A Remarkable New Genus of Tetraodontiform Fish with Features of Both Balistids and Ostraciids from the Eocene of Turkmenistan

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ABSTRACT

Tyler, James C., and Alexandre F. Bannikov. A Remarkable New Genus of Tetraodontiform Fish with Features of Both Balistids and Ostraciids from the Eocene of Turkmenistan. *Smithsonian Contributions to Paleobiology*, number 72, 14 pages, 4 figures, 1 table, 1992.—A new genus and species of tetraodontiform fish, *Eospinus daniltshenkoi*, is described from the Lower Eocene of Turkmenistan (Danatinsk Formation). It is referred to the Balistoidea because it has three large dorsal-fin spines; the pelvic fin reduced to a rudimentary but prominent structure apparently composed of two partially fused spines at the posterior end of the pelvis; and enlarged scale plates that form an incomplete carapace or loosely articulated armature around much of the body. It differs from all other balistoids in having a long median spine projecting forward from the snout and another spine projecting posteriorly from the middle of each side of the body; lower jaw teeth twice as long as the upper jaw teeth; and in lacking encasing scales around the rudimentary pelvic spine. *Eospinus* is the first record of a balistoid fish from the Eocene with three dorsal-fin spines and the pelvic spines fused together at the end of the pelvis, as otherwise only occurs in balistids, which are first recorded from the Oligocene.

Contents

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Introduction

Examination of the specimens of tetraodontiform and possibly related fishes in the collections of the Paleontological Institute in Moscow of the Russian Academy of Sciences has revealed new and unusual members of several families. Among them is a single specimen of a balistoid with specializations that include a long, anteriorly directed median spine on the snout, another spine directed posteriorly on each side of the body, and much larger teeth in the lower jaw than in the upper jaw. It has a covering of enlarged ostraciid-like scale plates forming a partial carapace around the body, three dorsal spines placed over the rear of the skull like balistids but without a locking mechanism, and a rudimentary pelvic fin at the end of the pelvis like balistids but without encasing scales. The uniqueness of this heavily armored species was recognized by P.G. Daniltshenko, the pioneering chronicler of the fossil fish fauna of Russia and adjacent regions, and a sketch he made of it accompanies the specimen in the collection. The specimen has remained undescribed, apparently because of uncertainty about its familial or even ordinal placement.

We place this new form in the Tetraodontiformes because it has a reduced number of caudal-fin rays (12), a reduced number of vertebrae (probably 18–20), and because it lacks anal-fin

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spines. We place it in the Balistoidea (sensu Winterbottom, 1974: the balistids, including monacanthids; the ostraciids, including aracanids; and the Eocene spinacanthids) because it has a reduced number (3) of dorsal-fin spines, a reduced pelvic fin (a rudimentary spine at the end of the pelvis), a reduced number of teeth, which are of heavy conical shape, and enlarged scale plates forming a partial carapace with spiny processes. In several ways the new form is anatomically intermediate between the ostraciid trunkfishes and the clade composed of the balistid triggerfishes and their Eocene spinacanthid sister group. We place the new form incertae sedis in an unresolved trichotomy with the balistids and spinacanthids. This is reflected in the following hierarchical synopsis.

Order TETRAODONTIFORMES Berg (1940), Winterbottom (1974), Tyler (1980)
    Suborder TETRAODONTOIDEI (this and other intraordinal categories sensu Winterbottom, 1974)
        Superfamily BALISTOIDEA
            Family OSTRACIIDAE
            Incertae sedis: *Eospinus*
            Family SPINACANTHIDAE
            Family BALISTIDAE

Museum, Tokyo, for their helpful reviews of the initial manuscript, which was further improved by the preacceptance reviews of C. Patterson, the Natural History Museum (London), J.D. Stewart, Los Angeles County Museum of Natural History, and V.G. Springer, National Museum of Natural History (Smithsonian Institution), and comments by G.D. Johnson and J.T. Williams, National Museum of Natural History. For much help with the cladistic analysis, we are greatly indebted to R. Winterbottom. At the National Museum of Natural History invaluable help was received from R. Clark for photographs, J. Lombardo for typing, and F. Grady for specimen conservation. At the Smithsonian Institution Press we thank J.C. Warren for his careful copy editing and typesetting and D.M. Tyler for preparing the table of characteristics of the taxa.

Eospinus, new genus

TYPE SPECIES.—*Eospinus daniltshenkoi* n. sp., by monotypy.

ETYMOLOGY.—*Eo* for the Eocene age, and *spinus* for the three large dorsal-fin spines, the carapace spines, and the fused pelvic-fin spine; masculine.

DIAGNOSIS.—*Eospinus* differs from all other Balistoidea by the presence of a large anteriorly directed median spine on the snout and a posteriorly directed spine on each side of the body, heterodont dentition, absence of a locking mechanism of the three dorsal-fin spines, and absence of encasing scales around the rudimentary pelvic fin at the end of the pelvis.

Eospinus daniltshenkoi, new species

FIGURES 1–3

MATERIAL.—Holotype and only known specimen, Paleontological Institute (PIN), Moscow, no. 2179-101, 31.5 mm SL, in part and counterpart, the more complete of the two halves being that with the head to the left, collected 16 October 1959 (Figure 1).

ETYMOLOGY.—The patronym is in honor of P.G. Daniltshenko, now retired from his grand work at the Paleontological Institute in Moscow of describing the fossil fishes of Russia and adjacent regions, who first recognized the uniqueness of this species. We spell the name in the manner he prefers for its Latinization, with a *ts* rather than a *c*, although in literature references below we use the more commonly cited western spelling Danilchenko.

DIAGNOSIS.—As for the monotypic genus.

TYPE LOCALITY AND HORIZON.—Middle part of Danatinsk Formation, Lower Eocene of southwestern Turkmenistan, close to the village of Uylya-Kushlyuk (38°38′N, 55°48′E). The Danatinsk Formation is composed of deposits from the Upper Paleocene to the Middle Eocene (Grossheim and Korobkov, 1975) and has a thickness of 200 m of mottled clays and argillaceous marls. The lower boundary of the Eocene in these deposits is marked by the replacement of foraminifera of the *Acarinina subsphaerica* Zone complex by those of the *Globorotalia subbotinae* Zone complex. The fish-bearing layer of brown clays (whose total thickness is about 9 m) lies at the base of the lower Eocene portion of the Danatinsk Formation (Solun, 1975). Danilchenko (1968) was in error in supposing that this layer belonged to the lower part of the Danatinsk Formation and therefore was Upper Paleocene in age.

ICHTHYOFAUNAL ASSOCIATIONS.—Up to now 23 species of teleost fishes have been described from the Lower Eocene of the middle part of the Danatinsk Formation (Danilchenko, 1968; Bannikov, 1985). These are mostly species of such pelagic families as the Scombridae, Carangidae, Clupeidae, Menidae, Chanidae, Turkmenidae, Kushlukiidae, and Luvaridae. However, at least one species, the acanthuroid *Siganopygaeus rarus* Danilchenko, is a member of the inshore, benthic family Siganidae, often associated with coral reefs and adjacent grass flats. We suppose that *Eospinus*, being heavily armored and probably slow moving, was benthic in habitat and perhaps associated with reefs, as would be expected of a balistoid fish.

