orbicularis*, were included in the study. The morphological data used for the total evidence analyses were taken from Winterbottom (1993).

In the first approach, Tang et al. (1999) found weak to very weak support (based on bootstrap and Bremer decay index values) at the nodes of the following clades (Fig. 3): Drepaneidae + Scatophagidae; (Drepaneidae + Scatophagidae) + Ephippidae; (Drepaneidae + Scatophagidae + Ephippidae) + the remaining acanthuroids; and, the restricted acanthuroids (Siganidae, Luvaridae, Zanclidae, and Acanthuridae). Weak support for the restricted acanthuroids was due to Siganidae falling out of the acanthuroids in trees two steps longer. However, the restricted acanthuroids (including Siganidae) were a highly-supported monophyletic group in the restricted analyses based on total evidence. In addition, *Naso*, an acanthurid, was depicted as the sister group to Zanclidae, and these two groups, collectively, as the sister group to the remaining acanthurids. Tang et al. (1999) dismiss this grouping of *Naso* and Zanclidae as artificial due to "an artifact of long-branch attraction." In the total evidence analyses (approaches 2 and 4), the overwhelming morphological evidence groups *Naso*, with the other acanthurids.

Excluding the relationships among Zanclidae and Acanthuridae, approaches 2-5 resulted in two hypotheses of relationships concerning Ephippidae, Scatophagidae, and Drepaneidae. Approaches 2 and 3 produced identical results (Fig 4a): a single most-parsimonious tree depicting Drepaneidae both as a member of the Acanthuroidei and as the sister group to Scatophagidae; these two taxa as the sister group to Ephippidae; and, this entire clade as the sister group to the rest of the acanthuroids (cf. Tang et al. 1999:422, figs 4, 5a, 6a). Based on bootstrap values, the clades Drepaneidae + Scatophagidae, the restricted acanthuroids, and Luvaridae + Zanclidae + Acanthuridae are highly supported. However, Bremer decay index values, show low support for the Drepaneidae + Scatophagidae node: it takes five additional steps to collapse this node.

Approaches 4 and 5 also produced identical results (Fig 4b): a single most-parsimonious tree with the sequence Drepaneidae + Scatophagidae +Ephippidae + restricted acanthuroids (cf. Tang et al. 1999: 422, fig. 5b). This topology is similar to that based on morphology (Tyler et al. 1989, Winterbottom 1993), except that the relative positions of Scatophagidae and Ephippidae are switched. (Winterbottom's [1993] myology study could not resolve the relationship between Scatophagidae and Ephippidae [Fig. 2b]). According to Wiley (pers. com.), the scatophagids are evolving twice as fast as the other acanthuroids, and that this can result in "misleading" parsimony analyses. Without correcting for the differences in rate, the scatophagids tend to be placed near the bottom of the tree, below Ephippidae. Correcting for the differences in rate results in Scatophagidae being placed above Ephippidae.

Relative to the relationships of Drepaneidae, Scatophagidae, and Ephippidae, findings based on molecular data have not fully supported those based on morphological data. In addition, the weakly supported clades listed above do little to elucidate sister-group relationships of the Ephippidae. Tang et al. (1999) demonstrated that the taxa used for rooting significantly affects the topology of relationships among the basal acanthuroids. Choosing Drepaneidae, Scatophagidae, and Ephippidae as the outgroups, resulted in Drepaneidae depicted as the sister group to Scatophagidae. Choosing Drepaneidae as the sole outgroup to the Acanthuroidei, resulted in a topology depicting Scatophagidae as the basalmost acanthuroid.

Choice of Outgroups for Phylogenetic Analyses of the Ephippidae

The choice of outgroups for a phylogenetic analysis of the Ephippidae is somewhat problematic. Although the sister group is usually the best choice for an outgroup (Wiley et al., 1991), there are multiple hypotheses that actually confound sister group relationships (see previous section).

Based on the results of the above-described studies, there are four reasonable options for outgroups: (1) first outgroup acanthuroids (less Ephippidae), second outgroup Drepaneidae (Tyler et al. 1989; Winterbottom 1993); (2) first outgroup Drepaneidae, second outgroup remaining acanthuroids, (Blum 1988); (3) first outgroup Drepaneidae + Scatophagidae, second outgroup restricted acanthuroids (Tang et al. 1999); (4) first outgroup restricted acanthuroids, second outgroup Scatophagidae, third outgroup Drepaneidae (Tang et al. 1999).

The ambiguity involving sister groups of the Ephippidae, combined with the fact that the presence of equivocal characters in the first outgroup (i.e., the sister group) or at the outgroup node could result in confounded analyses (Wiley et al. 1991), necessitated the exploration of various outgroup scenarios. Since there are no unambiguous choices of sister groups and sequential outgroups to the Ephippidae, all outgroup scenarios listed above were explored in multiple constraint analyses. Four additional families long considered by taxonomists to be close relatives of the Ephippidae were also included (i.e., Chaetodontidae, Pomacanthidae, Coracinidae, and Kyphosidae). Chaetodontidae and Pomacanthidae have been hypothesized to be more closely related to the ephippids than have Coracinidae and Kyphosidae (Cockerell 1915, Starks 1926, 1930, Burgess 1978, Blum 1988, Tyler et al. 1989).

The outgroup taxa selected for this study of ephippid relationships comprised the families Siganidae, Luvaridae, Zanclidae, Acanthuridae, Scatophagidae, Drepaneidae, Pomacanthidae, Chaetodontidae, Coracinidae, and Kyphosidae. The 11 families utilized in this study comprise the following numbers of genera and species, respectively (Nelson 1994): Kyphosidae (17, 45), Coracinidae (1, 3), Chaetodontidae (10, 144), Pomacanthidae (9, 74), Drepaneidae (1, 3), Ephippidae (8, 15), Scatophagidae (2, ~4), Siganidae (1, 27), Luvaridae (1, 1), Zanclidae (1, 1), Acanthuridae (6, ~72). In all 11 families, 19 genera, and 36 species were utilized in the construction of the data matrix. Species examined are listed in Appendix I. Of particular importance are the cleared and stained specimens and skeletons, which were used for the examination of internal morphology.

The choice of which taxa to use within two of the outgroups (i.e., Pomacanthidae and Chaetodontidae) was problematic, while in others (i.e., Kyphosidae, Siganidae, Acanthuridae) the choice was based solely on the availability of specimens. No formal cladistic hypotheses of intergeneric relationships are available for the Pomacanthidae. The family is highly diversified, with nine genera and 74 species (Nelson 1994), making choices of the basalmost genera or species difficult. Chaetodontidae is more speciose than Pomacanthidae, with 10 genera and 114 species (Nelson 1994). The only cladistic hypothesis of chaetodontid intergeneric relationships is that of Blum (1988). Unfortunately, his results depict a basal trichotomy between three clades, which he was unable to resolve (Fig. 5).

The lack of clear phylogenetic hypotheses of intergeneric relationships among the Pomacanthidae and the Chaetodontidae, combined with the high numbers of genera within these two families, and the observation that many genera appear to be highly derived, makes the choice of suitable genera for outgroup taxa extremely difficult. In addition, genera chosen at random could inhibit the study if relatively derived taxa were chosen. This is because primitive members of an outgroup have greater influence on hypotheses of ancestral states than those members that are more derived (Maddison et al. 1984). However, concerning polarity decisions and tree topology, the farther removed (i.e., more outgroup nodes) these two families are from the ingroup, the less influence they will exert on polarity decisions (Wiley et al. 1991). Four genera of each family were initially examined. The data matrix was completed using two genera from each family: *Centropyge* and *Holacanthus* (Pomacanthidae); *Forcipiger* and *Chaetodon* (Chaetodontidae) and augmented with others when possible (Appendix I).

Objectives

There were five main goals of this study: (1) produce a phylogenetic hypothesis of intrafamilial relationships of the Ephippidae; (2) examine and confirm the characters supporting monophyly of the Ephippidae (Johnson 1984) for all ephippid species; (3) search for additional characters relevant to the hypothesis of monophyly; (4) describe and illustrate the osteological features used to produce the phylogenetic hypothesis; and, (5) describe and discuss the current and historical zoogeographical distribution for all ephippid genera. The first four goals were accomplished primarily through the examination of the morphology of the ephippids and related fishes and the application of these morphological characters to a formal cladistic analysis. The fifth goal was accomplished by reviewing the literature, summarizing collection records for loan material and calculating probable ancestral areas for the family and various clades.

There were also two minor goals of this study. The first minor goal was to explore the various historical hypotheses of sister-group relationships of Blum (1988), Tyler et al. (1989), Winterbottom (1993), and Tang et al. (1999) using constraint trees (see "Sister-group Relationships). This cursory examination of hypotheses examined various outcomes when the tree is constrained to resemble the various trees found by these authors. It is important to note that only the relationships within the Ephippidae were critically tested in this study. A greatly-expanded data set would be necessary to critically test relationships of all taxa used in this study.

The second minor goal was to examine the descriptions of two extinct ephippid species known from fossils (Blot 1969). This included a comparison between the characters used by Blot (1969) to assign the species to Ephippidae, and those characters used by Johnson (1984) to define the family.

This study of evolutionary relationships of the Ephippidae was facilitated by the fact that 14 of the 15 currently-recognized valid ephippid species were available for loan (some are extremely rare). One species, *Chaetodipterus lippei*, was not available for loan, but radiographs of the two specimens were obtained. Specimens representing the 10 outgroup families were also available, and were cleared and counterstained for examination.

For comparative purposes, representatives of other perciform (suborder Percoidei) families, including some previously hypothesized to be closely related to Ephippidae were included: Moronidae, Serranidae, Centrarchidae, Percidae, Apogonidae, Carangidae, Sciaenidae, Stromateidae, and Sparidae. The use of these additional fishes facilitated comparisons among features as well as helped in the identification of various bones.

MATERIALS AND METHODS

Examination of osteological features was facilitated by the use of dried skeletons, radiographs, and cleared and stained specimens. Selected specimens were cleared and counterstained for bone and cartilage following the procedures of Potthoff (1984) as modified from Dingerkus and Uhler (1977). Specimens were dissected following the procedures of Weitzman (1974): this procedure essentially leaves one half of the fish intact. Whole specimens were used for the examination of external morphology. Gill rakers were counted for all arches on the right side only. Counts are reported as: number of rakers on upper limb + number of rakers on lower limb. In the case of a raker lying on the angle of the arch, the raker was included in the count for the lower limb (Strauss and Bond, 1990). Scale terminology is that of Roberts (1993). The term "supraneural", rather than "predorsal bone" is used in this study to indicate the two or three distinct bones anterior to the dorsal-fin pterygiophores (i.e., spine-supporting elements). Mabee (1988) demonstrated the presence of supraneurals in teleost fishes: these bones are not serial homologues to either pterygiophores or median neural spines, and hence, should not be termed predorsal.

Illustrations were made with the aid of a camera lucida mounted to a Wild M5 stereoscope. Illustrations were scanned using a HewlettPackard ScanJet 4C, and sized, manipulated, and labeled using Adobe Photoshop (version 3.0) and CorelDraw (version 6).

Loan material is listed in Appendix I. In list, "C&S" denotes cleared and counterstained specimens; all others are skeletons (labeled as such) or whole specimens. The cleared and stained specimens represent the minimum number of taxa examined for informative characters. Loan abbreviations used in this thesis are as follows: AMNH (American Museum of Natural History); AMS (Australian Museum); ANSP (Academy of Natural Sciences, Philadelphia); Beltran, B. (Beatriz Beltran-Leon, Instituto Nacional de Pesca y Acuicultura, INPA, Programa de pesca "VECEP", Colombia); BMNH (British Museum [Natural History] Department of Zoology); CSIRO (Commonwealth Science and Industrial Research Organization Division of Fisheries and Oceanography); IORD (Institute of Oceanic Research and Development, Tokai University); LACM (Los Angeles County Museum); MCZ (Harvard University Museum of Comparative Zoology); MNHN (Museue National D'Histoire Naturelle); NMW (Naturhistorisches Museum), NMV (National Museum of Victoria); NRM (Naturhistoriska Riksmuseet); NTM (Northern Territory Museum of Arts and Sciences); OSU (Oregon State University); PMBC (Phuket Marine Biological Center, Thailand); RUSI (J.L.B. Smith Institute of Ichthyology, South Africa); SMNS (Staatliches Museum Für Naturkunde Stuttgart); UCR (University of Costa Rica); USDZ (University of Singapore); USNM (National Museum of Natural History); VIMS (Virginia Institute of Marine Science); ZMB (Universitat Humboldt, Museum fur Naturkunde); and, ZMUC (Kobenhavns Universitet Zoologisk Museum). All acronyms except PMBC are from Leviton et al. (1985, 1988).

Phylogeny construction

Fine-scale anatomical examination of specimens was performed in search of characters that may have phylogenetic significance. Phylogenies were constructed following the cladistic methodology of Hennig (1965), as refined by subsequent authors (e.g., Watrous and Wheeler 1981; Maddison et al. 1984; see Wiley 1981 for review). Character polarity was determined by the outgroup comparison method with ingroup relationships determined by the presence of shared-derived characters (Watrous and Wheeler 1981; Wiley 1981; Maddison et al. 1984).

Ten outgroups were used to determine character polarity. Characters used by Tyler et al. (1989) to elucidate relationships among the restricted acanthuroids (Siganidae, Luvaridae, Zanclidae, Acanthuridae) were not examined. The relationships among the restricted acanthuroids are highly supported and are not in question here (Tyler et al. 1989, Winterbottom 1993, Tang et al. 1999). In addition, many of the characters used to elucidate relationships with the restricted acanthuroids are based on larval morphology, and larvae were not available for the majority of ingroup and outgroup taxa (see "DISCUSSION OF CONSTRAINT TREE ANALYSES").

Although the main objective of the study was to elucidate relationships within the Ephippidae, the nature of the analysis, with multiple outgroups, necessitated the inclusion of some characters that were shared among all ingroup members (i.e., not informative for relationships among the Ephippidae) and one of more of the outgroups (i.e., informative for relationships among Ephippidae and another group. For example, the same character states are held in common among all ephippids and Scatophagidae in characters 2 and 3 (see "RESULTS, Character Descriptions"); the same character states are held in common among all ephippids and the other acanthuroids in characters 11 and 12. Characters that varied within Ephippidae (i.e., potentially offered phylogenetic information) were compared with the outgroup taxa, beginning with Drepaneidae and continuing through all outgroup taxa.

A character matrix was constructed based on the presence or absence of derived characters. Characters in the matrix were grouped by anatomical region rather than the groups that they diagnose (recommended by Johnson, pers. com.). All taxa were examined for all characters. Multiple states exhibited among genera within the same family (e.g., Pomacanthidae and Chaetodontidae) were coded as "missing" and included in the analysis (e.g., Acanthuridae exhibits both possible states for characters 29 and 38). All characters coded as "missing" in the data matrix represent multiple states within the taxon except for character 56 for Coracinidae and Kyphosidae: these taxa were not examined for this character. Analysis of the data matrix and construction of phylogenies was performed using Phylogenetic Analysis Using Parsimony (PAUP; version 3.1.1; Swofford 1993). The data matrix was analyzed using the "Branch and Bound" search option of PAUP. This algorithm identifies all optimal trees given the distribution of characters and taxa. Multiple-state characters were left as unordered in the analyses because I had no *a priori* knowledge of character evolution (e.g., via ontogenetic transformations).

Characters 58 and 59 were weighted by 2 and 11, respectively to reduce the size of the data matrix. These characters, found by Tyler et al. (1989), represent a combined 13 synapomorphies of the restricted acanthuroids (character 59; 11 synapomorphies) and the restricted acanthuroids plus Scatophagidae (Character 58; 2 synapomorphies).

Character transformations and phylogenies were analyzed using MacClade (version 3.0; Maddison and Maddison 1992). Characters were optimized using both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) (Swofford and Madison 1987). The ACCTRAN tracing tends to maximize reversals by focusing on early gains near the root of the cladogram, thus leading to subsequent reversals, whereas the DELTRAN tracing tends to maximize parallelisms by delaying changes away from the root (Madison and Madison 1992). These two *a posteriori* optimizations produce trees with maximally-opposed interpretations of homoplasious character distributions. However, if all of the characters were unambiguous, these optimizations would yield the same results (Wiley et al. 1991). The ACCTRAN optimization was used for this section but the DELTRAN optimization is discussed under "Alternative hypothesis: DELTRAN optimization".

Autapomorphies for terminal taxa were excluded from the data matrix and subsequent analysis: autapomorphies are noninformative for the elucidation of relationships and produce the undesired effect of artificially inflating the confidence interval. Autapomorphies are described in a later section, "Autapomorphies and other features of interest".

Consensus trees, branch support, tree stability and bootstrap

A strict consensus was performed on multiple equally-parsimonious trees. The strict consensus is the most conservative consensus method (Siebert 1992), and is derived by retaining only those clades that are common to all trees being examined. That is, the consensus summarizes all trees and condenses them to a single tree representing all clades completely free from contradictions. However, in all consensus trees, polytomies can be broken down to represent the original trees (Siebert 1992). Consensus trees were used for estimates of branch support.

Branch support is commonly estimated through the examination of branch lengths (i.e., the number of steps); the longer the branch, the greater the hypothesized support. One problem with the use of branch lengths as a measure of support for a clade is that homoplastic characters artificially inflate branch lengths and may impart a false sense of security regarding a branch. To overcome this problem, branch support was also estimated using the methods of Bremer (1994).

Branch support (sensu Bremer) is a measure of the extra length (i.e., steps) required to collapse a branch in the consensus of the near-most-parsimonious trees. The more steps it takes to collapse a branch, the stronger the support for that branch. Although programs are available for the calculation of branch support (e.g., Treerot; Sorenson 1996), for small data sets, such as this one, visual inspection of the consensus trees of steps $s+1$, $s+2$, $s+3$, etc., (s = length of the most parsimonious tree) is all that is necessary to count the number of steps necessary to collapse a branch. One advantage of the branch support procedure over those such as the bootstrap or jack-knife procedures is that this approach is based on the original data and not on data perturbation (Bremer 1994). The bootstrap method, in contrast, results from resampling characters from the original data matrix; the jack-knife method results from sequential deletion of characters from the data matrix.

In addition to support for individual clades, branch support values can be combined to provide a measure of overall tree stability. Tree stability is usually measured in terms of homoplasies (i.e., consistency index) and synapomorphies (i.e., retention index). The consistency index (Kluge and Farris 1969) is the minimum amount of change possible for a character divided by the actual number of changes in the character on the tree. The greater the number of steps above the minimum required to place the characters on the tree, the greater the homoplasy. The consistency index can be artificially inflated with the inclusion of symplesiomorphies and autapomorphies. The retention index (Farris 1988) is a measure of the amount of synapomorphy as determined by comparing the actual amount of homoplasy as a fraction of the maximum possible homoplasy (Siebert 1992). The retention index is (m-o)/m, where m= the maximum possible extra steps, and o= the observed number of extra steps over the minimum. This measure is not influenced by symplesiomorphies or autapomorphies because they do not contribute to homoplasy.

Bremer (1994) proposed a method of measuring tree stability in terms of supported resolution. The total support index is defined as the sum of all branch support values divided by the length of the most-parsimonious tree: [$ti= t/s$], where: ti= total support index; t= total support, the sum of all branch support values (*b*) over the tree; and *s*= the length of the most-parsimonious tree. Branch support values (*b*) cannot exceed branch length, and total support (*ti*) cannot exceed the sum of all branch lengths (*s*) (Bremer 1994). Therefore, in the case of a completely unresolved polytomy, total branch support= 0, and the total support index= 0. In the case of a most-parsimonious tree with no homoplasy, total branch support= the sum of the branch lengths, and the total support index= 1. Bremer (1994) showed that there is some correlation between the retention index and the total support index, but that, depending on the data set, the total support index may differ widely from the retention and consistency indices because these indices measure different properties of the data than does the total support index.

A bootstrap analysis was performed as an additional indication of branch support (Felsenstein 1985). As mentioned above, the bootstrap method involves data perturbation, utilizing the data in a different manner than the total support index. Simply, the bootstrap method randomly samples the character matrix with replacement, building a new data matrix of the same size as the original. A most parsimonious tree is generated from the new data matrix. These simulated data sets are generated at least 100 times. Partitions found in one or more trees and their frequency of occurrence are tallied. The percentage of occurrence for each partition can be considered an estimate of support; the higher the percentage, the greater the support. Only those partitions with greater than 50% support are shown. The bootstrap, which involves data perturbation, is a statistical measure of the internal consistency of the data. That is, it is a measure of the amount of support offered by that particular data set. The addition of more data could change a well-supported branch found in this analysis. Nonetheless, a bootstrap analysis can offer insight into the data. Bootstrap values were calculated using the "Heuristic" search option and 1000 bootstrap replications (PAUP; version 3.1.1; Swofford 1993).

Area cladograms

Ancestral areas were estimated using Bremer's (1992) ancestral area analysis. Simply described, Bremer's ancestral area analysis is performed by mapping the distributions of the extant taxa on the cladogram (thereby producing an "area cladogram"), treating each area as a binary character (i.e., present or absent), and then optimizing each area character on the cladogram as in typical cladistic analysis. Areas are optimized using both forward- and reverse Camin-Sokal parsimony (i.e., allowing for only gains and losses, with no reversibility, respectively). The number of gains (G) and losses (L) are tallied per area in a table. The number of gains and losses by themselves offer nothing definitive regarding the locations of the ancestral areas. However, the gain/loss (G/L) quotient can be used to assign relative probabilities that each area was part of the ancestral area. The higher the value of G/L, the higher the probability that the area was part of the ancestral area. The G/L quotient can be rescaled for easier comparisons. This rescaled quotient (AA: estimated ancestral area) for each area is calculated by dividing each G/L quotient by the largest G/L quotient from the cladogram.

Bremer's (1992) ancestral area analysis is similar to the center of origin concept (descendents dispersed from a small geographical area) except that it does not constrain the place of origin to "a single spot" or an area smaller than the distributions of extant taxa. In Bremer's method, vicariance is not completely excluded; taxa can still spread out from an area after a vicariant event, but vicariance usually implies that the ancestral area is much closer to the size of the present distribution than does the center of origin concept (Bremer 1992). For detailed descriptions of 13 historical theories on biogeography, see Rosen (1988).

RESULTS

Character Descriptions

The following characters were compiled from both my own examination of specimens and the literature discussed above. Characters in bold were found in this study or first described by another author but amended here. Characters were grouped by anatomical region and are discussed below in numerical order. Each character description contains the derived state (in italics), a description of each state if the character has multiple states, a contrast between the derived and primitive states, and reference to pertinent literature. The associated data matrix comprises 18 taxa and 59 characters (Table 2). For ease of locating characters, the derived condition is summarized in Table 3.

The terms "derived" and "primitive" are relative terms: characters that are identified as "derived" may be identified as "primitive" in subsequent analyses if different outgroups are used. The labeling of some characters below as "derived" may seem somewhat arbitrary, but bear in mind that the term is relative to the group being discussed. In some characters (e.g., characters 11 and 12), the derived condition represents that the condition present in a group that includes the ephippids (i.e., the Acanthuroidei), and therefore, relative to the ephippids, the condition is primitive, but relative to fishes outside of the Acanthuroidei, the condition is derived. The analyses are not changed by changing the designation of the various character states.

1. ***Majority of primary ramus of premaxilla cancellous, with deep, tubular hollows oriented vertically.***

Derived condition: In Scatophagidae and all ephippids except *Rhinoprenes*, the primary ramus is cancellous along its entire length with deep, tubular hollows oriented vertically. In *Parapsettus, Platax*, and *Tripterodon*, the tubular hollows are located in a deep trough within the primary ramus (Fig. 6a). In the other ephippids and Scatophagidae, the hollows are flush with the dorsal surface of the primary ramus (Fig. 6b).

Other conditions: Three taxa (i.e., *Rhinoprenes*, Drepaneidae, Siganidae) possess premaxillae with reduced cancellous areas. In *Rhinoprenes*, the distal third of the premaxilla is not cancellous; this portion of the bone is reduced to a filamentous rod (narrow and toothless) (Fig. 6c). In Drepaneidae, only the basal half of the primary ramus is cancellous; the distal portion of the bone is not reduced as in *Rhinoprenes*. In Siganidae, less than one quarter of the primary ramus is cancellous, and the cancellations are present in a narrow band. In the other acanthuroids as well as the other outgroup taxa, the premaxilla is not cancellous.

2. ***Vertical lamina between the articular and ascending processes of the premaxilla.***

Derived condition: In Scatophagidae, all ephippids, and Kyphosidae, a vertically-extending lamina extends between the articular process and the ascending process of the premaxilla. It is somewhat variable, ranging from a lamina that is dorsally expanded, terminating just below the distal tip of the ascending process (*Ephippus* and *Tripterodon*; Fig. 7a) to a roughly triangular-shaped lamina that extends from the articular process to a position about midway up the ascending process (Scatophagidae, Kyphosidae, and the remaining ephippids; Fig. 7b).

Other conditions: The lamina is absent in the remaining taxa (e.g., Fig. 7c).

3. ***Distal end of premaxilla narrow and recurved.***

Derived condition: The distal end of the premaxilla of scatophagids and all ephippids (except *Rhinoprenes*) is narrow and recurved, with the tip extending ventrally to anteroventrally. In *Chaetodipterus, Tripterodon*, and *Zabidius* the distal tip is extremely recurved, with the tip extending anteroventrally (Figs. 7a, b). In the other ephippids (except *Rhinoprenes*), the distal tip extends ventrally. The condition is reduced but present in Scatophagidae, with only the extreme distal tip being recurved.

Other conditions: The distal end of the premaxilla of *Rhinoprenes* is greatly reduced, extremely narrow, and pointed (Fig. 6c). In *Drepane* and at least one chaetodontid (*Heniochus*), the distal end of the premaxilla is expanded and recurved both ventrally and dorsally (i.e., anchor-shaped) (Fig. 7c). In the other chaetodontids examined, as well as the restricted acanthuroids and all other outgroup taxa, the distal end of the premaxilla is straight.

4. ***Presence of a medially-positioned maxillary arch.***

Derived condition: In *Chaetodipterus, Platax,* and *Tripterodon*, the maxilla possesses a medially-positioned bony arch. This arch extends dorsolaterally to ventromedially, with the dorsal end originating ventral to the point of articulation with the palatine (Fig. 8a).

Other conditions: All other taxa examined lack an arch associated with the maxilla (Fig. 8b). *Zabidius* possesses a bony apophysis on the ventromedial surface of the maxilla, which could be interpreted as a reduced or incomplete arch, but was coded as absent.

5. ***Absence of distinct transverse fold over upper lip.***

Derived condition: In *Rhinoprenes, Parapsettus,* and Luvaridae there is an absence of a distinct transverse fold (i.e., frenum) over the upper lip.

Other conditions: In all other taxa examined, the distinct transverse fold is present.

6. *Length of ascending process of premaxilla less than length of alveolar process* (Rosen 1984).

Derived condition: In all acanthuroids, as well as Pomacanthidae, the length of the ascending process of the premaxilla is less than the length of the alveolar process (e.g., Figs. 6a-c, 7a,b). It is somewhat variable, with *Rhinoprenes* possessing an extremely short ascending process, and Zanclidae and Pomacanthidae possessing ascending processes that are slightly shorter (almost equal in lengths) than the alveolar processes.

Other conditions: In all other taxa examined, the ascending process is longer than the alveolar process (e.g., Fig. 7c).

7. ***Presence of relatively widely-separated bands of teeth in jaws.***

Derived condition: Widely-separated bands of teeth are present in the ephippids *Platax*, *Zabidius*, and *Tripterodon*, as well as Zanclidae (e.g., Fig. 9a). In these taxa, there are obvious distinct bands of teeth.

Other conditions: In all other ephippids, Drepaneidae, Chaetodontidae, Pomacanthidae, and Kyphosidae, the teeth are closely applied and bands are not easily differentiated. The bands are more noticeable by examining the tooth pedestals (Fig. 9b). In Siganidae, Luvaridae, Acanthuridae, and Coracinidae, only one row of teeth is present (coded as "absence of the derived condition").

Blum (1988) discussed the unique possession of a wave-like tooth replacement pattern in pomacanthids and chaetodontids (his character 9 in outgroup analysis: "Tooth replacement occurs in waves"; and character 18 in ingroup analysis; [cf. Blum 1988: 29, 142]). These two families exhibit a wave-like tooth-replacement pattern such that within each band of teeth, new teeth are added to each row posterolaterally, while older teeth are lost anteromedially. As teeth are lost and gained, the band appears to move posterolaterally. Although this is the case for chaetodontids and pomacanthids, Blum misinterpreted the condition in ephippids, drepaneids, and acanthurids. These three families also exhibit tooth replacement in a wave-like pattern, but the pattern is not as prominent. In chaetodontids and pomacanthids, there are distinct bands of teeth separated by gaps. These gaps are formed by immature, non-functioning teeth, developing between bands of mature teeth on pedestals (i.e., the tooth pedestals from different bands do not come in close contact with one another). Each band may have two or more overlapping rows of teeth (cf. Blum 1988: 148, 152, figs. 25 and 26 B, respectively). In Drepaneidae and all ephippids except *Platax*, *Zabidius*, and *Tripterodon*, the tooth rows are in close contact with one another and there is little or no separation between tooth pedestals of different bands (i.e., rows are compacted together both laterally and anteroposteriorly). Nonetheless, tooth replacement follows the same pattern as described by Blum for Pomacanthidae and Chaetodontidae.

Blum also misinterpreted the amount of overlap among rows of teeth. By Blum's account, tooth rows in chaetodontids are positioned such that there are always at least three rows of teeth overlapping within each band: there are actually only two overlapping rows in some genera (cf. Blum 1988: 148, 161, figs. 25a,b, 28b,d, respectively). Since Blum did not notice the bands of teeth in ephippids, he did not notice that there are many overlapping rows of teeth; there is simply no separation in bands.

8. ***Presence of tricuspidate teeth.***

Derived condition: Tricuspidate teeth are present in Pomacanthidae, Scatophagidae, and the ephippids *Platax*, *Proteracanthus*, *Rhinoprenes*, *Tripterodon*, and *Zabidius*. The percentage of tricuspidate teeth in the mouth varies from all teeth in all bands being tricuspidate (*Proteracanthus* and Scatophagidae) to all bands of teeth tricuspidate except the lingualmost band which possesses unicuspidate teeth (the other taxa mentioned above). The length of the middle cusp relative to the middle cusps also varies among taxa. In all the above-listed taxa except Pomacanthidae, the middle cusp is at most four times the length of the lateral cusps. In Pomacanthidae, the middle cusp extends far beyond the lateral cusps (i.e., middle cusp greater than 10 times the length of the lateral cusps). *Rhinoprenes* is the only taxon examined that possesses tricuspidate teeth in the lower jaw only; the upper jaw possesses unicuspidate teeth. In the character matrix (Table 2), presence of tricuspidate teeth in one jaw was coded as 1; presence of tricuspidate teeth in both jaws was coded as 2.

Other conditions: In all other taxa examined except Siganidae, all teeth are unicuspidate. However, the shape of the teeth does vary among taxa. In *Chaetodipterus, Ephippus, Parapsettus*, Drepaneidae, Coracinidae and Kyphosidae, the teeth are relatively stout. In Luvaridae, the teeth are relatively small and narrow. In Chaetodontidae, the teeth are all approximately the same size, elongate and filiform. In Acanthuridae, each tooth is serrated laterally with the number of serrations approximately 7-15. In Zanclidae, the labial row consists of teeth that are laterally flattened, while the lingual row consists of narrow, elongate conical teeth. Siganidae possesses non-symmetrical bicuspidate teeth, with the cusp on the medial side of the tooth being much larger on the lower jaw and the cusp on the lateral side being much larger on the upper jaw.

9. ***Reduction in the number of teeth.***

Derived condition (counts are approximate and may vary within a species): In *Platax, Proteracanthus, Rhinoprenes, Tripterodon, Zabidius,* Scatophagidae, the restricted acanthuroids, and Coracinidae, there is a reduction in the number of teeth associated with each jaw. In all taxa except the restricted acanthuroids and Coracinidae, there are between 35 and 75 teeth associated with each jaw (Table 4) (coded as 1 in the character matrix). In the restricted acanthuroids and Coracinidae, there is a further reduction in the number of teeth: less than 16 teeth associated with each jaw (coded as 2 in the data matrix). Siganidae, Luvaridae, and Zanclidae exhibit the greatest reduction with less than 10 teeth associated with each jaw.

Other conditions: In *Chaetodipterus, Ephippus,* Drepaneidae, Chaetodontidae, and Kyphosidae, there are greater than 100 teeth associated with each jaw (between 106 and 270 teeth; Table 4). *Parapsettus* appears to exhibit an intermediate condition, with differing numbers of teeth between jaws (120 in upper jaw, 84 in lower jaw; coded as "0").

10. ***Reduction in the number of bands of teeth.***

Derived condition: In all ephippids (except *Chaetodipterus* and *Ephippus,*), as well as Scatophagidae, the restricted acanthuroids, Pomacanthidae, and Coracinidae, there is a reduction in the number of bands of teeth. In all ephippids (except *Chaetodipterus* and *Ephippus*), Scatophagidae, and Pomacanthidae, and Zanclidae, there are less than six bands of teeth (but always at least two bands) (coded as 1 in the character matrix [Table 2]). In three members of the restricted acanthuroids, Siganidae, Luvaridae, and Acanthuridae, as well as Coracinidae, there is a further reduction in the number of bands of teeth to a single band (coded as 2 in the character matrix).

Other conditions: There are six or more bands of teeth in Kyphosidae, Chaetodontidae, Drepaneidae, *Chaetodipterus*, and *Ephippus*.

11. *Premaxillae non-protrusible and maxillae and premaxillae move relatively little* (Tyler et al. 1989).

Derived condition: In all acanthuroids, as well as Kyphosidae, the premaxillae are non-protrusible and are relatively tightly bound to the maxillae, resulting in little independent movement of the bones.

Other conditions: In Drepaneidae, Pomacanthidae, Chaetodontidae, and Coracinidae, the premaxillae and maxillae are both capable of extensive protrusion and functioning relatively independently.

12. *Length of articular less than or equal to length of dentary* (Tyler et al. 1989)

Derived condition: In all taxa examined except Drepaneidae, Pomacanthidae, Chaetodontidae, and Kyphosidae, the length of the articular is less than or equal to the length of the dentary (cf. Tyler et al. 1989: 54, fig. 38).

Other conditions: In Drepaneidae, Pomacanthidae, Chaetodontidae, and Kyphosidae, the length of the articular is much longer than the length of the dentary (cf. Tyler et al. 1989: 53, fig. 37).

13. ***Presence of a medially-projecting subocular shelf on infraorbital III.***

Derived condition: A medially-projecting subocular shelf on infraorbital III is present in *Ephippus, Platax, Tripterodon, Zabidius,* Scatophagidae, Zanclidae, Pomacanthidae, Chaetodontidae, Kyphosidae, Coracinidae (e.g., Figs. 10a-e). The subocular shelves of *Ephippus* and *Tripterodon* are relatively smaller in size than in the other taxa (not evident in Figs. 10a, b due to the perspective of the illustration). Kyphosidae and Coracinidae possess an additional subocular shelf on infraorbital IV.

Other conditions: In all other taxa examined, the third infraorbital does not possess an associated medially-projecting subocular shelf (e.g., Figs. 11a-e). Drepane punctata possesses a vertically-extending lamina rather than a horizontal shelf. Luvaridae possesses a greatly reduced infraorbital series which consists of the lachrymal and a small bone located ventral to the eye. Tyler et al. (1989) hypothesize this small bone to be the vestige of a subocular shelf associated with subocular III.

14. ***Posteriormost infraorbital closely articulates with the preceding infraorbital.***

Derived condition: In *Platax, Zabidius, Parapsettus, Rhinoprenes,* Chaetodontidae, Coracinidae, and Kyphosidae, the posteriormost infraorbital closely articulates with the preceding infraorbital, with flanges on these bones overlapping (e.g., Figs. 10c,d and 11b,c).

Other conditions: In all other taxa examined, there is a clear separation between these two bones (e.g., Figs. 10a, b, e and 11a, d, e). Two exceptions to this are in Acanthuridae and Pomacanthidae. In *Ctenochaetus* (Acanthuridae), the infraorbital bones come in contact with one another, but do not overlap. The infraorbitals of *Acanthurus* (Acanthuridae) are separate from one another. In the pomacanthids examined, two genera (i.e., *Pomacanthus, Holacanthus*) possess infraorbitals that are separate from one another and one (*Centropyge*) exhibits the derived condition. This equivocal condition within Pomacanthidae was coded as "missing".

15. ***Longitudinal edge of the lachrymal lies in the projected path of the infraorbital ring.***

Derived condition: In *Parapsettus, Proteracanthus,, Rhinoprenes,,* Siganidae, Zanclidae, Kyphosidae, and Coracinidae, the main body of the lachrymal (i.e., longitudinal edge) is oriented in the same path as the infraorbital ring (e.g., Figs. 11b-d). *Proteracanthus* exhibits a unique condition in that the lachrymal is highly hyperossified and is greatly enlarged relative to the other taxa (Fig. 11d).

Although not easily illustrated, the lachrymal of *Proteracanthus* is expanded medially resulting in the bone being bean-shaped and about half as wide as it is deep. The lachrymals of the other taxa are platelike or laminar.

Other conditions: In all other taxa examined, the main body of the lachrymal lies approximately perpendicular to the infraorbital ring (Figs. 10a-e and 11a, e). In addition, there is an elongate branched sensory canal in all genera with the primitive condition.

16. *Interopercle distinctly shaped* (Tyler et al. 1989).

Derived condition: In all acanthuroids, the interopercle is distinctly shaped, with a broad posterior portion and a narrow anteriorly-extending portion, either as bone (Scatophagidae, Siganidae, Luvaridae, Zanclidae, Acanthuridae) or as a narrow, ligamentous band (Ephippidae) (cf. Tyler et al. 1989: 53, fig. 37).

Other conditions: In Drepaneidae, Pomacanthidae, Chaetodontidae, Kyphosidae, and Coracinidae, the interopercle is roughly ovoid in shape, without any anterior projections (cf. Tyler et al. 1989: 54, fig. 38).

17. ***Posterior ramus of the palatine extends posteriorly and terminates dorsal to the mesopterygoid.***

Derived condition: In *Platax, Zabidius, Tripterodon*, and Kyphosidae, the posterior ramus of the palatine extends posteriorly and terminates dorsal to the mesopterygoid (Figs. 12a,b). That is, there is some portion of the mesopterygoid that is ventral to the palatine.

Other conditions: In the other ephippids examined, as well as all other taxa, the posterior ramus of the palatine does not terminate dorsal to the mesopterygoid, and the dorsal edges of these two bones are in the same plane (Fig. 12c).

18. ***Mandibulo-preopercular sensory canal in angular horizontally oriented.***
Derived condition: In Coracinidae and all acanthuroids except Acanthuridae, the portion of the mandibulo-preopercular sensory canal that passes through the angular is short, horizontally oriented, with the canal openings in the same plane. There is a slight modification in *Tripterodon*, in which the canal is greatly reduced in length and the anterior opening is oriented ventroanteriorly.

Other conditions: In Drepaneidae, Chaetodontidae, Pomacanthidae, and Kyphosidae, the mandibulo-preopercular canal is not horizontally-oriented: it extends dorsoanteriorly to ventroposteriorly. In *Acanthurus* (Acanthuridae), the canal is "s"-shaped, extending ventroanteriorly to dorsoposteriorly. In *Ctenochaetus* (Acanthuridae), the canal extends ventrally to dorsoposteriorly.

19. *Large, comblike series of blunt rakers loosely associated with the anterior margin of the broadened first epibranchial.* (Johnson 1984)
Derived condition: All adult ephippids possess rakers that are closely applied to one another, wide, and blunt (Figs. 13a-c). These rakers vary in shape and

proximity to one another: from relatively large, rounded, and not closely applied (e.g., *Proteracanthus* and *Parapsettus*) to relatively narrow, flat and extremely closely applied (e.g., *Platax*; some species with the distal rakers overlapping via laminate flanges. Ephippid larvae (*Platax*, *Chaetodipterus*) and small juveniles (*Platax*, *Chaetodipterus*, *Parapsettus*) possess rakers that resemble those of the outgroup, although they are more closely spaced. A change in raker morphology from early juvenile to adult most likely corresponds to a change in diet.

Other conditions: Non-ephippids possess rakers on the first epibranchial that are widely separated, narrow, and pointed (Fig. 13d).

20. ***Fourth pharyngobranchial (PB4) elongate and completely overlays the dorsal surface of the upper toothplate of the fourth branchial arch (UP4).*** Derived condition: In all ephippids, as well as Zanclidae, the fourth pharyngobranchial (PB4) is elongate and completely overlays the dorsal surface of the upper toothplate of the fourth branchial arch (UP4). In addition, the fourth epibranchial (E4) articulates with PB4 via loose connective tissue at the midpoint of PB4 (Figs. 14a, b), and the third epibranchial (E3) is in closer contact with PB4 than PB4 is with E4. The largest variation seen in this character is in the length of PB4, with *Proteracanthus* possessing the longest PB4, relatively.

Other conditions: In all other fishes examined, PB4 does not completely overlay the dorsal surface of UP4. In addition, E3 is usually in close contact with UP3, and PB4 is in close contact with E4. The shape and size of PB4 is variable, ranging from relatively short and narrow (Chaetodontidae, Pomacanthidae) to elongate and wide (e.g., Zanclidae, Acanthuridae). The PB4 of Zanclidae is relatively large and covers all but the dorsolateral side of UP4. Among the taxa examined, Drepaneidae is unique among these fishes in that PB4 inserts into a socket in UP4, and PB4 is closely applied to E4 (Fig. 14c).

21. *Reduction or absence of the basihyal* (Johnson 1984).

Derived condition: In all ephippids, the basihyal is either reduced or absent. In *Chaetodipterus, Ephippus, Parapsettus, Zabidius*, and *Tripterodon*, the basihyal is reduced to a short, ossified, and either stout or pear-shaped (Fig. 15a). The basihyal is reduced to a cartilaginous cap in some *Platax* species (i.e., *P. batavianus* and *P. pinnatus*) (Fig. 15b), and absent in others (e.g., *P. teira*). The basihyal is also absent in *Proteracanthus* and *Rhinoprenes*. The length of the basihyal may be, in part, a modification of a suite of characters related to feeding (e.g., overall oral cavity size, non-protrusive premaxillae and maxillae, gape size).

Other conditions: In all non-ephippids examined, the basihyal is elongate and slender (Fig. 15c). This character, as discussed by Johnson (1984) ("the absence or reduction of the basihyal buried in thick connective tissue") was altered by Blum (1988). Blum hypothesized a sister-group relationship between *Drepane* and Ephippidae based on the presence of thick connective tissue surrounding the basihyal. However, Blum omitted all discussion of the basihyal which is elongate and narrow in *Drepane*, unlike in Ephippidae.

22. *Absence of an interarcual cartilage* (Johnson 1984) *or* ***presence of a greatly reduced interarcual cartilage.***

Derived condition: Johnson (1984) used the absence of the interarcual cartilage as one of the synapomorphies to hypothesize the monophyly of the Ephippidae. Tyler et al. (1989) later found this character to be a synapomorphy of the Acanthuroidei. In all acanthuroids, except *Platax*, *Zabidius*, and Luvaridae, the interarcual cartilage is absent. In *Platax* and *Zabidius*, a reduced interarcual cartilage is present. In some specimens (e.g., *P. orbicularis*, *P. boersii*, *P. batavianus*) the interarcual cartilage is greatly reduced in length and girth relative to non-acanthuroids. In others (e.g., *P. teira*, *Z. novemaculeatus*) it is further reduced and resembles a small cartilaginous ball suspended in transparent connective tissue between the two bones (Fig. 13a). This character was coded as "missing" in *Platax* because of the presence of two states (i.e., equivocal) within the genus.

Other conditions: In all other taxa examined, the interarcual cartilage is large and provides structural support between the first epibranchial and the second pharyngobranchial (Fig. 13d). Tyler et al. (1989) erroneously stated that *Luvarus* lacks the interarcual cartilage; two of their figures depict the presence of the interarcual cartilage (cf. Tyler et al. 1989:15 and 16, figs. 9 and 10, respectively).

23. *Elongate first pharyngobranchial* (Johnson 1984)

Derived condition: This character was described by Johnson (1984), although he did not mention the condition in *Proteracanthus*. All ephippids except

Proteracanthus possess a relatively elongate first pharyngobranchial (Figs. 13a,c). That is, when the first pharyngobranchial is laid down on top of the other pharyngobranchials, it extends beyond them and the associated arches.

Other conditions: In all other taxa examined, as well as *Proteracanthus* , the first pharyngobranchial extends to approximately the third pharyngobranchial (e.g., Fig. 13d).

24. ***Presence of microbranchiospines.***

Derived condition: Microbranchiospines, which are small, dermal ossifications located at the base of the gill arches, are present in the ephippids *Chaetodipterus, Parapsettus, Platax, Proteracanthus*, and *Zabidius*, as well as Scatophagidae and Drepaneidae. The relative sizes of the patches of microbranchiospines are variable. In *Chaetodipterus, Proteracanthus, Parapsettus*, and Scatophagidae, the microbranchiospines are present in long patches on the anterior and posterior sides of at least the first three ceratobranchials. In *Platax* , *Zabidius*, and Drepaneidae, they form minute, isolated patches.

Other conditions: Microbranchiospines are absent in all other taxa examined (examined one small specimen representing Siganidae; microbranchiospines may be present in larger specimens).

25. ***Blunt, "bean-shaped" rakers associated with the anterior margin of the third ceratobranchial (CB3) and third hypobranchial (HB3).***

Derived condition: Blunt, "bean-shaped" rakers are associated with the anterior margin of the third ceratobranchial (CB3) and third hypobranchial (HB3) in the ephippids *Ephippus, Platax, Rhinoprenes, Tripterodon*, and *Zabidius*, as well as Zanclidae. These blunt rakers associated with the anterior margins of CB3 and HB3 are wider and rounder than other rakers associated with the arches (Fig. 16a).

Other conditions: In all other taxa examined, the rakers associated with CB3 and HB3 are similar in shape and size to all other rakers on the branchial arches (excluding those on the first epibranchial in ephippids); these rakers are somewhat flattened, triangle-shaped, with tooth arrangements that are somewhat tuft-like (Fig. 16b).

26. *Gill filaments free from epibranchials.*(Johnson 1984)

Derived condition: In Siganidae, Zanclidae, Acanthuridae, and all ephippids except *Rhinoprenes*, the gill filaments are free from the epibranchials. In these fishes, each row of gill filaments extends posteriorly from the associated distal end of the ceratobranchial with only a slight dorsal curvature. *Parapsettus* is unusual in that each row of gill filaments extends dorsomedially at approximately a 45-degree angle.

Other conditions: In all other taxa examined, each row of gill filaments curves sharply around the end of the associated ceratobranchial and extends onto the associated epibranchial. The filaments extend at least over the proximal portion of the epibranchial.

27. *Absence of a fontanel in the ceratohyal* (Rosen 1984).

Derived condition: In the restricted acanthuroids, some chaetodontids (e.g., *Heniochus acuminatus, Forcipiger flavissimus, Chaetodon sedentarius*), and *Proteracanthus*, the ceratohyal does not possess a fontanel.

Other conditions: In all other taxa examined, the ceratohyal possesses a fontanel. The chaetodontid, *Chaetodon trifasciatus*, possesses a fontanel: the presence of both the derived and primitive conditions in Chaetodontidae was interpreted as equivocal and coded as "missing" in the data matrix.

28. ***Ceratohyal firmly attached by connective tissue to dorsal and ventral hypohyals***.

Derived condition: In all ephippids, Siganidae, Luvaridae, Acanthuridae, and at least two chaetodontids (*Chaetodon sedentarius, C. trifasciatus*) the ceratohyal is connected to both the dorsal and ventral hypohyals via dense connective tissue. In the majority of taxa, the ceratohyal is stout along the anterior edge and it abuts the dorsal and ventral hypohyals. In some taxa (e.g., *Ctenochaetus* [Acanthuridae]), the ceratohyal (ventral half only) abuts only the dorsal hypohyal. In others (e.g., *Acanthurus* [Acanthuridae]) the ceratohyal is not stout but is rigidly attached to the dorsal and ventral hypohyals and is capable of little movement. The amount of movement capable between the ceratohyal and hypohyals varies from a small amount (e.g., *Rhinoprenes* and *Parapsettus*) to no movement (e.g., all other ephippids). This character was described, in part, by Blum (1988) (his character 26 in outgroup analysis: "ceratohyal - hypohyal joint"). Blum believed this character to be unique to ephippids, but it is present outside of the family.

Other conditions: In Scatophagidae, Zanclidae, Drepaneidae, Pomacanthidae, Coracinidae, Kyphosidae, and at least two chaetodontids (e.g., *Forcipiger flavissimus, Heniochus acuminatus*) the ceratohyal is laminar and is capable of extensive movement lateral to the dorsal and ventral hypohyals. The presence of both the derived and primitive conditions in Chaetodontidae was interpreted as equivocal and coded as "missing" in the data matrix.

29. ***Distal tips of anterior dorsal-fin pterygiophores not buttressed by bony flanges on anterior side of the posteriorly-associated neural spines.***

Derived condition: In all ephippids (except *Chaetodipterus* and *Proteracanthus*), Siganidae, Luvaridae, Zanclidae, and at least two acanthurids (e.g., *Naso* and *Acanthurus* spp.), the distal tip of each anteriorly-positioned dorsal-fin pterygiophore is not buttressed by bony flanges located on the anterior side of the neural spine positioned posteriorly to this pterygiophore. This condition is somewhat variable. In all ephippids (except *Chaetodipterus* and *Proteracanthus*), the distal ends of the dorsal-fin pterygiophores do not come in contact with the associated neural spines located posteriorly. In Siganidae, the third pterygiophore rests against the neural spine located anteriorly but does not insert into flanges . In Zanclidae, the distal end of the third pterygiophore touches the neural spine located posteriorly and a minute portion of the posterior edge of the pterygiophore is covered by bony flanges extending from the posterior neural spine (e.g., Zanclidae).

Other conditions: In all other taxa examined, the distal tip of at least one anterior dorsal-fin pterygiophore inserts between bony flanges of the posteriorly-located neural spine and is buttressed by these flanges (Fig. 17). This condition is variable among taxa. In *Chaetodipterus*, Drepaneidae, Scatophagidae, *Centropyge bicolor* (Pomacanthidae), *Forcipiger flavissimus*, and Kyphosidae, only the third dorsal-fin pterygiophore inserts into bony flanges. In *Ctenochaetus* (Acanthuridae), only the second dorsal-fin pterygiophore inserts into bony flanges. In *Proteracanthus* and Coracinidae, pterygiophores 3-5 insert into bony flanges. In *Holacanthus tricolor* (Pomacanthidae) several pterygiophores insert into flanges.

30. ***Absence of a vacant interneural space associated with the precaudal vertebrae* (excluding the first interneural space; see character 36).**

Derived condition: In the ephippids *Platax*, *Zabidius*, and *Rhinoprenes*, as well as Luvaridae, Chaetodontidae, Kyphosidae, and Coracinidae, at least one dorsal-fin pterygiophore interdigitates between each pair of neural spines (i.e., absence of a vacant interneural space anteriorly on the body) (Table 5).

Other conditions: In all other taxa examined, a vacant interneural space is present. The position of the vacant interneural space is variable. In Zanclidae and Acanthuridae, interneural space III is vacant. In Drepaneidae, interneural space V is vacant. In *Forcipiger* (Chaetodontidae), interneural space VII is vacant. In Scatophagidae, interneural spaces VI or VII are vacant.

31. ***Presence of minute vertically-oriented bony striations on the main ramus of the anterior dorsal- and anal-fin pterygiophores and basal portions of the anterior dorsal- and hemal spines.***

Derived condition: In all ephippids (except *Proteracanthus* and *Rhinoprenes*), as well as Drepaneidae and Coracinidae, the main ramus of the anterior dorsal- and anal-fin pterygiophores possesses minute vertically-oriented bony striations (e.g,. Fig. 17).

