

Relationships of the Fossil and  
Recent Genera of Rabbitfishes  
(Acanthuroidei: Siganidae)

*James C. Tyler*  
*and Alexandre F. Bannikov*



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## ABSTRACT

Tyler, James C., and Alexandre F. Bannikov. Relationships of the Fossil and Recent Genera of Rabbitfishes (Acanthuroidei: Siganidae). *Smithsonian Contributions to Paleobiology*, number 84, 35 pages, 21 figures, 1 table, 1997.—Four genera of fossil siganid fishes of early Eocene to early Oligocene age are recognized in addition to the single Recent genus. The osteological features of these five genera are described and illustrated. A phylogenetic analysis utilizing PAUP indicates that the genera have the following phyletic sequence convention: *Ruffoichthys* Sorbini (two species from the middle Eocene of Italy)—*Eosiganus*, new genus (one new species from the middle Eocene of Russia)—*Siganopygaeus* Danilchenko (one species from the early Eocene of Turkmenistan)—*Protosiganus* Whitley (one species from the early Oligocene of Switzerland)—*Siganus* Forsskål (27 Recent species in the Indo-Pacific).

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# Relationships of the Fossil and Recent Genera of Rabbitfishes (Acanthuroidei: Siganidae)

James C. Tyler  
and Alexandre F. Bannikov

## Introduction

Siganid rabbitfishes are one of the more prominent herbivorous components of the modern-day Indo-Pacific ichthyofauna. They are associated with coral reefs, the surrounding grass flats, and other algae-rich environments, such as mangroves and rocky shores. There is a single extant genus (*Siganus*), but it is exceptionally speciose (27 species that differ mostly in coloration and proportions). This genus is unique among Recent teleosts in having the palatine divided into two separate ossifications (palatine and prepalatine) and in having each pelvic fin with two spines (outer and inner, between which are three rays). Along with the description of a new fossil species in the morphologically primitive Eocene genus *Ruffoichthys* (palatine probably composed of two separate ossifications but no inner pelvic-fin spine), Tyler and Sorbini (1991) compared that genus with the two other fossil genera then known (the Eocene *Siganopygaeus* and Oligocene *Protosiganus*), but they did not analyze their phylogenetic relationships. We herein describe a new genus of Eocene siganid (*Eosiganus*), re-describe all of the other fossil taxa on the basis of our examination of all of the type materials, and utilize PAUP (Phylogenetic Analysis Using Parsimony, Version 2.4.1, written by D.L. Swofford, then of the Illinois Natural History Survey, now of the Smithsonian Institution) to analyze the relationships of the

five genera based on the 12 informative characters that can be determined in the Recent and most of the fossil taxa.

**METHODS.**—The methodology used for the phylogenetic hypotheses is given under “Analytical Protocols” at the beginning of the “Analysis of Characters” section.

Abbreviations for the repositories of materials are as follows: ANSP, Academy of Natural Sciences of Philadelphia; MCSNM, Museo Civico di Storia Naturale di Milano; MCSNV, Museo Civico di Storia Naturale di Verona; MCZ, Museum of Comparative Zoology, Harvard University; NMB, Naturhistorisches Museum Basel; PIN, Paleontological Institute, Moscow; USNM, National Museum of Natural History, Smithsonian Institution (collections of the former United States National Museum).

Specimen length is always standard length (SL). Vacant interneural spaces are given the number of the preceding neural spine (e.g., the first space is between the first and second neurals, as in Baldwin and Johnson, 1993), and the terms supraneural (as in Mabee, 1988) and epineural (as in Patterson and Johnson, 1995) are used rather than predorsal bone and epipleural intermuscular bone; all three of these terms are changes from those used in Tyler et al. (1989) for siganids and other acanthuroids.

For ease of comparison, descriptive features of the species are given in the same order, beginning with the few that are unique to either all or some siganids (palatine composed of two separate ossifications, two spines in each pelvic fin, deep notches on sides of teeth).

All five genera of siganids have 10 abdominal and 13 caudal vertebrae, and these data are not repeated. Most other families of acanthuroids (luvarids, zancuids, acanthurids) have a more specialized condition of one fewer abdominal vertebra, 9+13=22, but the fossil kushlukiids (sister group of luvarids) have a secondarily increased number of vertebrae 10+~19–

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James C. Tyler, National Museum of Natural History, Smithsonian Institution (MRC-106), Washington, D.C. 20560. Alexandre F. Bannikov, Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, 117647 Moscow, Russia.

Reviewers: Carole Baldwin, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Antony S. Harold, Department of Ichthyology and Herpetology, Royal Ontario Museum, Toronto, Ontario, Canada M5S 2C6. Robert L. Shipp, Department of Marine Sciences, University of South Alabama, Mobile, Alabama 36688.

20=29–30. Scatophagids are like siganids in having 10+13=23, itself a specialized reduction of one caudal vertebra from the 10+14=24 of ephippidids and other, lower, squamipinnes.

Other familial-level features not repeated herein that are common to all siganids are (1) the spines of the dorsal and anal fins are heteracanth; (2) some of the superficial skull bones, especially the frontal, are sculptured and cancellous (unknown in *Siganopygaeus*), more so in *Ruffoichthys*, *Eosiganus*, and *Protosiganus* than in *Siganus*; (3) the ethmoid is block-like, the supraoccipital has only a very low crest, and the maxilla and premaxilla appear to be immovably articulated and nonprotrusile, rotating around the ethmoid and flexible palatine (none of these features known in *Siganopygaeus*); (4) the distal ends of the pterygiophores of the dorsal and anal fins are laterally expanded; (5) the first two anal-fin spines are in supernumerary association with the first pterygiophore; (6) there are 17 principal caudal-fin rays (only probable in *Siganopygaeus*), nine in the upper lobe and eight in the lower, but we comment on the caudal fin because of variability in both its degree of preservation and the number of procurrent rays. In all five genera, the ventral shaft of the first pterygiophore of the dorsal fin is placed in the first interneural space, but the differences in the location of the ventral end of the shaft relative to the first neural spine are described.

Although they sometimes have been thought to be related to siganids or acanthurids, the Eocene fishes of the genera *Pygaeus*, *Acanthopygaeus*, *Malacopygaeus*, and *Parapygaeus* are chaetodontoids (Woodward, 1901; Eastman, 1904; Patterson, 1993).

The enigmatic *Gazolaichthys vestenanovae* Blot and Tyler (1991) was described from the Eocene of Monte Bolca, Italy, as an incertae sedis acanthuroid with characteristics suggestive of an intermediate position between acanthurids and siganids. However, we believe that it is more closely related to higher acanthuroids (the zanclid+acanthurid clade) than to siganids for the following reasons.

*Gazolaichthys* shares several derived features with zanclids and acanthurids (e.g., vertebrae reduced to 9+13; first pterygiophore of dorsal fin situated in front of neural spine of first vertebra; principal caudal-fin rays reduced to 16). By contrast, none of the similarities between *Gazolaichthys* and siganids are derived, and *Gazolaichthys* lacks such derived features of all or most siganids as increased numbers of dorsal- and anal-fin spines, reduced numbers of dorsal-, anal-, and pelvic-fin rays, pleural ribs on the second abdominal vertebra, and procumbent spine on first pterygiophore on the dorsal fin.

*Gazolaichthys* differs from both siganids and the zanclid+acanthurid clade by having the fourth interneural space vacant and having two well-developed uroneurals. *Gazolaichthys* differs most notably from acanthurids by lacking the highly specialized type of dorsal- and anal-fin spine locking mechanism by which the cap-like base of the first spine rotates into a deep indentation in front of the median flange at the distal end of the first basal pterygiophore of these fins.

The relationships of *Gazolaichthys* as a basal member of the zanclid+acanthurid clade will be discussed in a work in progress by one of us (JCT) redescribing the genus on the basis of newly examined Monte Bolca specimens.

ACKNOWLEDGMENTS.—We thank Lorenzo Sorbini, Museo Civico di Storia Naturale, Verona, Italy, and Daniel Goujet and Paulo Brito, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, for facilitating our work with specimens in their care.

Victor Springer, Division of Fishes, National Museum of Natural History, queried his ichthyophilatelic data base and made us aware of the existence of a stamp bearing a siganid and of the changed generic name for *Protosiganus glaronensis*. We were further aided in obtaining details about the issuance of this Swiss stamp by Joseph Geraci of the Smithsonian's National Philatelic Museum and by its librarian, Timothy Carr, and then by receiving copies of the issuance descriptive materials from Peter Meier of the Philatelic Office in Bern.

At the Naturhistorisches Museum Basel we are especially indebted to Peter Jung, Burkart Engesser, and Daniel Oppliger for their arduous and successful efforts to locate the long-misplaced holotype of *Protosiganus glaronensis*.

At the Naturwissenschaftliche Sammlungen des Kantons Glarus we received much help from Hanspeter and Edith Schlielly in our unsuccessful search for additional specimens of *P. glaronensis*. We hoped to find other specimens among their rich holdings of Oligocene fishes from the black schists of Glarus, many of them dating to the time of the study of these collections by Louis Agassiz (1833–1843) for his “Recherches sur les Poissons Fossiles.”

We thank the National Geographic Society, Washington, D.C., for grant no. 5037-93 that allowed one of us (AFB) to make excavations in the North Caucasus in 1993, from which two paratypes of *Eosiganus kumaensis* were obtained.

Carole Baldwin, Division of Fishes, National Museum of Natural History, introduced us to the use of PAUP and helped answer many questions of phylogenetic interpretation; her help in improving our analysis and in reviewing the manuscript is greatly appreciated. The manuscript was further improved by the preacceptance reviews of Anthony Herald, Royal Ontario Museum, and Robert Shipp, University of South Alabama, and by discussions of acanthuroid characters with Richard Winterbottom, Royal Ontario Museum.

We appreciate the copy editing of Craig Warren at the Smithsonian Institution Press.

### Systematic Descriptions of the Genera of Siganidae

DIAGNOSIS FOR BOTH FOSSIL AND EXTANT TAXA.—Acanthuroid fishes with the number of dorsal-fin spines increased to 11–14 (versus 3–9 in other acanthuroids), the number of dorsal-fin rays reduced to 9–11 (versus 20–42), the number of anal-fin spines increased to 4–8 (versus 0–3), the number of anal-fin rays reduced to 7–10 (versus 17–35), the

scales small and cycloid (versus larger and spinulose or ctenoid), the first pleural rib inserted on the second vertebra (only probably so in one of the fossil species) (versus inserted on the third vertebra), and the pelvic fin usually with only 3 rays (occasionally 5 rather than 3 in one of the fossil species) (versus always 5 rays).

The many other derived features known for the numerous species of the single Recent genus (*Siganus*) are either unknown in the fossil taxa (many features of the soft anatomy or those of regions not exposed in the fossil materials) or are present in some of the fossil taxa but not in others (e.g., inner pelvic-fin spine, palatine composed of two separate ossifications).

### †*Ruffoichthys* Sorbini, 1983

TYPE SPECIES.—*Ruffoichthys spinosus* Sorbini, 1983, by monotypy. Other species: *Ruffoichthys bannikovi* Tyler and Sorbini, 1991.

DIAGNOSIS.—Differs from all other siganids by having a I,3 or, rarely, a I,5 pelvic fin (versus I,3,I), no procumbent spine anterodorsally on the first dorsal-fin pterygiophore (versus prominent procumbent spine present), 4 anal-fin spines (versus 6–8), and sixth interneural space vacant (versus fifth).

### *Ruffoichthys bannikovi* Tyler and Sorbini, 1991 and *Ruffoichthys spinosus* Sorbini, 1983

FIGURES 1–4

DIAGNOSIS OF THE TWO SPECIES.—The two species of *Ruffoichthys* differ as follows: there are 10 dorsal- and anal-fin rays in *R. bannikovi* versus 9 in *R. spinosus*; there are 7–8 teeth on each side of the upper and lower jaws in *R. bannikovi* versus 5–6 in *R. spinosus*; the greatest body depth is 41%–43% SL in *R. bannikovi* versus 23%–34% in *R. spinosus*, with the neural and haemal spines in *R. bannikovi* correspondingly longer; the soft portions of the dorsal and anal fins are higher in *R. bannikovi* (height about 7–8 times in SL) than in *R. spinosus* (height about 10–11 times in SL).

DESCRIPTION.—Two additional specimens of *R. spinosus* (from Milan) have become available since the genus was redefined on the basis of 16 specimens (about 10–55.1 mm SL) of *R. spinosus* and two specimens (47.1–50.0 mm SL) of *R. bannikovi* (Tyler and Sorbini, 1991). We provide additional osteological information about these two species in the following description. The new information is given for both species together so that they can be compared more easily to the new genus and species described herein (*Eosiganus kumaensis*) and to the new data based on our examination of the holotypes of the other two species of fossil siganids (*Siganopygæus rarus* and *Protosiganus glaronensis*).

The pelvic fin in each of the two specimens of *R. bannikovi* has a single spine followed by three rays, whereas in *R. spinosus* the single spine is followed by either three or five rays. In neither species is there an inner spine that otherwise is typical of siganids. Of the eight specimens of *R. spinosus* in which the pelvic-fin counts could be obtained with some assurance, seven (including the holotype and one of the two newly examined Milan specimens in which the pelvic fin is clearly preserved) have three rays and one (MCSNV Tomelleri 53) has five rays. Tyler and Sorbini (1991) presumed that there was intraspecific variability in the number of pelvic-fin rays in this species, but another possibility is that the specimen with five rays represents a third species (or subspecies) of the genus. Many of the species of Recent *Siganus* differ from one another mainly in color pattern, with only subtle or no differences in the osteological features that are preserved in most fossils. Thus, if a fossil genus like *Ruffoichthys* was as speciose as *Siganus* and had as relatively minor differences between many of its species as is common in *Siganus*, the skeletons of several species could easily masquerade among the relatively numerous materials assigned here to *R. spinosus*.

One of the specimens of *R. spinosus* (MCSNV Mantovani, 32.3 mm SL) has evidence that the palatine was composed of two separate bony elements, as is the case in all of the Recent species of siganids.

The teeth are well exposed in several specimens of *R. spinosus*, including the holotype; they are distinctly notched on both the medial and lateral edges (Figure 19), and the teeth appear to have been fixed. In the upper jaw the medial notch is more distal and slightly less deep than the lateral notch, and the middle cusp is the largest. The teeth in the lower jaws of these specimens are not as completely preserved, but they seem to have the opposite pattern of notching, as is the case in the Recent *Siganus*. The teeth are less well exposed in *R. bannikovi* but seem to be somewhat less deeply notched than in *R. spinosus*, and there may be differences between the two species not only in the number of teeth (see diagnosis above) but in their shape as well; however, this cannot be determined until additional specimens of *R. bannikovi* with better preserved dentition become available.

The dorsal fin has 11 spines, with the first two in supernumerary association with the first pterygiophore; the first dorsal spine is between two-thirds and three-fourths the length of the second spine, and the second to the fourth or fifth spines are of similar length. The number of dorsal-fin rays differs between the two species (see diagnosis above). The anterodorsal end of the first pterygiophore of the spiny dorsal fin is not prolonged as a procumbent spine.

The anal fin has four spines. The number of anal-fin rays differs between the two species (see diagnosis above). The first anal-fin pterygiophore has a relatively vertical orientation, and the anteroventral process is short and well separated from the ventral end of the postcleithrum.

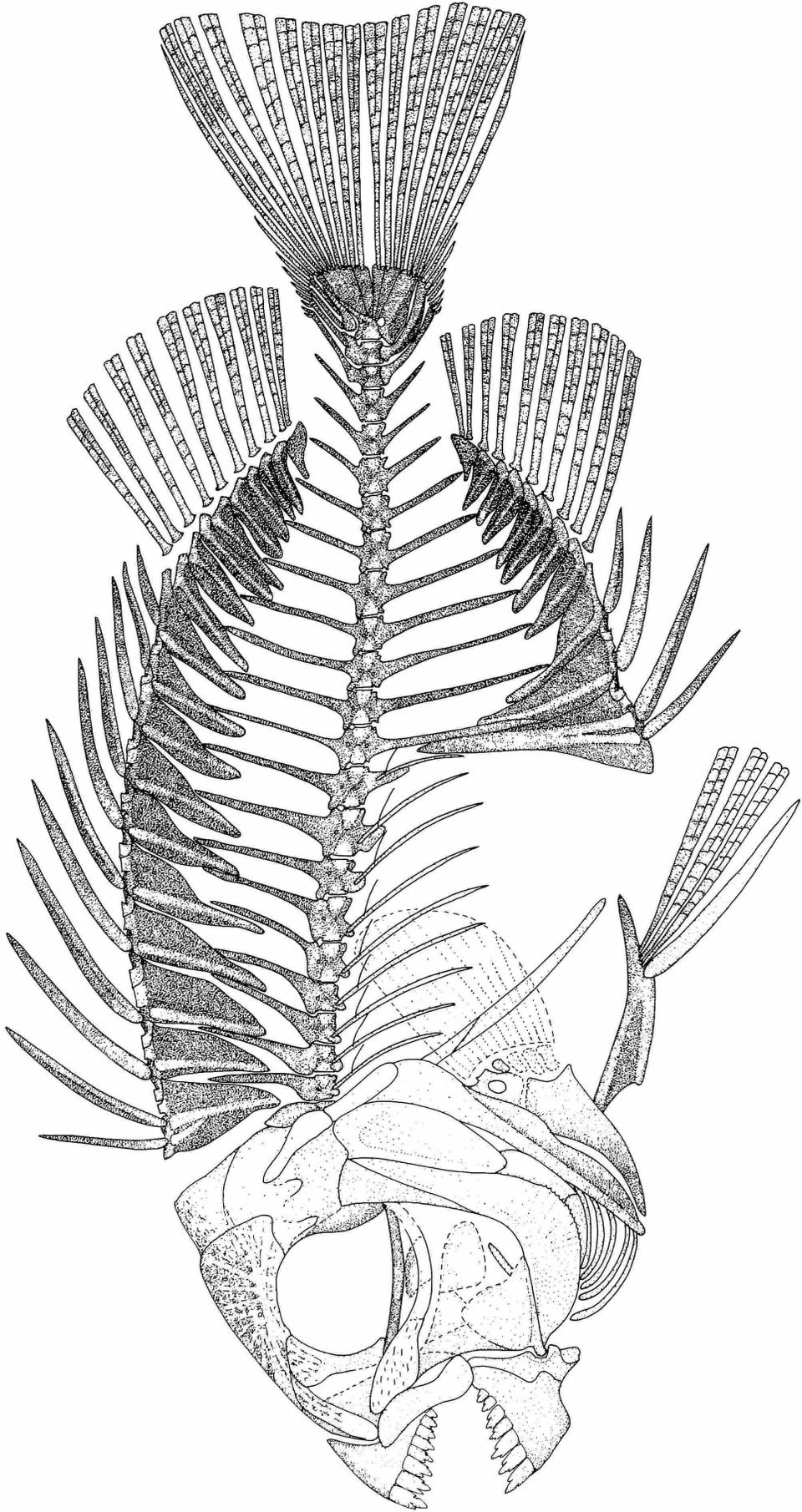


FIGURE 1.—Reconstruction of the skeleton of *Ruffoichthys bannikovi* Tyler and Sorbini, middle Eocene of Monte Bolca, Italy; based mostly on the holotype, MCSNV IG132595–132596, 47.1 mm SL, but with many details from the acid-prepared paratype (for which see Figure 2).

