Zeitschrift: Eclogae Geologicae Helvetiae

Herausgeber: Schweizerische Geologische Gesellschaft

Band: 91 (1998)

Heft: 3

Artikel: A new family for a long known but undescribed acanthopterygian fish from teh Eocene of Monte Bolca, Italy : Sorbiniperca scheuchzeri gen. & sp. nov.

Autor: Tyler, James C.

DOI: https://doi.org/10.5169/seals-168441

0012-9402/98/030521-20 $1.50 + 0.20/0
Birkhäuser Verlag, Basel, 1998

A new family for a long known but undescribed acanthopterygian fish from the Eocene of Monte Bolca, Italy: *Sorbiniperca scheuchzeri* gen. & sp. nov.

JAMES C. TYLER[1]

Key words: fish, fossil, Eocene, Monte Bolca, Italy, acanthopterygian

ABSTRACT

Sorbiniperca scheuchzeri, new species, new genus, new family (Sorbinipercidae), is described on the basis of three specimens from the Middle Eocene of Monte Bolca, Italy. One of these specimens was illustrated by Johann Jakob Scheuchzer as early as 1709 but was not described. The new taxon has a unique combination of derived characteristics that relate it to the zeiform + tetraodontiform and, perhaps, caproid clades of acanthopterygians, probably near to one of the branchings of the zeiform + tetraodontiform, beryciform, and lower percomorph clades from one another.

ZUSAMMENFASSUNG

Sorbiniperca scheuchzeri, nov. sp., nov. gen., nov. fam. (Sorbinipercidae), aus dem mittleren Eozän des Monte Bolca (Italien) wird anhand dreier Exemplare beschrieben. Eines dieser Exemplare wurde von Johann Jakob Scheuchzer bereits im Jahre 1709 abgebildet, aber nicht beschrieben. Das neue Taxon beruht auf einer einzigartigen Kombination abgeleiteter Merkmale, die in Beziehung zu den zeiformen + tetraodontiformen und vielleicht caproiden Ästen des Acanthopterygier-Kladogramms stehen, vermutlich nahe an einer der Zweigstellen zwischen den zeiformen + tetraodontiformen, beryciformen und percomorphen Gruppen.

RIASSUNTO

Sorbiniperca scheuchzeri, nuova specie, nuovo genere, nuova famiglia (Sorbinipercidae), viene descritto sulla base di tre esemplari dell'Eocene Medio di Monte Bolca, Italia. Uno di questi esemplari venne figurato per la prima volta da Johann Jakob Scheuchzer nel 1709 ma non descritto. Il nuovo taxon presenta una combinazione di caratteri derivati unica ed imparentato con i cladi zeiforme + tetraodontiforme e, forse, caproide del gruppo degli Acanthopterygii; va, probabilmente, situato vicino ad una delle diramazioni reciproche fra i cladi di Zeiformes + Tetraodontiformes, Beryciformes e Percomorpha inferiori.

Introduction

In both his great Herbarium Diluvianum (1709, 1723) and Kupfer-Bibel or Physica Sacra (1731a, 1731b) on the fossils resulting from the Great Deluge, the pioneering Swiss paleontologist Johann Jakob Scheuchzer (1672–1733; see Hünermann & Rieber 1988 and Gaudant & Bouillet 1997 for the life and publications of Scheuchzer) illustrated a deep-bodied little fish with elongate dorsal- and anal-fin spines from the Eocene of Monte Bolca, Italy.

In the Herbarium Diluvianum the Latin legend (first edition, 1709, p. 17; second edition, 1723, p. 22) for the illustration (Fig. 7 of Tab. V in both editions) comments on the elongate fins of the species and compares it to some American extant species (like the "toad fish") described in the 17th century by Marcgrave and Willughby, but states that no explanation is yet possible about how such a species has come to be found as a fossil in Italy.

In the Kupfer-Bibel the legend (1731a, p. 68) for the illustration (Fig. 34 of Tab. LIII) states: "Eine gantz fremde Art von Platteisz aus dem Veronesischen." Platteisz or platteisse in old German is a general term for a heterosomate plaice-like flatfish (e.g., see Grimm & Grimm 1889, p. 1909), and the quoted line can be translated as follows: "A completely strange species of flatfish from Verona" (personal communication, Dr. Heinz Balmer, July 1992). In the Physica Sacra the Latin legend (1731b, p. 51) for the illustration (Fig. 34 of Tab. LIII) is very brief but mentions the similarity to the "toad fish".

The same illustration of the fish appears in both editions of the Herbarium Diluvianum, and this is slightly different than

[1] National Museum of Natural History (MRC-106), Smithsonian Institution, Washington DC 20560

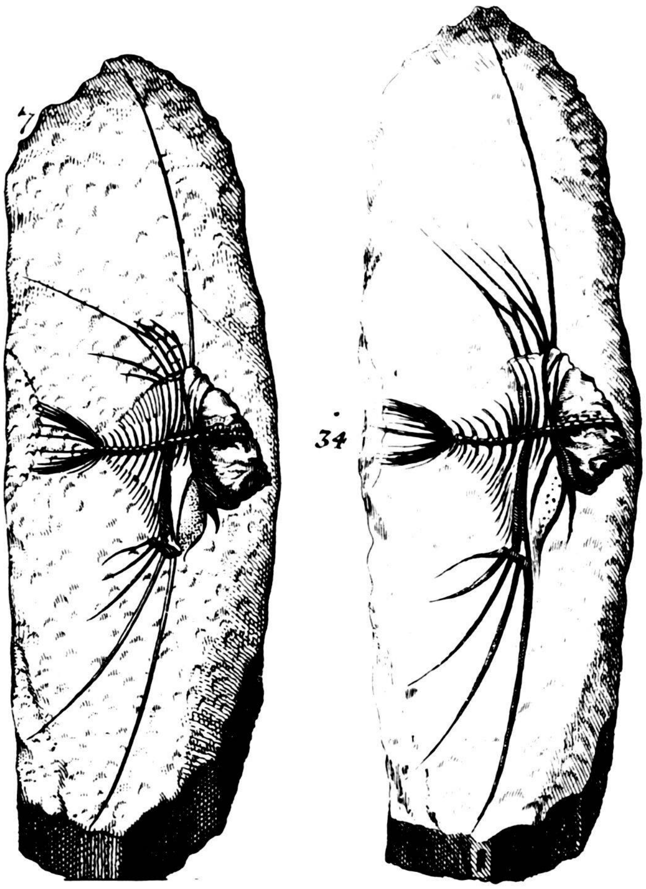

Fig. 1. *Sorbiniperca scheuchzeri*, as illustrated in Scheuchzer's works: to the left, from the 1709 Herbarium Diluvianum (the same figure appears in the 1723 second edition); to the right, from the 1731 Kupfer Bibel (the same figure appears in the 1731 Physica Sacra). These figures are reproduced here at the same size as in the original works, and this is very close to the natural size of the specimen.

the one in the Kupfer-Bibel and Physica Sacra (Fig. 1). The fish was re-drawn for each of the two composite plates in which it appeared with many other plants and animals.

The little specimen (25.9 mm standard length = SL) on which Scheuchzer based his illustrations and comments is among the old collections of the Paläontologisches Institut und Museum der Universität Zürich. The specimen had been donated to Scheuchzer by his Italian friend and colleague Antonio Vallisnerio (or Vallisnieri) (Scheuchzer, 1709, p. 17). It is now on display in a panel with other Monte Bolca fishes. It clearly is neither a flatfish nor a "toad fish". An ancient handwritten label on the back of the single plate of the specimen indicates that it subsequently had been identified as *Mene rhombea* (Perciformes, Menidae), a common deep-bodied fish of Monte Bolca, which it also certainly is not. A catalogue entry shows that this fish subsequently was also thought to be similar to *Enoplosus pygopterus* (Perciformes, Enoplosidae; personal communication, Dr. K.A. Hünermann, July 1995), but it has no derived features of similarity to members of that family.

This Zürich specimen does not appear in a small, earlier book by Scheuchzer (1708) devoted exclusively to fossil fishes. Since its illustration in the works of Scheuchzer between 1709 and 1731, mention of this specimen has occurred in the literature only twice, as *M. rhombea* in a list of Scheuchzer's specimens by Hünermann & Rieber (1988, p. 19) and as an undetermined perciform in a photograph by Frickhinger (1991, p. 871). A copy of the illustration of this fish from the Herbarium Diluvianum appears in the unpublished manuscript (Les Petrifications du Veronois) dating from about 1750 by the French scientist Jean-François Séguier on fossils from Monte Bolca, Italy (Gaudant, 1997; and personal communication, Dr. Jean Gaudant, May 1998).

Another small specimen (20.7 mm SL) of the same species from Monte Bolca is among the old collections of the Naturhistorisches Museum Wien. The Vienna museum archives indicate that this specimen (along with three minerals) had been received in 1843 in exchange for a selection of minerals sent to the Austrian Archduke (Erzherzog) Stephan, envoy to Hungary and a resident of Nassau near Frankfort. Johann Jacob Heckel, a preparator and then Adjunct Curator (see Wurzbach 1862, p. 184–189, and Steindachner 1901, p. 408–414) at the Vienna museum, intended to publish a description of the Vienna specimen, apparently unaware that Scheuchzer had previously illustrated a specimen of the same species. This intended manuscript with the description of the fish was never published, and the manuscript cannot be found in the archives of the Vienna museum (personal communication, Dr. Ortwin Schultz, July 1995). However, in two slightly different synopses of this manuscript, Heckel (1848, 1849) listed his intended name for the species as the nomen nudum *Platax quadrula*. This indicates that Heckel thought it was a member of the perciform Ephippididae, to which it does have some superficial resemblance. On a visit to the Vienna collections, Jacques Blot, the great monographer of the Monte Bolca ichthyofauna, examined Heckel's specimen and agreed that it was perhaps related to the Monte Bolca *Eoplatax* (Blot 1980, p. 374). It was Blot's intention to describe this species, but his early death in 1988 made this impossible, and there is nothing about this species among the manuscript materials of Blot, which were transferred from the Museum National d'Histoire Naturelle, Paris, to the Museo Civico di Storia Naturale di Verona in 1989.

An additional specimen (21.8 mm SL) of this little fish was recently located by Prof. Lorenzo Sorbini, late director of the Museo Civico di Storia Naturale di Verona. This specimen was among the more recently excavated (1984) materials from the Pesciara at Monte Bolca and generously made available to the author for comparison with the other two specimens.

This interesting species has never been properly described or formally named. It is an acanthopterygian with such a unique combination of derived conditions (high number of anal-fin spines, low number of both abdominal and caudal ver-

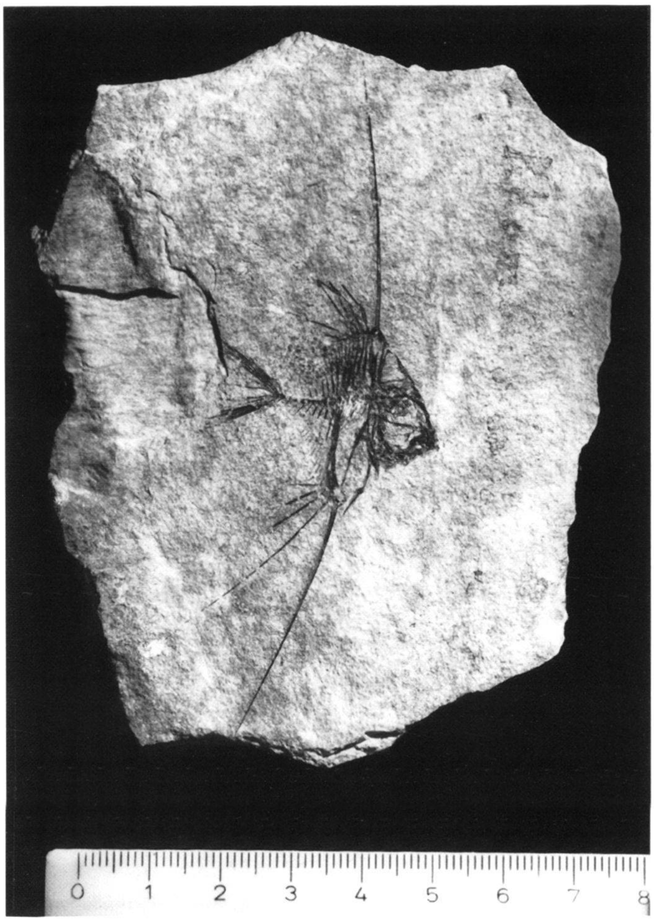

Fig. 2. *Sorbiniperca scheuchzeri*, photograph of the holotype, PIMUZ A/I 2488, 25.9 mm SL, lower Middle Eocene of Monte Bolca, Italy; the same specimen as illustrated by Scheuchzer. Scale is in millimeters.

tebrae, low number of caudal-fin rays, elongate median-fin spines, first dorsal pterygiophore in preneural space, two groups of vacant interneural spaces, no uroneural, long NPU2, molariform dentition, etc.) that it cannot be accommodated in any known fossil or Recent family. It is described below as *Sorbiniperca scheuchzeri*, gen. & sp. nov., family Sorbinipercidae.