DESCRIPTION.—The specimen is only moderately well preserved. The tear-drop shaped body tapers from a deep head to a short, deep, caudal peduncle; the eye is of moderate size in the upper part of the head; the mouth is small and slightly underslung, with distinct teeth of moderate (upper jaw) to large (lower jaw) size; especially prominent features are the long dorsal-fin spines and the median carapace spine on the snout. Very little of the internal structure is exposed because of the covering of enlarged but often fragmented or incomplete scale plates. The part of the parasphenoid under the orbit, the opercular bones, and the posterior edge of the pectoral girdle and postcleithrum are recognizable. There is no indication of a nasal organ. Nothing of diagnostic interest internally is clear, except in a portion of the vertebral column that curves upward over the abdominal region from the level of about the base of the posteriorly directed carapace spine. Somewhat vague contours and vertical grooves in the impression of the column offer faint evidence for the size of the individual centra. Our subjective interpretation is that the vertebrae were relatively large and few in number, consistent with the low number of about 18–20 as found in triacanthoid and most balistoid tetraodontiforms.

Measurements are standard length (SL) 31.5 mm, greatest depth of body 14.3 mm, approximate diameter of eye 4.0 mm, distance between tip of snout and base of spiny dorsal fin 13.4 mm, length of base of spiny dorsal fin 7.0 mm (with position of rear edge of recumbent third dorsal spine estimated as though it were erected), distance between posterior end of base of spiny dorsal fin and upper base of caudal fin 16.9 mm, caudal peduncle depth 4.6 mm, approximate length of caudal fin 7.0 mm (position of rear edge estimated), length of incomplete first dorsal spine 13.0 mm (based on the thickness and tapering of
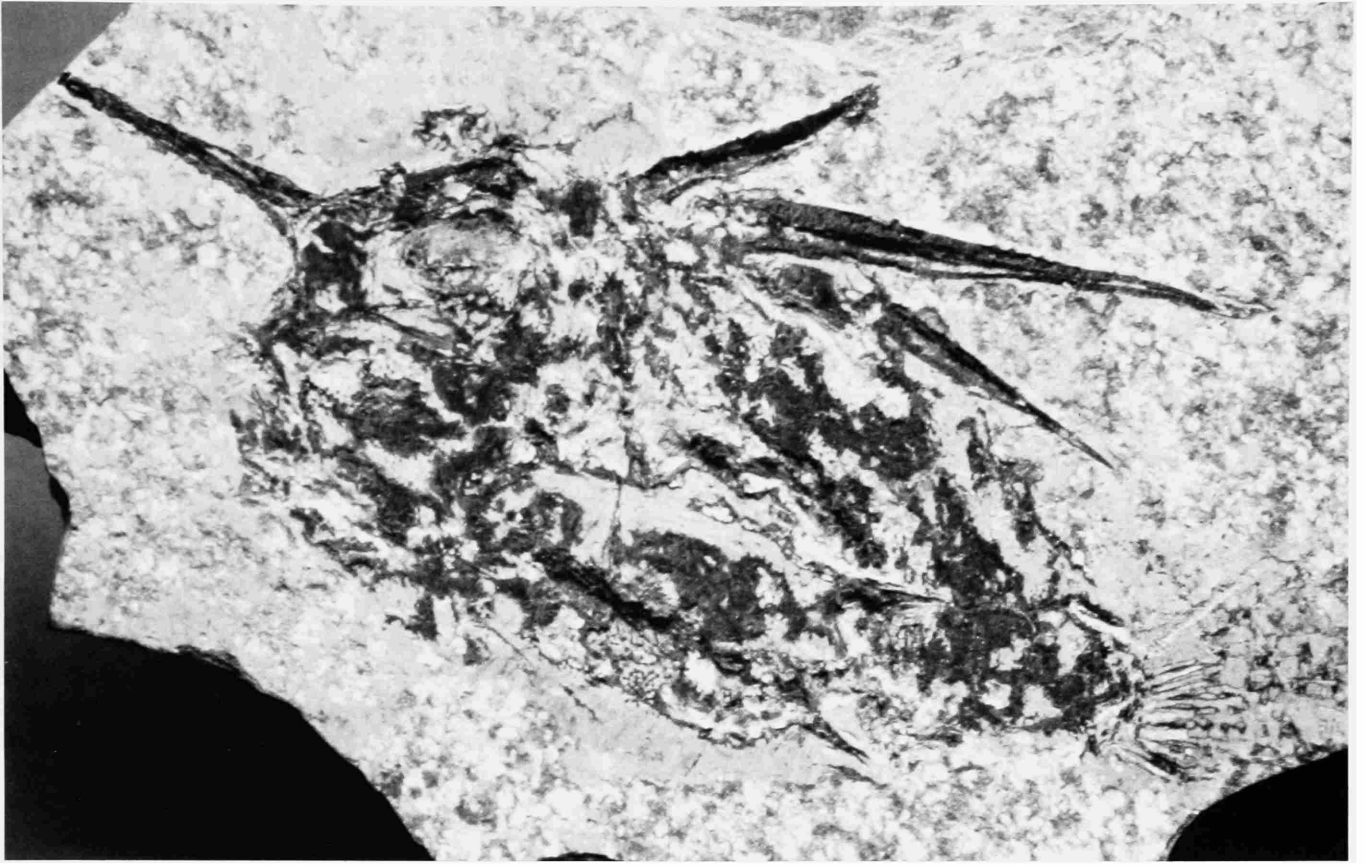
FIGURE 1.—Photograph of the holotype of *Eospinus daniltshenkoi*, new species, 31.5 mm SL, PIN 2179-101, Lower Eocene of Turkmenistan.

the preserved portion, the intact length is estimated to be about 23 mm), length of second dorsal spine 19.7 mm, length of third dorsal spine 13.1 mm, length of pelvic-fin apparatus protruding from ventral profile of body 4.3 mm, length of incomplete spine projecting anteriorly from snout 8.8 mm (intact length perhaps about 10 to 12 mm), length of longest tooth in lower jaw 1.4 mm, length of longest tooth in upper jaw approximately 0.7 mm.

The body is covered with enlarged scale plates bearing numerous low tubercles or granulations on their surface, with the most central tubercle often larger than the others. Although the peripheral edges of the plates are not well preserved, the plates appear to have varied from irregularly rounded to almost hexagonal. The plates are largest and in closest contact with one another in about the middle of the body, apparently forming an almost continuous covering of armor in the region that supports the posteriorly directed carapace spine and the rudimentary pelvic fin. It is possible that some of the plates were interdigitated, although there is no evidence of the type of more extensive suturing that characterizes the carapace of ostraciids. The scale plates of the head and caudal peduncle are somewhat smaller than those of the middle of the body and are more distantly spaced from one another.

Both the median snout spine and the posterior body spine on each side of the body appear to be processes of the enlarged dermal scale plates with which they are continuous basally; thus, both spines were probably fixed and inflexible. Continuing anteriorly from the base of the posterior body spine is a ridge along the enlarged scale plates, probably forming a crest along the body to below the pectoral-fin base. An even more prominent crest, along what are probably relatively consolidated scale plates, is present ventrolaterally from the region of the base of the rudimentary pelvic fin to the lower region of the cheek. Because this crest terminates at the base of the pelvic fin, we suppose that the pelvic girdle, which is not exposed, is positioned internal to it. The centers of the scale plates along this crest apparently were especially upraised, forming a spinous ventrolateral ridge. The snout spine bears shallow longitudinal grooves and low serrations, while the posterior body spine appears to be similarly but slightly less ornamented.