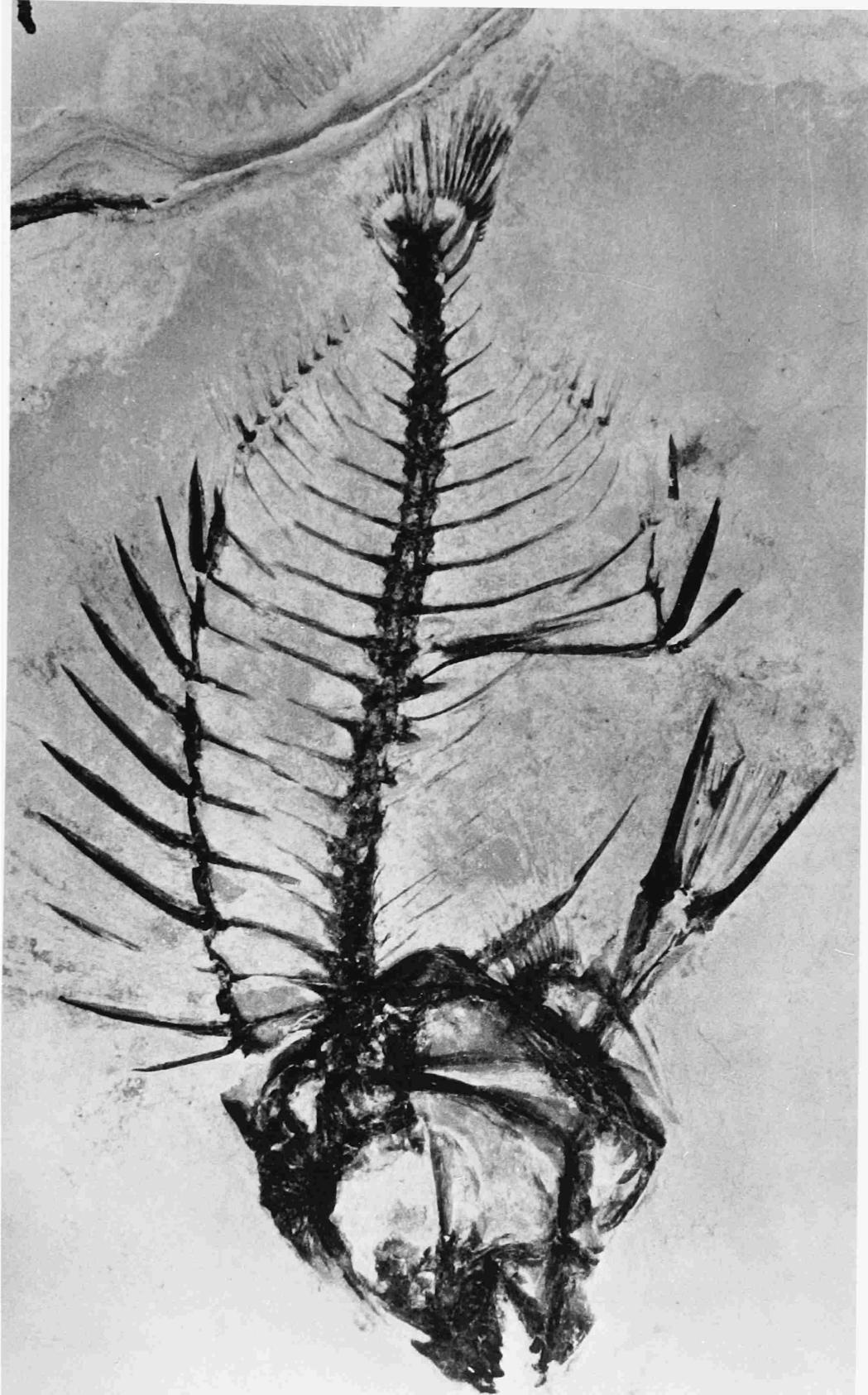


FIGURE 2.—Photograph of the acid-prepared paratype of *Ruffoichthys hannikovi* Tyler and Sorbini; MCSNV IIB65, 50.0 mm SL.

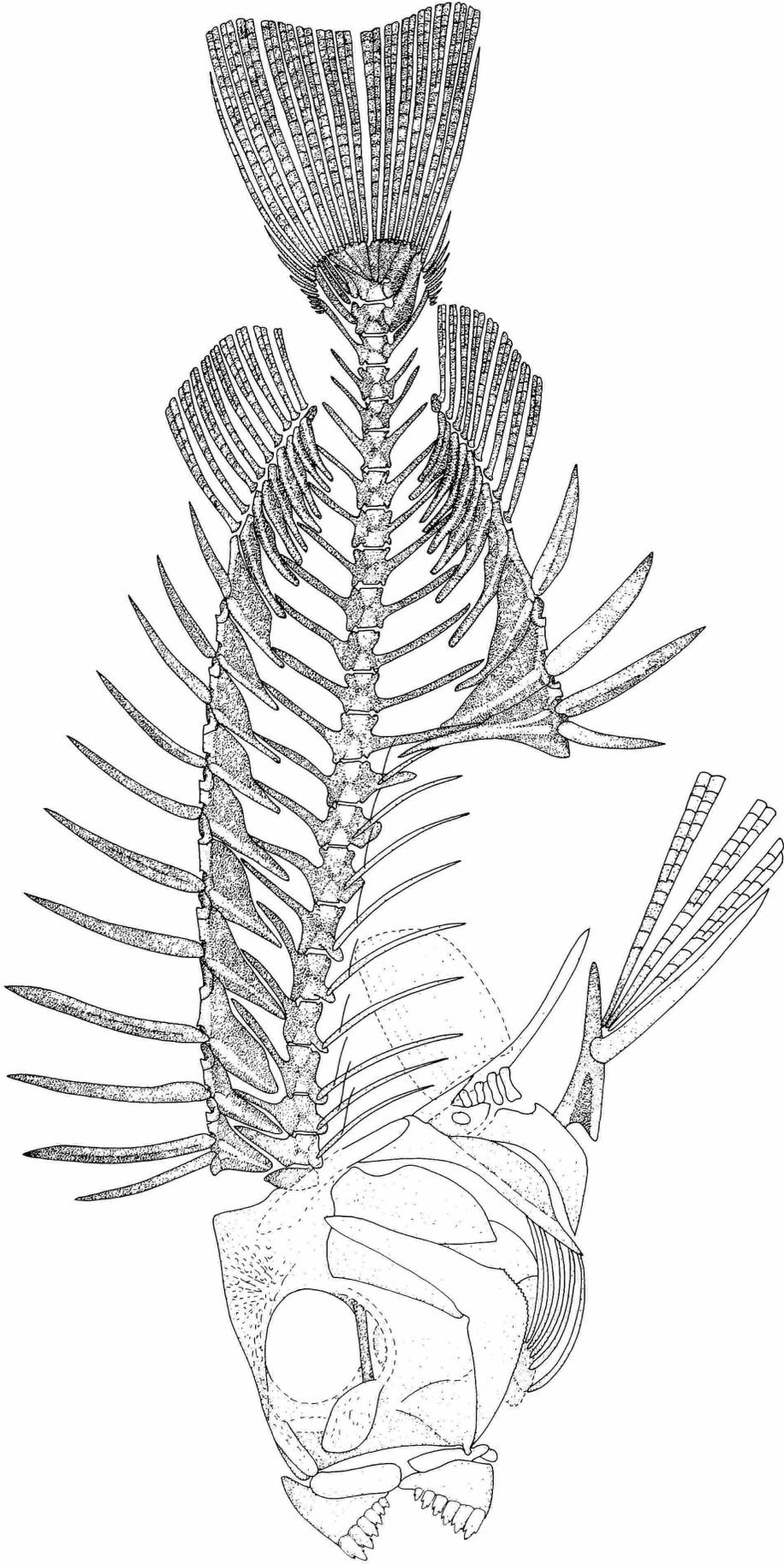


FIGURE 3.—Reconstruction of the skeleton of *Ruffoichthys spinosus* Sorbini, middle Eocene of Monte Bolca, Italy; based mostly on the holotype, MCSNV T920, 55.1 mm SL, but with some details from many other specimens (10.0–38.2 mm SL, see text for catalog data).

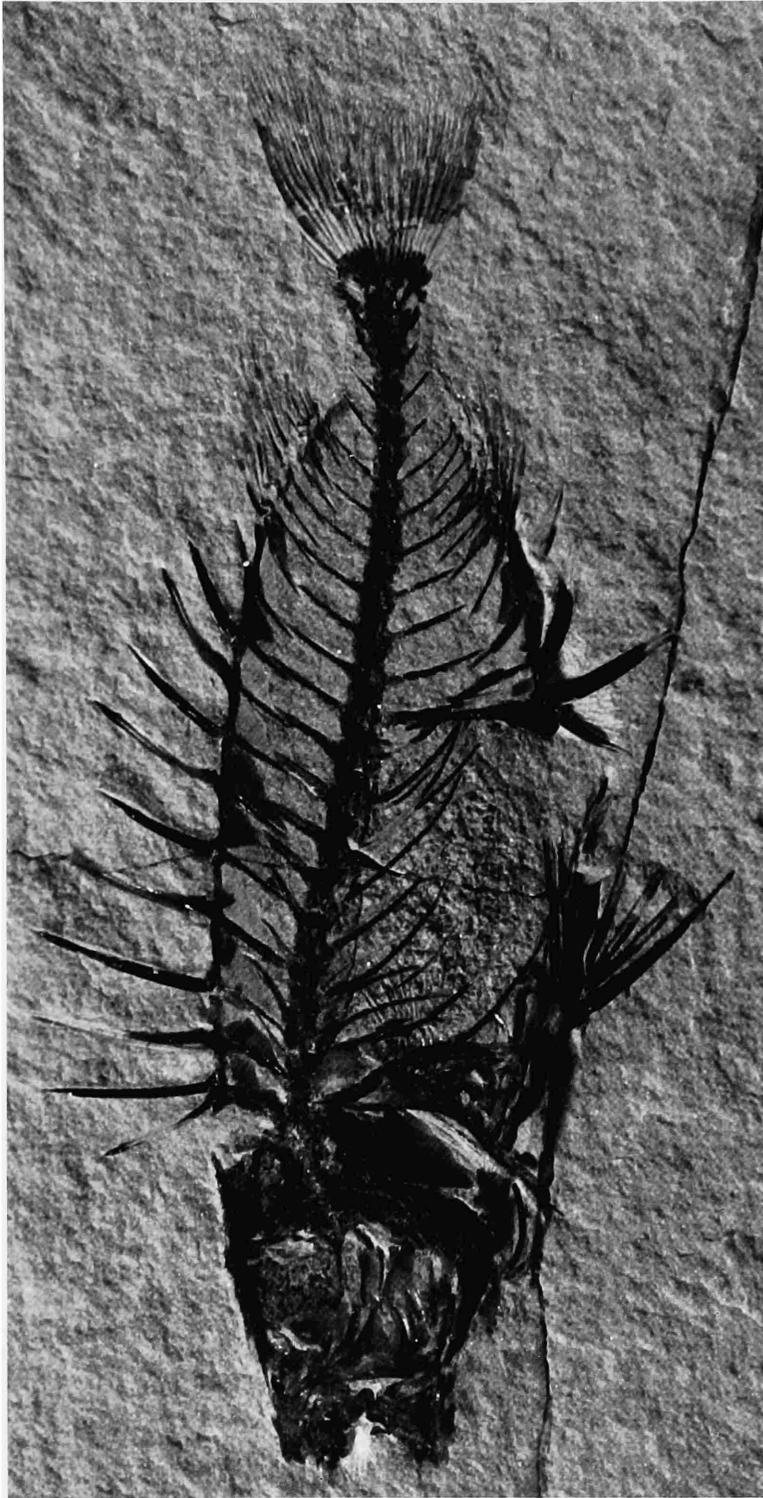


FIGURE 4.—Photograph of the holotype of *Ruffoichthys spinosus* Sorbini (see Figure 3 for data and reconstruction).

There are about 14–15 pectoral-fin rays. In a few specimens it is clear that the postcleithrum is formed of separate upper and lower elements.

The caudal fin has 17 principal rays and seven or eight procurrent rays above and below. There are five hypurals, three epurals, a large uroneural, and a free parhypural, with the haemal spines of PU2 and PU3 autogenous.

There is no supraneural. The ventral shaft of the first dorsal-fin pterygiophore is placed between the short neural spine of the first vertebra and the longer one of the second vertebra. The sixth interneural space is vacant.

There are pleural ribs from the second to last (tenth) abdominal vertebrae, most, if not all, of which bear epineural intermuscular bones.

The infraorbital series is well developed, with a large lachrymal and an unknown number of more-elongate elements in an arch to the middle of the rear of the orbit. It cannot be determined whether the second infraorbital is loosely articulated with the lachrymal and whether the main body of the lachrymal lies above the projected course of the infraorbital ring, both of which are synapomorphies of acanthuroids (Tyler et al., 1989). There is a well-developed subocular shelf, probably formed mostly from the third infraorbital. The posteroventral edge of the preopercle is serrate. There are 1+4=5 branchiostegal rays.

The scales are small and cycloid.

The illustrations of the two species of *Ruffoichthys* given in Tyler and Sorbini (1991) do not show surface sculpturing on the head bones. We have re-examined the specimens at the Museo Civico di Storia Naturale di Verona to confirm that they have the highly sculptured and cancellous condition typical of Recent siganids and higher squamipinnes, and these features are added to the lateral views of the skeletons of both species reproduced here (Figures 1, 3). We note that the descriptions of the teeth in both species of *Ruffoichthys* given by Tyler and Sorbini (1991) mention the notches that are present on both the medial and lateral edges but that the illustrations show only the deeper notch and larger cusp. This is rectified in the lateral views of the skeletons and is presented more clearly in the detailed drawing of a typical upper-jaw tooth of *R. spinosus* (Figure 19).

**AGE AND LOCALITY.**—Both species of *Ruffoichthys* are from the lower part of the middle Eocene (Lutetian; NP 14, *Discoaster sublodoensis* Zone) of Monte Bolca, Italy.

**HOLOTYPE AND OTHER SPECIMENS.**—*Ruffoichthys bannikovi*. *Holotype*: MCSNV IG132595 (head to right) and IG132596, in counterpart plates, 47.1 mm SL. *Paratype*: MCSNV IIB65, single plate, acid prepared, 50.0 mm SL.

*Ruffoichthys spinosus*. *Holotype*: MCSNV T920, single plate, 55.1 mm SL. *Additional Specimens*: MCSNV IG43394, single plate, 34.9 mm SL; MCSNV IG43360, single plate, 28.6 mm SL; MCSNV IG186668, single plate, 38.2 mm SL; MCSNV Mercoledt 17/8 84 Lina, in counterpart plates,

34.0 mm SL; MCSNV Mantovani, single plate, 32.3 mm SL; MCSNV Mantovani, single plate, 30.4 mm SL; MCSNV Mantovani, single plate, 26.0 mm SL; MCSNV Mantovani, in counterpart plates, 22.3 mm SL; MCSNV Mantovani, single plate, ~25.5 mm SL; MCSNV Mantovani, single plate, ~21.0 mm SL; MCSNV Mantovani, in counterpart plates, ~10.0 mm SL; MCSNV Tomelleri 41, single plate, 17.7 mm SL; MCSNV Tomelleri 53, single plate, ~32.2 mm SL; MCSNV Tomelleri 40, single plate, ~28 mm SL; MCSNM MMV1194, single plate, 41.3 mm SL; MCSNM MMV148, single plate, 31.8 mm SL; BM(NH) P20931, single plate, 37.4 mm SL.

### †*Eosiganus*, new genus

**TYPE SPECIES.**—*Eosiganus kumaensis*, new species, by monotypy.

**DIAGNOSIS.**—Differs from all other siganids by having a single supernumerary dorsal-fin spine (versus 2), this first dorsal-fin spine slightly to distinctly longer than the others (versus first spine shorter than the others), and by having about 7 anal-fin rays (versus 9–10).

**ETYMOLOGY.**—*Eo*, for the Eocene age, and *siganus* for the extant genus of the family.

### *Eosiganus kumaensis*, new species

FIGURES 5–9

This species is listed as “Siganidae, Gen. et sp. nov.” in a preliminary list of the Kuma ichthyofauna (Bannikov, 1993).

**DIAGNOSIS.**—That of the genus, of which it is the only known representative.

**DESCRIPTION.**—Each pelvic fin has an outer and inner spine and what we interpret as three rays, but the rays are compressed between the spines, and the fins from both sides are superimposed, so we cannot be as sure of the number of rays as we are of the spines. The outer pelvic-fin spine is smooth in the 34.2 mm SL holotype, but it has prominent serrations in the ~18 mm SL paratype and perhaps slight serrations in the 19.6 mm SL paratype. We presume the presence of these serrations indicates that at least the ~18 mm SL paratype is a pelagic late larval stage or a juvenile, which has just settled into a benthic habitat, as this stage is also indicated by the serrations on its first dorsal spine (see below). Most Recent species of siganids metamorphose from pelagic larvae to benthic juveniles at about 20–30 mm SL (Leis and Rennis, 1983; Woodland, 1990, and contained references).

The condition of the palatine is unknown.

The teeth are well preserved. They are strong and bluntly conical, with smooth edges and no notches (Figure 19), and appear to have been fixed. There are about eight teeth to each side of both the upper and lower jaws.