The derived features of *Sorbiniperca* are compared to conditions in what are probably the related tetraodontiform + zeiform and lower percomorph clades. However, a cladistic analysis is not attempted here because of the present uncertainty about the relationships of the putative zeiform + tetraodontiform clade with caproids and of these taxa with various percomorph groups. These matters are under active investigation by the author and two colleagues, R. Winterbottom and B. O'Toole of the Royal Ontario Museum. Upon the completion of that research, it will probably be relatively easy to more precisely access the relationships of *Sorbiniperca* in a cladistic context.

Systematics

Sorbiniperca scheuchzeri: new species, new genus, and new family (Sorbinipercidae)

Holotype
Paläontologisches Institut und Museum der Universität Zürich (PIMUZ) A/I 2488, single plate, 25.9 mm SL (length from tip of snout to end of hypural plate).

Paratypes
Naturhistorisches Museum Wien (NMW) 1843.XXV.4a–b, part and counterpart (head to left in 4a), 20.7 mm SL; Museo Civico di Storia Naturale di Verona (MCSNV) 533 and I.G.129751, part and counterpart (head to left in 533), 21.8 mm SL.

Age and Locality
All three specimens are from the lower part of the Middle Eocene (Lutetian; NP 14, Discoaster sublodoensis Zone) of Monte Bolca, Italy.

Diagnosis
Unique among acanthopterygians by the following combination of derived features: vertebrae 8 + 12 – 13 = 20 – 21; five anal-fin spines; pelvic fin I,4; 14 principal caudal-fin rays; one supernumerary dorsal-fin spine; stout ventral shaft of first dorsal-fin pterygiophore in preneural space; three vacant interneural spaces in two groups (second group of varying location); elongate median-fin spines; long NPU2; uroneurals absent; teeth large, few, molariform and mostly rounded, a few anteriorly somewhat more elongate.

Etymology
Generic name: *Sorbini,* for Prof. Lorenzo Sorbini (1939–1997), the distinguished late director of the Museo Civico di Storia Naturale di Verona, a leading authority on the fishes of the Eocene of Monte Bolca, and a valued friend and helpful colleague to all who worked with him; and *perca,* in allusion to its many percomorph-like features in addition to those of the zeiform + tetraodontiform fishes (masculine).

Specific name: *scheuchzeri,* in honor of the historically important Swiss geologist and paleontologist Johann Jakob Scheuchzer (1672–1733).

Description

The three type specimens are all relatively small (20.7–25.9 mm SL) but are fully ossified. The great elongation of the first two dorsal- and anal-fin spines (equal to or greater than SL) and the great body depth (equal to or slightly less than SL) may in part be juvenile features. If this is the case, larger specimens can be expected to have significantly less elongate anterior median-fin spines and a somewhat lesser body depth.

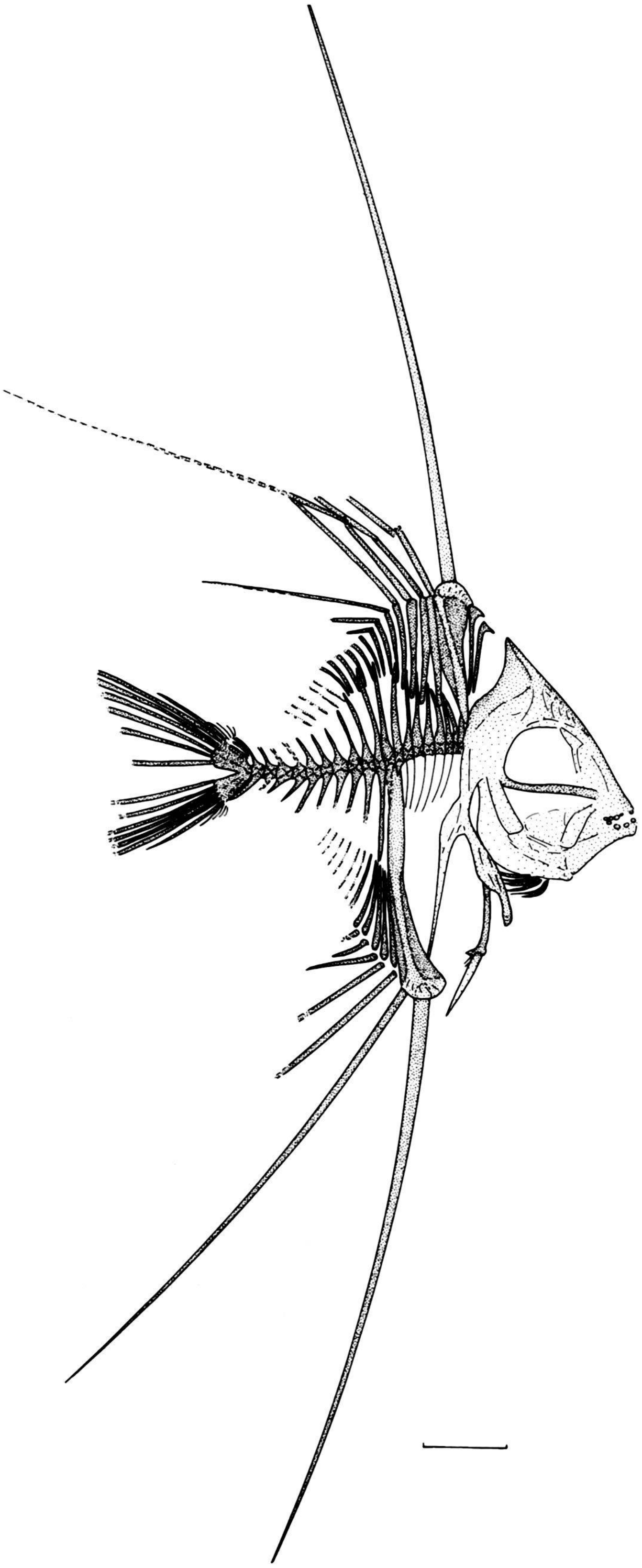

Fig. 3. *Sorbiniperca scheuchzeri*, reconstruction of the holotype (see Fig. 2 for specimen data). Scale line is 5 mm.

The head length (tip of snout to anterior edge of pectoral arch) ranges from 41–44% SL. The body depth from the distal edges of the first pterygiophores at the spiny dorsal- and anal-fin origins ranges from 99–102% SL.

The first dorsal- and anal-fin spines are most fully exposed in the holotype (Figs. 2 and 3); the first dorsal spine is at least 151% SL and the first anal spine is at least 139% SL, with the possibility that the extreme tips of both spines are missing beyond fractures in the plate. The second anal-fin spine in the holotype is 127% SL, but most of the other dorsal- and anal-fin spines in the holotype are incomplete distally or are represented only by impressions. The fourth dorsal spine is probably about 108% SL and the fifth anal spine is probably about 17% SL. In the Vienna paratype (Figs. 4 and 6A) the first two dorsal-fin spines, as exposed, are about 99% SL, but they are obviously incomplete distally where they seem to be buried in matrix. The more anterior anal-fin spines in this paratype are incomplete distally and probably are buried in matrix. In the Verona paratype (Figs. 5 and 6B) all of the anterior dorsal-fin spines are incomplete distally, as are most of those of the anal fin; however, the first and second anal-fin spines may have been only about 106% SL based on their distal impressions in one of the plates. If so, these anal spines are less elongate than those in the holotype.

There are eight dorsal-fin spines and five anal-fin spines in the holotype (Fig. 7) and in the Vienna paratype, with the last elements in both fins relatively short. In the Verona paratype the last few dorsal-fin spines are absent and the last few anal-fin spines have only the bases indicated; the bases of the last few preserved dorsal spines are displaced slightly forward and the anterior region of the spiny dorsal fin is displaced upward so that the distal ends of the dorsal pterygiophores and supraneurals are unnaturally above the profile. Dorsal-fin rays are not preserved in any of the specimens; however, the Verona paratype has at least 12 pterygiophores posterior to the eight pterygiophores of the spiny dorsal fin, and the soft dorsal fin presumably had at least 12 rays, and perhaps a few more. A relatively complete series of anal-fin rays are preserved as impressions or bases only in the Verona paratype, which seems to have a total of about 14 soft rays and 13 pterygiophores. In the holotype only the first two anal-fin rays are preserved (only the first relatively completely), and no anal rays are preserved in the Vienna paratype. None of the dorsal- and anal-fin rays are sufficiently preserved distally to determine whether they were branched or simple, except that the first anal ray in the holotype is probably unbranched. Each dorsal-fin spine is borne on its own pterygiophore (i.e., there is a single supernumerary spine on the first dorsal pterygiophore); the first two anal-fin spines are borne on the first pterygiophore (i.e., there are two supernumerary spines on the first anal pterygiophore), and the other spines are each borne on their own pterygiophore.

The pectoral fin is indicated only in the Verona paratype, but the number of rays cannot be determined.

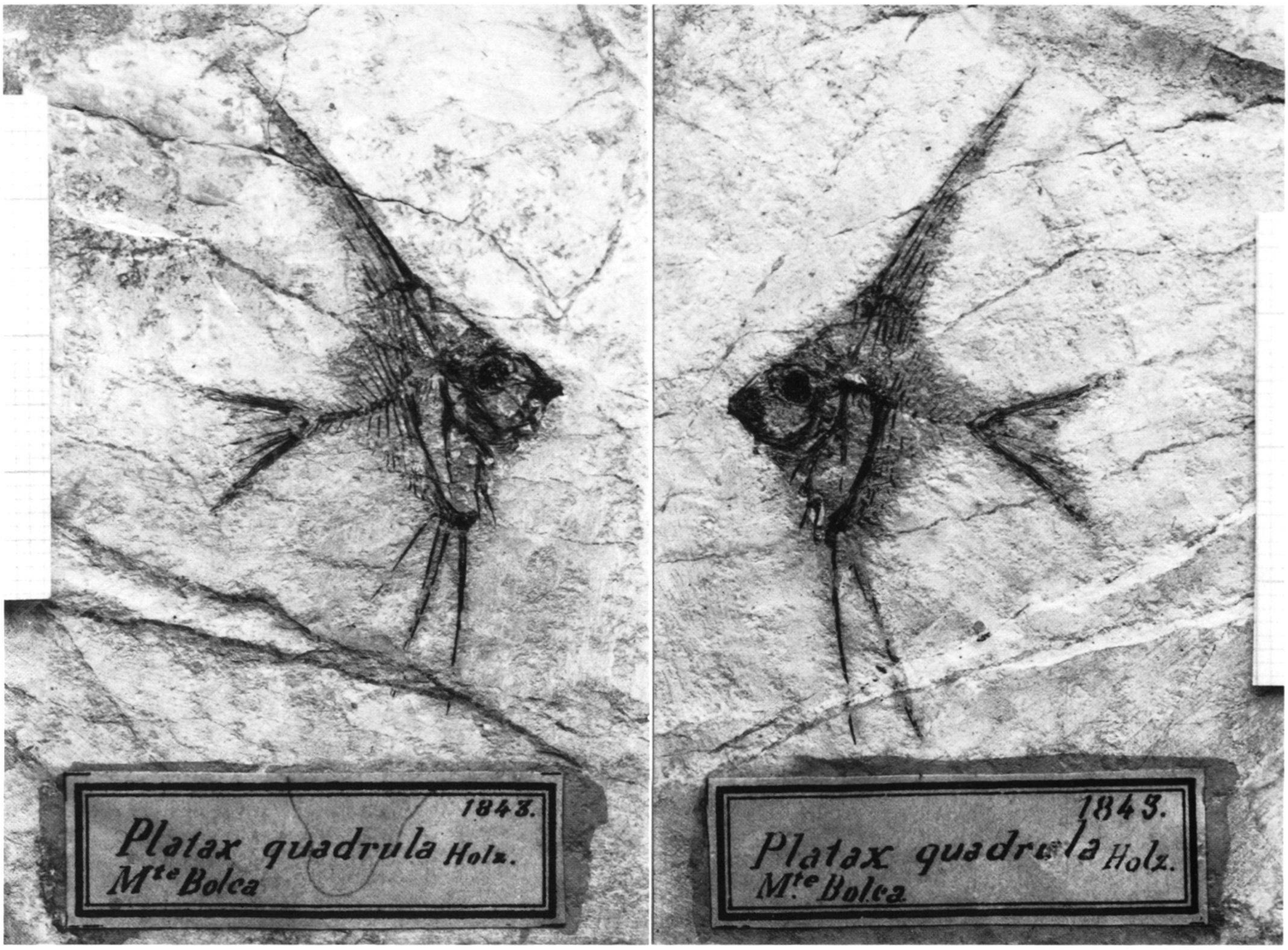

Fig. 4. *Sorbiniperca scheuchzeri*, photographs of the part and counterpart of the Vienna paratype, NMW 1843.XXV.4a (head to left) and 4b, 20.7 mm SL, lower Middle Eocene of Monte Bolca, Italy.