Other conditions: In all other taxa examined, the anteriormost pterygiophores and dorsal- and hemal spines are smooth along their main rami (e.g., Fig. 18). This condition is somewhat variable. In all taxa except Luvaridae and Kyphosidae, striations are absent from all of these bones. In Luvaridae, there appear to be small striations at the distal end of the first pterygiophore and basally on the anterior hemal spines. This condition may be ontogenetic as it is not mentioned (or illustrated) in the larger specimens examined by Tyler et al. (1989). In Kyphosidae, minute striations are present on the first anal-fin pterygiophore only.

32. ***Proximal radials of soft dorsal- and anal fins with symmetrical diamond-shaped heads*** (Rosen 1984).

Derived condition: In all ephippids (except *Proteracanthus* and *Rhinoprenes*) (variously in *Ephippus* and *Zabidius*), as well as Scatophagidae and Drepaneidae, the proximal radials of the soft dorsal- and anal fins possess symmetrical diamond-shaped heads (cf. Rosen 1984:15, fig.15b). This condition is variable ranging from the majority of proximal radials with symmetrical diamond-shaped heads (e.g., *Chaetodipterus*) to only the posteriormost proximal radials being symmetrical (e.g., Drepaneidae). Variation is seen within the genera *Ephippus* and *Zabidius*, with some specimens possessing symmetrical heads posteriorly, and others with no symmetrical heads at all. This equivocal condition was coded as "missing" in the data matrix.

Other conditions: In all other taxa examined, except Zanclidae, the proximal radials of the soft dorsal- and anal fins are asymmetrical (e.g., Siganidae; Rosen 1984:7, fig. 4). In Zanclidae, the proximal radials are symmetrical but are box-shaped rather than diamond-shaped.

33. ***Presence of middle radials associated with soft dorsal- and anal-fin pterygiophores.***

Derived condition: In the ephippids *Chaetodipterus, Ephippus*, and *Tripterodon*, as well as Coracinidae and Kyphosidae, middle radials are associated with the soft dorsal- and anal-fin pterygiophores (cf. Rosen 1984: 15, fig. 15a).

Other conditions: In all other taxa examined, the soft dorsal- and anal-fin pterygiophores lack middle radials (cf. Rosen 1984: 15, fig. 15b).

34. ***First two supraneurals do not extend ventrally beyond the distal tip of the first neural spine.***

Derived condition: The first two supraneurals are relatively short and do not extend beyond the distal tip of the first neural spine. This condition is exhibited by the ephippids *Ephippus, Platax, Tripterodon*, and *Rhinoprenes*, as well as Scatophagidae (e.g., Fig. 19a).

Other conditions: In all other ephippids, as well as Drepaneidae, Coracinidae, Kyphosidae, and at least one chaetodontid (i.e., *Forcipiger flavissimus*), the first two supraneurals are relatively elongate and extend beyond the tip of the first neural spine (e.g., Figs. 17, 19b,c). Zanclidae and Pomacanthidae (*Centropyge* and *Holacanthus*) possess only one supraneural, which is relatively elongate and extends beyond the first neural spine. Supraneurals are absent in Siganidae, Luvaridae, and the acanthurids *Naso, Acanthurus*, and *Ctenochaetus*. The acanthurid *Prionurus* possesses a single supraneural that does not extend beyond the first neural spine (coded as a primitive condition in the data matrix). If the possession of at least one short supraneural represented the derived condition, then *Prionurus* would exhibit the derived condition, and optimization at the acanthurid node would be equivocal: this would not change optimization at the restricted acanthuroid node.

35. ***Dorsal-fin spines sequentially increase in length.***

Derived condition: Dorsal-fin spines sequentially increase in length, with the posteriormost spine being the longest. This condition is exhibited by the ephippids *Platax*, *Zabidius*, and *Parapsettus*, as well as Luvaridae, Acanthuridae, Pomacanthidae, Kyphosidae, and some chaetodontids.

Other conditions: In all other taxa examined, there is an elongation of one or more spines variously located in the dorsal fin, giving a notched appearance in the spinous dorsal fin or between the spinous dorsal and the soft-rayed dorsal fin. In *Chaetodipterus*, *Ephippus*, *Tripterodon*, and *Proteracanthus*, as well as Drepaneidae, Scatophagidae, Zanclidae, and some chaetodontids the third, fourth, or fifth dorsal-fin spine is the longest. In *Rhinoprenes*, the first spine is the longest, the last spine is the second longest, and the third spine is the next longest; this results in a double-notched appearance. In Siganidae, the first dorsal-fin spine is relatively short, spines 2-10 are relatively longer and approximately equal in length, and spines 11-13 are relatively shorter: exhibiting more of a depression rather than a distinct notch. Due to the presence of both the derived and primitive conditions in Chaetodontidae, the character was coded as "missing". In Coracinidae, spines 1-5 ascend in length, spines 6-9 descend in length, and the last spine (spine 10) is longer than the ninth.

36. ***Two anteriormost neural spines closely applied.***

Derived condition: In the ephippids *Chaetodipterus*, *Ephippus*, *Tripterodon*, and *Zabidius*, as well as Chaetodontidae, the first two neural spines are closely applied to one another, there is little or no space between the two neural spines, and there is no space for the insertion of a supraneural or pterygiophore (Figs. 20, 21).

Other conditions: In all other taxa examined, the two anteriormost neural spines are separate from one another (i.e., enough space to allow the insertion of a supraneural or pterygiophore) (e.g., Figs. 19b,c).

37. ***Anterior haemal spines without anteriorly- or posteriorly-directed vertically-oriented lamina.***

Derived condition: In the ephippids *Parapsettus, Rhinoprenes*, and *Proteracanthus*, as well as Luvaridae, Pomacanthidae, Chaetodontidae, Kyphosidae, and Coracinidae, the main ramus of each anterior haemal spine is rounded and smooth: there are no lamina associated with the haemal spines (e.g., cf. Tyler et al. 1989: 45, fig. 30). Although the second haemal spine of Kyphosidae possesses two small lamina anteriorly, these lamina are closely associated with one another basally, flare out anteriorly (v-shaped), and do not represent the same condition as described above.

Other conditions: In all other taxa, the main stem of each anterior haemal spine possesses either a posteriorly-directed vertically-oriented lamina (e.g., Siganidae: cf. Tyler et al. 1989: 44, fig. 29) or two lamina, one extending posteriorly, the other anteriorly (e.g., Scatophagidae: cf. Tyler et al. 1989: 48, fig. 33).

38. ***Dorsal- and anal-fin spines approximately symmetrical in cross-section.***

Derived condition: In the ephippids *Parapsettus, Platax,* and *Rhinoprenes,* as well as Acanthuridae (in part), Luvaridae, Pomacanthidae, and Coracinidae, the dorsal- and anal-fin spines are approximately symmetrical in cross-section.

Other conditions: In all other taxa examined, the dorsal- and anal-fin spines are asymmetrical in cross-section. That is, in all taxa except *Proteracanthus,* the dorsal-and anal-fin spines, except the posteriormost spine, each possess a single posteriorly-directed flange. These spines appear apostrophe-shaped in cross-section (Fig. 22a). These flanges sequentially alternate in position, one on left side of the spine, the next on the right side, allowing each spine to lie slightly adjacent to the next spine in succession: this allows the fin to lie closer to the body when the fin is depressed. *Proteracanthus* is unique in that it possesses alternating flanges on the anterior side of each spine, excluding the anteriormost spine (Fig. 22b). Scatophagidae and Siganidae are unique in that in addition to the flanges associated with each spine, successive spines are physically offset from one another (i.e., not in a line).

39. ***Presence of hyperostosis.***

Derived condition: Presence of hyperostosis. The ephippids *Chaetodipterus, Platax,* and *Proteracanthus,* as well as Scatophagidae and Drepaneidae, exhibit hyperostosis. Although variation is seen among these taxa, bones that may become hyperossified include the occipital crest, frontals, ascending process of the posttemporal, lachrymal, supraneurals, first dorsal-fin pterygiophore, dorsal-fin spines, neural spines, ribs, cleithrum, ventral process of the postcleithrum, first anal-fin pterygiophore, and the haemal spines.

Other conditions: All other taxa examined do not exhibit hyperostosis.

40. ***First epural positioned posterior to the reduced neural spine of preural centrum 2 (PU$_2$).***

Derived condition: The first epural is positioned posterior to a vertical extended from the reduced neural spine of preural centrum 2 (PU$_2$). This is exhibited in all ephippids except *Ephippus* and *Tripterodon*, as well as Zanclidae, Drepaneidae, Pomacanthidae, Chaetodontidae, Kyphosidae, and Coracinidae.

Other conditions: In *Ephippus*, *Tripterodon*, Scatophagidae, Acanthuridae, Luvaridae, and Siganidae, the first epural is positioned dorsal to the reduced neural spine of preural centrum 2 (PU$_2$).

41. *Presence of 8+8 principle caudal-fin rays* (Tyler et al. 1989)

Derived condition: Scatophagidae, Luvaridae, Zanclidae, and Acanthuridae possess 8+8 principle caudal-fin rays.

Other conditions: All other taxa examined possess 9+8 principle caudal-fin rays.

42. *Reduction in the number of pectoral-fin actinosts articulating with the scapula.*

Derived condition: A reduction in the number of pectoral-fin actinosts articulating with the scapula from three to two or one. The derived condition is present in all acanthuroids as well as Coracinidae. In all of these taxa except *Rhinoprenes*, the two dorsalmost pectoral-fin actinosts completely articulate with the scapula (Fig. 23a): the two ventralmost actinosts articulate with the coracoscapular cartilage and the coracoid or just the coracoscapular cartilage. *Rhinoprenes* is unique in that only the dorsalmost actinost completely articulates with the scapula and the other three articulate with the widened coracoscapular cartilage (Fig. 23b).

Other conditions: In Drepaneidae, Pomacanthidae, Chaetodontidae, and Kyphosidae, the three dorsalmost pectoral-fin actinosts articulate with the scapula and the ventralmost actinost articulates entirely with the coracoscapular cartilage, the coracoid, or straddles both (Fig. 23c).

43. *Ventral process of the coracoid elongate and articulates with the main ramus of the cleithrum.*

Derived condition: The ventral process of the coracoid is elongate, overlays the median lamina, and articulates with the main ramus of the cleithrum in all ephippids (except *Chaetodipterus*, *Ephippus*, and *Proteracanthus*) and Siganidae (Figs. 24a,b).

Other conditions: In all other taxa examined, the ventral process is relatively shorter and articulates with either the outer edge of the median lamina of the cleithrum (e.g., Scatophagidae, Drepaneidae; Fig. 24d) or the ventral process of the coracoid sightly overlaps the median lamina (e.g., *Chaetodipterus*, *Ephippus*, *Proteracanthus* and Drepaneidae ; Fig. 24c).

44. ***Posteroventral edge of scapula concave.***

Derived condition: The posteroventral edge of the scapula is concave in the ephippids *Chaetodipterus*, *Ephippus*, *Platax*, *Tripterodon*, and *Zabidius*, as well as Siganidae, Luvaridae, and Drepaneidae (e.g., Fig. 25b). The ventral portion of the scapula is filled with cartilage and articulates synchondrally with the coracoid.

Other conditions: In all other taxa examined, the ventral portion of the scapula is filled with cartilage, but the posteroventral edge of the scapula is flat (e.g., Fig. 25a).

45. ***Presence of a cancellous sulcus on the medioantero edge (i.e., internal crest) of the cleithrum.***

Derived condition: In all ephippids, Acanthuridae, Drepaneidae, and Coracinidae, the medioantero edge (i.e., the internal crest) of the cleithrum possesses a cancellous sulcus. The condition is variable among the taxa. In all ephippids, except *Rhinoprenes* and *Proteracanthus*, as well as Drepaneidae, the internal crest of the cleithrum possesses a large deep cancellous sulcus located in the middle of the cleithrum (Figs. 24a,d): the cancellations located within this sulcus are deep and extend in a convoluted fashion laterally toward the edge of the cleithrum that articulates with the scapula. In Coracinidae, the sulcus is relatively narrow and the cancellations shallow. In *Rhinoprenes* and *Proteracanthus*, the sulcus is both narrow and smaller (i.e., dorso-ventrally compressed) relative to the other taxa (Fig. 24b). In Acanthuridae, the sulcus ranges from greatly reduced and difficult to discern (e.g., *Acanthurus* and *Ctenochaetus*) to deep with few cancellations (e.g., *Naso*). In *Acanthurus* and *Naso*, one side of the rim of the sulcus is noticeably higher than the other.

Other conditions: In all other taxa examined, the internal crest of the cleithrum does not possess a cancellous sulcus. In many taxa, the internal crest is laminar: cancellations may be present but not in a sulcus.

46. ***Posterior processes of the pelvic-fin girdle elongate, pointed, parallel and separate from one another along their entire lengths.***

Derived condition: All ephippids possess posterior processes (i.e., the ischial processes) of the pelvic-fin girdle (basiterygia) that are elongate, pointed, and parallel, and separate from one another along their entire lengths (Fig. 26a). *Rhinoprenes* is unique in that the processes are extremely elongate, relative to the others.

Other conditions: All other taxa possess one of three conditions: (1) The distal ends of the posterior processes of the pelvic fins either curve laterally or are clublike (e.g., Fig. 26b), as in Scatophagidae, Drepaneidae, Chaetodontidae, Pomacanthidae, Kyphosidae, and Coracinidae; (2) The posterior processes of the pelvic-fin girdle are elongate, pointed, parallel to one another, but are in contact with one another along their entire lengths (e.g., Fig. 26c), as in Siganidae, Acanthuridae, and Zanclidae; (3) The posterior processes are absent as in Luvaridae.

47. ***Four lamina of membrane bone (i.e., wings) associated with the basipterygium.***

Derived condition: The presence of four lamina of membrane bone (i.e., wings) associated with the basipterygium. These lamina (i.e., internal wing, ventral wing, external dorsal wing, external ventral wing) (see Fig. 27a) are discussed by Stiassny and Moore (1992). Four wings are present in the ephippids *Ephippus, Platax, Tripterodon*, and *Zabidius*, as well as, Acanthuridae (in part; i.e, *Naso*), Drepaneidae, Pomacanthidae, Kyphosidae, and Coracinidae. The origin of the ventral wing is variable: it originates on the central part of the basipterigium in all taxa except *Zabidius* and Acanthuridae (i.e., *Naso*). In *Zabidius*, the ventral wing is reduced to a small ridge and has its origin on the internal wing (similar to the condition described by Stiassny and Moore (1992). In *Naso*, the external ventral wing is shelf-like and extends medially: the ventral wing originates on the external ventral wing.

Other conditions: In all other taxa examined (including two acanthurids, *Acanthurus* and *Ctenochaetus*), only three lamina of membrane bone are associated with the basipterygia: the ventral wing is lost in all of these taxa (Fig. 27b).

48. ***Pelvic-fin spine reduced in length and equal to the length of the posterior process of the pelvic fin.***

Derived condition: In the ephippids *Parapsettus* and *Rhinoprenes*, the pelvic-fin spine is reduced in length and equal to the length of the posterior process of the pelvic fin.

Other conditions: In all other taxa examined, the pelvic-fin spine is much longer than the posterior process of the pelvic fin.

49. ***External dorsal wing of the basipterygium is reduced in size.***

Derived condition: The external dorsal wing (i.e., membrane bone associated with the basipterygium) of the basipterygium is reduced in size and smaller than the external ventral wing. This condition is exhibited by the ephippids *Parapsettus* and *Rhinoprenes*, as well as Scatophagidae and Acanthuridae.

Other conditions: In all other taxa examined the external ventral wing is much larger than the external dorsal wing.

50. ***Primary ramus of basipterygium reduced in length and width.***

Derived condition: The primary ramus of the basipterygium is relatively short and narrow in the ephippids *Parapsettus* and *Rhinoprenes*.

Other conditions: All other taxa examined possess basipterygia that are relatively large and stout.

51. **Mandibulopreopercular sensory canal branched between the dentary and the angular.**

Derived condition: In all ephippids except *Rhinoprenes*, as well as Siganidae, and Acanthuridae (in part), the mandibulopreopercular sensory canal branches ventrally between the dentary and the angular; a single, large, ventrally-oriented pore is at the terminus of this canal (Fig. 28a). A large space between the dentary and the angular allows for the passage of the canal. In Siganidae and *Acanthurus* (Acanthuridae), the canal is relatively elongate relative to the condition exhibited in the ephippids.

Other conditions: In *Rhinoprenes*,, the dentary possesses a posteriorly-projected bony flange that approaches the anteroventral edge of the angular, with little or no room for a large canal; no branching canal is evident. However, multiple minute branching canals are evident. This may be related to the highly cancellous nature of the dentary. In the other taxa examined, the canal between the dentary and angular is horizontal, without a ventrally-directed branch; if a pore is present, it is in the same plane as the canal (Fig. 28b). This condition is also apparent in two acanthurids examined (*Naso, Ctenochaetus*). The presence of the equivocal condition in Acanthuridae was coded as "missing" in the character matrix.

52. **Lateral line extends onto the caudal fin and is branched.**

Derived condition: The lateral line extends onto the caudal fin and branches in the ephippids *Proteracanthus* and *Rhinoprenes*. In his description of *Rhinoprenes*, Munro (1964) did not illustrate or describe the condition of lateral line scales extending onto the caudal fin of the holotype or paratypes. Including the scales on the caudal fin, the number of total lateral line scales would increase from 46-50 (Munro 1964) to 58-60. Clearing and staining renders these small scales more noticeable.

Other conditions: In all other taxa examined, except Coracinidae and Acanthuridae, the lateral line terminates prior to the caudal fin. In Coracinidae, the lateral line extends between the dorsal- and ventral caudal-fin primary rays about two thirds across the fin, but does not branch. In Acanthuridae, the lateral line extends onto the caudal fin, along the dorsal margin of the eighth dorsalmost primary ray.

53. **Presence of dorsoanterior swimbladder diverticula.**

Derived condition: Dorsoanterior bilateral swimbladder diverticula are present in the ephippids *Chaetodipterus*, *Ephippus*, *Tripterodon*, *Platax*, and *Zabidius*, as well as Drepaneidae and Chaetodontidae. The condition is somewhat variable among taxa. In *Chaetodipterus*, *Platax* and *Zabidius*, the swimbladders possess short, blunt diverticula bifurcating dorsoanteriorly (Fig. 21). In *Ephippus*, *Tripterodon*, and Drepaneidae, the diverticula are more elaborate. These taxa possess elongate tube-like bilateral diverticula that extend from, and are a continuation of, the short, blunt diverticula. *Ephippus* and *Tripterodon* possess elongate diverticula of varying lengths; the shortest extends to a position lateral to the basioccipital (Fig. 20); the longest are open-ended and insert to the back of the skull. These are very fragile tubes and are easily pulled from the skull by manipulating the specimen. It appears the tubes enter the skull and terminate in the otic capsules. In *Drepane punctata* and *D. africana*, the tube-like diverticula extend to a position lateral to the ventroposterior edge of the parasphenoid. The anterior diverticulum was absent in one specimen of *D. africana*, but this may be a reflection of the size of the specimen (88 mm SL). *Drepane longimanus* possesses a unique swimbladder that is further modified, with many branching diverticula located laterally and anteriorly; rather than a single tube extending anteriorly, there are several small diverticula extending anteriorly.

Blum (1988) misinterpreted a swimbladder character (his character 8.0-8.2, pp. 121-122). He states that pomacanthids, drepaneids, and ephippids either possess swimbladders without anterior diverticula or, if present, the diverticula are "derived differently than they are in chaetodontids." He describes 10 chaetodontid genera as possessing swimbladders with "bilaterally paired, bulbous, antero-lateral diverticula, that are attached to the medial surfaces of the supracleithra", as well as two additional genera with more narrow and elongate diverticula. Blum states that the connection between the swimbladder and the supracleithrum is the "most substantial modification of internal anatomy known to occur in the family." Of the ephippid genera he examined, anterior diverticula are absent in *Rhinoprenes*, and short and blunt in *Chaetodipterus* and *Platax*. *Drepane* possesses diverticula that are relatively longer and tube-like. However, the ephippids *Ephippus* and *Tripterodon* express a similar condition as that seen in chaetodontids: the diverticula attach to the medial surfaces of the supracleitha.

Other conditions: Absence of anterior bilateral swimbladder diverticula. The ephippids *Proteracanthus*, *Parapsettus*, and *Rhinoprenes*, as well as all other acanthuroid families, Pomacanthidae, Coracinidae, and Kyphosidae do not possess anterior diverticula.

54. **Absence of posterior bilateral swimbladder diverticula**.

Derived condition: Absence of posterior bilateral swimbladder diverticula is exhibited in the ephippids *Parapsettus*, *Proteracanthus*, and *Rhinoprenes*, as well as Siganidae, Luvaridae, Zanclidae, Chaetodontidae, Kyphosidae, and Coracinidae.

Other conditions: The ephippids *Chaetodipterus*, *Ephippus*, *Tripterodon*, *Platax*, and *Zabidius*, as well as Scatophagidae, Acanthuridae, Drepaneidae, and Pomacanthidae all possess posteriorly-extending swimbladder diverticula. The diverticula are variable among the taxa. The diverticula of ephippids are elongate, may extend posteriorly as far as the second precaudal vertebra, and are located relatively high on the body (i.e., located at a level equal to or dorsal to the medial tips of the anal-fin pterygiophores (Fig. 29a). The diverticula of Drepaneidae are shorter and located lower on the body (i.e., extend laterally to the midpoint of the anal-fin pterygiophores) than those of ephippids (Fig. 29b). In the majority of ephippids and Drepaneidae, the posterior diverticula are highly sclerotized, with the distal portions difficult to pierce with a needle. In Scatophagidae, Acanthuridae, and Pomacanthidae, the diverticula are not sclerotized, are relatively short, and extend to a position lateral to haemal spines II-V.

55. Gill membranes broadly united at the isthmus (Tyler et al. 1989).
Derived condition: Gill membranes broadly united at the isthmus, restricting the branchial aperture ventrally (Tyler et al. 1989) is exhibited by all acanthuroid fishes.

Other conditions: In all other taxa examined, the gill membranes are not connected to the isthmus, but may be continuous or discontinuous ventrally.

56. Presence of a myocommatum (i.e., septum between two adjacent myotomes) in adductor mandibulae section (Winterbottom 1993).
Derived condition: The presence of a myocommatum (i.e., septum between two adjacent myotomes) in adductor mandibulae section (Winterbottom 1993) is exhibited by all acanthuroids.

Other conditions: Absence of a mycommatum. This condition is exhibited by Drepaneidae, Pomacanthidae, and Chaetodontidae. The condition is unknown for Coracinidae and Kyphosidae.

57. **Presence of dark vertical bar extending through the eye.**

Derived condition: In the ephippids *Chaetodipterus*, *Ephippus* (in part), *Platax*, *Tripterodon*, and *Zabidius*, as well as Acanthuridae (in part) and Chaetodontidae (in part), a dark vertical bar extends from the top of the head, through the eye, and terminates anterior to the pelvic fins. In addition, a second vertical bar extends from the nape, through the pectoral-fin base and the posterior margin of the opercle, and terminates at the pelvic fins. *Ephippus goreensis* possesses a dark bar through the eye, but *E. orbis* does not.

Other conditions: In all other taxa examined, there is no dark vertical bar through the eye. Scatophagid larvae possess a dark bar that extends through the eye. This bar is not present in adults. *Ephippus*, Acanthuridae, and Chaetodontidae were coded as "missing" in the character matrix because of the equivocal condition exhibited by these taxa: some taxa possess a dark vertical bar through the eye, others do not.

58. Characters of Scatophagidae + Siganidae + Luvaridae + Zanclidae + Acanthuridae (Tyler et al. 1989) (weighted by 2).

Derived condition: Tyler et al. (1989; chars. VII and VIII, p. 52) describe two synapomorphies that are shared by all acanthuroids except ephippids. These characters, presence of 13 caudal vertebrae, and the presence of only the anterior pair of uroneurals, are not shared by any of the outgroup taxa. The characters were considered as a single character with a weight of two in the data matrix.

59. Eleven synapomorphies of Siganidae + Luvaridae + Zanclidae + Acanthuridae (Tyler et al. 1989) (weighted by 11).

Derived condition: Tyler et al. (1989) describe 11 synapomorphies based on adult morphology of the restricted acanthuroids. Elucidating relationships of this well-supported monophyletic group is not an issue here. In the data matrix, these characters were considered as a single character with a weight of 11. See Tyler et al. (1989; cf. p. 58) for detailed description of these characters. Tyler et al. (1989) also describe seven additional characters supporting monophyly based on larval morphology. These characters were not included in the matrix because larvae were not available for all outgroup taxa (but see "DISCUSSION OF CONSTRAINT TREE ANALYSES").

CONSTRAINT TREE ANALYSES

A data matrix (Table 2) was constructed utilizing the characters described above. Based on the discussion in "Choice of Outgroups for Phylogenetic Analyses of the Ephippidae," seven constraint trees were used for the elucidation of sister-group relationships. Data were analyzed in PAUP (version 3.1.1; Swofford 1993). The Branch and Bound algorithm, and the "enforce constraint trees" option were used to evaluate all maximally-parsimonious unrooted trees given the constraints.

It is important to note that all analyses utilizing the below-described constraint trees resulted in a monophyletic Ephippidae with the same topology in all. For this reason, the results of the constraint-tree analyses will be discussed briefly followed by a discussion of the phylogeny of the Ephippidae.

The combined constraint tree searches resulted in maximally-parsimonious trees of 183 to 196 steps (CI = 0.393 - 0.421, RC = 0.250 - 0.284). The low rescaled consistency indices (RC) indicate that, concerning all 11 families, the data do not have hierarchical structure. One conclusion that can be made from this lack of structure is that there is a high amount of homoplastic evolution among the families. The RC excludes all autapomorphies (these were excluded before the analysis) and totally homoplastic characters, but retains those that partially support the tree topology.

The topologies of the seven contraint trees and results from each search are as follows:

Constraint Tree 1. Ingroup: polytomy with all acanthuroid taxa + Drepaneidae (from Tang et al. 1999); first outgroup, Chaetodontidae + Pomacanthidae; second outgroup Coracinidae + Kyphosidae (Fig. 30a).

Results: Six equally-parsimonious trees of 185 steps were obtained (CI = 0.416 , HI = 0.584, RI = 0.670, RC = 0.279). The six trees differed from one another in two respects. First, Scatophagidae was placed as either the sister group to the Ephippidae (present in three trees; consensus tree shown in Fig. 31a), or as the sister group to the restricted acanthuroids (present in three trees; consensus tree shown in Fig. 31b). Second, the positions among Acanthuridae, Siganidae, and

Luvaridae rotated (the three possible pairing combinations using these three taxa were exhibited in the two types of trees described above). A strict consensus of the six trees resulted in one tree with a polytomy involving Siganidae, Luvaridae, and Acanthuridae, and another polytomy involving Ephippidae, Scatophagidae, and the restricted acanthuroids.

Four key observations can be made utilizing the two consensus trees (Figs. 31a,b): (1) Drepaneidae always falls outside of the currently-recognized Acanthuroidei and never groups with Scatophagidae. In their restricted total evidence analysis utilizing both mitochondrial DNA and morphological data for 15 taxa (14 acanthuroid taxa plus Drepaneidae; Ephippidae, Scatophagidae, and Drepaneidae were designated as the outgroups), Tang et al. (1999) found Drepaneidae to be the sister group of the Scatophagidae; (2) Scatophagidae is either the sister taxon to the Ephippidae or the sister taxon to the restricted acanthuroids; (3) In all trees, Zanclidae is shown to be the basalmost member of the restricted acanthuroids; (4) The positions of the families Siganidae, Luvaridae, and Acanthuridae are not stable. Note the relationships among the restricted acanthuroids are based on this data set alone and that the addition of characters found by Tyler et al. (1989) would support only one topology concerning these taxa (Fig. 2a).

The clade comprising Siganidae, Luvaridae, and Acanthuridae is weakly supported (bootstrap = 54%, Bremer support value = 1). There is moderate support for the clade comprising Coracinidae,, Kyphosidae, and Chaetodontidae (bootstrap = 88%, Bremer support value = 2). There is high support for the restricted acanthuroids (bootstrap = 84%, Bremer support value > 6) and very high support for the Acanthuroidei (bootstrap = 93%, Bremer support value = 5).

Constraint Tree 2 (Fig. 30b). Ingroup: polytomy with acanthuroid taxa + Drepaneidae (relationships within the restricted Acanthuroidei defined as in Tyler et al. 1989 and Winterbottom 1993); first outgroup, Chaetodontidae + Pomacanthidae; second outgroup Coracinidae + Kyphosidae.

Results: Two equally-parsimonious trees of 188 steps were found (CI = 0.410, HI = 0.584, RI = 0.661, RC = 0.271) (Figs. 32a,b). As in Constraint Tree 1, Drepaneidae is not depicted as the sister group to Scatophagidae. The only difference between the two trees from this analysis is in the placement of Scatophagidae. In one tree, Scatophagidae is the sister group to Ephippidae, and both are the sister group to the restricted acanthuroids (Fig. 32a). In the other tree, Scatophagidae is the sister group to the restricted acanthuroids, and both are the sister group to the Ephippidae (Fig. 32b). In the consensus tree, a polytomy is represented by Scatophagidae, the restricted acanthuroids, and Ephippidae. Support for all clades is the same as that described for Constraint Analysis 1.

Constraint Tree 3 (Fig. 33a). Ingroup: polytomy with acanthuroid taxa + Drepaneidae (relationships within the restricted Acanthuroidei defined as in Tyler et al. 1989 and Winterbottom 1993); first outgroup, polytomy with Chaetodontidae, Pomacanthidae, Coracinidae, and Kyphosidae.

Results: Two equally-parsimonious trees of 188 steps with the exact same topologies as those resulting from the use of Constraint Tree 2 (see above; Figs. 32a,b).

Constraint Tree 4 (Fig. 33b). Ingroup: polytomy with acanthuroid taxa (relationships within the restricted acanthuroids defined as in Tyler et al. 1989 and Winterbottom 1993); first outgroup, polytomy with Drepaneidae, Chaetodontidae, Pomacanthidae, Coracinidae, and Kyphosidae.

Results: one maximally-parsimonious tree of 186 steps (CI = 0.414, HI = 0.586, RI = 0.667, RC = 0.276) (Fig. 34). The tree topology depicts Scatophagidae as the sister group to the Ephippidae, and these two families as the sister group to the restricted acanthuroids. There is no support for the sister-group relationship between Scatophagidae and Ephippidae: the branch collapsed, leaving a trichotomy with these two taxa and the restricted acanthuroids in the bootstrap (bootstrap < 50%). There is also no support for any of the clades among the outgroup taxa: the clades collapsed to one polytomy in the bootstrap (bootstrap < 50%). Assuming the relationships of the restricted acanthuroids are as defined by Tyler et al. (1989) and Winterbottom (1993), the single tree represents the most parsimonious hypothesis of relationships among all taxa.

Constraint Tree 5 (Fig. 35a). Ingroup: polytomy with all acanthuroid taxa; outgroup, polytomy with Drepaneidae, Chaetodontidae, Pomacanthidae, Coracinidae, and Kyphosidae.

Results: Three equally-parsimonious trees of 183 steps (CI = 0.421, HI = 0.579, RI = 0.676, RC = 0.284). All three trees are identical in topologies except for the placement of taxa within the restricted acanthuroids. The strict consensus of these three trees is shown in Fig. 35b. In all trees, Zanclidae is depicted as the basalmost restricted acanthuroid, and the other three taxa rotate positions. Placement of Zanclidae as the sister group to Acanthuridae (see Constraint Tree 4) results in one tree that is three steps longer (186). There is no bootstrap support (<50%) for the Ephippidae + Scatophagidae clade: this branch is collapsed leaving a trichotomy with these two taxa and the restricted acanthuroids. There is very weak support for the clade comprising Siganidae, Luvaridae, and Acanthuridae (bootstrap = 52%). There is moderate support for the restricted acanthuroids (bootstrap = 78%).

Constraint Tree 6 (Fig. 36a). Ingroup: topology defined as in Tang et al. (1999; Fig. 5A), with the exception of the ephippid taxa which were left as a polytomy; first outgroup, Chaetodontidae + Pomacanthidae; second outgroup Coracinidae + Kyphosidae.

Results: One maximally-parsimonious tree of 196 steps (CI = 0.393, HI = 0.607, RI = 0.636, RC = 0.250) (Fig. 36b). Of the seven constraint analyses, this is the longest most parsimonious tree found. Due to the resulting tree being the same as the constraint tree, bootstrap and Bremer support values are not available.

Constraint Tree 7 (Fig. 37a). Ingroup: topology defined as in Tang et al. (1999; Fig. 5B), with the exception of the ephippid taxa which were left as a polytomy; first outgroup, Chaetodontidae + Pomacanthidae; second outgroup, Coracinidae + Kyphosidae.

Results: One maximally-parsimonious tree of 189 steps (CI = 407, HI = 0.593, RI = 0.657, RC = 0.268) (Fig. 37b). This single most parsimonious tree is seven steps shorter than the single most parsimonious tree found in Constraint Analysis 6.

DISCUSSION OF CONSTRAINT TREE ANALYSES

Eight key observations can be made from the above-listed analyses: (1) The suborder Acanthuroidei is monophyletic; (2) Using this data set only, it is more parsimonious to hypothesize that Zanclidae is the basalmost member of the restricted acanthuroids; (3) Similar to the results of Tang et al. (1999), the exact placement of Scatophagidae within the Acanthuroidei can not be determined with this data set; (4) Drepaneidae is not the sister taxon to Scatophagidae; (5) The family Ephippidae is monophyletic; (6) Relationships within the Ephippidae are invariant no matter what outgroup scenarios are chosen; (7) Constraint Tree Analyses 1 and 5 require the minimum amount of assumptions (i.e., they represent the least structure); and, (8) It takes an additional 13 steps to go from the shortest most-parsimonious tree in these analyses to the longest most-parsimonious tree.

In all maximally parsimonious trees, the suborder Acanthuroidei is depicted as a monophyletic group (Figs. 31, 32, 34-37). Using total evidence, Tang et al. (1999) found conflicting hypotheses regarding the Acanthuroidei. One hypothesis placed Drepaneidae as the sister group to the Scatophagidae within the Acanthuroidei (making Acanthuroidei *sensu stricto* paraphyletic). The other hypothesis, based on outgroup choice, placed Drepaneidae as the sister group to the entire Acanthuroidei (similar to other hypotheses [e.g., Winterbottom 1993]). Comparison of the Constraint Analysis 6 and all others reveals that it is more parsimonious to hypothesize that Drepaneidae is not a member of the Acanthuroidei. The single most parsimonious tree resulting from Constraint Analysis 6 (Fig. 36b) is the longest most parsimonious tree resulting from all analyses.

In all analyses where the relationships of the restricted acanthuroids were left as an unresolved polytomy, Zanclidae was always placed as the basal member of the group (i.e., Constraint Trees 1 and 5). This is an artifact of the data set not including all characters used by the Tyler et al. (1989) and Winterbottom (1993) to elucidate relationships with the restricted acanthuroids. Tyler et al. (1989) used the following number of characters to hypothesize monophyly of the following clades (based on adult morphology, based on larval morphology): restricted acanthuroids (11, 7); Luvaridae + Zanclidae + Acanthuridae (8, 7); Zanclidae + Acanthuridae (5, 4) (Fig. 2A). Winterbottom (1993), using myology, found one additional character each, supporting the first two clades, and six characters supporting the last clade (Fig. 2B). These additional characters, which were not examined in this study offer overwhelming support for the restricted acanthuroid phylogeny as hypothesized by Tyler et al. (1989) and Winterbottom (1993). The inclusion of these characters would certainly result in Zanclidae being depicted as the sister taxon to the Acanthuridae.

Within this data set, only two characters, 10 and 28, influence the placement of Zanclidae as either the basal member of the restricted acanthuroids or as the sister taxon to the Acanthuridae (from comparison between Constraint Analyses 1 and 2). Zanclidae, Scatophagidae, and Ephippidae (less *Chaetodipterus* and *Ephippus*) exhibit a reduction in the number of bands of teeth (between 2 and 6)(character 10). The remaining restricted acanthuroids possess a single band of teeth. If Zanclidae is the basal member of the restricted acanthuroids, then a further reduction to a single row of teeth (as seen in Luvaridae, Siganidae, and Acanthuridae) represents a synapomorphy for the last three taxa. This state is homoplastically shared with Coracinidae. If Zanclidae is the sister taxon to Acanthuridae as hypothesized by (Tyler et al. 1989, Winterbottom 1993, Tang et al. 1999) then the possession of 2 rows represents a reversal.

Character 28, the possession of a ceratohyal firmly attached by connective tissue to dorsal and ventral hypohyals, is exhibited by Siganidae, Luvaridae, Acanthuridae, and all ephippids. In Scatophagidae and Zanclidae, the ceratohyal is laminar and is capable of extensive movement lateral to the dorsal and ventral hypohyals. The same arguments that were made for character 10 above apply here. Unfortunately, there is not enough structure in the data to resolve the relationships between Luvaridae, Acanthuridae, and Siganidae. Due to the overwhelming evidence supporting a sister group relationship between Zanclidae and Acanthuridae (Tyler et al. 1989, Winterbottom 1993), it is better to hypothesize a reversal for this character in Zanclidae. Considering characters 10 and 28 and the additional evidence offered by Tyler et al. (1989) and Winterbottom (1993), it is easier to justify placement of Zanclidae as the sister group to Acanthuridae, with reversals occurring in Zanclidae. This results in a tree that is three steps longer (compare results from Constraint Analyses 4 and 5).

Similar to the results of Tang et al. (1999), these analyses resulted in two equally-parsimonious hypotheses regarding the placement of Scatophagidae. Utilizing both molecular and total evidence approaches, Tang et al. (1999) concluded Scatophagidae was either the sister taxon to Drepaneidae, and the two were the sister group to Ephippidae, or Scatophagidae was the basal member of the Acanthuroidei, and Ephippidae was the next basalmost member. In many constraint analyses herein, it was equally parsimonious to hypothesize a sister group relationship between either Scatophagidae and Ephippidae (and these two as the sister group to the restricted acanthuroids), or between Scatophagidae and the restricted acanthuroids (and these two as the sister group to the Ephippidae). Unfortunately, this data set is not powerful enough to resolve the placement of Scatophagidae.

Tang et al. (1999) hypothesized that Drepaneidae was either the sister taxon to Scatophagidae (within the Acanthuroidei) or the basal member of the Acanthuroidei. In the constraint tree analyses herein, it is more parsimonious to hypothesize that Drepaneidae is not within the Acanthuroidei. Constraining the analyses to include Drepaneidae within the Acanthuroidei (e.g., Constraint Analyses 1, 2, 3 and 6) resulted in maximally parsimonious trees that were longer than those that excluded Drepaneidae from the Acanthuroidei (Constraint Analyses 4 and 5) (given the same ingroup topologies). In all trees where Drepaneidae was included in the Acanthuroidei, but not constrained to a particular clade (Constraint Analyses 1-3), the family is depicted as the basalmost member of the Acanthuroidei, and never as the sister group to Scatophagidae. Constraining Drepaneidae as the sister group to Scatophagidae (Constraint Tree 6) resulted in a single most parsimonious tree of 196 steps; the longest most parsimonious tree found in the constraint analyses. There were no morphological characters found in this study that are unique to Drepaneidae and Scatophagidae. In addition, Drepaneidae does not possess a single morphological character currently used to hypothesize monophyly of the Acanthuroidei (see Winterbottom 1993), and the inclusion of Drepaneidae in the suborder would necessitate the independent loss of these characters. Therefore, results of this study do not support one hypothesis of Tang et al. (1999), and concludes that Drepaneidae is not a member of the Acanthuroidei. Blum's (1989) hypothesis of a sister group relationship between Drepaneidae and Ephippidae is also not supported by this data set. Constraint Analysis 1 placed Drepaneidae in a polytomy with the acanthuroid taxa. In the topologies of the six resulting trees, Drepaneidae was always depicted as the basalmost taxon within the clade, and was two to three nodes away from Ephippidae (Figs. 31a,b).

All trees resulting from the constraint analyses depicted a monophyletic Ephippidae. In addition, it is important to note that the topology of the within-

Ephippidae relationships was invariant under all outgroup scenarios. Constraint Trees 1 and 5 represent the trees with the least amount of assumptions. That is, there is minimal structure before analysis. They also represent the maximally parsimonious trees with the fewest steps (185 and 183, respectively). Although, the shortest tree is the best hypothesis of relationships, based on parsimony, it does not measure the degree of confidence that can be placed on this phylogenetic hypothesis relative to alternatives that are slightly less parsimonious. Constraint Analyses 1 and 5 did not take into account the highly-supported phylogeny of the restricted acanthuroids (Tyler et al. 1989, Winterbottom 1993). If the restricted acanthuroids are constrained to reflect the relationships hypothesized by these authors (i.e., Constraint Tree 4), then the most parsimonious tree is 186 steps. For this reason, the single most parsimonious tree resulting from Constraint Analysis 4 will be used to describe the phylogeny of the Ephippidae and related taxa.

SISTER GROUPS TO THE EPHIPPIDAE

In the following discussion, Constraint Analysis 4 (Fig. 34) will be used for description of the sister groups and other taxa in relation to the Ephippidae, as well as a base for comparison among sister group hypotheses resulting from the other constraint analyses. In the seven constraint analyses described above, there is a 13 step difference between the shortest most-parsimonious tree and the longest most-parsimonious tree. It takes few additional steps to create trees with significantly different topologies. For example, the separation of Pomacanthidae and Drepaneidae by one node is not supported (Bootstrap support <50%), and it takes only two additional steps to switch the relative positions of these two families (compare results from Constraint Analyses 3 and 4).

A single tree resulted from Constraint Analysis 4 (Fig. 34): 186 steps, CI = 0.414, HI = 0.586, RI = 0.667, RC = 0.276. The low RC is indicative of the high amount of homoplastic evolution among the families examined. The RC excludes all autapomorphies (these were excluded before the analysis) and totally homoplastic characters, but retains those that partially support the tree topology. There are too many character changes to plot on a single tree. However, character changes for all taxa and the list of apomorphies for each branch are listed in Tables 6 and 7, respectively.

Refer to Table 8 throughout the following discussion: this table summarizes the characters offering unambiguous support for the various sister group hypotheses resulting from the seven constraint analyses.

Although the tree from Constraint Analysis 4 depicts Scatophagidae as the sister group to the Ephippidae, this node is not supported by bootstrap analysis (bootstrap < 50%). In the next most-parsimonious tree (one tree of 187 steps), the only difference in the topology is a switch in position of Scatophagidae from the sister group of the Ephippidae to the sister group to the restricted acanthuroids. Similar to the findings of Tang et al. (1999), the data provide little support for one hypothesis over another. Three characters (1, 2, 3) offer unambiguous support for a sister group relationship between Scatophagidae and Ephippidae (Constraint Analysis 4); two characters (26, 28) offer unambiguous support for a sister group relationship between the restricted acanthuroids and Ephippidae (Constraint Analysis 7). There are also two characters (40, 58) that offer unambiguous support for a sister group relationship between Scatophagidae and the restricted acanthuroids (Constraint Analyses 1, 2, and 3).

These results differ from those of Tang et al. (1999) in that Drepaneidae is not hypothesized to be the sister group to the Scatophagidae. In fact, there are no characters that offer unambiguous support for a Scatophagidae + Drepaneidae sister group relationship, and none that offer support for the clade Scatophagidae + Drepaneidae + Ephippidae (Constraint Analysis 6; Table 8).

The best supported clade depicted in Constraint Analysis 4 is the Acanthuroidei *sensu stricto*, with eight unambiguous characters (11, 12, 16, 18, 22, 42, 55, 56). Pomacanthidae is depicted as the sister group to the Acanthuroidei. Although three characters (6, 10, 47) offer unambiguous support for this clade, this is a weakly supported node (bootstrap < 50%, Bremer support value = 2). Hypothesizing Drepaneidae as the sister group to the Acanthuroidei (Constraint Analyses 2 and 7) is just as weak , with one character, 37, offering unambiguous support for the clade.

The clades Drepaneidae + Pomacanthidae + Acanthuroidei, and these taxa plus Chaetodontidae (Constraint Analysis 4) are supported by three (14, 30, 54) and two (15, 33) unambiguous characters, respectively. There is weak support for these nodes (bootstrap < 50%, Bremer support value = 2).

PHYLOGENY OF THE EPHIPPIDAE

Phylogenetic Reconstruction

Constraint Analysis 4, utilizing all eight ephippid genera, resulted in a tree topology that depicts a monophyletic Ephippidae (Figs. 38, 39), in support of Johnson's (1984) hypothesis. The phylogeny of the Ephippidae will be described in detail below. Bear in mind that the character designations of derived versus primitive are relative terms and some characters would switch designations depending on outgroups used. However, the morphology would not change, and therefore, the following descriptions offer valuable information regarding morphology of these fishes. Character changes for all taxa and the list of apomorphies for each branch are listed in Tables 6 and 7, respectively.

The tree topology (Figs. 38, 39) depicts two distinct clades (25 and 27). One clade (25) comprises the genera *Chaetodipterus, Ephippus, Tripterodon, Platax*, and *Zabidius*.. The other clade (27) comprises the genera *Proteracanthus, Parapsettus*, and *Rhinoprenes*.

Consensus trees, branch support, tree stability and bootstrap

Although one maximally-parsimonious tree of 186 steps was found, all trees up to 192 steps were examined. Branch support values were calculated by visual inspection of the strict consensus trees of one to six steps greater than the most parsimonious tree: 187 (1 tree), 188 (17 trees), 189 (34 tree), 190 (118 trees), 191 (260 trees), 192 (677 trees). (A consensus was not necessary for the single tree of 188 steps.) All clades except the restricted acanthuroids collapsed in the consensus of trees 192 steps or longer, resulting in two unresolved polytomies with the topology of the original constraint tree (i.e., Acanthuroidei represented as one polytomy, all other taxa represented by another). The restricted acanthuroid clade is strongly supported (e.g., character 59, weighted by 11), with a minimum of at least the 1108 most parsimonious trees (all trees of steps 186 - 192) exhibiting the same topology.

Branch lengths, bootstrap values, and Bremer support values were plotted on each non-terminal branch of the most-parsimonious tree (ACCTRAN optimization) (Fig. 39). Branch lengths only were plotted on terminal branches. Branch lengths range from 6 - 11, bootstrap values range from <50 - 85%, Bremer support values range from 2 - 4. The branch lengths offer little information as to the support of the clades because they can be artificially increased by homoplasies and reversals. A bootstrap (i.e., heuristic search) was performed using PAUP with 1000 replicates. The resultant tree has a different topology than the most-parsimonious tree: node 27 is not supported and is collapsed, resulting in a trichotomy with nodes 25 and 26. All other nodes are supported by the bootstrap analysis, with nodes 28 and 25 being the best supported, as was also shown in the Bremer branch support analysis.

Based on Bremer branch support values, there is minimal support for nodes 24, 23, 27, and 26, (Bremer support value = 2), medium support for node 25 (Bremer support value = 3), and relatively high support for node 28 (Bremer support value = 4). Nodes 24, 23, 27, and 26 are only supported by the two most-parsimonious trees (all trees of steps 186 and 187) (although some of the trees of steps 188 could also support these topologies). The 19 most parsimonious trees (all trees of steps 186 - 188) offer support for node 25. The 53 most parsimonious trees (all trees of steps 186 - 189) offer support for monophyly of the Ephippidae.

Forty-seven of the total 59 characters were used in the construction of the ephippid phylogeny (Fig. 38). Of these characters, six are multi-state characters and one is weighted by two. The minimum number of steps for these characters is 55. The overall consistency index (CI) for the tree representing Ephippidae is: minimum number of steps/actual number of steps (55/80) = 0.687.

The Bremer (1994) total support index, a measure of overall tree stability, was calculated for the most-parsimonious tree. Excluding the 10 characters at the ingroup node (10 characters, 11 steps), cladogram of ephippid relationships is 69 steps. The total support index, derived from summing the branch support values depicted in Figure 39, is $ti = t/s = (3+2+2+4+2+2)/69 = 0.22$. This low total support index is indicative of the high amount of homoplastic evolution within the Ephippidae. As discussed by Bremer (1994), a low total support index does not mean that all branches are weakly supported. In fact, there may be individual groups with high branch support (e.g., nodes 25, 22).

Monophyly of the Ephippidae

As in all acanthuroids, the interarcual cartilage is absent or reduced, the premaxillae are nonprotrusive, and the maxillae and premaxillae do not move independently. The major anatomical modifications that have occurred within the family Ephippidae also involve the mouth and the branchial region, as well as the hyoid region. These modifications are most likely for food handling and processing (see "DISCUSSION"). There are also alterations to the pectoral and pelvic girdles. Of the 59 characters used in this study, 47 are mapped on the portion of the tree depicting the phylogeny of the Ephippidae (Fig. 38).

The clade Ephippidae is well supported (Fig. 38). There are 10 characters associated with basal node of the Ephippidae (13, 19, 20, 21, 23, 40, 45, 46, 51, 58) (Tables 6 and 7). Only three of which (19, 21, 46) offer unambiguous support for monophyly of the Ephippidae, and they are not shared with any other taxa in this study. The derived conditions of characters 19 and 21 were used by Johnson (1984) to hypothesize monophyly of the family. Character 46, which is a multi-state character, was found in this study. The derived condition of character 20, is present in all members of the Ephippidae, but it is also homoplastically shared with Zanclidae. Character 23 is present only in Ephippidae and is exhibited by all taxa except *Proteracanthus.* Character 51 is present in all ephippids except *Rhinoprenes.* It is homoplastically shared with Siganidae. The remaining four characters (13, 40, 45, 58) offer no support for monophyly.

Phylogeny of the Ephippid Clades

Chaetodipterus + Ephippus + Tripterodon + Platax + Zabidius

At this clade, there are anatomical modifications to the mouth, vertebrae, swimbladder, pectoral girdle, external pigment pattern, and fin supports. Nine characters (4, 9, 10, 31, 33, 36, 44, 53, 57) are mapped at this node (Fig. 38). Only one character (57) provides unambiguous support for this clade. This character, the presence of a dark vertical bar extending through the eye, supports monophyly of this clade, as it is present in all species except *Ephippus orbis*. This condition is homoplastically shared with some species of the families Acanthuridae and Chaetodontidae. However, within these two families, both the derived and primitive conditions are exhibited (coded as "missing"). All other characters associated with this node are ambiguous. That is, either an atavistic reversal occurs with at least one genus of this clade, or the derived condition is shared with many other taxa outside of the clade. Character 4 is found only in this clade, but is represented by a reversal in two taxa (*Ephippus* and *Zabidius*). Character 33 is present in three of the taxa, with a reversal in the clade comprising *Platax* and *Zabidius*. The derived condition is also homoplastically shared with Coracinidae, Kyphosidae, and Scatophagidae. Character 36 is present in all members of this clade except *Platax*. The derived condition is homoplastically shared with Chaetodontidae. Character 53 is present in all members of this clade, but is homoplastically shared with Drepaneidae and Chaetodontidae.

Ephippus + *Tripterodon* + *Platax* + *Zabidius*

This node is characterized by modifications to the suborbital bones, axial skeleton, supraneurals, branchial region, and pelvic-fin skeleton. Eight characters are mapped at this node (13, 24, 25, 29, 34, 39, 40, 47), none of which offer unambiguous support for the clade (Fig. 38). The derived condition of character 25 is present in all members of this clade, but it is also homoplastically shared with Zanclidae and *Rhinoprenes*. Character 29 is homoplastically shared with the restricted acanthuroids, *Parapsettus*, and *Rhinoprenes*. Character 34 is exhibited by all members of this clade except *Zabidius*, and it is homoplastically shared with Scatophagidae and *Rhinoprenes*. All other characters are ambiguous, either through atavisms or homoplasy with other taxa.