The dorsal fin has 11 spines, with a single spine in supernumerary association with the first pterygiophore; the

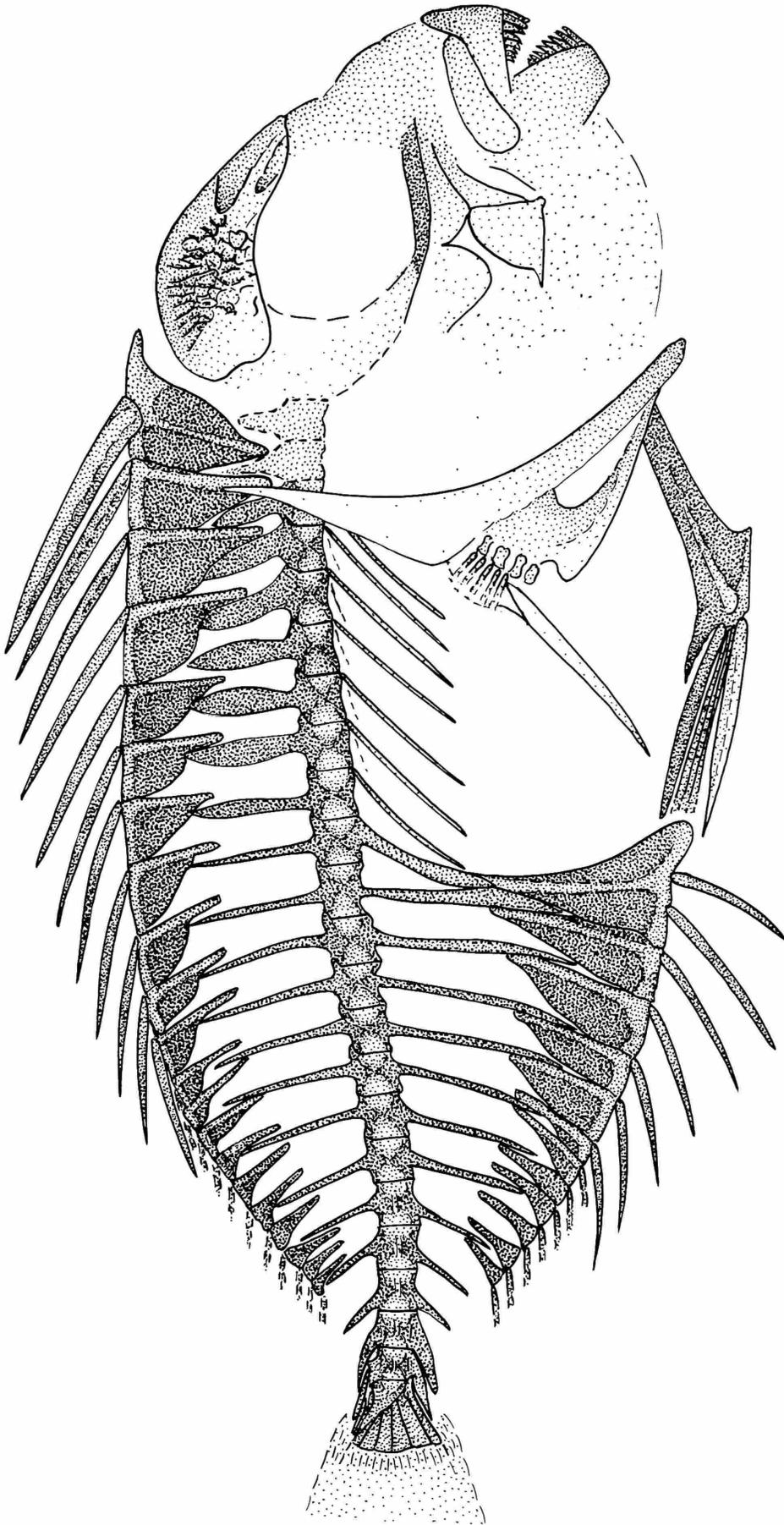


FIGURE 5.—Reconstruction of the skeleton of *Eosiganus kumaensis*, new genus and species, middle Eocene of North Caucasus, Russia; based on the holotype, PIN 4425-17A, 34.2 mm SL; because the paratypes are substantially smaller than the holotype, they are not used to render parts missing in the holotype.



FIGURE 6.—Photograph of the holotype of *Eosiganus fumaensis*, new genus and species; the right frontal is displaced ventrally into the upper orbit (see Figure 5 for data and reconstruction).

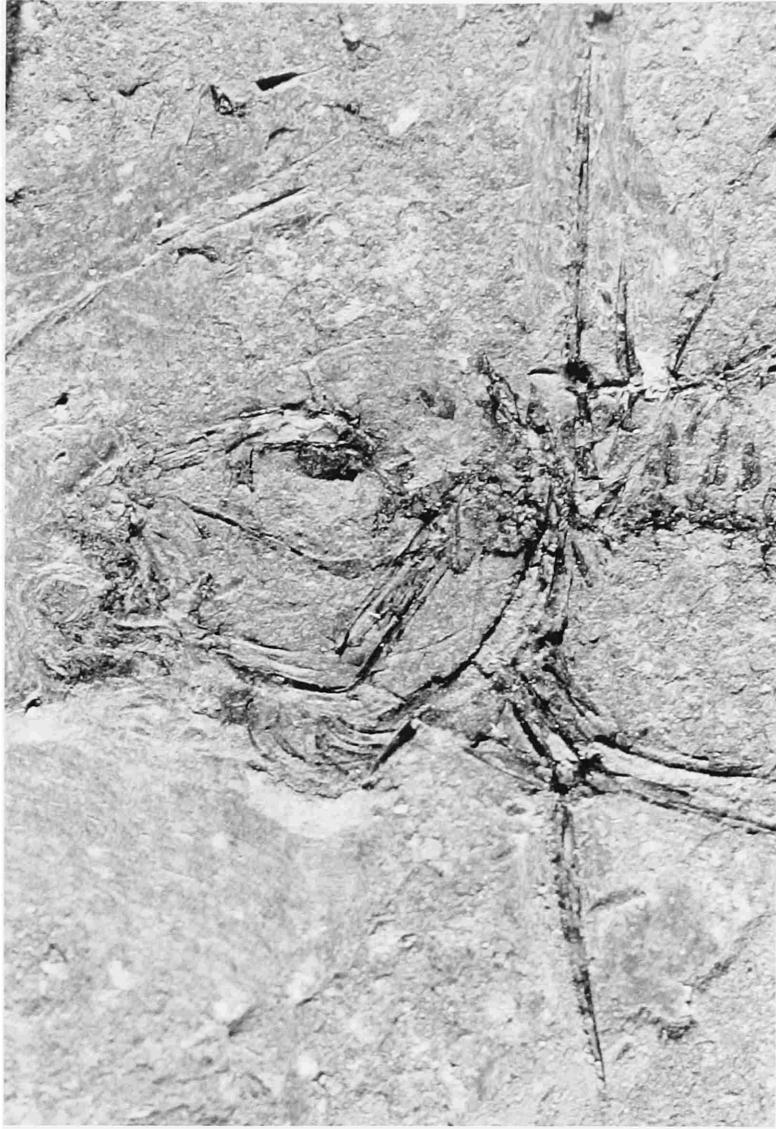


FIGURE 7.—Photograph of the smallest paratype of *Eosiganus kumaensis*, new genus and species; PIN 4425-21A, ~18 mm SL, with larval serrations on the first dorsal- and pelvic-fin spines and on the nasal (see Figure 8 for details).

supernumerary spine is slightly longer than the succeeding spines in the holotype but is much longer than the second spine in the two much smaller paratypes. The first dorsal spine is smooth in the holotype and the 19.6 mm SL paratype, but it is serrate in the ~18 mm SL paratype. There are 11 dorsal-fin rays based on a combination of those that can be counted (in the paratypes) and the number of pterygiophores in places where the rays are not preserved. The anterodorsal end of the first pterygiophore of the spiny dorsal fin is prolonged as a prominent procumbent spine, with longitudinal grooves apparent in one of the paratypes (Figure 9).

The anal fin has seven spines. The anal-fin rays are poorly preserved, but it is clear on the basis of the number of

pterygiophores that there were no more than about seven rays. The first anal-fin pterygiophore has a relatively vertical orientation, and the anteroventral process is of moderate length but well separated from the ventral end of the postcleithrum.

The total number of pectoral-fin rays cannot be determined. The postcleithrum is formed from separate upper and lower pieces.

The caudal fin is well preserved only in one of the paratypes (PIN 4425-20A), but it is somewhat distorted. Our interpretation is that the total number of principal rays is 17, with up to eight procurent rays both above and below. There are five hypurals, three epurals, and a free parhypural; there is an element that we interpret as an uroneural, but it is incomplete

and these are incomplete and poorly preserved; they may have been especially slender.

The infraorbital series is not well-enough preserved to describe. The number of branchiostegals and the condition of the posteroventral edge of the preopercle cannot be determined.

Scales are not preserved.

AGE, LOCALITY, AND ICHTHYOLOGICAL ASSOCIATIONS.—

The type materials are all from the upper part of the middle Eocene (Kuma Horizon, also spelled Kumsky, which correlates with the Bartonian) of the North Caucasus in southwest Russia, on the Pshekha River, Apsheronsk District, about 0.5 km from the Gorny Luch farmstead. The Kuma Horizon is characterized by several late Eocene foraminiferans, and the rich fish fauna has a preponderance of oceanic pelagic species (e.g., representatives of stomiiforms, trichiurids, acronurus-stage acanthurids, *Bregmaceros* cf. *filamentosus*, *Thunnus abchasicus*, *Palaeorhynchus parini*, *Palimphyes pshekhaensis*, *Eomola bimaxillaria*) (Tyler and Bannikov, 1992a; Bannikov, 1993).

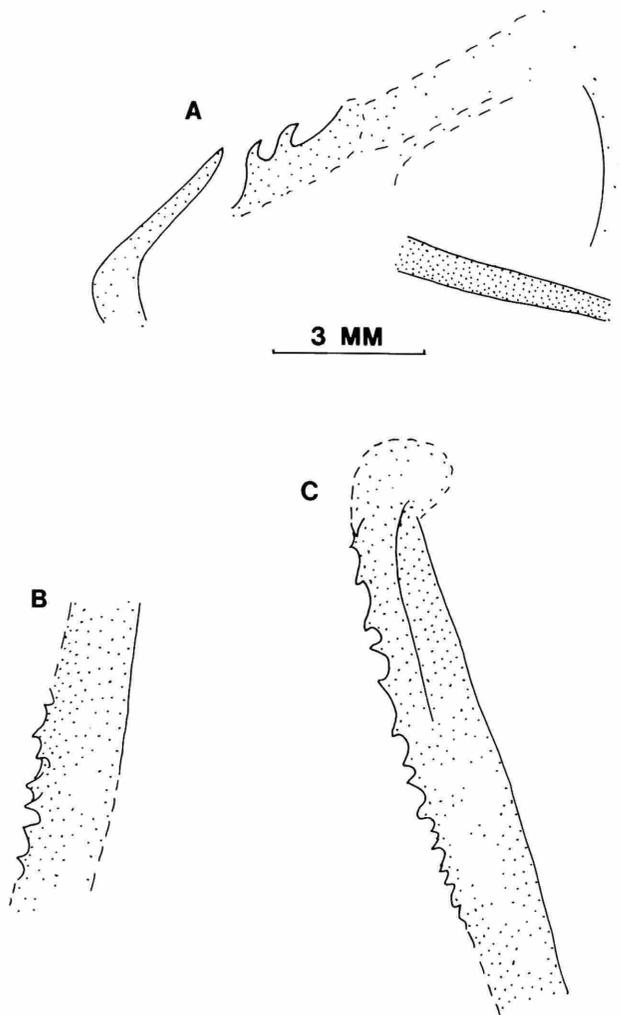


FIGURE 8.—Camera lucida drawings of parts of the smallest paratype of *Eosiganus kumaensis*, new genus and species; PIN 4425-21A, ~18 mm SL, with some larval serrations present: A, ascending process of the premaxilla and serrate nasal bone, with part of the somewhat upwardly displaced parasphenoid; B, part of the lower region of the serrate first dorsal-fin spine; C, lower region of the serrate outer pelvic-fin spine. Anterior to left; scale applies to all three illustrations.

and we cannot determine its full size. Because the haemal spine on PU3 appears to be autogenous, we presume PU2, the base of which is less clear, is also autogenous.

There is no supraneural. The ventral shaft of the first dorsal-fin pterygiophore is placed between the poorly preserved neural spines of the first and second vertebrae. The fifth interneural space is vacant.

Pleural ribs are present on most of the abdominal vertebrae and, from its position, it appears that the first rib was attached to the second vertebra, but we cannot be absolutely sure of this. There is evidence of only a few epineural intermuscular bones,

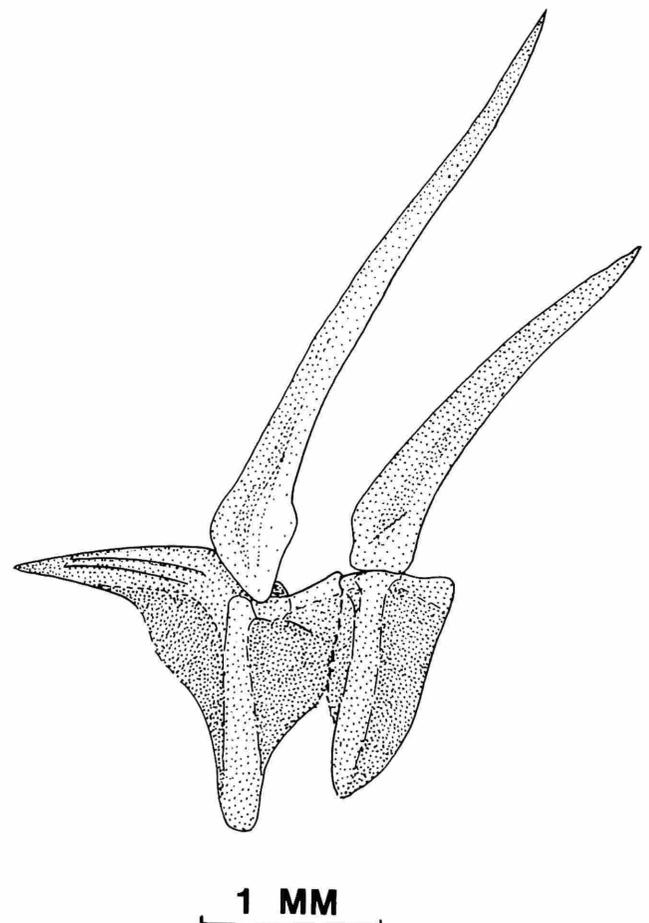


FIGURE 9.—Camera lucida drawing of the first two dorsal-fin spines and pterygiophores of a paratype of *Eosiganus kumaensis*, new genus and species, PIN 4425-20A, 19.6 mm SL; larval serrations absent.

However, there are also some species typical of inshore benthic habitats, such as priacanthids and a syngnathiform (*Paraeoliscus bannikovi* Parin, 1992). We presume that the holotype and the 19.6 mm SL paratype were in a benthic reef or grass-flat habitat, whereas the ~18 mm SL paratype, with larval serrations, was either pelagic or had just recently settled to the bottom.

The Kuma Horizon has been assigned previously to the upper Eocene (Tyler and Bannikov, 1992a; Bannikov, 1993) but according to Cavalier and Pomerol (1986) only the Priabonian (but not the Bartonian) should be included in the upper Eocene.

TYPE SPECIMENS.—*Holotype*: PIN 4425-17A (head to right) and 17B, in counterpart plates, 34.2 mm SL. *Paratypes*: PIN 4425-20A (head to left) and 20B, in counterpart plates, 19.6 mm SL; PIN 4425-21A (head to left) and 21B, in counterpart plates, ~18 mm SL.

ETYMOLOGY.—The specific name is for the Kuma Horizon that contains a wonderfully rich assemblage of middle Eocene marine fishes.

#### †*Siganopygaeus* Danilchenko, 1968

TYPE SPECIES.—*Siganopygaeus rarus* Danilchenko, 1968, by monotypy and original description.

DIAGNOSIS.—Differs from all other siganids by having 14 dorsal-fin spines (versus 11–13), 8 anal-fin spines (versus 4–7), one supraneural (versus no supraneural), the first of two supernumerary dorsal-fin spines very short (versus long when present), and the third dorsal-fin spine by far the longest (versus the third spine of similar length to the immediately preceding and succeeding spines).

#### *Siganopygaeus rarus* Danilchenko, 1968

FIGURES 10, 11

This species originally was described on the basis of two specimens at PIN, but only the single plate of the holotype can now be located.

DIAGNOSIS.—That of the genus, of which it is the only known representative.

DESCRIPTION.—Most of the head is missing, with the exception of the opercular bones; the opercle and subopercle are well preserved and in place, whereas the preopercle is partially preserved and is displaced in front of the first dorsal-fin pterygiophore. Two other bones are displaced in the region of the mouth; we interpret these as the supracleithrum partially overlying a bone we cannot identify.

The pelvic fin is well preserved and clearly has an outer spine followed by three rays and an inner spine (one other spine from the opposite pelvic fin also is exposed). The first ray is slender, the second ray slightly thicker, and the third ray

substantially thicker than the other two, about as thick as the inner spine. The distal portions of the rays are incomplete, and, although there is evidence of them being composed of paired halves, no cross-striations are apparent.

The palatine and teeth are not preserved.

The dorsal fin has 14 spines, with the first two in supernumerary association with the first pterygiophore; the first dorsal spine is very short (2.2% SL) and was not mentioned by Danilchenko (1968). The second spine has only the base preserved but because this is somewhat less thick than the base of the third spine, we estimate that the second spine, although many times longer than the first spine, was shorter than the long third spine (28.8% SL for the third spine). The fourth and succeeding spines are all significantly shorter (19.2% SL for the fourth spine) than the third spine. The dorsal-fin rays are only partially preserved, mostly anteriorly, and the complete number cannot be determined; however, in most siganids (*Eosiganus* being exceptional) the dorsal fin has about the same number of rays as the anal fin, and because there are 10 anal-fin rays, we presume that there are about 10 dorsal-fin rays. The anterodorsal end of the first pterygiophore of the spiny dorsal fin is prolonged as a prominent procumbent spine, without evidence of grooves.

The anal fin is well preserved and relatively complete. It has eight spines and 10 rays. The first anal-fin pterygiophore has a relatively vertical orientation, and the anteroventral process is moderately long but well separated from the ventral end of the postcleithrum.

The pectoral fin is poorly preserved, but there appears to be a minimum of 10 rays; Danilchenko (1968) gave the count as 12–14, perhaps based on the missing paratype. The postcleithrum is formed of separate dorsal and ventral pieces.

The caudal fin is essentially absent except for the impressions of rays from the upper lobe, in which there appear to have been about nine principal rays and an undetermined number of procurrent rays (there are only the impressions of the posterior three). The impression of the caudal skeleton is too vague to interpret how many separate elements were present.

A well-developed supraneural is present, with a prominent anterior process from its dorsal end. The ventral shaft of the first dorsal-fin pterygiophore is placed between the neural spines of the first and second vertebrae. The fifth interneural space is vacant.