The pelvic fin is best exposed and preserved in one of the counterparts of the Vienna paratype (NMW 1843.XXV.4a), in which the pelvis and the two pelvic-fin spines are turned and displayed in more or less dorsal view rather than in lateral view (Fig. 8B). In this paratypic plate (head to left) there are three well-preserved rays of decreasing length just medial to the spine on the left side, and medial to them is one even shorter, less well-preserved ray. The poorly preserved ray seems to be close to the midline, just to the left of where the two halves of the pelvis would be in contact, based on the vacant space that can be seen between the two halves more anterodorsally on the pelvis. This innermost ray seems to be the fourth ray of the left-side pelvic fin and a continuation medially of the series of three better preserved rays; however, this putative fourth and innermost ray of the left-side fin is situated close to the base of the right-side pelvic spine, and it could also be interpreted as a poorly preserved innermost ray of the right-side fin. If that is the case, then there are only three rays and not four in each pelvic fin. Nevertheless, from the positional evidence relative to the presumed midline, it seems more likely that this innermost ray is the fourth from the left side, and that no rays are preserved or exposed from the right-side fin. It is, therefore, presumed that the pelvic fin is I,4. In the holotype the pelvic fin is preserved in lateral view: two rays are clearly evident just behind the base of the spine (which has two deep lengthwise grooves along the basal region). There are indistinct remains of a few other rays internal to these, but whether these remains are from one or both sides is uncertain. Therefore, the condition of the fin in the holotype does not shed light on the total number of pelvic-fin rays. The pelvic fin is not preserved in the Verona paratype.

The caudal fin is relatively well preserved in the holotype (Fig. 8A) and Vienna paratype; in both specimens there are 14 principal rays (branched rays plus long upper and lower un-

Fig. 5. *Sorbiniperca scheuchzeri*, photograph of one of the two plates of the Verona paratype, MCSNV 533, 21.8 mm SL, lower Middle Eocene of Monte Bolca, Italy.

branched rays) and four procurrent rays both above and below (iv,I,6 + 6,I,iv). The caudal fin in the Verona paratype is displaced forward over the hypural plate and cannot be counted accurately, but it seems similar to that of the other two specimens.

The teeth (Fig. 8C) are relatively large and few in number; although scattered, there were probably no more than 8–10 to each side of the midline of the upper and lower jaws (on each premaxilla and dentary). Most of the teeth are more or less rounded or oval, with a round basal half that was held in a concave socket and a slightly less wide exposed upper half that terminates in a dark, slightly upraised cap. In both the holotype and Verona paratype there is at least one tooth evident that is somewhat more stoutly elongate and incisor-like than the other more rounded teeth; in both cases the more elongate tooth is toward the front of the jaw, and it is likely that there was a gradation in tooth morphology from front to back.

The ascending process of the premaxilla is long, reaching to the level of about the front of the lateral ethmoid, somewhat anterior to the orbit.

The frontal and supraoccipital form a high crest above and behind the eye. Most of the skull bones are too indistinct to be meaningfully described, with only the parasphenoid shaft under the orbit clear in all three specimens. The hyomandibular and some of the opercular and pterygoid series are preserved in the holotype but are unremarkable as far as exposed (the metapterygoid seems to be of moderate size and close to the quadrate). There is an infraorbital ring of bone, but the individual limits of the elements are not clear.

The branchiostegal rays are well preserved and exposed in the holotype and Vienna paratype; they are 2 + 4 = 6. The urohyal is faintly indicated in the Vienna paratype.

The pectoral girdle has a relatively narrow cleithral-coracoid region and a long postcleithrum that at least below the level of the pectoral-fin base seems to be composed of a single piece. The ventral end of the postcleithrum closely approaches or actually contacts the anterior edge of the lower region of the first pterygiophore of the anal fin. The supracleithrum is relatively vertically oriented, but its attachment to the skull is unclear.

The pelvis is oriented relatively vertically to the vertebral axis and attaches to the cleithral-coracoid arch at the level of the branchiostegal rays. Based on the Vienna paratype (in which the pelvis is seen in dorsal view), the two halves of the pelvis are narrowly separated from one another throughout most of their length anterodorsal to the origin of the pelvic fin. Based on the holotype, the posterior process of the pelvis is short, about as long as the width of the base of the pelvic-fin spine.

There are two long and sturdy supraneural (predorsal) bones in all three specimens, the first a little shorter than the second.

The eight pterygiophores of the spiny dorsal fin decrease in length posteriorly in the series, with the first being particularly long and stout. The distal end of the first pterygiophore seems to have thin, bilateral, upright flanges to either side of the base of the first spine, through which the basal region of the spine can be seen as an impression (best preserved in the holotype; in the paratypes only the upright flanges behind the spine base are preserved). This pair of upright lateral flanges also covers the anterior end of the base of the second spine, although the latter is borne primarily on the second pterygiophore. None of the other dorsal pterygiophores has such an upright lateral flange along the side of the bases of the spines. Although obscured by the lateral flange, there is indication in the impressions and sculpturing of the bones that the base of the first dorsal spine rotates over a median flange. Because of the incomplete preservation it cannot be determined if there is a foramen in the medial flange for interlocking with the base of the spine.

The stout ventral shaft of the first dorsal pterygiophore contacts the rear of the skull just in front of the upper end of

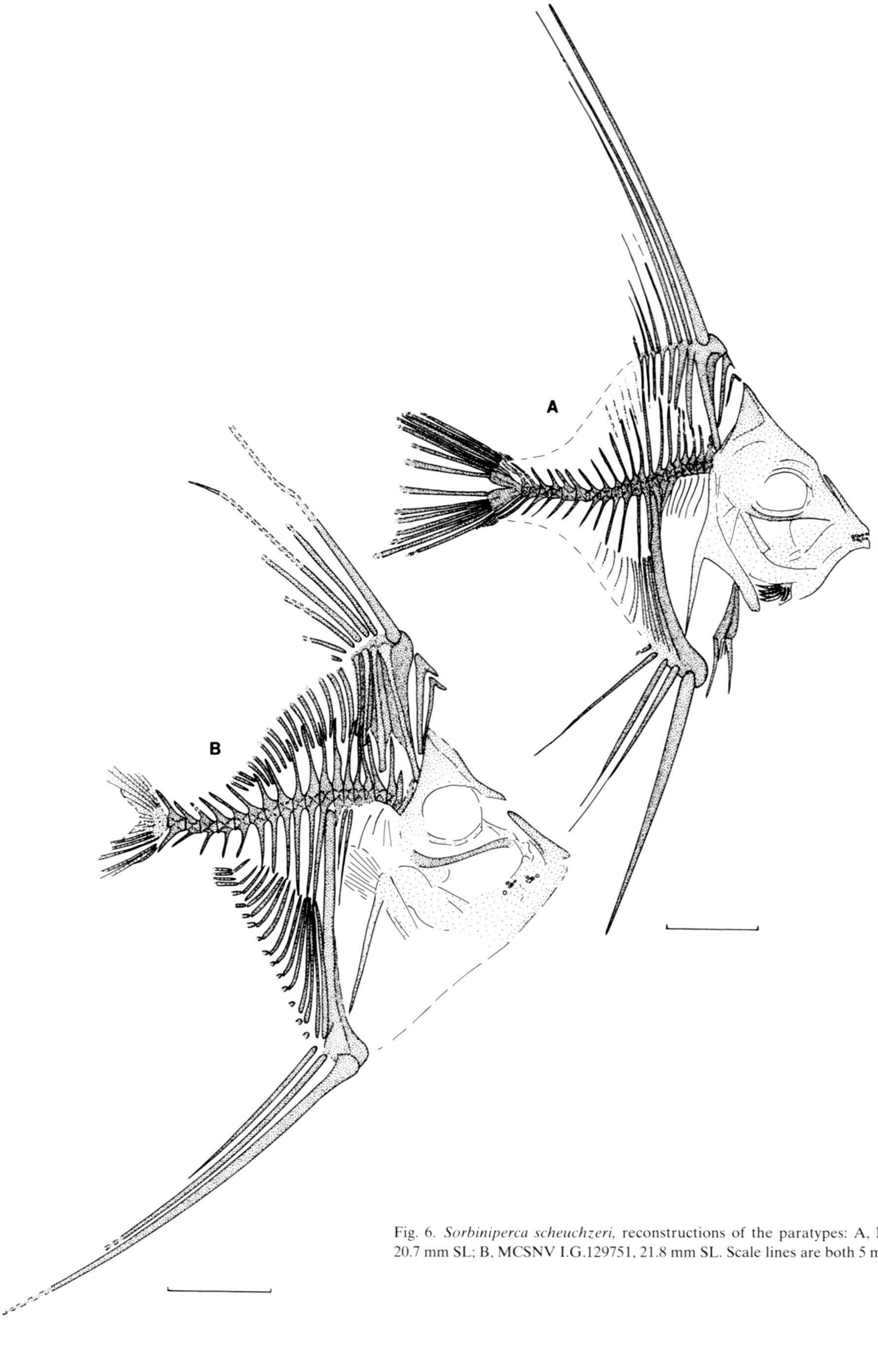

Fig. 6. *Sorbiniperca scheuchzeri*, reconstructions of the paratypes: A, NMW 1843.XXV.4b, 20.7 mm SL; B, MCSNV I.G.129751, 21.8 mm SL. Scale lines are both 5 mm.

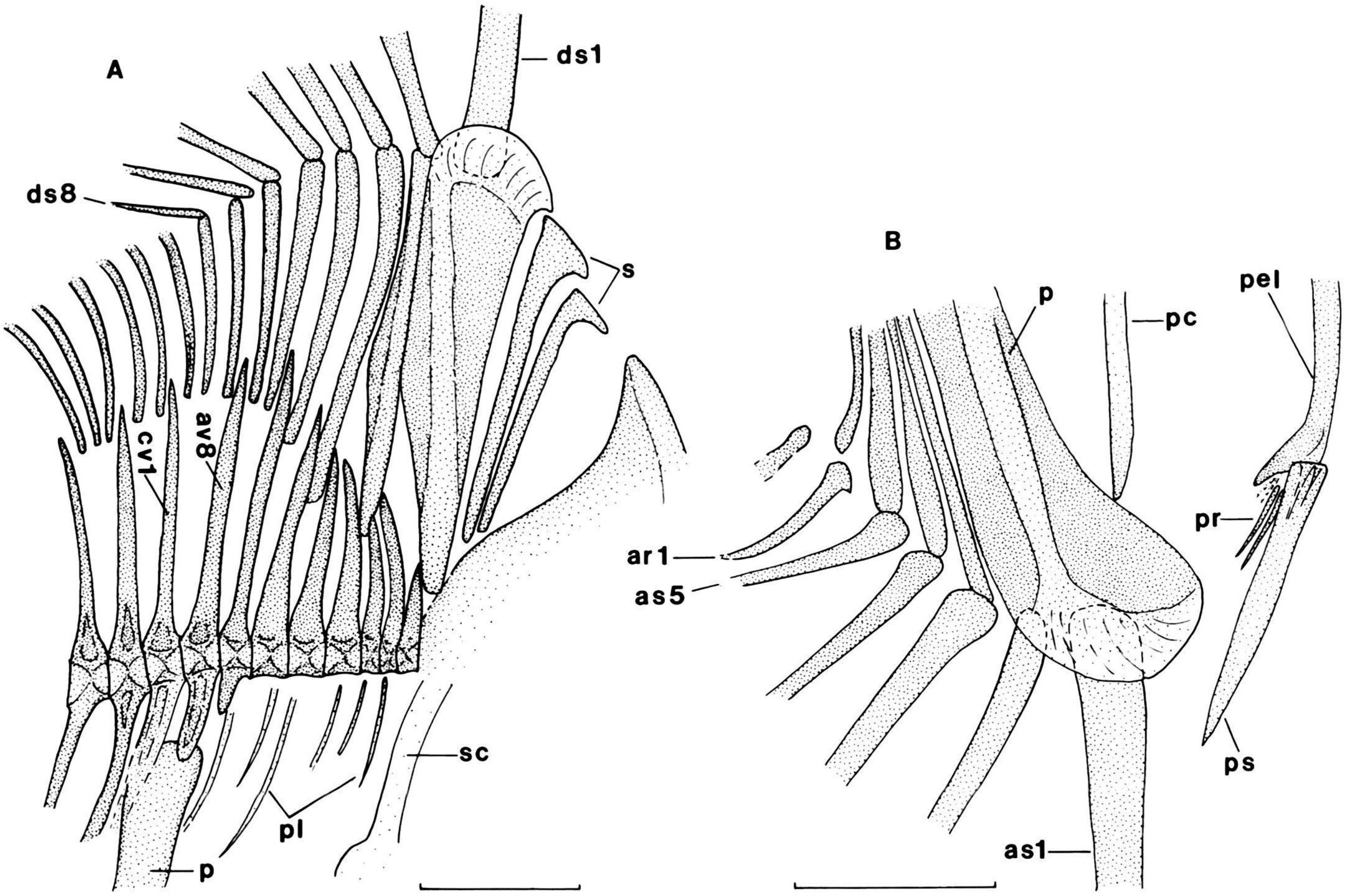

Fig. 7. *Sorbiniperca scheuchzeri*, holotype, PIMUZ A/I 2488, 25.9 mm SL: A, anterior part of vertebral column, dorsal fin pterygiophores, and bases of dorsal-fin spines; B, pelvic fin, distal ends of anal-fin pterygiophores, bases of anal-fin spines, and first two anal-fin rays. Scale lines are both 3 mm. Abbreviations: ar – anal-fin ray; as – anal-fin spine (first and fifth); av – abdominal vertebra (eighth); cv – caudal vertebra (first); ds – dorsal-fin spine (first and eighth); p – anal-fin pterygiophore; pc – postcleithrum; pel – pelvis; pl – pleural rib; pr – pelvic-fin ray; ps – pelvic-fin spine; s – supraneural; sc – supracleithrum.