All three dorsal-fin spines are long and robust and at least the first two bear low serrations along the anterior and, especially on the second spine, lateral edges. The distal end of the first dorsal spine is missing, but based on the thickness and degree of tapering of the basal region we estimate that the first spine was only slightly longer (73% SL) than the second (63% SL),

while by measurement the length of the third (42% SL) is slightly more than half that of the second. The large rounded base of the second dorsal spine does not appear to make close contact with the posterior edge of the base of the first spine. Therefore, we think it unlikely that the complex locking mechanism of the first spine by the second spine as found in Recent and fossil (as early as the Oligocene) balistids is present. The origin of the spiny dorsal fin is at a level about half way between the eye and the region of the gill slit and pectoral-fin base, and the anterior end of its supporting basal pterygiophores (which cannot be seen because of overlying large scale plates) probably articulated with the posterodorsal surface of the skull.

The base of the caudal fin is preserved and there appear to have been 12 rays, but we cannot determine how many were branched or unbranched because the distal part of the fin is only a faint impression. There are no remains of the pectoral, soft dorsal, or anal fins, and these are shown hypothetically by dashed lines in the reconstruction (Figure 2). We presume that there were no anal-fin spines because if such were present they could be expected to be as easily visible as the dorsal-fin spines, the rudimentary pelvic-fin spine and the carapace spines.

The pelvic fin, although rudimentary, protrudes prominently from the ventral contour of the body. The apparatus as exposed is seen in dorsoventral view (Figure 3) and, therefore, its bilateral symmetry is clear, especially with the clay-like matrix having been carefully removed from along its length. The bony element appears to represent the consolidation of the right and left pelvic spines, as it is a continuous, solid, uninterrupted piece without cross-striations (segmentations) or branching as would be found in a soft ray. The two halves of the spine are fully fused to one another medially except at the distal end. Indentations and irregularities medially along the length of the spine also are evidence of the region of fusion. Strong spiny processes are present along its lateral edges, the more distal of which tend to be retrorse. These spiny processes appear to be fully continuous outgrowths of the spine itself. The base of the pelvic spine abuts against the enlarged scale plate at the posterior end of the ventrolateral ridge along the body armor. At the end of the ventrolateral ridge this scale plate curves medially to meet the base of the spine and presumably overlies the posterior end of the pelvic girdle where the spine would probably be attached. Just above the base of the pelvic spine the body is indented, undoubtedly for the anus. There is no evidence of elongate scales between the anus and the base of the spine, such as those in Recent and fossil balistids that strengthen the somewhat expansible dewlap or fan of skin in
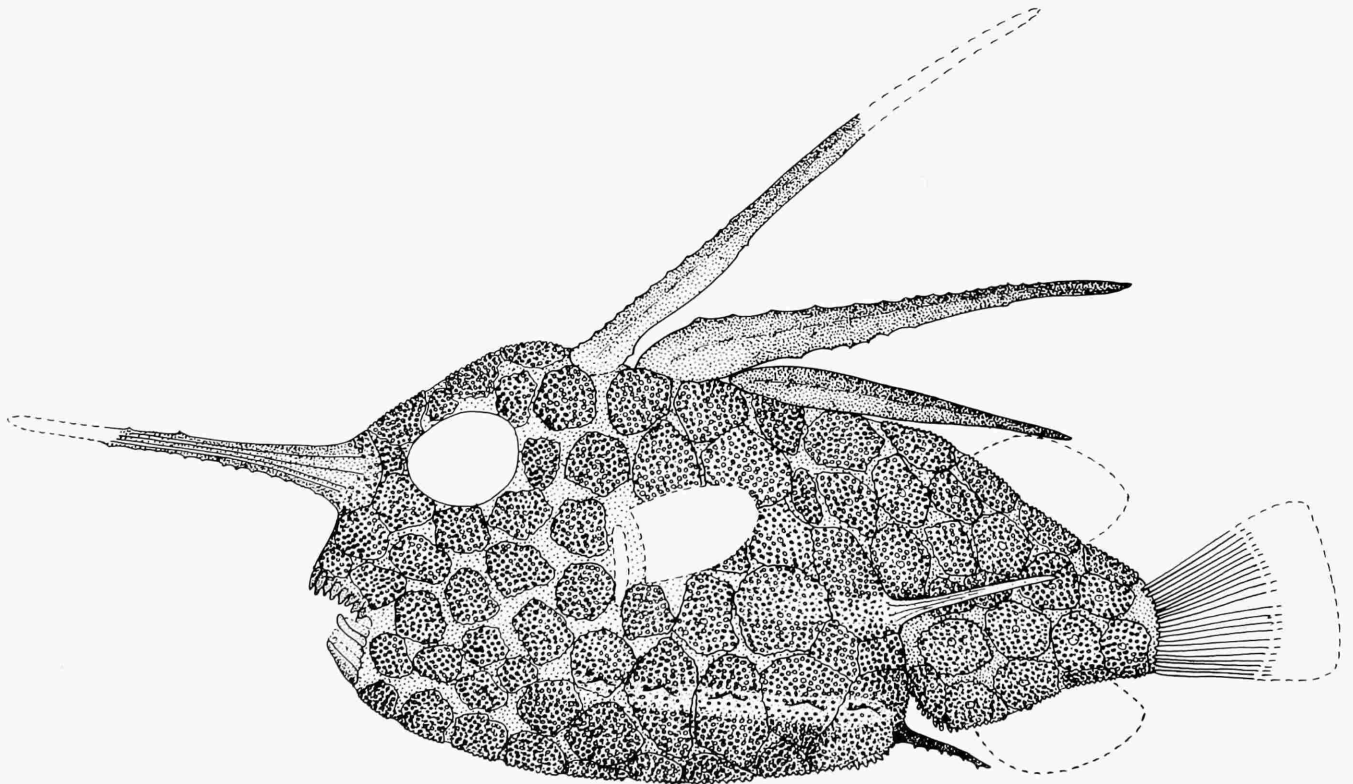

FIGURE 2.—Reconstruction of the holotype of *Eospinus daniltshenkoi*, new species, 31.5 mm SL, PIN 2179-101, Lower Eocene of Turkmenistan.
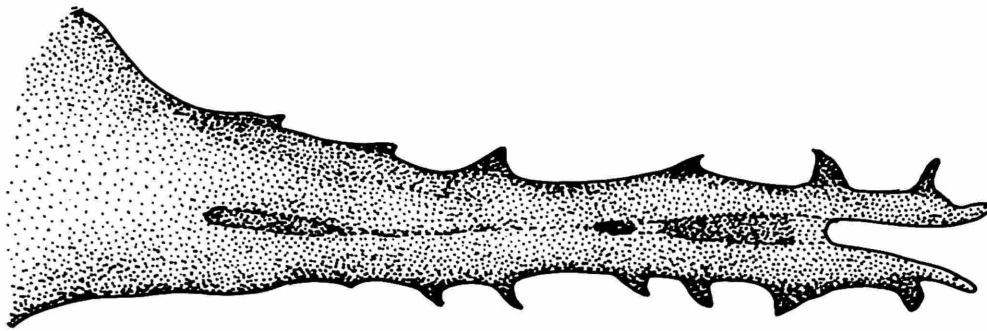
FIGURE 3.—Rudimentary pelvic-fin element of the holotype of *Eospinus daniltshenkoi*, new species, as seen in dorsoventral view, base of element to left, the pelvic spines from the right and left sides fused together except distally.

this region. Neither is there evidence of a distinct series of scales forming a sheath around the pelvic spine.