Pleural ribs are present on the second to ninth abdominal vertebrae. There is no evidence of epineural intermuscular bones, but this could as well be because of poor preservation or exposure of the vertebral centra and upper regions of the pleural ribs as from the true absence of epineurals.

The infraorbitals and branchiostegals are not preserved. The displaced preopercle has at least a few large serrations along its posteroventral edge.

Scales are not preserved in the holotype, but Danilchenko (1968) said that they are small and cycloid, with about 60–80

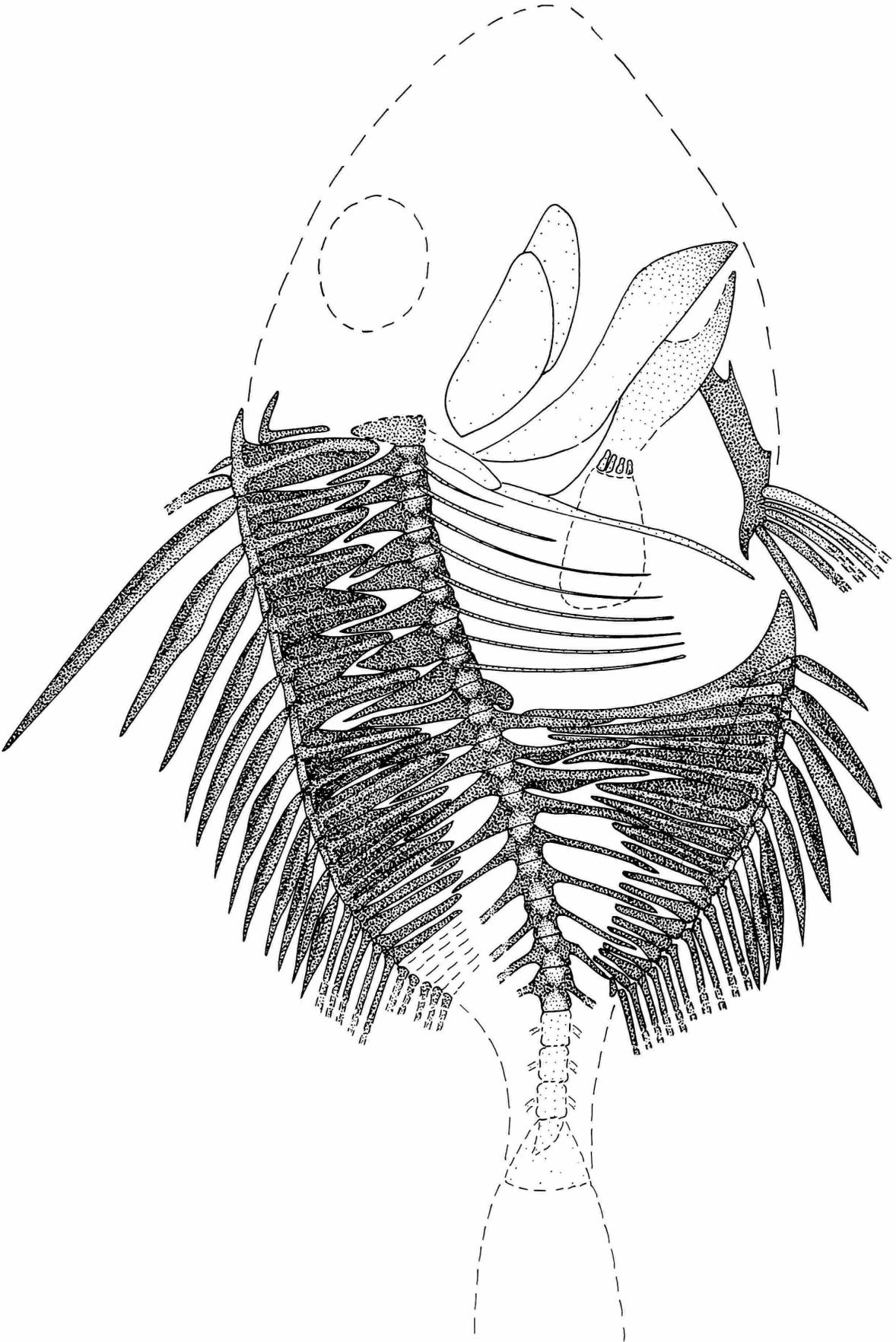


FIGURE 10.—Reconstruction of the skeleton of *Siganypygaeus rarus* Danilichenko, early Eocene of Turkmenistan; holotype, PIN 2179-100, 31.2 mm SL.

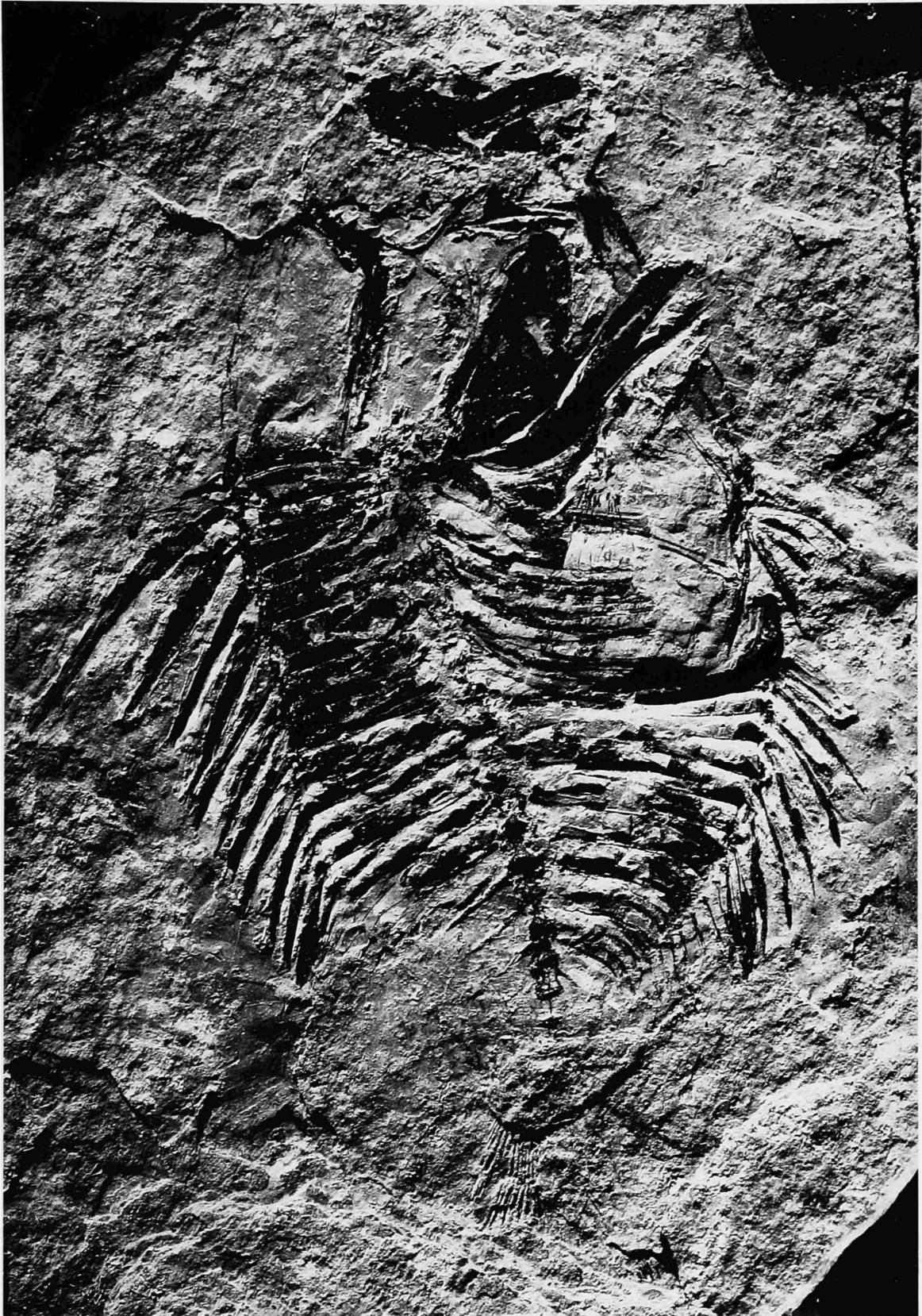


FIGURE 11.—Photograph of the holotype of *Siganopygæus rarus* Danilichenko (see Figure 10 for data and reconstruction).

rows from just behind the opercle to the caudal-fin base. This information must have been obtained from the missing paratype.

AGE AND LOCALITY.—Both specimens (holotype and missing paratype) are from the lower Eocene Danatinian (Danata) Formation of Ulyla-Kushlyuk, southwestern Turkmenistan (see Tyler and Bannikov, 1992b, and Bannikov, 1993, for the geology and ichthyological associations of the Danatinian Formation); based on nannoplankton, it is possible that the thin fish-bearing layer of the Danatinian Formation belongs to the upper Paleocene rather than to the lower Eocene (N. Muzylyov, Jan., 1995, pers. comm.).

TYPE SPECIMEN.—*Holotype*: PIN 2179-100, 31.2 mm SL, single plate; the missing paratype was never catalogued.

### †*Protosiganus* Whitley, 1935

*Archaeoteuthis* Wettstein (1886), preoccupied by *Archaeoteuthis* Roemer (1855), a cephalopod; Whitley (1935) gave the replacement name *Protosiganus*, which therefore takes the same type species.

TYPE SPECIES.—*Archaeoteuthis glaronensis* Wettstein, 1886, by monotypy and original designation.

DIAGNOSIS.—Differs from all other siganids by having 6 anal-fin spines (versus 4 or 7–8).

### *Protosiganus glaronensis* (Wettstein, 1886)

FIGURES 12–14

*Archaeoteuthis glaronensis* Wettstein (1886):67–68.

This species is known on the basis of the single plate of the holotype. At the time of its original description, the plate of black schist had not been prepared in any way, and the photograph of the specimen by Wettstein (1886, pl. 8: fig. 11) indicates that there was much matrix superimposed on the imprint. Sometime more than 30 years ago the holotypic plate was prepared at the Naturhistorisches Museum Basel using the air-brush abrasive technique to remove the excess matrix and enhance the exhibition qualities of the specimen, with outstanding results. The far greater detail of the skeleton that can now be seen is described below.

We know that this preparation was done prior to 1961 because a postage stamp issued by Switzerland in 1961 as the 20 Rp denomination in the Pro Patria series has a representation of this species clearly based on the prepared specimen. The stamp does not bear the name of the fish, and the descriptions of this stamp in catalogs (e.g., Zumstein) simply state that it is a fossil fish (in German, Versteinerter Fisch). However, the publicity material issued from Bern by the Swiss Philatelic Office in 1961 relative to this fossil fish stamp states (in German) that it is “*Scorpaena porcus* Linne (Familie Scorpaenoidei)” from the early Oligocene of Canton Glarus, an inexplicable error because the specimen was properly identified

when on exhibit at the Basel museum and the holotypic plate bears a label on the back side identifying it as the holotype of *Archaeoteuthis glaronensis* Wettstein. The erroneous identification associated with the stamp was corrected by Bearse (1976), Bearse et al. (1977), and Rice (1976), all of whom used the name *Protosiganus glaronensis* for it.

DIAGNOSIS.—That of the genus, of which it is the only known representative.

DESCRIPTION.—The pelvic fin is well preserved and clearly has an outer spine followed by three rays and an inner spine (one other spine from the opposite pelvic fin also is exposed).

The condition of the palatine is unknown.

The teeth are relatively well preserved. They are long and slender (up to about 1.4 mm in length or 1.2% SL), with at least 14 exposed in the upper jaw and 20 in the lower jaw as based on actual teeth and the gaps in the series (Figure 19). The teeth have smooth anterior edges, but the distal half of the posterior edge has faint indications of what could be low lobations or irregularities. Because the teeth are relatively long and slender, we presume that they were probably moveable, as is typical of setiform teeth when present in other acanthuroids and higher squamipinnes.

The dorsal fin has 13 spines, with the first two in supernumerary association with the first pterygiophore; the first dorsal spine is about three-fourths the length of the second spine, and the third spine (22% SL) is slightly longer than the others. There are 10 dorsal-fin rays. The anterodorsal end of the first pterygiophore of the spiny dorsal fin is prolonged as a prominent procumbent spine, with delicate longitudinal grooves.

The anal fin has six spines and 10 rays. The first anal-fin pterygiophore has an oblique orientation and a long anteroventral process that closely approaches and probably directly contacts the ventral end of the postcleithrum (the actual point of probable contact is overlain by a narrow layer of matrix). Although some small portion of the oblique orientation of the anal pterygiophore may be attributable to distortion of the matrix, its close relationship with the postcleithrum is entirely natural.

The total number of pectoral-fin rays cannot be determined. The postcleithrum is formed of separate upper and lower pieces.

The caudal fin is well preserved. It has 17 principal rays, with nine procurrent rays above and seven or eight below. There are five hypurals, three epurals, and a large uroneural, but the region of the parhypural is covered with matrix. The haemal spine of PU2 is probably autogenous but that of PU3 appears to be fused with the centrum.

There is no supraneural. Although matrix obscures the details, the ventral shaft of the first dorsal-fin pterygiophore seems to be placed directly over the short neural spine of the first vertebra and just in front of the longer neural spine of the second vertebra. The fifth interneural space is vacant.

Pleural ribs are present on the second to ninth abdominal vertebrae; a well-preserved epineural intermuscular bone is

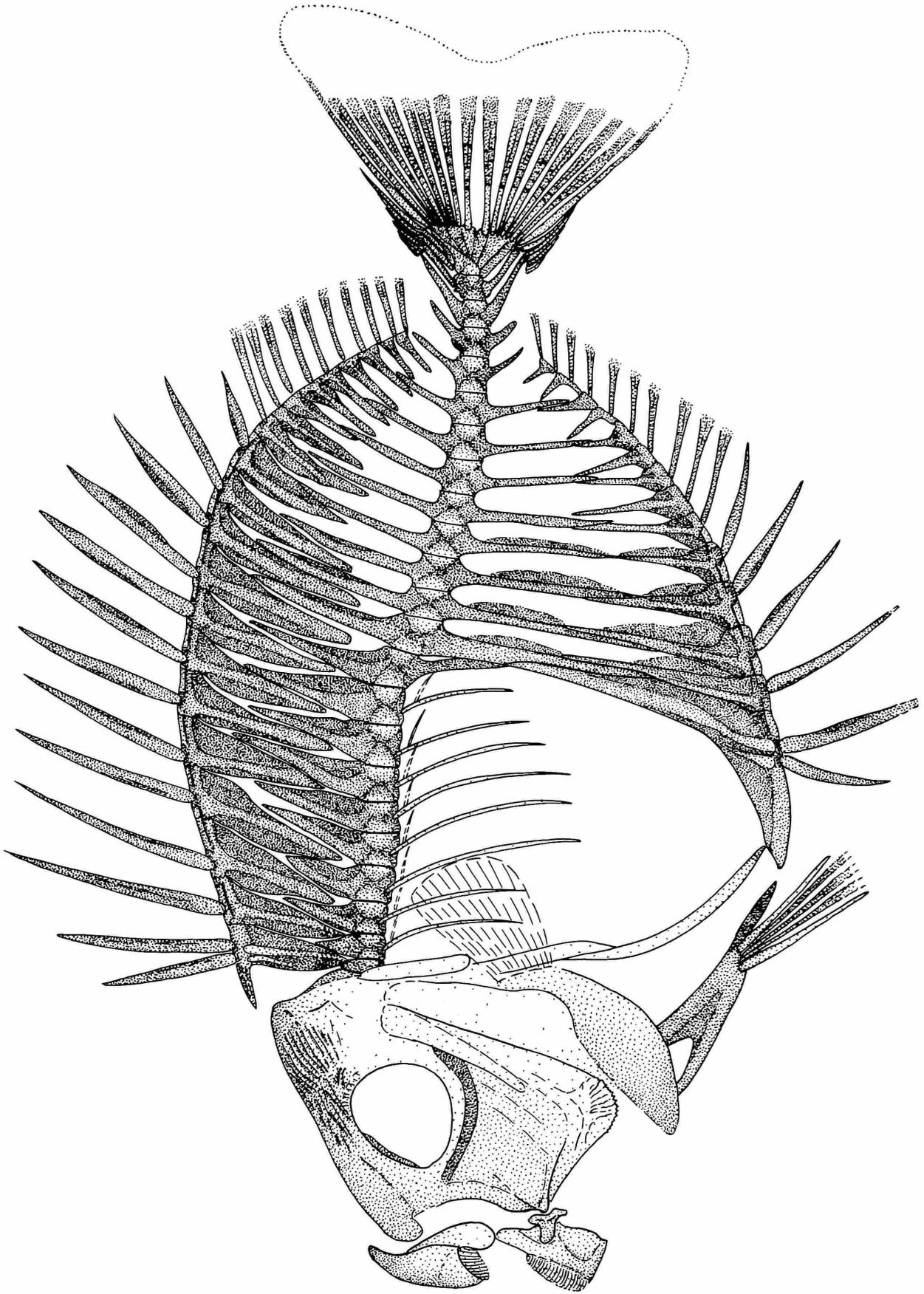


FIGURE 12.—Reconstruction of the skeleton of *Protosiganus glaronensis* (Wettstein), early Oligocene of Canton Glarus, Switzerland; holotype, NMB E177, 113.6 mm SL.



FIGURE 13.—Photograph of the holotype of *Protosiganus glaronensis* (Wettstein) (see Figure 12 for data and reconstruction), as described and figured by Wettstein (1886, pl. 8: fig. 11), prior to preparation (compare with Figure 14, after preparation).