the neural spine of the first vertebra (best seen in the holotype), in the preneural space; in the Verona specimen the shaft makes contact higher up on the rear of the skull than in the other two specimens, probably because of distortion in this region (see below under abdominal vertebrae). The more slender second pterygiophore bears the second spine distally, and its ventral shaft is situated between the distal regions of the neural spines of the third and fourth vertebrae in all three specimens; there are no pterygiophore shafts placed in the spaces between the neural spines of the first-second and second-third vertebrae. The third pterygiophore, bearing the third spine, has its ventral shaft situated between the distal regions of the neural spines of the fifth and sixth vertebrae in the holotype and Vienna paratype, but it is between the neural spines of the fourth and fifth vertebrae in the Verona paratype; thus, there are no pterygiophores placed between the neural spines of the fourth-fifth vertebrae in two specimens and between the fifth-sixth in the other. The fourth and more posterior pterygiophores, including those of the soft dorsal fin, are placed between successive neural spines, with one, two, or three pterygiophores per space.

The vacant interneural spaces described above are, in summary, the first and second in all three specimens, the fourth in two specimens, and the fifth in one.

The first anal-fin pterygiophore is similar to the first dorsal-fin pterygiophore but longer, with a stouter proximal shaft. The dorsal end of the shaft is situated between the haemal process of the last (8th) abdominal vertebra and the long haemal spine of the first caudal vertebra. The distal end of the first anal pterygiophore has bilateral upright lateral flanges (like those of the first dorsal pterygiophore) alongside the base of the first anal spine and, to a lesser extent, along the base of the second spine (as with the first dorsal pterygiophore, there may be a median flange for the first anal spine that is obscured

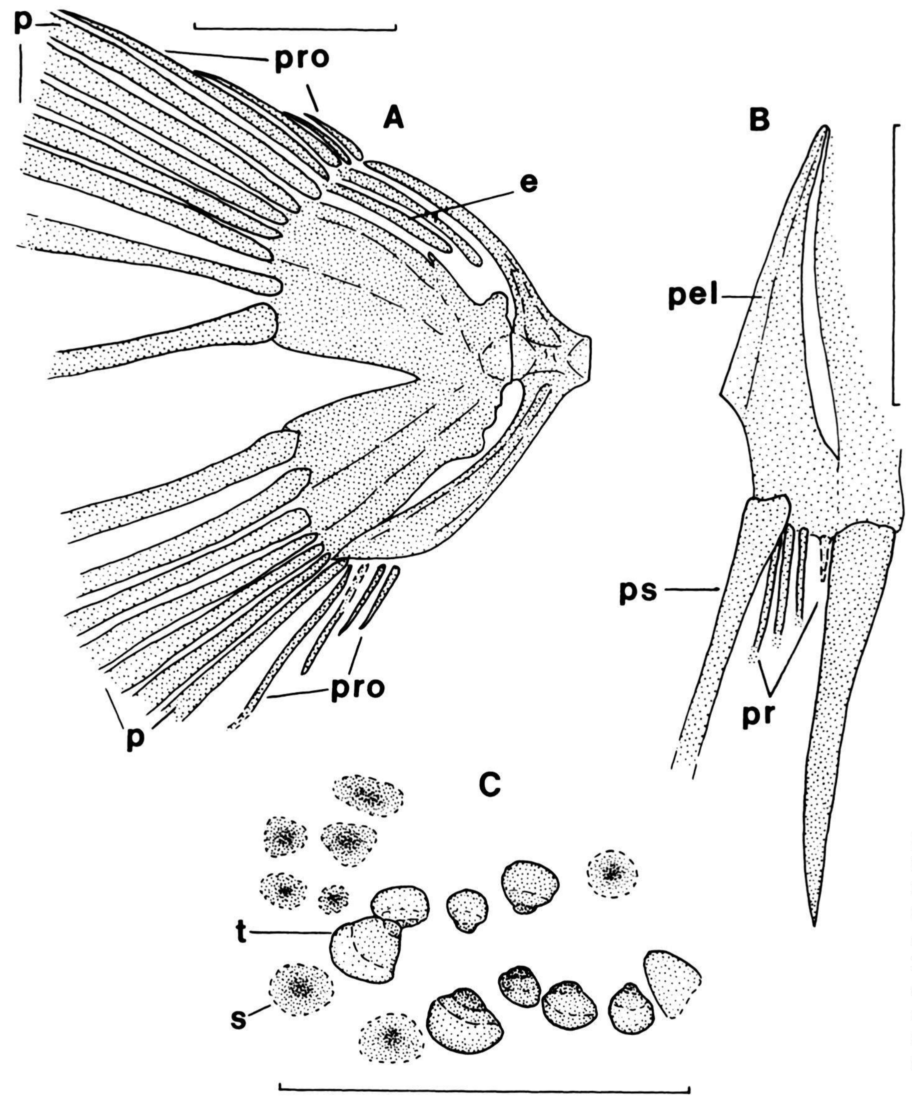

Fig. 8. *Sorbiniperca scheuchzeri:* A, caudal skeleton, and C, teeth and tooth sockets, holotype, PIMUZ A/I 2488, 25.9 mm SL, anterior to right in both illustrations; B, dorsal view of pelvis and pelvic fin, paratype, NMW 1843.XXV.4a, 20.7 mm SL, anterior to left. All three scale lines are 2 mm. Abbreviations: e – epural; s – socket of dislodged tooth; t – tooth; p – principal caudal-fin ray; pel – pelvis; pr – pelvic-fin ray; pro – procurrent caudal-fin ray; ps – pelvic-fin spine.

by the paired lateral flanges). The second to fourth anal pterygiophores, bearing the third to fifth spines, are considerably shorter and slenderer than the first pterygiophore. Their proximal shafts are placed just in front of and behind the haemal spine of the first caudal vertebra, but the state of preservation does not permit detailing of these arrangements.

The holotype has the first anal-fin ray and its slender pterygiophore relatively completely preserved, but the subsequent rays and pterygiophores are poorly preserved. In the Verona paratype the 13 slender pterygiophores of the soft anal fin are placed between the haemal spines of the first to seventh caudal vertebrae.

There are clearly eight abdominal vertebrae in all three specimens.

The centrum of the first vertebra is clearly discernable in all three specimens, but the neural arch and spine are variously preserved. In all three specimens the lower, or neural, arch region seems to be in contact with the rear of the skull, but at least in the holotype the distal region of the neural spine is free from the skull and is placed against the lower posterior edge of the shaft of the first dorsal-fin pterygiophore. The distal end of this first neural spine is less well exposed and preserved in the paratypes, and its precise position is difficult to determine; however, it seems to be oriented so that it would be just behind the base of the first pterygiophore, as in the holotype.

The neural spines increase in length from the second to about the seventh and eighth abdominal and first caudal vertebrae and then decrease in length. A few of these neural spines have a slight anterodorsal slant, and a few others are relatively vertical. The last (8th) abdominal vertebra has a strong haemal process that contacts the upper front region of the first anal pterygiophore, and at least in the Vienna paratype there is evidence that haemal processes from the sixth and seventh abdominal vertebra abut that of the eighth vertebra to strengthen the support of the pterygiophore. There are a series of slender pleural ribs of moderate length on most of the second to seventh abdominal vertebrae (best seen in the holotype). In the Verona specimen there is a strong upward arch to the abdominal vertebrae that is probably a distortion because it is not present in the other two specimens, and the shaft of the first dorsal-fin pterygiophore also seems displaced dorsally.

The holotype has 12 caudal vertebrae and the Vienna paratype has 13; the Verona paratype probably has 12 caudal vertebrae but the anteriorly displaced and slightly disarticulated caudal-fin base makes this less than certain. The caudal skeleton is best preserved in the holotype (Fig. 8A). The penultimate vertebra (PU2) has long neural and haemal spines, with no evidence of them being autogenous. There are two epurals. The hypurals are closely spaced and apparently highly consolidated, with only faint lines indicating the areas of fusion or close apposition between the lower four of the presumed five primordial elements; the parhypural contacts the centrum anteriorly. There is an especially deep cleft between the region of hypurals two and three. There is no free uroneural, but the stegural region above the first centrum is large. The antepenultimate vertebra (PU3) is not well preserved in the holotype, but in the Vienna paratype the neural and haemal spines of PU3 are much more elongate than the preceding ones. In the Vienna paratype there is clear evidence of the fifth (uppermost) hypural being free. The caudal skeleton of the Verona paratype does not add information to the above.

Comparison of Derived Features of *Sorbiniperca* with Other Taxa

Among the acanthopterygian fishes, *Sorbiniperca* has many features of similarity to the Percomorpha. Of the derived percomorph features discussed by Johnson & Patterson (1993) that can be determined in *Sorbiniperca,* the following are present: absence of a second ural centrum, five or fewer hypurals, pelvic fin with less than six soft rays, and 17 or fewer caudal-fin rays. However, *Sorbiniperca* possesses a large array of derived features, and this combination of features is not found within any of the 92 families and incertae sedis genera of the largest subgroup of Percomorpha, the Percoidei or perciforms (Johnson 1984), although a few of the derived features of *Sorbiniperca* are found in various combinations in a few of the perciform groups. Therefore, *Sorbiniperca* cannot be accommodated in any existing higher category of perciform fishes.

Two of the derived percomorph features mentioned above (hypural and caudal-fin numbers) also are found in zeiforms (Johnson & Patterson 1993, give several more features that cannot be determined in *Sorbiniperca*). *Sorbiniperca* also has several important derived features characteristic of either zeiforms and/or their tetraodontiform sistergroup and of caproids, with the latter of uncertain monophyly and relationship to either perciforms or zeiforms + tetraodontiforms (see Johnson & Patterson 1993; Bonde & Tyler, in press; Winterbottom et al., manuscript). Some of the derived features of *Sorbiniperca* also are found in the perciform Acanthuroidei and to a lesser extent in their higher-squamipinne sistergroups, and Bannikov (1991) has proposed that the caproids and acanthuroids (in which he includes the Monte Bolca Acanthonemidae) are all closely related. For the acanthuroid fishes, highly corroborated hypotheses based on osteological and myological evidence (Tyler et al. 1989; Winterbottom 1993; Winterbottom & McLennan 1993; Guiasu & Winterbottom 1993) indicate that the families have the phyletic sequence of Siganidae – Luvaridae (and its entirely fossil sistergroup, the Kushlukiidae) – Zanclidae – Acanthuridae (Nasinae – Acanthurinae) and that the first and second outgroups are, respectively, the higher squamipinne Scatophagidae and Ephippididae.

Because a few of the derived features of *Sorbiniperca* are shared with each of the above groups, Table 1 summarizes the conditions in these groups for 16 features useful in either systematically defining or phylogenetically relating them. Each of these features is discussed below.

Analysis of Characters

1. First dorsal-fin pterygiophore position

In *Sorbiniperca* the ventral end of this pterygiophore is placed between the rear of the skull and the tip of the first neural spine, in the preneural space. This derived condition (relative to a more posterior placement in the first or second interneural space in most perciforms; see Johnson 1984; and Tyler et al. 1989) also is found in all caproids, all zeiforms, and those tetraodontiforms with the ancestral condition of a well-developed spiny dorsal fin. In the more advanced tetraodontiforms with a well-developed spiny dorsal fin, the pterygiophore becomes plastered to the top of the skull. The shaft also is placed in the preneural space in many acanthuroids, but the ancestral condition for this clade is that found in siganids (and its scatophagid outgroup), in which the shaft is in the first interneural space (except by specialization above the short first neural spine in one of the five genera, *Siganus*), with the shaft shifted forward into the preneural space only in the more derived clades of luvarids, zanclids, and acanthurids (Tyler et al. 1989). In the †kushlukiid sistergroup of luvarids the shaft is placed in the third or fourth space because of the posterior placement of the spiny dorsal fin, a secondarily derived condition within acanthuroids (Bannikov & Tyler 1995). The stoutness of the shaft could be considered a specialization separate from that of its placement, but for present purposes these two features are treated herein as a single correlated complex.