Tripterodon + *Platax* + *Zabidius*

This node is characterized by four modifications to the teeth, and modifications to the palatine and pectoral girdle. Six characters (Characters 7, 8, 9, 10, 17, 43) are mapped at this node (Fig. 38). None of which offer unambiguous support for the clade. The derived condition of character 7 is present in the three taxa of this clade, but is homoplastically shared with Zanclidae. Character 17 is homoplastically shared with Kyphosidae. The other characters are shared with many taxa outside of the clade.

Platax + *Zabidius*

This clade is characterized by modification to the interarcual cartilage. Seven characters are mapped at this node (Characters 14, 22, 24, 30, 33, 35, 40; Fig. 38). Only one unambiguous character supports the monophyly of this clade: the presence of a reduced interarcual cartilage (character 22). The derived condition of character 14 is homoplastically shared with two clades, *Parapsettus* + *Rhinoprenes*, and Chaetodontidae + Kyphosidae + Coracinidae. Characters 24, 33, and 40 are represented by reversals at this node. Characters 30 and 35 are homoplastically shared with many taxa.

Proteracanthus + *Parapsettus* + *Rhinoprenes*

This clade is characterized by modifications to the infraorbital bones, pterygiophores, axial skeleton, pectoral girdle, and swimbladder. Six characters are mapped at this node (15, 32, 37, 45, 52, 54; Fig. 38). The derived conditions of characters 45 and 52 are present in *Proteracanthus* and *Rhinoprenes*, with a reversal in *Parapsettus*. The other characters are shared with at least three other taxa outside of the clade.

Parapsettus + *Rhinoprenes*

This clade is characterized by modifications to the mouth, axial skeleton, spines, pectoral and pelvic girdles. Nine characters are mapped at this node (5, 14, 29, 38, 39, 43, 48, 49, 50), of which two (48, 50) unambiguously support this clade (Fig. 38). Four characters are shared with only members of the Acanthuroidei. Character 5 is homoplastically shared with Luvaridae only. Character 29 is homoplastically shared with all acanthuroids except Scatophagidae, *Chaetodipterus*, and *Proteracanthus*. Character 43 is homoplastically shared with four other acanthuroids (Siganidae, *Platax*, *Zabidius*, *Tripterodon*). Character 49 is homoplastically shared with Acanthuridae and Scatophagidae. The other characters (14, 38, 39) are homoplastically shared with at least three other widely-separated taxa.

Alternative hypothesis: DELTRAN optimization

DELTRAN optimization was applied to the most-parsimonious tree resulting from Constraint Analysis 4 (ACCTRAN optimization discussed above). This optimization resulted in changes in character distributions on the tree. These changes indicate the amount of homoplasy among the taxa. As discussed earlier, DELTRAN optimization delays the transformation of an equivocal character. This movement of characters up the tree favors parallelisms, in contrast to ACCTRAN, which favors reversals. Given the same tree topology and number of steps, these two *a posteriori* optimizations will result in extremes in character placement if the characters are equivocal. If the tree was free of homoplasy, ACCTRAN and DELTRAN would yield identical character distributions.

The number of characters distributed among internal and terminal nodes (i.e., branch length) for the ACCTRAN and DELTRAN optimizations is summarized in Table 9. The tree resulting from the ACCTRAN optimization is one step longer than the tree resulting from the DELTRAN optimization. This is a result of character 58, which fell out of the Ephippidae in the DELTRAN optimization. Total branch lengths at the terminal nodes in the DELTRAN optimization increased by 12 due to characters moving from internal nodes to terminal nodes.

Using ACCTRAN optimization (Fig. 38, Tables 7 and 9), 11 characters were mapped at the node representing the family Ephippidae. Using DELTRAN optimization, the number of characters decreased to seven. Five characters (19, 20, 21, 46, 51) remained constant in both optimizations. Five characters (13, 23, 40, 45, 58 [weighted as 2]) mapped from the ACCTRAN optimization were placed farther up the tree using the DELTRAN optimization and represented as independent acquisitions. In the DELTRAN optimization, two characters (26, 28) were added that were placed outside of the Ephippidae in the ACCTRAN optimization.

Autapomorphies and other features of interest

Some of the following features were not polarized in this analysis but may have phylogenetic significance. Additional characters were autapomorphous and their presence is noted for future analyses. Not all of these characters were quantified for all taxa in this study.

1. ***Scales.*** Three types of scales are exhibited among ephippids: transforming ctenoid, cycloid, and spinoid. All ephippids possess transforming ctenoid scales except *Platax pinnatus* and *Rhinoprenes pentanemus*. *Platax pinnatus* possesses cycloid scales. *Rhinoprenes pentanemus* is unique in possessing three types of scales: 1) cycloid scales with many radii (up to 58 radii, although not all complete) covering the majority of the body; 2) spinoid scale Type A, which possess up to four spines; and 3) spinoid scale Type B, which possesses one buttressed spine that extends laterally from the main body of the scale- this spine is widened in some scales and forms a wall-like structure. Type A scales are located anteriorly on the body, extending from just above the lateral line origin, over the dorsal edge of opercle, onto the pectoral fin base, and to the area below the preopercle. They do not extend to the ventral midline. These scales most closely resemble those of the myctophid *Notoscopelus japonicus* (Roberts 1993; his Fig. 2e). Type B scales are located in a patch between the pectoral and anal fins.

Tyler et al. (1989) state that *Ephippus* sp. possess cycloid scales, while Roberts (1993) states that *Ephippus orbis* possesses spinoid scales. All specimens examined herein possess transforming ctenoid scales. Tyler et al. (1989) also state *Ephippus* and *Rhinoprenes* are the only squamipinnean fishes with cycloid scales. This is erroneous; *P. pinnatus* also possesses cycloid scales; *Ephippus* sp. possess transforming ctenoid scales. Drepaneidae possesses cycloid scales. Scale type is variable among the other acanthuroids: spinoid scales in Scatophagidae, Luvaridae, and Zanclidae; cycloid scales in Siganidae; transforming ctenoid and spinoid scales in Acanthuridae. Chaetodontids possess transforming ctenoid scales, while pomacanthids possess spinoid scales.

2. ***Number of anterior dorsal-fin pterygiophores that come in contact with the vertebral centra*** (Table 10). There is variability in this character within and among genera. The number of anteriormost (beginning at the first) dorsal-fin pterygiophores that come into contact with the vertebral centra are as follows: Drepaneidae (2), *Parapsettus* (2), *Tripterodon* (2), *Ephippus* (2 or 1), *Chaetodipterus* (1), *Zabidius* (1), *Platax* (1 or 0), *Rhinoprenes* (1 or 0), *Proteracanthus* (0).

3. ***Number of infraorbitals***. Drepaneidae, and all ephippids except *Proteracanthus, Rhinoprenes*, and *Zabidius* possess five infraorbital bones. *Proteracanthus* and *Zabidius* each possess four infraorbitals; *Rhinoprenes* possesses six.

4. ***Maxilla with large caudally-directed flange***. This condition is present in Drepaneidae and three ephippid genera, *Chaetodipterus, Ephippus*, and *Tripterodon*. The flange is large and forms a cleft with the remainder of the maxilla. The flange is present but reduced in *Platax, Proteracanthus* and *Zabidius*, and absent in *Parapsettus* and *Rhinoprenes*. A similar condition of a reduced flange is seen in *Scatophagus*, and Pomacanthidae. No flange is present in Zanclidae, Acanthuridae, Siganidae, Luvaridae, and Chaetodontidae.

5. **Presence of an uncinate process on the third epibranchial.** Mok and Shen (1983) proposed a sister-group relationship between Drepaneidae and Ephippidae based on the absence of an uncinate process on the third epibranchial. This was later refuted by Tyler et al. (1989) who found only one ephippid genus, *Ephippus*, to lack an uncinate process. In this study, some specimens of *E. goreensis* and *E. orbis* possessed a reduced cartilage-tipped uncinate process on the third epibanchial. Tyler et al. also found some of the other acanthuroids to lack an uncinate process.

6. ***Cephalic sensory canals.*** All ephippids as well as Drepaneidae possess extensive minute sensory canal systems associated with the head. There are differences in the number and position of canals/pores among genera. Drepaneidae appears to possess the most canals (ca. 233 canals counted on one side of the head). *Ephippus* and *Tripterodon* appear to possess the most among ephippids. A reduction in the number of canals is evident in *Proteracanthus*, *Parapsettus*, and *Rhinoprenes*. The locating and mapping of these canals is tedious, but appears to offer phylogenetic information. Locations of major sensory canal regions include: two distinct rows associated with the preopercle (one associated with the posterior margin); many canals positioned around anterior terminus of lateral line; extensive branching of canals on cheek (canals branch off of infraorbital series); branching canals around nares and extending to margin of maxilla; extensive branching on frontals; and extensive branching (originating from rows of canals) on top of head (posterior to a line connecting the posterior margins of the eyes).

7. **Mandibular sensory pores *Rhinoprenes*.** In all ephippids except *Rhinoprenes*, the chin pores associated with the dentary are large. In *Rhinoprenes*, rather than individual large pores, each "pore" is comprised of several small pores arranged in a circle. This may be associated with the highly cancellous nature of the dentary (i.e., multiple routes for canals rather than a few large ones).

8. ***Presence of a single moveable dermal flap associated with the posterior margin of the posterior nare.*** In all ephippids except *Parapsettus* and *Rhinoprenes*, there is a large dermal flap associated with the posterior margin of the posterior nare. This flap is typically folded against the posterior margin, but when expanded, covers the entire opening of the nare. *Parapsettus, Rhinoprenes,* as well as Scatophagidae and Siganidae, possess a dermal flap associated with the anterior margin of the posterior nare that is fixed in position (i.e., not capable of being folded against margin of nare) and large (i.e., covers the majority of the nare. Acanthuridae, Zanclidae, Luvaridae, Kyphosidae, and Coracinidae do not possess any dermal flaps associated with the posterior nare. Drepaneidae and Chaetodontidae possess two small dermal flaps associated with the posterior nare; one associated with the anterior margin, the other with the posterior margin. Pomacanthidae possesses a very small non-moveable flap associated with the ventroposterior margin.

KEY TO THE GENERA OF THE EPHIPPIDAE

A key to the genera of Ephippidae is presented below. Meristic data for genera are summarized in Table 11. Illustrations were not provided with this key as they are readily available in the published literature. In addition, Heemstra (In press) provides a key (with illustrations) to nine of the 15 species.

1a. Posterior dorsal-fin spines longest; dorsal-fin soft rays 27-39 2

1b. Posterior dorsal-fin spines shorter than anterior spines (anterior spines I or III-V distinctly longer than rest); dorsal-fin soft rays 14-16 or 18-23 4

2a. Body with two or three distinct, wide bars, with the first extending through the eye; outer bands of teeth tricuspidate, lingualmost band unicuspidate. 3

2b. Body uniformly pigmented (no bars); all teeth unicuspidate; dorsal-fin spines IX; soft dorsal and anal fins falciform; pelvic fin much smaller than pectoral fin; snout extends beyond mouth; found from Gulf of California south to northern Peru; monotypic . . . . ***Parapsettus***

3a. Two or three wide, vertically-oriented bars (the second bar originating at the origin of the spinous dorsal fin); dorsal-fin spines V-VII; juveniles (ca. 50-200 mm) with greatly elongated anterior dorsal-, anal- and pelvic-fin rays, rays become relatively shorter with age; up to 650 mm TL, found in Japan, south to Australia, Midway Island, Tuamoto Archipelago, west to the Red Sea and east African coast; five species . . . . ***Platax***

3b. Two narrow bars not vertically-oriented (the second bar originating on the nape); dorsal-fin spines IX; up to 480 mm, northern Australia to Papua New Guinea; monotypic . . . . ***Zabidius***

4a. Body without 5-9 wide, evenly-spaced vertical bars; dorsal-fin spine I or IV elongate; mouth subterminal 5

4b. Body with 5-9 wide, evenly-spaced bars; dorsal fin spines III, III-V, or III-VI elongate; mouth terminal 6

5a. First dorsal-fin spine, first pelvic-fin ray, fourth pectoral-fin ray greatly elongated and delicate, reaching beyond dorsal and anal fins; body laterally compressed; head naked; mouth small and inferior; upper jaw with unicuspidate only, lower jaw with tricuspidate only; dorsal fin spines VIII; pelvic-fin origin far in advance of pectoral fin origin; up to 150 mm; found in the muddy bottoms of river mouths in the Gulf of Papua, New Guinea; monotypic .... ***Rhinoprenes***

5b. Dorsal-fin spine IV elongate and irregularly swollen (i.e., hyperossified); body fusiform, not laterally compressed, with about 24 longitudinal stripes; all teeth tricuspidate, those on outer margin large; greatly enlarged lacrymal (i.e., first circumorbital bone); up to 325 mm; found in Singapore, Sumatra, and Borneo; monotypic .... ***Proteracanthus***

6a. Dorsal-fin spines III-V or III-VI elongate; margin of soft dorsal fin smooth, not falciform 7

6b. Dorsal-fin spine III longest; margin of soft dorsal fin slightly falciform to falciform; all teeth unicuspidate; up to 504 mm; found in the western Atlantic (only ephippid) and eastern Pacific (San Diego, CA to northern Peru, including the Gulf of California); two species ..... ***Chaetodipterus***

7a. Dorsal-fin spines III-VI elongate; margin of anal fin smooth, not falciform; all teeth unicuspidate; up to 250 mm, commonly about 150 mm; found from throughout Indo-west Pacific and in the east Pacific (West Africa- Cape Verde to Gaboon); three species .... ***Ephippus***

7b. Dorsal-fin spines III-V elongate; margin of anal fin falciform, not smooth; outer bands of teeth tricuspidate, lingualmost band unicuspidate; up to 500 mm; found in south Africa only (Natal to Mombasa); monotypic
.... ***Tripterodon***

BIOGEOGRAPHY OF THE EPHIPPIDAE

The Ephippidae are distributed throughout the coastal regions of the oceans ranging from tropical to temperate latitudes. Figures 40 and 41 depict the known distributions for the 15 ephippid species. Maximum diversity occurs in the Indo-west Pacific. Minimum diversity is found in three areas: the western Atlantic with one species (*Chaetodipterus faber*), the eastern Atlantic with two species (*C. lippei* and *Ephippus goreensis*), and the eastern Pacific with two species (*C. zonatus* and *Parapsettus panamensis*). Most species are found in marine waters, but some are found in hypersaline waters of the Red Sea (*Platax pinnatus, P. teira, P. orbicularis*) and mesohaline waters of estuaries and river mouths (*C. faber, C. lippei, Proteracanthus sarissophorus, Rhinoprenes pentanemus*) (Desoutter 1986, in part).

The geographic ranges vary widely within the family, with some species with reduced ranges (e.g., *C. lippei, R. pentanemus, Platax boersii*), while others have extensive ranges (e.g., *C. faber, P. orbicularis, E. orbis*). A few species have populations with disjunct distributions: *R. pentanemus*, known only from the Gulf of Papua, New Guinea and northwestern Australia; *Platax pinnatus*, although widespread throughout the Indo-west Pacific, is absent from Pakistan, India, and Bangladesh; *Platax batavianus*, found primarily in northern Australia and Indonesia, but also in Madagascar, Africa; *Platax orbicularis* and *P. teira*, known throughout the Indo-west Pacific, but absent in parts of Indonesia. Although some of the distributions may represent true geographical separations, the perceived absence of some of the relatively ubiquitous species from certain areas (e.g., *Platax pinnatus* absent from India) may be a result of inadequate collecting efforts or poor reporting of fish collections.

In general, the clade comprising *Proteracanthus, Parapsettus* and *Rhinoprenes* is much more restricted in individual ranges than is the clade comprising *Chaetodipterus, Tripterodon, Ephippus, Platax,* and *Zabidius* (Figs. 40, 41). The current geographic distributions of the ephippids are a result of both micro- and macroevolutionary processes. The microevolutionary processes operate at the population level (genetic), while the macroevolutionary processes are a result of vicariance. In the following, I seek to describe biogeographic pattern in present distributions that is congruent with the hypothetical relationships.

In a well-supported analysis, Winterbottom and McLennan (1993) demonstrated the utility of a cladogram for biogeographic analysis. Following the methods of Bremer (1992), these authors using the highly-corroborated cladogram of acanthuroid relationships (discussed in "Introduction"), mapped regional distributions of each extant member, and optimized these distributions to hypothesize the geographical distribution of the ancestors at each node (Fig. 42). The Ephippidae was excluded from their final analysis of biogeographical distributions since Ephippidae and Scatophagidae were considered outgroups for some optimization arguments.

As a result of this analysis, Winterbottom and McLennan (1993) hypothesized that the ancestors of the Acanthuroidei (excluding the ephippids), the Acanthuridae, and the Acanthurinae, each had an Indo-west Pacific distribution. They cite support for an Indo-west Pacific origin of the Acanthuroidei (excluding the ephippids) by noting that extant siganids and scatophagids are absent from the eastern Pacific, Caribbean, and the eastern Atlantic.

Extant ephippids are widely distributed and could be considered circumglobal, although they are absent from islands in the eastern Pacific. Since distributions of extant ephippid taxa do not support Winterbottom and McLennan's hypothesis, a cladistic reinterpretation of the ancestral areas, similar to the study of Winterbottom and McLennan (1993) was warranted.

According to Bremer (1992), distributions observed in extant taxa are more likely a result of dispersal from some ancestral area than a result of vicariant events. In addition, those "areas that are plesiomorphic in the area cladogram are more likely parts of the ancestral area than are positionally apomorphic areas."

Area distributions for the ephippid genera were mapped onto the terminal branches of the most-parsimonious cladogram resulting from Constraint Analysis 4 (Fig. 43). Values for gains, losses, gain/loss ratio, and ancestral area (see "Materials and Methods") corresponding to Figure 43 are presented in Table 12. For this analysis, I used the geographical areas delineated by Winterbottom and McLennan (1993), with the addition of the western Atlantic (WA). If the ancestral area was less than the present area, the results of this analysis indicate that the Indian Ocean was most likely part of the ephippid ancestral area (AA value of 1.0). The western Pacific was also likely to be part of the ancestral area (AA = 0.89). This corresponds to the results of Winterbottom and McLennan (1993) for the other acanthuroids, and provides evidence that the Acanthuroidei as a whole most likely had an ancestral area that included the Indo-west Pacific (Fig. 42). These results also indicate that the western Atlantic and Caribbean were least likely to be part of the ancestral area (AA values of 0.33).

A second analysis was performed with the Indian Ocean delineated by east and west halves, as was done with the Atlantic and Pacific Oceans in the previous analysis. Justification for this delineation is based on three observations: (1) *Tripterodon* is found only in the western part of the Indian Ocean; (2) *Zabidius*, *Rhinoprenes*, and *Proteracanthus* are found only in the easternmost part of the Indian Ocean; and (3) the Indian Ocean actually lies on three lithospheric plates: the largest being the Indian-Australian Plate; the second largest being the African Plate; and a relatively minute plate, the Arabian Plate (Springer 1982). The results of this analysis, with delineated east Indian (EI) and west Indian (WI) areas (Table 13, Fig. 44) indicate that if the ancestral area was less than the present area, the Ephippidae not only had an Indo-west Pacific distribution, but specifically, had an east Indian/west Pacific distribution (AA values 1.0). As in the first analysis, the areas least likely to be part of the ancestral range were the Caribbean and the western Atlantic.

Within the Ephippidae (Table 13, Fig. 44), it appears the two main clades, B and F, diverged with the ancestors of these clades most likely in two distinctly different ancestral areas. In clade B, the eastern Atlantic was most likely part of the ancestral area (AA value = 1.0) with the next most likely area being the western Indian ocean (AA value = 0.75). In clade F, the western Pacific and eastern Indian oceans were the most likely ancestral areas (AA values = 1.0). Within clade B, ancestral areas of ancestors of the other clades (C, D, E) moved progressively east (western Indian, to eastern Indian, to western Pacific). The same easterly progression can be seen in clade F (western Pacific to eastern Pacific).

DISCUSSION

Seven constraint tree analyses were conducted to take a cursory look at the various sister group hypotheses proposed by Blum (1988), Tyler et al. (1989), Winterbottom (1993), and Tang et al. (1999). After correcting for weaknesses in the data set concerning the restricted acanthuroids (see "DISCUSSION OF CONSTRAINT TREE ANALYSES"), the single most parsimonious tree resulting from Constraint Analysis 4 was chosen as the best hypothesis of relationships concerning all taxa. This tree of 187 steps (CI = 0.412, HI = 0.588, RI = 0.665, RC = 0.274) depicts a monophyletic Ephippidae, and a monophyletic Acanthuroidei. Scatophagidae is shown as the sister group to the Ephippidae, but this is hypothesis is weakly supported with the data set: it takes one additional step for Scatophagidae to switch to the sister group to the restricted acanthuroids. Unfortunately, the results of Tang et al. (1999) are substantiated here. That is, the position of Scatophagidae within the Acanthuroidei is unknown, the sister group to the Ephippidae is either Scatophagidae or the clade comprising Scatophagidae and the restricted acanthuroids. The phylogeny of the Ephippidae was invariant with all constraint analyses indicating the data provided structure for the ingroup.

The monophyly of the family Ephippidae is hypothesized based on the possession of three shared specializations exhibited by all ephippid taxa and no other taxa surveyed. Two of these characters were used by Johnson (1984) to hypothesize monophyly of the family. This study confirms the presence of these characters in all species except *Chaetodipterus lippei*, for which whole specimens were not available. The third character, the possession of posterior processes of the pelvic girdle that are elongate, pointed, parallel, and separate from one another, was discovered in this study. One additional character found in this study, the possession of an elongate fourth pharyngobranchial that completely overlays the dorsal surface of the upper toothplate of the fourth branchial arch, is present in all members of the Ephippidae, but it is also homoplastically shared with Zanclidae. The third specialization used by Johnson (1984) to hypothesize monophyly was found in this study to be present in all ephippids except *Proteracanthus*. Therefore, this character does not diagnose the Ephippidae without considering an independent loss within *Proteracanthus*.

If the most-parsimonious cladogram resulting from Constraint Analysis 4 (Figs. 34, 38, 39) is the best estimate of relationships among the Ephippidae, then we must accept a high degree of homoplastic evolution within the family. The majority of characters transformations are homoplastic. The consistency index (CI) for the family is 0.68. Recent phylogenetic analyses have found other families with similarly-high amounts of homoplasy: the similarly-distributed chaetodontids (CI = 0.66) (Blum 1989); dactyloscopids with CI = 0.64 (Doyle 1998). Testing the homology of these ambiguous characters is paramount to fully understanding and possibly reducing the high incidence of apparent homoplasy in the cladogram. The application of the ontogenetic criterion is the best approach to test these transformations.

When Johnson (1984) hypothesized monophyly of the Ephippidae based on four shared specializations of adults, he believed that early life history characters (in particular, larval morphology) could provide valuable information into the interrelationships of the ephippid genera. At that time, the only described larval representative of Ephippidae was *Chaetodipterus faber*. To date, larvae of at least five species representing three genera are known (i.e., *C. faber, C. zonatus, Platax orbicularis, P. batavianus, Ephippus orbis*). Complete series are available for the first three, as well as for *Drepane*. Eggs are known from *C. faber, C. zonatus, P. orbicularis*, and *Triperodon orbis*. (See Appendix II for historical taxonomy of ephippid larvae.)

An ontogenetic perspective could not be applied to this study because larvae of only three genera are known. However, much of the early life history information that is known for ephippids and drepaneids has been summarized in two manuscripts (Appendices III and IV).

Larval morphology could benefit this study in three ways: the ontogenetic criterion could be applied in tests of homology; characters unique to larvae could be discovered and applied to the elucidation of relationships; and characters derived from larvae could be used in an independent test of relationships.
For example, the unique condition of broad rakers associated with the first epibranchial of ephippid adults is not present in the few described larvae. The rakers in these larvae are narrow and resemble those of non-ephippids. With the discovery of more larvae, this character could be tested to see if it is homologous among ephippids.

Differences in head spination, pigmentation, and fin morphology have been observed in *Chaetodipterus, Ephippus*, and *Platax* larvae, potentially offering many characters for the elucidation of relationships (Appendix III; Ditty et al. 1994). Tyler et al. (1989) found that morphology of larval acanthuroids

(Scatophagidae and Ephippidae not examined) distinctly differed from that of the adults; a total of 30 shared specializations were found only in larvae.

Tyler et al. (1989) hypothesized the phyletic sequence Siganidae-Luvaridae-Zanclidae-Acanthuridae based on 60 specialized characters of adults. This sequence was corroborated using the 30 specialized characters of larvae exclusive of those of the adults. It is probable that a similar analysis could be applied to the Ephippidae.

Winterbottom and McLennan (1993), optimized feeding mode onto their cladogram for the Acanthuroidei and hypothesized that within the Acanthuroidei, foraging on benthic invertebrates was plesiomorphic, while herbivory was derived. Although ephippids are nearly circumglobally distributed, little is known of their biology and feeding habits. Information on the feeding habits of ephippids is available for only four genera: *Chaetodipterus*, *Ephippus*, *Platax*, and *Tripterodon*. *Tripterodon* has been observed feeding on invertebrates (not identified) on reefs (Smith 1965). *Platax* and *Ephippus* species are omnivores, feeding primarily on benthic invertebrates, zooplankton, small fishes, and algae (*Platax* only). The most detailed information regarding feeding among ephippids is known for *Chaetodipterus*. In a study of stomach contents, Hayse (1990) found *Chaetodipterus faber* to be an omnivore, feeding primarily on jellyfish, hydroids, anenomes, sponges, polychaetes, amphipods, algae, and copepods.

It is likely that *Zabidius*, *Proteracanthus*, *Parapsettus*, and *Rhinoprenes* are also omnivores. Justification for this hypothesis is based on two observations. First, fishes of these genera all inhabit open bottom areas, away from reefs: *Zabidius* in relatively deep water (34 - 64 m); *Proteracanthus* in marine to mesohaline bottom waters; *Parapsettus* over sand and mud bottoms along the coast; and *Rhinoprenes* in dark water of river mouths over sand and mud bottoms. It is probable that these fishes are feeding on benthic animals such as polychaetes, amphipods, and small fishes.

Second, the majority of anatomical modifications that have occurred within the family have been structural innovations to the mouth, branchial, and hyoid regions. In addition, there have been apparent elaborations to the sensory system of the head (i.e., numerous pores on head; large pores on chin). It is believed that these unique and numerous modifications all work in concert for food capture and manipulation. The nonprotrusive maxillae and premaxillae, broad rakers on the first epibranchial, reduced or absent interarcual cartilage, ceratohyal-hypohyal joint, elongate fourth pharyngobranchials, laminae associated with the premaxillae, and reduction or absence of the basihyal, all indicate an evolutionary trend toward increased mastication ability and pressure. For example, the absence of the interarcual cartilage probably results in increased mobility of the first epibranchial and associated rakers. The relative "shortening" of structures probably results in greater mastication pressures within the oral cavity and pharynx for processing a variety of foods. Indeed, the Ephippidae can be defined by the evolutionary trend toward increased food manipulation rather than food capture (e.g., protrusive jaws in piscivores). The presence of omnivorous feeding within at least four genera (and probably all) supports Winterbottom and McLennan's (1993) hypothesis that herbivory is derived within the Acanthuroidei.

The cladistic reinterpretation of ancestral areas (see "BIOGEOGRAPHY OF THE EPHIPPIDAE") resulted in three general conclusions: (1) the ancestor of both the Ephippidae and the Acanthuroidei had an east Indian/west Pacific distribution (Fig. 42); (2) future studies involving ancestral area estimates should treat the Indian ocean as two distinct regions (east and west); and, (3) Bremer's (1992) hypothesis of the center of origin concept is supported.

Winterbottom and McLennan (1993), concluded that the ancestor of each family within the Acanthuroidei (ephippids not included in their analysis) had an ancestral range that included the Indo-west Pacific (Fig. 42). In their study, the Indian Ocean was not delineated into eastern and western halves. Results from this study support Winterbottom and McLennan's hypothesis and extends the Indo-west Pacific (specifically east Indian/west Pacific) origin to the Ephippidae and the entire Acanthuroidei. The results of this study, combined with the fact that the Indian ocean overlays three lithospheric plates, and that Springer (1982) found a higher correlation between distributions of shorefishes and continental plates than with oceanic plates, it is recommended that future studies differentiate the Indian ocean into at least two areas (east and west) and possibly a third (north).

Within the Acanthuroidei, extensive dispersal (as evident by distributions of extant fishes) has occurred in three families: Ephippidae, Luvaridae (monotypic), and Acanthuridae (in particular, *Acanthurus*), and to a lesser extent Zanclidae. On whole, ephippids, *Luvarus*, and acanthurids have the same distributions (i.e., C, EA, I, EP, WP; see Figs. 41, 43), with the addition of west Atlantic for the Ephippidae. The distribution of ephippids is explained in more detail below.

It is likely that the range of the ancestor to the Ephippidae had an east Indian/west Pacific distribution (Fig. 44). Within the family there has been extensive geographic dispersal in some genera, and little in others. The family diverged into two distinct clades, with the ancestor of one most likely with an east Atlantic distribution (clade B), and the ancestor of the other most likely with an east Indian/west Pacific distribution (clade F) (Fig. 44). Within these two clades, ancestors to successive clades had progressively eastern distributions. Within clade B, the ancestral ranges migrated from the eastern Atlantic (node B), to the western Indian (nodes C and D), to the eastern Indian and western Pacific (node E). Within clade F, the ancestral ranges migrated from the eastern Indian and western Pacific, to the eastern Pacific.

Extensive geographic dispersal occurred in two genera: *Chaetodipterus* and *Ephippus*. If the ancestor of *Chaetodipterus* and the other ephippids in clade B had an east Atlantic distribution, then it is most parsimonious to assume that unlike the eastern movement of ancestors represented by each node, there has been an apparent westward migration within *Chaetodipterus*: from the eastern Atlantic to the western Atlantic, to the Caribbean, to the eastern Pacific. *Ephippus* (node C) migrated in both an east and west direction: from the western Indian to the eastern Atlantic; and from the western Indian to the eastern Indian, to the western Pacific. All other clades exhibit a current distribution similar to or smaller than that of the respective ancestors (Figs. 40, 44).

The limited and relatively small distribution (i.e., east Indian/west Pacific) of the ancestor to the Ephippidae supports the center of origin concept (Bremer 1992). That is, descendents dispersed from a small geographical area. Assuming the ancestor(s) of the extant ephippids were present during the Eocene, the warmer waters of the west Pacific and Indian Oceans of the Eocene (56.5-35.5 mya) and the presence of the Tethys Sea may have provided the conduit for dispersal from the ancestral area. At least one ephippid, *Eoplatax*, is known from Eocene deposits (but see below). It seems plausible that the unimpeded equatorial current of the Eocene followed by relatively rapid changes in the environment (e.g., vicariant events such as closing of the Tethys Sea) would lead to both dispersal from ancestral areas and relatively rapid adaptational and evolutionary responses.

During the Eocene, the Tethys Sea was one of the predominant oceanic features. The presence of the Tethys Sea, combined with the separation of North and South America (i.e., absence of the Isthmus of Panama), and the separation of India from Eurasia (i.e., India had not yet collided with Eurasia), allowed for uninterrupted interoceanic circulation at the equatorial latitudes. The Indian Ocean was relatively warmer than the other oceans due to warm equatorial currents coming from the east. These currents had very long residence times and were warmed by their long trip across the Indo-Pacific equatorial zone (Kennett 1982).

By the late Oligocene (25 mya), the Tethys Current was greatly restricted because of the close proximity and impending collisions of both Africa and Asia, and India and Asia (cf. Kennett 1982: 726, fig. 19-16). This essentially halted equatorial circulation. By the late Miocene (18 mya), the ocean basins resembled those of today. This was a result of four main geological events (Kennett 1982): 1) the Tethys Sea was completely restricted; 2) Asia and Africa collided; 3) the raising of the Ishtmus of Panama occurred; and 4) the continued northward movement of Australia, which separated the equatorial Indian Ocean from the equatorial Pacific Ocean.

More recent vicariant events are likely to have resulted in rapid speciation within the Ephippidae. For example, as a result of glaciation, the Pleistocene (1.6-0.01 mya) was marked by sea level lowering , increased salinity, and decreased ocean tempertatures: this resulted in isolated oceanographic regions (Kennett 1982).

Two studies (McMillan and Palumbi [1995], Woodland [1983]) offer support for this hypothesis. McMillan and Palumbi (1995) conducted a molecular phylogenetic analysis of two monophyletic groups of butterflyfishes (Chaetodontidae). These authors found a significant genetic difference between members of the Indian Ocean and those of the Pacific Ocean. As a result of low genetic differences within species groups, and strong temporal and phylogenetic concordance between the two groups, the authors concluded: (1) that there were distinct intraoceanic basin genetic relationships within each complex; (2) the two complexes formed in parallel; (3) there are two centers of diversification, one in the Indian Ocean and the other in the Pacific Ocean, with overlap of the two faunas occurring in Indonesia, the Philippines, and New Guinea; and (4) rapid speciation occurred during the Pleistocene (1.6 - 0.01 mya). One could postulate a similar explanation for the ephippids, but information derived from molecular studies is needed to measure differentiation within and among genera and ocean basins.

Woodland (1983) examined five pairs of sibling species of the family Siganidae, with one of each pair with a distribution center in the Indian Ocean, and the other of the pair centered in the Pacific Ocean. He concluded that the high diversity in the Indonesian area was a result of overlapping of two faunas, one from the Indian Ocean, the other from the Pacific Ocean. As in McMillan and Palumbi (1995), Woodland concluded that environmental changes in the form of sea level lowerings during the Pleistocene were probably responsible for the distinct faunas of the two oceans.

Blot (1969) described two ephippid genera, *Archaephippus* and *Eoplatax*. The translations of the diagnoses of these genera are in Appendices VI and VII. *Archaephippus*, as described by Blot, cannot be definitively placed in the family Ephippidae using the current synapomorphies of extant ephippids.

Blot expresses doubt regarding the placement of *Archaephippus* within Ephippidae. He states that *Archaephippus* is similar in morphology to *Psettopsis* (Monodactylidae) in many ways, and could possibly be placed in that family. Some of these similarities between these two families include the head skeleton, teeth on the endopterygoid, similar sagittal crests, and identical pectoral girdles and caudal skeletons. In many ways, these characters are just as convincing an argument for transferring *Archaephippus* to Monodactylidae as Blot had for placing *Archaephippus* in Ephippidae. Based on the fact that there are no characters mentioned in the diagnosis that are uniquely ephippid, it is recommended that *Archaephippus* be removed from the Ephippidae.

Eoplatax, as described by Blot, also possesses features that make it difficult to assign it to the Ephippidae. *Eoplatax* shares some of the same features present in *Archaephippus* (e.g., teeth on the ecto- and endopterygoids, presence of supramaxillaries) to the exclusion of extant ephippids. However, unlike *Archaephippus*, *Eoplatax*, possesses tricuspidate teeth and nonprotrusive premaxillae. Even with these features, it is not possible to definitively place *Eoplatax* in the Ephippidae. The fact that the minute skeletal and soft tissue features apparent in cleared and stained extant specimens are not evident in fossil "ephippids" casts doubt on whether these fossils will ever offer substantial evolutionary insights into evolutionary relationships.

Future research efforts regarding ephippids should be directed toward the identification and description of ephippid larvae, additional morphological examination of adults, particularly concentrating on myology, patterns of innervation, patterns of cephalic sensory pores, and molecular analysis within and among families. The ontogenetic criterion should be used for tests of homology. Molecular analysis within Ephippidae should be used to confirm the hypotheses of Woodland (1983) and McMillan and Palumbi (1995). That is, that rapid environmental changes (i.e., sea level lowering, changes in ocean salinity and temperature) during the Pleistocene lead to rapid speciation within different groups of shorefishes.

Appendix I. List of loan material for phylogenetic study of Ephippidae. Each taxonomic name is spelled as on the identification label and has not been emendated.

Taxon		Number	Catalogue Number	Origin of Loan
Larvae:				
Chaetodipterus faber		3	uncatalogued	VIMS
Platax	*batavianus*	1	I.24209-019	AMS
Platax	*batavianus*	1	I.26350-003	AMS
Platax	*batavianus*	1	I.24209-020	AMS
Platax	*tiera*	1	I.23159-002	AMS
Platax	*teira?*	1	I.24240-005	AMS
Platax	*teira*	1	I.24238-001	AMS
Platax	*teira*	1	I.24243-001	AMS
Platax	*teira*	1	I.24256-001	AMS
Platax	*teira*	1	I.24246-001	AMS
Platax	sp. 1	1	I.23534-006	AMS
Platax	sp. 2	1	I.26757-001	AMS
Platax	sp. 3	1	I.26511-001	AMS
Platax	type 2	1	I.23526-001	AMS
Platax	type 2	1	I.23595-003	AMS
Platax	type 2	1	I.24210-003	AMS
Platax	type 2	1	I.26349-002	AMS
Platax	type 2	1	I.26381-001	AMS
Platax	type 2	1	I.23581-005	AMS
Platax		1	31005-12	LACM
Platax		6	I.26505-001	AMS
Platax		1	I.25132-003	AMS
Platax		1	I.21754-005	AMS
Platax		1	I.23525-001	AMS
Platax		6	I.26503-003	AMS
Platax		1	I.26503-004	AMS
Platax		1	I.26515-001	AMS
Platax		1	I.26759-003	AMS
Platax		1	I.26985-001	AMS
Platax		1	I.23808-005	AMS
Platax		1	I.24210-004	AMS
Platax		1	I.24196-005	AMS
Platax		2	I.23552-002	AMS
Platax		1	I.26249-001	AMS
Platax		1	I.23592-007	AMS
Platax		1	I.26508-021	AMS
Ephippidae	(unidentified)	6	I.26511-002	AMS
Ephippidae	(unidentified)	1	I.23579-005	AMS
Ephippidae	(unidentified)	3	I.26515-002	AMS

Appendix I (continued)

Taxon	Number	Catalogue Number	Origin of Loan
Larvae (continued):			
Ephippidae (unidentified)	1	UCR-ICP-88-249	UCR
Ephippidae (unidentified)	1	I.23578-004	AMS
Ephippidae (unidentified)	2	44432-10	LACM
Ephippidae (unidentified)	1	I.26493-004	AMS
Ephippidae (unidentified)	~3	I.26531-006	AMS
Ephippidae (unidentified)	13	I.26504-022	AMS
Ephippidae (unidentified)	9	I.26510-012	AMS
Ephippidae (unidentified)	5	I.26508-011	AMS
Ephippidae (unidentified)	~2	I.26513-006	AMS
Ephippidae (unidentified)	18	I.26507-013	AMS
Ephippidae (unidentified)	14	I.26509-022	AMS
Ephippidae (unidentified)	~2	I.26469-004	AMS
Drepane punctata	4	S.10101-001	NTM
Drepane punctata	1	I.26388-001	AMS
Drepane punctata	1	I.24191-003	AMS
Drepane punctata	4	I.26544-007	AMS
Drepane	2	I.24191-006	AMS
Drepane	1	I.24205-005	AMS
Drepane	1	I.24206-010	AMS
Drepane	2	I.26385-001	AMS
Drepane	1	I.24190-005	AMS
Drepane	3	I.28984-021	AMS
Adults or juveniles:			
Chaetodipterus faber	4	uncatalogued	VIMS
Chaetodipterus faber	13	uncatalogued 13 C&S	VIMS
Chaetodipterus faber	~50	uncatalogued	VIMS
Chaetodipterus faber	2	03212	VIMS
Chaetodipterus faber	1	079544SD skeleton	AMNH
Chaetodipterus faber	1	090837SD skeleton	AMNH
Chaetodipterus faber	1	01533	VIMS
Chaetodipterus faber	2	08099 1 C&S	VIMS
Chaetodipterus faber	6	08021 1 C&S	VIMS
Chaetodipterus faber	1	00523	VIMS
Chaetodipterus faber	1	6104	LACM
Chaetodipterus faber	2	43528-2	LACM
Ephippus gigas (= *Chaetodipterus faber*)	1	109112 skeleton	ANSP

Appendix I (continued)

Taxon	Number	Catalogue Number	Origin of Loan
Chaetodipterus lippei (= *Ephippus lippei*)	1	1971-0065 radiograph	MNHN
Chaetodipterus lippei (= *Ephippus lippei*)	1	1967-0857 radiograph	MNHN
Chaetodipterus zonatus	1	107087	ANSP
Chaetodipterus zonatus	3	220721 1C&S	USNM
Chaetodipterus zonatus	1	220719 C&S	USNM
Chaetodipterus zonatus	1	38104-4	LACM
Chaetodipterus zonatus	5	38087-1	LACM
Chaetodipterus zonatus	5	W53-196	LACM
Chaetodipterus zonatus	3	W55-2	LACM
Chaetodipterus zonatus	2	32086-19	LACM
Chaetodipterus zonatus	1	23765	LACM
Chaetodipterus zonatus	1	32085-19	LACM
Chaetodipterus zonatus	1	uncatalogued (Banford)	VIMS
Chaetodipterus zonatus	3	3682	LACM
Chaetodipterus zonatus	1	32542-5	LACM
Parephippus (= *Chaetodipterus*)	3	030220 1C&S	USNM
Ephippus argus	1	284499	USNM
Chaetodipterus goreensis (= *Ephippus goreensis*)	4	55193 2C&S	ANSP
Chaetodipterus goreensis (= *Ephippus goreensis*)	1	041506	AMNH
Ephippus orbis	1	38133-28	LACM
Ephippus orbis	3	123281 1C&S	ANSP
Ephippus orbis	1	257868 C&S	USNM
Ephippus orbis	1	52749	ANSP
Ephippus orbis	1	285325 C&S	USNM
Ephippus orbis	1	S.11001-004	NTM
Ephippus orbis	1	S.13157-001	NTM
Ephippus orbis	2	27738 1C&S	ANSP
Ephippus orbis	1	284507	USNM
Ephippus orbis	5	62749 1C&S	ANSP
Ephippus orbis	1	62754	ANSP
Ephippus orbis	1	5307	PMBC
Ephippus rubescens	1	3132	SMNS
Parapsettus panamensis	1	306455 C&S	USNM
Parapsettus panamensis	1	340961 C&S	USNM
Parapsettus panamensis	1	9577 C&S	VIMS
Parapsettus panamensis	1	9578 C&S	VIMS
Parapsettus panamensis	2	uncatalogued (Banford)	VIMS

Appendix I (continued)

Taxon		Number	Catalogue Number	Origin of Loan
Parapsettus	*panamensis*	1	33806-41	LACM
Parapsettus	*panamensis*	1	W49-464	LACM
Parapsettus	*panamensis*	1	W54-55	LACM
Parapsettus	*panamensis*	1	W52-26	LACM
Parapsettus	*panamensis*	2	31310-36	LACM
Parapsettus	*panamensis*	1	6917-11	LACM
Parapsettus	*panamensis*	1	38463-4	LACM
Parapsettus	*panamensis*	5	32290-18	LACM
Parapsettus	*panamensis*	14	33808-11	LACM
Paropsettus	*panamensis*	1	285335	USNM
Parapsettus	*panamensis*	9	uncatalogued 3C&S	Beltran, B.
Platax	*batavianus* (= teira)	1	S.10141-003 C&S	NTM
Platax	*batavianus*	1	S.10939-003	NTM
Platax	*batavianus*	3	S.10959-089 1C&S	NTM
Platax	*batavianus*	1	103816	ANSP
Platax	*batavianus*	1	098768SD skeleton	AMNH
Platax	*batavianus*	1	098800SD skeleton	AMNH
Platax	*batavianus*	1	103818	ANSP
Platax	*batavianus*	1	103820	ANSP
Platax	*batavianus?*	1	S.11127-041	NTM
Platax	*batavianus*	1	CA1431	CSIRO
Platax	*boersii*	1	629	SMNS
Platax	*boersii*	1	85-309 C&S	IORD
Platax	*ehrenbergii* (= *Platax orbicularis*)	1	109069 skeleton	ANSP
Platax	*orbicularis*	2	24200 1C&S	ANSP
Platax	*orbicularis*	1	63140	ANSP
Platax	*orbicularis*	1	77646	ANSP
Platax	*orbicularis*	1	78250 skeleton	ANSP
Platax	*orbicularis*	2	91692 1C&S	ANSP
Platax	*orbicularis*	4	167380 1C&S	ANSP
Platax	*orbicularis*	1	37285-10	LACM
Platax	*orbicularis*	1	37398-13	LACM
Platax	*orbicularis*	1	37407-8	LACM
Platax	*orbicularis*	1	5838	PMBC
Platax	*orbicularis*	3	300618 1C&S	USNM
Platax	*orbicularis?*	1	S.10939-004	NTM
Platax	*orbicularis*	1	268668 C&S	USNM
Platax	*vespertilio* (= *P. orbicularis*)	1	167382	ANSP
Platax	*pinnatus*	1	90650	ANSP
Platax	*pinnatus*	1	5839	PMBC

Appendix I (continued)

Taxon		Number	Catalogue Number	Origin of Loan
Platax	*pinnatus*	1	273720	USNM
Platax	*pinnatus*	1	07810	VIMS
Platax	*pinnatus*	1	274680 C&S	USNM
Platax	*pinnatus*	1	42466-1	LACM
Platax	*pinnatus*	1	088344SW C&S	AMNH
Platax	*pinnatus*	1	37407-9	LACM
Platax	*pinnatus*	1	42467-2	LACM
Platax	*pinnatus*	1	37406-1	LACM
Platax	*raynaldi*	1	11043	ANSP
(=*P. teira*)				
Platax	*teira*	2	I.24233-001	AMS
Platax	*teira*	1	82305	ANSP
Platax	*teira*	1	134736	ANSP
Platax	*teira*	1	37420-16	LACM
Platax	*teira*	1	37416-4	LACM
Platax	*teira*	1	148724 C&S	ANSP
Platax	*teira*	1	C1597	CSIRO
Platax	*teira*	1	088349SW C&S	AMNH
Platax	*teira*	1	3772	SMNS
Platax	*teira*	2	4231	SMNS
Platax	*teira*	1	4264	SMNS
Platax	*teira*	1	056011	USNM
Platax	*teira*	1	084208	USNM
Platax	*tiera*	1	S.10735-002	NTM
Platax	*teira*	1	6230	PMBC
Platax	*tiera (= batavianus)*	1	S.11690-002C&S	NTM
Platax	*tiera*	1	S.11838-001	NTM
Platax	*tiera (= batavianus)*	1	S.12263-009C&S	NTM
Platax (skeleton)		1	38291-31 S-318	LACM
Platax		1	S.10356-001	NTM
Platax	*vespertilio*	1	1295	SMNS
Proteracanthus	*sarissophorus*	1	S.13177-001	NTM
Proteracanthus	*sarissophorus*	1	ZRC.3361 C&S	USDZ
Rhinoprenes	*pentanemus*	1	I.21625-001	AMS
Rhinoprenes	*pentanemus*	1	56860	MCZ
Rhinoprenes	*pentanemus*	1	134859 C&S	ANSP
Rhinoprenes	*pentanemus*	1	134860 C&S	ANSP
(on loan to USNM: borrowed from Dr. Johnson)				
Rhinoprenes	*pentanemus*	1	A3077(paratype)	CSIRO
Rhinoprenes	*pentanemus*	1	CA1651	CSIRO
Tripterodon	*orbis*	2	273721	USNM
Tripterodon	*orbis*	1	261384 C&S	USNM

Appendix I (continued)

Taxon		Number	Catalogue Number	Origin of Loan
Tripterodon	*orbis*	1	53124	ANSP
Tripterodon	*orbis*	2	39869	RUSI
Tripterodon	*orbis*	2	8508 C&S	RUSI
Zabidius	*novemaculatus*	1	S.388	NTM
Zabidius	*novemaculatus*	4	S.10031-080 1C&S	NTM
Zabidius	*novemaculatus*	1	S.10083-005	NTM
Zabidius	*novemaculatus*	1	S.10120-002	NTM
Zabidius	*novemaculatus*	1	S.10164-001	NTM
Zabidius	*novemaculatus*	1	S.11930-001 C&S	NTM
Zabidius	*novemaculatus*	1	S.12164-001 C&S	NTM
Zabidius	*novemaculatus*	1	S.12434-025	NTM
Zabidius	*novemaculatus*	1	CA1501	CSIRO
Drepaneidae				
Drepane	*africana*	3	306260 1C&S	USNM
Drepane	*africana*	1	306252 C&S	USNM
Drepane	*longimana*	3	306246	USNM
Drepane	*longimana*	1	38294-11 skeleton	LACM
Drepane	*longimana*	1	38294-29 skeleton	LACM
Drepane	*longimanus*	3	284483 1C&S	USNM
Drepane	*longimanus*	1	284472 C&S	USNM
Drepane	*longimanus*	1	S.13157-007	NTM
Drepane	*punctata*	1	38117-68 skeleton	LACM
Drepane	*punctata*	1	C4492	CSIRO
Drepane	*punctata*	1	306455 C&S	USNM
Drepane	*punctata*	1	284825 C&S	USNM
Drepane	*punctata*	2	006531	USNM
Drepane	*punctata*	1	S.1168	NTM
Drepane	*punctata*	3	S.12373-002 1C&S	NTM
Drepane	*punctata*	1	07540	VIMS
Drepane	*punctata*	9	S.12510-012 1C&S	NTM
Drepane	*punctata*	1	S.12898-022	NTM
Drepane	*punctata*	1	S.13003-003 C&S	NTM
Drepane	*punctatus*	1	284499	USNM
Drepane		6	S.10057-001 1C&S	NTM
Scatophagidae				
Scatophagus	*argus*	1	180258 C&S	USNM
Scatophagus	*argus*	1	5444	OSU
Scatophagus	*argus*	1	4807	OSU
Scatophagus	*argus*	3	224393 C&S	USNM

Appendix I (continued)

Taxon	Number	Catalogue Number	Origin of Loan
Scatophagus tetracanthus	2	75584 1C&S	ANSP
(misidentified on loan and label as *Tripterodon orbis*)			
Selenotoca multifasciata	1	173514 C&S	USNM
Siganidae			
Siganus marmoratus	1	018791 C&S	AMNH
Siganus spinus	1	029387 C&S	AMNH
Siganus javus	2	07511	VIMS
Luvaridae			
Luvarus imperialis	2	231697 C&S	USNM
Luvarus imperialis	1	4942	OSU
Acanthuridae			
Acanthurus achilles	1	140006 C&S	USNM
Acanthurus leucosternon	1	043437SW C&S	AMNH
Ctenochaetus striatus	1	038133SW C&S	AMNH
Naso unicornis	1	309439 C&S	USNM
Zebrasoma xanthurum	1	342913 C&S	USNM
Zanclidae			
Zanclus canescens	1	038139SW C&S	AMNH
Zanclus cornutus	1	342965 C&S	USNM
Zanclus cornutus	1	342966	USNM
Pomacanthidae			
Centropyge bicolor	1	056995 C&S	USNM
Centropyge bispinosus	1	336477 C&S	USNM
Holacanthus tricolor	1	021351SW C&S	AMNH
Pomacanthus maculosus	1	147894 C&S	USNM
Pomacanthus paru	1	263253 C&S	USNM
Pygoplites diacanthus	1	261764 C&S	USNM
Chaetodontidae			
Chaetodon auriga	1	340963 C&S	USNM
Chaetodon sedentarius	1	159275 C&S	USNM
Chaetodon trifasciatus	1	140142 C&S	USNM
Forcipiger flavissimus	1	340962 C&S	USNM
Heniochus acuminatus	1	147893 C&S	USNM
Prognathodes aculeatus	1	088374SW C&S	AMNH

Appendix I (continued).