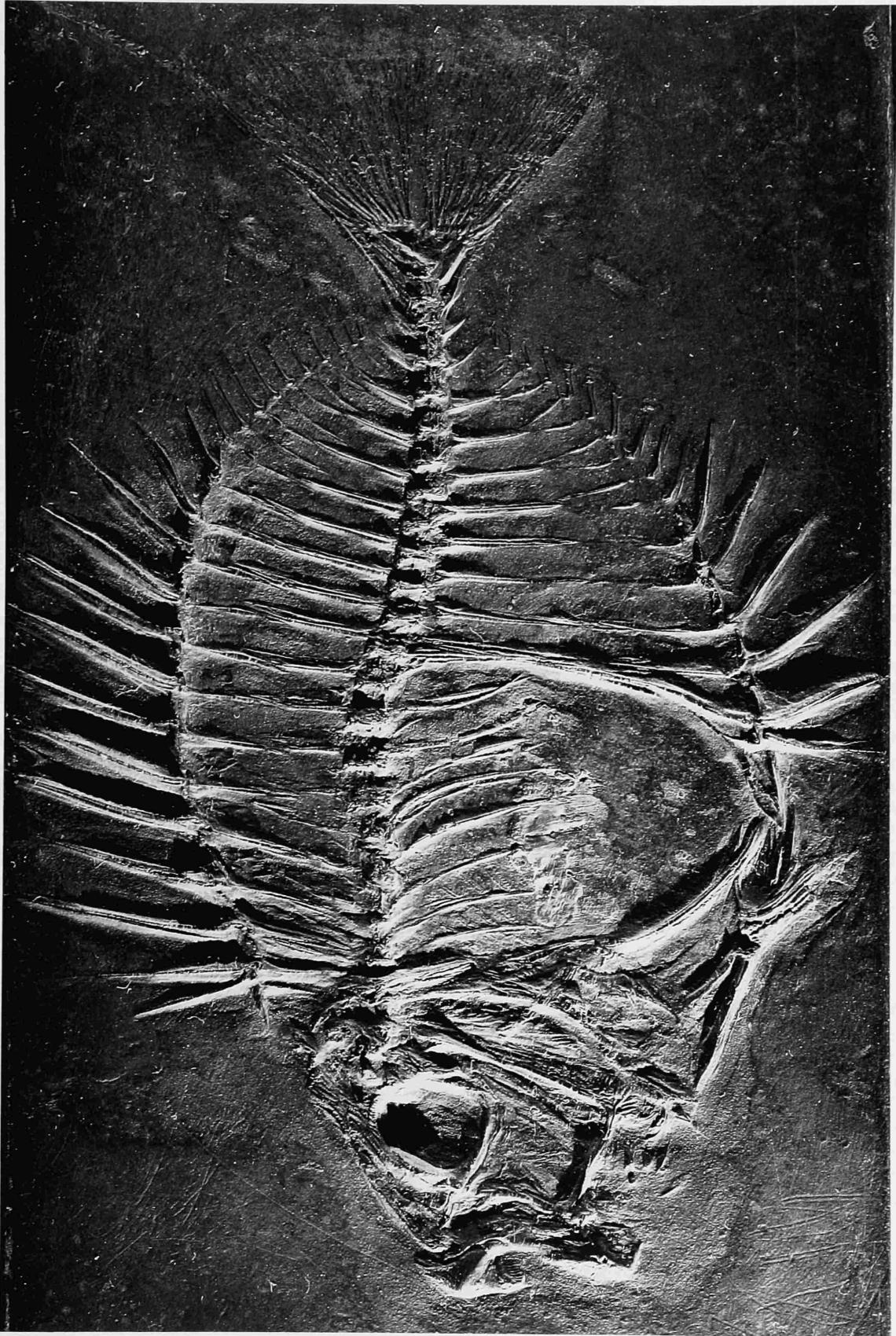


FIGURE 14.—Photograph of the holotype of *Protosiganus garonensis* (Wettstein) (see Figure 12 for data and reconstruction), as described herein after air-brush preparation at the Naturhistorisches Museum Basel.

present on the pleural rib attached to the eighth vertebra, but there are only faint traces of other epineurals.

The limits of the individual elements in the infraorbital series are not well-enough differentiated to describe. The posteroventral edge of the preopercle is serrate. Most of the branchiostegals are preserved, but those from both sides are not well separated and it is impossible to determine their total number and grouping.

Scales are not preserved.

AGE AND LOCALITY.—The holotype is from the early Oligocene (Rupelian) of Canton Glarus, Switzerland.

TYPE SPECIMEN.—*Holotype*: NMB EI77, 113.6 mm SL, single plate.

### *Siganus* Forsskål, 1775

TYPE SPECIES.—*Scarus rivulatus* Forsskål, 1775, by monotypy; for the history of the nomenclatural confusion over the names *Siganus* = *Teuthis* and the respective type species, see Gill (1884), Woodland (1990), and Eschmeyer (1990). Other species: see *Siganus* species, below.

DIAGNOSIS.—Differs from all other siganids by the presence of a posterior barb on the procumbent spine of the first pterygiophore of the dorsal fin (versus no posterior barb). Three synapomorphies (long first dorsal spine, postcleithral-ptyerygiophore contact, 9–10 dorsal rays) indicate that *Siganus* is most closely related to the Oligocene *Protosiganus*, and both have 13 dorsal-fin spines (versus 11 or 14 in other genera). *Siganus* differs from *Protosiganus* by having the teeth wide and deeply notched (versus slender and with probable low lobations on one side in *Protosiganus*, but deeply notched teeth are also independently present in *Ruffoichthys*), seven anal-fin spines (versus six in *Protosiganus*, but seven spines are also present in *Eosiganus*), and shorter dorsal-fin spines (longest spines ranging between 11%–18% SL versus 22% SL in *Protosiganus*).

### *Siganus* species

FIGURES 15–18

The species differ mainly in coloration, body proportions (including length and stoutness of rays and spines), numbers of scale rows, and, for the two subgenera, length of snout.

Woodland (1990) has thoroughly treated the taxonomy and distribution of the 27 species of *Siganus* (22 in the subgenus *Siganus* and 5 in the subgenus *Lo*), all of which are Recent in the tropical and subtropical Indo-Pacific. We therefore limit ourselves to the osteology of the genus and its phylogenetic relationships within the family, topics not covered by Woodland.

MATERIALS.—Our description of the osteology of *Siganus* is based on the following cleared and stained, radiographed, and alcohol preserved specimens.

*Cleared and Stained*: *Siganus* (*S.*) *canaliculatus* (Park), ANSP 77804, 1, 55.9 mm SL. *Siganus* (*S.*) *corallinus* (Valenciennes), ANSP 49224, 1, 139 mm SL. *Siganus* (*S.*) *luridus* (Rüppell), USNM 218868, 2, 41.2–61.0 mm SL. *Siganus* (*S.*) sp., USNM 109355, 3, 16.0–31.5 mm SL; MCZ 63119, 2, 7.7–9.7 mm SL. *Siganus* (*Lo*) *vulpinus* (Schlegel and Müller), USNM 270217, 1, 91.6 mm SL; USNM 325277, 2, 69.5–80.4 mm SL.

*Radiographed*: *Siganus* (*S.*) *argenteus* (Quoy and Gaimard), USNM 336445, 8, 96.4–124 mm SL. *Siganus* (*S.*) *fuscescens* (Houttuyn), USNM 336444, 11, 69.8–94.2 mm SL. *Siganus* (*S.*) *luridus* (Rüppell), USNM 235620, 3, 105–156 mm SL. *Siganus* (*S.*) *rivulatus* Forsskål, USNM 336446, 3, 134–151 mm SL. *Siganus* (*S.*) *virgatus* (Valenciennes), USNM 173031, 7, 81.7–95.4 mm SL. *Siganus* (*Lo*) *vulpinus* (Schlegel and Müller), USNM 182882–182883, 72.6–96.5 mm SL.

*Alcohol Preserved*: *Siganus* (*S.*) *fuscescens* (Houttuyn), USNM 235569, 1, 56.7 mm SL. *Siganus* (*S.*) *spinus* (Linnaeus), USNM 273859, 1, 61.1 mm SL. *Siganus* (*S.*) *argenteus* (Quoy and Gaimard; prior to Woodland, 1990, better known as *rostratus* Valenciennes), USNM 32508, 1, 106 mm SL. *Siganus* (*S.*) *rivulatus* Forsskål, USNM 235326, 1, 112 mm SL. *Siganus* (*S.*) *doliatus* Cuvier, USNM 324412, 1, 121 mm SL. *Siganus* (*S.*) *stellatus* Forsskål, USNM 235297, 1, 204 mm SL. *Siganus* (*Lo*) *vulpinus* (Schlegel and Müller), USNM 182883, 1, 96.5 mm SL. *Siganus* (*L.*) *uspi* Gawel and Woodland, USNM 243961, 1, 158 mm SL. (Compare Figure 18 of Recent species to Figure 19 of fossil species.)

DESCRIPTION.—The pelvic fin has outer and inner spines and three rays.

The palatine is composed of two separate ossifications, a character unique to siganids among teleosts, which was first described by Starks (1907) for *Siganus fuscescens*; the palatine and its upper-jaw articulation is well illustrated by Rosen (1984).

The teeth are always deeply notched (Figure 18), with those of the upper jaw having a major notch medially (and most species with a lesser or more distally placed notch laterally) and those of the lower jaw with an opposite pattern, the major notch being lateral and the lesser notch, if present, medial. The teeth are fixed, with usually about 10–14 to each side of both the upper and lower jaws. Two dental autapomorphies of Recent siganids are that the replacement teeth lie free in connective tissue on the inner surface of the jaws rather than being enclosed by bone (Tyler et al., 1989) and that the tooth rows on the fifth ceratobranchial are preceded by deep, transverse, tooth-replacement trenches (Guiasu and Winterbottom, 1993); however we cannot determine these features in any of the fossil taxa.

The dorsal fin has 13 spines, with the first two in supernumerary association with the first pterygiophore; the first dorsal spine is about two-thirds to three-fourths the length of the second spine, and the slightly longest spines usually are the third to the eighth (see Woodland, 1990). There is

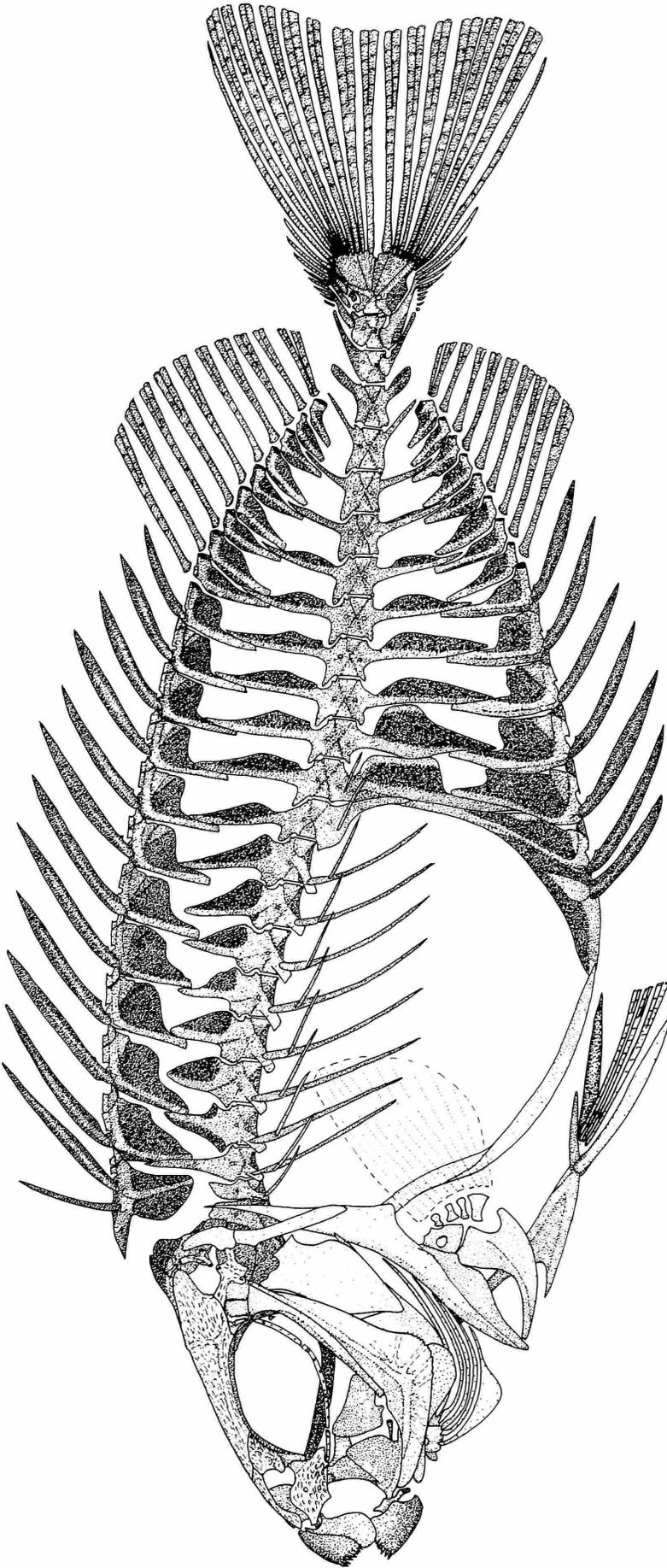


FIGURE 15.—Skeleton of cleared and stained specimen of *Siganus canaliculatus* (Park), Recent, ANSP 77804, 55.9 mm SL.

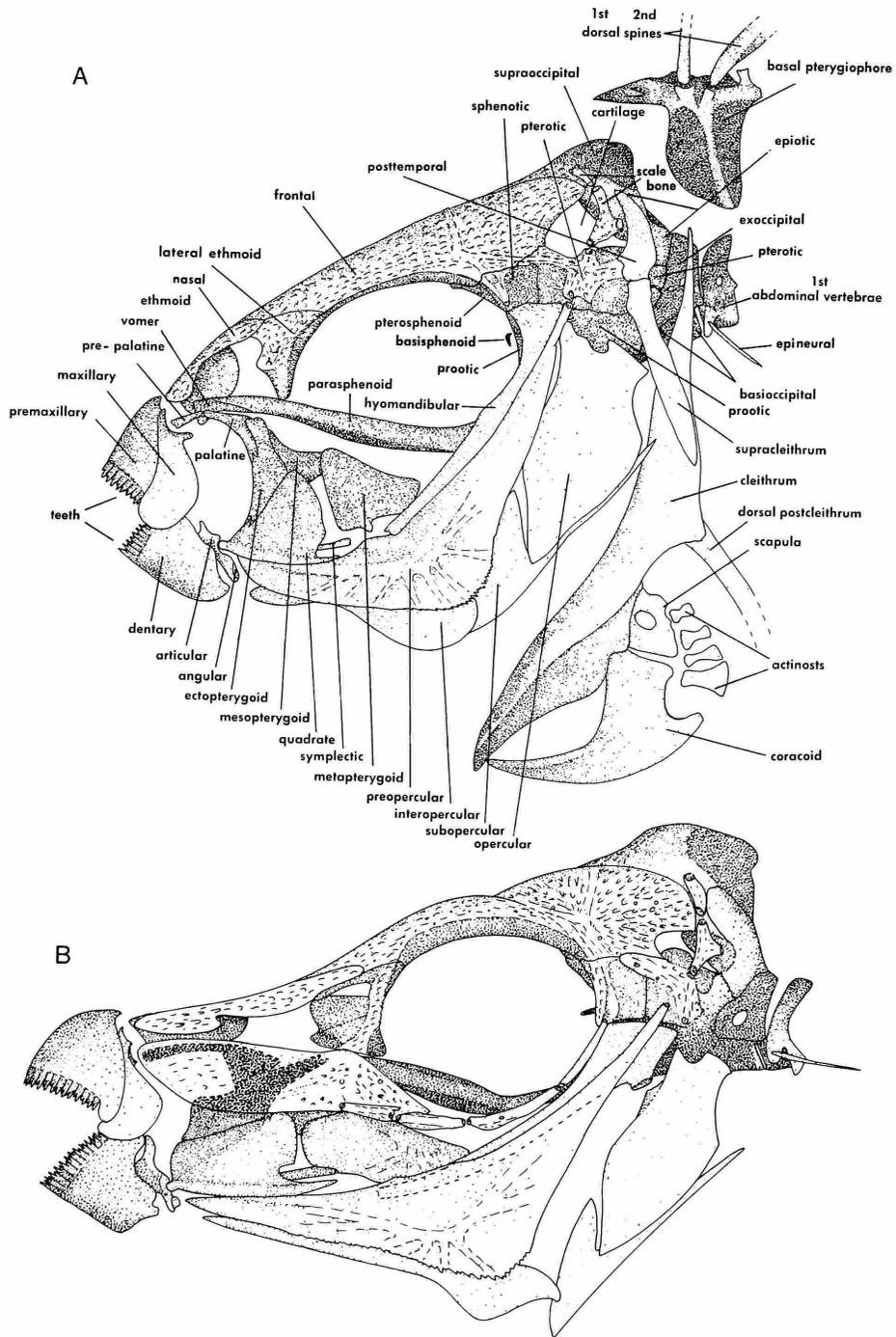


FIGURE 16.—Head bone configuration in species representative of the two subgenera of Recent *Siganus*: A, *Siganus (Siganus) canaliculatus* (Park), ANSP 77804, 55.9 mm SL, infraorbitals removed; B, *Siganus (Lo) vulpinus* (Schlegel and Müller), USNM 325277, 80.4 mm SL, infraorbitals in place, with the parts of the ectopterygoid and the two separate ossifications of the palatine that are obscured from view by the lachrymal indicated by dashed lines and dark stipple. The differences in snout length are not so extreme between some of the other species of the two subgenera.