There is an important difference, however, between the condition of the first neural spine in *Sorbiniperca* and in the putative caproid + zeiform + tetraodontiform clade. In *Sorbiniperca* the region of the neural arch is in contact with the rear of the skull, but the region of the neural spine is free from the skull. In caproids, zeiforms, and tetraodontiforms the neural spine has most or all of its length in close contact with the skull (a few zeiforms have a free elongate portion of the neural spine extending up beyond the broadly attached portion) and the ventral end of the pterygiophore abuts the skull between the bifid end of the neural spine (with the exception of the zeiform *Parazen*, in which the end of the pterygiophore is placed in the middle of the first interneural space, out of contact with the skull). Thus, the plastering of the first neural spine and the attachment of the first pterygiophore to the skull are more specialized in caproids, zeiforms (with the exception of *Parazen* for the pterygiophore), and tetraodontiforms than in *Sorbiniperca*, but the latter condition could be ancestral to that of the others. Whether the form of adherence to the skull of the first vertebra is exactly homologous in caproids and zeiforms has been called into question by Johnson & Patterson (1993). Because the fine details of the attachment of the first vertebra and its neural spine to the skull are unknown in *Sorbiniperca*, only the placement of the shaft of the first pterygiophore in the preneural space, in contact with the skull, is utilized herein as a clear synapomorphy with the putative caproid + zeiform + tetraodontiform clade.

2. Supernumerary dorsal-fin spines

In *Sorbiniperca* there is a single dorsal-fin spine borne on the first pterygiophore. Among the groups under consideration, this derived condition (Patterson 1992) is found only in the single species of Eocene acanthonemid, a few ephippidids *(Platax, Monodactylus)*, one of the two genera of zanclids *(Zanclus)*, one of the five genera of siganids *(Eosiganus)* and, most importantly, in all zeiforms. Two supernumerary spines is the ancestral condition in zanclids and siganids (Tyler & Bannikov 1997). Caproids and tetraodontiforms also have two supernumerary dorsal-fin spines, and the single supernumerary dorsal spine is therefore a synapomorphy of zeiforms (Tyler & Sorbini 1996).

3. Length of penultimate neural spine (NPU2)

In *Sorbiniperca* NPU2 is long. This is a derived condition because NPU2 is short in most beryciforms (Zehren 1979) and perciforms (Johnson 1984), and a long or complete NPU2 is found mainly in far more primitive groups. A long NPU2 otherwise is found in the groups under consideration only in all zeiforms, in nearly all tetraodontiforms (the exceptions being secondary reductions in length in a few specialized forms), and in the two fossil genera of scatophagidae (Tyler & Sorbini, in prep.; the two Recent genera have short NPU2 like all taxa of the acanthuroid sistergroup and the ephippidid outgroup).

4. Uroneurals

In *Sorbiniperca* there are no free uroneurals. This is a derived condition because there are one or two free uroneurals, including the stegural element, in most beryciforms (Zehren 1979) and perciforms (Johnson 1984). The absence of uroneurals in the groups under consideration otherwise is found only in all zeiforms and most tetraodontiforms (but a uroneural is probably present ancestrally in tetraodontiforms because it is present in the most primitive groups: most plectocretacicoids, triacanthoids, and triodontids). All of the other groups have the primitive condition of one (caproids, scatophagids, acanthurids) or two (acanthonemids, ephippidids) uroneurals.

5. Epurals

In *Sorbiniperca* there are two epurals. This is a derived condition because the primitive condition for both beryciforms and perciforms is three epurals (Zehren 1979; Johnson 1984; Fujita 1990). Most of the other groups under consideration have the primitive condition of three epurals: caproids, acanthonemids, ephippidids, scatophagids, and all acanthuroids except a few derived acanthurids with only two (in the genus *Naso*) and adult luvaroids with only one (but three in some larvae). There are only two epurals in zeiforms, except for some species of zeids with a further reduction to only one epural. In tetraodontiforms there is either one epural or none, with the exception of one of the three Upper Cretaceous taxa, *Plectocretacicus clarae*, with three, an apparent reversal from the ancestral tetraodontiform condition of a single epural.

6. Hypurals

In *Sorbiniperca* the hypurals are highly consolidated, and there is an especially deep cleft between the regions of the second and third elements. Consolidated hypurals is a derived condition because the primitive condition for most beryciforms is five or six separate elements and that for perciforms is five separate elements (Zehren 1979; Johnson 1984; Fujita 1990; Johnson & Patterson 1993), with many linages of derived perciforms independently consolidating hypurals. In the groups under consideration, the primitive condition of unconsolidated hypurals is present in caproids, acanthonemids, ephippidids, scatophagids, and most acanthuroids (secondarily consolidated only in luvarids and *Naso* among acanthurids); consolidated hypurals otherwise are only found among zeiforms and tetraodontiforms. Because all zeiforms have some consolidation of hypurals (usually 1 + 2 and 3 + 4 fused together and one or both of these fused to the urostylar centrum), including the earliest known ones, from the Upper Paleocene (Bonde & Tyler, in press), this can be considered the ancestral zeiform condition. The putative Middle Cretaceous *Palaeocyttus* Gaudant, which has consolidated hypurals, is not a zeiform, but, rather, probably a beryciform (Bonde & Tyler, in press).

Hypural consolidation also is found in most families of tetraodontiforms, including the earliest known ones, from the Upper Cretaceous (Tyler & Sorbini 1996). If consolidated hypurals are ancestral for tetraodontiforms, then the unconsolidated hypurals in triacanthodids, triodontids, and the Eocene eoplectids are reversals, but this has not yet been documented. Thus, it can only be noted that the derived hypural consolidation found in *Sorbiniperca* is also the condition in all zeiforms and most tetraodontiforms (including the most primitive clade of the latter).

There is a deep cleft between hypurals two and three in *Sorbiniperca*, but equally deep clefts are found in some genera of a wide variety of perciform and beryciform families (Fujita 1990) and also in many other acanthomorph groups, as well as in at least one zeiform *(Parazen)*. Deep clefting has obviously occurred independently so often in so many groups that it is not useful in establishing the relationships of *Sorbiniperca*.

7. Caudal-fin rays

In *Sorbiniperca* there are 14 principal caudal-fin rays (i,6 + 6,i). This is a derived condition because most beryciforms have 18–19 principal rays (i,8 – 9 + 8,i) (Zehren 1979) and the primitive condition for percomorphs and perciforms is 17 principal rays (i,8 + 7,i) (Johnson 1984; Johnson & Patterson 1993), although within perciforms a few groups have reduced the number of principal rays to 15 or 16, or rarely fewer. In the groups under consideration there are many with reduced caudal-fin numbers, and only the acanthonemids, ephippidids, and the most primitive family of acanthuroids, the siganids, have 17 principal rays (all other acanthuroids and the closely related scatophagids have 16 principal rays). In tetraodontiforms the caudal fin is reduced to 12 or fewer principal rays in all species except for one of the three Upper Cretaceous taxa, *Plectocretacicus clarae*, in which there is a reversal to 14 principal rays (12 is the ancestral number for tetraodontiforms, see Tyler & Sorbini 1996). Caproids have either 12 *(Antigonia)* or 14 *(Capros)* principal rays; it is undocumented which condition is ancestral for the family; the putative Middle Cretaceous caproid *Microcapros* Gayet has 15 principal rays but it is a trachichthyid rather than a caproid (Bonde & Tyler, in press). Zeiforms have 13 principal rays, except that there is a secondary increase to 15 rays in one probably derived family (grammicolepidids), and a decrease to 12 rays in one of the two Paleocene taxa (Bonde & Tyler, in press).

8. Vertebrae

In *Sorbiniperca* there is reduction in the numbers of both the abdominal and caudal series of vertebrae to 8 + 12 – 13 = 20 – 21, an exceptionally low number. Among perciforms, 10 + 14 – 15 is accepted as the ancestral number (Gosline 1968; Johnson 1984), with many groups increasing the number but only two families, priacanthids and scatophagids, reducing the number to 10 + 13 = 23; most beryciforms have more than 24 vertebrae (but 24 in Berycidae), usually 25–35 and up to more than 50 in some (Keene & Tighe 1984). Among the groups under consideration, only ephippidids have the primitive vertebral count of 10 + 14 = 24, with a reduction to 10 + 13 = 23 in acanthonemids, scatophagids, and the most basal of the families of acanthurids, the siganids; all other acanthuroids have a further secondary reduction to 9 + 13 = 22, except for a secondary increase to 10 + 19 – 20 = 29 – 30 in kushlukiids (Bannikov & Tyler 1995). Caproids have 10 + 12 = 22. Tetraodontiforms have 20 or 21 vertebrae as the ancestral condition, with 9 or 10 abdominal vertebrae in the Upper Cretaceous clade but typically 8 + 12 = 20 or fewer in the other major clades, at least ancestrally. There are, however, many independent further slight increases and decreases in vertebral numbers within various tetraodontiform clades (see Tyler 1980). Zeiforms have relatively higher vertebral numbers, between 27–46 total (usually 30 or more), of which 10–15 (usually 11 or more) are abdominal and 16–35 are caudal. Among these zeiforms, only *Zenion* has as few as 27 vertebrae (11 + 16).

9. Supraneurals

In *Sorbiniperca* there are two supraneural (predorsal) bones. Three supraneurals is considered the primitive condition for perciforms (Johnson 1984), and beryciforms usually have two or three supraneurals (Zehren 1979). Therefore, the two supraneurals in *Sorbiniperca* is not a notably derived condition, whereas many of the other groups under consideration have the clearly derived condition of only one supraneural or none. Tetraodontiforms and acanthonemids have no supraneurals. A single supraneural is ancestral for acanthuroids (with subsequent loss of the element in luvaroids and some siganids and acanthurids; Tyler & Bannikov 1997). Ephippidids have three supraneurals, scatophagids have two, and among caproids one genus has two *(Antigonia)* and the other genus has none *(Capros)*. Most zeiforms have a single supraneural, but this is absent in parazenids and in two highly derived genera of zeids (*Zeus* and *Zenopsis*), with the absence probably secondary. Therefore, of the groups under consideration, all but the two families of higher squamipinnes and one of the two genera of caproids have a more derived condition of supraneural loss than in *Sorbiniperca*.

10. Vacant interneural spaces

Spaces between successive neural spines without the presence of basal regions of dorsal-fin pterygiophores are considered to be vacant, and the spaces take the number of the vertebra bearing the more anterior of the two neural spines bordering the vacancy. In *Sorbiniperca* there are three vacant interneural spaces in two groups (variable location of the second group).

In the more morphologically generalized perciforms, there are usually no vacant interneural spaces behind the first pterygiophore of the dorsal fin, and the presence of vacant spaces there is considered derived. However, in the groups under consideration there is great variation both intraspecifically (especially among many zeiforms) and within higher taxa in the number of vacant spaces and in their position, and the positional differences are difficult to homologize. In spite of these limitations, having two or more vacant interneural spaces in two groups can be considered more derived than a single vacant space or several spaces in a single group.

All of the groups under consideration have one or more vacant interneural spaces, but there is only a single space vacant in caproids (variously the 5th, 6th, or 7th space), acanthonemids (the 5th), ephippidids (the 6th, except none in *Platax*, *Eoplatax*, and *Archaephippus*), scatophagids (usually the 6th or 7th, rarely the 5th or 8th), and acanthuroids (variously the 3rd through 6th, but none in the acanthurid *Marosichthys* and many luvaroids; see Bannikov & Tyler 1995; Tyler & Bannikov 1997; Tyler 1997). The more derived condition of two or more vacant interneural spaces in two or more groups is present only in *Sorbiniperca*, many zeiforms and some tetraodontiforms. For example, among zeiforms there is a single vacant space (usually the 7th) in parazenids, but zeniontids have two spaces (usually the 6th and 8th) in two groups, grammicolepidids have four spaces (usually the 3rd through the 5th, and the 7th) in two groups, oreosomatids have a total of seven to nine spaces (too variable in position to enumerate here) in three groups, and most zeids have two to five spaces (variable in position) in two to four groups (two species have only a single space, the 7th). In tetraodontiforms the ancestral condition is probably two spaces (the 2nd and 4th or 5th) in two groups, but the anterior migration of the spiny dorsal fin in many specialized groups gives rise to a highly derived condition of numerous spaces in a single large gap. Therefore, the vacant interneural space condition in *Sorbiniperca* is most similar to that of many zeiforms and some of the more primitive tetraodontiforms.