The lower jaw teeth are bluntly conical, slightly curved posteriorly toward the distal end, and twice as long as those of the upper jaw. The first four teeth on the side of the jaw are clearly indicated (the second and third by impressions only) and are of about similar length and width, while the few more posterior teeth (probably two) apparently decrease in size (these are not so evident as the first four). The upper jaw teeth are more numerous, with about eight teeth clearly evident in a single row. At least some of the upper jaw teeth, especially those toward the middle of the series, have more constricted distal regions than in the lower jaw, forming blunt nipples. In neither jaw is there evidence of inner series teeth, although such teeth, especially if small, could be hidden behind the large outer teeth.

Analysis of Characters of *Eospinus*

For purposes of establishing the systematic position of *Eospinus* we accept Winterbottom's (1974) higher classification and phylogenetic analysis of the relationships of the Tetraodontiformes, i.e., the Suborder Triacanthoidei (Triacanthodidae and Triacanthidae) is the sister group of the Suborder Tetraodontoidei (all of the other families; see Table 1 for a synopsis of the classification of tetraodontiforms and Figure 4 for their phylogenetic relationships). Within the Tetraodontoidei, the Superfamily Balistoidea (with, among other characters, individual teeth protruding from the jaws; plesiomorphic) is the sister group of the Superfamily Tetraodontoidea (teeth incorporated with jaw bones into a beak; apomorphic). Within the Balistoidea, the Spinacanthidae (two Eocene species) is the sister group of the Balistidae (including monacanthids), while the sister group of the balistid-spinacanthid clade is the Ostraciidae (including aracanids). We follow these categories in the text discussion and in Table 1 summarizing the characters of *Eospinus* in comparison to all of the other major

groups of tetraodontiforms, but in the cladogram (Figure 4) we follow the scheme of Tyler (1980) and recognize the monacanthids and aracanids at the familial level rather than the subfamilial as accorded them in Winterbottom (1974, on which the cladogram is based).

On the basis of 96 osteological and myological autapomorphies, Winterbottom and Tyler (1983) defined the Recent Balistoidea (20 autapomorphies), Balistidae (20), and Ostraciidae (56). Only a few of these are external features that can be seen in both fossil and Recent species. The Spinacanthidae were not treated by Winterbottom and Tyler (1983) and are analyzed here on the basis of the descriptions in Tyler (1980). While the phylogeny of the Recent balistoids as proposed by Winterbottom (1974) and Winterbottom and Tyler (1983) is robust in osteological and myological characters, the placement of the poorly known Eocene spinacanthids (single specimens of each of the two species, with only external features evident) with the balistoids and its sister group relationship with the balistids is based on far fewer characters (elongate ethmoid region, eye high in head, spiny dorsal fin forward on head over eye; Winterbottom, 1974). Even with the limitations from the lack of knowledge of the osteology of spinacanthids we accept these relationships of the balistoids and believe that the few additional features analyzed here for *Eospinus* will not substantially change them. Obviously, however, as more and more data become available in new taxa like *Eospinus* with unique combinations of balistoid characters, or from additional specimens of spinacanthids, the previous phylogenetic hypothesis for balistoids should be reanalyzed rather than having the new data appended to it.

On the basis of a phylogenetic analysis of data from early life history stages, Leis (1984) tentatively placed the ostraciids in an unresolved trichotomy with the diodontids and molids as the sister group of the tetraodontids, which in turn were the sister group of the balistids (including monacanthids). The placement of the ostraciids with the tetraodontoids was based on nine characters, but was proposed only with the caution that no data were available for two of the included families, the Triodont-

TABLE 1.—Synopsis of the phylogenetically informative features of *Eospinus daniltshenkoi*, new species, in comparison to the comparable conditions in all of the other groups of Tetraodontiformes. (– indicates feature is not applicable.)

Taxa	Number dorsal-fin spines	Size dorsal-fin spines	Pelvic-fin composition	Pelvic-fin placement	Scale size	Carapace and carapace spines	Number teeth each side of jaw, outer series	Teeth size and shape
Order TETRAODONTIFORMES								
Suborder TRIACANTHOIDEI								
Triacanthodidae	6	moderate	I, ii or I, i	thoracic	small	absent	modally 12–37*	usually small to moderate, conical ‡
Triacanthidae	6	moderate	I, i or I	thoracic	small	absent	4–5	large, incisiform
†*Cryptobalistes* incertae sedis	4	moderate	I, rays unknown	thoracic	small	absent	unknown	unknown
Suborder TETRAODONTOIDEI								
Superfamily BALISTOIDEA								
†*Eospinus* incertae sedis	3	large	rudimentary spine, no encasing scales	abdominal	large	partial; with spines	6–8	moderate to large, stoutly conical
†Spinacanthidae	5–6	large	rudimentary(?) or absent	?	moderate to large	absent or partial; no spines	4–7	large, stoutly conical to molariform and incisiform
Balistidae	1–3	moderate	rudimentary spine with encasing scales, or absent	abdominal	small §	absent	2–4	large, stout, notched or incisiform
Ostraciidae	0	–	absent	–	large	well developed; spines present or absent	3–9	moderate to large, stoutly conical
Superfamily TETRAODONTOIDEA								
†Eoplectidae	6	moderate	I, iv	thoracic	moderate	absent	teeth incorporated with jaw bones into beak-like structure, but with separate teeth still recognizable on outer surface of jaws as small rounded units or elongate rods (except in Molidae, dental units indistinct), while distinct trituration or mastication teeth of moderate to large size often are present on internal surface	
Triodontidae	0–2	rudimentary	absent	–	small	absent		
†Zignoichthyidae	0	–	absent	–	small	absent		
Tetraodontidae	0	–	absent	–	absent to large	usually absent∞		
Diodontidae	0	–	absent	–	large	absent		
Molidae	0	–	absent	–	small	absent or present; with spines in larvae		

* Two derived genera have long tubular snouts in which the number of teeth may be reduced, and absent entirely in the upper jaw.

‡ Several derived genera with teeth either compressed and rounded to truncate distally, or with reduced conical teeth.

§ A few genera with secondarily derived scales of moderate size.