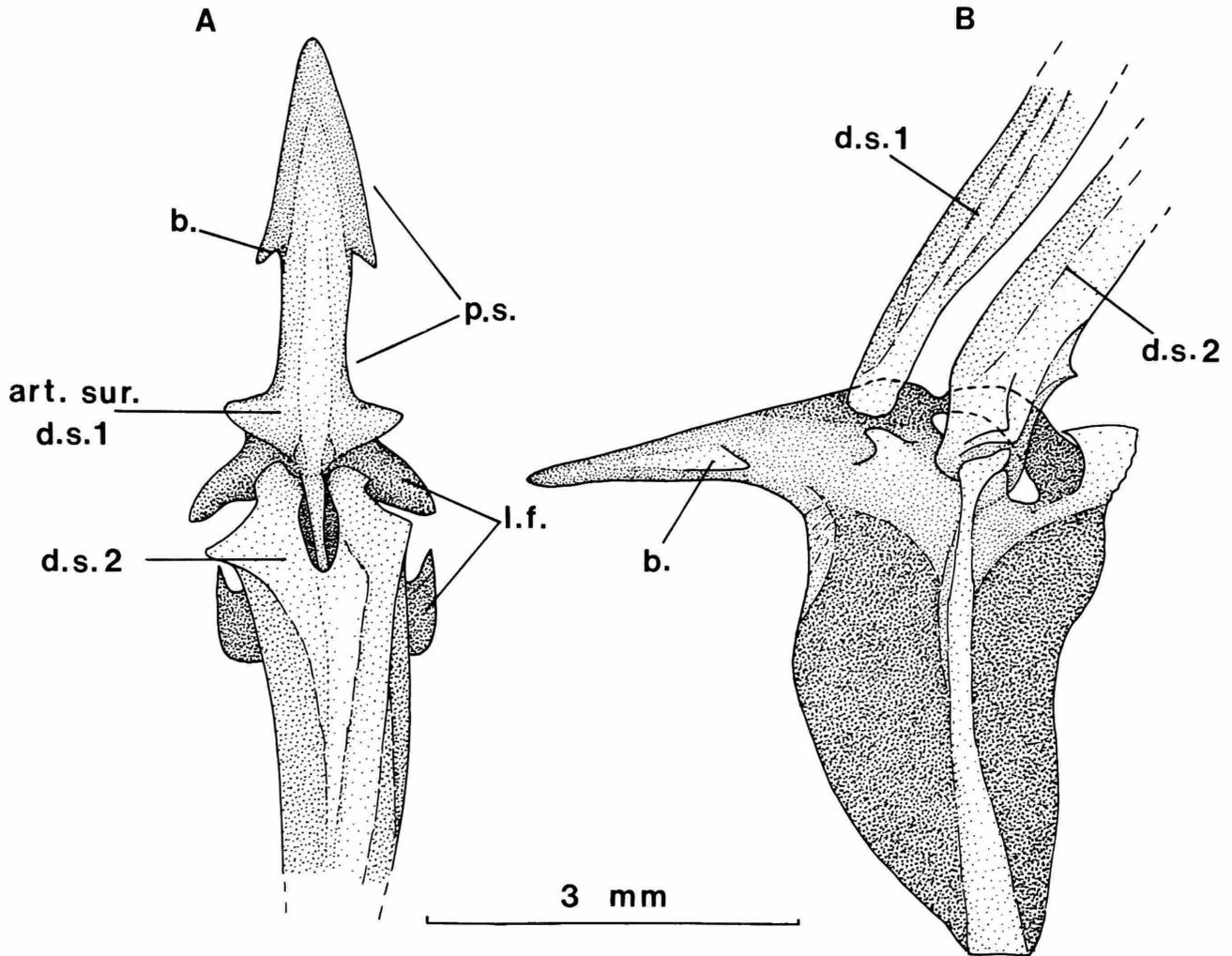


FIGURE 17.—Procumbent spine and posterior barb of the first dorsal-fin pterygiophore in *Siganus (S.) luridus* (Rüppell), USNM 218868, 61.0 mm SL: A, in dorsal view, with the first dorsal-fin spine removed, and B, in lateral view, with both supernumerary dorsal-fin spines in place. The edges of the median articular flanges of the pterygiophore that are clasped by the spines (chain-link type for the second spine) are shown by dashed lines in B. Distal radial removed in both figures. Abbreviations: art. sur., articular surface for the removed first dorsal-fin spine; b., barb on the procumbent spine; d.s.1 and 2, first and second dorsal-fin spines; l.f., lateral flanges of the pterygiophore below the first and second dorsal-fin spines; p.s., procumbent spine of the first pterygiophore.

extremely little variation in the norm of 10 dorsal-fin rays in all species of *Siganus*. The anterodorsal end of the first pterygiophore of the spiny dorsal fin is prolonged as a procumbent spine, which bears a posteriorly directed barb from about the middle of its lateral surface. Whereas the dorsal-, anal-, and pelvic-fin spines have poison glands associated with them, neither the procumbent spine nor its barb is poisonous, but these are still formidable armature (Halstead et al., 1971).

The anal fin has seven spines and nine rays, with just as little variation as is the case of the elements in the dorsal fin. The first anal-fin pterygiophore has an oblique orientation and a long

anteroventral process that contacts the ventral end of the postcleithrum, to which it is firmly held by connective tissue.

The pectoral fin most commonly has either 16 or 17 rays, but sometimes 15 or 18 (Woodland, 1990). The postcleithrum is formed of separate upper and lower pieces.

The caudal fin has 17 principal rays and 7 to 11 (usually 8 to 10) procurrent rays above and below. There are five hypurals, three epurals, a small uroneural, and a free parhypural, with the haemal spines of PU2 and PU3 autogenous.

There is no supraneural. The ventral shaft of the first dorsal-fin pterygiophore is placed directly over the short and

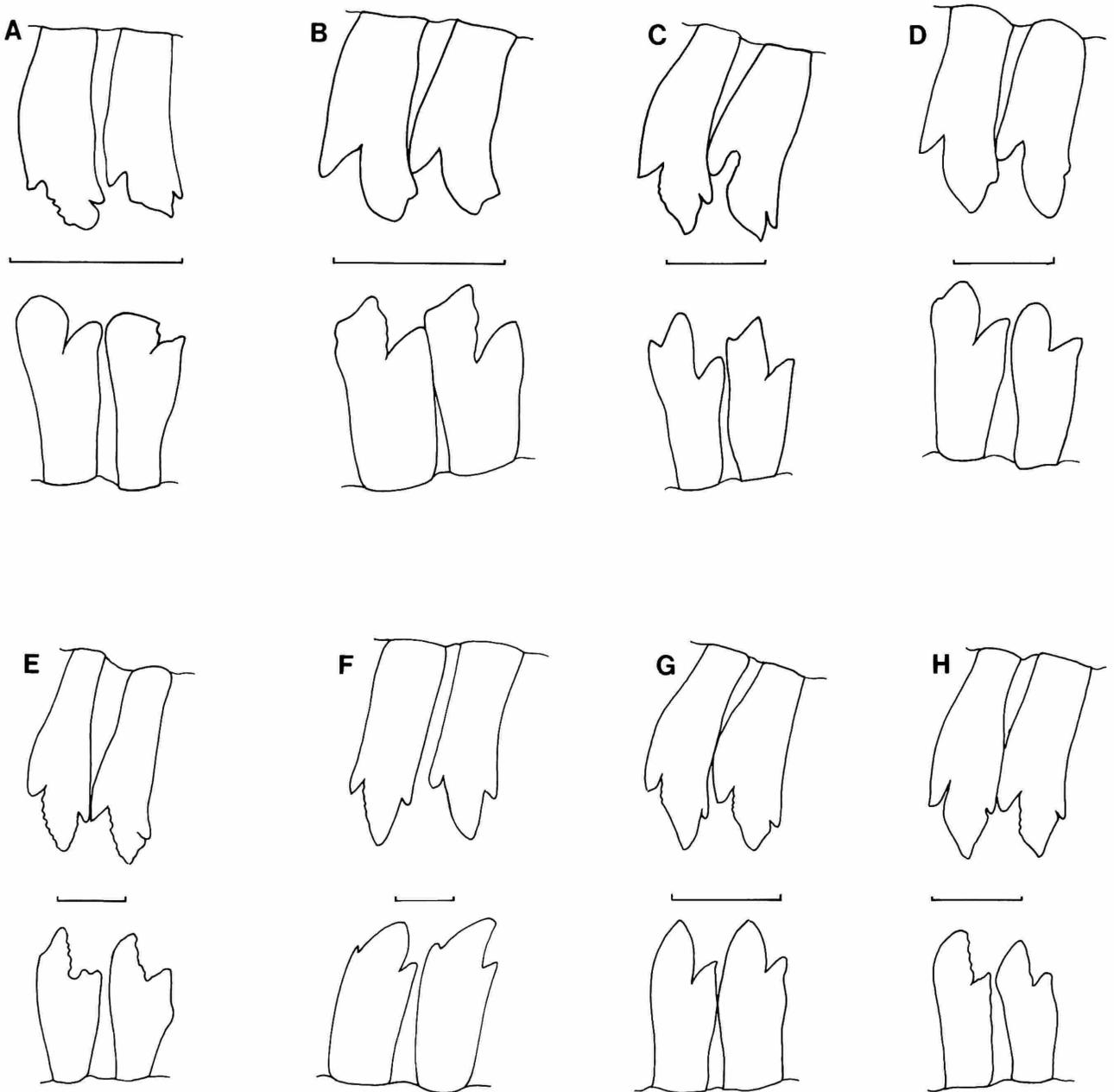


FIGURE 18.—Teeth in a representative selection of species of the two subgenera (*Siganus* and *Lo*) of the Recent *Siganus*; numbers of teeth are for those to each side of the midline, i.e., on each premaxilla and each dentary. Camera lucida drawings of adjacent teeth from the middle of the left side of the upper (above) and lower jaws; anterior to left; in: A, *Siganus* (*S.*) *fuscescens* (Houttuyn), 14 teeth in both jaws; B, *S.* (*S.*) *spinus* (Linnaeus), 10 teeth in both jaws, with teeth relatively wider and fewer in number than in the other illustrated species; C, *S.* (*S.*) *argenteus* (Quoy and Gaimard; prior to Woodland, 1990, better known as *rostratus* Valenciennes), 13 teeth in upper jaw and 12 in lower jaw; D, *S.* (*S.*) *rivulatus* Forsskål, 13 teeth in upper jaw and 14 below; E, *S.* (*S.*) *dolius* Cuvier, 13 teeth in upper jaw and 14 below; F, *S.* (*S.*) *stellatus* Forsskål, 14 teeth in both jaws; G, *S.* (*L.*) *vulpinus* (Schlegel and Müller), 12 teeth in upper jaw and 13 below; H, *S.* (*L.*) *uspi* Gawel and Woodland, 14 teeth in both jaws. The basal regions of the teeth are illustrated here as exposed distal to the edges of the sockets in the jaws bones and do not include the more posteriorly expanded anchoring regions at the base of the teeth within the bony sockets. Scale lines are all 0.5 mm. Nomenclature follows that of the systematic revision of *Siganus* by Woodland (1990).

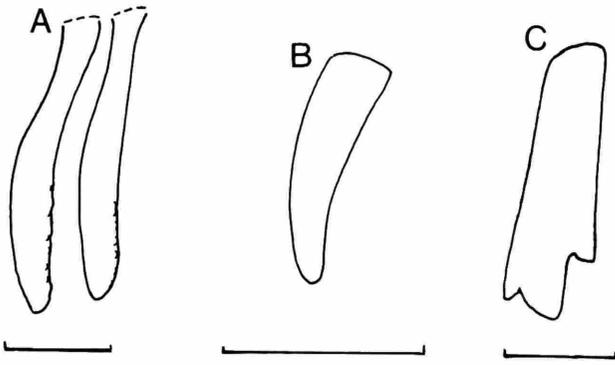


FIGURE 19.—Teeth in the fossil species of Siganidae. Camera lucida drawings of the teeth in the left side of the upper jaw from wherever they are best preserved (usually toward the front); anterior to left; teeth not consistently well-enough preserved in comparable places in both the upper and lower jaws to present drawings of opposing teeth like those given in Figure 18 for Recent species: A, two teeth from *Protosiganus glaronensis* (Wettstein), NMB E177, 113.6 mm SL, holotype, with the possibility that there are slight irregularities or low lobations along the distal half of the posterolateral edge; B, *Eosiganus kumaensis*, new genus and species, PIN 4425-17A-17B, 34.2 mm SL, holotype, simple, conical teeth; C, *Ruffoichthys spinosus* Sorbini, MCSNV T920, 55.1 mm SL, holotype, teeth with notches on anteromedial and posterolateral edges (the teeth are probably less deeply notched in the other species of the genus, *R. bannikovi*). Scale lines are all 0.5 mm. The teeth are unknown in *Siganopygaeus rarus* Danilchenko, representative of the only other fossil siganid genus.

open neural spine of the first vertebra and just in front of the longer neural spine of the second vertebra (with the neural canal effectively roofed over by the connective tissue binding the proximal tip of the pterygiophore to the side walls of the neural arch of the first vertebra). The fifth interneural space is vacant (rarely the sixth as an intraspecific variation).

Pleural ribs are present from the second to ninth abdominal vertebrae, with epineural intermuscular bones present from the first vertebra posteriorly, usually until the first caudal vertebra.

The infraorbital series has a large lachrymal and usually four more-tubular elements with pores or broad openings, with the dermosphenotic firmly attached or fused to the sphenotic. At least in the species of the subgenus *Lo* with especially long snouts, the lachrymal is likewise especially elongate and the second infraorbital element is positioned entirely below the posteroventral edge of the lachrymal, whereas in most species of the subgenus *Siganus* the lachrymal is shorter and the second element has most of its length projecting behind the posterior edge of the lachrymal. In smaller specimens of species of the subgenus *Lo*, the second infraorbital has the same specialized loose attachment to the lachrymal as in most other acanthuroids (Tyler et al., 1989:58), although in larger specimens it is more firmly held to the lachrymal by fibrous tissue, but it is not in direct contact with it. There is no subocular shelf. The posteroventral edge of the preopercle is serrate. There are 1+4=5 branchiostegal rays.

The scales are small and cycloid.

## Analysis of Characters

### ANALYTICAL PROTOCOLS

Highly corroborated hypotheses based on osteological and myological evidence (Tyler et al., 1989; Winterbottom, 1993; Winterbottom and McLennan, 1993; Guiasu and Winterbottom, 1993) indicate that the families of acanthuroid fishes (sensu stricto, as in Tyler et al., 1989) have the phyletic sequencing convention of Siganidae—Luvaridae—Zanclidae—Acanthuridae (Nasinae—Acanthurinae), and that the first and second outgroups are, respectively, the Scatophagidae and Ephippididae (with *Drepane* of uncertain relationship to the ephippidids).

The monophyly of the Siganidae is supported by a total of 18 autapomorphies (references above), but this is based only on the Recent species (i.e., those of *Siganus*). Three of the siganid autapomorphies are myological, and many others are cartilaginous features or those of the pharyngeals or other regions in which characters cannot be determined in the available fossil materials. However, the fossil siganids do have some of these 18 autapomorphies exposed: all four fossil genera have reduced numbers of dorsal- and anal-fin rays relative to all other acanthuroids; all have the first pleural rib attached to the second vertebra (only probably so in *Eosiganus*); the scales are small and cycloid when known (*Ruffoichthys* and *Siganopygaeus*); and the palatine probably is composed of two separate ossifications in the one genus (*Ruffoichthys*) in which at least one specimen has this bone exposed. Three of the fossil genera have an inner pelvic-fin spine, although this is absent in *Ruffoichthys*, and two of them (*Ruffoichthys* and *Protosiganus*) are known to have larger uroneurals than the specialized small size found in the Recent *Siganus*. The exposure of at least several of these siganid autapomorphies in each of the fossil taxa gives assurance that they are siganids.

Winterbottom and McLennan (1993) believe that scatophagids and ephippidids should be included in an expanded Acanthuroidei, but in this paper we follow the more traditional usage of four families of acanthuroids, with scatophagids and ephippidids considered as higher squamipinnes.

In the present analysis, the Luvaridae (and their fossil sister group, the Kushlukiidae), Zanclidae, and Acanthuridae are used as the sequential convention members of the first outgroup (the sister group) of the Siganidae, with the Scatophagidae and Ephippididae as other sequential outgroups, in that order. When appropriate, conditions in *Drepane* and chaetodontoids are mentioned.

Statements about osteological conditions in all of these acanthuroid and higher squamipinne outgroups are based on the cleared and stained specimens listed in Tyler et al. (1989). These statements include the conditions, when known, for at least the more fully preserved and described of the fossil representatives of these groups, all of which are from the Eocene: for the Ephippididae, *Archaehippus asper* (Volta) and *Eoplatax papilio* (Volta); for the Scatophagidae, *Scatopha-*

*gus frontalis* Agassiz (for the three preceding species see Blot, 1969); for the Zanclidae, *Eozanclus brevirostris* (Agassiz) (see Blot and Voruz, 1970, 1974); for the Luvaridae and Kushlukiidae, the several species of the genera *Avitoluvarus*, *Luvarus*, and *Kushlukia* described by Bannikov and Tyler (1995); and for the Acanthuridae, the numerous genera and species of acanthurids described by Blot and Tyler (1991). Also included as appropriate are data on the poorly known acanthurids from the Oligocene and Miocene that one of us (JCT) is in the process of redescribing.

Character polarity is hypothesized using the outgroup comparison method of Maddison et al. (1984). The ancestral states in Table 1 represent those hypothesized at the outgroup node (i.e., the ancestral acanthuroid states) based on conditions in the siganid sister group and outgroups. The matrix for the 12 polarizable osteological features (Table 1) present in both the Recent genus and in at least most of the fossil genera was analyzed using the "Branch and Bound" option of the software package PAUP, an approach that is designed to find all of the most-parsimonious trees.

Characters were optimized using both ACCTRAN (accelerated transformation; favoring reversal over independent acquisition) and DELTRAN (delayed transformation; favoring independent acquisition over reversal). No differences were found in tree structure with these two methods of optimization. In the phylogeny given in Figure 20, we have chosen to show the DELTRAN optimization; other equally parsimonious distributions of states are discussed in the analysis of each character as appropriate.

Four of the characters included in the matrix, namely numbers of dorsal- and anal-fin spines and soft rays, have

multiple states (characters 3, 7, 8, and 9 in the "Analysis of Characters" and in Table 1 and Figure 20). The numbers of dorsal- and anal-fin elements are conservative within siganids, ranging for all taxa from 11–14 dorsal spines, 9–11 dorsal rays, 4–8 anal spines, and 7–10 anal rays, and are relatively invariable within taxa. We presume that our sampling of fossil siganid species is highly incomplete. We also have very few specimens of most of the fossil species, all except *Ruffoichthys spinosus* being known on the basis of only one to three specimens. There is no variation in the dorsal- and anal-fin counts in the 16 specimens of *Ruffoichthys spinosus*, and it differs in fin meristics from the other known species of the genus only by having one fewer dorsal- and anal-fin ray. The 27 species of Recent *Siganus* have a remarkable constancy in the numbers of dorsal- and anal-fin spines and rays, almost invariably D.XIII,10 and A.VII,9.

Relative to the outgroups, the numbers of dorsal- and anal-fin rays in siganids are especially constant (e.g., dorsal rays 20–30 in luvarids+kushlukiids, 20–33 in acanthurids, and 15–53 in ephippidids; anal rays 17–26 in luvarids+kushlukiids, 19–33 in acanthurids, and 14–46 in ephippidids).

The evidence above suggests that the numbers of dorsal- and anal-fin spines and rays evolved conservatively in siganids. Therefore, we believe it justified to treat the four multi-state characters in the analysis as an ordered transformation series. However, because such ordering of data has been criticized (Michevich, 1982), we have analyzed the multi-state characters by treating them as both unordered (Swofford, 1985) and ordered.

TABLE 1.—Numerical character matrix: 0 = primitive; 1 = derived, or 1, 2, 3 progressive degrees of specialization; 9 = either unknown because of incompleteness of fossil material (i.e., teeth and dorsal rays in *Siganopygæus*) or character undeterminable (i.e., length of absent first supernumerary dorsal spine in *Eosiganus*, and lack of procumbent pterygial spine and, therefore, of a possible barb in *Ruffoichthys*). Ancestral states represent those hypothesized at the outgroup node (i.e., the ancestral acanthuroid states) based on conditions in the siganid sister group and outgroups.