Taxon	Number	Catalogue Number	Origin of Loan
Kyphosidae			
Microcanthus strigatus	1	267047 C&S	USNM
Moronidae			
Morone americana	1	785 C&S	VIMS
Morone saxatilis	1	4251 C&S	VIMS
Serranidae			
Centropristes philadelphicus	1	1418 C&S	VIMS
Mycteroperca microlepis	1	3218 C&S	VIMS
Centrarchidae			
Ambloplites rupestris	1	2363 C&S	VIMS
Lepomis auritus	1	242 C&S	VIMS
Percidae			
Perca flavescens	1	3370 C&S	VIMS
Apogonidae			
Epigonus pandonius	1	7468 C&S	VIMS
Carangidae			
Caranx crysos	1	9080 C&S	VIMS
Sciaenidae			
Bairdiella chrysura	1	2764 C&S	VIMS
Coracinidae			
Coracinus multifasciatus	1	274682 C&S	USNM
Dichistius multifasciatus	1	28391	RUSI
Dichistius capensis	1	2861	RUSI

Appendix II. Historical taxonomy of ephippid larvae.

Of the eight genera and 15 ephippid species, larvae are known for three genera and approximately six species, although representatives of only two genera have been illustrated. Hildebrand and Cable (1938) gave the first description of verified larvae of *Chaetodipterus faber.* Johnson (1978) supplied additional information on larvae of this species. The eggs of *C. faber* were later described by Gaspar (1984). Ditty et al. (1994) redescribed larvae of *C. faber.* Martinez-Pecero et al. (1990), followed by Ambrose (1996) described eggs and larvae of *C. zonatus.* Leis and Trnski (1989) described larvae of *Platax batavianus,* at least two identified *Platax* species, and *Ephippus orbis*; only the *Platax* species were illustrated. No additional species were described for the revision of this book (see Appendix III). The *Ephippus orbis* larvae mentioned above were not available for loan during the revision and have yet to be illustrated. Masanet (1994) described and sketched larvae of *Platax orbicularis* reared in an aquarium.

Appendix III. Chapter on larval ephippids of the Indo-Pacific. Chapter submitted for review for inclusion in The Larvae of Indo-Pacific Shorefishes, second edition (see Leis and Trnski 1989). Every ephippid larva on loan was examined for this manuscript. Figures were omitted, as they will most likely remain the same as the first edition.

Ephippidae — Batfishes, Spadefishes

Martin R. Cavalluzzi, Jeffrey M. Leis, Thomas Trnski

Adults Ephippids are extremely deep-bodied, laterally compressed fishes of medium size. They are semi-pelagic, form schools in relatively shallow water, and are usually loosely associated with coral and rocky reefs, mangrove swamps, grass beds, or manmade structures. Primary foods include plant material, sponges, gorgonians, zooplankton, and benthic invertebrates (mainly molluscs and polychaete worms). We follow Johnson's (1984) definition of the family, and amend it to include *Zabidius* (Eschmeyer 1990). There are six Indo-Pacific genera and eleven species (Maugé and Heemstra 1984b, Sainsbury *et al* 1984).

Spawning Mode Known for only one Indo-Pacific genus, *Platax*. Naturally-spawned eggs of *P. orbicularis* held in a public aquarium were collected, reared and described (Mansanet 1994). Eggs of this species are positively buoyant, spherical, 1.5 mm in diameter, with a single oil globule; they hatched at an estimated 28-36 h at 26 °C and a salinity of 35 ppt. Eggs of *Chaetodipterus faber* (western Atlantic) and *C. zonatus* (eastern Pacific) are small (about 1 mm), transparent, with a smooth chorion, a minimum perivitelline space, a segmented yolk, and one oil globule (*C. zonatus*, mean diameter 0.13 mm; *C. faber*, diameter range 0.25-0.35 mm) (Ambrose 1996, Johnson 1984, Martínez-Pecero et al. 1990). *Chaetodipterus faber* eggs hatch by 26 h at 24.5-28.5 °C (31 - 32 h at 20-23.5 °C) and salinities of 37.5-38.5 ppt (Gaspar 1984).

Development at Hatching Known for only one Indo-Pacific genus, *Platax*. *Platax orbicularis* hatch at about 2.5 mm TL, with a large yolk sac and unpigmented body (Masanet 1994). The single oil globule is located in the middle of the yolk sac and the larva initially floats belly up. *Chaetodipterus* (western Atlantic, eastern Pacific) hatch at about 2 mm with a large yolk sac (about 1.2 mm in total length in *C. faber*), incipient preopercular spines, functional mouth and digestive tract, pigmented eyes, and melanophores on the yolk-sac; larvae initially float belly up (Gaspar 1984, Martínez-Pecero et al. 1990).

Larvae *Morphology*— Young ephippid larvae have a moderate to deep body, with the head and trunk combined into a ball-like unit, nearly as broad as high. The tail is relatively compressed. Postflexion larvae are initially deep-bodied and laterally compressed, but become extremely deep-bodied with growth. There are 24 myomeres (8-13+11-16). The gut is triangular to round and tightly coiled, normally reaching to 47-68 percent BL. A conspicuous gas bladder is present in all specimens examined; it is located dorsal to the anterior portion of the gut, but expands posteriorly with growth. The large head is initially round to rhomboid, and becomes deeply ovate in postflexion larvae. Later the head becomes increasingly deeper than long. The profile becomes steep during the preflexion stage and remains so. The mouth is initially large, slightly oblique, with subequal jaws. The maxilla reaches to the posterior margin of the eye in preflexion larvae; in postflexion larvae relative mouth size decreases with the maxilla reaching only to midpupil. In larger larvae (> 13 mm) the mouth becomes more or less horizontal. Teeth are present by 2.5-2.8 mm, and are large, numerous, and cuspidate (tricuspidate teeth begin forming as early as 12.3 mm). The eye is small to moderate and round and does not change relative size with growth. Gill membranes are initially free from the isthmus; they become attached to each other anteriorly by 3 mm, broadly attached to one another during flexion, and then become broadly attached to the isthmus as early as late in the flexion stage in some species. During the early postflexion stage, the nasal capsule differentiates into separate nares, and a prominent sensory canal located medial to the nares becomes apparent. Head spination is well-developed in most species. The anterior margin of the preopercle may have up to four very small spines on a ridge; the ridge is present in all larvae examined. The posterior margin of the preopercle possesses small, smooth spines in some species by 2.5 mm; some spines, particularly the one at the angle, may become long, increasing head width to 65-80 percent SL. The spines are initially naked, but are soon covered basally by thick dermal tissue; in postflexion larvae at least the basal half of each spine is covered. After about 13 mm, the preopercular spines are short, rounded and almost completely enclosed by the tissue and may persist in this state to about 80 mm. A posteriorly-directed supraoccipital spine with a weakly to strongly serrate leading edge (i.e., crest) is present by 2.5-2.9 mm; the crest may extend up to 21 percent SL. The supraoccipital crest and spine is variously covered by flesh: in some, the crest is fully exposed; in others, the crest may be completely covered except for the tip of the spine. The supraoccipital spine becomes reduced and completely engulfed by flesh by as early as 11 mm in some species. A weak opercular spine is apparent by 2.8-3.7 mm, and disappears in *Platax* by 12-14 mm; the spine is unreduced in the largest *Ephippus* (6.1 mm). A posttemporal spine appears as early as 3.6 mm. It is retained in postflexion larvae of some species but is reduced to a low ridge in others. A supracleithral spine appears during the flexion stage in *Ephippus* and is unreduced in the largest specimen (6.1 mm). A supracleithral spine and/or ridge appears in some *Platax* species by 6.2 mm, may be absent in others, and disappears by 9-14 mm. A supraocular ridge appears by 2.6-3.3 mm and varies among species from low and smooth to large and strongly serrate; most with one prominent spine. The supraocular ridge is unreduced in the 6.1 mm *Ephippus* larva, but disappears by 10-12 mm in *Platax*. One interopercular spine appears at 2.6-3.3 mm; it is reduced but present in the largest *Platax* larva examined. A small pterotic spine is present in *Ephippus* by 4.8 mm; a small ridge is present on only two *Platax* larvae (10.6 and 12.3 mm). A small, serrate infraorbital series and a small tabular spine are present in our largest *Ephippus* (6.1 mm). Dorsal- and anal-fin anlagen form in preflexion larvae by 3.3-3.8 mm and incipient rays appear during flexion. All dorsal and anal elements are present by 6.1-7.7 mm, and the spines and posteriormost rays are the last to ossify. The first anal ray and, in some species, the first dorsal ray transforms to a spine by 9 mm. The fin membranes become thick and fleshy and the elements become very long in postflexion larvae, continuing to increase in length through the early juvenile stage. Pectoral-fin rays begin to form during preflexion and all rays are ossified in postflexion larvae by 6.1-8.9 mm. Small pelvic-fin buds appear prior to flexion and all elements are ossified in early postflexion larvae. The pelvic fin becomes extremely elongate and reaches beyond the anus in larvae larger than 8 mm; the longest ray may reach as far as the base of the thirteenth anal-fin ray and measure up to 64 percent SL. Scales are present only in the largest larva (14.4 mm) and they cover nearly the entire body; each scale with a single small spine. Lateral line pores may be apparent by 11 mm. Specializations to larval life include the globose body, large mouth and head spination.

Size of smallest examined specimen — 2.5-3.5 mm
Size at initial ossification of dorsal-fin elements — 4.8-5.6 mm
Size at caudal flexion — 3.8-6.2 mm
Size of largest examined pelagic specimen — 6.1-14.4 mm

Morphometrics (proportion of body length):

	preflexion larvae	*postflexion larvae*
PAL	.45-.68	.51-.67
PDL	.31-.59	.31-.48
HL	.32-.50	.32-.50
SnL	.06-.14	.08-.20
ED	.09-.12	.07-.13
BD	.34-.54	.56-.87
BW	.17-.41	.22-.42
[BD/BW][a]	1.14-2.91	1.58-3.29
VAFL	0-.03	0-.04

[a] Not a proportion of body length.

Pigment — Ephippid larvae initially are lightly pigmented. Preflexion larvae variously possess the following: a pigment patch associated with the anterior margin of the nasal capsules; melanophores associated with the occiput and dorsal midline, between the supraoccipital crest and the dorsal fin; a pigment patch on the roof of the mouth (vomer); a pigment patch on the retroarticular and the cleithral symphysis; scattered melanophores on the chin, isthmus, opercle, preopercle, preopercular spines, abdomen, pectoral-fin base, and pelvic-fin buds; a band of melanophores extending from the abdomen to the posttemporal; a single-file row of melanophores extending between the cleithral symphysis and the anus; the ventral midline with up to one melanophore per myomere; single melanophores associated with basal ends of a few anteriorly-located anal-fin pterygiophores; pigment patches posteriorly on gut; and, one or two small melanophores dorsal to the gas bladder. The rest of the body is unpigmented.

Early-stage postflexion larvae possess similar pigment to preflexion larvae except that it is usually more pronounced. One species, *Platax batavianus*, remains lightly pigmented until about 8 mm, at which time, a distinct bar of melanophores forms, extending from the dorsal margin of the eye to the dorsal fin spines. At this length, it will also possess light pigmentation on the cheek, preopercle, opercle, abdomen, and scattered pigment on the pectoral-fin rays. At about 11 mm, there is a proliferation of melanophores covering the majority of the body. Other species with a proliferation of melanophores as early as 5.7 mm. This pigment is usually heavy over the entire body except in the following areas, which are naked or lightly pigmented: occiput, often with only a few melanophores; cheek; snout, except for a few melanophores on the maxilla; caudal fin and posterior portion of caudal peduncle; pectoral fin, except at base and usually base of a few rays; posteriormost dorsal- and anal-fin rays completely naked, others naked distally. By 11 mm, larvae are usually heavily pigmented, with melanophores present on entire head and body, including the lips; pigment absent only distally on the caudal peduncle, dorsal- and anal fins, and the entire caudal fin. This pattern involving the dorsal-, anal-, and caudal fins is distinctive and is present in some larvae from as early as 5.7 mm to at least 14 mm.

Similar Families — Ephippids are characterized by their head spination, particularly the supraoccipital crest and large preopercular spines, the rotund head and gut, pigment, subequal jaws, and in later larvae, by the elongate fin rays. The larvae most likely to be confused with ephippids are the very closely related drepaneids. Other larvae likely to be confused with ephippids are carangids, lobotids, and perhaps cepolids and bramids, because of similarities in head spination. Drepaneid larvae are similar in body shape and head spination but differ from ephippids in that they possess the following: a less rotund body prior to notochord flexion; an inferior mouth from the flexion stage onwards; a larger supraoccipital crest with many more serrations; prominent supraneurals; more prominent head spines, particularly the pterotic, sphenotic, parietal, tabular, and posttemporal; the second anal-fin spine is the longest (each successive spine is longer than the previous in ephippids); pigment on the pectoral fin at all stages; and, heavy concentrations of pigment on the snout and tip of the upper jaw. In many characters, *Ephippus* is intermediate between *Platax* and *Drepane* making identification difficult. In contrast to ephippids, carangid larvae lack interopercular and opercular spination. Most carangids are laterally compressed with a lateral midline melanophore series. In addition, the first two anal-fin spines are widely separated from the third, the origin of the dorsal fin is posterior to the pectoral fin base (*Selene* is an exception), and most with pelvic-fin rays that do not extend beyond the anus (*Selene* is an exception). The carangid most likely to be confused with ephippids is *Parastromateus niger*, but this species has over 40 dorsal rays, over 35 anal rays and smaller preopercular spines than ephippids. Lobotid larvae are similar to ephippids in that they are deep-bodied, with similar head spination and pigmentation, particularly the lack of pigment distally on the dorsal- and anal-fin rays, caudal peduncle, and caudal fin. They differ from ephippids in that they are not rotund, the supraoccipital crest is much larger relative to that of ephippid larvae, the pelvic fins form early and are heavily pigmented (rays develop before those of other fins), and they possess fewer dorsal- and anal-fin rays, none of which are elongate. They also obtain the "tripletail" appearance by about 7 mm. Early *Platax* larvae have a shape similar to that of bramid and cepolid larvae, but both the latter have many more than 24 myomeres. Bramids also lack a supraoccipital crest, have heavy pigmentation associated with the brain and nape, and may have pigment associated with the notochord tip.

Description is based on a complete set consisting of *Ephippus orbis* and three or four *Platax* spp.

Meristic Characters of Indo-Pacific Ephippid Genera.

	D	A	P_1	P_2	C	Vertebrae
Ephippus	VIII-IX,19-20	III,15-16	18-19	I,5	9+8	10+14=24
Platax	V-VII,28-39	III,19-29	16-20	I,5	9+8	10+14=24
Proteracanthus	X,14-16	III,13-15	19	I,5	9+8	10+14=24
Rhinoprenes	VIII,19-21	III,16-19	19-21	I,5	9+8	10+14=24
Tripterodon	IX,19-21	III,15-17	17-19	I,5	9+8	10+14=24
Zabidius	IX,27-29	III,20-22	19-21	I,5	9+8	10+14=24

Fig 33 *Larvae of the ephippid genus* ***Platax*** *from the Great Barrier Reef Lagoon: A-C near Lizard Island (plankton tows), D off Townsville (midwater trawl).*

A *2.9 mm.*

B *4.5 mm.*

B' *Dorsal view of B, pigment omitted.*

C *7.5 mm* ***P. batavianus.***

D *11.6 mm* ***P. batavianus.***

D' *Dorsal view of D, pigment omitted.*

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Appendix IV. Chapter on larval drepaneids of the Indo-Pacific. Chapter submitted for review for inclusion in The Larvae of Indo-Pacific Shorefishes, second edition (see Leis and Trnski 1989). Every ephippid larva on loan was examined for this manuscript. Figures were omitted, as they will most likely remain the same as the first edition.

Drepaneidae — Blunt Spadefishes, Sicklefishes, Spotted batfish, Concertina fish

Martin R. Cavalluzzi, Jeffrey M. Leis, Thomas Trnski

Adults Drepaneids are moderately sized (up to 40 cm), deep bodied, laterally compressed fishes. They possess a protractile mouth which extends downward when open, rows of brushlike teeth, and long, falcate pectoral fins which reach the base of the caudal fin. Found in relatively shallow water over sand, mud, or mixed sand- and shell-covered bottoms, often near reefs. There is one genus with two Indo-Pacific species (Druzhinin 1977, Lloris and Rucabado 1987, Masuda *et al* 1984, Maugé and Heemstra 1984a).

Spawning Mode Mature ovarian eggs of *Drepane punctata* are small (0.8-0.9 mm) (Thresher 1984).

Development at Hatching Unknown.

Larvae *Morphology*— Larval drepaneids are initially deep-bodied with a relatively rotund head and trunk and a relatively compressed tail. They become increasingly deep-bodied and laterally compressed with growth. There are 24 myomeres (10-13+11-14) which become obscured by heavy pigment in postflexion larvae. The large triangular gut is tightly coiled and the anus is located at 47-64 percent BL. The gas bladder is inconspicuous, centered over the gut, and elongates posteriorly with growth. The head is large and initially round but, after notochord flexion, it develops a steep profile and becomes increasingly deep. The short snout is slightly concave in preflexion larvae, becomes rounded during the flexion and early postflexion stages, and develops an irregular profile as the ascending process of the premaxilla elongates. The mouth is initially relatively large, slightly oblique, with the maxilla reaching to the posterior margin of the pupil. With growth, the mouth becomes inferior and relatively smaller; from about 16 mm, the maxilla reaches only to the anterior margin of the eye. In the smallest specimen, the lower jaw projects slightly beyond the upper jaw; in all other specimens, the opposite occurs. Small, pointed teeth are present in the lower jaw by 2.2 mm and in both jaws by 3.2 mm. The lips become fleshy by 10 mm and may conceal the teeth. A lateral flange, distally on the maxilla, is apparent by 7 mm. The eye is large and round in the smallest specimen, but in all others, relative eye size ranges from small to moderate. Gill membranes become broadly attached to the isthmus between 7 and 8 mm. Head spination is well-developed, complex, and present in all specimens examined; spination generally increases from preflexion to postflexion, and then variably decreases at about 20 mm. Spination in the smallest specimen comprises a supraoccipital ridge, a narrow spine associated with the dorsoposterior margin of the interopercle, spines associated with the anterior and posterior margins of the preopercle, a reduced supraocular ridge, and a small bony ridge associated with the angular. The supraoccipital ridge in the 2.2 mm larva is initially long (39 percent HL), strongly-serrate, and located dorsally on the body. With growth, this ridge is displaced anteroventrally as the dorsal-fin pterygiophores elongate, the supraneurals enlarge, and the body deepens. The ridge initially is serrated, but later gains up to 10 spines. Preopercular spines are smooth with the one at the angle of the posterior margin being the longest (41 percent HL in the 2.2 mm larva). With growth, spines are added to the preopercle; at most, there will be four spines anterior to the one at the angle and two dorsal to the spine at the angle. The anterior margin of the preopercle possesses three to seven small spines on a ridge. A narrow, weak spine is associated with the dorsoposterior margin of the interopercle in larvae between 2.2 and 13 mm. One or two weak spines are associated with the ventroposterior margin of the subopercle in larvae between 3.2 and 13 mm. A blunt spine is present on the dorsoposterior margin of the opercle by 10 mm. A small bony ridge associated with the lateral margin of the angular is present in larvae beginning at 2.2 mm; although present in all larvae examined, this ridge becomes relatively smaller in larvae larger than 10 mm. The retroarticular is pointed and spine-like in larvae between 4.3 and about 24 mm; with growth it becomes more rounded. The maxilla possesses a bony ridge that projects anteriorly over the premaxilla near the ascending process in larvae between 3.2 and 10 mm. Spines associated with the infraorbital sensory canal system form early. Those associated with the anterior infraorbitals are present by 4.3 mm, and are in three distinct areas: a small group of up to five spines located beneath the posterior margin of the pupil; a small group of up to three spines located beneath the anterior margin of the eye; a large group of up to seven spines associated with the lachrymal. Spines associated with the posterior infraorbitals are present by 7.1 mm, and consist of up to two groups of small spines located at a height equal to the dorsal- and ventral margins of the pupil, respectively. Parietal and tabular spines are present by 7.1 mm. The supraocular, pterotic, sphenotic, posttemporal, and supracleithral bones have extensive spination. In larvae between 7 and 10 mm, when spination associated with these bones is at a maximum, a nearly complete bony ridge is formed with these bones. The supraocular ridge is present but reduced in the smallest specimen; the posttemporal is present by 3.2 mm. Spines or ridges associated with the other bones are present by 7 mm, but reduced or absent in the largest larvae examined. A low nasal ridge is present from about 8 to 20 mm. Barbels associated with the chin, angular, and isthmus begin to appear in pairs by 7 mm. Development of barbels is variable, but by 14 mm, 11 pairs of barbels are present; these persist until about 250 mm (Maugé and Heemstra 1984a). Sensory pores on the chin begin to develop at about 7 mm but are not distinct until 13 mm. Dorsal- and anal-fin anlagen are present by 2.2 mm; both soft rays and then spines appear during the flexion stage. All dorsal- and anal-fin elements are present by 7.1 mm, but the first soft ray of each fin transforms into a spine by 8 mm. Spines are weak when they begin to ossify, but become very robust by 7 mm. The second anal-fin spine is slightly longer than the third; the first is the shortest. The procumbent spine of the first dorsal-fin pterygiophore is present in postflexion larvae. Supraneurals are apparent between the supraoccipital crest and the dorsal-fin origin in postflexion larvae. Pelvic-fin buds are present at 2.2 mm, and incipient rays are present by the end of the flexion stage. In flexion-stage larvae, the pelvic-fin rays are relatively short; the longest being 23 percent BL. In postflexion larvae the rays become relatively longer, extending up to 46 percent BL; the outermost ray is much longer than the other rays. The two branches of the outermost ray are of two different lengths; the median half is up to 55 percent longer than the lateral half. Pelvic rays begin to branch at 4.3 mm (rays 1 and 5 branch first), and all rays branch once by 13.8 mm. Ossification of the pelvic fins is complete by the end of flexion, at which time the fins reach to or beyond the anus. Pectoral-fin rays begin to ossify early in the flexion stage and all rays are present by the time flexion is complete. The caudal-fin rays become relatively elongate in postflexion larvae; rays up to 43 percent BL. The lateral line begins to form at about 8 mm and is complete by 14 mm; at this length, non-lateral line scales are present on the entire body. Larvae 13 mm and larger possess some scales with a single small spine on each; these scales are distributed among the others scales anteriorly on the body above the lateral line, including the top and sides of the head, the opercle, the cheek, the pectoral-fin base, and the side of the body ventral to the pectoral fin. There is no distinct settlement stage, instead, a gradual transition to the juvenile form and habitat takes place. Specializations to pelagic life include the large head with associated spination and the large mouth.

Size of smallest examined specimen — 2.2 mm
Size at initial ossification of dorsal-fin elements — 3.4 mm
Size at caudal flexion — 3.3 - 4.3 mm
Size of largest examined pelagic specimen — 27.3 mm

Morphometrics (proportion of body length):

	preflexion larvae	postflexion larvae
PAL	.51-.64	.47-.59
PDL	.45-.53	.34-.49
HL	.36-.47	.37-.44
SnL	.08-.21	.08-.12
ED	.11-.14	.08-.11
BD	.45-.56	.42-.73
BW	.10-.16	.11-.25
[BD/BW][a]	2.9-5.0	2.0-4.8
VAFL	.01-.03	.03-.07

[a] Not a proportion of body length.

Pigment — Drepaneid larvae initially are lightly pigmented. The majority of pigment in preflexion larvae is on the snout, in three distinct locations: 1) a large pigment patch on the anterodorsal surface of the premaxilla; this is the most prominent pigment character in preflexion larvae; 2) anteriorly on the maxilla;

this pigment increases with growth; 3) the inside perimeter of the nasal capsules, particularly anteriorly and posteriorly; at this stage, the nares are beginning to differentiate. Scattered melanophores are present on the abdomen, initially concentrated on the descending portion of the gut and later scattered over entire abdomen. The pectoral- and pelvic-fin rays are lightly pigmented; melanophores are evenly distributed along the lengths of the pectoral rays except for the few dorsalmost rays, which are almost void of pigment. The large spines on the posterior margin of the preopercle are often lightly pigmented on their anterior edges. Internal pigment consists of a pigment patch on the dorsal surface of the gas bladder, and two pigment patches associated with the posterior side of the gut, just above the anus. The rest of the body is unpigmented. Early-stage postflexion larvae possess snout pigment similar to that of preflexion larvae, as well as, lightly pigmented pectoral and pelvic fins, large melanophores evenly distributed lateral to the dorsal- and anal-fin pterygiophores, and usually one pair of melanophores on each side of the occiput. The caudal fin is the last fin to become pigmented; in early-stage larvae only the basal ends are pigmented; in later stage larvae only the basal third of the rays is pigmented. By 7.2 mm, large melanophores are scattered over the entire body including the lateral and ventral sides of the head. Paired melanophores are located on the occiput. There are also scattered melanophores on the brain, primarily posteriorly. By 8.3 mm, pigment associated with the snout is reduced to one large melanophore on each side of the premaxilla, associated with the base of each ascending process; this pigment is present in larvae of all sizes examined. By 10.4 mm, the body is covered by two distinct sizes of melanophores; small melanophores randomly distributed on the body and all fins; large melanophores arranged on the body in inconspicuous lines (see below). In addition, the dorsal-, anal-, and pelvic fins are darkly pigmented. By 13.8 mm, pigmentation on the body has increased and the barbels on the chin are now pigmented. Pigment on the caudal fin is confined to the basal portion (ca. 15 percent of fin is pigmented). The large melanophores on the body are in inconspicuous lines, however, distinct lines of uniformly distributed melanophores are apparent in the vicinity of the dorsal- and anal fins (lateral to the pterygiophores) and midbody (lateral to the vertebrae). By 17.6 mm, the dorsal and anal fins are completely pigmented except for the posteriormost rays which are unpigmented distally. A large melanophore is associated with the membrane between the bases of each dorsal- and anal-fin ray. Pigment remains constant until about 25 mm when the cornea becomes partially covered dorsally and ventrally with pinpoint melanophores. By 27.3 mm the only addition to pigmentation is that the branchiostegal rays become pigmented.

Similar Families — Drepaneid larvae are characterized by their: initially rotund head and trunk which later become very compressed and deep; head spination, particularly the long, serrate supraoccipital crest, serrate infraorbital and pterotic ridges; pigment, particularly on the snout, pectoral fins, and mixed large and small melanophores on the body and fins (large melanophores in obscure lines); barbels; and the somewhat oblique and, in postflexion larvae, inferior mouth. Drepaneid larvae are likely to be confused with the closely-related and very similar ephippid larvae and larvae similar to them (see chapter on ephippids: the characters which separate ephippids from the other groups will also separate the drepaneids from them).

Description is based on an incomplete set of five preflexion larvae and sixteen postflexion larvae of at least *Drepane punctata*.

Meristic Characters of the Indo-Pacific Drepaneid Genus

	D	A	P_1	P_2	C	Vertebrae
Drepane	VIII-IX,19-23	III,17-19	15-18	I,5	3-5+9+8+3-5	10+14=24

Fig 31 *Larvae of the drepaneid genus* ***Drepane*** *from the Great Barrier Reef Lagoon, near Townsville; A-C from midwater trawls taken nearshore; D from an epibenthic sled tow in a mangrove estuary.*

A *2.3 mm.*
B *3.6 mm.*
C *7.1 mm* ***D. punctata.***
D *16.7 mm* ***D. punctata.***
E **Dorsal view of head spination?**

Index terms: *Drepane*, *Drepane punctata*, Drepaneidae, Blunt Spadefishes, Sicklefishes, Spotted batfish, Concertina fish

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Appendix V. Translation of Blot's (1969) description of the genus *Archaephippus*, placed in the family Ephippidae. Only select portions are presented here. Translation by Laurent Mezin (pers. com.), with help on bone terminology by me. Nothing in the translation has been modified. For example, Bleeker (1859) first diagnosed the family Ephippidae, as opposed to Blot's designation of Gill (1862). Blot, J. 1969. Les poissons fossiles du Monte Bolca: Carangidae, Menidae, Ephippidae et Scatophagidae. Studi e ricerche sui giacimenti terziari di Bolca, Verona, 1: 1-540.

Family of Ephippidae Gill 1862

Diagnosis

Body strongly compressed, tall, covered with scales of medium size, smaller on the head, continuing on the soft dorsal, anal, and caudal fins. Lateral line arch forming an angle. Head much shorter than high, densely and irregularly covered with scales. Postemporal articulated to the cranial wall. Very small mouth, terminal, almost horizontal. Jaws with rows of setiform teeth. Six to eight branchiostegal rays. Dorsal fin very marginated with a spiny portion and a soft portion preceeded by a spiny ray. Anal fin with three spines and a soft part similar to that of the dorsal. Obtuse caudal. Pectorals small or medium. Pelvics pointed with a longer spine.

Genus *Archaephippus* nov. gen.

Diagnosis

Fairly small mouth, non-protractile jaws. Suspensorium almost perpendicular to the axis of the body. Strong neural spines, slightly flattened at their extremities but not lanceolated. The last parapophysis does not present a widening (not basin-shaped). Hemal spine complex of type IIIa. Triangular pectorals, continuing almost to first caudal "hemocanth". Dorsal fin with a strong spiny portion (D_1), slightly less elevated than rays of soft portion. Caudal truncated with posterior edges very slightly concave. Scales weakly ctenoid, cycloid on the head. Lateral line slightly arched, parallel to the dorsal profile.

The samples from Monte Bolca placed in this new genus had first been placed in the genus *Chaetodon* by Volta (1796), Blainville (1818), and Krüger (1923), and the genus *Ephippus* by Agassiz and his successors. After a more thorough study, I felt the need to create the new genus *Archaephippus*. Without necessarily implying a direct phylogeny between this new genus and the existing genus *Ephippus*. This genus is represented by fossil forms only, and is represented by a species of the Eocene from Monte Bolca, and perhaps a species from the mid-Eocene of Val Sordina of Lonigo (Province of Vicence): *Ephippus nicolisi* Bassani 1888.

Systematic Position

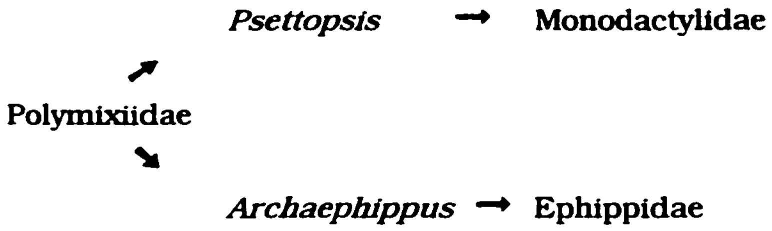
The preceeding study allowed us to notice the new genera *Archaephippus* as clearly separated from the genus *Ephippus*. Indeed the size of the mouth, the presence of the supramaxillaries, the probable presence of teeth on the ectopterygoids and the endopterygoids, the eight pairs of branchiostegal rays, the presence of epipleural bones, the well-developed pelvics, the lateral line very weakly arched, are so many characters that distinguish the two genera, and as one can notice within these characters, a number of which indicate the primitiveness of the genus *Archaephippus*. The supramaxillaries, the palatine teeth, the muscular ribs, and the number of branchiostegal rays. One needs to notice that this does not imply a direct phylogenetic relationship between *Archaephippus* and *Ephippus*.

The genus *Archaephippus* seems as if it needs to be placed within the Ephippidae even though some of its characteristics would place it close to the Monodactylidae and more precisely to the genus *Psettopsis*. Indeed, the skeleton of the head of these to genera are fairly comparable. In *Psettopsis*, the endopterygoid is toothed. It seems also to be in *Archaephippus*, though we know this character is only observed today in the families Monodactylidae, Kyphosidae, and Scorpidae. The sagittal crest in these two genera (*Archaephippus* and *Psettopsis*) is of the knife-blade type and presents a very-finely serrated anterodorsal edge. The pectoral girdle is identical and so is the internal caudal skeleton. However, *Archaephippus* has a double dorsal fin (i.e., spiny and soft dorsals) which is not found in Psettopsis, where the dorsal is unique and continuous, with a very small spiny portion. The "hemal spine" complex is similar between the two, but it's orientation ("obliquity") is very different: where it goes forward in *Psettopsis*, it is very clearly oriented backwards in *Archaephippus*. Thus, *Archaephippus* is strongly connected in one part to the *Ephippus* genus, but also has many common points with *Psettopsis*, and this allows us to pose the problem of relationships between the Ephippidae and the Monodactylidae. Two solutions come to mind: either this is convergence within two clearly distinct lines or, and this seems more probable to me, one must accept a commonality of origin for the two families, and in the Eocene, and in the levels of the Pesciara, where the two families are represented, the types are still fairly close to their origins so that their common points are more numerous than in the modern genera *Ephippus* and *Monodactylus* (= *Psettus*) that derived from them.

This outlook is not completely new since Jordan (1923), Arambourg of Bertin (1958), and E. of Y. Le Danois (1963) considered that the ephippids needed to be brought closer to the Monodactylidae, the Kyphosidae, and the Pempheridae.

According to Patterson (1964), those three families could find their origins in the Polymixiidae. It does not seem impossible to also bring in the Ephippidae line, but then it would probably be necessary to separate this family from the Chaetodontidae group, within which many authors place it (Boulenger 1895).

The sagittal crest of ephippids is of an entirely different type than that of the Chaetodontidae. This position can be put thus:


Psettopsis
Monodactylidae
Polymixiidae
Archaephippus
Ephippidae

Appendix VI. Translation of Blot's (1969) description of the genus *Eoplatax*, placed in the family Platacidae. Only select portions are presented here. Translation by Laurent Mezin (pers. com.), with help on bone terminology by me. Nothing in the translation has been modified. Blot, J. 1969. Les poissons fossiles du Monte Bolca: Carangidae, Menidae, Ephippidae et Scatophagidae. Studi e ricerche sui giacimenti terziari di Bolca, Verona, 1: 1-540.

Family of Platacidae Jordan 1923

Diagnosis (from Weber and Beaufort 1936, corrected)

Compressed body, rhomboid, very high, about as high as long, changing considerably with age. Ctenoid or slightly ctenoid scales, medium or small, getting in size on the sides of the head and on base of dorsal, caudal, and anal fins. Complete lateral line arched. High head, more or less short, with a semicircular profile or very slightly angulated. Neurocranium more or less oblique when compared to the axis of the body. High sagital crest, but more or less compressed (anteroposterior). Lateral eyes roughly in middle of the head. Small mouth, horizontal or slightly oblique. Slightly or non-protractile mouth with very small teeth, conical and simple or tricuspid and mobile in a thin line in each jaw. Six to eight branchiostegal rays. Double structure of vertebral apophysis that is observable. Hemal spine (arch?) complex of type IIIb-discontinuous. Spiny dorsal non-differentiated from the soft part. The five to seven (nine) anterior spines increase in length posteriorly, and are mostly hidden by scales. Three interior spines at the anal tightly spaced close together to the rays. The anterior rays of the dorsal and anal fins are elongate in the young and getting shortened with age. In the adult the posterior rays are much shorter. Segmentation of the dorsal and anal rays is secondary. It starts from the basal segments and the extremities are not segmented. The caudal fin is rounded, truncated or emarginated. Short pectorals. Pelvic with strong spine and five rays, anterior rays lengthened but get relatively shorter with age. In addition to the genus *Platax*, one must place within this family the genus *Eoplatax* as well as the doubtful genus *Paraplatax* Bogatshov 1938.

Genus Eoplatax nov. gen.

Diagnosis

Medium head representing more than one third the total length without the tail. Neurocranium elongate with ventral profile approximately parallel to the axis of the body. Sagittal crest spread out and knife-blade shaped. Teeth conical, simple and short. Teeth on ectopterygoids and endopterygoids. Elongated maxillary. Supramaxillary present. Eight branchiostegal rays. Eight pairs of small ribs not exceeding half the height of the visceral cavity. Epicentral bones. Pelvics in anterior position at level of posterior edge of the orbital cavity. Anterior rays of dorsal fin (18) non-segmented but divided. Posterior rays segmented but the segmentation progresses towards the extremity from the basal segments. The anterior rays of the anal fin (13) non-segmented but divided.

Segmentation of posterior rays identical to that of the dorsal. Three vertebrae participate to the caudal skeleton. Medium scales very slightly ctenoid.

Agassiz placed in the genus *Platax* all of the fish that Volta and his successors had placed in the genus *Chaetodon*. Confronted with the important differences existing between the modern genera and the samples from Monte Bolca, I had to create the new genus *Eoplatax*.

Systematic Position

The fossils studied here though they present a general look fairly comparable to the genus *Platax* cannot be placed in that genus. The length of the neurocranium and the weak obliquity of the parasphenoid, the sagittal crest spread out and knife-blade shaped, the teeth conical and simple, the lengthening of the maxillaries and the presence of supramaxillaries, the eight pairs of branchiostegal rays, the weak development of the ventral ribs and the presence of epicentrals, the positions of the pelvics are so many characters that allowed me to define the new genus *Eoplatax* that I place near the modern *Platax* genus. Depending on the authors, the position of *Platax* and the *Eoplatax* varies somewhat. Günther (1860), Woodward (1901), and d'Erasmo place it in the big group Carangidae, but one knows how this family is full of genera very different from one another and clearly without tight phylogenetic relations. A fair number of authors place *Platax* in the Ephippidae: Gregory (1933-1959), Romer (1945-1966), Arambourg and Bertin (1958), and Obruchev (1964); the later also placing in the Ephippidae family the genera *Semiophorus* (= *Exellia*) and *Amphistium*. Jordan (1923), J.L.B. Smith (1950), E.S. Herald (1961), and Greenwood, Rosen, Weitzman and Meyers (1966) placed *Platax* in the Platacidae and Weber and Beaufort (1936) agree with them, while thinking like Berg (1940-1958) that it is a subfamily of the Platacinae.

I place myself in this later point of view and place *Eoplatax* with the genus *Platax*, and maybe the genus *Paraplatax* in the Platacidae. However, this family must be separated from the Chaetodontidae (Weber and Beaufort, Goodrich 1930), as should be the Ephippidae[1], to be placed near the Monodactylidae as had Günther (1860) already done. One can notice indeed in the samples of *Platax*, as in those of *Mondactylus* that the visceral cavity is asymmetrical and spreads backwards past the "hemal spine" complex[2].

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[1] See page 369.

[2] This is a personal observation made from dissection of multiple individuals of both types.

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Table 1. Classification, type locality and location of type specimens. Information on types from Eschmeyer (1998) and literature search. Full citations for authorities can be found in Eschmeyer (1998).

- Ephippidae Bleeker, 1859
  - *Chaetodipterus* Lacepède, 1802
    - *C. faber* (Broussonet, 1782)
      - Jamaica. Museum Banks. Type apparently lost
    - *C. lippei* Steindachner, 1895
      - Freetown, Liberia. Syntypes: NMV 52020 (1), ?72022 (1)
    - *C. zonatus* (Girard, 1858)
      - Off San Diego, California. Syntypes: USNM 690 (were two specimens, now one)
  - *Ephippus* Cuvier, 1816
    - *E. goreensis* Cuvier in Cuvier and Valenciennes, 1831
      - Gorée, Senegal. Holotype (unique): MNHN A.412
    - *E. orbis* (Bloch, 1787)
      - East Indies. Syntypes: ZMB 8166 (1, right skin), ZMB 8167 (1, left skin)
  - *Parapsettus* Steindachner, 1875
    - *P. panamensis* Steindachner, 1875
      - (Pacific) Panama. Syntypes: (several) MCZ 17281 (1), NMW 78789 (1)
  - *Platax* Cuvier, 1816
    - *P. batavianus* Cuvier in Cuvier and Valenciennes, 1831
      - Jakarta [Batavia], Java, Indonesia Holotype (unique): MNHN A.184
    - *P. boersii* Bleeker, 1852
      - Makasar [Ujung Pandang], Sulawesi [Celebes], Indonesia. Holotype (unique): whereabouts unknown
    - *P. orbicularis* (Forsskål, 1775)
      - Jidda, Saudi Arabia, Red Sea. Holotype (unique): ZMUC P5168 (dried skin)
    - *P. pinnatus* (Linnaeus, 1758)
      - Indian Ocean. Probable type: NRMS LP 57 (1)
    - *P. teira* (Forsskål, 1775)
      - Luhaiya, Yemen, Red Sea. No types known
  - *Proteracanthus* Gunther, 1859
    - *P. sarissophorus* (Cantor, 1849)
      - Sea of Pinang, [Penang], Malaysia; Malay Peninsula. Syntypes: (2) BMNH uncat. (skin)
  - *Rhinoprenes* Munro, 1964
    - *R. pentanemus* Munro, 1964
      - Off Port Romilly, Kerema Bay, Gulf of Papua, Papua New Guinea. Holotype: CSIRO A1826. Paratypes: CSIRO A1825 (1), A1834-35 (1, 1), A3077-78 (1, 1)

Table 1 (continued)

Tripterodon Playfair in Playfair and Günther, 1866
    T. orbis Playfair in Playfair and Günther, 1866
        Zanzibar. Holotype (unique): BMNH 1867.3.9.133 (skin in preservative)
Zabidius Whitley, 1930
    Z. novemaculeatus (McCulloch, 1916)
        Queensland, Australia. Holotype: AMS E.2766. Paratypes: (22) AMS I.13863-68(1 ea.), ?E.2743 (?), E.2539-41(1, 6, 1), E.2635 (1), E.2766 (1)

Extinct taxa
    Archaephippus
        A. asper (Volta, 1796)
            Gazola, Italy. Holotype: MNHN 10777
    Eoplatax
        E. papilio (Volta, 1796)
            Gazola, Italy. Holotype: MNHN 10769-10770

Table 2. Character matrix for the phylogenetic study of the Ephippidae. 0= primitive state; 1-2 = derived states. Bold text designates ingroup.

	1-5	**6-10**	**11-15**	**16-20**	**21-25**	**26-30**	**31-35**	**36-40**	**41-45**	**46-50**	**51-55**	**56-59**
Coracinidae	00000	00022	01111	00100	00010	00001	01100	01110	01010	00000	00110	?000
Kyphosidae	01000	00000	10111	01000	00010	00001	11101	01010	00012	00000	00110	?000
Chaetodontidae	00000	00000	00110	00000	00010	00?01	1100?	11010	00012	00000	00010	0?00
Pomacanthidae	00000	10201	001?0	00000	00010	00000	11001	01110	00012	01000	00100	0000
Drepaneidae	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	0000
Siganidae	00000	10022	11001	10100	02010	11110	11000	00011	01102	21000	10111	1011
Luvaridae	00001	10022	11100	10100	00010	01111	11001	01111	11002	31000	00111	1011
Zanclidae	00000	11021	11101	10101	02011	11010	11000	00010	11012	21000	00111	1011
Acanthuridae	00000	10022	11000	10000	02010	111?0	11001	00?11	11010	2?010	?0101	1?11
Scatophagidae	11100	10211	11100	10100	02000	00000	10010	00001	11012	01010	00101	1010
Chaetodipterus	**11110**	**10000**	**11000**	**10111**	**12100**	**10100**	**00100**	**10000**	**01000**	**11000**	**10001**	**1100**
Ephippus	**11100**	**10000**	**11100**	**10111**	**12111**	**10110**	**0?110**	**10011**	**01000**	**10000**	**10001**	**1?00**
Parapsettus	**11101**	**10001**	**11011**	**10111**	**12100**	**10110**	**00001**	**01110**	**01110**	**11111**	**10111**	**1000**
Platax	**11110**	**11211**	**11110**	**11111**	**1?101**	**10111**	**00011**	**00100**	**01100**	**10000**	**10001**	**1100**
Proteracanthus	**11100**	**10211**	**11001**	**10111**	**12000**	**11100**	**11000**	**01000**	**01011**	**11000**	**11111**	**1000**
Rhinoprenes	**01001**	**10111**	**11011**	**10111**	**12111**	**00111**	**11010**	**01110**	**01111**	**11111**	**01111**	**1000**
Tripterodon	**11110**	**11211**	**11100**	**11111**	**12111**	**10110**	**00110**	**10011**	**01100**	**10000**	**10001**	**1100**
Zabidius	**11100**	**11211**	**11110**	**11111**	**11101**	**10111**	**0?001**	**10010**	**01100**	**10000**	**10001**	**1100**

Table 3. Characters used to infer phylogenetic relationships among the Ephippidae. See "RESULTS, Character Descriptions" for detailed descriptions of characters. See Table 2 for the character matrix. Characters in bold were found in this study.

1. **Majority of primary ramus of premaxilla cancellous, with deep, tubular hollows oriented vertically.**
2. **Vertical lamina between the articular and ascending processes of the premaxilla.**
3. **Distal end of premaxilla narrow and recurved.**
4. **Presence of a medially-positioned maxillary arch.**
5. **Absence of distinct transverse fold over upper lip.**
6. Length of ascending process of premaxilla less than length of alveolar process (Rosen 1984).
7. **Presence of relatively widely-separated bands of teeth in jaws.**
8. **Presence of tricuspidate teeth in both jaws.**
9. **Reduction in the number of teeth.**
10. **Reduction in the number of bands of teeth.**
11. Premaxillae non-protrusible and maxillae and premaxillae move relatively little (Tyler et al. 1989).
12. Length of articular less than or equal to length of dentary (Tyler et al. 1989)
13. **Presence of a medially-projecting subocular shelf on infraorbital II.**
14. **Posteriormost infraorbital closely articulates with the preceding infraorbital.**
15. **Longitudinal edge of the lachrymal lies in the projected path of the infraorbital ring.**
16. Interopercle distinctly shaped (Tyler et al. 1989).
17. **Posterior ramus of the palatine extends posteriorly and terminates dorsal to the mesopterygoid.**
18. **Mandibulo-preopercular sensory canal in angular horizontally oriented.**
19. Large, comblike series of blunt rakers loosely associated with the anterior margin of the broadened first epibranchial. (Johnson 1984)
20. **Fourth pharyngobranchial (PB4) elongate and completely overlays the dorsal surface of the upper toothplate of the fourth branchial arch (UP4).**
21. Reduction or absence of the basihyal (Johnson 1984).
22. Absence of an interarcual cartilage (Johnson 1984).
23. Elongate first pharyngobranchial (Johnson 1984)
24. **Absence of microbranchiospines.**
25. **Blunt, "bean-shaped" rakers associated with the anterior margin of the third ceratobranchial (CB3) and third hypobranchial (HB3).**
26. Gill filaments free from epibranchials.(Johnson 1984)
27. Absence of a fontanel in the ceratohyal (Rosen 1984).
28. **Ceratohyal firmly attached by connective tissue to dorsal and ventral hypohyals.**

Table 3 (continued)

29. **Distal tips of anterior dorsal-fin pterygiophores not buttressed by bony flanges on anterior side of the posteriorly-associated neural spines**
30. **Absence of a vacant interneural space associated with the precaudal vertebrae (excluding the first interneural space; see character 7).**
31. **Absence of minute vertically-oriented bony striations on the main ramus of the anterior dorsal- and anal-fin pterygiophores and basal portions of the anterior dorsal- and hemal spines**
32. Proximal radials of soft dorsal- and anal fins without symmetrical diamond-shaped heads (Rosen 1984).
33. **Presence of middle radials associated with soft dorsal- and anal-fin pterygiophores.**
34. **First two supraneurals do not extend ventrally beyond the distal tip of the first neural spine.**
35. **Dorsal-fin spines sequentially increase in length.**
36. **Two anteriormost neural spines closely applied.**
37. **Anterior haemal spines without anteriorly- or posteriorly-directed vertically-oriented lamina**
38. **Dorsal- and anal-fin spines approximately symmetrical in cross-section.**
39. **Absence of hyperostosis.**
40. **First epural positioned above the reduced neural spine of preural centrum 2 (PU_2).**
41. Presence of 8+8 principle caudal-fin rays (Tyler et al. 1989)
42. **Reduction in the number of pectoral-fin radials articulating with the scapula.**
43. **Ventral process of the coracoid elongate and articulates with the main ramus of the cleithrum.**
44. **Posteroventral edge of scapula flat (not concave).**
45. **Reduced or absent cancellous sulcus on the medioantero edge (i.e., internal crest) of the cleithrum.**
46. **Posterior processes of pelvic-fin girdle elongate, pointed, parallel and separate from one another along their entire lengths.**
47. **Reduction to three laminae of membrane bone (i.e., wings) associated with the basipterygium**
48. **Pelvic-fin spine reduced in length and equal to the length of the posterior process of the pelvic fin.**
49. **External dorsal wing of the basipterygia is reduced in size.**
50. **Primary ramus of basipterygia reduced in length and width.**
51. **Mandibulo-preopercular sensory canal branched between the dentary and the angular.**
52. **Lateral line extends onto the caudal fin and is branched.**
53. **Presence of dorsoanterior swimbladder diverticula.**
54. **Absence of posterior bilateral swimbladder diverticula.**
55. Gill membranes broadly united at the isthmus (Tyler et al.).

Table 3 (continued)

56. Presence of a myocommatum (i.e., septum between two adjacent myotomes) in adductor mandibulae section (Winterbottom 1993).
57. **Presence of dark vertical bar through eye.**
58. Characters of Scatophagidae + Siganidae + Luvaridae + Zanclidae + Acanthuridae (Tyler et al. 1989) (weighted by 2).
59. Eleven synapomorphies of restricted acanthuroids (Tyler et al. 1989) (weighted by 11).

Table 4. **Approximate numbers of teeth associated with the premaxilla and dentary (premaxilla/dentary; right side only)**

Chaetodontidae (2 species):	270/190; 110/112
Ephippus:	160/160
Chaetodipterus:	150/140
Kyphosidae	128/128
Drepaneidae:	110/106
Pomacanthidae:	108/116
Parapsettus:	120/84
Scatophagidae:	74/66
Platax:	67/70
Zabidius:	64/75
Tripterodon:	63/59
Rhinoprenes:	48/46
Proteracanthus:	36/36
Acanthuridae:	15/11
Coracinidae	15/9
Siganidae:	9/9
Zanclidae:	9/9
Luvaridae:	8-9/6-8

Table 5. **Supraneural formulae and interdigitation patterns for the anterior portion of the dorsal fin. 0 = supraneural; # = number of spines associated with each pterygiophore; multiple numbers (e.g., 1 + 1) refer to the number of pterygiophores interdigitating in the same interneural space.**

Drepaneidae	0/0+0/1/1+1/1/ /1
	0/0+0/2/1+1/1/ /1
Chaetodipterus	0+0+0/ /2/1+1/1/1/ /1
	0+0+0/ /3/1+1/1/1/ /1
Ephippus	0+0+0/ /2/1+1/1/1/ /1
Parapsettus	0/0+0/2/1/1+1/1/ /1
	0/0+0/2/1+1/1/1/ /1
Platax	0/0+0/2/1+1/1/1/1+1/1+1/1
	0/0+0/2/1+1/1/1+1/1/1+1/
	/0+0+0/1/1/1+1/1+1/1/1+1+1/
	0+0/ /1+1+1/1+1/1+1/1/1+1/1+1/
	0+0/2/1+1/1+1/1+1/1/1+1/1+1
	0+0/2/1+1/1+1/1+1/1+1/1/1+1
Proteracanthus	0/0/0+2/1+1/1/1/ /1/1
Rhinoprenes	0+0/0/P/1/1/1/1/1/1/
Tripterodon	0+0+0/ /2/1+1/1/1/ /1/1
Zabidius	0+0+0/ /2/1+1/1/1/1/1/1/1+1

Table 6. Character change list for cladogram of Ephippidae and related taxa. Nodes are numbered in Figs. 34, 38, 39. CI = Consistency Index. Double-lined arrow (==>) indicates a change that occurs in all possible reconstructions (i.e., is unambiguous). A single-lined arrow (---->) indicates that the change occurs under some reconstructions, but not others.