11. Neural spine orientation

In *Sorbiniperca* some of the neural spines of the more posterior abdominal vertebrae have a slight anterodorsal slant. This is a derived condition because nearly all of the more typical and basal perciforms and beryciforms have these neural spines with a posterodorsal orientation, like the preceding and succeeding ones. Anterodorsally slanting neurals, however, are found in some genera in a wide variety of at least perciform families, and this derived condition apparently has appeared numerous times independently. Among the groups under consideration, only tetraodontiforms have no species with some anterodorsally slanting abdominal neural spines. By contrast, three (zeids, oreosomatids, grammicolepidids) of the five families of zeiforms have nearly all of their species with anterodorsally slanting neurals. All of the other groups under consideration have at least some species with anterodorsally slanting neurals, even though in most cases the majority of species of these groups have the primitive posterodorsally slanting condition. Those taxa with anterodorsally slanting neurals are as follows: slightly so in *Antigonia* among caproids; very slightly so in some specimens of the acanthonemid *Acanthonemus subaureus*, at least of the strengthening ridge; slightly so in *Platax* and strongly so in *Eoplatax* among ephippidids; slightly so in some *Selenotoca* among scatophagids; slightly so in zanclids, some luvarids and some Eocene acanthurids among acanthuroids. Just as with the hypural cleft character, there are so many independent acquisitions of slightly anteriorly slanting abdominal neural spines that this feature is not useful in establishing the relationships of *Sorbiniperca*.

12. Branchiostegals rays

In *Sorbiniperca* there are 2 + 4 = 6 branchiostegal rays. Among acanthopterygians, this is a derived condition because most beryciforms have eight branchiostegals and most perciforms have seven (Zehren 1979; Johnson 1984; Johnson & Patterson 1993), although within perciforms many families have reduced (often independently) the number to six (McAllister 1968; Johnson 1984). Among the groups under consideration, all zeiforms have the primitive perciform number of 3 + 4 = 7, with the single exception of the perhaps paedomorphic and poorly known *Macrurocyttus acanthopodus*, which has 2 + 4 = 6. There is no reason to believe that *Macrurocyttus* is a basal zeiform, but, rather, it is probably a specialized zeniontid. The ancestral condition for tetraodontiforms also is 3 + 4 = 7 as found in the morphologically primitive Upper Cretaceous clade (Tyler & Sorbini 1996), although all of the Eocene to recent clades have 2 + 4 = 6 or fewer branchiostegals. In most of the other groups (caproids, acanthonemids, ephippidids, scatophagids) there are 2 + 4 = 6 branchiostegals. In acanthuroids the rays are reduced to 1 + 4 = 5 in all species of the four Recent families (branchiostegals unknown in the fossil Kushlukiidae), except they are further reduced to four in a few *Zanclus* among zanclids and *Naso* among acanthurids.

13. Anal-fin spines

In *Sorbiniperca* there are five anal-fin spines. This is a derived condition because three anal-fin spines is accepted as the primitive condition for perciforms (Johnson 1984), and beryciforms usually have between two and four anal spines, often three or none, and in only one family are there as many as five (Keene & Tighe 1984). Of the other groups under consideration, many have three (caproids, ephippidids) or four (acanthonemids, scatophagids) anal spines. Zeiforms have between one and four anal spines, usually two or three (with four anal spines only in one derived genus of zeid, *Zeus*, in which a small minority of specimens of one species, *Z. faber*, have five anal spines), with the single exception of no anal spines in *Macrurocyttus acanthopodus*, which is of uncertain relationships. Tetraodontiforms have a specialized loss of all anal spines. Acanthuroids have variable numbers of anal-fin spines, with three in acanthurids and zanclids, none in luvaroids, and an increased number in siganids. In the latter family, four anal-fin spines has been shown to be the ancestral condition and the further increase up to between six and eight more derived (Tyler & Bannikov 1997; none of the taxa of siganids so far known have five anal-fin spines). Thus, the five anal spines of *Sorbiniperca* is similar only to the trend within the siganids and not to any particular taxon or to the ancestral condition for that family.

14. Dorsal-fin spines

In *Sorbiniperca* there are eight dorsal-fin spines. This is a moderate number that helps distinguish the family but which cannot be polarized because of the wide range of numbers of dorsal spines found even among the various families of beryciforms and perciforms among acanthopterygians. Among the groups under consideration, dorsal-fin spine numbers are as follows: zeiforms 5–10; tetraodontiforms 6 primitive, but reduced or absent in many groups; caproids usually 8 or 9, rarely 7 or 10; acanthonemids 9; ephippidids 5–11; scatophagids 11–12; acanthuroids 0–14 (with as many as 11–14 only in siganids; 3 or fewer with ontogenetic change in luvaroids; 7 in zanclids; and 4–9 in acanthurids). Thus, the range in dorsal-fin spine counts in all of the major groups includes or is close to the number found in *Sorbiniperca,* with the exception of tetraodontiforms, which always have fewer dorsal spines than in *Sorbiniperca.*

15. Pelvic-fin

In *Sorbiniperca* the pelvic fin has a spine and four soft rays. This is a derived condition because the primitive condition for perciforms is five rays (with representatives of only five families of perciforms reducing that number; Johnson 1984) and beryciforms have five or more rays in all families except for two with reduced or absent rays (Keene & Tighe 1984), with reductions from seven or eight rays considered specialized (Zehren 1979; Johnson & Patterson 1993). In most of the groups under consideration (caproids, acanthonemids, ephippidids, scatophagids), the perciform ancestral I,5 condition is present.

In acanthuroids a wide variety of pelvic fin conditions are present: I,5 in zanclids and most acanthurids, except reduced to three rays in several genera of acanthurids; I,4 or fewer rays with ontogenetic change in luvaroids; and I,3 or I,3,I in siganids (a minority of specimens of one fossil siganid, *Ruffoichthys spinosus,* have five rays; Tyler & Bannikov 1997). The I,5 condition can be considered ancestral for acanthuroids, as that is the condition in all of its near outgroups.

In tetraodontiforms the ancestral condition can be documented on the basis of all known fossil and Recent taxa as I,2 (Tyler & Sorbini 1996), with this being the condition found in the two most primitive clades (the Upper Cretaceous plectocretacicoids and the Recent triacanthoids). However, one primitive tetraodontoid, the Eocene *Eoplectus bloti* (Eoplectidae), has a reversal to an I,4 pelvic fin that probably represents an even more ancestral condition that can be expected to be found in some even earlier tetraodontiform clade than presently known. Thus, it is instructive that one primitive fossil clade of tetraodontiforms, the eoplectids, has the same slight reduction in pelvic rays as found in *Sorbiniperca.*

Those zeiforms with a pelvic-fin spine usually have six to seven rays (but I,5 in one species of oreosomatid, *Pseudocyttus maculatus*); when the pelvic spine is absent, there are six to nine rays. Exceptional to this among zeiforms is *Macrurocyttus acanthopodus,* of uncertain relationships, which has a I,3 pelvic fin.

Thus, of all the groups under consideration, only some luvaroids and one tetraodontiform have the same pelvic-fin formula as *Sorbiniperca,* and neither represent the documented ancestral conditions for their groups.

16. Teeth

In *Sorbiniperca* the teeth are mostly rounded, with slightly less wide, bluntly tapering cones distally. This is a highly specialized condition. This condition is unknown among beryciforms and most other major groups of acanthopterygians, including all of the groups under consideration herein, which at least ancestrally have small to moderate-sized conical or slender elongate teeth, although with many secondary specializations within many of the families, especially among tetraodontiforms and acanthuroids.

Among perciforms, there is only one family, the Sparidae, that has teeth at least somewhat like those of *Sorbiniperca.* In many sparids the outer series of teeth along the sides of the jaw are rounded and have a slightly tapering or constricted distal region, somewhat similar to those along the side of the jaw in *Sorbiniperca.* In addition, the teeth in the front of the jaw of *Sorbiniperca* and sparids are larger than those positioned posterolaterally. These front teeth are only slightly enlarged in *Sorbiniperca* but often much enlarged and heavily conical in sparids. In both cases the lateral crushing and grinding teeth are probably a similar adaptation for a hard-shelled diet of mollusks and crustaceans.

Sparids lack most of the more significant derived features of *Sorbiniperca.* For example, sparids have 10 + 14 vertebrae, three anal-fin spines, I,5 pelvic fin, 17 principal caudal-fin rays, first dorsal pterygiophore in second interneural space, no vacant interneural spaces, no anterodorsally slanting abdominal neural spines, two supernumerary dorsal-fin spines, three supraneurals, and three epurals, whereas *Sorbiniperca* has derived conditions for all of these characters. Given that there are many convergences in dentition among perciforms and that sparids are typical generalized perciforms in most respects, it can be presumed that the single derived dentition feature of similarity between *Sorbiniperca* and sparids is convergent. The consolidated hypurals and deep cleft between the second and third hypurals in some sparids is similarly considered independent of these conditions in *Sorbiniperca* because these are so homoplastic among perciforms.

Another group with the outermost row of lateral teeth somewhat like those of *Sorbiniperca* is the non-teleost pycnodontids, which became extinct in the Eocene but which also is present at Monte Bolca and with which *Sorbiniperca* would perhaps have competed for food. Pycnodontids are so remote phylogenetically from acanthopterygians that the partial similarity in dentition with *Sorbiniperca* is convergent. The teeth laterally in the jaws of some perciform labrids are somewhat rounded, but these probably are not ancestral for that family. *Sorbiniperca* otherwise has no suite of shared derived features with labrids, and it shows no evidence of a specialized pharyngeal mill that is characteristic of labrids.

Discussion

As detailed above and summarized in Table 1, *Sorbiniperca* shares one or more derived features with each of the groups under consideration. Excluding the few characters that are exceptionally variable within the higher taxa (no. 11) or in which *Sorbiniperca* has relatively primitive (no. 9), unpolarizable (no. 14), or unique (no. 16) conditions, these combinations are as follows.

Sorbiniperca shares with zeiforms the following characters: no. 1; no. 2; no. 3; no. 4; no. 5 (with the exception of a few specialized taxa that have lost one of the two epurals that are ancestral for zeiforms); no. 6; no. 7 (in the sense of reduction of principal caudal-fin rays to less than 16 or 17; 14 in *Sorbiniperca* and 13–15 in zeiforms); no. 10 (in the sense of vacant interneural spaces increased to two or more spaces in two or more groups, with three vacant in two groups in *Sorbiniperca*, and zeiforms usually with two to five spaces in two to four groups); no. 12 (but this in only a single species of zeiform, *Macrurocyttus acanthopodus*, that is probably paedomorphic and not basal to zeiform phylogeny, all other zeiforms having seven branchiostegals); no. 15 (in the sense of reduction of rays to less than five, and this only in *Macrurocyttus acanthopodus* (I,3), all other zeiforms having five to nine rays).

Sorbiniperca shares with tetraodontiforms the following characters: no. 1; no. 3 (shared with all of the more basal tetraodontiforms, with only some of the more derived taxa having shorter NPU2); no. 4 (but only in part, and only with the more derived taxa within tetraodontiforms, the ancestral condition for tetraodontiforms being the presence of a uroneural, as found in two of the three taxa of Upper Cretaceous plectocretacicoids and in the phyletically basal triacanthoids and triodontids); no. 6 (but only in part, with consolidated hypurals probably ancestral for the order and reversed in a few families, albeit some of the more morphologically primitive ones among the Recent taxa); no. 7 (in the sense of reduction of principal caudal-fin rays to less than 16 or 17; 14 in *Sorbiniperca* and 12–14 in tetraodontiforms); no. 8 (in the sense of reduced vertebral numbers of 20 or 21 in *Sorbiniperca* and 20 or 21 primitively for tetraodontiforms and often further reduced in its more specialized clades); no. 10 (in the sense of vacant interneural spaces increased to two or more spaces in two or more groups, with three vacant in two groups in *Sorbiniperca* and ancestrally for tetraodontiforms two spaces in two groups, even thought many advanced tetraodontiforms have many spaces vacant in one group); no. 12 (but only with the advanced Eocene to Recent clades, with seven branchiostegals being ancestral for tetraodontiforms, as found in the Upper Cretaceous clade); no. 15 (in the sense of reduction of rays to less than five, with I,2 ancestral for tetraodontiforms and one primitive Eocene species, *Eoplectus bloti*, having I,4 like *Sorbiniperca*).

Sorbiniperca shares with caproids the following characters: no. 1; no. 7 (in the sense of reduction of principal caudal-fin rays to less than 16 or 17; 14 in *Sorbiniperca* and 12–14 in caproids); no. 12.

Sorbiniperca shares with acanthonemids the following characters: no. 2; no. 12.

Sorbiniperca shares with ephippidids the following characters: no. 2 (but only in part, with the derived condition found only in a few taxa that are not known to be basal in ephippidid phylogeny; the ancestral condition for ephippidids is two supernumerary spines, as found in the scatophagid basal member of the acanthuroid sistergroup and in the higher squamipinne outgroup); no. 12.

Sorbiniperca shares with scatophagids the following characters: no. 3 (but only with the two fossil genera, in which this condition is derived relative to the ancestral condition of a short NPU2, as found in the acanthuroid sistergroup and the ephippidid outgroup); no. 12.

