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

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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 be-

ruht 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, caproid del gruppo degli Acanthopterygii; va, probabilmente, situato vicino ad una delle diramazioni reciproche fra i cladi di Zeiformes + Tetraodontiformes, Beryciformes e Per-

comorpha 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 eel 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 ganz fremde Art von Platteisz aus dem Veronesischen.” Platteisz or platteisese 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

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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 Hünemann & Rieber (1988, p. 19) and as an undetermined perciform in a photograph by Frickinger (1991, p. 871). A copy of the illustration of this fish from the Herbarium Diluvianum appears in the unpublished manuscript (Les Petrifactions 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 Frankfurt. Johann Jacob Heckel, a preparator and then Adjunct Curator (see Würzbach 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 *Platix 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 monograph of the Monte Bolca ichthyofauna, examined Heckel’s specimen and agreed that it was perhaps related to the Monte Bolca *Eoplatix* (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-

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*Fig. 1. Sorbini*perca 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.*
Systematics

*Sorbiniperca scheuchzeri*: new species, new genus, and new family (Sorbinipericidae)

Holotype
Paläontologisches Institut und Museum der Universität Zürich (PIMUZ) A/12488, 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, Discaster sublodoensis Zone) of Monte Bolca, Italy.

Diagnosis
Unique among acanthuriforms 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 ziform + 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.
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.
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 1,4. 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-
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

Branched rays) and four procurent rays both above and below (iv, l, 6 + 6, l, 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.

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.

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Fig. 6. *Sorbusperca 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.

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the neural spine of the first vertebra (best seen in the holotype), in the pre neural 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 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. 7. Sorbiniperca scheuchzeri, holotype, PIMUZ A/1 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); ps – pelvic-fin ray; pc – pelvic-fin spine; s – supranal; sc – supracleithrum.
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 ab-

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Fig. 8. Sorhiniperca scheuchzeri: A, caudal skeleton, and C, teeth and tooth sockets, holotype, PIMUZ A/1 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 – procurent caudal-fin ray; ps – pelvic-fin spine.
dominal 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 stegeural 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 urocentrum, 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 large subgroup of Perciformes, the Percoidae 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 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 Acanthonemidiae) are all closely related. For the acanthuran fishes, highly corroborated hypotheses based on osteological and myological evidence (Tyler et al. 1989; Winterbottom 1993; Winterbottom & McLennan 1993; Guissard & Winterbottom 1993) indicate that the families have the phyletic sequence of Siganidae – Luvoridae (and its entire fossil sistergroup, the Kushlukidae) – Zancididae – Acanthuridae (Nasinae – Acanthurinae) and that the first and second outgroups are, respectively, the higher squamipinne Scatophagidae and Ephippidae.

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, zanelids, and acanthurids (Tyler et al. 1989). In the kushlukid 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.

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(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 platyzation 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 *Sorbiniiperca*, 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 *Sorbiniiperca*, 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 *Sorbiniiperca* 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 & Bankov 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 *Sorbiniiperca* 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 acanththiod sistergroup and the ephippidid outgroup).

4. Uroncuals

In *Sorbiniiperca* 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 plecotocacti, triacanthids, and triodontids). All of the other groups have the primitive condition of one (caproids, scatophagids, acanthurids) or two (acanthonemids, ephippidids) uroneurals.