∞ One species with enlarged midbody scales forming a partial carapace without spines in large specimens.
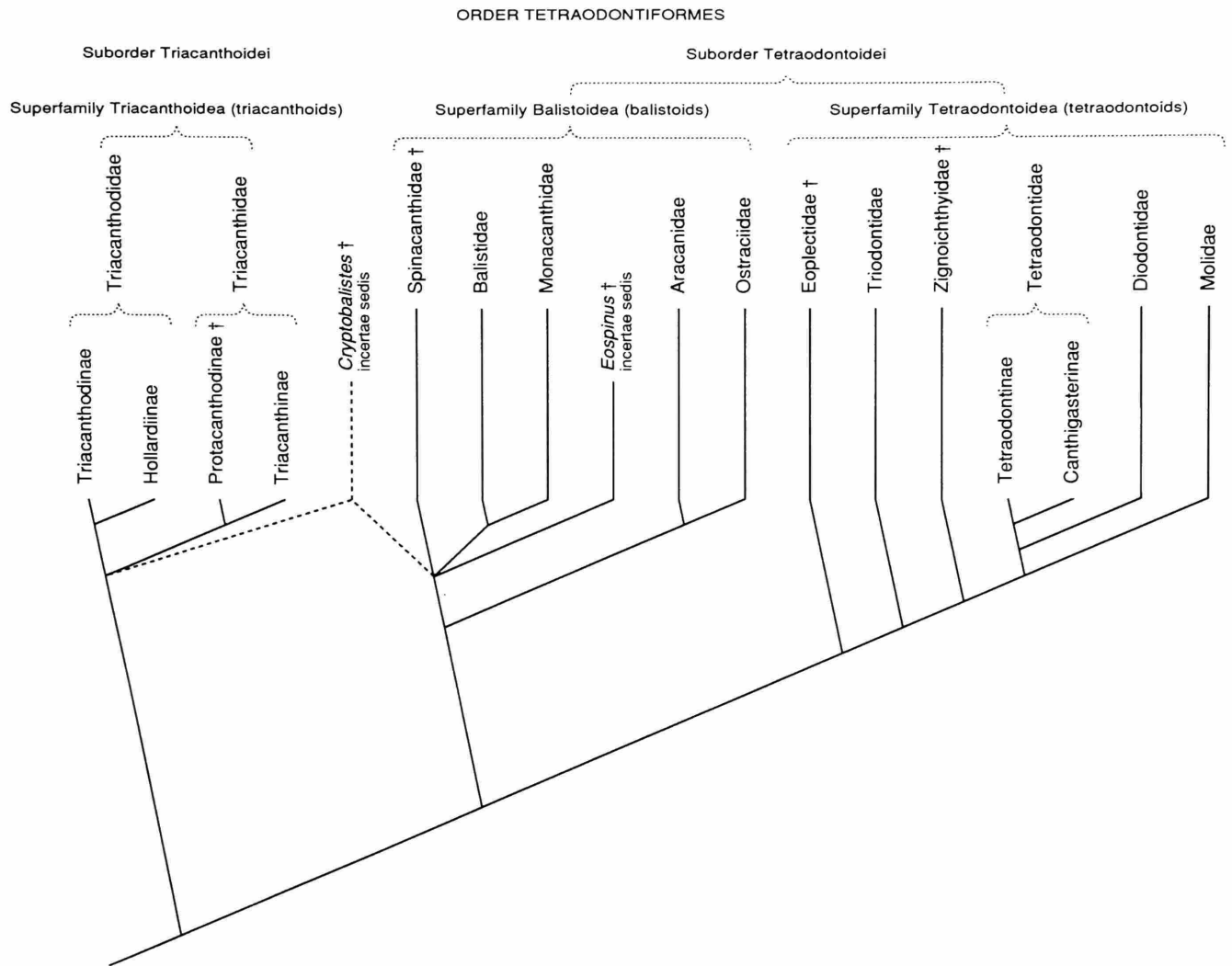
ORDER TETRAODONTIFORMES

FIGURE 4.—Cladogram of relationships within the Tetraodontiformes, based on Winterbottom (1974), except for changes in the placement of a few fossil groups (*Cryptobalistes* as incertae sedis rather than a subfamily of Triacanthodidae; Zignoichthyidae as more closely related to Tetraodontidae than to Eoplectidae) and the recognition of families within the balistoids (aracaniids, ostraciids, balistids, and monacanthids as families rather than subfamilies).

idae and Aracanidae, the two most morphologically primitive of their respective lines. Although we highly value the evidence offered by early life history stages, in this case we believe that the 20 synapomorphies from the osteology and myology of adults by which Winterbottom and Tyler (1983) defined the balistid-ostraciid clade offer far stronger evidence for the monophyly of that group than do the nine synapomorphies of early life history stages by which Leis (1984) related ostraciids to tetraodontoids, especially as such data were absent for critically important groups of both ostraciids and tetraodontoids.

In Rosen's (1984) proposal of the zeiforms as the primitive sister group of the tetraodontiforms, a rigorous analysis of the

inter-relationships of the families of the latter was not intended, and Rosen's placement of the ostraciids in an unresolved trichotomy with the triodontids and other tetraodontoids based on a single synapomorphy (dorsal fins and radials remote from occipital region of skull) and four others, all reductive, linking ostraciids and tetraodontoids (absence of pelvis, ribs, and uncinate process on first epibranchial, and consolidation of the caudal skeleton) obviously is weak in comparison to the evidence presented by Winterbottom and Tyler (1983).

The few known and almost exclusively external characters of *Eospinus* are compared below with those of spinacanthids, balistids, and ostraciids, and with those of their triacanthoid and tetraodontoid outgroups. The triacanthoids are, in general, the

most plesiomorphic tetraodontiforms. Among the tetraodontoids we compare *Eospinus* especially to the Eocene *Eoplectus*, the most morphologically primitive member of the Superfamily Tetraodontoidea, and to *Triodon*, the most generalized extant member of the superfamily and the sister group of all of the other extant families of that group.

NUMBER AND PLACEMENT OF DORSAL-FIN SPINES.—*Eospinus* has three dorsal spines. The plesiomorphic condition for tetraodontiforms is six spines, as found in all Triacanthoidei and in *Eoplectus*, the most generalized representative of the Tetraodontoidea. Within the Tetraodontoidei, reduction in the number of dorsal spines has taken place independently in the Balistoidea (5–6 spines in Spinacanthidae, 2–3 or rarely 1 in Balistidae, and none in Ostraciidae) and Tetraodontoidea (6 spines in the Eocene Eoplectidae, 1–3 rudimentary spines or none in Triodontidae, and none in the Eocene Zignoichthyidae, Tetraodontidae, Diodontidae, and Molidae).

Winterbottom's (1974) phylogeny of the balistoids indicates that an a posteriori synapomorphy of the ostraciids is the posterior migration of the basal pterygiophore of the spiny dorsal fin toward the origin of the soft dorsal fin and the complete loss of the spiny dorsal fin, with the pterygiophores becoming the prominent supraneural element found just in front of the first basal pterygiophore of the soft dorsal fin in all ostraciids. Conversely, the sister group relationship of balistids and spinacanthids is supported by the anterior migration of the dorsal spines and their pterygiophores to at least the rear of the skull, which condition is apomorphic relative to the position just behind the rear of the skull in the triacanthoid and eoplectid-based outgroups. Spinacanthids retained five or six dorsal spines from the ancestral triacanthoid-eoplectid condition and these spines migrated even further forward onto the top of the skull over the eye and greatly increased in length relative to the moderate length in triacanthoids and eoplectids. The reduction of the number of dorsal spines in balistids to three in balistins and to two (rarely one) in monacanthins is independent of the loss of spines in ostraciids. Balistins retained the position of the spiny dorsal fin and their supports at the rear of the skull, plesiomorphic for the balistid-spinacanthid clade, while monacanthins further specialized by the migration of the spines further forward onto the top of the skull, usually to the region of the eye or even in front of the eye. The forward migration of the spiny dorsal fin in monacanthins is here interpreted as independent of that in spinacanthids.

The presence of three dorsal spines in *Eospinus* relates it to balistids within the spinacanthid-balistid clade, while the origin of the spines at the rear of the skull is the ancestral condition for that clade.

On the basis only of the number of dorsal spines and not of their position (nor of the supraneural in their absence), spinacanthids with five or six spines would be the sister group of both balistids and ostraciids, with three or fewer spines being a synapomorphy for a balistid-ostraciid clade and the complete loss of the dorsal spines a synapomorphy of ostraciids.