Sorbiniperca shares with various families of acanthuroids the following characters: no. 1 (but only in part, and this is not the ancestral condition for acanthuroids, which is the shaft situated in the first interneural space as in siganids and the scatophagid outgroup, with the preneural placement of the shaft a derived feature of only three families higher in the clade, namely luvarids, zanclids, acanthurids, with further specialization by the shaft being in the third or fourth space in kushlukiids associated with posterior migration of the spiny dorsal fin); no. 2 (but only in part, with the derived condition found in only a few taxa of siganids and zanclids that are not known to be basal in acanthuroid phylogeny; the ancestral condition for acanthuroids is two supernumerary spines, as found in the scatophagid sistergroup); no. 5 (but only in part, with the derived condition found in only a few taxa of acanthurids deeply nested within the clade and whose ancestral condition is three epurals, and in adult but not larval luvarids); no. 6 (but only in part, with luvaroids and a few highly specialized taxa of acanthurids, whereas the ancestral condition for acanthuroids clearly is unconsolidated hypurals); no. 13 (in the sense of anal-fin spine numbers increased to five or more, and this only with the trend in the more advanced of the genera of siganids, in which the number increases from four to eight, with three or four anal spines being ancestral for acanthuroids); no. 15 (in the sense of reduction of rays to less than five, with many genera of several families, namely siganids, luvaroids, acanthurids, having only three or four rays, even though the ancestral number of acanthuroids is five rays, as in the scatophagid sistergroup and ephippidid outgroup).

It is obvious from the above, as well as the synopsis of characters given in Table 1, that *Sorbiniperca* shares only a few derived features with acanthonemids and the higher squamipinne ephippidids and scatophagids. Moreover, the somewhat larger number of derived features that *Sorbiniperca* shares with the acanthuroid sistergroup of these higher squamipinnes are

Tab. 1. Comparison of morphological features of Sorbinipercidae with other higher taxa. Earliest occurrence of these higher taxa are Upper Cretaceous: Tetraodontiformes; Upper Paleocene: Zeiformes; Lower Eocene: Siganidae, Luvaridae, Kushlukiidae; and Middle Eocene: Caproidae, Acanthonemidae, Ephippididae, Scatophagidae, Zanclidae, Acanthuridae. There is good evidence for a sistergroup relationship between zeiforms and tetraodontiforms, but caproids are of uncertain relationship to them and to perciforms. The relationships of acanthonemids (monotypic) are uncertain (e.g., carangid, acanthuroid?), but the higher squamipinne perciforms and acanthuroids have a well-documented phyletic sequence as given in the table for the ephippidid through acanthurid famial clades.

Character	†SORBINIPERCIDAE	ZEIFORMES	TETRAODONTIFORMES	CAPROIDAE	†ACANTHONEMIDAE
1. First dorsal pterygiophore position	In preneural space, to rear to skull	In preneural space, to rear of skull*	In preneural space, to rear of skull*	In preneural space, to rear of skull	In first interneural space
2. Supernumerary dorsal-fin spines	1	1	2	2	1
3. NPU2 length	Long	Long	Long*	Short	Short
4. Uroneurals	0	0	1 ancestrally; 0 secondarily	1	2
5. Epurals	2	2*	1–0*	3	3
6. Hypural consolidation	Nos. 1–4 consolidated	Nos. 1–4 consolidated	Nos. 1–4 separate or consolidated	All separate	All separate
7. Caudal fin principal rays	14	13 in four families; 15 in one family*	12 or fewer in all except 14 in one family	12 or 14	17
8. Vertebrae	20–21	27–46	20–21 or less*	22	23
9. Supraneurals	2	1 in most; 0 in a few	0	0 or 2	0
10. Vacant interneural spaces	3 spaces in 2 groups	1–9 spaces in 1–4 groups	1–8 spaces in 1–2 groups	1 space (5th to 7th)	1 space (5th)
11. Neural spine orientation	Some anterodorsal	Some anterodorsal in 3 of 5 families	Posterodorsal	Posterodorsal or anterodorsal	Vertical to posterodorsal*
12. Branchiostegals	2 + 4 = 6	3 + 4 = 7*	3 + 4 = 7; 2 + 4 = 6 or fewer	2 + 4 = 6	2 + 4 = 6
13. Anal-fin spines	5	1–4*	0	3	4
14. Dorsal-fin spines	8	5–10	0–6	8–9*	9
15. Pelvic-fin rays	4	6–9 in most; 5 in one; 3 in one	2 ancestrally; 0–1 secondarily; 4 in one	5	5
16. Teeth	Rounded, large, molariform	Small, conical	Small, conical ancestrally; many secondary modifications	Small, conical	Small, conical

† Exclusively fossil taxa.
* Exceptions, none of which are ancestral for that higher taxon, discussed in the text.

nearly all with features that are not ancestral for acanthuroids but, rather, are found only as specializations within a few families or genera to which *Sorbiniperca* otherwise has few derived similarities. Moreover, these few derived features of similarity of *Sorbiniperca* with acanthuroids are widely scattered among the many families of acanthuroids and not to any one of them in particular. In each case *Sorbiniperca* lacks the majority of the defining synapomorphies of these various families of higher squamipinnes and acanthuroids.

Sorbiniperca shares a few notable derived features with caproids, especially the shaft of the first dorsal pterygiophore in the preneural space (no. 1), caudal fin reduced to 12–14 principal rays (no. 7), and 2 + 4 = 6 branchiostegals (no. 12); caproids also have reduced the numbers of vertebrae to 22, although not so reduced as in *Sorbiniperca* to 20 or 21. However, two of these features (pterygiophore position and caudal-fin ray reduction) also are found in zeiforms and tetraodontiforms, and it remains unclear whether these and a few other similarities are indications of a relationship between caproids, zeiforms, and tetraodontiforms or whether caproids are more closely related to percomorphs (Johnson & Patterson 1993).

What is most obvious is that *Sorbiniperca* shares a much larger number of derived features with zeiforms and tetraodontiforms than with the other groups. This is especially true for those features documented to be ancestral for one or both of these orders, or in which zeiforms or tetraodontiforms

		ACANTHUROIDEI			
EPHIPPIDIDAE	SCATOPHAGIDAE	SIGANIDAE	LUVARIDAE (L) †KUSHLUKIIDAE (K)	ZANCLIDAE	ACANTHURIDAE
In second interneural space	In first interneural space	In first interneural space	In preneural space, sometimes to rear of skull(L); in 3rd or 4th interneural space(K)	In preneural space, to rear of skull	In preneural space, to rear of skull
2*	2	2*	2	1 or 2	2
Short	Short or long	Short	Short	Short	Short
2	1	1	1	1	1
3	3	3	1–3	3	3*
All separate	All separate	All separate	Nos. 1–4 consolidated	All separate	All separate*
17	16	17	16	16	16
24	23	23	22(L); 29–30(K)	22	22
3	2	0 in most; 1 in one	0	1	0 or 1
1 space (6th) in most; none in several	1 space (usually 6th or 7th)	1 space (5th or 6th)	1 space (3rd to 5th) or none	1 space (3rd)	1 space (3rd)*
Usually vertical to posterodorsal; anterodorsal in some	Usually vertical to posterodorsal; anterodorsal in a few	Usually vertical to posterodorsal; anterodorsal in a few	Usually posterodorsal; anterodorsal in some	Some anterodorsal	Usually posterodorsal; anterodorsal in a few
2 + 4 = 6	2 + 4 = 6	1 + 4 = 5	1 + 4 = 5	1 + 4 = 5*	1 + 4 = 5; 0 + 4 = 4
3	4	4–8	0	3	3
5–11	11–12	11–14	0–3	7	4–9
5	5	3*	0–4	5	5 in most; 3 in some
Elongate, setiform	Elongate, setiform	Conical to flattened	Small, conical; or absent	Elongate, setiform	Small, stout, conical to flattened and elongate, setiform

have even more specialized conditions in reductive features that could be easily derived from the condition as found in *Sorbiniperca*. Some of these are shared with both of these orders and some are shared only with one or the other order.

Thus, *Sorbiniperca* shares with both zeiforms and tetraodontiforms the following features: the positioning of the first dorsal-fin pterygiophore in the preneural space (no. 1, but with a less specialized plastering of the first neural spine to the skull in *Sorbiniperca*); the reduction in principal caudal-fin rays to 14 or less (no. 7, with the exception of apparently secondary increase to 15 in one specialized family of zeiforms, and even further reduction in most tetraodontiforms to 12); the increase to two or more vacant interneural spaces in two or more groups (no. 10); epurals reduced to two or fewer (no. 5, with tetraodontiforms usually further reduced to one or none but by reversal to three in one of the Upper Cretaceous species); the long neural spine on the penultimate centrum (no. 3, with only some specialized tetraodontiforms secondarily shortening the NPU2).

Sorbiniperca shares with zeiforms but not tetraodontiforms several other derived features: consolidated hypurals (no. 6, these being free ancestrally for tetraodontiforms, but consolidated in many advanced families); a single supernumerary dorsal-fin spine (no. 2, there always being two supernumerary spines in those tetraodontiforms with a spiny dorsal fin); the absence of free uroneurals (no. 4, with a uroneural being present ancestrally in tetraodontiforms, but lost in most advanced families); some slightly anterodorsally oblique neural spines (three of the five families of zeiforms have this condition, probably ancestrally, but not any tetraodontiforms).

Sorbiniperca shares with tetraodontiforms but not zeiforms the following derived features: reduction in number of pelvic-fin rays (to four in both *Sorbiniperca* and one primitive tetraodontiform indicating reversal to a hypothetical ancestral condition even though all other tetraodontiforms presently known have only two or fewer pelvic rays; one specialized zeiform has only three rays but this is not an ancestral condition, and nearly all other zeiforms have six to nine rays); reduction in number of vertebrae to 20 or 21 (whereas most zeiforms have 30 or more vertebrae, and only one genus has as few as 27 or 28).

In spite of the many derived features *Sorbiniperca* shares with zeiforms and/or tetraodontiforms, some of which are also present in many percomorph groups, *Sorbiniperca* lacks many of the more fundamental derived features of both zeiforms and tetraodontiforms.

For example, all tetraodontiforms have completely lost anal-fin spines, whereas *Sorbiniperca* has an opposite trend, to an increased number of five anal spines; tetraodontiforms have a reduced number of dorsal-fin spines, no more than six and usually three to none, whereas *Sorbiniperca* has a moderate number of eight dorsal spines; with one exception by reversal, all tetraodontiforms have 12 or fewer principal caudal-fin rays (the exception being the Upper Cretaceous *Plectocretacicus* with 14), whereas *Sorbiniperca* has 14; with one exception by reversal, all tetraodontiforms have only one or no epurals (the exception being *Plectocretacicus* with three), whereas *Sorbiniperca* has two; at least ancestrally, tetraodontiforms lack pleural ribs (a few taxa by reversal have pleurals present, see Tyler 1980, and Tyler & Sorbini 1996), whereas *Sorbiniperca* has a full complement of pleural ribs.

Of the 16 features analyzed above, only one is somewhat more derived ancestrally for zeiforms than the condition in *Sorbiniperca:* the ancestral number of principal caudal-fin rays in zeiforms is 13 and thus more reduced than the 14 of *Sorbiniperca* (reversal among zeiforms to a higher number, 15, only in grammicolepidids). There are, however, several other derived features (see Winterbottom et al., manuscript, and Bonde & Tyler, in press) of zeiforms that are absent in *Sorbiniperca.* For example, all zeiforms have lost the pleural ribs on the first four abdominal vertebrae, whereas *Sorbiniperca* has the more primitive condition of pleurals beginning on the second abdominal vertebra; all zeiforms have a specialized parhypural, which ancestrally is foreshortened and out of contact with the centrum (but with a secondarily derived ball and socket articulation with the centrum in grammicolepidids), whereas *Sorbiniperca* has a normal parhypural making unmodified contact with the centrum; at least ancestrally, zeiforms have a locking mechanism between two or more of the dorsal-fin spines (secondarily lost in some zeids and one oreosomatid), whereas it is apparent from the positioning of the bases of the dorsal spines in *Sorbiniperca,* out of contact with one another, that no locking mechanism is present; at least ancestrally, zeiforms have a locking mechanism between the first and second anal-fin spines (when two or more spines are present) (secondarily lost in some zeids and one grammicolepidid), whereas this is absent in *Sorbiniperca,* the spine bases not being in contact; all zeiforms have a metapterygoid that is reduced in size and somewhat remote from the quadrate, whereas this bone apparently is of moderate size and not remote from the quadrate in *Sorbiniperca;* all zeiforms have the distal ends of the dorsal fin pterygiophores laterally expanded (Johnson & Patterson 1993, p. 596), whereas *Sorbiniperca* lacks these but has a different derived condition of upright flanges alongside the base of the first spine.

Moreover, *Sorbiniperca* lacks three derived conditions found in both zeiforms and tetraodontiforms. *Sorbiniperca* has at least the upper region of the neural spine of the first vertebra free from the skull, whereas this is far more extensively plastered to the skull in zeiforms and tetraodontiforms (and caproids). *Sorbiniperca* has two supraneurals, but these are reduced to one or none in zeiforms and are completely absent in tetraodontiforms (two or none in caproids). *Sorbiniperca* has somewhat asymmetrical or posteriorly curved distal regions of the soft dorsal- and anal-fin pterygiophores, like most other acanthopterygians, versus these being symmetrical or relatively straight in zeiforms and tetraodontiforms (and caproids) (Rosen 1984; Winterbottom et al., manuscript).