5. Epurals

In *Sorbiniiperca* 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 acanthurids except a few derived acanthurids with only two (in the genus *Naso*) and adult luvurids 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 *Sorbiniiperca* 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 acanthurids (secondarily consolidated only in luvurids 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 *Palaecycus* 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 tricanthodids, triodontids, and the Eocene eopletids are reversals, but this has not yet been documented. Thus, it can only be noted that the derived hypural consolidat-
tion 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 clefs are found in some genera of a wide variety of percomorph and beryciform families (Fujita 1990) and also in many other acanthomorph groups, as well as in at least one zeiform (Parazen). Deep clef tings 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 percomorphs is 17 principal rays (i.8 + 7.i) (Johnson 1984; Johnson & Patterson 1993), although within percomorphs 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 acanthomids, ephippidids, and the most primitive family of acanthoideans, the siganids, have 17 principal rays (all other acanthoideans 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, Plectocretacius clarus, 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 (grammicoideids), 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 = 20 – 21, an exceptionally low number. Among percomorphs, 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 acanthomids, scatophagids, and the most basal of the families of acanthoideans, the siganids; all other acanthoideans have a further secondary reduction to 9 + 13 = 22, except for a secondary increase to 10 + 19 – 20 = 29 – 30 in kushukiids (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 percomorphs (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 acanthomids have no supraneurals. A single supraneural is ancestral for acanthoideans (with subsequent loss of the element in luaroids and some siganids and acanthoideans; 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 parazeniids and in two highly derived genera of zeoids (Zenus and Zenopsis), with the absence probably secondary. Therefore, of the groups under consideration, all but the two families of higher squamipinnipes 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 vertebrae 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 percomorphs, 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 (usually the 5th, 6th, or 7th space), acanthonemids (the 5th), ephippidids (the 6th, except none in Platax, Eoplatax, and Archaeophiippus), scatophagids (usually the 6th or 7th, rarely the 5th or 8th), and acanthurids (variously the 3rd through 6th, but none in the acanthurid Marosichthys and many luaroids; see Bannikov & Tyler 1995; Tyler & Bannikov 1997; Tyler 1997). The more derived condition of two or more more 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 parazeniids, 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 postoral orientation, like the preceding and succeeding ones. Anterodorsally slanting neural spines, 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 neural spines. All of the other groups under consideration have at least some species with anterodorsally slanting neural spines, even though in most cases the majority of species of these groups have the primitive postoral dorsally slanting condition. Those taxa with anterodorsally slanting neural spines are as follows: slightly so in Antigonia among caproids; very slightly so in some specimens of the acanthonemid Acanthonemus subarreis, at least of the strengthening ridge; slightly so in Platax and strongly so in Eoplatax among ephippidids; slightly so in some Seleotroca among scatophagids; slightly so in zanclids, some luaroids and some Eocene acanthurids among acanthuroids. Just as with the hypural cleft character, there are 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 Macrurus acanthopus, which has 2 + 4 = 6. There is no reason to believe that Macrurus acanthopus 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 acanthurids 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 Macrurus acanthopus, 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 luaroids, 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 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.

An acanthopterygian fish from the Eocene of Monte Bolca, Italy 533
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 & Tigne 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 pericorm ancestral I,5 condition is present.

In acanthuroids a wide variety of pelvic fin conditions are present: I,5 in zanclids and most acanthuroids, except reduced to three rays in several genera of acanthuroids; I,4 or fewer rays with ontogenetic change in luvaroids; and I,3 or I,3,1 in siganids (a minority of specimens of one fossil siganid, Rufiochthys 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 plectoceractioids and the Recent triacanthoids). However, one primitive tetraodontoid, the Eocene Eoplectus blunt (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 oresomatid, Pseudocottus maculatus); when the pelvic spine is absent, there are six to nine rays. Exceptional to this among zeiforms is Macrurocottus 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 known 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 spaces, 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 homoplasic among perciforms.