It is clear that the position of the spiny dorsal fin was anterior, toward the rear of the skull, in the ancestral balistoid. One could hypothesize that the spines were lost in ostraciids while still in this position and that only then did the basal pterygiophores, having lost their original function of spine support, migrate posteriorly to the origin of the soft dorsal fin to become the supraneural. However, in triodontids, which are the only tetraodontiforms with a rudimentary spiny dorsal fin, the spiny dorsal fin and its pterygiophores have migrated posteriorly to just in front of the soft dorsal fin. Moreover, when the rudimentary spiny dorsal fin is absent (Indian Ocean populations) in the only Recent species, *Triodon macropterus* Lesson, the basal pterygiophores are entirely comparable to the posteriorly placed supraneural of ostraciids. This analogous positioning of the pterygial supports of the absent spiny dorsal fin in triodontids and ostraciids is in conformity with Winterbottom's (1974) contention of the sister group relationship of spinacanthids and balistids, both of which have anterior migration of the spiny dorsal fin, and the sister group relationship of that clade with the ostraciids, which have posterior migration of the pterygiophores and loss of the spines. This scenario also is consistent with Rosen's (1984) hypothesis of ostraciid relationships.

Eospinus lacks a mechanism by which the second dorsal spine locks the first spine in an erect position. Such a complex specialized locking mechanism is present among tetraodontiforms (and all other fishes) only in the Balistidae (present in all species except for a few highly specialized monacanthins that have lost the second spine). If *Eospinus* is more closely related to balistids than to other balistoids this would indicate that the reduction in the number of dorsal spines to three in *Eospinus* and balistids took place in that lineage prior to the development of the locking mechanism in balistids alone, in which case *Eospinus* would be the sister group of balistids.

LENGTH OF DORSAL-FIN SPINES.—*Eospinus* has exceptionally long and robust dorsal spines, the first being about 73% SL and the second 63% SL. The plesiomorphic condition for tetraodontiforms is a moderate dorsal-spine length of 17%–43% SL as found in the Triacanthoidei (for specimens over 60 mm SL; smaller specimens with somewhat longer spines, Tyler, 1968). In the only group of Tetraodontoidea with a relatively well-developed spiny dorsal fin, the primitive Eocene *Eoplectus* (Tyler, 1973b), the spines are incompletely preserved, but from the shape and size of the parts that remain the spines were obviously of only moderate length and probably somewhat shorter than in triacanthoids. In the Balistidae the longest (first) dorsal spine is plesiomorphically moderate in length, usually between 20% and 30% SL, and always less than 40% SL. In the Spinacanthidae the dorsal spines are exceptionally long and strong in both of the monotypic genera, 54% and 92% SL in *Protobalistum imperiale* (Massalongo) and *Spinacanthus cuneiformis* (de Blainville), respectively. The greatly increased length of the dorsal spines is a synapomorphy

of the two genera of Spinacanthidae, as is their origin far forward on the head over the small and highly placed eye.

A hypothesis of moderate dorsal-spine length as found in triacanthoids and eoplectids being ancestral for balistoids and increased length acquired by spinacanthids and *Eospinus* (one step if spinacanthids and *Eospinus* are sister groups or two steps if balistids and *Eospinus* are sister groups) is more parsimonious than increased length being ancestral for balistoids and there having been reduction in the length of the spine in balistoids and ostraciids (three steps). Within the balistoids, however, it is equally parsimonious to assume that the spinacanthid-balistid ancestor had increased spine length that was reversed in balistids or that this ancestor had moderate length and that spinacanthids and *Eospinus* independently acquired increased length if, as evidenced by the number of dorsal spines, *Eospinus* and balistids are sister groups (two steps in both scenarios).

The evidence from the 73% SL dorsal-spine length in *Eospinus* indicates relationship with spinacanthids, while the evidence from the number of spines indicates relationship with balistids. If *Eospinus* is proposed as the sister group of spinacanthids on the basis of dorsal-spine length, then the number of spines had to be reduced from the ancestral six to three or fewer independently in *Eospinus* and balistids (two steps). If *Eospinus* is proposed as the sister group of balistids on the basis of the number of spines, then the size of the spines had to be increased from the ancestral moderate size to large independently in *Eospinus* and spinacanthids (two steps). None of the other characteristics of *Eospinus* supports one versus the other of these equally parsimonious alternatives.

PELVIC FIN.—*Eospinus* has the pelvic fin reduced to a pair of partially fused and relatively large rudimentary spines placed posteriorly at the end of the pelvis. The plesiomorphic condition for tetraodontiforms is a pelvic fin of one spine and two (triacanthoids) to four (eoplectids) rays placed thoracically along the middle of the length of the pelvis below the pectoral fin (condition of pelvis unknown in eoplectids but pelvic fin thoracic). Among the alternate outgroups for tetraodontiforms, most acanthuroids and some zeiforms have a pelvic fin with a spine and five well-developed rays (in some zeiforms up to seven rays if a spine is present or up to 10 rays if the spine is absent; rays reduced to three or four in some specialized acanthuroids). The pelvic fin in zeiforms and acanthuroids is like that of morphologically primitive tetraodontiforms in being placed thoracically along the side of the pelvis, which usually has a prominent posterior process behind the fin; i.e., the fin is never at the extreme posterior end of the pelvis as in balistids.

The pelvic fin of tetraodontiforms has become much reduced, apparently independently, in both lineages of the Tetraodontoidei. In the Tetraodontoidea the pelvic fin is completely lost in all groups except the Eoplectidae, although the Triodontidae retain the pelvis. In the Balistoidea the pelvic fin is either reduced to a complex rudimentary structure at the end of the pelvis in front of the anus or absent altogether. In the Balistidae the pelvic fin rudiment is thought to be the partial fusion product of the pelvic spines from both sides of the body. Except at its distal end, this rudimentary fused spine is surrounded by a series of enlarged encasing scales (in balistins and most monacanthins, while the rudiment and its encasing scales are secondarily further reduced or completely lost in some of the more specialized monacanthins, even though the pelvis is always present: Tyler, 1962; Matsuura, 1979). In the Ostraciidae both the pelvis and pelvic fin are completely lost. In the Eocene Spinacanthidae there is no clear evidence in either of the single specimens of the two species of a pelvic fin or pelvis, and the pelvic fin must be considered to have been either extremely rudimentary or entirely lost.

The spiny structure at the end of the pelvis in *Eospinus* is less specialized than that of balistids because of its larger or less apomorphically reduced size and its lack of development of the specialized series of encasing scales that surround the rudiment in the more primitive balistids (subsequently lost by some specialized monacanthins). The spiny processes along the lateral edges of the reduced and partially fused pelvic spines in *Eospinus* also can be interpreted as plesiomorphic relative to the smooth edges of the smaller rudiment in balistids because such spiny processes are present on the pelvic spines of both the more generalized triacanthoid (the triacanthodids) and eoplectid-based outgroups.

In assessing the condition of the pelvic fin in balistoids we presume that there is an ordered, polarized, transformation series from the ancestral condition of a relatively well-developed pelvic fin with a spine and at least a few rays (triacanthoids, eoplectids, extraordinal outgroups) to a progressively smaller rudimentary fin before it is entirely lost. In this scenario the pelvic fin became reduced to a large rudiment in the ancestral balistoid, a condition retained by *Eospinus*, while balistids further reduced the size of the rudiment and ostraciids lost it. Given the frequency of reductive tendencies among many lineages of tetraodontiforms in both pelvic- and dorsal-fin spines, with the numbers and size progressively reduced and then eventually lost, this scenario seems far more reasonable to us than to assume that the ancestral balistoid entirely lost the pelvic fin and it was regained to much different degrees by balistids and *Eospinus*.

Any further analysis of the pelvic fin in balistoids is severely limited by the unknown condition in spinacanthids. Nevertheless, on the basis only of its relatively large and ornamented rudimentary pelvic fin *Eospinus* is the sister group of a clade including at least balistids and ostraciids (and spinacanthids if their pelvic fin is no more than a small rudiment, if not absent entirely). The ancestor of such a clade would have had the pelvic fin further reduced to a small rudiment, which was retained by balistids and lost by ostraciids, while the balistids developed a complex specialized series of encasing scales around the rudiment.