Genera	1. Pelvic spines	2. Procumbent pterygial spine	3. Anal spines	4. Supernumerary dorsal spines	5. Length of first supernumerary	6. Postcleithrum—basal pterygiophore contact	7. Dorsal spines	8. Dorsal rays	9. Anal rays	10. Supraneural	11. Teeth	12. Barb on procumbent pterygial spine
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ruffoichthys</i>	0	0	0	0	1	0	0	2	1	1	1	9
<i>Eosiganus</i>	1	1	2	1	9	0	0	1	2	1	0	0
<i>Siganopygæus</i>	1	1	3	0	0	0	2	9	1	0	9	0
<i>Protosiganus</i>	1	1	1	0	1	1	1	2	1	1	0	0
<i>Siganus</i>	1	1	2	0	1	1	1	2	1	1	1	1

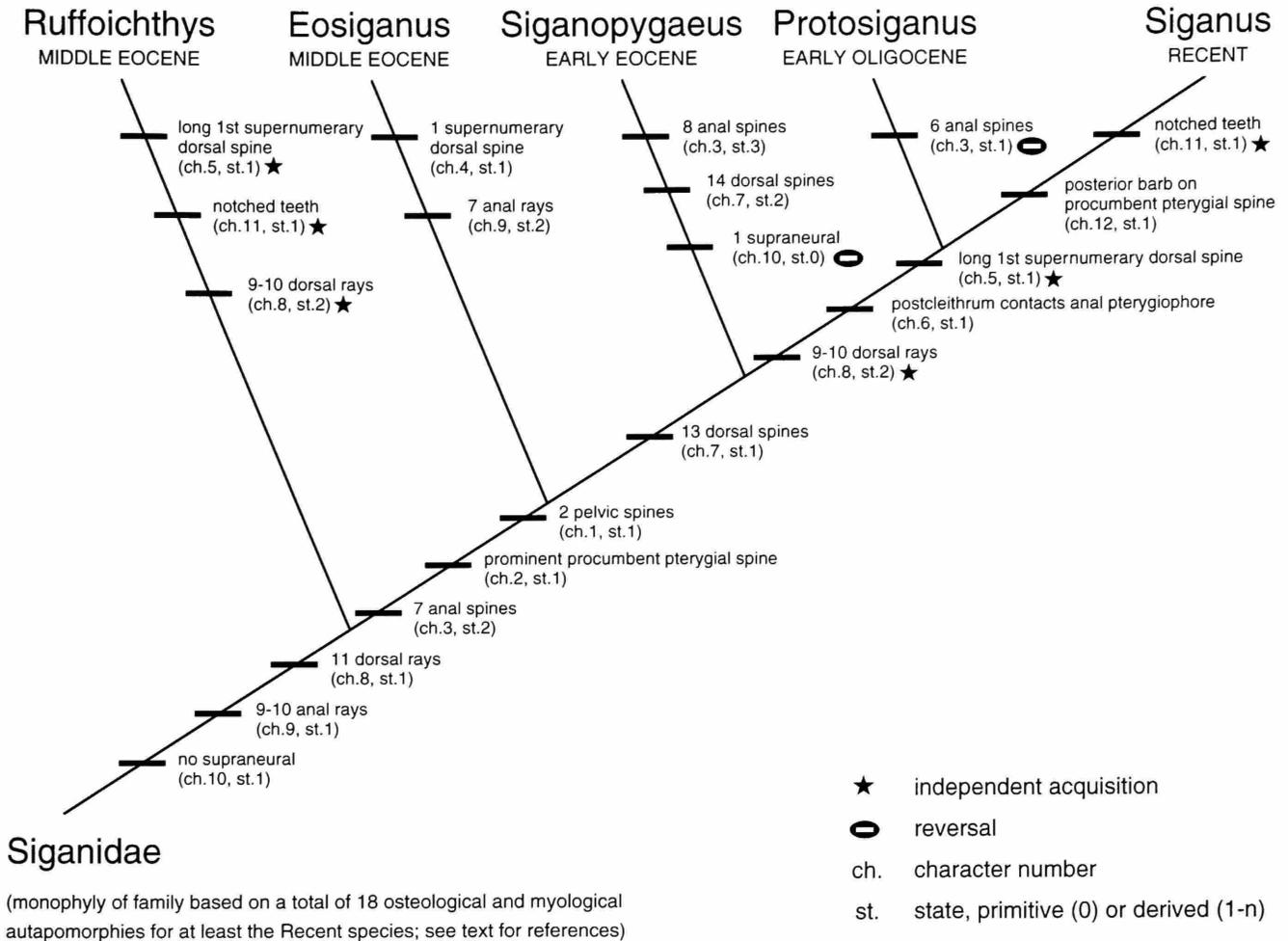


FIGURE 20.—Cladogram of the relationships of the five genera of the family Siganidae; character and state numbers correspond to those in the "Analysis of Characters"; four multi-state characters are ordered.

Treating all four multi-state characters as ordered yields a single most-parsimonious tree (Figure 20), with a length of 22 steps and a consistency index of 0.773. It has two reversals (from zero to one supraneural in *Siganopygaeus* and from seven to six anal-fin spines in *Protosiganus*) and three independent acquisitions (of notched teeth in *Ruffoichthys* and *Siganus*, and of 9–10 dorsal-fin rays and long first supernumerary dorsal spines in *Ruffoichthys* and in the ancestor of *Protosiganus*+*Siganus*).

Treating all four multi-state characters as unordered yields four equally parsimonious trees (Figure 21), each with a length of 20 steps and consistency index of 0.85. One of these (Figure 21A) indicates the same phyletic relationships as the single most-parsimonious tree resulting from the ordered data analysis. In all of these trees, *Protosiganus* and *Siganus* are sister taxa, always linked by at least the derived condition of the postcleithrum contacting the first anal-fin pterygiophore. In

two (Figure 21B,C) of the three trees based on unordered data, *Ruffoichthys* is the sister group of the other four genera, based on the latter clade having at least the derived conditions of two pelvic spines and a procumbent spine on the first dorsal-fin pterygiophore. These unordered trees differ from the ordered trees in that *Eosiganus* is either the sister group of *Protosiganus*+*Siganus* or *Eosiganus*+*Siganopygaeus* are together the sister group of *Protosiganus*+*Siganus*. The different interpretations of relationships within this clade of four genera revolve in the unordered data analysis around whether seven or eight anal-fin spines are ancestral for them and in the details of the increase in numbers of dorsal-fin spines. Both hypotheses require some liberal changes in numbers of fin-ray elements; e.g., dorsal spines increase from 11 to 13 in *Protosiganus*+*Siganus* and from 11 to 14 in *Siganopygaeus*.

In the one tree (Figure 21D) that does not have *Ruffoichthys* as the sister group of the other four genera, *Siganopygaeus* is

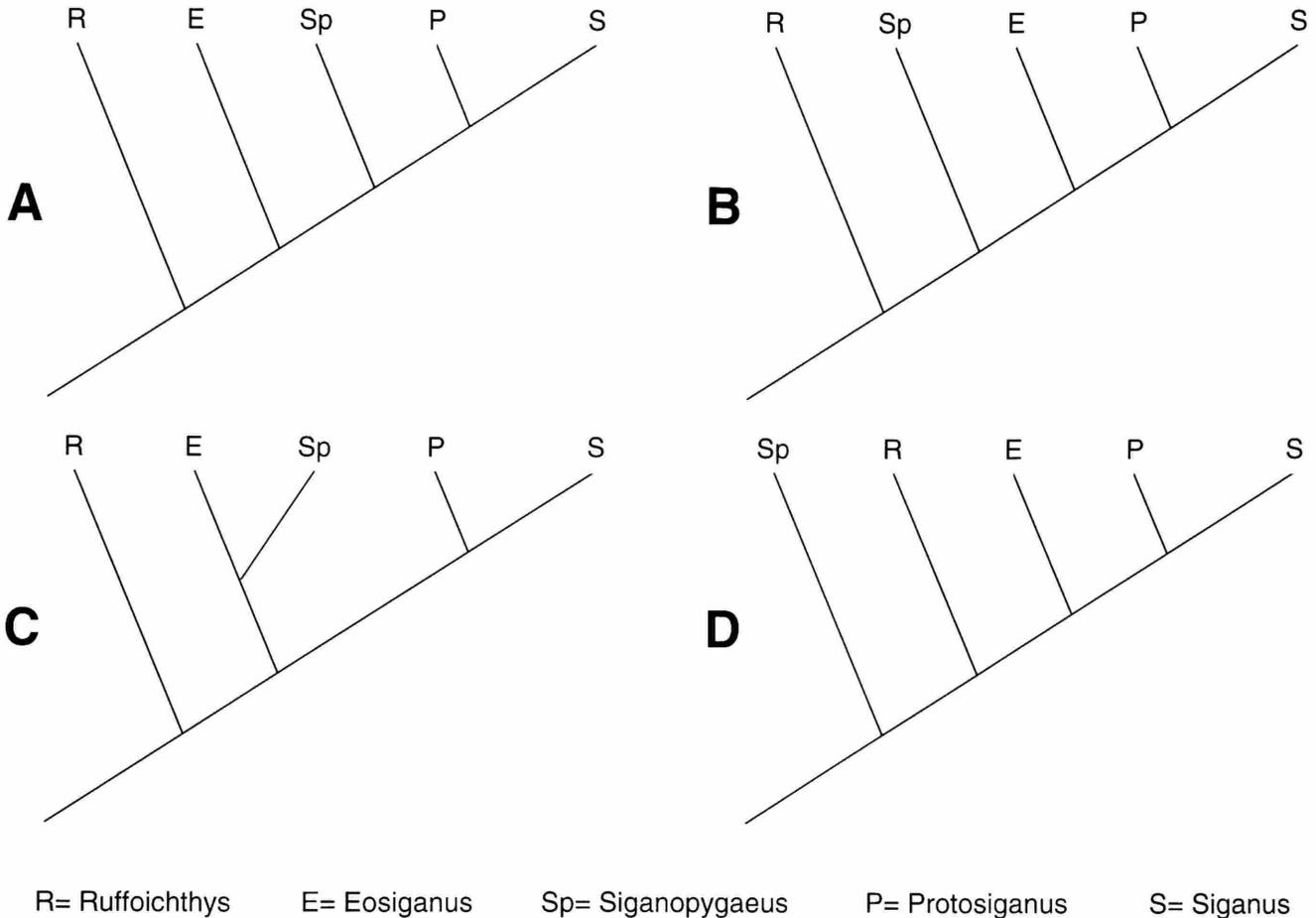


FIGURE 21.—Four equally parsimonious cladograms when four multi-state characters are unordered, each with a consistency index of 0.85 and length of 20 steps.

the sister group of the other four genera, differing from the other interpretations in having the independent acquisition of two pelvic spines and a procumbent spine by *Siganopygaeus* and the clade composed of *Eosiganus*+*Protosiganus*+*Siganus*. This hypothesis also requires that the number of dorsal- and anal-fin elements changes liberally; e.g., anal spines increase from four or fewer to seven in the ancestor of *Eosiganus*+*Protosiganus*+*Siganus* and again from four or fewer to eight in *Siganopygaeus*.

We believe that, because of the especially conservative nature of the numbers of dorsal- and anal-fin spines and rays in siganid fishes, especially as exemplified in the Recent species, ordering the four multi-state characters so that the numbers of dorsal- and anal-fin elements change incrementally is justified. It is reassuring that one most-parsimonious tree resulting from the unordered data analysis gives the same relationships as the single most-parsimonious tree from the ordered data analysis, and that many other features are comparable among the trees resulting from both analyses, such as the sister-group relation-

ship between *Protosiganus* and *Siganus*, and that between *Ruffoichthys* and the other four genera. We acknowledge that additional characters are needed to corroborate the phylogeny depicted in Figure 20, which is based on only 12 characters, especially the relationships among *Eosiganus*, *Siganopygaeus*, and the *Protosiganus*+*Siganus* clade.

#### CHARACTERS USED IN PHYLOGENETIC ANALYSIS

The following 12 characters are polarized and are used in the PAUP analysis. The numbers of the characters correspond to those in the cladogram. Character states are designated primitive (0) or derived (1–n).

1. *Number of Pelvic-Fin Spines*: Among siganids, only *Ruffoichthys* has a single spine (outer) in each pelvic fin. The other four genera (*Eosiganus*, *Siganopygaeus*, *Protosiganus*, *Siganus*) have two spines (outer and inner) in each fin, a unique condition among teleosts. In the acanthuroid sister groups (*Luvaridae*+*Kushlukidae*, *Zanclidae*, *Acanthuridae*) and in the

higher squamipinne outgroups (Scatophagidae, Ehippididae, *Drepane*), there is a single pelvic-fin spine (outer).

The single pelvic spine in *Ruffoichthys* is considered primitive (0), with the presence of two spines derived (1) for the other four genera.

2. *Procumbent Spine on First Pterygiophore of Spiny Dorsal Fin*: Among siganids, only *Ruffoichthys* has essentially no anterior extension of the distal end of the first pterygiophore of the spiny dorsal fin. The other four genera have this region prolonged into a prominent sharp process that protrudes through the skin of the nape as a procumbent spine. In luvareids+kushlukiids and zanclids the anterodorsal region of this pterygiophore is a prong of moderate length but it never forms a sharp procumbent spine that protrudes through the surface; it is also prong-like in most acanthurids, except in genera like *Naso* in which this pterygiophore is laterally expanded as a housing around the specialized short first dorsal-fin spine.

In scatophagids the anterodorsal end of the first pterygiophore of the spiny dorsal fin has a moderately to well-developed sharp-pointed prong with a point that sometimes protrudes through the skin as a small procumbent spine in juveniles or small specimens, but never as prominently as in siganids. This small, juvenile procumbent spine is reduced and often absent in adults. In ehippidids there is a short to moderate prong but no procumbent spine at any specimen size in most species, but a small procumbent spine is present in juveniles of *Ehippus* and *Proteracanthus* and, sometimes, in *Drepane*.

Although a small juvenile procumbent spine could be primitive for higher squamipinnes and siganids rather than independently acquired among some ehippidids and scatophagids, and lost by all acanthuroids except some siganids, it is clear that the presence of a larger and more prominently protruding procumbent spine at all sizes is a derived feature (1) of *Eosiganus*, *Siganopygaeus*, *Protosiganus*, and *Siganus*.

The lack of any kind of anterior prong on this pterygiophore in *Ruffoichthys* is probably an autapomorphic reduction from the primitive condition in other acanthuroids and higher squamipinnes of having at least a moderate prong in this region (0).

3. *Number of Anal-Fin Spines*: *Ruffoichthys* has four anal-fin spines, *Protosiganus* has six, *Eosiganus* and *Siganus* have seven, and *Siganopygaeus* has eight. Zanclids and acanthuroids have three anal-fin spines, whereas a specialization of luvareids+kushlukiids is the absence of anal spines (Tyler et al., 1989; Bannikov and Tyler, 1995). Scatophagids have four anal-fin spines and ehippidids have three (as does *Drepane*).

We consider three or four anal-fin spines as primitive for acanthuroids, with the four spines in *Ruffoichthys* being primitive for siganids (0) and the six (1), seven (2), or eight (3) anal spines of the other siganid genera derived. The most-parsimonious hypothesis (Figure 20) is that the ancestor of the clade composed of all siganid genera except *Ruffoichthys* had

seven anal-fin spines, as retained by *Eosiganus* and *Siganus*, with *Protosiganus* reducing the number to six and *Siganopygaeus* increasing the number to eight.

In one of the trees resulting from analysis of unordered multi-state characters, the eight anal-fin spines in *Siganopygaeus* evolved independently of the six and seven anal-fin spines in *Eosiganus*, *Protosiganus*, and *Siganus*. We consider this an unlikely scenario because of the apparent conservatism in numbers of dorsal- and anal-fin elements in siganids.

4. *Number of Supernumerary Dorsal-Fin Spines*: Among siganids, only *Eosiganus* has a single supernumerary dorsal-fin spine borne on the first pterygiophore, the other four genera have two supernumerary spines on this pterygiophore. There are two supernumeraries in all acanthuroids (the first spine short to moderate in length) and in luvareids (the first spine short and becoming reduced in size and lost at large sizes, at least in the Recent species; the presence and potential loss of the first spine is unclear in the fossil taxa of luvareids and is unknown in kushlukiids because of preservation problems and the lack of adequate size series, but the spine perhaps is lost at smaller specimen sizes than in the Recent species). In zanclids there are two supernumeraries in the Eocene *Eozanclus* but only one in the Recent *Zanclus*.

Scatophagids and ehippidids have two supernumerary spines (including all of the species of *Platax*, although in a small minority of specimens of *P. pinnatus* there is a single spine; on the basis of the position of the remaining spine, it appears to be the first spine that is lost).

It is most parsimonious to consider two supernumerary dorsal-fin spines as primitive (0) for acanthuroids, with the specialized loss of one of the spines (1) occurring independently in *Eosiganus* and *Zanclus* (and as a rare variant in one species of *Platax* among ehippidids).

Independent loss of one of the supernumerary spines (presumably the first based on the position of the remaining spine) also occurs in one of the several species of *Drepane* (two supernumeraries in *D. africana* and *D. punctata*; one in *D. longimana*) and in chaetodontoids (nearly all species with two, including several species of *Holacanthus*, but with *H. bermudensis* having a minority of specimens with only one). An opposite variability is present in *Monodactylus*, with *M. falciformis* and *M. argenteus* usually having only one supernumerary but the latter species sometimes having two (the Eocene *Psettopsis subarcuatus* has two).

5. *Length of First Supernumerary Dorsal-Fin Spine*: Among siganids with two supernumerary dorsal-fin spines, *Siganopygaeus* is unique in having the first of these spines short (far less than one-half the length of the second spine). The first supernumerary is long (two-thirds to three-fourths the length of the second spine) in *Ruffoichthys*, *Protosiganus*, and *Siganus*. There is only one supernumerary spine in *Eosiganus*, and this is presumably the second based on its position. The first supernumerary spine is very short in luvareids and is lost with increasing specimen size (this

condition is unclear or unknown in fossil luvarids and kushlukiids), whereas in acanthurids the first supernumerary is of short to moderate (less than one-half the length of the second spine) length. In those zancids with two supernumerary spines (*Eozanclus*), the first is short, and, when only one is present (*Zanclus*), it is likewise short. Although the serial homology of this single supernumerary spine in Recent zancids is difficult to establish (Johnson and Washington, 1987), based on the position of the remaining spine, we believe it is the first that is lost.