Character	CI	Weighted steps	Changes
1	0.500	1	node 30 0 ==> 1 node 29
		1	node 26 1 ==> 0 *Rhinoprenes*
2	0.500	1	node 34 0 ==> 1 Kyphosidae
		1	node 30 0 ==> 1 node 29
3	0.500	1	node 30 0 ==> 1 node 29
		1	node 26 1 ==> 0 *Rhinoprenes*
4	0.333	1	node 28 0 ----> 1 node 25
		1	node 24 1 ----> 0 *Ephippus*
		1	node 22 1 ----> 0 *Zabidius*
5	0.500	1	node 20 0 ==> 1 Luvaridae
		1	node 27 0 ==> 1 node 26
6	1.000	1	node 31 1 ==> 0 node 32
7	0.500	1	node 19 0 ==> 1 Zanclidae
		1	node 24 0 ==> 1 node 23
8	0.400	1	node 31 0 ==> 2 Pomacanthidae
		1	node 29 0 ==> 2 Scatophagidae
		1	node 24 0 ==> 2 node 23
		1	node 26 0 ==> 1 *Rhinoprenes*
		1	node 27 0 ==> 2 *Proteracanthus*
9	0.333	1	node 34 0 ==> 2 Coracinidae
		1	node 31 0 ----> 1 node 30
		1	node 30 1 ----> 2 node 21
		1	node 28 1 ----> 0 node 25
		1	node 24 0 ----> 1 node 23
		1	node 26 1 ----> 0 Parapsettus
10	0.333	1	node 31 1 ==> 0 node 32
		1	node 34 0 ==> 2 Coracinidae
		1	node 30 1 ==> 2 node 21
		1	node 19 2 ==> 1 Zanclidae
		1	node 28 1 ----> 0 node 25
		1	node 24 0 ----> 1 node 23
11	0.500	1	node 34 0 ==> 1 Kyphosidae
		1	node 31 0 ==> 1 node 30
12	0.500	1	node 34 0 ==> 1 Coracinidae
		1	node 31 0 ==> 1 node 30

Table 6 (continued)

13	0.200	1	node 32	1 ==> 0	Drepaneidae
		1	node 21	1 ==> 0	Siganidae
		1	node 19	1 ==> 0	Acanthuridae
		1	node 29	1 ----> 0	node 28
		1	node 25	0 ----> 1	node 24
14	0.333	1	node 32	0 ==> 1	node 33
		1	node 23	0 ==> 1	node 22
		1	node 27	0 ==> 1	node 26
15	0.250	1	node 33	0 ==> 1	node 34
		1	node 21	0 ==> 1	Siganidae
		1	node 19	0 ==> 1	Zanclidae
		1	node 28	0 ==> 1	node 27
16	1.000	1	node 31	0 ==> 1	node 30
17	0.500	1	node 34	0 ==> 1	Kyphosidae
		1	node 24	0 ==> 1	node 23
18	0.333	1	node 34	0 ==> 1	Coracinidae
		1	node 31	0 ==> 1	node 30
		1	node 19	1 ==> 0	Acanthuridae
19	1.000	1	node 29	0 ==> 1	node 28
20	0.500	1	node 19	0 ==> 1	Zanclidae
		1	node 29	0 ==> 1	node 28
21	1.000	1	node 29	0 ==> 1	node 28
22	0.667	1	node 31	0 ==> 2	node 30
		1	node 20	2 ==> 0	Luvaridae
		1	node 23	2 ----> 1	node 22
23	0.500	1	node 29	0 ----> 1	node 28
		1	node 27	1 ----> 0	*Proteracanthus*
24	0.200	1	node 32	1 ==> 0	Drepaneidae
		1	node 30	1 ==> 0	node 29
		1	node25	0 ----> 1	node 24
		1	node 23	1 ----> 0	node 22
		1	node 26	0 ==> 1	*Rhinoprenes*
25	0.333	1	node 19	0 ==> 1	Zanclidae
		1	node25	0 ==> 1	node 24
		1	node 26	0 ==> 1	*Rhinoprenes*
26	0.250	1	node 31	0 ----> 1	node 30
		1	node20	1 ----> 0	Luvaridae
		1	node29	1 ----> 0	Scatophagidae
		1	node26	1 ==> 0	*Rhinoprenes*
27	0.500	1	node 30	0 ==> 1	node 21
		1	node 27	0 ==> 1	*Proteracanthus*
28	0.333	1	node 31	0 ----> 1	node 30
		1	node19	1 ==> 0	Zanclidae
		1	node29	1 ----> 0	Scatophagidae

Table 6 (continued)

29	0.333	1	node 30	0 ==> 1	node 21
		1	node 25	0 ==> 1	node 24
		1	node27	0 ==> 1	node 26
30	0.250	1	node 32	0 ==> 1	node 33
		1	node20	0 ==> 1	Luvaridae
		1	node 23	0 ==> 1	node 22
		1	node 26	0 ==> 1	*Rhinoprenes*
31	0.250	1	node 34	1 ==> 0	Coracinidae
		1	node 32	1 ==> 0	Drepaneidae
		1	node 28	1 ==> 0	node 25
		1	node 26	1 ==> 0	*Parapsettus*
32	0.250	1	node 32	1 ==> 0	Drepaneidae
		1	node 30	1 ----> 0	node 29
		1	node 28	0 ----> 1	node 27
		1	node 26	1 ----> 0	*Parapsettus*
33	0.333	1	node 33	0 ==> 1	node 34
		1	node 28	0 ==> 1	node 25
		1	node 23	1 ==> 0	node 22
34	0.250	1	node 29	0 ==> 1	Scatophagidae
		1	node 25	0 ==> 1	node 24
		1	node22	1 ==> 0	*Zabidius*
		1	node 26	0 ==> 1	*Rhinoprenes*
35	0.167	1	node 34	0 ==> 1	Kyphosidae
		1	node 31	0 ==> 1	Pomacanthidae
		1	node 21	0 ----> 1	node 20
		1	node 19	1 ----> 0	Zanclidae
		1	node 23	0 ==> 1	node 22
		1	node 26	0 ==> 1	*Parapsettus*
36	0.333	1	node 33	0 ==> 1	Chaetodontidae
		1	node 28	0 ==> 1	node 25
		1	node 22	1 ==> 0	*Platax*
37	0.250	1	node 32	0 ----> 1	node 33
		1	node 31	0 ----> 1	Pomacanthidae
		1	node 20	0 ==> 1	Luvaridae
		1	node 28	0 ==> 1	node 27
38	0.200	1	node 34	0 ==> 1	Coracinidae
		1	node 32	0 ==> 1	Pomacanthidae
		1	node20	0 ==> 1	Luvaridae
		1	node 22	0 ==> 1	*Platax*
		1	node 27	0 ==> 1	node 26
39	0.200	1	node 32	1 ==> 0	Drepaneidae
		1	node 30	1 ----> 0	node 29
		1	node 25	0 ----> 1	node 24
		1	node22	1 ==> 0	*Platax*
		1	node 27	0 ----> 1	node 26

Table 6 (continued)

40	0.200	1	node 31	0 ----> 1	node 30
		1	node 19	1 ==> 0	Zanclidae
		1	node 29	1 ----> 0	node 28
		1	node 25	0 ----> 1	node 24
		1	node 23	1 ----> 0	node 22
41	0.500	1	node 21	0 ==> 1	node 20
		1	node 29	0 ==> 1	Scatophagidae
42	0.500	1	node 34	0 ==> 1	Coracinidae
		1	node 31	0 ==> 1	node 30
43	0.333	1	node 21	0 ==> 1	Siganidae
		1	node 24	0 ==> 1	node 23
		1	node 27	0 ==> 1	node 26
44	0.250	1	node 32	1 ==> 0	Drepaneidae
		1	node 30	1 ----> 0	node 21
		1	node 20	0 ----> 1	node 19
		1	node 28	1 ==> 0	node 25
45	0.333	1	node 34	2 ==> 0	Coracinidae
		1	node 32	2 ==> 0	Drepaneidae
		1	node 19	2 ==> 0	Acanthuridae
		1	node 29	2 ----> 0	node 28
		1	node 28	0 ----> 1	node 27
		1	node 26	1 ----> 0	Parapsettus
46	1.000	1	node 30	0 ==> 2	node 21
		1	node 20	2 ==> 3	Luvaridae
		1	node 29	0 ==> 1	node 28
47	0.500	1	node 31	1 ==> 0	node 32
		1	node 25	1 ==> 0	node 24
48	1.000	1	node 27	0 ==> 1	node 26
49	0.333	1	node 19	0 ==> 1	Acanthuridae
		1	node 29	0 ==> 1	Scatophagidae
		1	node 27	0 ==> 1	node 26
50	1.000	1	node 27	0 ==> 1	node 26
51	0.333	1	node21	0 ==> 1	Siganidae
		1	node 29	0 ==> 1	node 28
		1	node 26	1 ==> 0	*Rhinoprenes*
52	0.500	1	node 28	0 ----> 1	node 27
		1	node 26	1 ----> 0	*Parapsettus*
53	0.333	1	node 31	1 ----> 0	node 32
		1	node 33	0 ----> 1	node 34
		1	node 28	1 ==> 0	node 25
54	0.250	1	node 32	0 ==> 1	node 33
		1	node 30	0 ==> 1	node 21
		1	node 19	1 ==> 0	Acanthuridae
		1	node 28	0 ==> 1	node 27
55	1.000	1	node 31	0 ==> 1	node 30

Table 6 (continued)

56	1.000	1	node 31	0 ==> 1	node 30
57	1.000	1	node 28	0 ==> 1	node 25
58	0.500	2	node 31	0 ----> 1	node 30
		2	node 29	1 ----> 0	node 28
59	1.000	11	node 30	0 ==> 1	node 21

Table 7. List of apomorphies by branch. Nodes are numbered in Figs. 34, 38, 39. CI = consistency index. Double-lined arrow (==>) indicates a change that occurs in all possible reconstructions (i.e., is unambiguous). A single-lined arrow (---->) indicates that the change occurs under some reconstructions, but not others.

Branch	Character	Weighted steps	CI	Change
node 31 —> node 32	6	1	1.000	1 ==> 0
	10	1	0.333	1 ==> 0
	47	1	0.500	1 ==> 0
	53	1	0.333	1 ----> 0
node 32 —> node 33	14	1	0.333	0 ==> 1
	30	1	0.250	0 ==> 1
	37	1	0.250	0 ----> 1
	54	1	0.250	0 ==> 1
node 33 —> node 34	15	1	0.250	0 ==> 1
	33	1	0.333	0 ==> 1
	53	1	0.333	0 ----> 1
node 34 —> Coracinidae	9	1	0.333	0 ==> 2
	10	1	0.333	0 ==> 2
	12	1	0.500	0 ==> 1
	18	1	0.333	0 ==> 1
	31	1	0.250	1 ==> 0
	38	1	0.200	0 ==> 1
	42	1	0.500	0 ==> 1
	45	1	0.333	2 ==> 0
node 34 —> Kyphosidae	2	1	0.500	0 ==> 1
	11	1	0.500	0 ==> 1
	17	1	0.500	0 ==> 1
	35	1	0.167	0 ==> 1
node 33 —> Chaetodontidae	36	1	0.333	0 ==> 1
node 32 —> Drepaneidae	13	1	0.200	1 ==> 0
	24	1	0.200	1 ==> 0
	31	1	0.250	1 ==> 0
	32	1	0.250	1 ==> 0
	39	1	0.200	1 ==> 0
	44	1	0.250	1 ==> 0
	45	1	0.333	2 ==> 0
node 31 —> Pomacanthidae	8	1	0.400	0 ==> 2
	35	1	0.167	0 ==> 1
	37	1	0.250	0 ----> 1
	38	1	0.200	0 ==> 1

Table 7 (continued)

Branch	Character	Weighted steps	CI	Change
node 31 —> node 30	9	1	0.333	0 ---> 1
	11	1	0.500	0 ==> 1
	12	1	0.500	0 ==> 1
	16	1	1.000	0 ==> 1
	18	1	0.333	0 ==> 1
	22	1	0.667	0 ==> 2
	26	1	0.250	0 ---> 1
	28	1	0.333	0 ---> 1
	40	1	0.200	0 ---> 1
	42	1	0.500	0 ==> 1
	55	1	1.000	0 ==> 1
	56	1	1.000	0 ==> 1
	58	2	0.500	0 ---> 1
node 30 —> node 21	9	1	0.333	1 ---> 2
	10	1	0.333	1 ==> 2
	27	1	0.500	0 ==> 1
	29	1	0.333	0 ==> 1
	44	1	0.250	1 ---> 0
	45	1	1.000	0 ==> 2
	54	1	0.250	0 ==> 1
	59	11	1.000	0 ==> 1
node 21 —> Siganidae	13	1	0.200	1 ==> 0
	15	1	0.250	0 ==> 1
	43	1	0.333	0 ==> 1
	51	1	0.333	0 ==> 1
node 21 —> node 20	35	1	0.167	0 ---> 1
	41	1	0.500	0 ==> 1
node 20 —> Luvaridae	5	1	0.500	0 ==> 1
	22	1	0.667	2 ==> 0
	26	1	0.250	1 ---> 0
	30	1	0.250	0 ==> 1
	37	1	0.250	0 ==> 1
	38	1	0.200	0 ==> 1
	46	1	1.000	2 ==> 3
node 20 —> node 19	44	1	0.250	0 ---> 1

Table 7 (continued)

Branch		Character	Weighted steps	CI	Change
node 19 —>	Zanclidae	7	1	0.500	0 ==> 1
		10	1	0.333	2 ==> 1
		15	1	0.250	0 ==> 1
		20	1	0.500	0 ==> 1
		25	1	0.333	0 ==> 1
		28	1	0.333	1 ==> 0
		35	1	0.167	1 ---> 0
		40	1	0.200	1 ==> 0
node 19 —>	Acanthuridae	13	1	0.200	1 ==> 0
		18	1	0.333	1 ==> 0
		45	1	0.333	2 ==> 0
		49	1	0.333	0 ==> 1
		54	1	0.250	1 ==> 0
node 30 —>	node 29	1	1	0.500	0 ==> 1
		2	1	0.500	0 ==> 1
		3	1	0.500	0 ==> 1
		24	1	0.200	1 ==> 0
		32	1	0.250	1 ---> 0
		39	1	0.200	1 ---> 0
node 29 —>	Scatophagidae	8	1	0.400	0 ==> 2
		26	1	0.250	1 ---> 0
		28	1	0.333	1 ---> 0
		34	1	0.250	0 ==> 1
		41	1	0.500	0 ==> 1
		49	1	0.333	0 ==> 1
node 29 —>	node 28	13	1	0.200	1 ---> 0
		19	1	1.000	0 ==> 1
		20	1	0.500	0 ==> 1
		21	1	1.000	0 ==> 1
		23	1	0.500	0 ---> 1
		40	1	0.200	1 ---> 0
		45	1	0.333	2 ---> 0
		46	1	1.000	0 ==> 1
		51	1	0.333	0 ==> 1
		58	2	0.500	1 ---> 0

Table 7 (continued)

Branch		Character	Weighted steps	CI	Change
node 28 —>	node 25	4	1	0.333	0 ----> 1
		9	1	0.333	1 ----> 0
		10	1	0.333	1 ----> 0
		31	1	0.250	1 ==> 0
		33	1	0.333	0 ==> 1
		36	1	0.333	0 ==> 1
		44	1	0.250	1 ==> 0
		53	1	0.333	1 ==> 0
		57	1	1.000	0 ==> 1
node 25 —>	node 24	13	1	0.200	0 ----> 1
		24	1	0.200	0 ----> 1
		25	1	0.333	0 ==> 1
		29	1	0.333	0 ==> 1
		34	1	0.250	0 ==> 1
		39	1	0.200	0 ----> 1
		40	1	0.200	0 ----> 1
		47	1	0.500	1 ==> 0
node 24 —>	*Ephippus*	4	1	0.333	1 ----> 0
node 24 —>	node 23	7	1	0.500	0 ==> 1
		8	1	0.400	0 ==> 2
		9	1	0.333	0 ----> 1
		10	1	0.333	0 ----> 1
		17	1	0.500	0 ==> 1
		43	1	0.333	0 ==> 1
node 23 —>	node 22	14	1	0.333	0 ==> 1
		22	1	0.667	2 ----> 1
		24	1	0.200	1 ----> 0
		30	1	0.250	0 ==> 1
		33	1	0.333	1 ==> 0
		35	1	0.167	0 ==> 1
		40	1	0.200	1 ----> 0
node 22 —>	*Platax*	36	1	0.333	1 ==> 0
		38	1	0.200	0 ==> 1
		39	1	0.200	1 ==> 0
node 22 —>	*Zabidius*	4	1	0.333	1 ----> 0
		34	1	0.250	1 ==> 0

Table 7 (continued)

Branch		Character	Weighted steps	CI	Change
node 28 —>	node 27	15	1	0.250	0 ==> 1
		32	1	0.250	0 ----> 1
		37	1	0.250	0 ==> 1
		45	1	0.333	0 ----> 1
		52	1	0.500	0 ----> 1
		54	1	0.250	0 ==> 1
node 27 —>	node 26	5	1	0.500	0 ==> 1
		14	1	0.333	0 ==> 1
		29	1	0.333	0 ==> 1
		38	1	0.200	0 ==> 1
		39	1	0.200	0 ----> 1
		43	1	0.333	0 ==> 1
		48	1	1.000	0 ==> 1
		49	1	0.333	0 ==> 1
		50	1	1.000	0 ==> 1
node 26 —>	*Parapsettus*	9	1	0.333	1 ----> 0
		31	1	0.250	1 ==> 0
		32	1	0.250	1 ----> 0
		35	1	0.167	0 ==> 1
		45	1	0.333	1 ----> 0
		52	1	0.500	1 ----> 0
node 26 —>	*Rhinoprenes*	1	1	0.500	1 ==> 0
		3	1	0.500	1 ==> 0
		8	1	0.400	0 ==> 1
		24	1	0.200	0 ==> 1
		25	1	0.333	0 ==> 1
		26	1	0.250	1 ==> 0
		30	1	0.250	0 ==> 1
		34	1	0.250	0 ==> 1
		51	1	0.333	1 ==> 0
node 27 —>	*Proteracanthus*	8	1	0.400	0 ==> 2
		23	1	0.500	1 ----> 0
		27	1	0.500	0 ==> 1

Table 8. Characters offering unambiguous support for competing hypotheses.

Taxa United	Characters
Constraint Analysis 4	
Scatophagidae + Ephippidae	1, 2, 3, 24 (R)
Acanthuroidei	11, 12, 16, 18, 22, 42, 55, 56, 58(R)
Pomacanthidae + Acanthuroidei	6, 10, 47
Drepaneidae + Pomacanthidae + Acanthuroidei	14, 30, 54
Chaetodontidae + Drepaneidae + Pomacanthidae + Acanthuroidei	15, 33
Constraint Analyses 1-3	
Scatophagidae + restricted acanthuroids	40, 58
Constraint Analyses 2 and 7	
Drepaneidae + Acanthuroidei	37
Constraint Analysis 6	
Drepaneidae + Scatophagidae	no characters
Drepaneidae + Scatophagidae + Ephippidae	no characters
Constraint Analysis 7	
Restricted acanthuroids + Ephippidae	26, 28

Table 9. Number of characters (i.e., branch length) per internal node and terminal node for ACCTRAN and DELTRAN optimizations of the cladogram of ephippid relationships (Fig. 38).

Node	No. of characters per node (ACCTRAN)	No. of characters per node (DELTRAN)
28	11	7
25	9	9
24	8	4
23	6	5
22	7	4
27	6	5
26	9	9
Total:	56	43
Terminal node		
Chaetodipterus	0	4
Ephippus	1	3
Tripterodon	0	3
Platax	3	4
Zabidius	2	2
Proteracanthus	3	5
Parapsettus	6	4
Rhinoprenes	9	11
Total:	24	36
Grand total:	80	79

Table 10. **Number of anterior dorsal-fin pterygiophores that come in contact with the vertebral centra in Ephippidae and Drepaneidae.**

Genus	None	First Pterygiophore	First Two Pterygiophores
Drepane			X
Chaetodipterus		X	
Ephippus		X	X
Parapsettus			X
Platax	X	X	
Proteracanthus	X		
Rhinoprenes	X	X	
Tripterodon			X
Zabidius		X	

Table 11. Meristic data of ephippid genera. Counts for caudal fin are for principle rays only.

	Dorsal	Anal	Pectoral	Pelvic	Caudal	Vertebrae
Chaetodipterus	IX,18-23	III,16-20	16-18	I,5	9+8	10+14=24
Ephippus	VIII-IX,19-20	III,15-16	18-19	I,5	9+8	10+14=24
Parapsettus	IX,27-28	III,24-26	18	I,5	9+8	10+14=24
Platax	V-VII,28-39	III,19-29	16-20	I,5	9+8	10+14=24
Proteracanthus	X,14-16	III,13-15	19	I,5	9+8	10+14=24
Rhinoprenes	VIII,19-21	III,16-19	19-21	I,5	9+8	10+14=24
Tripterodon	IX,19-21	III,15-17	17-19	I,5	9+8	10+14=24
Zabidius	IX,27-29	III,20-22	19-21	I,5	9+8	10+14=24

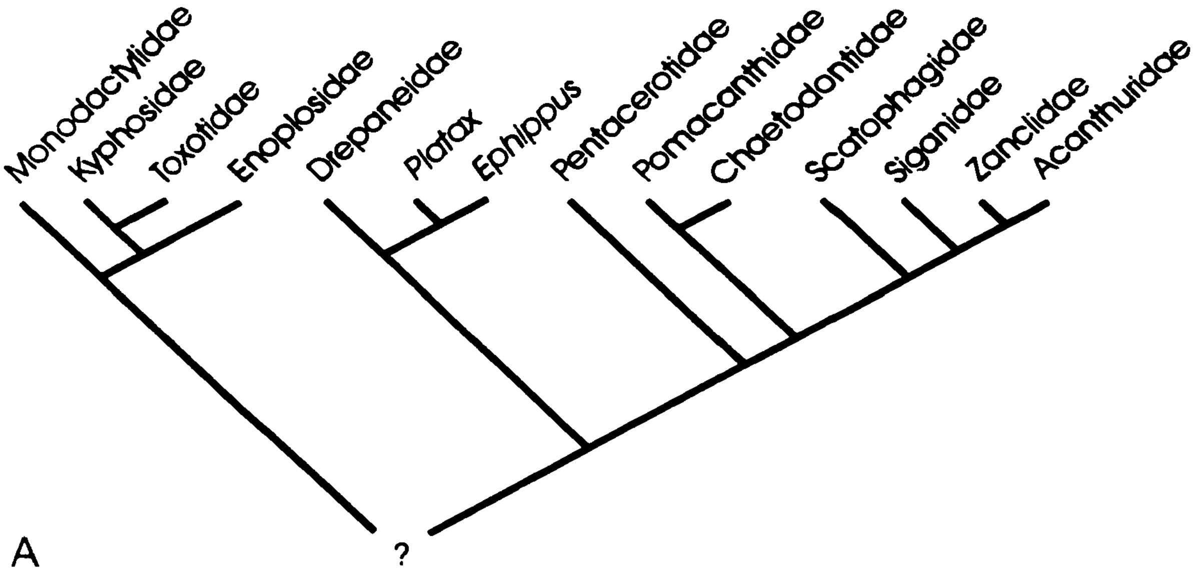
Table 12. Bremer calculations for ancestral areas of Ephippidae and the ephippid clades. Indian Ocean not delineated into two halves. G = number of gains using forward Camin-Sokal parsimony; L = number of losses using reverse Camin-Sokal parsimony; G/L = the gain/loss quotient; AA (ancestral area) = the rescaled G/L quotient.

Clade	Area	G	L	G/L	AA
A	Western Pacific	4	3	1.33	0.89
	Eastern Pacific	2	3	0.67	0.45
	Western Atlantic	1	2	0.50	0.33
	Eastern Atlantic	2	2	1.00	0.67
	Indian Ocean	3	2	1.50	1.00
	Caribbean	1	2	0.50	0.33
B	Western Pacific	2	2	1.00	0.50
	Eastern Pacific	1	1	1.00	0.50
	Western Atlantic	1	1	1.00	0.50
	Eastern Atlantic	2	1	2.00	1.00
	Indian Ocean	1	1	1.00	0.50
	Caribbean	1	1	1.00	0.50
C	Western Pacific	2	1	2.00	
	Eastern Atlantic	4	0	undefined	decisive
	Indian Ocean	1	1	1.00	
D	Western Pacific	1	1	1.00	
	Indian Ocean	1	0	undefined	decisive
E	Western Pacific	1	0	undefined	decisive
	Indian Ocean	1	0	undefined	decisive
F	Western Pacific	2	1	2.00	1.00
	Eastern Pacific	1	2	0.50	0.25
	Indian Ocean	2	1	2.00	1.00
G	Western Pacific	1	1	1.00	1.00
	Eastern Pacific	1	1	1.00	1.00
	Indian Ocean	1	1	1.00	1.00

Table 13. Bremer calculations for ancestral areas of Ephippidae and the ephippid clades. Indian Ocean delineated into east/west halves. G = number of gains using forward Camin-Sokal parsimony; L = number of losses using reverse Camin-Sokal parsimony; G/L = the gain/loss quotient; AA (ancestral area) = the rescaled G/L quotient.

Clade	Area	G	L	G/L	AA
A	Western Pacific	4	3	1.33	1.00
	Eastern Pacific	2	3	0.67	0.50
	Western Atlantic	1	2	0.50	0.37
	Eastern Atlantic	2	2	1.00	0.75
	Western Indian	3	3	1.00	0.75
	Eastern Indian	4	3	1.33	1.00
	Caribbean	1	2	0.50	0.37
B	Western Pacific	2	2	1.00	0.50
	Eastern Pacific	1	1	1.00	0.50
	Western Atlantic	1	1	1.00	0.50
	Eastern Atlantic	2	1	2.00	1.00
	Western Indian	3	2	1.50	0.75
	Eastern Indian	2	2	1.00	0.50
	Caribbean	1	1	1.00	0.50
C	Western Pacific	2	1	2.00	0.67
	Eastern Atlantic	1	1	1.00	0.33
	Western Indian	3	1	3.00	1.00
	Eastern Indian	2	1	2.00	0.67
D	Western Pacific	1	1	1.00	0.50
	Western Indian	2	1	2.00	1.00
	Eastern Indian	1	1	1.00	0.50
E	Western Pacific	1	0	undefined	decisive
	Western Indian	1	1	1.00	
	Eastern Indian	1	0	undefined	decisive
F	Western Pacific	2	1	2.00	1.00
	Eastern Pacific	1	2	0.50	0.25
	Eastern Indian	2	1	2.00	1.00
G	Western Pacific	1	1	1.00	1.00
	Eastern Pacific	1	1	1.00	1.00
	Eastern Indian	1	1	1.00	1.00

Figure 1. Relationships among the Squamipennes, as proposed by Mok and Shen (1983) (A) and Blum (1988, unpubl. Ph.D. diss.) (B).


Monodactylidae
Kyphosidae
Toxotidae
Enoplosidae
Drepaneidae
Platax
Ephippus
Pentacerotidae
Pomacanthidae
Chaetodontidae
Scatophagidae
Siganidae
Zanclidae
Acanthuridae
?
A

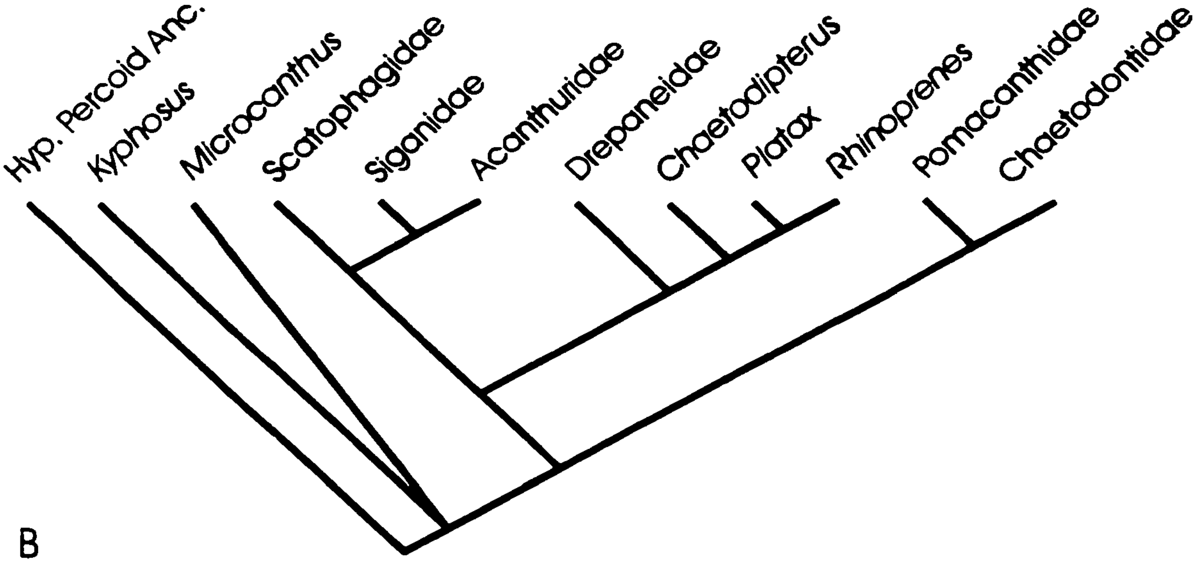
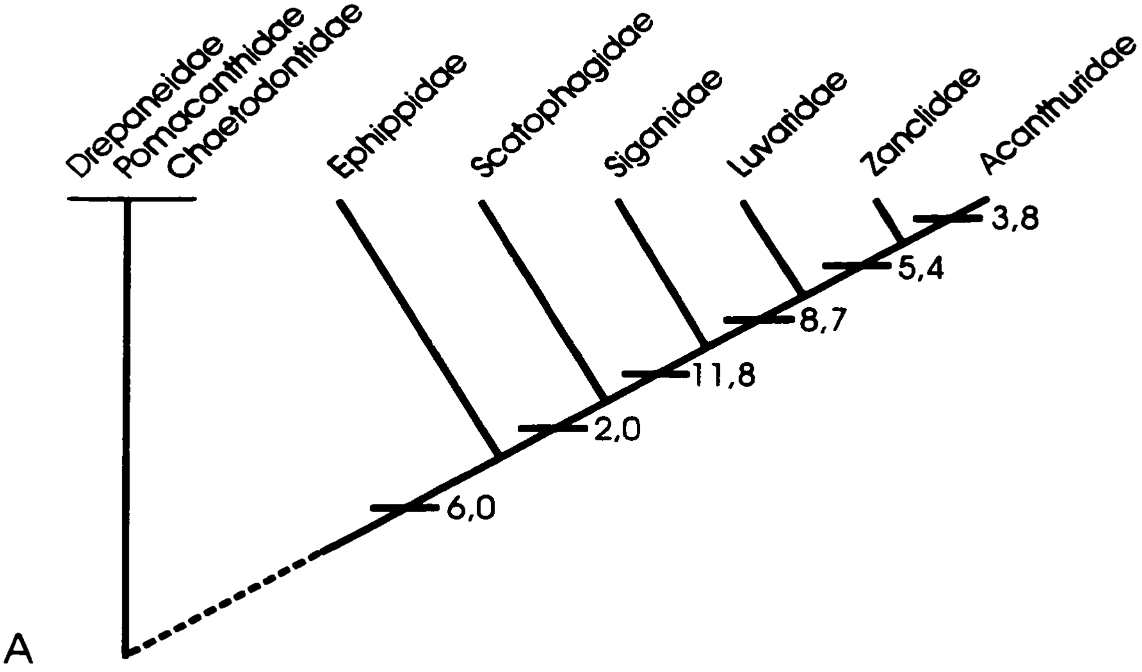

Hyp. Percoid Anc.
Kyphosus
Microcanthus
Scatophagidae
Siganidae
Acanthuridae
Drepaneidae
Chaetodipterus
Platax
Rhinoprenes
Pomacanthidae
Chaetodontidae
B

Figure 2. Relationships among the higher Squamipennes, as proposed by Tyler et al. (1989) (A); Relationships among the Acanthuroidei as proposed by Winterbottom (1993) (B). In A, numbers refer to the number of synapomorphies at each node based on adult morphology and larval morphology, respectively. In B, numbers refer to the number of synapomorphies at each node based on myology.


Drepaneidae
Pomacanthidae
Chaetodontidae
Ephippidae
Scatophagidae
Siganidae
Luvaridae
Zanclidae
Acanthuridae
3,8
5,4
8,7
11,8
2,0
6,0
A

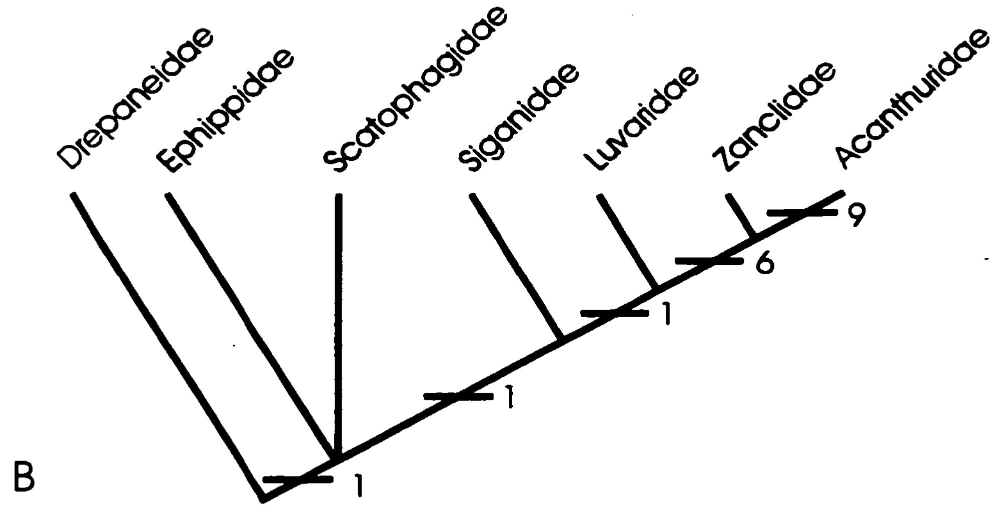

Drepaneidae
Ephippidae
Scatophagidae
Siganidae
Luvaridae
Zanclidae
Acanthuridae
9
6
1
1
1
B

Figure 3. Relationships among the Acanthuroidei and related taxa, as proposed by Tang et al. (1999); based on molecular analysis utilizing 21 taxa. Numbers at each node refer to Bremer decay index values (top), bootstrap values for 1000 replicates (middle), and branch lengths (bottom)

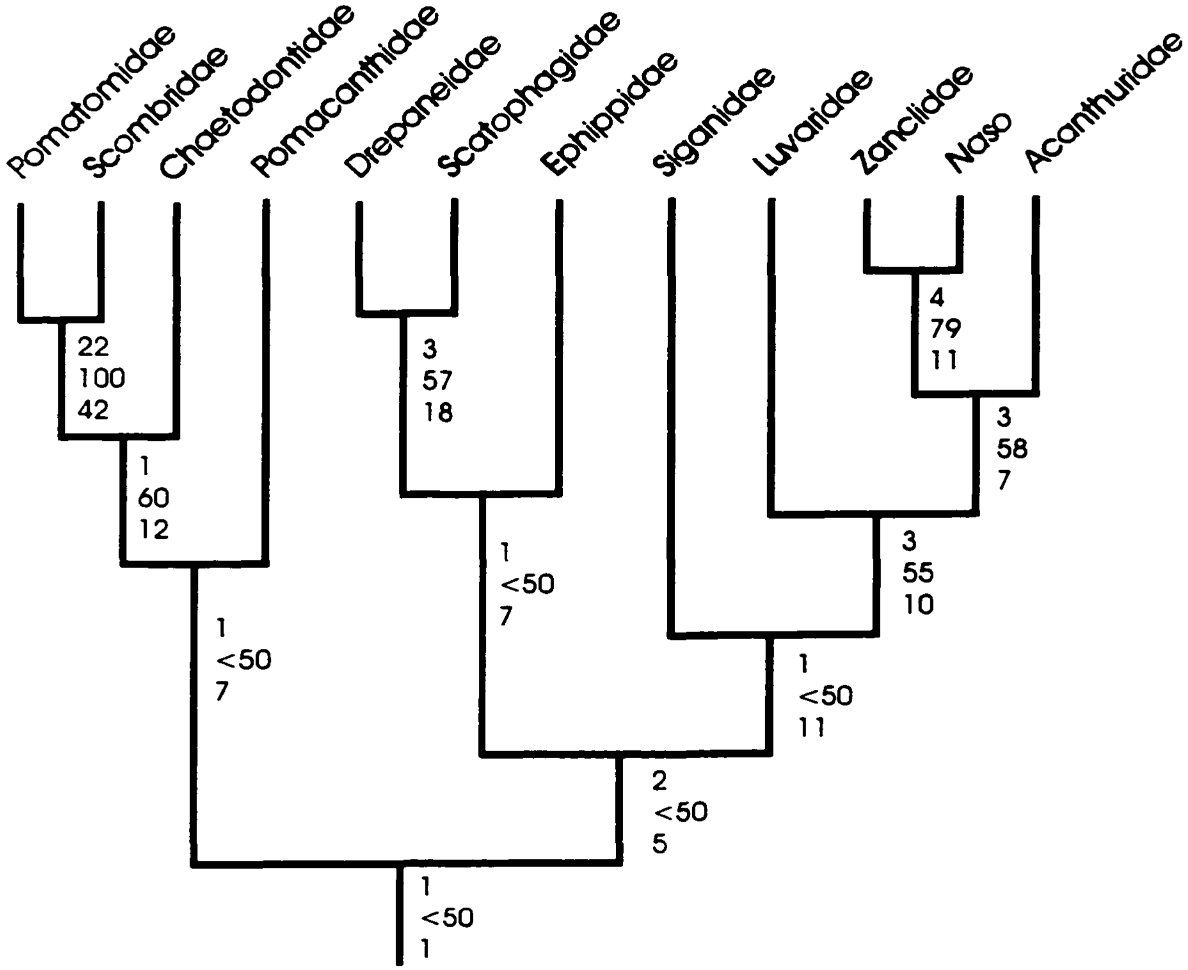

Pomatomidae
Scombridae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Ephippidae
Siganidae
Luvaridae
Zanclidae
Naso
Acanthuridae
22 100 42
1 60 12
3 57 18
4 79 11
3 58 7
3 55 10
1 <50 7
1 <50 7
1 <50 11
2 <50 5
1 <50 1

Figure 4. Relationships among the Acanthuroidei, as proposed by Tang et al. (1999), based on total evidence with (A) Drepaneidae, Ephippidae, and Scatophagidae designated as outgroup; and (B) Drepaneidae designated as the outgroup. Numbers at each node refer to Bremer decay index values (top), bootstrap values for 1000 replicates (middle), and branch lengths (bottom).

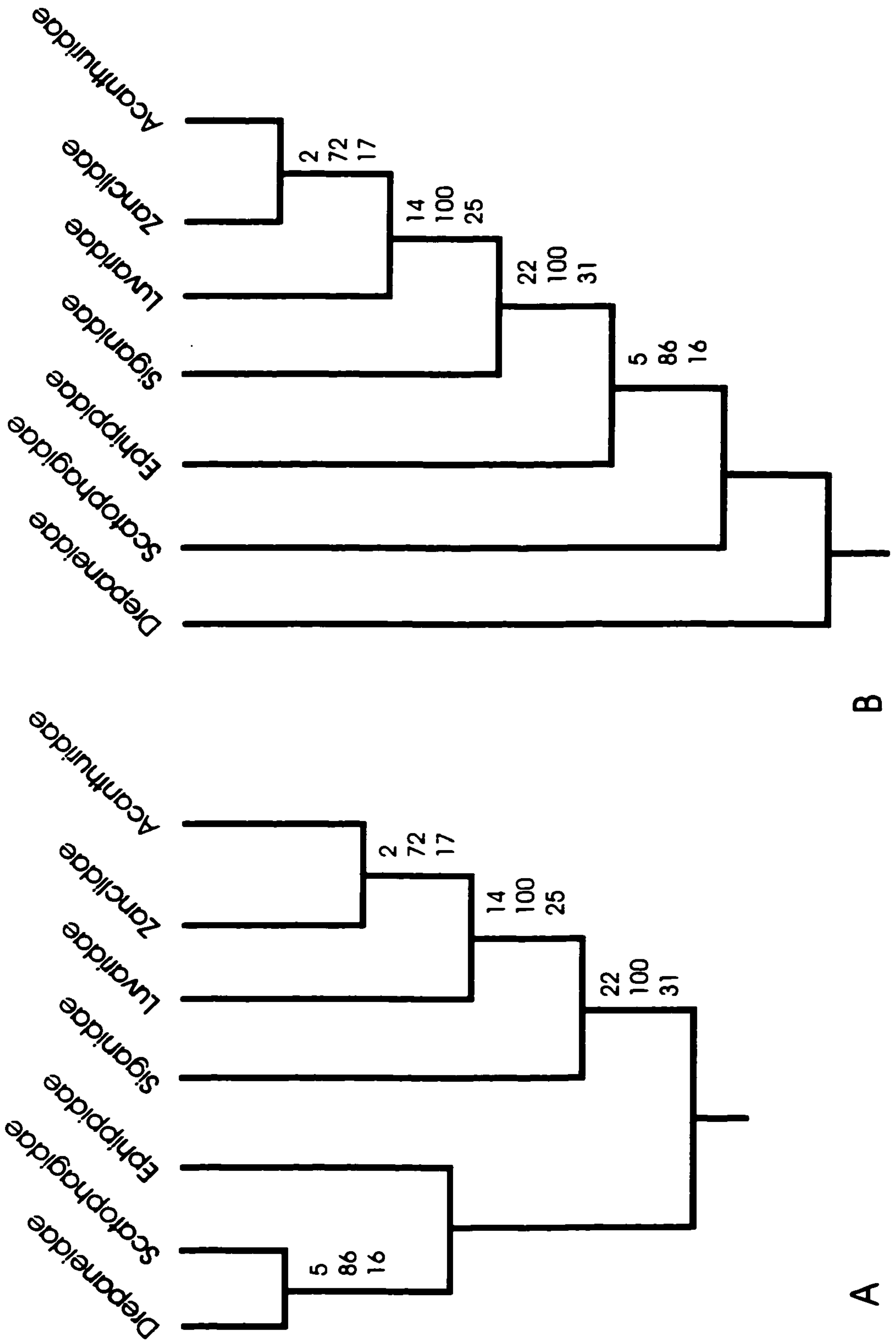

A
Acanthuridae
Zanclidae
Luvaridae
Siganidae
Ephippidae
Scatophagidae
Drepaneidae
2
72
17
14
100
25
22
100
31
5
86
16
B
Acanthuridae
Zanclidae
Luvaridae
Siganidae
Ephippidae
Scatophagidae
Drepaneidae
2
72
17
14
100
25
22
100
31
5
86
16

Figure 5. **Relationships among the chaetodontid genera, as proposed by Blum (1988).**

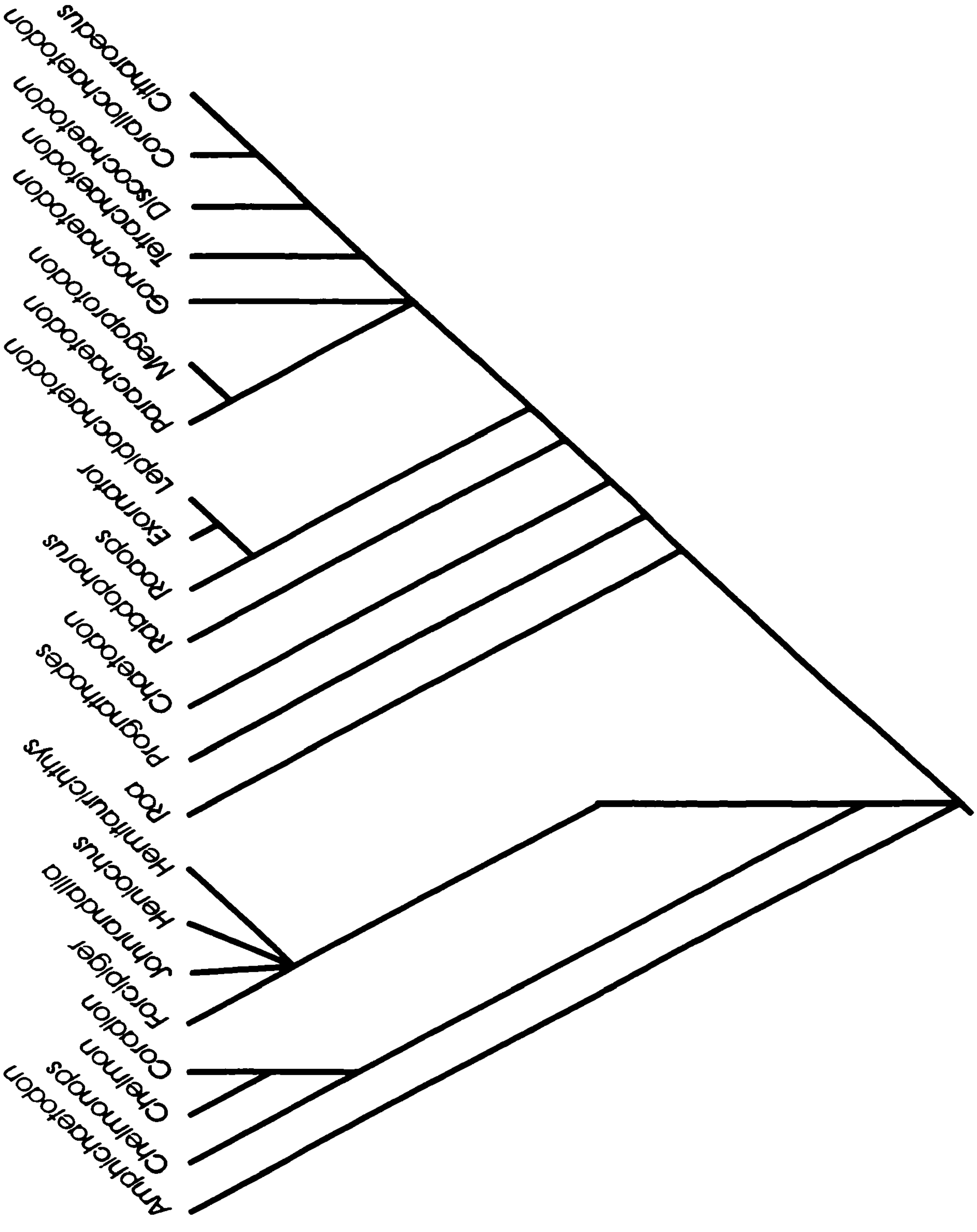
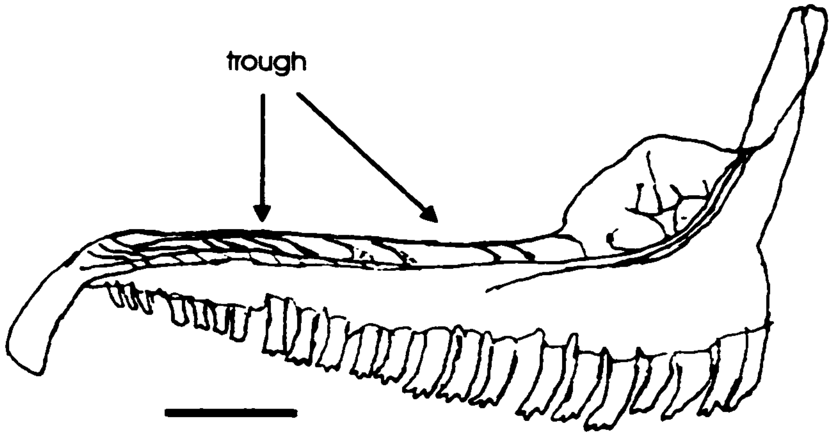
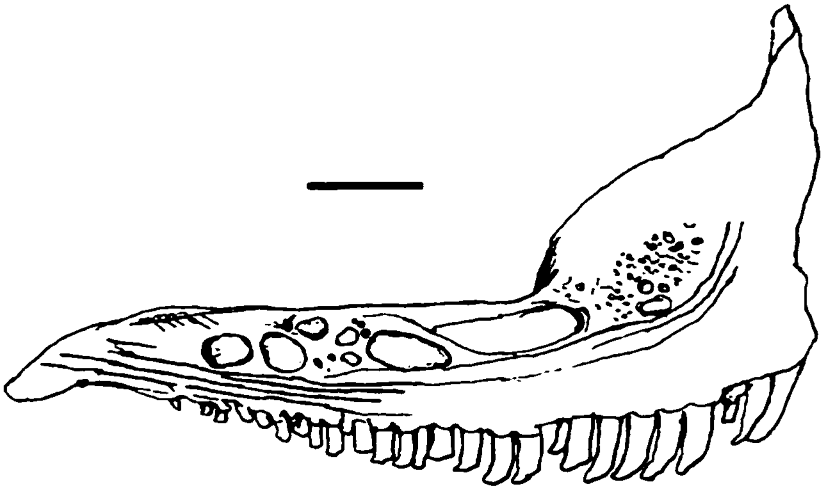

Citharoedus
Corallochaetodon
Discochaetodon
Tetrachaetodon
Gonochaetodon
Megaprotodon
Parachaetodon
Lepidochaetodon
Exornator
Roaops
Rabdophorus
Chaetodon
Prognathodes
Roa
Hemitaurichthys
Heniochus
Johnrandallia
Forcipiger
Coradion
Chelmonops
Chelmon
Amphichaetodon

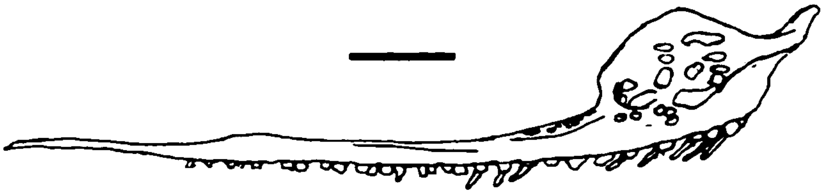
Figure 6. Dorsolateral view of the premaxilla of *Platax orbicularis* (A), *Ephippus orbis* (B), and *Rhinoprenes pentanemus* (C). *Platax*: ANSP 91692, 70 mm SL. *Ephippus*: ANSP 52749, 97 mm SL, *Rhinoprenes*: ANSP 134859, 100 mm SL. Scale bars = 1 mm.