Another group with the outermost row of lateral teeth somewhat like those of Sorbiniperca is the non-teledont 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 some-
what 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), un polarizable (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, *Macrourycytus 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 *Macrourycytus acanthopodus* (13), 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 unconeural, as found in two of the three taxa of *Upper Cretaceous plectocretacoids* and in the phyletically basal triaenothoids and triodontoids); 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 respectively 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 1,2 ancestral for tetraodontiforms and one primitive Eocene species, *Eoplectus britoii*, having 1,4 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 acanthoid 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 acanthonemid 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 acanthurid 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 acanthuroids 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 acanthurid sistergroup of these higher squamipinnes are
Tab. 1. Comparison of morphological features of Sorbiniperca with other higher taxa. Earliest occurrence of these higher taxa are Upper Cretaceous: Tetraodontiformes; Upper Paleocene: Zeiformes; Lower Eocene: Siganidae, Luvaridae, Kushkidae; and Middle Eocene: Caproidae, Acanthonemidae, Ephippididae, Scatophagidae, Zancidiae, 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 epiphypid through acanthurid familial clades.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>SORBINIPERCIDA</em></th>
<th>ZEIFORMES</th>
<th>TETRAODONTIFORMES</th>
<th>CAPROIDAE</th>
<th><em>ACANTHONEMIDA</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1. First dorsal pterygiophore position</td>
<td>In preural space, to rear to skull</td>
<td>In preural space, to rear of skull*</td>
<td>In preural space, to rear of skull*</td>
<td>In preural space, to rear of skull</td>
<td>In first interneural space</td>
</tr>
<tr>
<td>2. Supernumerary dorsal-fin spines</td>
<td>1</td>
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<td>2</td>
<td>2</td>
<td>1</td>
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<td>3. NPU2 length</td>
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<td>Long</td>
<td>Long*</td>
<td>Short</td>
<td>Short</td>
</tr>
<tr>
<td>4. Urobranchiostegals</td>
<td>0</td>
<td>0</td>
<td>1 ancestral; 0 secondarily</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>5. Epurals</td>
<td>2</td>
<td>2*</td>
<td>1-0*</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>6. Hyural consolidation</td>
<td>Nos. 1-4 consolidated</td>
<td>Nos. 1-4 consolidated</td>
<td>Nos. 1-4 separate or consolidated</td>
<td>All separate</td>
<td>All separate</td>
</tr>
<tr>
<td>7. Caudal fin principal rays</td>
<td>14</td>
<td>13 in four families; 15 in one family*</td>
<td>12 or fewer in all except 14 in one family</td>
<td>12 or 14</td>
<td>17</td>
</tr>
<tr>
<td>8. Vertebræ</td>
<td>20-21</td>
<td>27-46</td>
<td>20-21 or less*</td>
<td>22</td>
<td>23</td>
</tr>
<tr>
<td>9. Supraneurals</td>
<td>2</td>
<td>1 in most; 0 in a few</td>
<td>0</td>
<td>0 or 2</td>
<td>0</td>
</tr>
<tr>
<td>10. Vacant interneural spaces</td>
<td>3 spaces in 2 groups</td>
<td>1-9 spaces in 1-4 groups</td>
<td>1-8 spaces in 1-2 groups</td>
<td>1 space (5th to 7th)</td>
<td>1 space (5th)</td>
</tr>
<tr>
<td>11. Neural spine orientation</td>
<td>Some anterodorsal</td>
<td>Some anterodorsal in 3 of 5 families</td>
<td>Posterodorsal</td>
<td>Posterodorsal or antero-dorsal</td>
<td>Vertical to posterodorsal*</td>
</tr>
<tr>
<td>12. Branchiostegals</td>
<td>2 + 4 = 6</td>
<td>3 + 4 = 7*</td>
<td>3 + 4 = 7; 2 + 4 = 6 or fewer</td>
<td>2 + 4 = 6</td>
<td>2 + 4 = 6</td>
</tr>
<tr>
<td>13. Anal-fin spines</td>
<td>5</td>
<td>1-4*</td>
<td>0</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>14. Dorsal-fin spines</td>
<td>8</td>
<td>5-10</td>
<td>0-8</td>
<td>8-9*</td>
<td>9</td>
</tr>
<tr>
<td>15. Pelvic-fin rays</td>
<td>4</td>
<td>6-9 in most; 5 in one; 3 in one</td>
<td>2 ancestral; 0-1 secondarily; 4 in one</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>16. Teeth</td>
<td>Rounded, large, molari-form</td>
<td>Small, conical</td>
<td>Small, conical ancestrally; many secondary modifications</td>
<td>Small, conical</td>
<td>Small, conical</td>
</tr>
</tbody>
</table>

*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 squamipinnies and acanthuroids.

Sorbiniperca shares a few notable derived features with caproids, especially the shaft of the first dorsal pterygiophore in the preural 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
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 pre-

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

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sent 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 *Plectocraticus* with 14), whereas *Sorbiniperca* has 14; with one exception by reversal, all tetraodontiforms have only one or no epurals (the exception being *Plectocraticus* 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 oncosomatid), 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 suprayeal, 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

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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 branching 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.

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