Thus, *Sorbiniperca* can have no more than a sistergroup relationship to the combined zeiform + tetraodontiform clade, and it may be a sister taxa at an even lower level to a group that includes some caproid-like "perciforms".

And *Sorbiniperca* has more derived conditions of three features than is ancestral for zeiforms and tetraodontiforms, which would be autapomorphic at this level. *Sorbiniperca* has highly specialized rounded teeth, versus conical in zeiforms and primitive tetraodontiforms, in which, however, many secondary dental specializations occur in advanced clades (conical also in caproids). *Sorbiniperca* has a moderately specialized branchiostegal ray condition of 2 + 4 = 6, versus 3 + 4 = 7 ancestrally in zeiforms and tetraodontiforms, even though most tetraodontiforms have secondarily reduced the number to 2 + 4 = 6 (also 2 + 4 = 6 in caproids). *Sorbiniperca* has an increase to five anal-fin spines, versus usually 1–3, rarely 4 in zeiforms and none in tetraodontiforms (3 in caproids).

Conclusion

Sorbiniperca scheuchzeri, gen. & sp. nov., shares many derived features with zeiforms and tetraodontiforms, some of which are also found in several groups of percomorph fishes. But *Sorbiniperca* also lacks many of the fundamental defining synapomorphies of both zeiforms and tetraodontiforms individually, and of the combined zeiform + tetraodontiform clade. Moreover, *Sorbiniperca* has a unique combination of derived features found in none of the other groups under discussion. *Sorbiniperca* is unique enough to warrant familial recognition as the Sorbinipercidae, but it cannot be accommodated conveniently within any ordinal category, especially because of the uncertain relationship of the zeiform + tetraodontiform clade with caproids and of the latter with percomorphs and more typical perciforms.

Therefore, it can only be suggested here that the Sorbinipercidae diverged near to the common ancestry of the zeiform + tetraodontiform clade with the caproid-like percomorphs and the euacanthopterygians; i.e., *Sorbiniperca* may have a sistergroup relationship with zeiforms + tetraodontiforms, or with them plus caproids, or within some even larger clade including caproids and other lower percomorphs. Until the issue of caproid, percomorph, and zeiform + tetraodontiform relationships is resolved, the Sorbinipercidae can be placed incertae sedis among the acanthopterygians near to one of the branchings of the zeiform + tetraodontiform, beryciform, and percomorph clades from one another.

If, as proposed here, *Sorbiniperca* is in some ill-defined way a linage in proximity to the branching of the zeiform + tetraodontiform and caproid-like percomorph clades, then it is especially interesting that the earliest known members of these clades are all relatively small in size. The specimens of the three Upper Cretaceous taxa of tetraodontiforms range from 10–25 mm SL (Tyler & Sorbini 1996), those of the two Paleocene taxa of zeiforms from 9–11 mm SL (Bonde & Tyler, in press), the single Eocene specimen of caproid is 21 mm SL (Sorbini 1988), and the three specimens of *Sorbiniperca* range from 21–26 mm SL. These diminutive sizes may indicate that paedomorphic influences were associated with the early evolution of these groups, all of which today have the great majority of their species with far larger body sizes.

Acknowledgments

The generous help received from the following individuals and institutions toward the completion of this study is greatly appreciated.

Prof. Dr. H. Rieber (Direktor), Dr. K.A. Hünermann, and Dr. Heinz Furrer, of the Paläontologisches Institut und Museum der Universität Zürich, and Dr. Heinz Balmer, Medizinhistorisches Museum der Universität Zürich, provided access to and information about the history of the specimen of *Sorbiniperca* that was first illustrated by J.J. Scheuchzer, arranged to have it taken temporarily off exhibit to facilitate this study, and provided me with excellent photographs of it. Dr. Urs Leu, Zentralbibliothek, Zürich, made available several of the Scheuchzer books.

Dr. Ortwin Schultz, of the Naturhistorisches Museum Wien, was equally helpful in the examination of the Vienna specimen. He provided much information about the history of its acquisition and study by J.J. Heckel, as well as excellent photographs of it.

Prof. Dr. Lorenzo Sorbini, the late and much beloved director of the Museo Civico di Storia Naturale di Verona, knowing of my interest in the Zürich and Vienna specimens, located the third specimen among the more recent excavations from Monte Bolca and encouraged its study and inclusion in this paper. Also at the Verona museum, I thank Dr. Alessandra Aspes for her help since the absence of Prof. Sorbini.

Dr. Jean Gaudant, Université Paris, provided information on the history of Scheuchzer's work on fossil fishes.

Mrs. Diane M. Tyler composed and typeset the table.

The manuscript was improved by the reviews of: Dr. Toni Bürgin, Naturmuseum, St. Gallen, and Dr. Norbert Micklich, Hessisches Landesmuseum, Darmstadt.

REFERENCES

BANNIKOV, A.F. 1991: On the systematic position of the family Caproidae with reference to the Eocene genus *Acanthonemus*. Voprosy Ikhtiologii 31/2, 179–188 [in Russian; translated in Journal of Ichthyology 31/2, 47–58].

BANNIKOV, A.F. & TYLER, J.C. 1995: Phylogenetic revision of the fish families Luvaridae and †Kushlukiidae (Acanthuroidei), with a new genus and two new species of Eocene luvarids. Smithsonian Contributions to Paleobiology 81, 1–45.

BLOT, J. 1980: La fauna ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie). Catalogue systématique présentant l'état actuel des recherches concernant cette faune. Bulletin du Muséum National d'Histoire Naturelle, series 4, 2/c,4, 339–396.

BONDE, N. & TYLER, J.C. In press: Two new genera and species of zeiform fishes from the Late Paleocene (Mo-clay) of Denmark; the earliest record of the order. Meddelelser fra Dansk Geologisk Forening.

DEAN, B. 1923: A bibliography of fishes. Volume III. American Museum of Natural History, New York, 1–707.

FRICKHINGER, K.A. 1991: Fossilien Atlas. Fische. Verlag für Natur- und Heimtierkunde, H.A. Baensch, Melle, 1–1088.

FUJITA, K. 1990: The caudal skeleton of teleostean fishes. Tokai University Press, Tokyo, 1–897.

GAUDANT, J. 1997: Les poissons pétrifiés du Monte Bolca (Italie) et leur influence sur les théories de la Terre au milieu du Siècle des lumières, d'après un manuscrit inachevé de Jean-François Séguier (1703–1784). Bulletin de la Société Géologique de France, 168/5, 675–683.

GAUDANT, J. & BOUILLET, G. 1997: Aux sources de la paléoichthyologie: les Doléances et Revendications des Poissons (Piscium Querelae et Vindiciae) de Johann Jakob Scheuchzer (1708). Comité des Travaux Historiques et Scientifiques, Section de la Géologie à Son Histoire, 1997, 37–59.

GOSLINE, W.A. 1968: The suborders of perciform fishes. Proceedings of the United States National Museum 124/3647, 1–77.

GRIMM, J. & GRIMM, W. 1889: Deutsches Wörterbuch. Band 13. Deutscher Taschenbuch Verlag, Leipzig, 2386 columns.

GUIASU, R.C. & WINTERBOTTOM, R. 1993: Osteological evidence for the phylogeny of Recent genera of surgeonfishes (Percomorpha, Acanthuridae). Copeia 1993/2, 300–312.

HECKEL, J.J. 1848: Untersuchungen über die fossilen Fische des österreichischen Kaiserstaates. Berichte über die Mittheilungen von Freunden der Naturwissenschaften in Wien (Haidinger) 3/1–6, 327–330.

– 1849: Untersuchungen der fossilen Fische des Österreichischen Kaiser-Staates. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde (Leonhard und Bronn), Jahrgang 1849, 499–500.

HÜNERMANN, K.A. & RIEBER, H.P. 1988: Johann Jakob Scheuchzer (1672–1733), ein bedeutender Sohn Zürichs. Ausstellung des Paläontologischen Institutes und des Museums der Universität Zürich in der SBG Zürich-Römerhof, 1–24.

JOHNSON, G.D. 1984: Percoidei: development and relationships. In: Ontogeny and systematics of fishes (Ed. in chief, H.G. MOSER). American Society of Ichthyologists and Herpetologists, Special Publication 1, 464–498.

JOHNSON, G.D. & PATTERSON, C. 1993: Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52/1, 554–626.

KEENE, M.J. & TIGHE, K.A. 1984: Beryciformes: development and relationships. In: Ontogeny and systematics of fishes (Ed. in chief, H.G. MOSER). American Society of Ichthyologists and Herpetologists, Special Publication 1, 383–392.

MCALLISTER, D.E. 1968: The evolution of branchiostegals and associated opercular, gular, and hyoid bones and the classification of teleostome fishes, both living and fossil. Bulletin of the National Museum of Canada, 221/Biol. Ser. 77, 1–239.

PATTERSON, C. 1992: Supernumerary median fin-rays in teleostean fishes. Zoological Journal of the Linnean Society 106, 147–161.

ROSEN, D.E. 1984: Zeiforms as primitive plectognath fishes. American Museum Novitates 2782, 1–45.

SCHEUCHZER, J.J. 1708: Piscium querelae et vindiciae. Typis Gessnerianis, Tiguri [Zürich], 1–36, 5 plates.
– 1709: Herbarium diluvianum collectum. Literis Davidis Gessneri, Tiguri, 1–44, 10 plates.
– 1723: Herbarium diluvianum, editio novissima, duplo auctior. Petri Vander Aa, Lugduni Batavorum [Leiden], 1–119, 14 plates.
– 1731a: Kupfer-Bibel. In welcher Die Physica Sacra. 1. Band. C.U. Wagner, Augsburg und Ulm, 1–276, 174 plates. [Latin version of this published in 1731 in Ulm, see Dean 1923].
– 1731b: Physica sacra ... Iconibus aeneis illustrata. Tomus I. Auguste Vindelicorum, Ulmae, 1–272, 225 plates. [French version of this published in 1732 in Amsterdam, see Dean 1923].
SORBINI, L. 1988: *Antigonia veronensis*, an Eocene caproid from Bolca (Italy). Bollettino del Museo Civico di Storia Naturale di Verona 14/for 1987, 255–269.
STEINDACHNER, F. 1901: Geschichte der Zoologie in Österreich von 1850 bis 1900. Fische. Festschrift [Anlässich des Fünfzigjährigen Bestandes] der Kaiserlich-Koenigliche Zoologisch-Botanische Gesellschaft in Wien 1901, 407–443.
TYLER, J.C. 1980: Osteology, phylogeny, and higher classification of the fishes of the Order Plectognathi (Tetraodontiformes). National Oceanic and Atmospheric Administration, Technical Report, National Marine Fisheries Service, Circular 434, 1–422.
– 1997: The Miocene fish *Marosichthys*, a putative tetraodontiform, actually a perciform surgeon fish (Acanthuridae) related to the Recent *Naso*. Beaufortia 47/1, 1–10.
TYLER, J.C. & BANNIKOV, A.F. 1997: Relationships of the fossil and Recent genera of rabbitfishes (Acanthuroidei: Siganidae). Smithsonian Contributions to Paleobiology 84, 1–35.
TYLER, J.C., JOHNSON, G.D., NAKAMURA, I. & COLLETTE, B.B. 1989: Morphology of *Luvarus imperialis* (Luvaridae), with a phylogenetic analysis of the Acanthuroidei (Pisces). Smithsonian Contributions to Zoology 485, 1–78.
TYLER, J.C. & SORBINI, L. 1996: New superfamily and three new families of tetraodontiform fishes from the Upper Cretaceous: the earliest and most morphologically primitive plectognaths. Smithsonian Contributions to Paleobiology 82, 1–59.
WINTERBOTTOM, R. 1993: Myological evidence for the phylogeny of the Recent genera of surgeonfishes (Percomorpha, Acanthuridae), with comments on the Acanthuroidei. Copeia 1993/1, 21–39.
WINTERBOTTOM, R. & MCLENNAN, D.A. 1993: Cladogram versatility: evolution and biography of acanthuroid fishes. Evolution 47/5, 1557–1571.
WINTERBOTTOM, R., TYLER, J.C. & JOHNSON, G.D. Manuscript: A preliminary analysis of the interrelationships of the zeiform families, with comments on their relationship to tetraodontiforms and caproids.
WURZBACH, C. von. 1862: Biographisches Lexikon des Kaiserthums Oesterreich. Achter Theil (Hartmann–Henser). Kaiserlich-königliche Hof- und Staatsdruckerei, Wien, 1–498.
ZEHREN, S.J. 1979: The comparative osteology and phylogeny of the beryciforms (Pisces: Teleostei). Evolutionary Monographs 1, 1–389.

Manuscript received January 23, 1998
Revision accepted June 13, 1998