A



B



C

Figure 7. **Medial view of premaxillae of *Tripterodon orbis* (A), *Chaetodipterus faber* (B), and *Drepane punctata* (C). *Tripterodon*: RUSI 8508 (1 of 2; 70 mm SL). *Chaetodipterus*: VIMS 8021, 49 mm SL. *Drepane*: USNM 284825, 91 mm SL. Scale bars = 1 mm.**

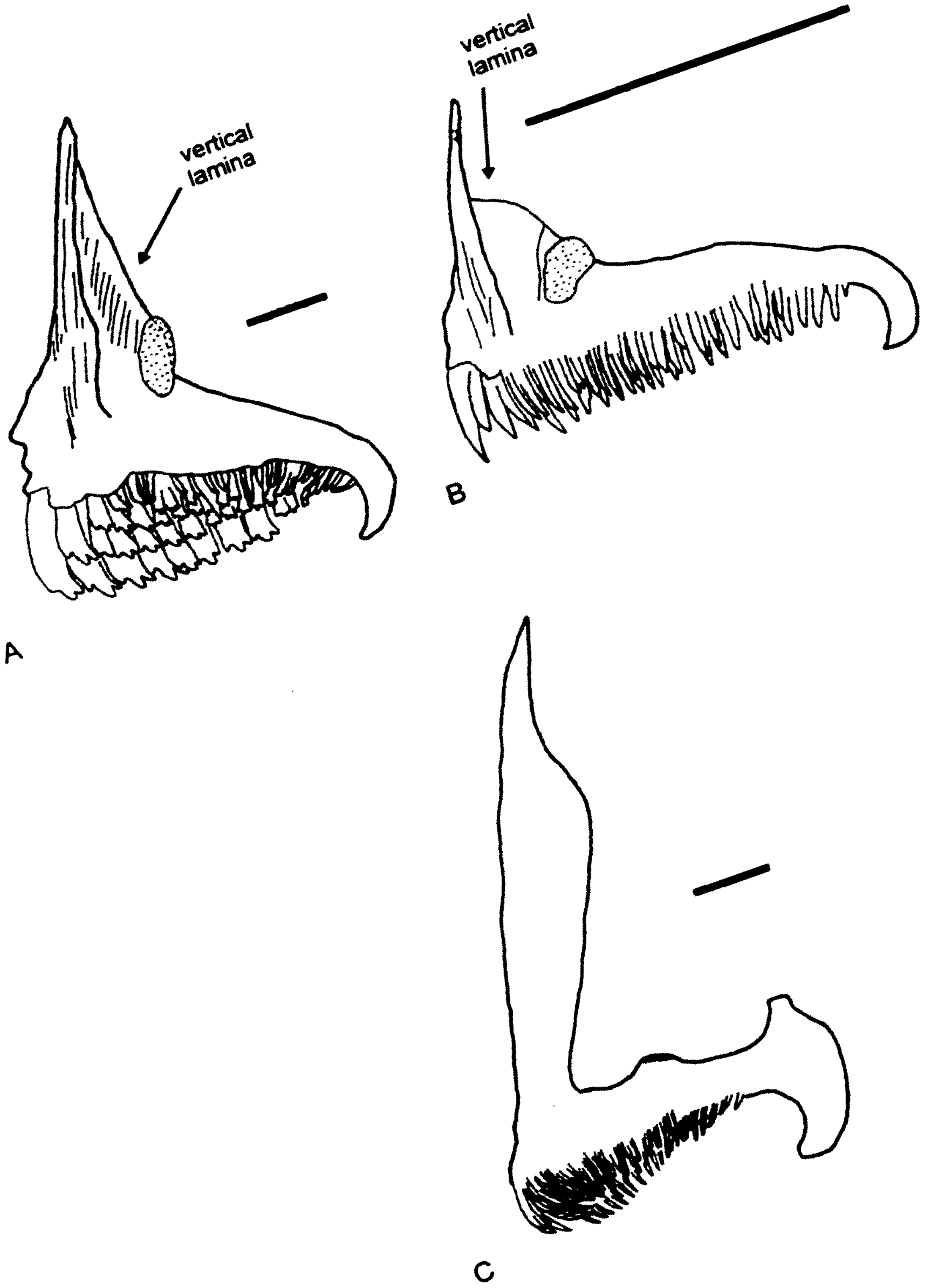
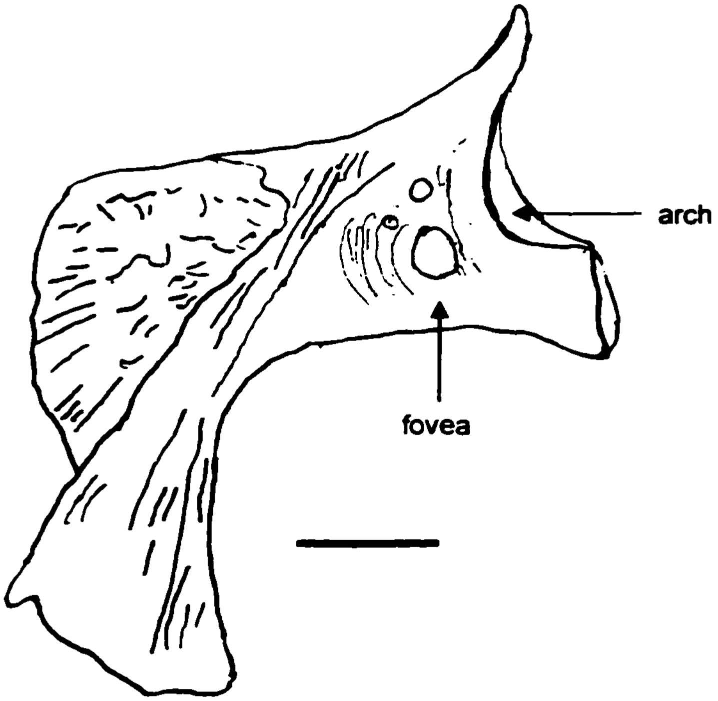
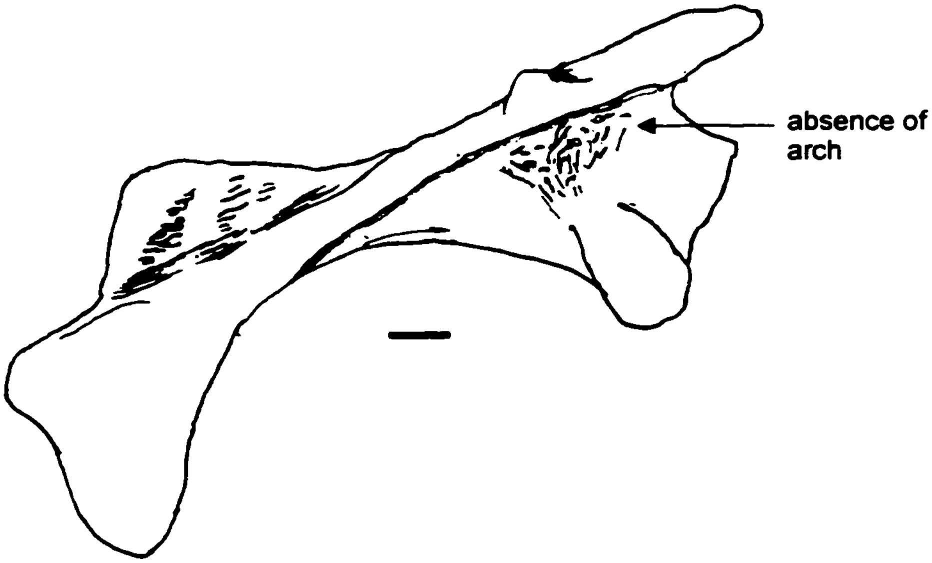

vertical lamina
vertical lamina
A
B
C

Figure 8. Anterolateral view of the maxilla of *Tripterodon orbis* (A) and *Proteracanthus sarissophorus* (B). *Tripterodon*: RUSI 8508, 68 mm SL. *Proteracanthus*: ZRC (USDZ) 3361, 183 mm SL. Scale bars = 1 mm.

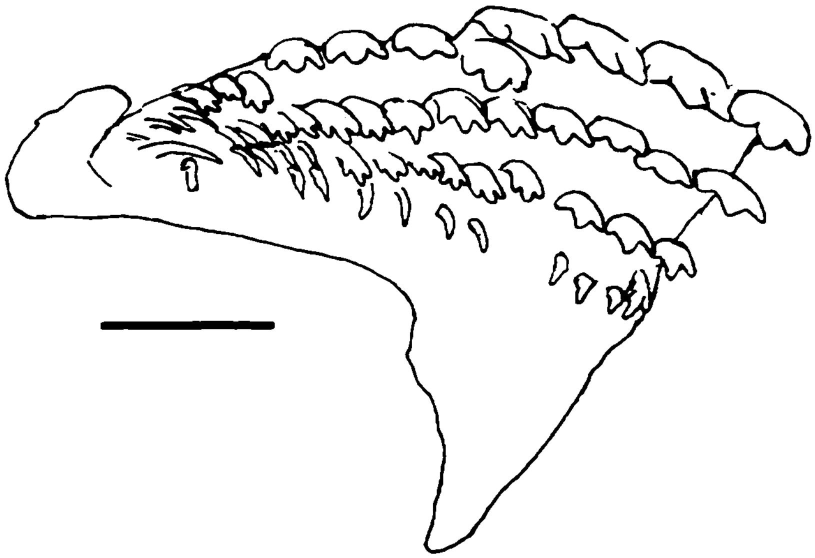


A

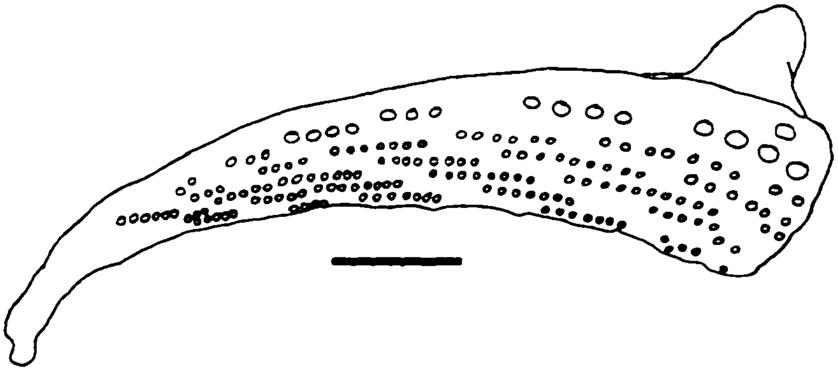


B

Figure 9. Ventromedial view of toothcaps of right premaxilla of *Tripterodon orbis* (A). Ventrolateral view of tooth pedestals of the right premaxilla of *Ephippus orbis* (B). *Tripterodon*: RUSI 8508, 68 mm SL. *Ephippus*: ANSP 27738, 107 mm SL. Scale bars = 1 mm.



A



B

Figure 10. Lateral view of the infraorbital series of *Tripterodon orbis* (A), *Ephippus goreensis* (B), *Zabidius novemaculeatus* (C), *Platax batavianus* (D), and *Scatophagus argus* (E). *Tripterodon*: Rusi 8508, 68 mm SL. *Ephippus*: ANSP 55193, 81 mm SL. *Zabidius*: NTM S.12164-001, 110 mm SL. *Platax*: NTM S.11690-002, 100 m SL. *Scatophagus*: USNM 224393, 54.5 mm SL. I - V = infraorbital bones. Scale bars = 1 mm.

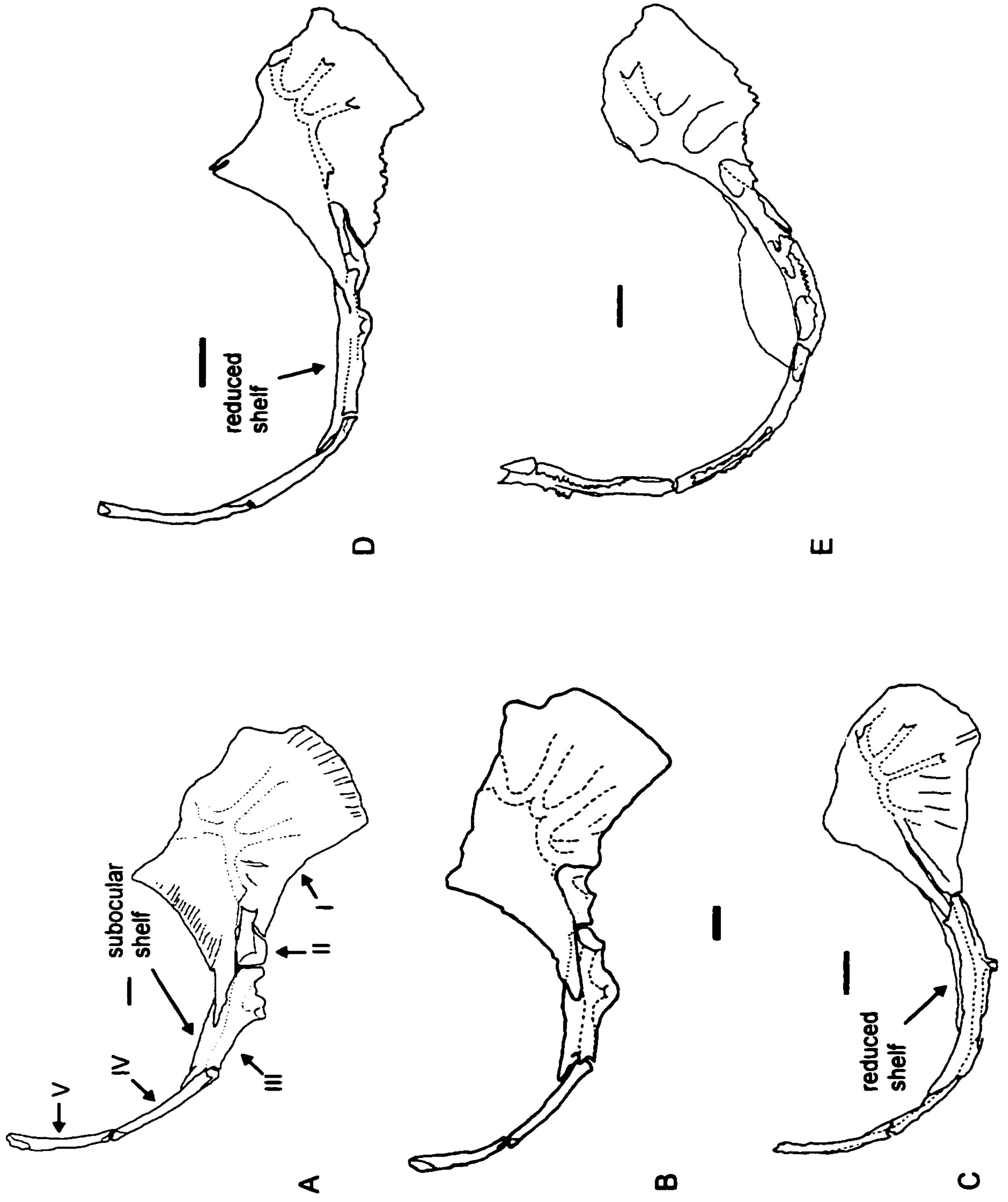

A
B
C
D
E
subocular shelf
I
II
III
IV
V
reduced shelf
reduced shelf

Figure 11. Lateral view of infraorbital series of *Drepane punctata* (A), *Rhinoprenes pentanemus* (B), *Parapsettus panamensis* (C), *Proteracanthus sarissophorus* (D), and *Chaetodipterus faber* (E). *Drepane*: USNM 284825, 91 mm SL. *Rhinoprenes*: ANSP 134859, 100 mm SL. *Parapsettus*: USNM 306455, 107 mm SL. *Proteracanthus*: ZRC.3361 (USDZ), 183 mm SL. *Chaetodipterus*: VIMS 8099, 91 mm SL. I - IV = Infraorbital bones. Scale bars = 1 mm.

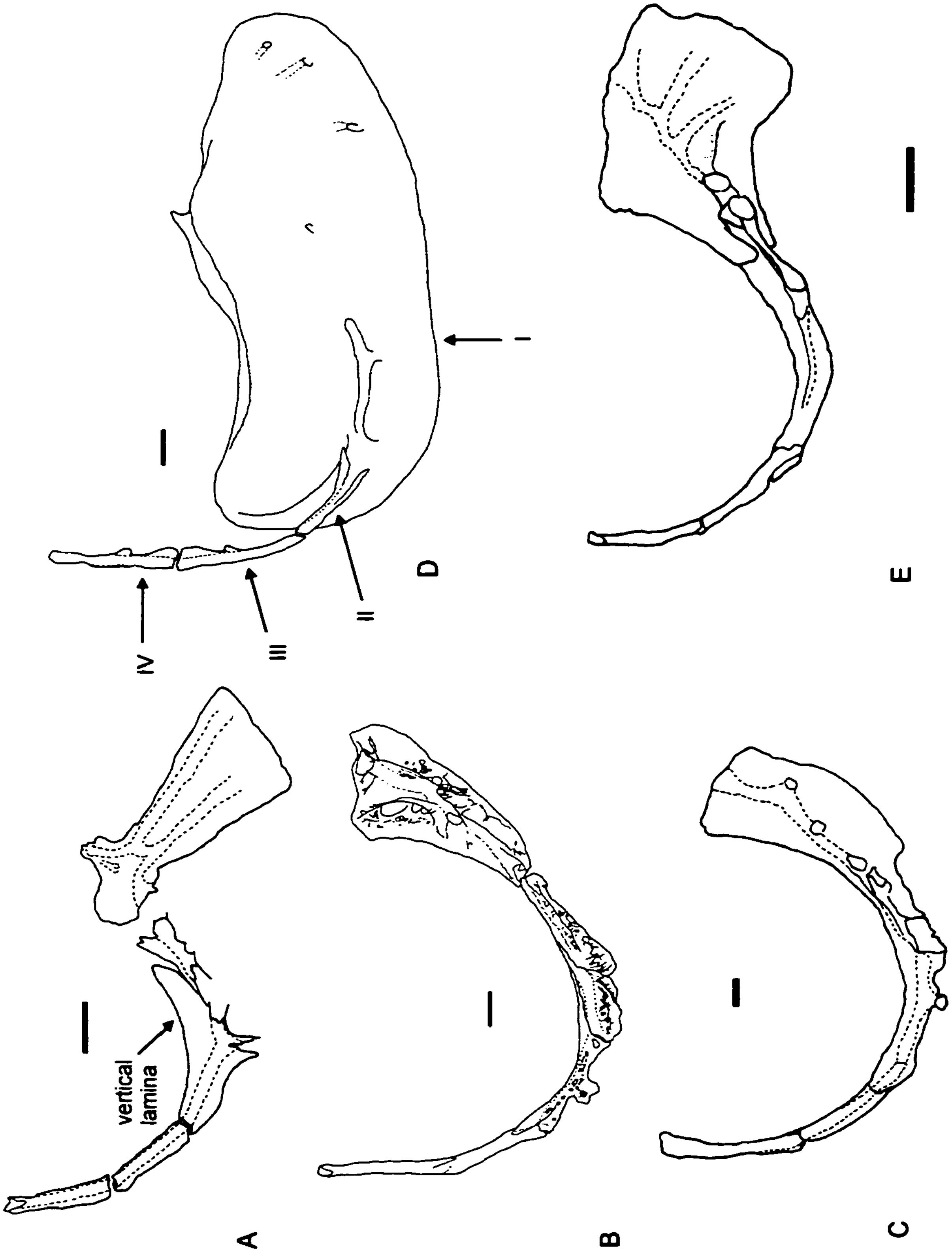

vertical lamina
A
B
C
D
E
I
II
III
IV

Figure 12. Medial view of the suspensorium, upper and lower jaws, and opercular series (left side for A, right side for B and C) of *Zabidius novemaculeatus* (A), *Tripterodon orbis* (B), and *Chaetodon trifasciatus* (C). *Zabidius*: NTM S.11930-001, 99 mm SL; left side photographically reversed. *Tripterodon*: RUSI 8508, 68 mm SL. *Chaetodon*: USNM 140142, 92 mm SL. Scale bars = 1 mm.

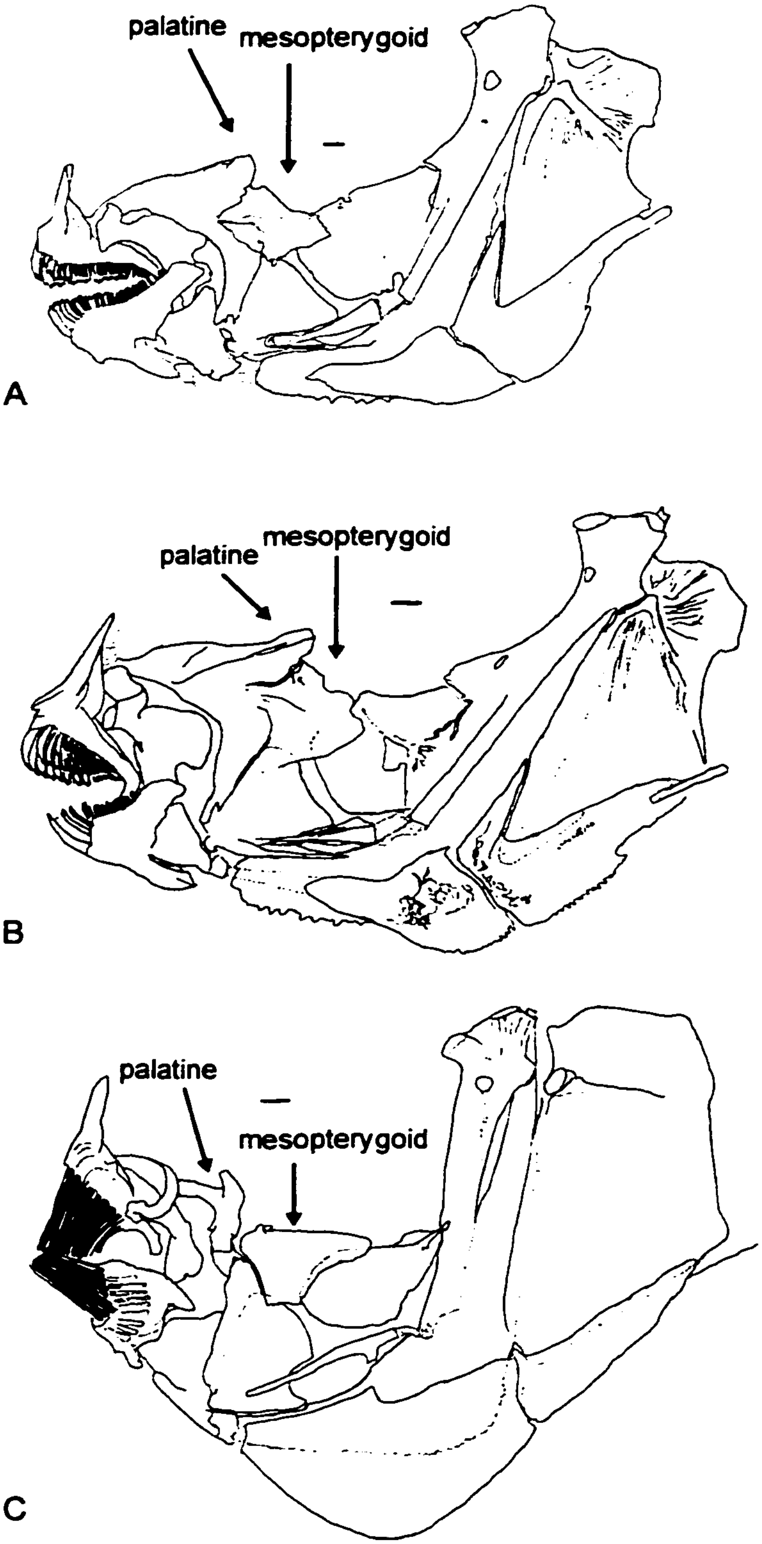

palatine
mesopterygoid
A
palatine
mesopterygoid
B
palatine
mesopterygoid
C

Figure 13. Dorsoanterior view of branchial bones (in part) and rakers associated with first epibranchial of *Platax tiera* (A), *Rhinoprenes pentanemus* (B), *Ephippus orbis* (C), and *Chaetodon sedentarius* (D). *Platax*: NTM S.11690-002, 100 mm SL. *Rhinoprenes*: ANSP 134859, 127 mm TL. *Ephippus*: ANSP 52549, 97 mm SL. *Chaetodon*: USNM 159275, 87 mm SL. PbI and II = pharyngobranchials I and II, EbII = epibranchial II. Scale bars = 1 mm.

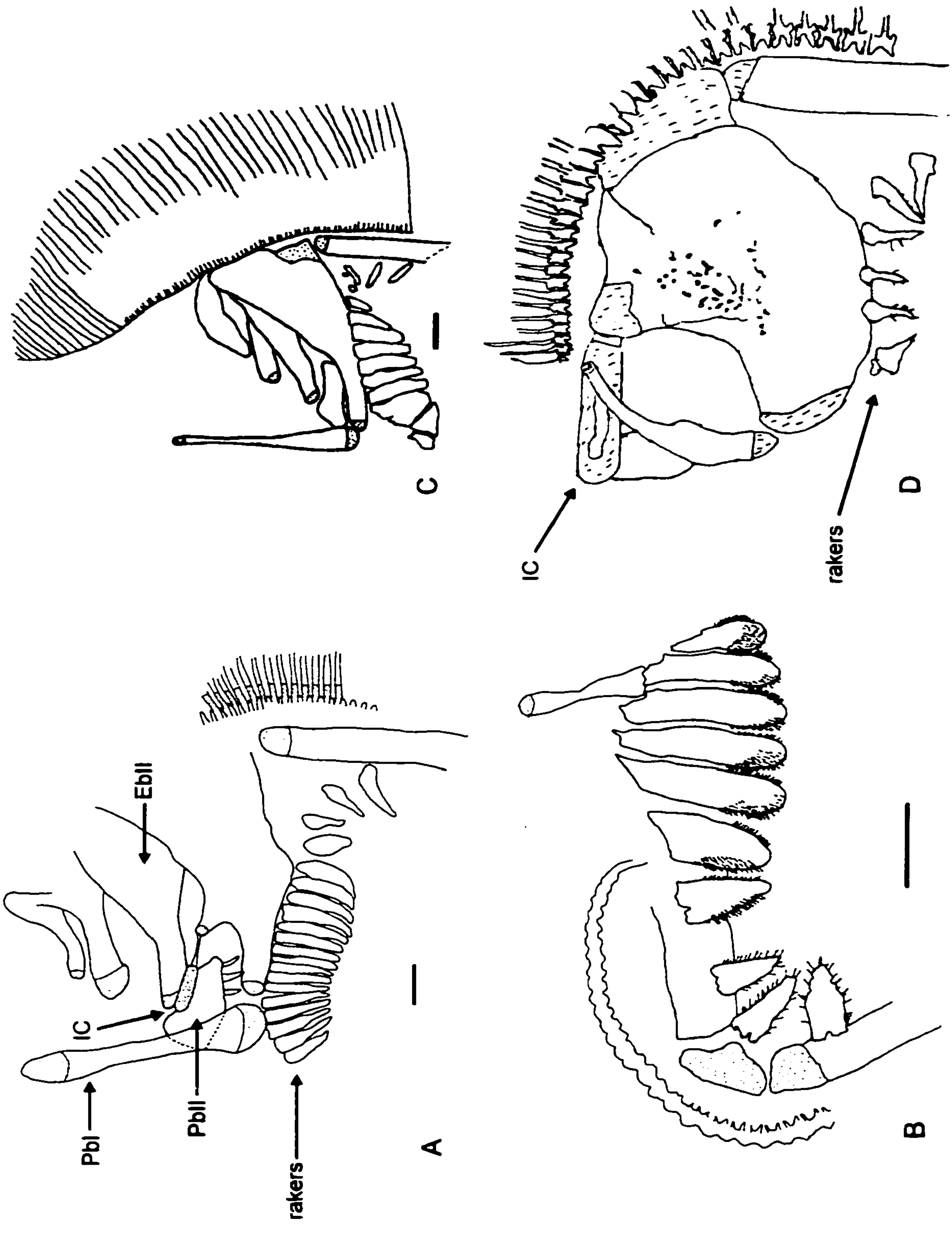

PbI
PbII
IC
EbII
rakers
A
B
C
IC
rakers
D

Figure 14. Oblique view of branchial system of *Platax tiera*, right side, (A), *Chaetodipterus faber*, left side (B), and *Drepane africana*, right side (C). *Platax*: NTM S.10141-003, 82 m SL. *Chaetodipterus*: VIMS 8099, 91 mm SL. *Drepane*: USNM 306260, 89 mm SL. E = epibranchials, Pb = pharyngobranchials, UP = branchial arch, IC =interarcual cartilage. Scale bars = 1 mm.

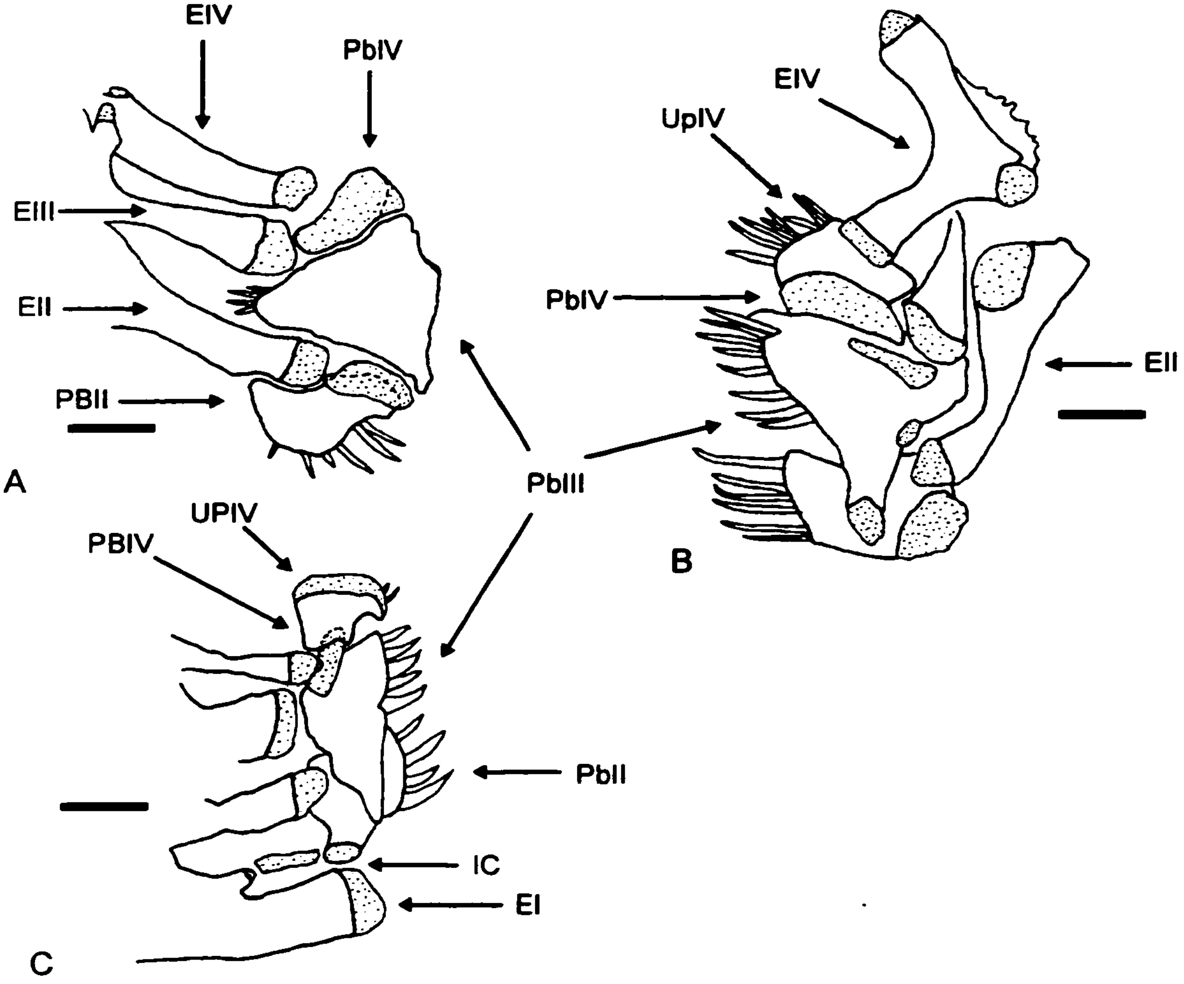

EIV
PbIV
EIII
EII
PBII
A
PbIII
UpIV
EIV
PbIV
EII
B
UPIV
PBIV
PbII
IC
EI
C

Figure 15. **Basihyals of** ***Zabidius novemaculeatus*** **(A),** ***Platax batavianus*** **(B), and** ***Heniochus acuminatus*** **(C).** ***Zabidius*****: NTM S.11930-001, 99 mm SL.** ***Platax*****: NTM S.10141-003, 82 mm SL.** ***Heniochus*****: USNM 147893, 80 mm SL. Scale bars = 1 mm.**

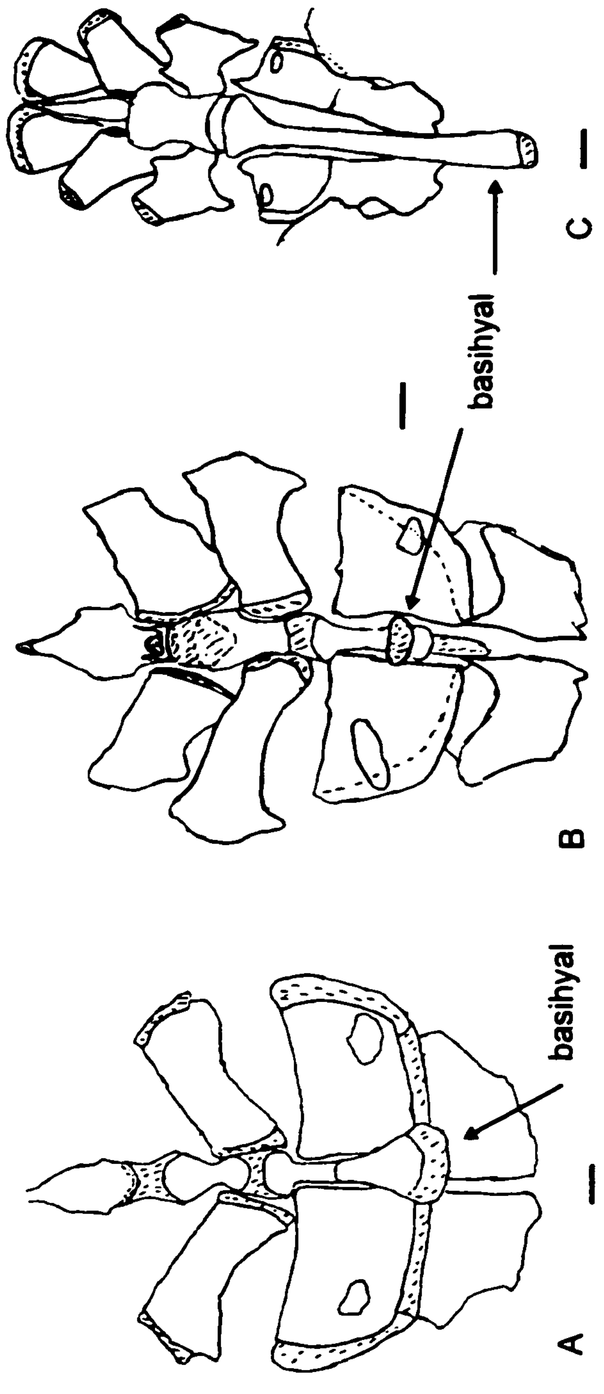
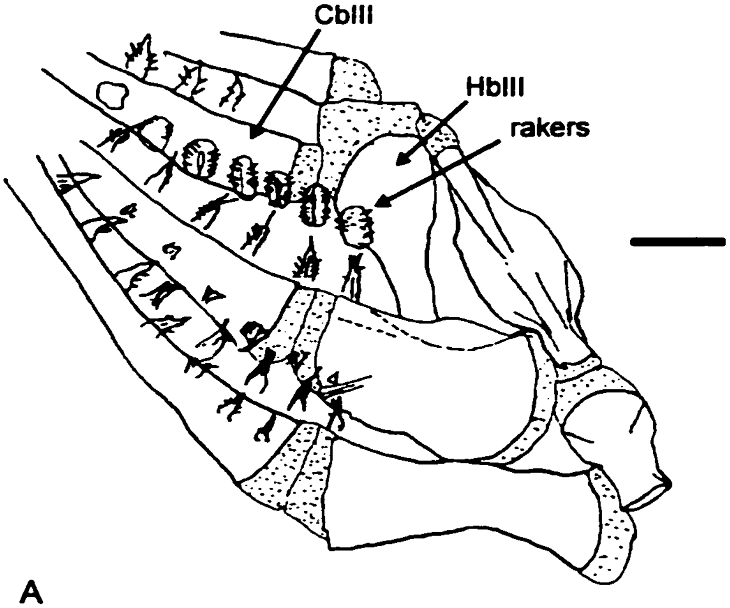
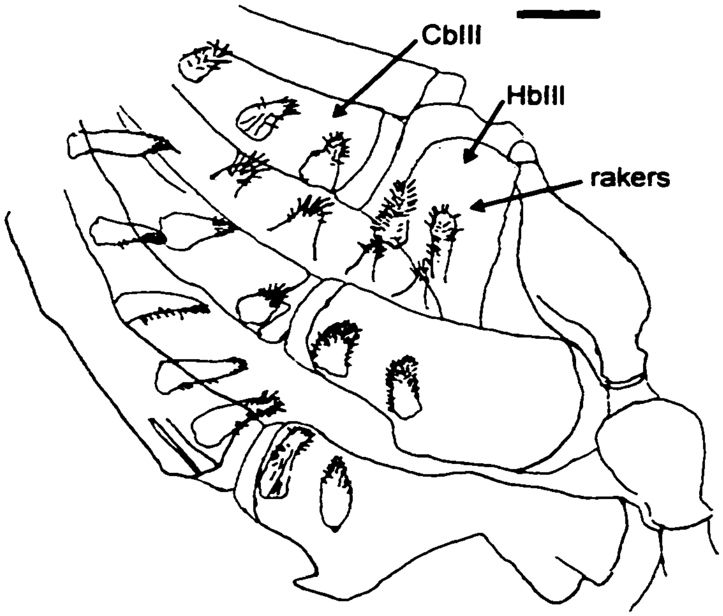

A
basihyal
B
basihyal
C

Figure 16. Basibranchials, hypobranchials, and ceratobranchials (in part) of *Rhinoprenes pentanemus* (A) and *Chaetodipterus zonatus* (B). *Rhinoprenes*: ANSP 134859, 127 mm TL, *Chaetodipterus*: USNM 220719, 85 mm SL. CBIII = ceratobranchial III, HbIII = hypobranchial III. Scale bars = 1 mm.



A



B

Figure 17. **Lateral view of anterior neural spines, pterygiophores, and supraneurals of *Drepane africana*. USNM 306260, 89 mm TL. Scale bar = 1 mm.**

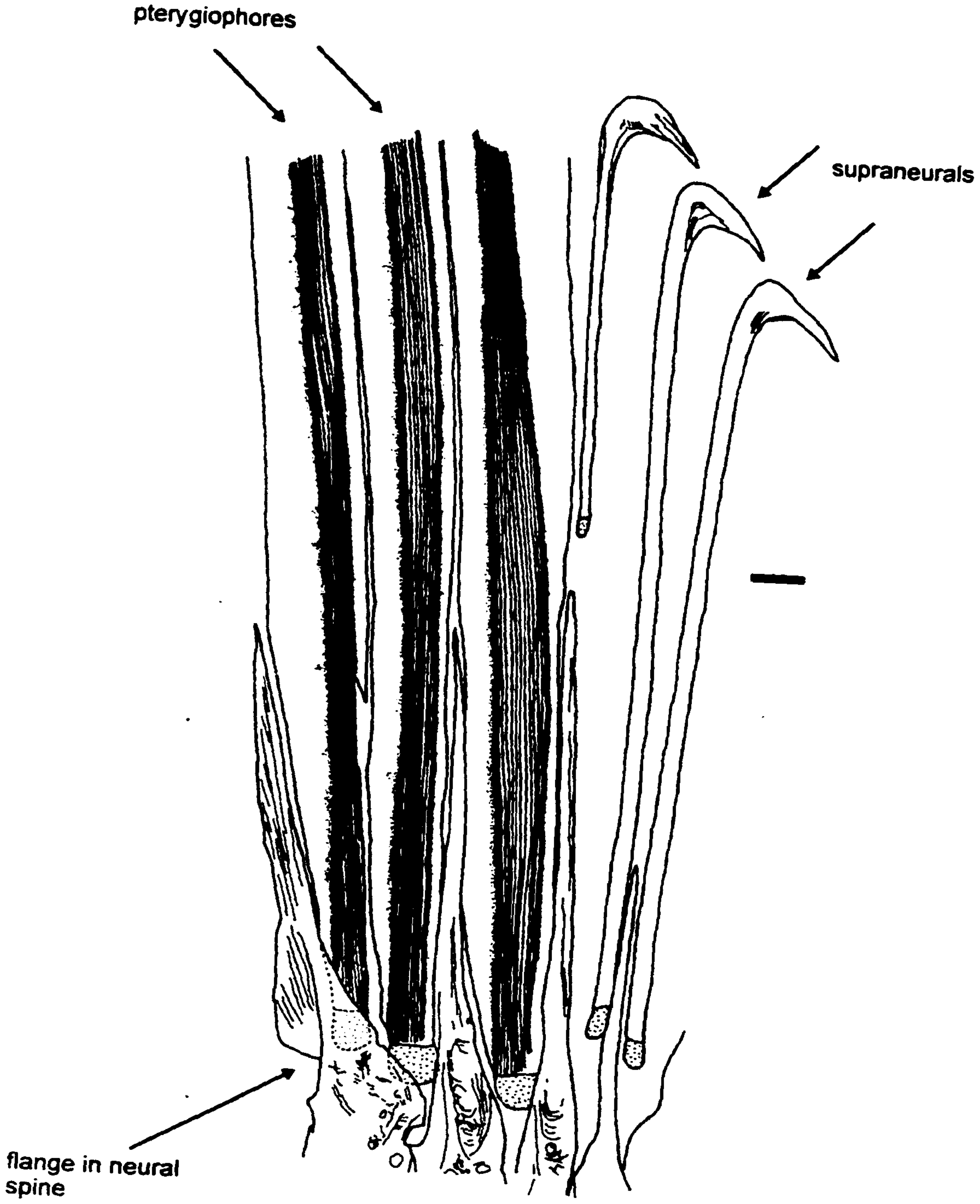

pterygiophores
supraneurals
flange in neural spine

Figure 18. Lateral view (right side) of fifth anteriormost vertebra and fifth anteriormost pterygiophore of *Rhinoprenes pentanemus*. ANSP 134859, 100 mm SL. Scale bar = 1 mm.

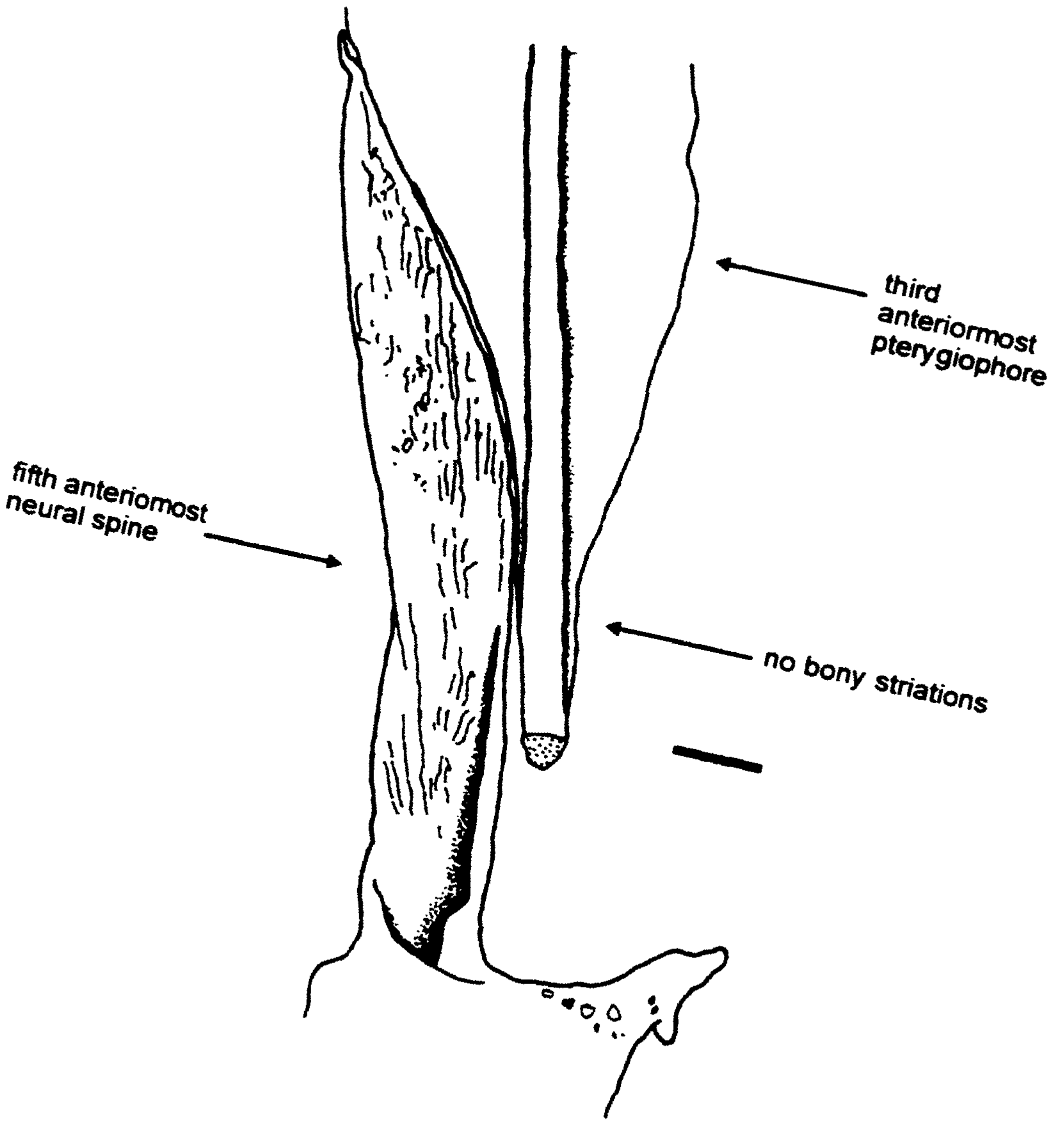

third anteriormost pterygiophore
fifth anteriomost neural spine
no bony striations

Figure 19. **Lateral view of supraneurals, anteriormost pterygiophores, and anteriormost neural spines of *Platax pinnatus* (A), *Parapsettus panamensis* (B), and *Proteracanthus sarissophorus* (C). *Platax*: AMNH 88344SW, 58 mm SL. *Parapsettus*: Beltran, B. (personal loan, uncatalogued), 50 mm SL. *Proteracanthus*: ZRC 3361 (USDZ), 183 mm SL. Scale bars = 1 mm.**

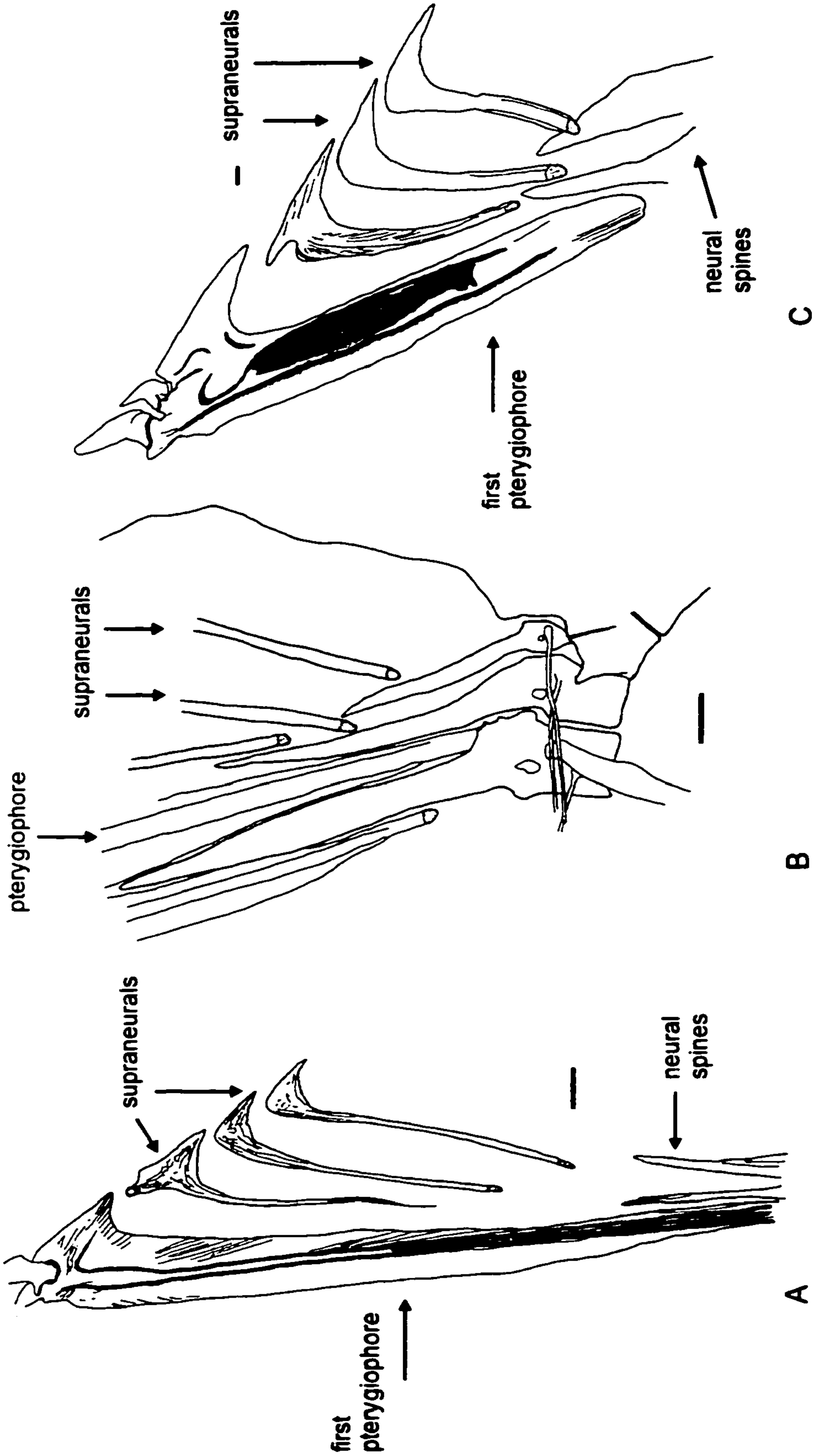

first pterygiophore
supraneurals
neural spines
A
first pterygiophore
supraneurals
supraneurals
B
supraneurals
neural spines
first pterygiophore
C

Figure 20. Lateral view of anterior vertebrae and swimbladder diverticulum of *Ephippus goreensis*. ANSP 55193, 68 mm SL. Scale bar = 1 mm.

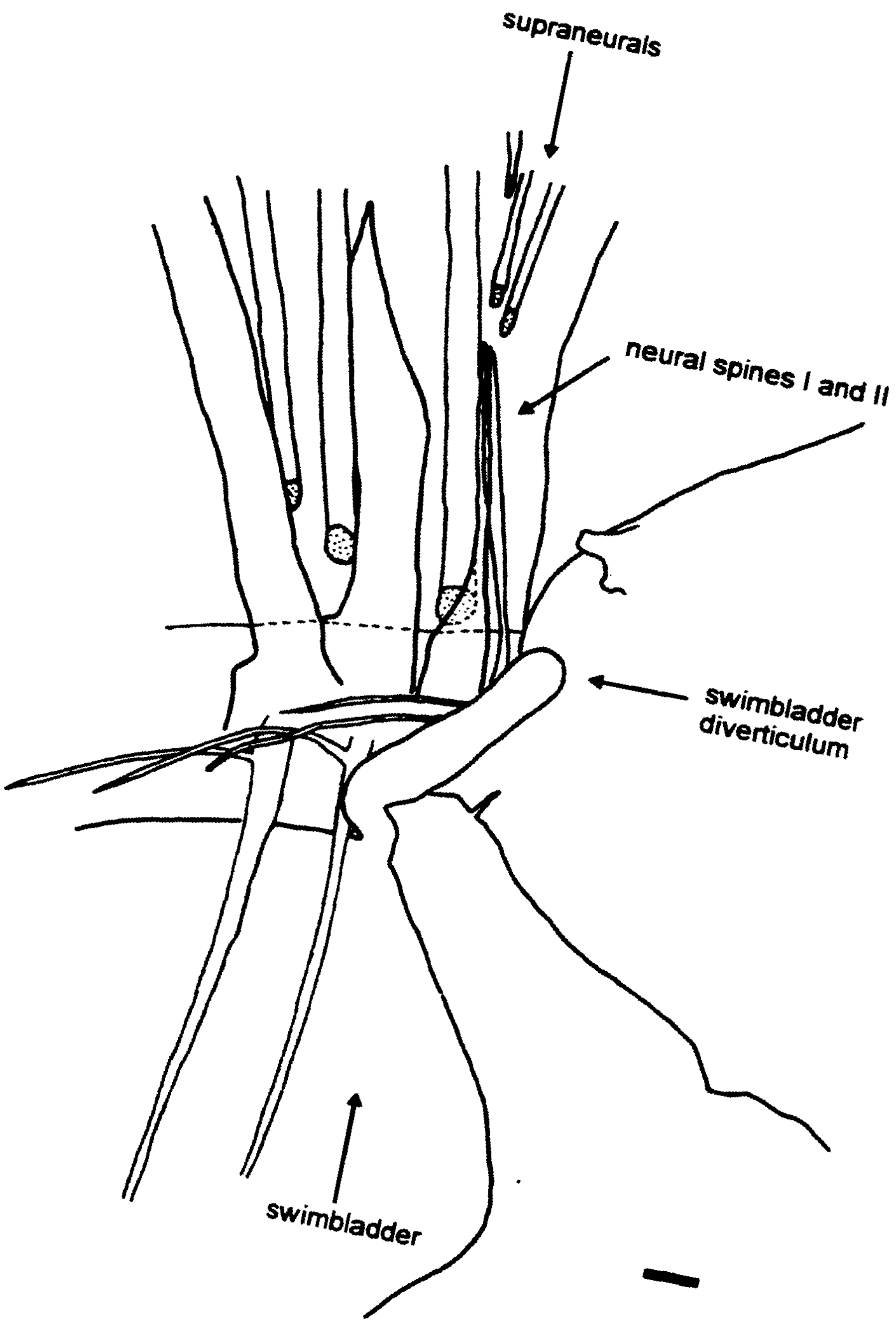

supraneurals
neural spines I and II
swimbladder diverticulum
swimbladder

Figure 21. Lateral view (left side) of anterior swimbladder diverticulum of *Zabidius novemaculeatus*. NTM S.11930-001, 99 mm SL. Scale bar = 1 mm.