Without knowing the condition of the pelvic fin in

spinacanthids we cannot assess the implications of the placement of the rudimentary pelvic fin at the posterior end of the pelvis just in front of the anus in *Eospinus* and balistids, versus thoracically placed in all other tetraodontiforms with a pelvic fin (triacanthoids and eoplectids) and in the extraordinal outgroups. If one presumes that the loss of the pelvic fin in ostraciids took place after its migration posteriorly to the end of the pelvis, as was probably the comparable situation with the posterior migration of the spiny dorsal fin associated with its loss, then the position of the pelvic-fin rudiment in *Eospinus* and balistids is plesiomorphic for balistoids.

We note that if *Eospinus* had encasing scales around the rudimentary pelvic spine we would accept this as important evidence linking it with the balistids (just as we would if *Eospinus* had a locking mechanism between the first and second dorsal spines). We believe it unlikely that the loss of the pelvic fin in ostraciids, even if it involved migration to the posterior end of the pelvis, proceeded through a stage in which the rudimentary spine became encased in the specialized series of flexible scale segments found in balistids. This complex apparatus in balistids serves variously to wedge the species into crevices and to flare a dewlap of skin to increase apparent body size in a presumably protective-defensive behavior, and the development of this apparatus has apparently been a key factor in the diversification of the group. We doubt that ostraciids also developed this complex pelvic apparatus only to subsequently lose it before their probable pre-Eocene origins (the ostraciin *Eolactoria* and the aracaniin *Proaracana*, both without a pelvis or pelvic fin of any kind, being known from the early Eocene). The balistid pelvic apparatus (and the dorsal-spine locking mechanism) is fully developed in all of the fossil balistids. Balistins are first recorded from the Oligocene by the three species of *Balistomorphus* from Switzerland and the monotypic *Oligobalistes* from Russia (Tyler, 1980), while monacanthins are first known from the Pliocene by several species of *Aluterus* and *Cantherhines* reported by Sorbini (1987, 1991) from Italy.

CARAPACE SCALE PLATES.—*Eospinus* has enlarged tuberculate scale plates over the entire body, the largest of which are between 12% and 13% SL and tend to form a continuous carapace around the middle of the body, although the plates are not as regularly hexagonal or extensively sutured to one another as in ostraciids. In ostraciids the mostly hexagonal tuberculate scale plates are firmly sutured to one another to form a rigid carapace over most of the body, with scale plates of up to 13% SL (larger in the Eocene *Proaracana*, up to 24% SL).

In spinacanthids one genus, *Spinacanthus*, has moderately enlarged scales of 4.8% SL, while the other, *Protobalistum*, has greatly enlarged scales of 12.3% SL, and in both cases the scales bear numerous tubercles on the surface, like those of *Eospinus* and the ostraciids. In *Spinacanthus* the plates are more or less isolated and only cover a total of about one-fourth of the surface of the body, without much contact between the

plates except ventrally. In *Protobalistum*, however, the scale covering is much more complete, like that of *Eospinus*. In the anterior half of the body (exclusive of the head) of *Protobalistum* many of the plates are distinctly hexagonal and articulate with one another by interdigitations, just as in ostraciids. This is similar to the situation in *Eospinus*, in which the greatest consolidation of the scale plates and their closest articulation to one another is in the anterior half of the body below the spiny dorsal fin and in front of the pelvic spine and the posteriorly oriented carapace spine.

Scale size in balistids is not well quantified in the literature. Therefore, we made a survey of the size of the scales from the side of the body (i.e., excluding the sometimes larger and more elongate scales at the rear of the abdomen associated with the expansible dewlap) from specimens in the collections of the National Museum of Natural History. Examination of 21 species of balistin triggerfishes (the more generalized of the two groups of balistids), representing nearly all of the genera, shows that the greatest dimension of the scales is usually between 2%–3% (range 1%–4%) SL, but as much as 5% SL in *Pseudobalistes flavomarginatus* (Rüppell) and 7% SL in *Odonus niger* (Rüppell). The thick scales in the aberrant *Xenobalistes* (enlarged coracoid, postcleithra, and frontal), which has some superficial ostraciid characteristics, are about 3.3% SL (Matsuura, 1981:194). The scales in the Oligocene genera *Balistomorphus* and *Oligobalistes* are only impressions that are difficult to measure, but from their pattern they obviously were small and in the size range of 2%–3% SL like those of most Recent balistins. The scales of monacanthin filefishes tend to be slightly smaller and thinner than those of balistins, and to bear upright spinules, while in some specialized species the scales are almost entirely lost. Thus, the scales in balistids are small, except in a few derived genera of balistins with scales of moderate size, even though the basal scale plate may be thicker in balistins than in triacanthoids.

Among the Tetraodontoidea, the monotypic Eocene *Zignoichthys* (Zignoichthyidae) has small scales (0.9% SL) with upright spinules very similar to those of the Triacanthodidae, the most generalized family of the order, while the monotypic Eocene *Eoplectus* (Eoplectidae) has moderately enlarged scales (5.8% SL) with stellate radiations from the base of a central upright spinule. In the Triodontidae, another relatively generalized family of tetraodontoids, the scales are relatively small (3% SL) except where more elongate in the expansible dewlap of the abdomen. Elsewhere in the Tetraodontoidea the scales often are enlarged as either fixed or erectable spines in most Tetraodontidae and Diodontidae, except where the spines are secondarily reduced or lost in some tetraodontids. However, enlarged plate-like scales similar to those of ostraciids are found in the tetraodontid *Ephippion* and in the molid *Ranzania*. The scale plates of *Ephippion* are up to 9.2% SL in large adults and form a firmly sutured girdle around the middle of the body (more extensively so than in *Eospinus*, although the latter has a girdle at a much smaller body size than does *Ephippion*). The

scale plates of *Ranzania* are relatively thin and small, up to 1.2% SL, but form a complete, if somewhat flexibly sutured, carapace around the entire body. These two genera of different families of the Tetraodontoidea apparently have developed a carapace-like structure independently of one another and of *Eospinus, Protobalistum*, and the ostraciids among the Balistoidea.

In the triacanthoids, which overall are the most morphologically plesiomorphic group of tetraodontiforms, the scales are relatively small (1%–3% SL), with either upright spinules (triacanthodids) or emarginate ridges (triacanthids), including the only Eocene representative, *Protacanthodes*. Because triacanthoids have small scales, the moderately enlarged plate-like scales of some spinacanthids (*Spinacanthus*), balistids (*Pseudobalistes* and *Odonus*), and eoplectids (*Eoplectus*) and the greatly enlarged plates of *Eospinus*, ostraciids, and some spinacanthids (*Protobalistum*) and tetraodontids (*Ephippion*) are derived conditions. It seems clear that many of these plate-like enlargements are independent acquisitions (e.g., in tetraodontids and balistids; as are the smaller plate-like scales forming the carapace in the molid *Ranzania*). Enlarged scales, as either plates or spines, are of such frequent if phylogenetically sporadic occurrence among spinacanthids, eoplectids, ostraciids, tetraodontids, and diodontids, that it also seems clear that scale enlargement is an especially homoplastic feature in tetraodontiforms (as is extreme reduction and loss of scales). Nevertheless, the small scales of triacanthoids must be considered the primitive condition, and enlargement apomorphic.