The first of the two supernumerary spines is of short to moderate length (always less than one-half the length of the second spine) in both ehippidids and scatophagids, as it is in the single species of ehippidid with a single supernumerary spine. In *Drepane*, there are either one or two supernumerary spines, and these are short.

Therefore, we consider a short to moderate length for the first supernumerary spine as primitive (0) for acanthuroids, with the very short first spine of *Siganopygaeus* primitive and the long first spine in *Ruffoichthys*, *Protosiganus*, and *Siganus* derived (1). As shown in Figure 20, the long first spine of *Ruffoichthys* may have been gained independently from that in the ancestor of *Protosiganus*+*Siganus* (DELTRAN optimization); alternatively, the long first spine may be a synapomorphy of siganids, with a reduction of spine length in *Siganopygaeus*.

For purposes of the numerical matrix of characters in the computer analysis, the single supernumerary spine of *Eosiganus* is presumed to correspond to the second supernumerary of the other genera; therefore, it is the first spine that is considered to be absent and its condition of length is coded as missing in Table 1.

**6. Association of Postcleithrum with First Anal-Fin Pterygiophore:** In *Protosiganus* and *Siganus* the ventral end of the ventral postcleithrum closely approaches or is in contact with the anterior end of the anteroventral process of the first anal-fin pterygiophore, whereas in the other three genera of siganids the postcleithrum does not closely approach this pterygiophore. The postcleithrum is far removed from the first anal-fin pterygiophore in all luvarids+kushlukiids and zancids. They are also far removed from one another in all acanthurids, with two exceptions. In *Zebbrasoma* the postcleithrum is only moderately removed from the pterygiophore. In those species of *Naso* in which the first anal-fin pterygiophore is swung far forward, the postcleithrum is only moderately removed from the pterygiophore. However, in neither *Zebbrasoma* nor *Naso* is there as close an association of the postcleithrum with the pterygiophore as in *Protosiganus* and *Siganus*.

The postcleithrum is moderately removed from the first anal-fin pterygiophore in scatophagids and far removed from it in ehippidids (and *Drepane*).

Therefore, we consider the distinct separation of the postcleithrum and first anal-fin pterygiophore as primitive (0) for siganids and the close association or contact between these two bones as a derived feature (1) of *Protosiganus* and *Siganus*.

**7. Number of Dorsal-Fin Spines:** There are 11 dorsal-fin spines in *Ruffoichthys* and *Eosiganus*, 13 in *Protosiganus* and *Siganus*, and 14 in *Siganopygaeus*. There are no more than three dorsal-fin spines in luvarids (the first very short and at least sometimes lost with increasing size; conditions unclear or unknown in fossil luvarids and kushlukiids), seven in zancids, and five to nine in acanthurids (including the very short first spine in *Naso*).

There are 11 or 12 dorsal-fin spines in scatophagids and 5 to 9 in all ehippidids except *Proteracanthus*, which has 10 or 11, whereas *Drepane* has 8 or 9.

Therefore, we consider 12 or fewer dorsal-fin spines as primitive for acanthuroids (0), with, among siganids, the 11 of *Ruffoichthys* and *Eosiganus* being primitive and the 13 (1) to 14 (2) of the other three genera being derived. In our phylogeny (Figure 20), the ancestor of the clade composed of *Siganopygaeus*+*Protosiganus*+*Siganus* has 13 dorsal-fin spines, with *Siganopygaeus* alone further increasing the number to 14.

As noted above in the "Analytical Protocols," two trees resulting from the analysis of multi-state characters as unordered require that the primitive siganid condition of 11 dorsal spines gave rise to the 13 and 14 dorsal spines of other siganids independently, which seems unlikely given the conservative nature of the fin-ray elements in siganids.

**8. Number of Dorsal-Fin Rays:** There are 9 or 10 dorsal-fin rays in the two species of *Ruffoichthys*, 10 rays in *Protosiganus* and *Siganus*, and 11 rays in *Eosiganus*; the number of dorsal-fin rays is unknown in *Siganopygaeus* (and coded as missing in the numerical character matrix, Table 1). There are 20 to about 30 dorsal-fin rays in luvarids+kushlukiids (reduced in number from anteriorly in the series with increasing specimen size in *Luvarus*), 38–42 in zancids, and 20–33 in acanthurids.

There are 13–18 dorsal-fin rays in scatophagids, 15–53 in ehippidids (the high of 53 being in the Eocene species of *Eoplatax*), and 19–22 in *Drepane* (chaetodontoids have about 15–30).

Therefore, we consider 13 or more dorsal-fin rays as ancestral for acanthuroids (0), and, among siganids, the highest number of 11, as found in *Eosiganus*, as less derived (1) than the more specialized lower number of 9 or 10 (2) as found in the other four genera. The most-parsimonious hypothesis (Figure 20) is that the ancestor of all siganids had 11 dorsal-fin rays and that the reduced number of 9 or 10 rays was obtained independently by *Ruffoichthys* and the clade composed of at least *Protosiganus*+*Siganus* (and potentially *Siganopygaeus* if its number of dorsal-fin rays is 9 or 10).

**9. Number of Anal-Fin Rays:** Among siganids, there are about seven anal-fin rays in *Eosiganus* (based on the number of pterygiophores) and 9 to 10 in the other four genera. There are 17–26 anal-fin rays in luvarids+kushlukiids (reduced in number from anteriorly in the series in *Luvarus*), 31–35 in zancids, and 19–33 in acanthurids.

There are usually 14–16 anal-fin rays in Recent scatophagids but 11 in the Eocene species of *Scatophagus*, 14–46 in ehippidids (the high of 46 being in the Eocene species of *Eoplatax*), and 16–19 in *Drepane* (chaetodontoids have about 14–23).

Therefore, we consider 11 or more anal-fin rays as ancestral for acanthuroids (0), and, among siganids, the higher numbers of 9–10 as less derived (1) than the more specialized reduction to about seven (2) in *Eosiganus*.

10. *Number of Supraneurals*: Among siganids, there is a single supraneural in *Siganopygaeus* but none in the other four genera. There is no supraneural in luvarids+kushlukiids, one in zancids, and either one or none among acanthurids (one in all of the Eocene genera and in the Recent genus *Prionurus*, but none in the other five Recent genera and in the Oligocene and Miocene genera).

There are usually two supraneurals in scatophagids (rarely only one as an intraspecific variant) and three in ehippidids and *Drepane* (chaetodontoids have one or two).

Winterbottom and McLennan (1993) have discussed extensively the various interpretations of the presence or absence of the supraneural in fossil and Recent acanthuroids (especially on the basis of the generic phylogeny within acanthurids documented by Winterbottom, 1993, and Guisau and Winterbottom, 1993, and on what we agree is the reasonableness of the limited data supporting their hypothesis that *Prionurus* is more closely related to the other Recent acanthurin genera than to those of the Eocene, as well as the assumption that the Eocene genera of acanthurids are more closely related to *Naso* than to the other Recent genera; the relationships of the Oligocene and Miocene genera of acanthurids are unstudied, but they seem to be more similar morphologically to the Recent *Naso* than to the Eocene *Naso*-like genera, although they have many distinctive apomorphies).

On the basis of the Recent and better known fossil taxa (i.e., the Eocene siganids *Ruffoichthys* and *Siganopygaeus* and the Eocene acanthurids), Winterbottom and McLennan (1993) concluded that interpretations based on both accelerated transformation and delayed transformation led to three equally parsimonious five-step hypotheses of the evolution of acanthuroid supraneurals. One is that the supraneural was retained by the acanthurid ancestor from its higher squamipinne ancestry and was lost independently by *Ruffoichthys* and by Recent siganids (and by *Protosiganus*, the then poorly-known sister group of *Siganus* not included by Winterbottom and McLennan), was lost by luvarids+kushlukiids, and was lost by *Naso* independently of the loss in other Recent genera except *Prionurus* (and by the Oligocene and Miocene genera); this DELTRAN-based hypothesis is shown in Winterbottom and McLennan (1993:1567, fig. 5b). The second is that the supraneural was lost by the acanthuroid ancestor and regained independently by the siganid *Siganopygaeus*, by zancids, by Eocene acanthuroids, and by *Prionurus*; this ACCTAN hypothesis only with reversals is shown in Winterbottom and

McLennan (1993, fig. 5d). The third is that the supraneural was lost by the acanthuroid ancestor and regained by the ancestor of the zancid+acanthurid clade and lost therein by *Naso* independently of the loss in the other Recent genera except *Prionurus*; this ACCTAN based hypothesis is shown in Winterbottom and McLennan (1993, fig. 5b).

However, when the analysis includes the additional taxa of fossil siganids described or redescribed herein and their newly hypothesized relationships, the ambiguity for the interpretation within the siganid clade is fully resolved. The most-parsimonious hypothesis (Figure 20) for the distribution of the supraneural is that the absence of the supraneural is a synapomorphy of the siganid clade (1) and that the supraneural reappeared (0) in *Siganopygaeus* alone (two steps), rather than the retention of the supraneural in siganids primitively, with independent losses in *Ruffoichthys*, *Eosiganus*, and the clade composed of *Protosiganus*+*Siganus* (three steps).

Moreover, the placement of the new siganid taxon, *Eosiganus*, in the sequence partially clarifies the evolution of supraneurals among all acanthuroids. When *Eosiganus* is added to the cladograms of Winterbottom and McLennan (1993:1567) between *Ruffoichthys* and *Siganopygaeus*, their optimization of the character in their cladograms B and D becomes the most parsimonious, to the exclusion of that in their cladogram C, with the ancestor of all acanthuroids as well as that of siganids lacking the supraneural (adding *Protosiganus* next to *Siganus* in this case is uninformative because both lack the supraneural). This clarification based on the conditions in *Eosiganus* and the other taxa examined herein reinforces Winterbottom and McLennan's (1993) statement about the importance of fossils in understanding the presence versus absence of the supraneural in acanthuroids.

It remains, however, equally parsimonious that the ancestor of the zancid+acanthurid clade regained the supraneural and it was lost independently by *Naso* and by the four other Recent genera except *Prionurus*, or that this ancestor lacked the supraneural and it was regained independently by zancids, Eocene fossil acanthurids, and *Prionurus*.

11. *Shape of Teeth*: The teeth are deeply and asymmetrically notched in *Ruffoichthys* and *Siganus* but are conical in *Eosiganus* and *Protosiganus* (although *Protosiganus* may have low lobations along part of the rear edge of the otherwise long conical teeth); the teeth are unknown in *Siganopygaeus* (and coded as missing in the numerical character matrix, Table 1).

Luvarids+kushlukiids have smoothly conical teeth, when teeth are present (some taxa lose all of the teeth with increasing specimen size, and some are edentulous even at small size). Zancids have long, moveable, conically setiform teeth with smooth edges. Acanthurids have teeth that range from simple, short, conical, with smooth edges or with low lobations in *Naso*, to deeply lobate along both edges in most genera, but with long, moveable, setiform teeth with small to moderate lobes along the posterior edge of an expanded distal region in

*Ctenochaetus* (see Tyler, 1970; Guiasu and Winterbottom, 1993; and Purcell and Bellwood, 1993, for illustrations of the teeth and jaws in acanthurids).

Higher squamipinnes have a wide variety of dentition, from short to long conical, smooth-edged to distally notched, and fixed to moveable. Among scatophagids, the Eocene *Scatophagus frontalis* has long, smoothly conical teeth that presumably are moveable (setiform), but in the Recent species of *Scatophagus* and in the Recent *Selenotoca* the teeth are likewise long and conical but are symmetrically double-notched at the extreme distal end (trident). Among Eocene ehippidids, *Eoplatax papilio* has short, smoothly conical, fixed teeth, whereas *Archaehippus asper* has similarly short, smoothly conical teeth but these were perhaps moveable because they apparently were not implanted in sockets (Blot, 1969:353, 378). Among Recent ehippidids, the species of *Ehippus*, *Chaetodipterus*, and *Psettus* (including *Parapsettus*) have long and smoothly conical setiform teeth in multiple rows, but the species of *Platax*, *Tripteron*, *Proteracanthus*, and *Zabidius* have the more external multiple rows similar to those of *Chaetodipterus* except the teeth are trident distally (in *Rhinoprenes* only the outer teeth in the lower jaw are trident), whereas the more internal rows are simply long, conical, and setiform without distal notching (including at the extreme posterolateral edge of the series where the otherwise inner series teeth are exposed). *Drepane* has long, smoothly conical setiform teeth, as do most chaetodontoids (except usually trident distally in pomacanthids).

Outgroup comparison indicates that short, conical teeth with smooth edges are primitive (0) for siganids, with the deeply notched teeth of *Ruffoichthys* and *Siganus* derived (1). We presume that the longer and perhaps movable and slightly lobed teeth of *Protosiganus* represent another specialization, but because we are not sure of the anatomy of the teeth we do not utilize it as an autapomorphy. The most-parsimonious hypothesis (Figure 20) is that the notched teeth of *Ruffoichthys* were gained independently of those in *Siganus*.

12. *Ornamentation of Procumbent Spine:* Among the four genera of siganids with procumbent spines on the first pterygiophore of the spiny dorsal fin, *Eosiganus*, *Siganopygæus*, and *Protosiganus* have no large processes associated with it, although there may be shallow longitudinal grooves (*Eosiganus*, *Protosiganus*) along the surface. All species of *Siganus* have a prominent posteriorly directed barb along the middle of the lateral surface of the first dorsal pterygiophore. The procumbent spine is absent in *Ruffoichthys* (and thus coded as missing in the numerical character matrix, Table 1).

There is no barb on the anterodorsal process of the first dorsal pterygiophore in any of the siganid outgroups and none on the smaller procumbent spine that occurs in some scatophagids and ehippidids (0).

Therefore, the barb on the procumbent spine of all Recent species of siganids is considered derived (1).

## OTHER CHARACTERS

The following characters are phylogenetically problematic and were not used in the analysis but are useful in distinguishing between siganid genera.

*Vacant Interneural Space:* In *Ruffoichthys* the sixth interneural space is vacant, whereas in the other four genera it is the fifth space that is vacant. In luvarids there is no vacant interneural space in the two species of Eocene *Avitoluvarus* and in the Recent *Luvarus imperialis*, but the Eocene *L. necopinatus* has a vacant interneural space that varies from the third, fourth, or fifth; the Eocene *Kushlukia permira* has the first and second interneural spaces vacant but none vacant posterior to the origin of the dorsal fin, with the short first pterygiophore associated with the third or fourth space. In zancids and acanthurids the third space is vacant.

In scatophagids the vacant space is usually either the sixth or seventh (rarely the fifth or eighth; the sixth space is vacant in the Eocene *Scatophagus frontalis*, but this is not correctly shown in Blot, 1969, pl. N). In ehippidids the vacant space is usually the sixth, except that none is vacant in the Eocene *Eoplatax papilio* and *Archaehippus asper*, and none in *Platax* posterior to the origin of the dorsal fin, with the first pterygiophore in the second space and only supraneurals above the first space. In *Drepane* the fifth space is vacant.

In luvarids+kushlukiids, the cladistically primitive sister group to siganids, the most-parsimonious interpretation is that the ancestor had no vacant interneural space posterior to the origin of the dorsal fin and that the presence of vacant spaces in the Eocene *Luvarus necopinatus* is a reversal (Bannikov and Tyler, 1995). Given this, as well as the great variation in position of the vacant interneural space in the squamipinne outgroups, and that the space that is vacant in zancids and acanthurids is different than either of the ones in siganids, we cannot polarize neural space vacancy for the Siganidae.

*Size of Uroneural:* In *Ruffoichthys* and *Protosiganus* the uroneural is relatively large, whereas it is especially small in *Siganus*; the size of the uroneural is unknown in *Eosiganus* and *Siganopygæus*. In all of the outgroups the uroneural is relatively large. The small size of the uroneural in *Siganus* is considered derived (Tyler et al., 1989), but because we do not know the condition in two of the other genera of siganids we do not use this as an autapomorphy.

*Subocular Shelf:* A well-developed subocular shelf is present in *Ruffoichthys*, probably formed mostly from the third infraorbital, but there is no subocular shelf in *Siganus*; the infraorbitals are not well-enough preserved in the other three genera of siganids to determine if a subocular shelf was present. In luvarids there is a large lachrymal but the rest of the infraorbital series is reduced or absent (and essentially unknown for the fossil species of luvarids and kushlukiids, except for the lachrymal in a few species), and there is no subocular shelf. A well-developed shelf is present on the third

infraorbital in zancids and in three of the six genera of acanthurids, with the analysis by Guíasu and Winterbottom (1993) indicating that the shelf was present in the ancestor of the zancid+acanthurid clade and lost by some acanthurids. Because a large shelf is present on the third infraorbital of scatophagids (although a shelf is absent in some ehippidids and in *Drepane*), we consider the presence of a shelf as primitive for acanthuroids and for *Ruffoichthys* among siganids, with the loss of a shelf derived in *Siganus*. However, because we do not know the condition of the shelf in the other three genera of siganids, we cannot hypothesize the universality of the character and do not use it as an autapomorphy.

*Longest Dorsal-Fin Spine:* *Siganopygæus* is unique among siganids in having the third dorsal-fin spine far longer than the others, and *Eosiganus* is unique in having the first spine slightly or distinctly (in the two smallest specimens) longer than the others. In *Protosiganus* the third dorsal spine is slightly longer than the others, and in *Ruffoichthys* the second to about the fourth or fifth are the longest and the first is much shorter. In *Siganus* the third or fourth to the seventh or eighth dorsal spines are usually the longest, although sometimes the last is longest (see Woodland, 1990, for spine lengths in all Recent species). There is so much variation in which dorsal-fin spine is the longest among the outgroups that this character

cannot be polarized in siganids, and we simply call attention to the unique features of dorsal-spine length in *Siganopygæus* and *Eosiganus*.

### Conclusion

Analysis of the 12 characters that can be determined in at least most of the taxa of siganids supports the hypothesis that the five genera have the following phyletic sequencing convention: *Ruffoichthys* (middle Eocene)—*Eosiganus* (middle Eocene)—*Siganopygæus* (early Eocene)—*Protosiganus* (early Oligocene)—*Siganus* (Recent). Siganids were more anatomically diverse at the generic level in the Eocene than at present, but we have no idea whether any of them were as speciose as the single Recent genus (*Siganus*, with 27 species). Although the Recent *Siganus* can be defined readily by a combination of characters, it has only one derived feature (barb on procumbent spine) unique to it among siganids, and the fossil genera are not remarkably distinctive in most of their osteological features from the Recent genus. With several fossil siganids of relatively modern appearance known from as early as the Eocene (including the early Eocene), one suspects that the Paleocene or Upper Cretaceous eventually will yield an earlier and overall more-primitive taxon of the family.

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