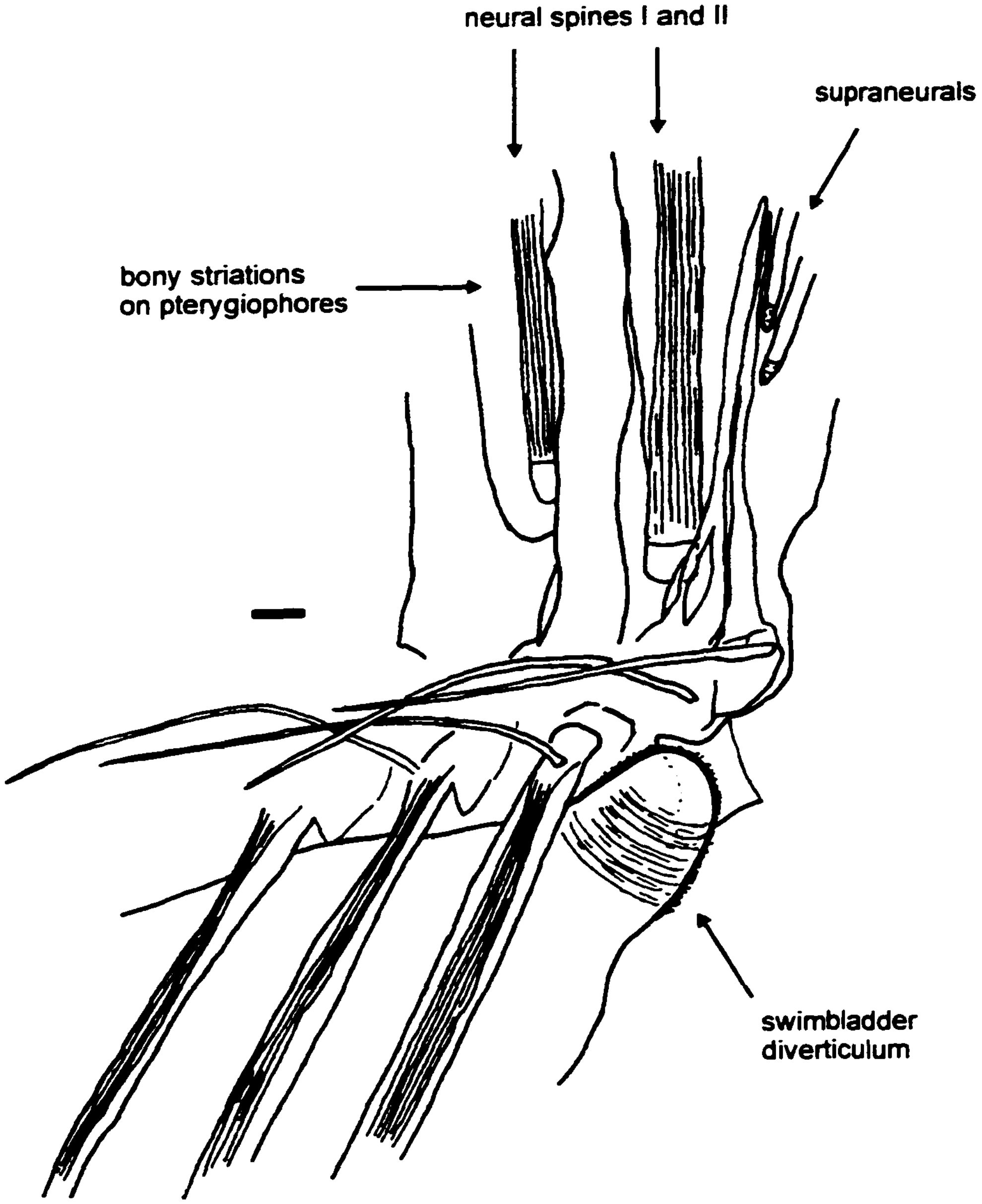
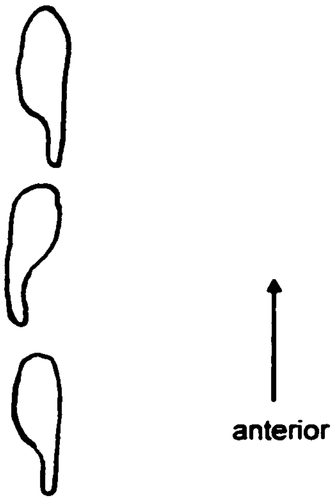
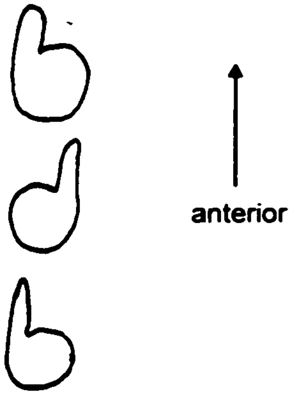

neural spines I and II
supraneurals
bony striations on pterygiophores
swimbladder diverticulum

Figure 22. Diagrammatic representation of cross-section through three dorsal spines of *Tripterodon orbis* (A), and *Proteracanthus sarissophorus* (B). Scale bar = 1 mm.



A



B

Figure 23. Lateral view of pectoral girdle of *Platax batavianus* (A), *Rhinoprenes pentanemus* (B), *Drepane punctata* (C). *Platax*: NTM S.10141-003, 82 mm SL. *Rhinoprenes*: ANSP 134859, 100 mm SL. *Drepane*: USNM 284825, 91 mm SL. Scale bars = 1 mm.

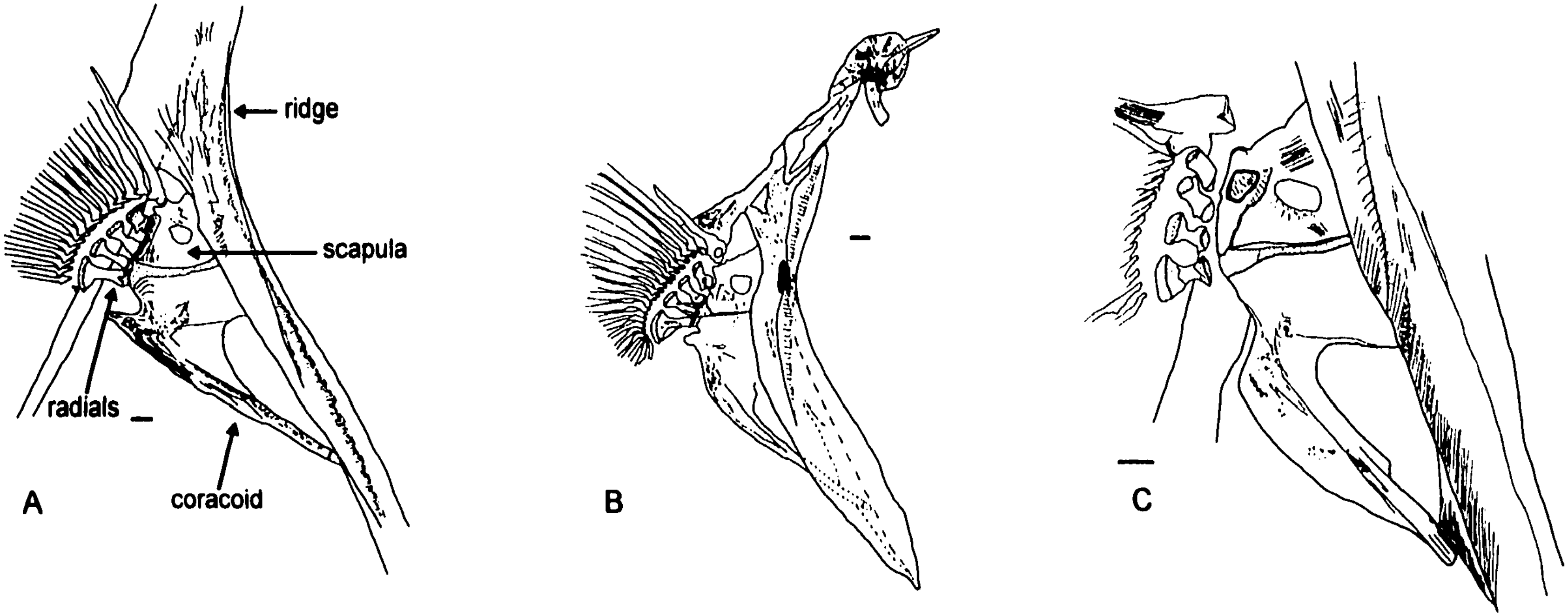

ridge
scapula
radials
coracoid
A
B
C

Figure 24. Medial view of right pectoral girdle of *Platax batavianus* (A), *Rhinoprenes pentanemus* (B), and *Drepane longimanus* (D). Lateral view of pectoral girdle of *Drepane punctata* (C): USNM 284825, 91 mm SL. *Platax*: NTM S.10141-003, 82 mm SL. *Rhinoprenes*: ANSP 134859, 100 mm SL. *Drepane longimanus*: USNM 284472, 93 mm SL. Scale bars = 1 mm.

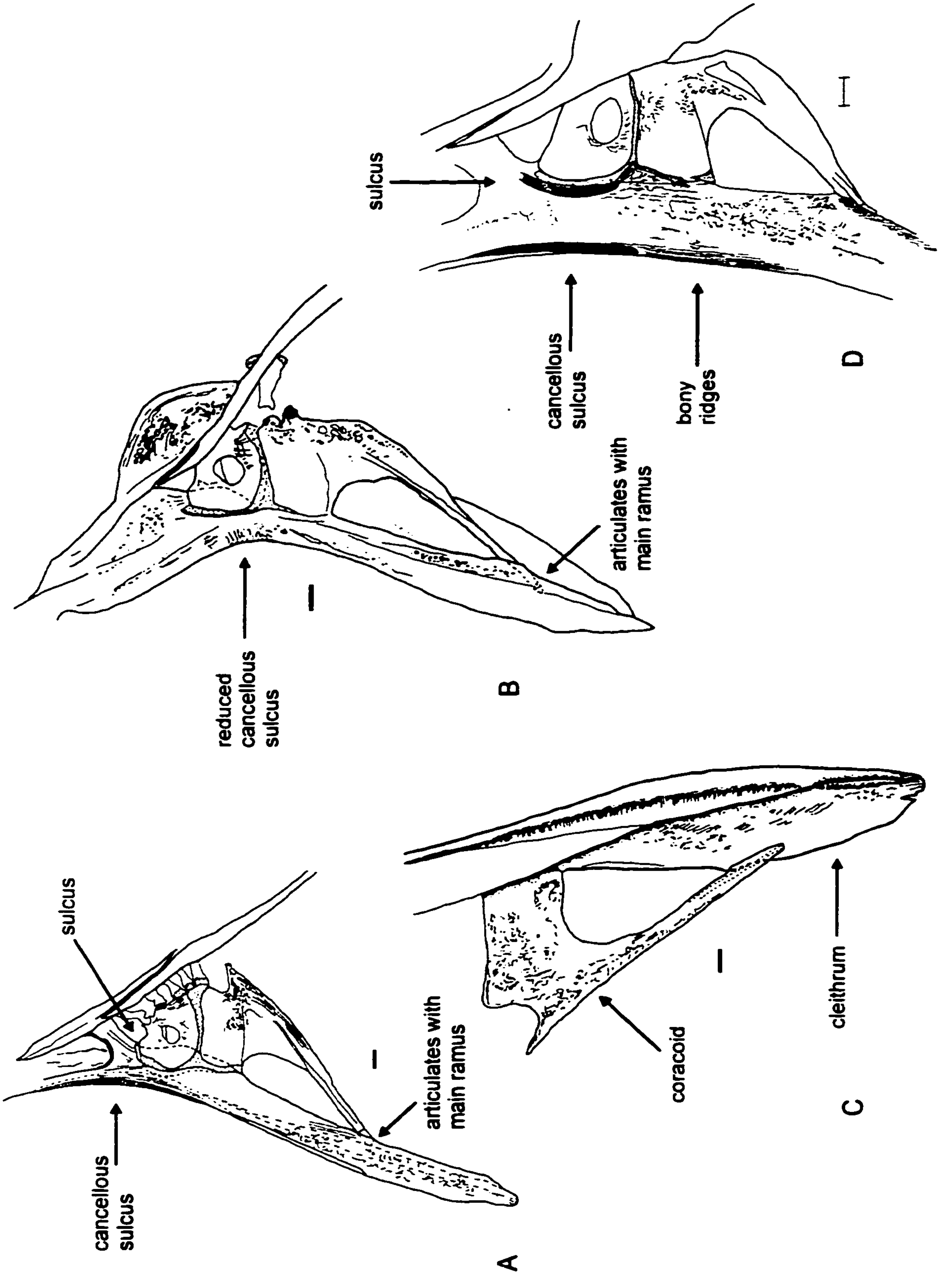
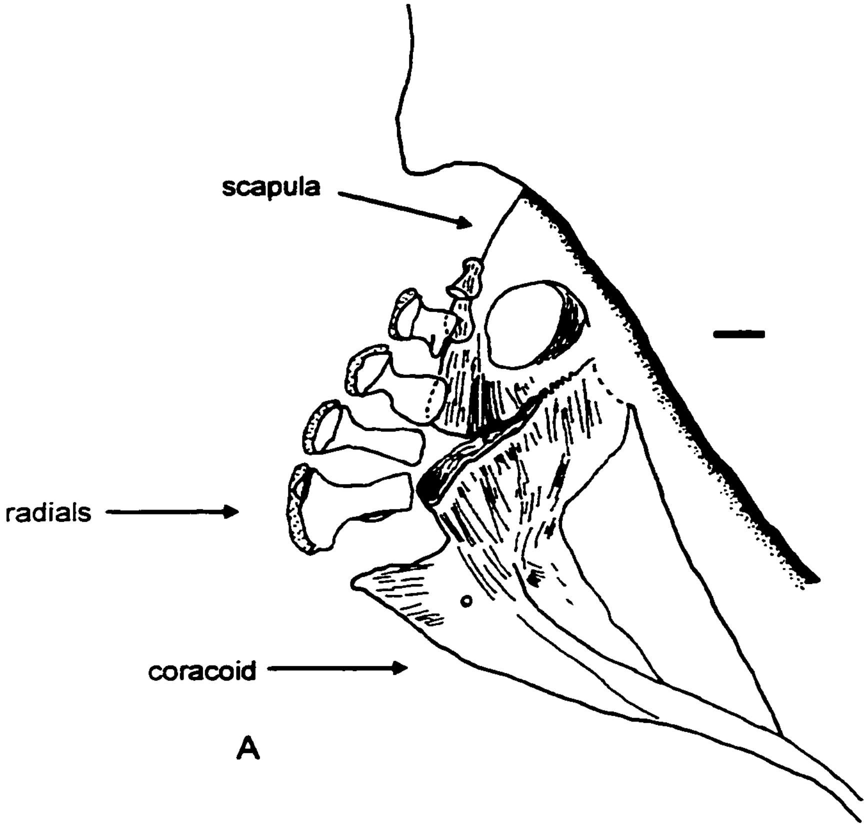

A
cancellous sulcus
sulcus
articulates with main ramus
B
reduced cancellous sulcus
articulates with main ramus
C
coracoid
cleithrum
D
sulcus
cancellous sulcus
bony ridges

Figure 25. Posterolateral view of right pectoral girdle (in part) of *Rhinoprenes pentanemus* (A), and *Ephippus orbis* (B). *Rhinoprenes*: ANSP 134859, 100 mm SL. *Ephippus*: ANSP 27738, 107 mm SL. Scale bars = 1 mm.


scapula
radials
coracoid
A

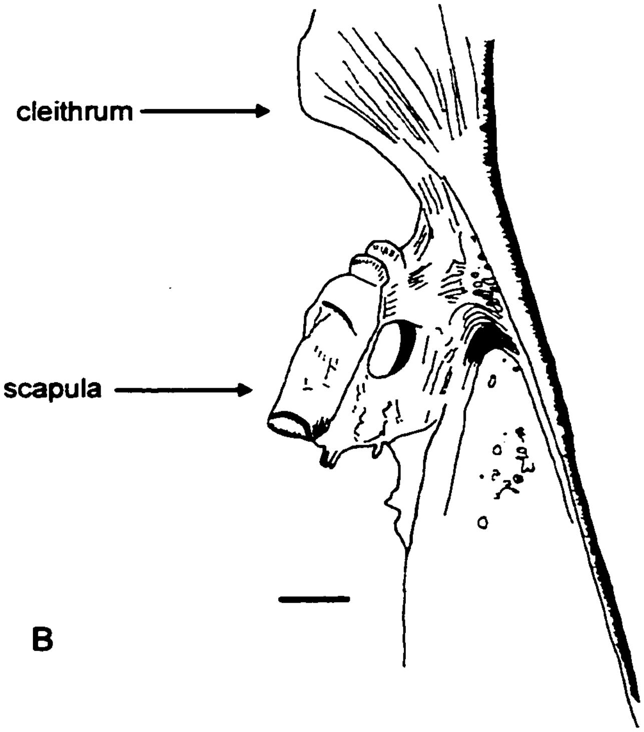

cleithrum
scapula
B

Figure 26. Dorsal view of ischial processes of pelvic fin girdle of *Chaetodipterus faber* (A), *Drepane africana* (B), and *Ctenochaetus striatus* (Chaetodontidae) (C). *Chaetodipterus*: VIMS 8099, 91 mm SL. *Drepane*: USNM 306252, 88 mm TL. *Ctenochaetus*: AMNH 38133SW, 72 mm SL. Scale bars = 1 mm.

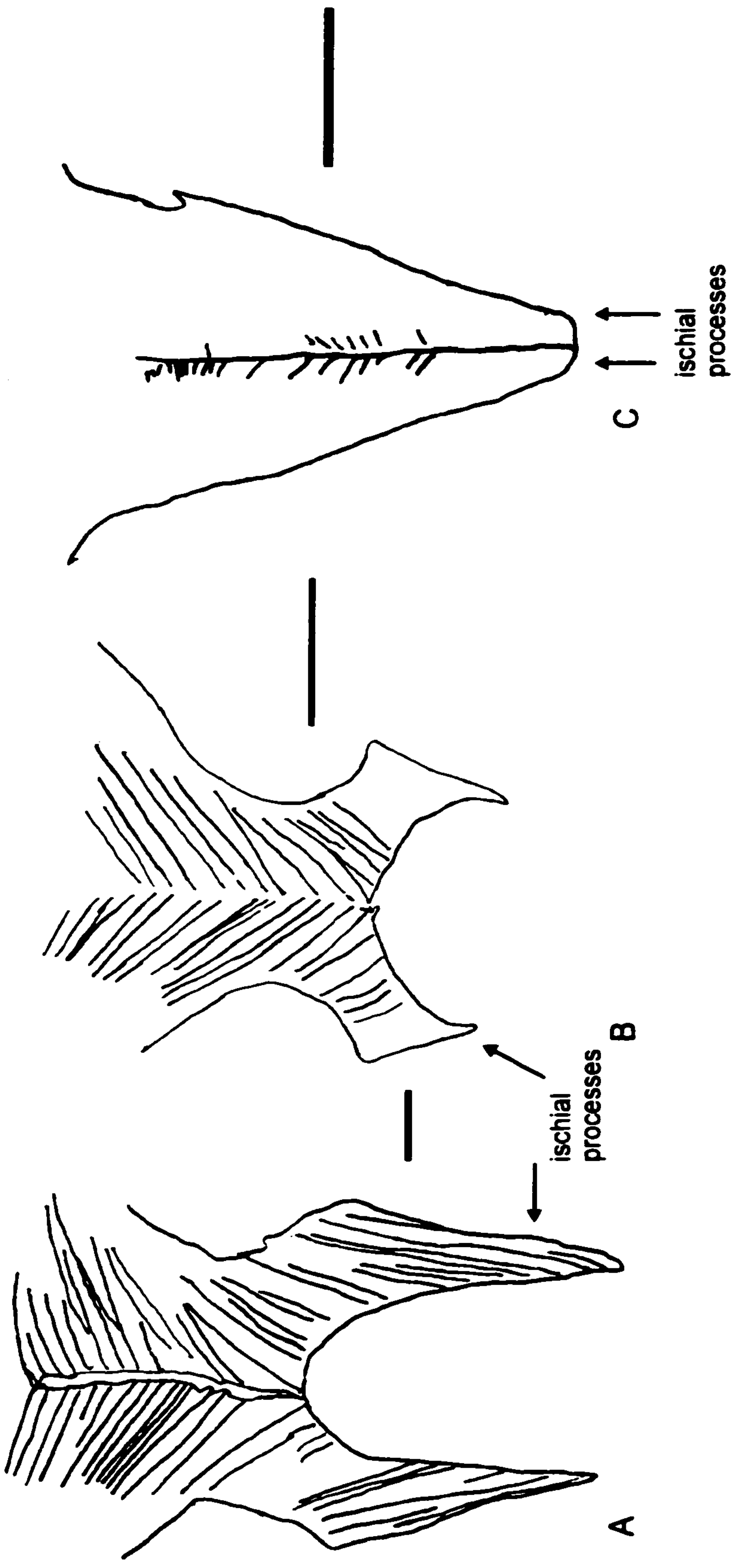

A
B
C
ischial processes
ischial processes

Figure 27. Diagrammatic representation of pelvic-fin wings (lamina): four lamina (A), three lamina (B). Diagram is a cross-section through the pelvic girdle (basipterygia). EDW = external dorsal wing; EVW = external ventral wing; IW = internal wing; VW = ventral wing; CP = central part.

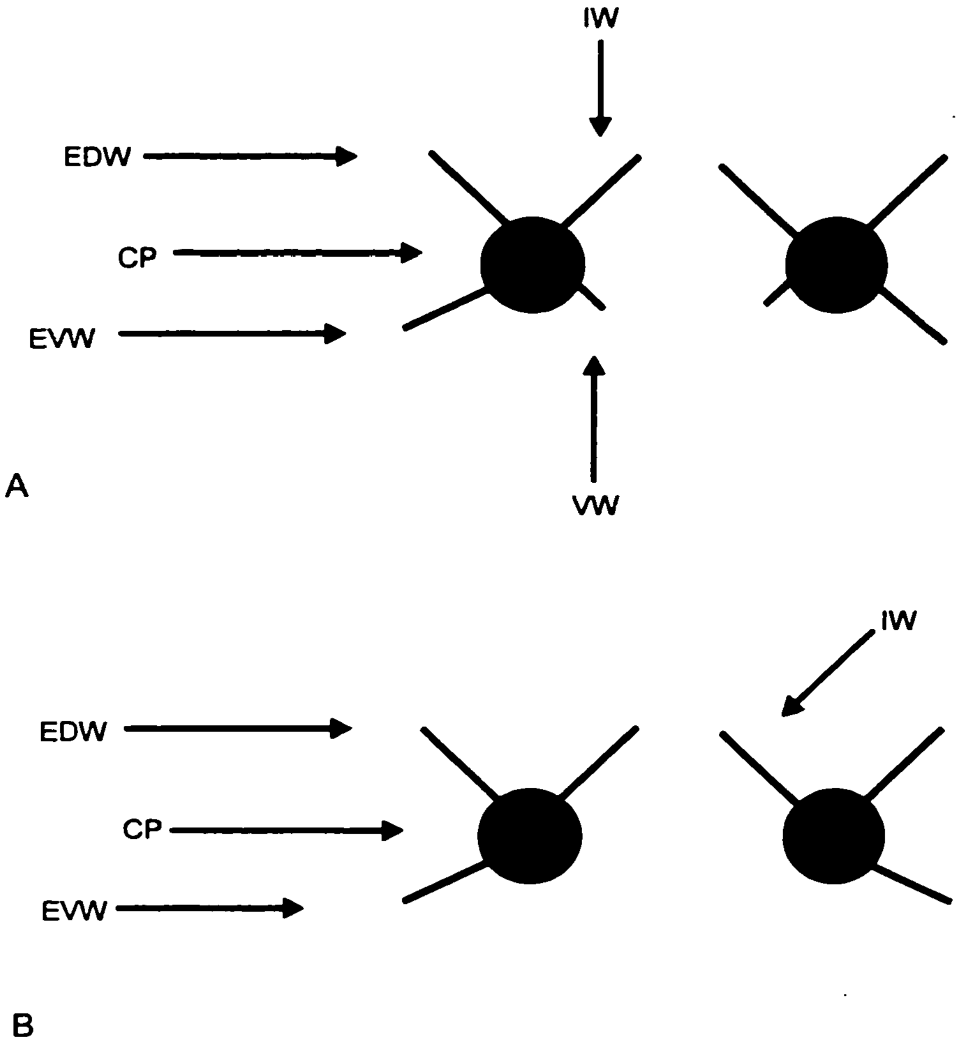

IW
EDW
CP
EVW
A
VW
IW
EDW
CP
EVW
B

Figure 28. Lateral view of the angular, dentary (in part), and preoperculomandibular sensory canal of *Ephippus orbis* (A), and *Chaetodon sedentarius* (B). *Ephippus*: ANSP 52749, 97 mm SL. *Chaetodon*: USNM 159275, 87 mm SL. Scale bars = 1 mm.

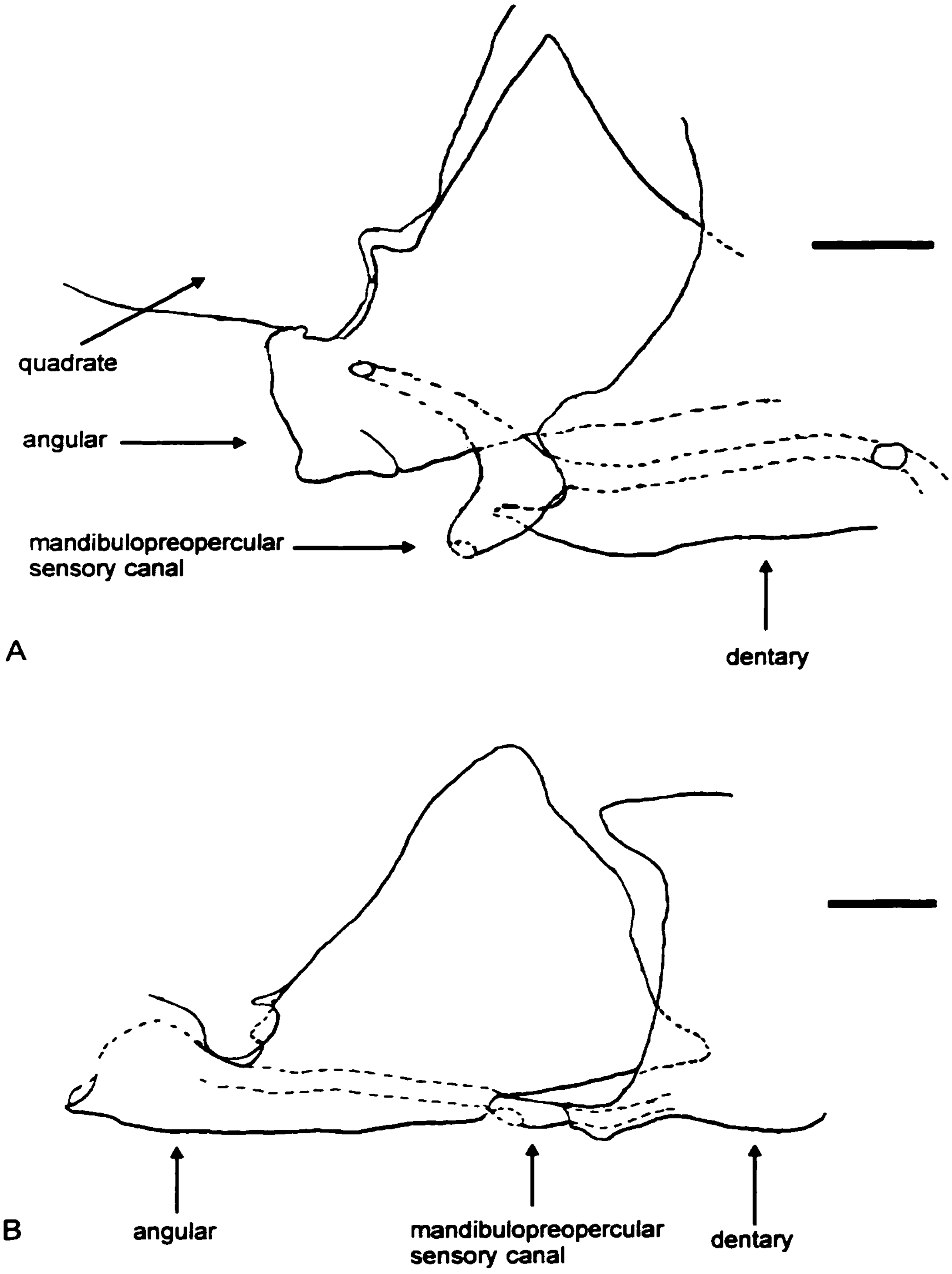
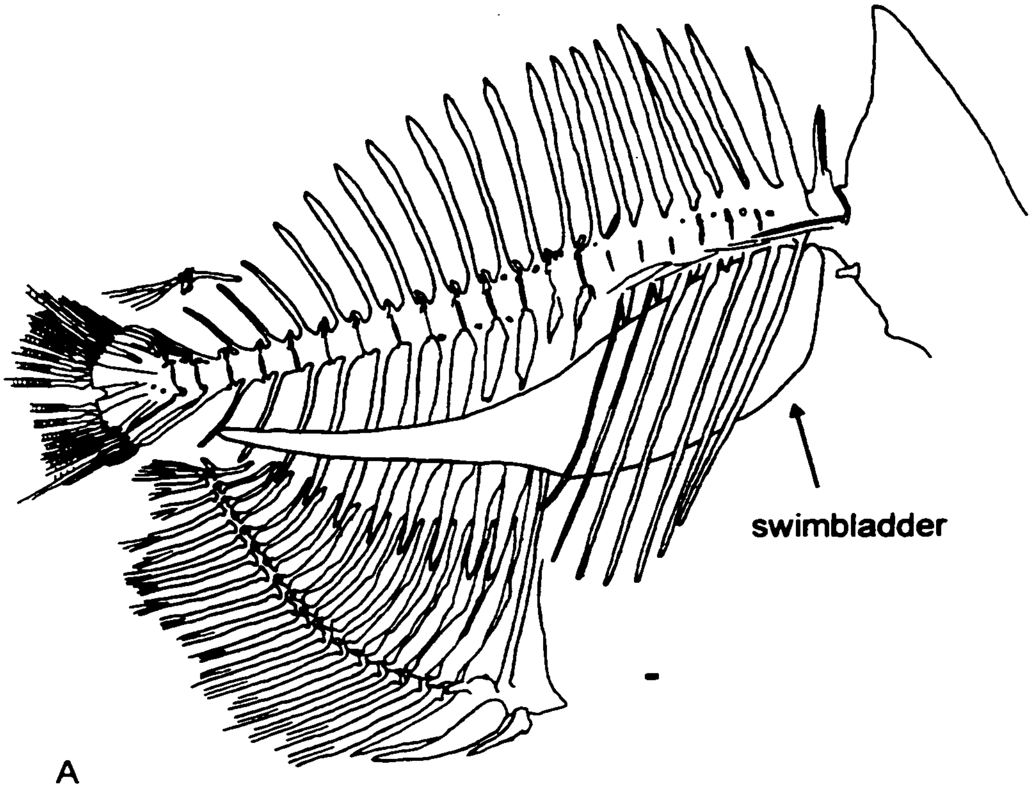
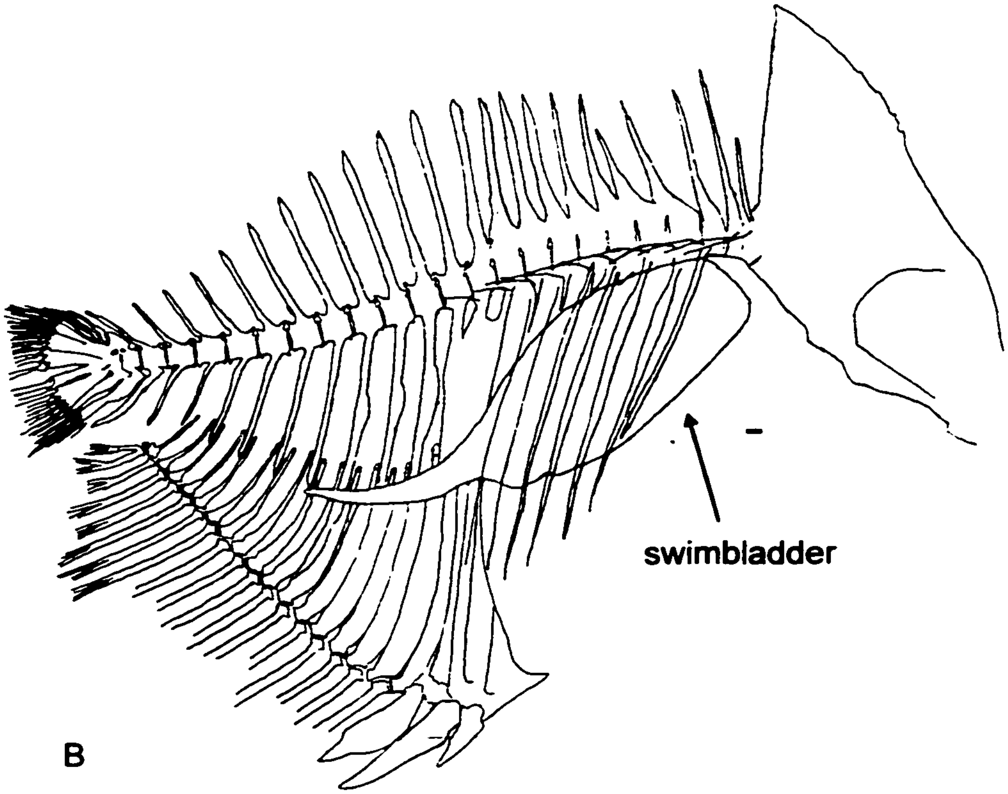

quadrate
angular
mandibulopreopercular sensory canal
A
dentary
B
angular
mandibulopreopercular sensory canal
dentary

Figure 29. Lateral view of skeleton and swimbladder of *Chaetodipterus zonatus* (A), and *Drepane africana* (B). *Chaetodipterus*: USNM 220719, 85 mm SL. *Drepane*: USNM 306260, 64 mm SL. Scale bars = 1 mm.



A



B

Figure 30. Constraint trees 1 (A), and 2 (B). Topology of Constraint tree 1 from results of Tang et al. (1999).

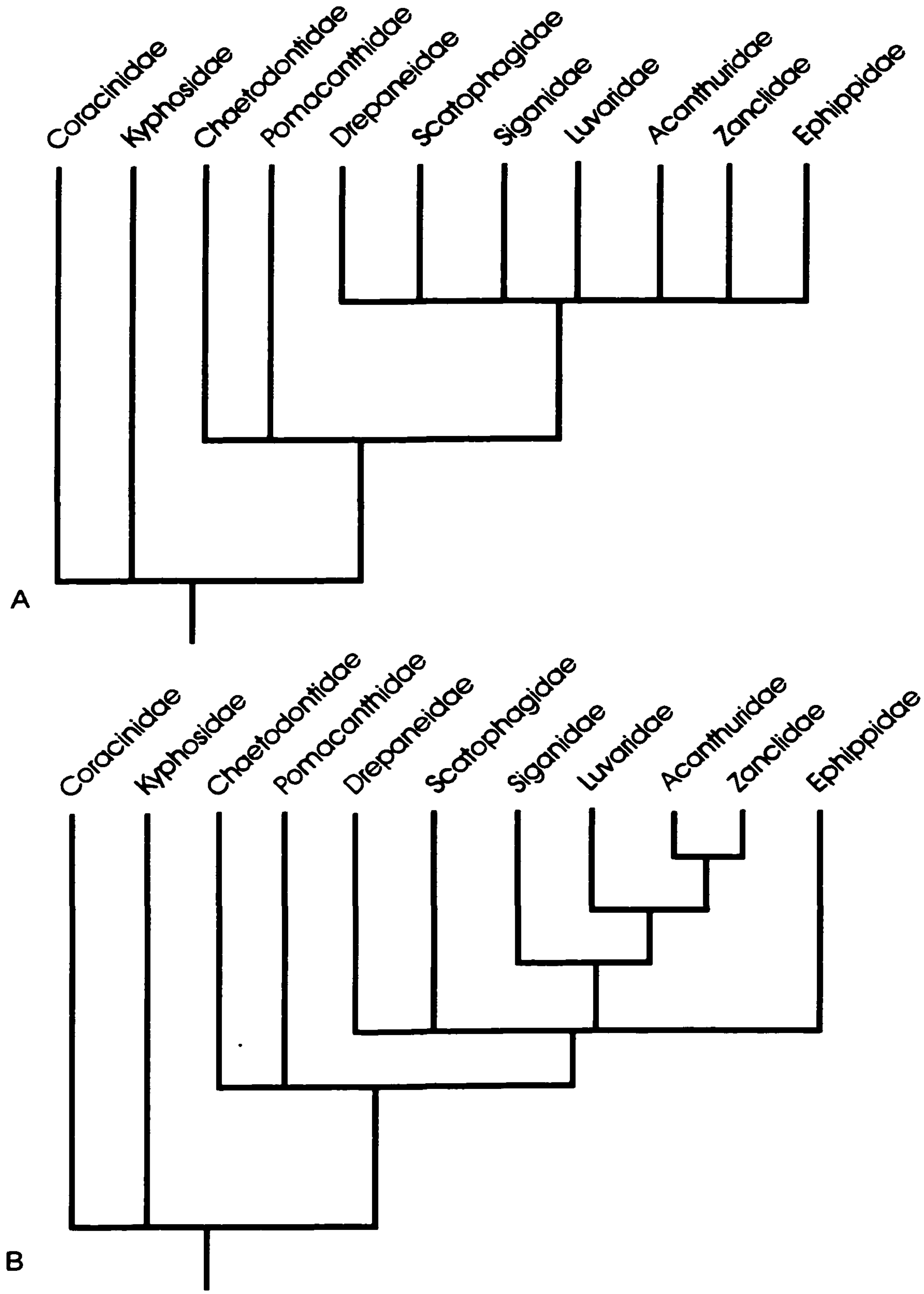

Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
Ephippidae
A
Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
Ephippidae
B

Figure 31. Two consensus trees (A, B) resulting from Constraint Analysis 1. Top: branch length; middle: bootstrap value; bottom: Bremer support value. NA = not available due to constraint tree topology.

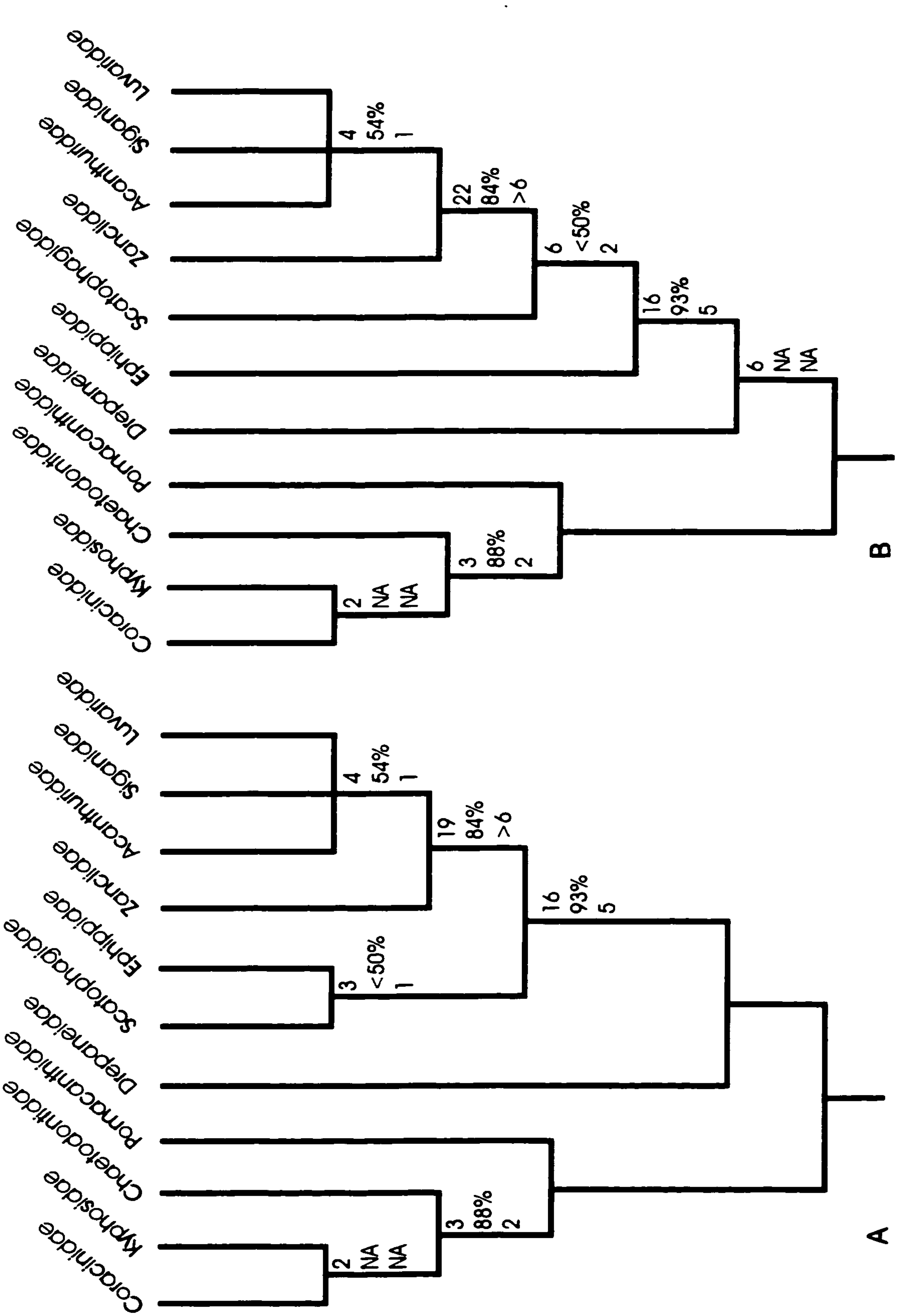

Luvaridae
Siganidae
Acanthuridae
Zanclidae
Ephippidae
Scatophagidae
Drepaneidae
Pomacanthidae
Chaetodontidae
Kyphosidae
Coracinidae
4 54% 1
19 84% >6
3 <50% 1
16 93% 5
3 88% 2
2 NA NA
A
Luvaridae
Siganidae
Acanthuridae
Zanclidae
Scatophagidae
Ephippidae
Drepaneidae
Pomacanthidae
Chaetodontidae
Kyphosidae
Coracinidae
4 54% 1
22 84% >6
6 <50% 2
16 93% 5
6 NA NA
3 88% 2
2 NA NA
B

Figure 32. Two equally-parsimonious trees (A, B) resulting from Constraint Analysis 2. Top: branch length; middle: bootstrap value; bottom: Bremer support value. NA = not available due to constraint tree topology.

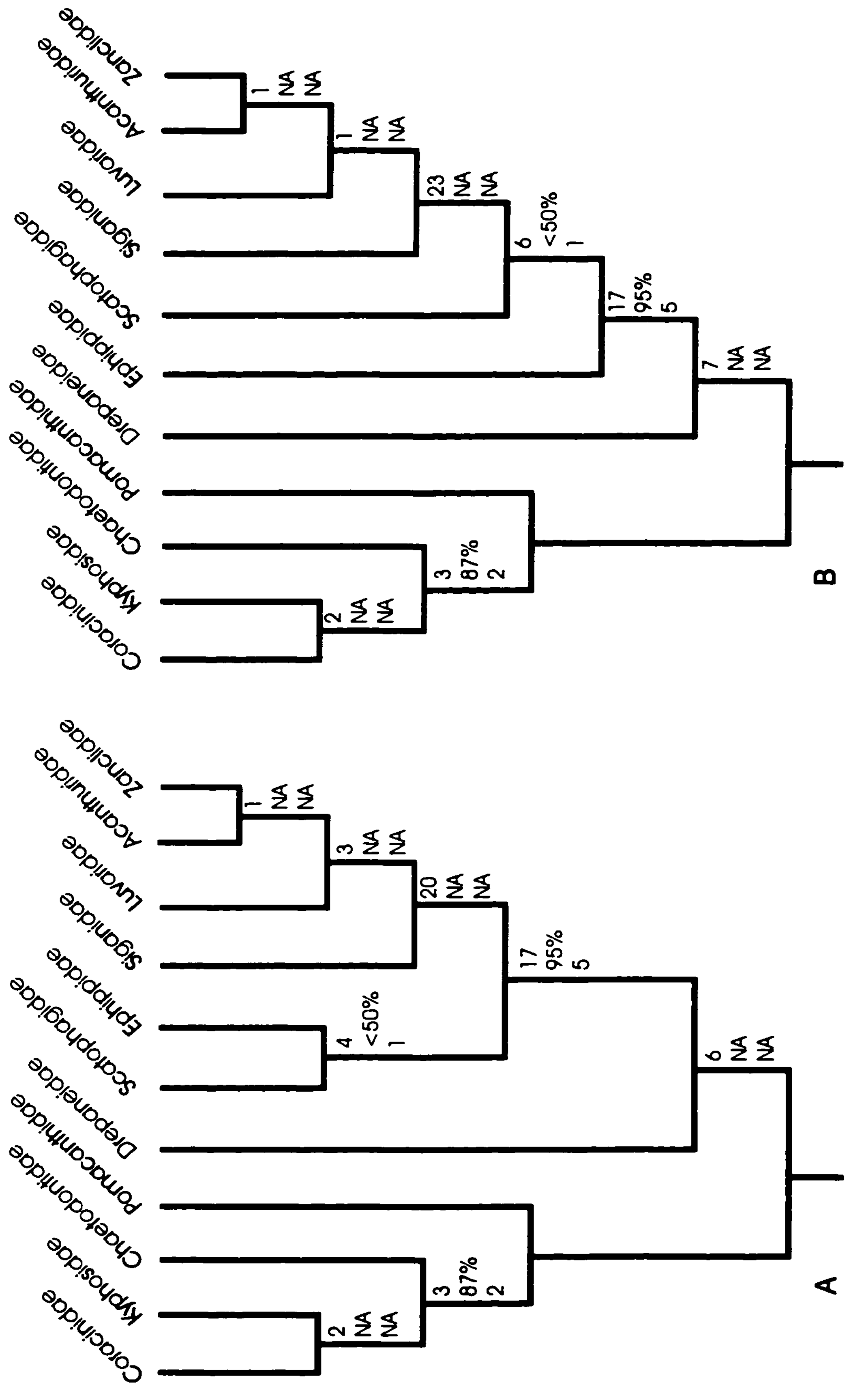
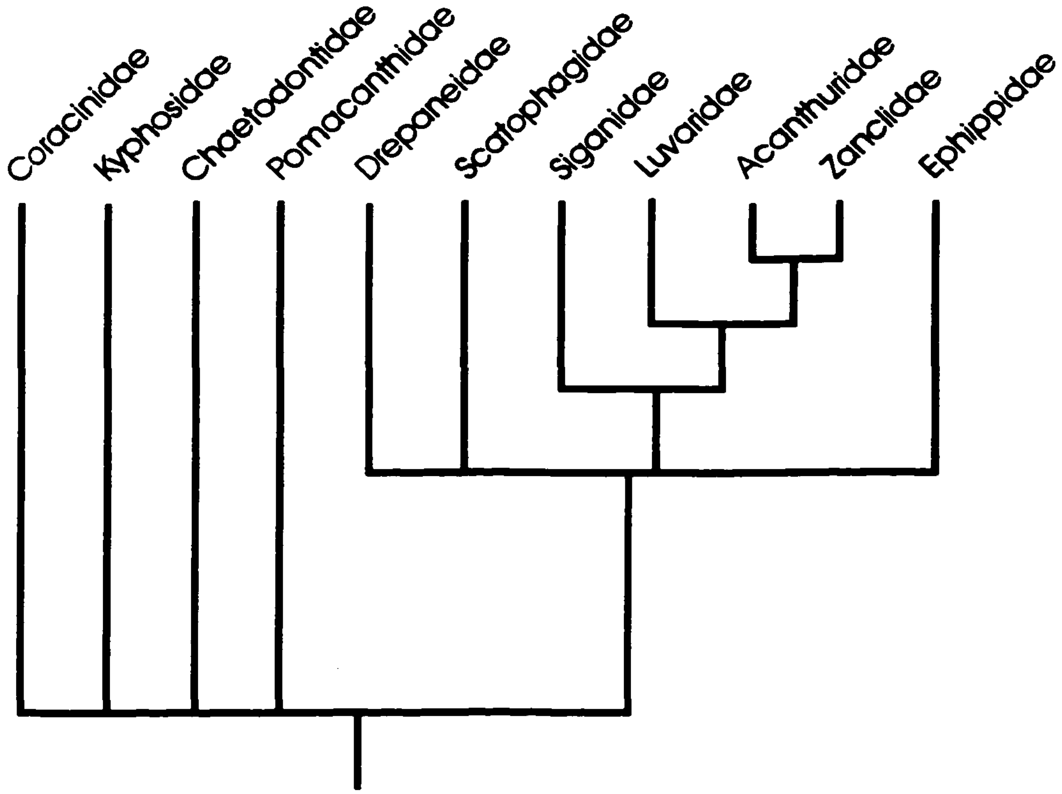
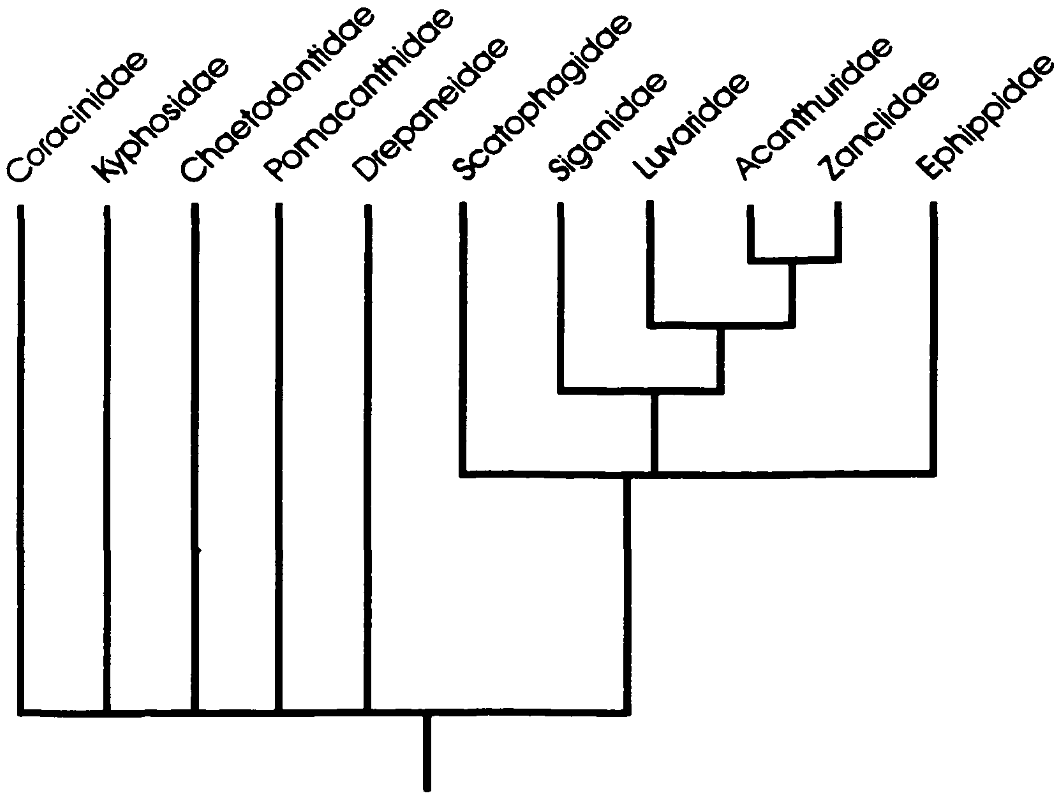

A
Zanclidae
Acanthuridae
Luvaridae
Siganidae
Ephippidae
Scatophagidae
Drepaneidae
Pomacanthidae
Chaetodontidae
Kyphosidae
Coracinidae
1 NA NA
3 NA NA
20 NA NA
4 <50% 1
17 95% 5
6 NA NA
3 87% 2
2 NA NA
B
Zanclidae
Acanthuridae
Luvaridae
Siganidae
Scatophagidae
Ephippidae
Drepaneidae
Pomacanthidae
Chaetodontidae
Kyphosidae
Coracinidae
1 NA NA
1 NA NA
23 NA NA
6 <50% 1
17 95% 5
7 NA NA
3 87% 2
2 NA NA

Figure 33. Constraint trees 3 (A), and 4 (B).


Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
Ephippidae

A


Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
Ephippidae

B

Figure 34. Single most-parsimonious tree resulting from Constraint Analysis 4. Top: branch length; middle: bootstrap value; bottom: Bremer support value. NA = not available due to constraint tree topology. Numbers in parentheses refer to nodes referenced in Tables 6 and 7.

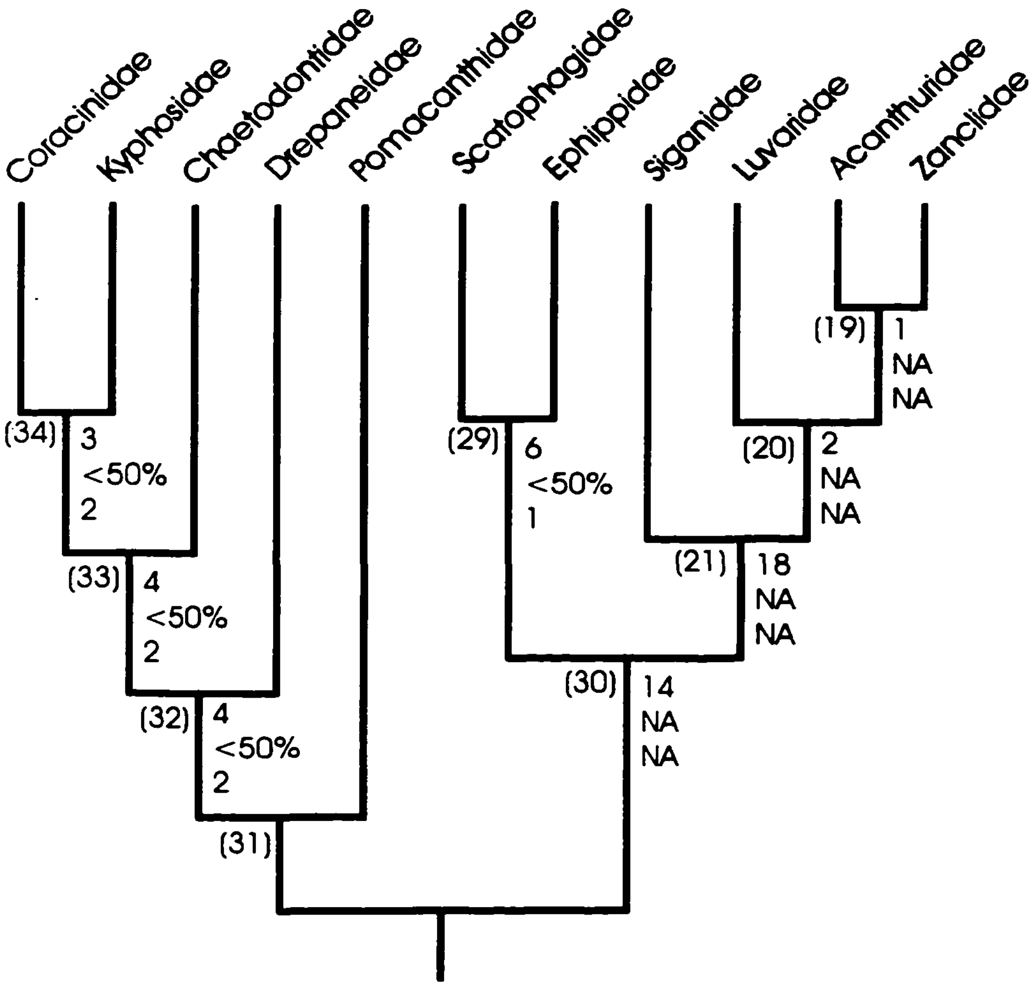

Coracinidae
Kyphosidae
Chaetodontidae
Drepaneidae
Pomacanthidae
Scatophagidae
Ephippidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
(19) 1 NA NA
(20) 2 NA NA
(21) 18 NA NA
(29) 6 <50% 1
(30) 14 NA NA
(34) 3 <50% 2
(33) 4 <50% 2
(32) 4 <50% 2
(31)

Figure 35. Constraint tree 5 (A) and the consensus tree of the three most parsimonious trees resulting from Constraint Analysis 5 (B). Top: branch length; middle: bootstrap value; bottom: Bremer support value. NA = not available due to constraint tree topology.

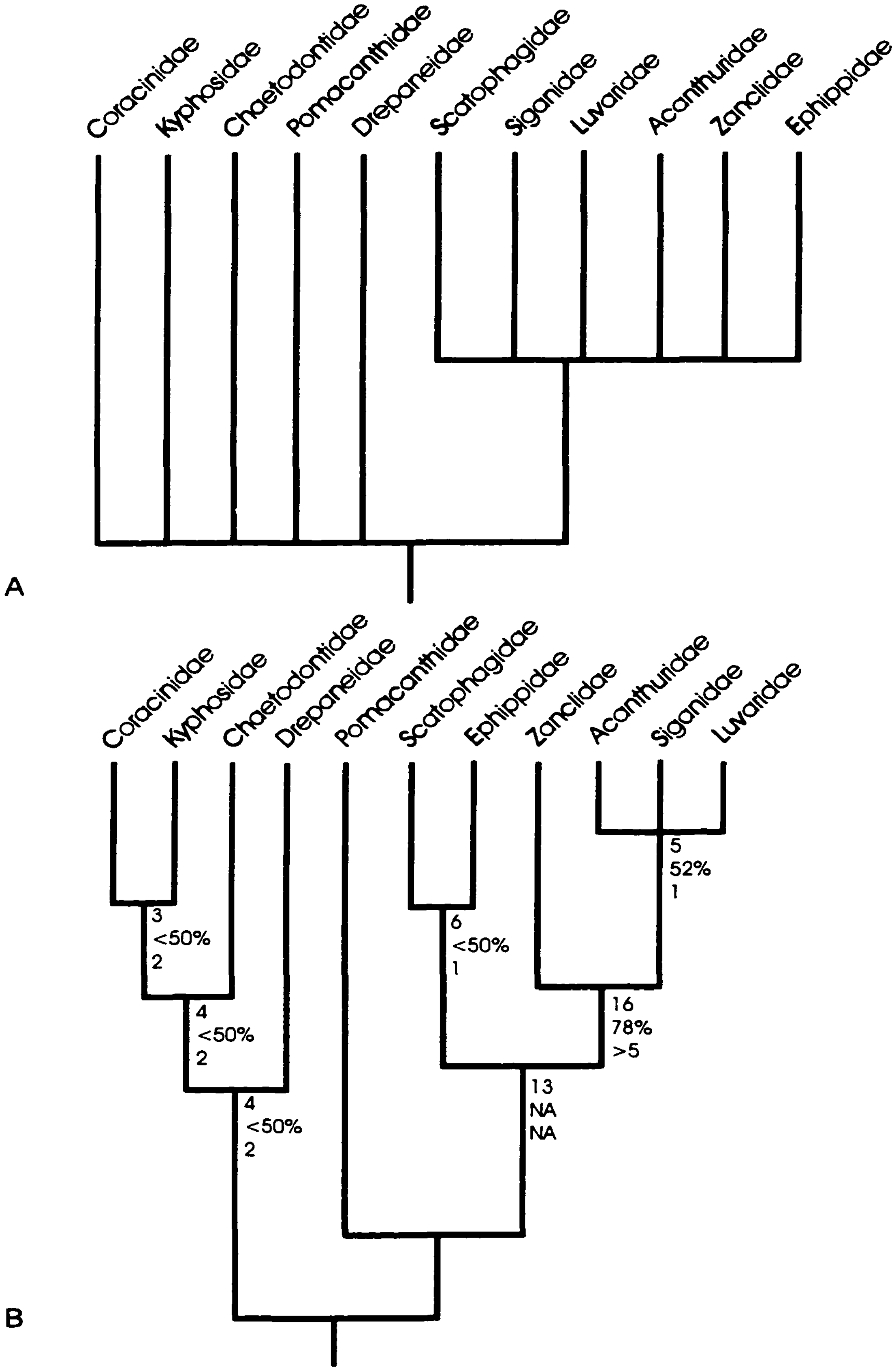

Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
Ephippidae
A
Coracinidae
Kyphosidae
Chaetodontidae
Drepaneidae
Pomacanthidae
Scatophagidae
Ephippidae
Zanclidae
Acanthuridae
Siganidae
Luvaridae
5
52%
1
3
<50%
2
6
<50%
1
4
<50%
2
16
78%
>5
13
NA
NA
4
<50%
2
B

Figure 36. Constraint tree 6 (A), and the single most parsimonious tree resulting from Constraint Analysis 6 (B). Top: branch length; middle: bootstrap value; bottom: Bremer support value. NA = not available due to constraint tree topology.

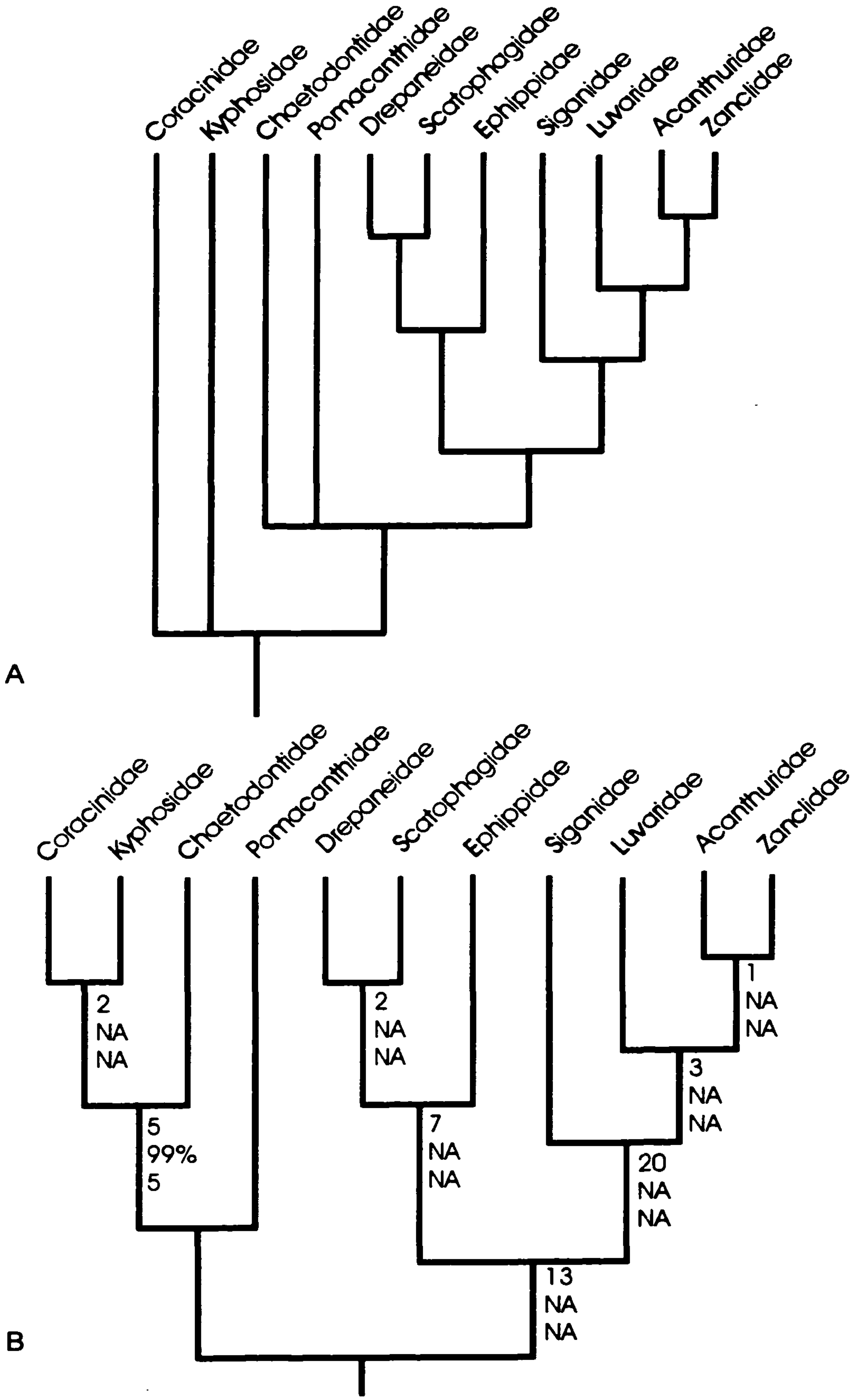

Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Ephippidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
A
Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Ephippidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
2 NA NA
5 99% 5
2 NA NA
7 NA NA
1 NA NA
3 NA NA
20 NA NA
13 NA NA
B

Figure 37. Constraint tree 7 (A), and the single most parsimonious tree resulting from Constraint Analysis 7 (B). Top: branch length; middle: bootstrap value; bottom: Bremer support value. NA = not available due to constraint tree topology.

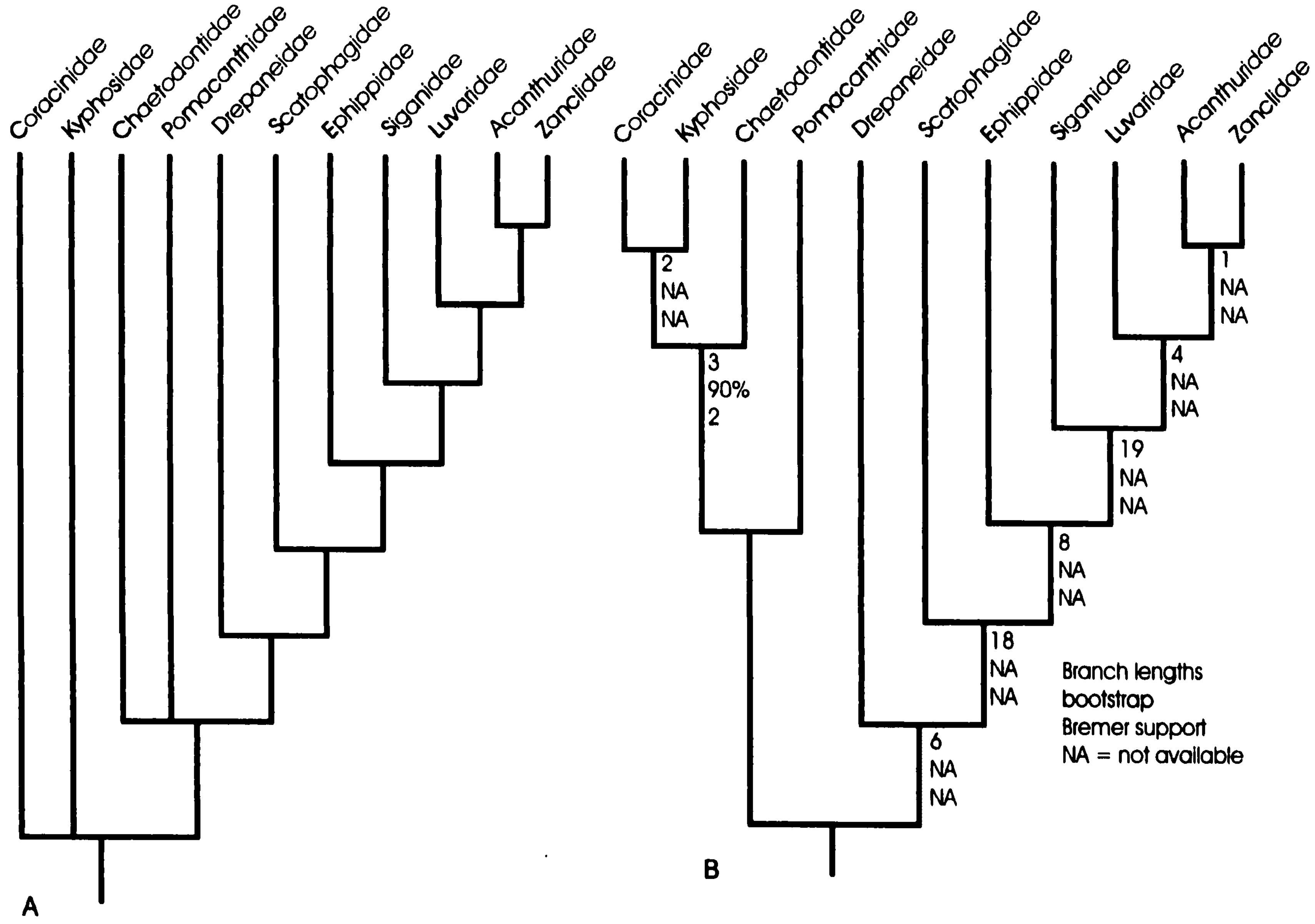

Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Ephippidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
A
Coracinidae
Kyphosidae
Chaetodontidae
Pomacanthidae
Drepaneidae
Scatophagidae
Ephippidae
Siganidae
Luvaridae
Acanthuridae
Zanclidae
2 NA NA
3 90% 2
1 NA NA
4 NA NA
19 NA NA
8 NA NA
18 NA NA
6 NA NA
Branch lengths
bootstrap
Bremer support
NA = not available
B

Figure 38. Distribution of character states among ephippid genera. Cladogram was derived from Constraint Analysis 4. Black bars denote non-homoplasious changes; open bars denote homoplasious changes. Characters are listed to the left of the bars; character state changes are listed to the right of the bars. Numbers in parentheses refer to nodes referenced in Tables 6 and 7.

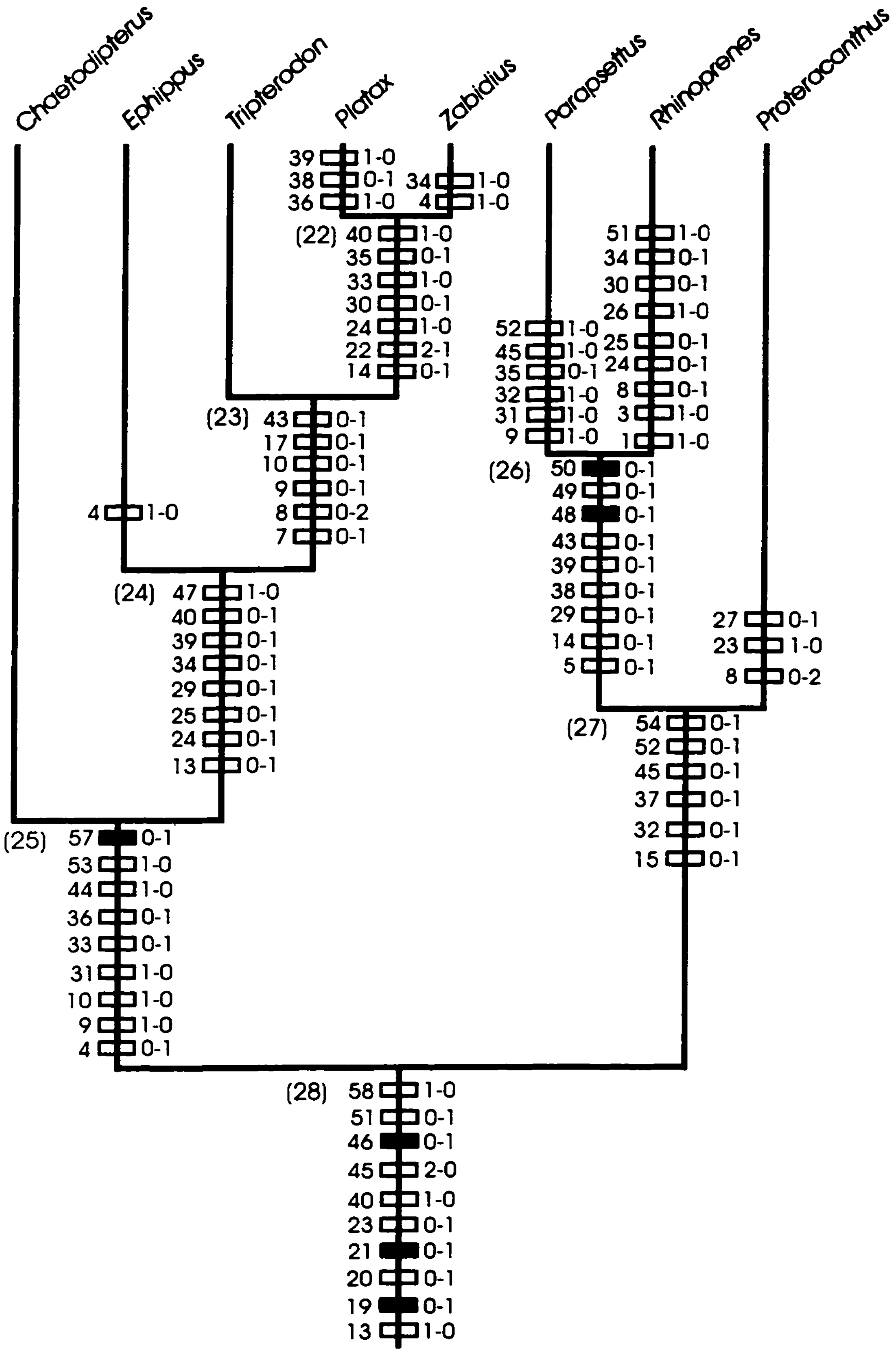

Chaetodipterus
Ephippus
Tripterodon
Platax
Zabidius
Parapsettus
Rhinoprenes
Proteracanthus
39 1-0
38 0-1
36 1-0
34 1-0
4 1-0
(22)
40 1-0
35 0-1
33 1-0
30 0-1
24 1-0
22 2-1
14 0-1
(23)
43 0-1
17 0-1
10 0-1
9 0-1
8 0-2
7 0-1
4 1-0
(24)
47 1-0
40 0-1
39 0-1
34 0-1
29 0-1
25 0-1
24 0-1
13 0-1
(25)
57 0-1
53 1-0
44 1-0
36 0-1
33 0-1
31 1-0
10 1-0
9 1-0
4 0-1
52 1-0
45 1-0
35 0-1
32 1-0
31 1-0
9 1-0
51 1-0
34 0-1
30 0-1
26 1-0
25 0-1
24 0-1
8 0-1
3 1-0
1 1-0
(26)
50 0-1
49 0-1
48 0-1
43 0-1
39 0-1
38 0-1
29 0-1
14 0-1
5 0-1
27 0-1
23 1-0
8 0-2
(27)
54 0-1
52 0-1
45 0-1
37 0-1
32 0-1
15 0-1
(28)
58 1-0
51 0-1
46 0-1
45 2-0
40 1-0
23 0-1
21 0-1
20 0-1
19 0-1
13 1-0

Figure 39. Cladogram of the relationships of the family Ephippidae. Cladogram was derived from Constraint Analysis 4. Top: branch length; middle: bootstrap value; bottom: Bremer support value. NA = not available due to constraint tree topology. Numbers on terminal nodes are branch lengths. Numbers in parentheses refer to nodes referenced in Tables 6 and 7.

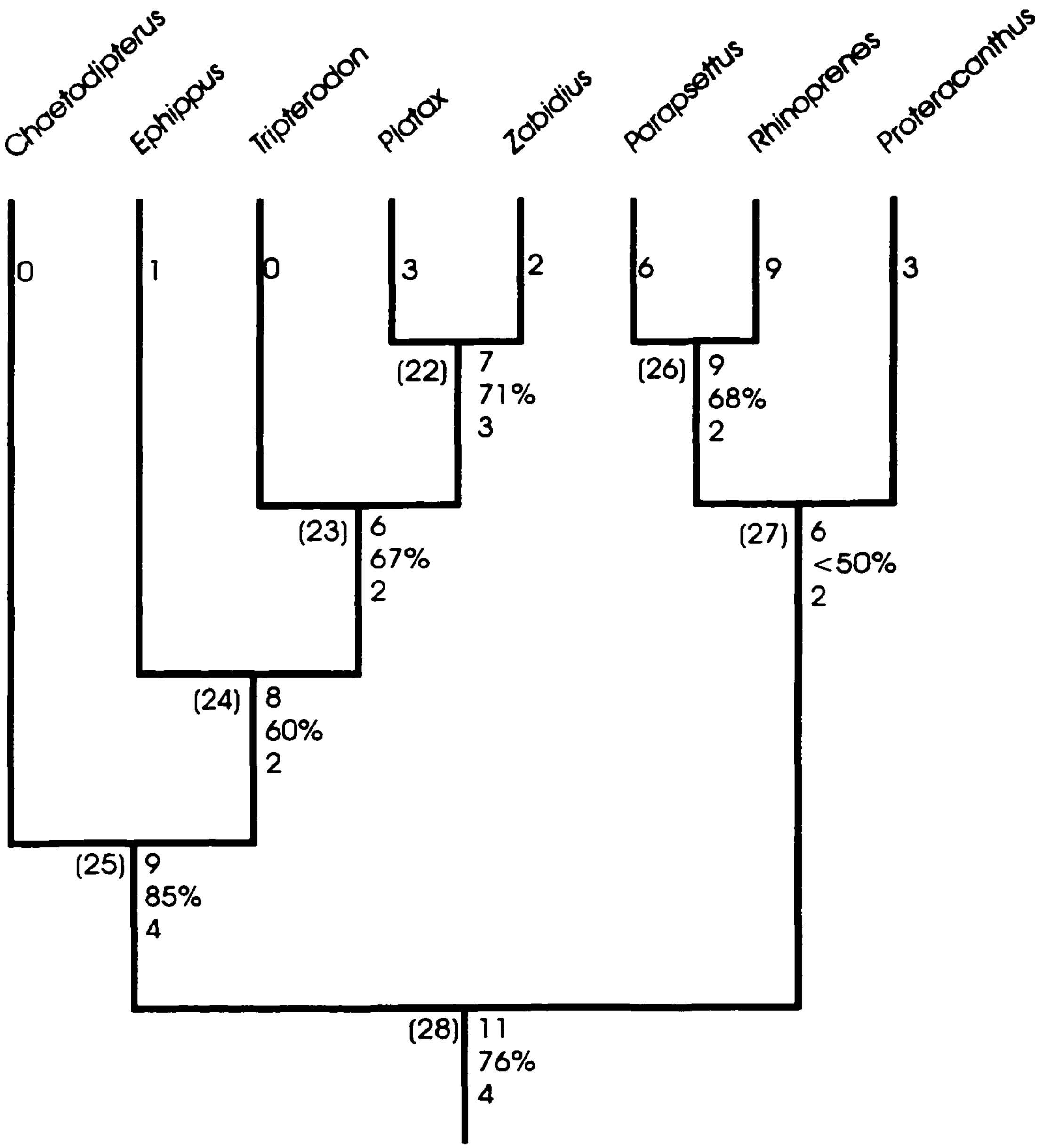

Chaetodipterus
Ephippus
Tripterodon
Platax
Zabidius
Parapsettus
Rhinoprenes
Proteracanthus
0
1
0
3
2
6
9
3
(22)
7
71%
3
(26)
9
68%
2
(23)
6
67%
2
(27)
6
<50%
2
(24)
8
60%
2
(25)
9
85%
4
(28)
11
76%
4

Figure 40. Geographic distribution of the ephippid species of clade 25 (see Fig. 38). Cf, *Chaetodipterus faber*; Cl, *C. lippei*; Cz, *C. zonatus*; Eg, *Ephippus goreensis;* Eo, *E. orbis*; Pb, *Platax batavianus*; Pbo, *P. boersii*; Po, *P. orbicularis*; Ppi, *P. pinnatus*; Pt, *P. teira*; To, *Tripterodon orbis*; Zn, *Zabidius novemaculeatus*.

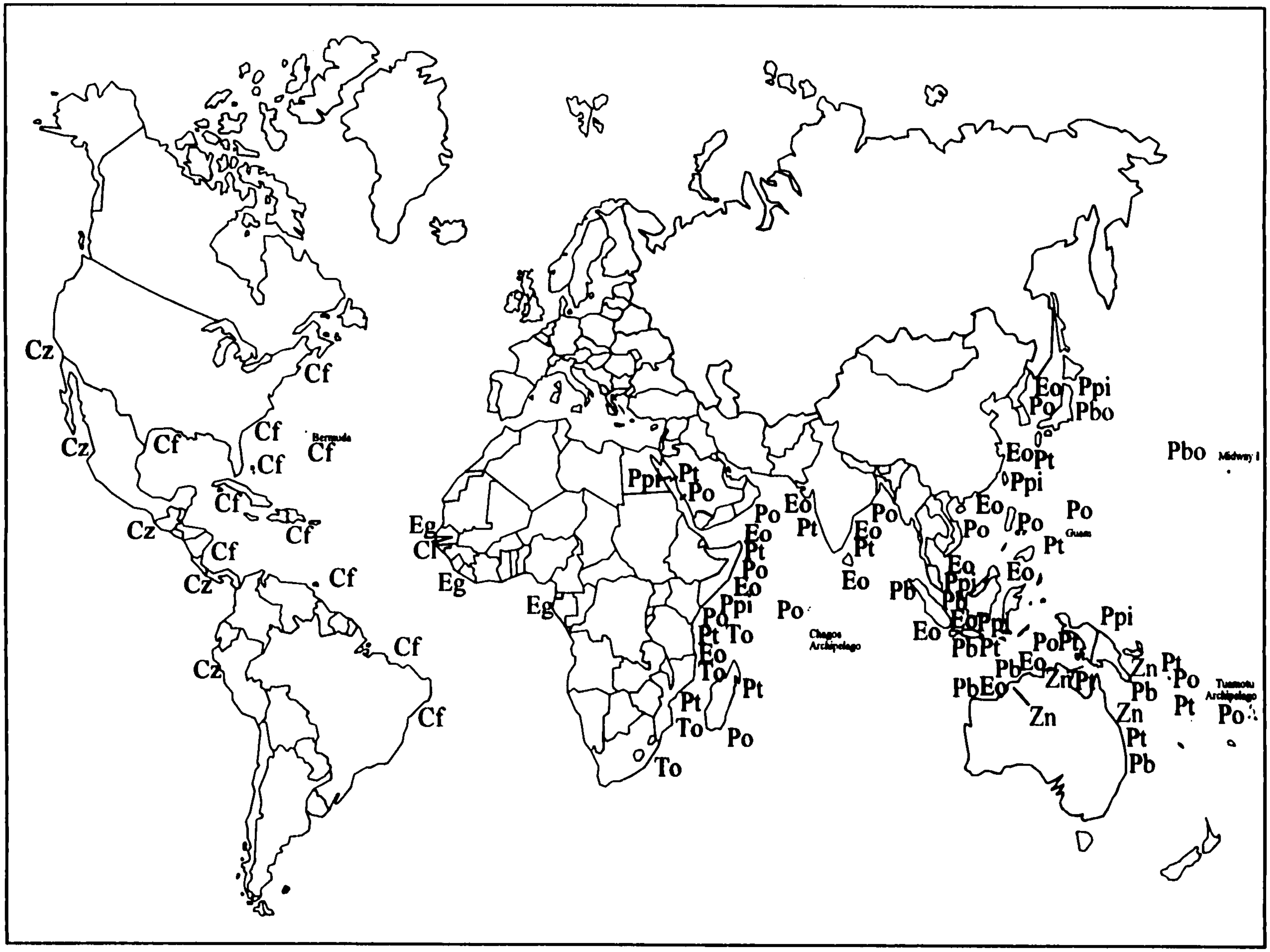

Cz
Cz
Cz
Cz
Cz
Cf
Cf
Bermuda
Cf
Cf
Cf
Cf
Cf
Cf
Cf
Cf
Cf
Cf
Eg
Cf
Eg
Eg
Ppi
Pt
Po
Po
Eo
Pt
Po
Eo
Pt
Po
Eo
Ppi
Po
Pt
To
Eo
To
Pt
Pt
To
Po
To
Po
Chagos Archipelago
Eo
Pt
Po
Eo
Pt
Eo
Pb
Eo
Eo
Ppi
Po
Pbo
EoPt
Ppi
Eo
Po
Po
Po
Po
Guam
Pt
Eo
Ppi
Pb
Eo
EoPpi
PbPt
PoPt
Ppi
PbEo
ZnPt
PbEo
Zn
Zn
Pt
Po
Pb
Pt
Zn
Pt
Pb
Pbo
Midway I
Tuamotu Archipelago
Po

Figure 41. Geographic distribution of the ephippid species of clade 27 (see Fig. 38): Pp, *Parapsettus panamensis*; Ps, *Proteracanthus sarissophorus*; Rp, *Rhinoprenes pentanemus*.

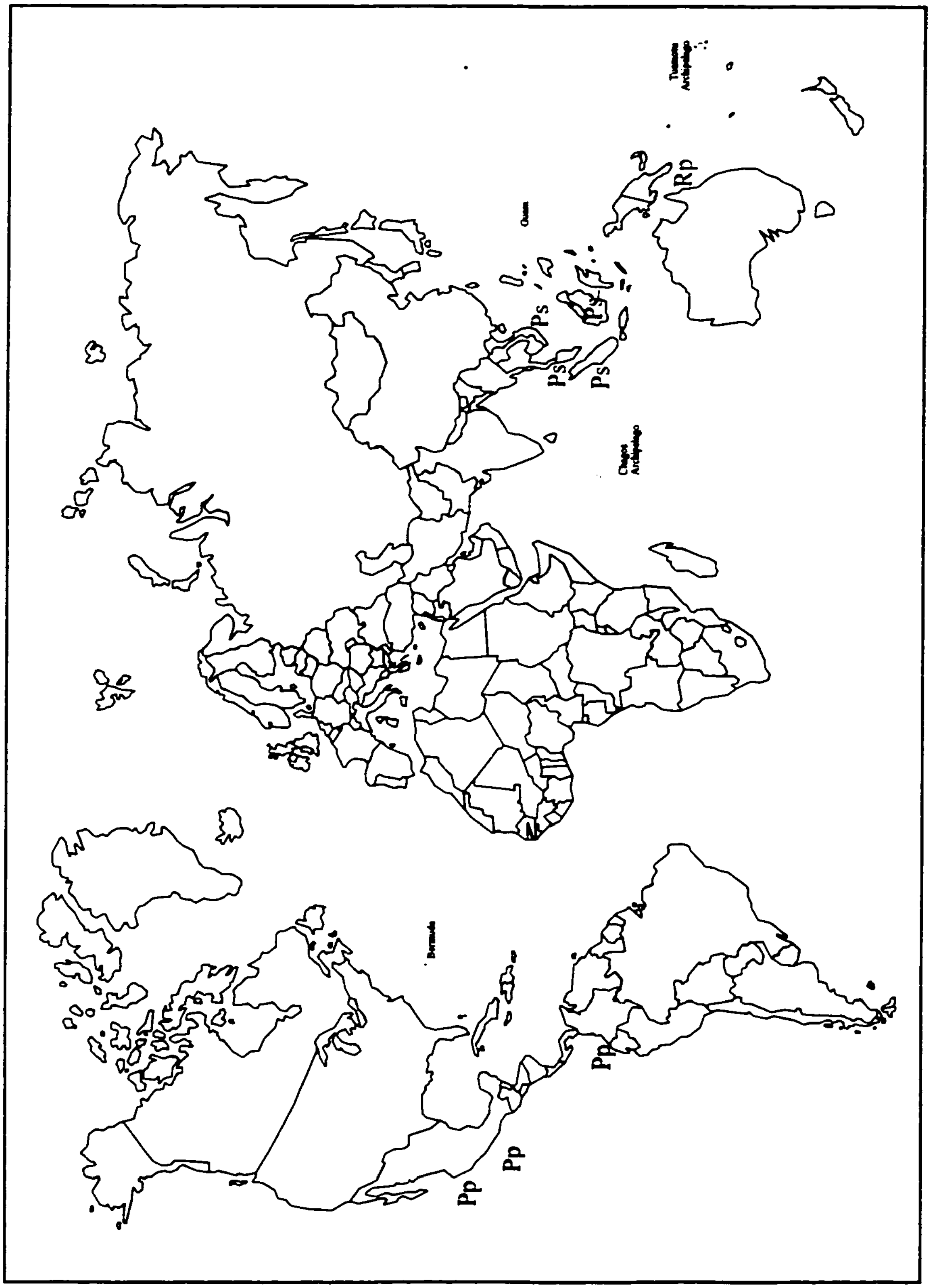
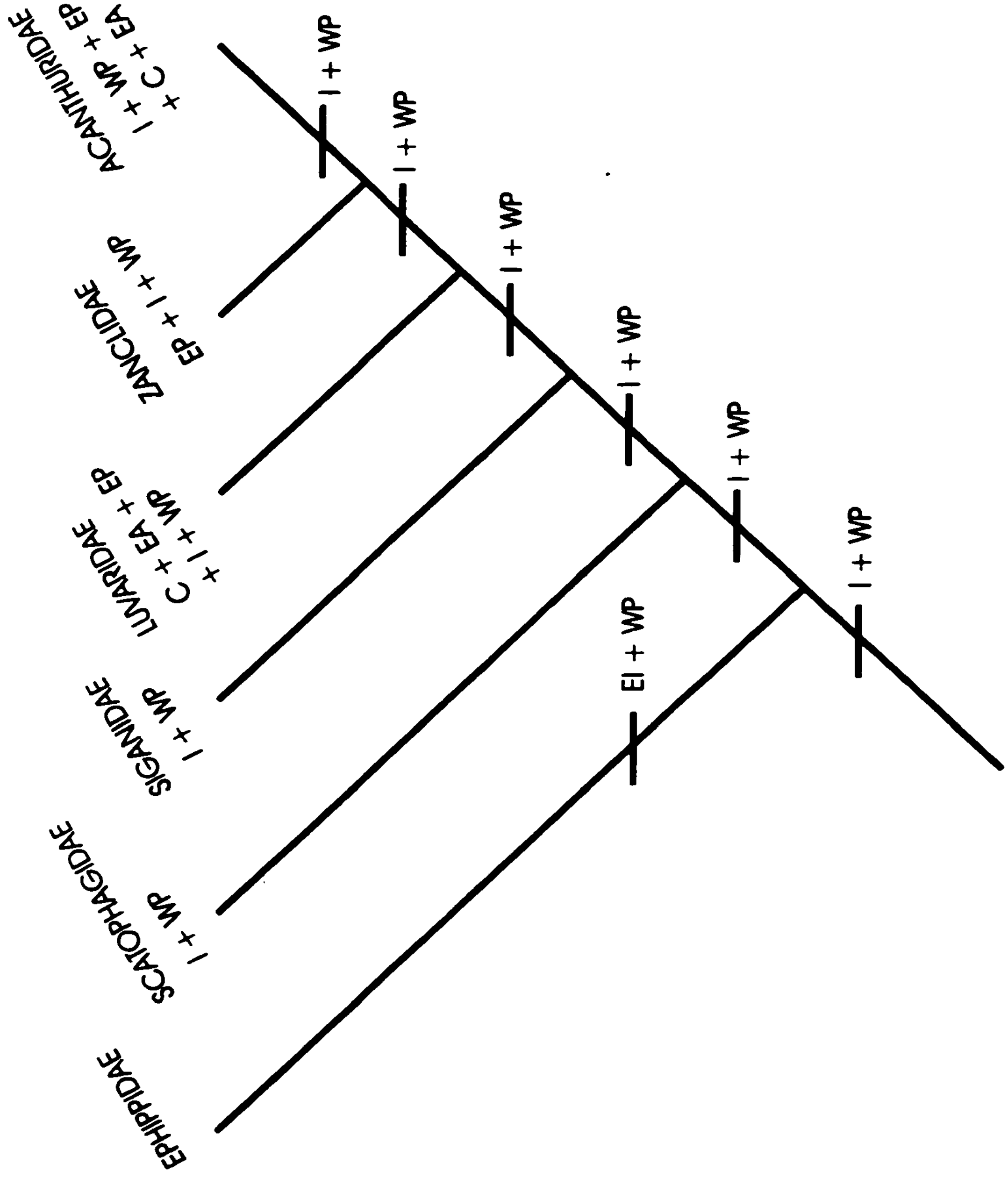

Tuamotu Archipelago
Rp
Guam
Ps
Ps
Ps
Ps
Chagos Archipelago
Bermuda
Pp
Pp
Pp

Figure 42. Cladogram of the Acanthuroidei with hypothesized ancestral areas mapped for each clade. All mapped areas are from Winterbottom and McLennan (1993) except those for the Ephippidae and the Acanthuroidei node, which are from this study. I, Indian Ocean; EI, east Indian Ocean; WP, west Pacific Ocean; EP, east Pacific Ocean; C, Caribbean; EA, east Atlantic Ocean.



ACANTHURIDAE
I + WP + EP
+ C + EA
ZANCLIDAE
EP + I + WP
LUVARIDAE
C + EA + EP
+ I + WP
SIGANIDAE
I + WP
SCATOPHAGIDAE
I + WP
EPHIPPIDAE
I + WP
I + WP
I + WP
I + WP
I + WP
I + WP
EI + WP

Figure 43. Cladogram of the Ephippidae with hypothesized ancestral areas mapped for each clade. I, Indian Ocean; WP, west Pacific Ocean; EP, east Pacific Ocean; C, Caribbean; WA, west Atlantic Ocean; EA, east Atlantic Ocean.

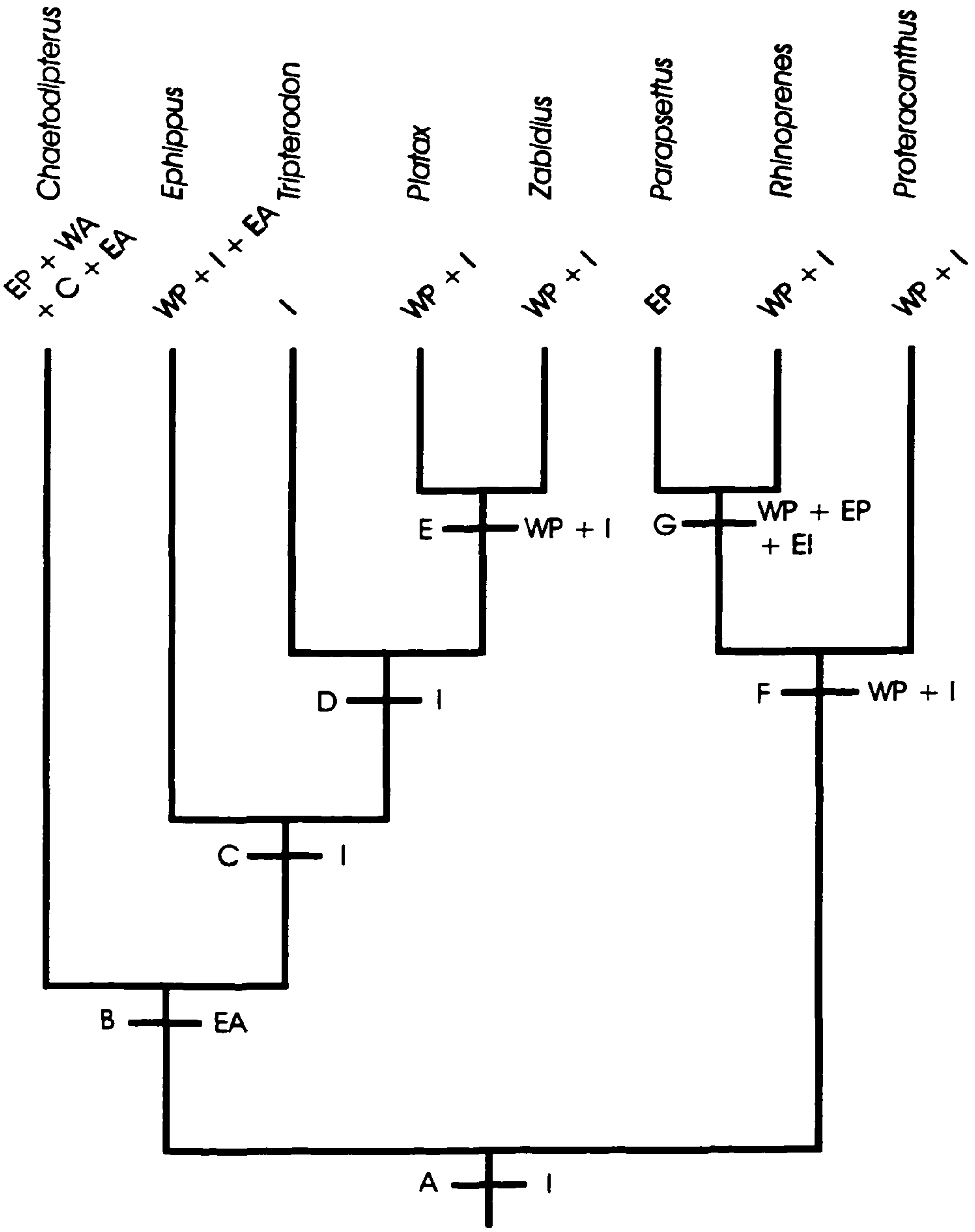
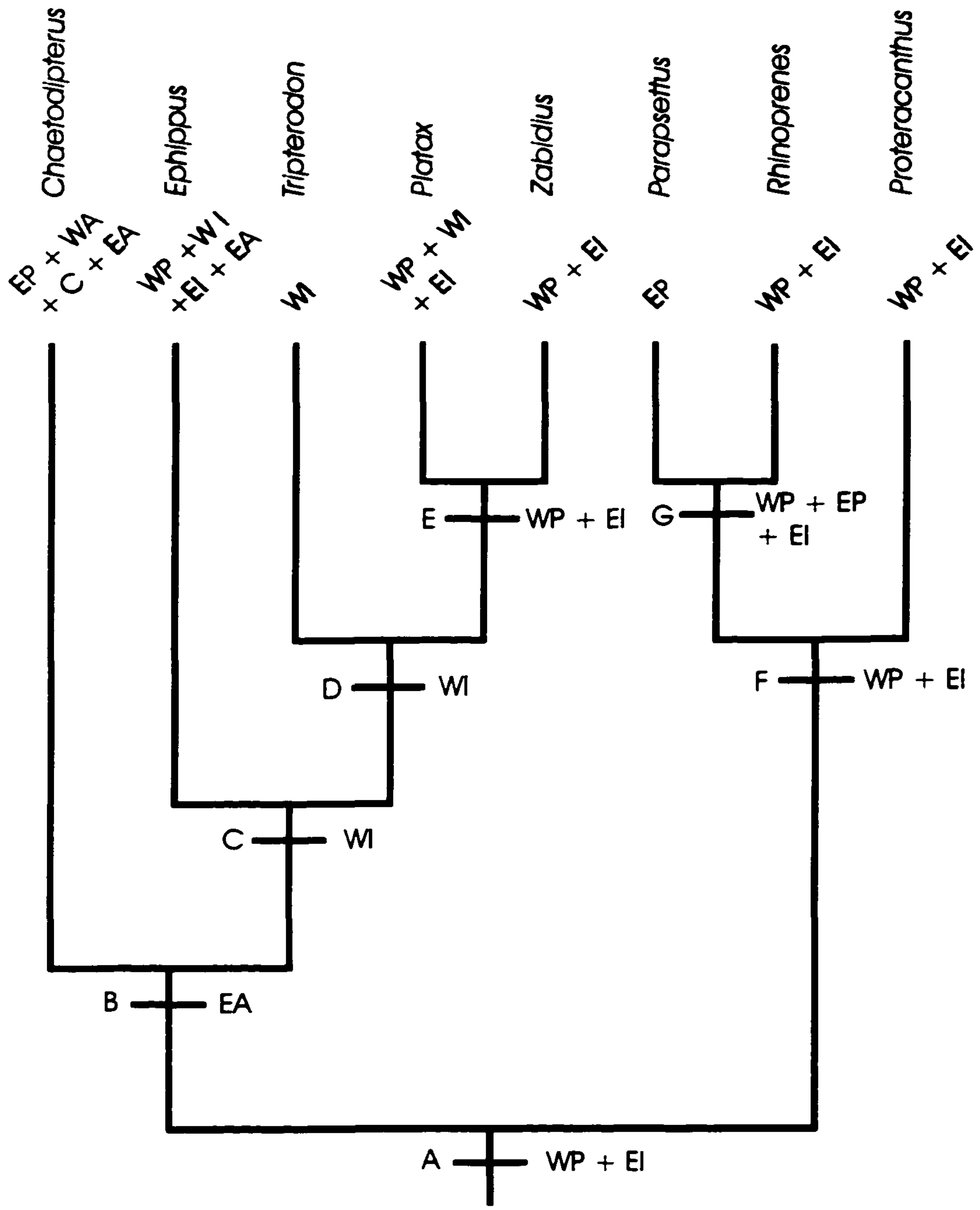

Chaetodipterus
Ephippus
Tripterodon
Platax
Zabidius
Parapsettus
Rhinoprenes
Proteracanthus
EP + WA + C + EA
WP + I + EA
I
WP + I
WP + I
EP
WP + I
WP + I
E
WP + I
G
WP + EP + EI
D
I
F
WP + I
C
I
B
EA
A
I

Figure 44. Cladogram of the Ephippidae with hypothesized ancestral areas mapped for each clade. WI, west Indian Ocean; EI, east Indian Ocean; WP, west Pacific Ocean; EP, east Pacific Ocean; C, Caribbean; WA, west Atlantic Ocean; EA, east Atlantic Ocean.


Chaetodipterus
Ephippus
Tripterodon
Platax
Zabidius
Parapsettus
Rhinoprenes
Proteracanthus
EP + WA + C + EA
WP + WI + EI + EA
WI
WP + WI + EI
WP + EI
EP
WP + EI
WP + EI
E WP + EI
G WP + EP + EI
D WI
F WP + EI
C WI
B EA
A WP + EI

VITA

Martin Ray Cavalluzzi was born in Wichita Falls, Texas in 1960. He moved with his family to New York, and then California. He earned an AA degree from Orange Coast College in 1981, and a BS from Humboldt State University in 1987. He taught marine science for three years at the Orange County Marine Institute, CA. Martin earned a MA from The College of William and Mary in 1992, and finally, a Ph.D. from The College of William and Mary in 2000. In January, 1999, he began work as a faculty research assistant at Oregon State University. Who knows where he goes from here...