Given that small scales are primitive for the Triacanthoidei (all species with small scales) and Tetraodontoidea (small scales in morphologically primitive forms like the Eocene *Zignoichthys* and the Eocene to Recent *Triodon*, although moderate size scales in the Eocene *Eoplectus*), it is equally parsimonious (3 steps) to assume that the scales in the ancestral balistoids were of either large or small size, but not of moderate size (4 steps). If the balistoid ancestral line had small scales like triacanthoids, then this requires changes for the moderate scale size in *Spinacanthus*, the large scale size in *Protobalistum*, and the large scale size of ostraciids. If the balistoid ancestral line had large scales, then this requires changes from the small scale size of triacanthoids, the moderate scale size of *Spinacanthus*, and the small scale size of nearly all balistids.

Our preferred hypothesis is that the ancestral balistoids had small scales like the triacanthoids and some of the more primitive tetraodontoids, simply because we have no particular reason to believe that a large-scaled balistoid ancestral line is more probable than the proposed small-scaled ancestry. If one accepts small scales as ancestral to balistoids, then the enlargement of scales in *Eospinus* relates it to either ostraciids or spinacanthids (*Protobalistum*) in the accepted phylogeny or indicates, contrary to other evidence, that spinacanthids and ostraciids are sister groups to which *Eospinus* has an unresolved relationship. None of these alternatives are refuted by the possibility that the ancestral balistoids had large scales, in which case the large scales of *Eospinus* are phyletically uninformative within the balistoids.

In *Protobalistum* the partial carapace has a ventrolateral ridge, similar to the ridges in this position in most ostraciids and in *Eospinus*. Just as with scale enlargement, we postulate that the carapace ridge in *Protobalistum* is an independent acquisition from that in *Eospinus* and ostraciids. Thus, ridges are interpreted as a common functional aspect of carapace construction irrespective of the phylogenetic origin of the carapace.

CARAPACE SPINES.—*Eospinus* has a large median carapace spine directed forward from the snout and another fixed spine directed posteriorly from the middle of each side of the body. No such spines are present in spinacanthids and balistids (among the latter neither the flexible quill-like spines found on the side of the body of males of the monacanthin *Amanses scopas* (Cuvier) nor the enlarged tubercles and spiny processes borne on the scales of the caudal peduncle in many balistins and monacanthins seem homologous to the fixed carapace spines of *Eospinus*). Among ostraciids only the Eocene *Eolactoria* has a median, but much shorter, carapace spine on the snout, in the same position as that of *Eospinus* (the Recent *Ostracion rhinorhynchus* Bleeker has a blunt, rounded enlargement on the snout, but not a spine). Bilateral carapace spines are present in many ostraciids, either on the supraorbital ridge or along the dorsolateral and ventrolateral ridges of the carapace, but none has a large spine projecting posteriorly from the middle of each side of the body.

While the median snout spines of *Eospinus* and *Eolactoria* could be considered a synapomorphy, we discount the significance of this evidence because of the great degree of homoplasy in carapace spines in ostraciids. For example, seemingly identical large carapace spines bilaterally in front of the eyes have been acquired independently by genera in two different phyletic lines of Recent ostraciins, and this is also homoplastic to the occurrence of such preorbital spines in the Oligocene *Oligolactoria* (Tyler and Gregorova, 1991). Moreover, the numerous spiny scale processes of pelagic larval molids, which apparently act as flotation and defensive devices, include a long anteriorly projecting median snout spine and one projecting posteriorly from each side of the middle of the body (especially in *Masturus*). These are similar in size and placement to those of *Eospinus* but they are not associated with a carapace. As molids are one of the most derived groups of tetraodontoids and more closely related to tetraodontids and diodontids than to ostraciids, it is reasonable to assume that the molid snout and body spines have been acquired independently from those of ostraciids. Because there is no other evidence of a close relationship between *Eospinus* and *Eolactoria*, we postulate that the snout spines in these two genera (and in larval molids) are homoplastic, and that the presence of carapace spines of any kind in *Eospinus* is not evidence of relationship with ostraciids.

TEETH.—*Eospinus* has a moderate number (6 to 8 on each side) of basically conical teeth; those of the lower jaw are stoutly conical and larger than those above, and some of the latter are constricted distally. The plesiomorphic condition for tetradontiforms is relatively numerous (modally 12 or more on each side), simple, conical teeth without distal constrictions and of equal (small to moderate) size in both jaws. This is the condition found in all species of the Triacanthodidae except for several derived genera with thin, wide, and distally rounded or truncate scraping teeth (sometimes reduced in number or absent in the upper jaw) and/or long tubular snouts. In the Triacanthidae, the more derived of the two families of Triacanthoidei, the teeth are larger, more incisor-like, and reduced in number to four or five on each side in an outer series and one or two in an inner series on each side.

Within the Tetraodontoidei, all Tetraodontoidea have the derived condition of the teeth incorporated with the jaw bones into a specialized beak, while the Balistoidea have teeth that vary from conical to heavy incisors, as follows. Of the two species of Spinacanthidae, *Spinacanthus cuneiformis* has about seven stoutly conical teeth on each side of the lower jaw (the upper jaw teeth are less visible in the single specimen), some of which taper distally into a strongly constricted blunt nipple. In the other species, *Protobalistum imperiale*, there are four or five teeth on each side of both jaws, some with straight or rounded distal edges as in incisors or molars, but others with a distinct blunt nipple-like cusp. In the Balistidae the teeth are relatively few, large, compressed, and more-or-less notched and incisor-like, three to four in an outer series on each side, and two or three in an inner series in the upper jaw and two to four in a single series in the lower jaw. In the Ostraciidae the teeth are of moderate size and more or less conical but usually constricted distally, often into a blunt nipple, with between three and nine (usually four to six) in a single series on each side of both jaws. In the two Eocene genera of ostraciids, *Eolactoria* and *Proaracana*, the teeth are somewhat larger, heavier, and more notched distally than in the Recent species and bear at least some similarity to the outer teeth of balistids (Tyler, 1973a).

Relative to the simple conical teeth of triacanthodids, the teeth of all three families of balistoids have a derived condition of being enlarged to some degree, less numerous, and in various ways notched, distally constricted, or incisor-like. Within the balistoids, the basically conical, distally constricted teeth of ostraciids and spinacanthids are less derived than are the larger, less numerous, incisor-like teeth in the outer series of balistids. The teeth of *Eospinus* are more similar to those of spinacanthids and ostraciids than to those of balistids in that they are basically conical and some of them are distally constricted. However, the lower jaw teeth of *Eospinus* are enlarged, being at least as large as those in the two Eocene genera of ostraciids and not much smaller than those of balistids; and some of the teeth in the spinacanthid *Protobalistum* are incisor-like.

Thus, there are significant differences in the size and shape of the teeth within each of the families of balistoids, and even within each of the species of the two monotypic genera of spinacanthids, *Protobalistum* and *Spinacanthus*. Given this degree of ambiguity, we interpret the teeth of *Eospinus* as simply relating it to the balistoids but not to a particular family within it. The dentition of *Eospinus* is best considered as modified for its function in a unique mouth in which the upper jaw teeth are only half as long as and more distally constricted than those in the lower jaw.

PLESIOMORPHIC FEATURES.—*Eospinus* has 12 principal caudal-fin rays as also found in triacanthoids, spinacanthids, balistids, eoplectids, triodontids, and zignoichthyids rather than the derived condition of 11 or less found in ostraciids, tetraodontids, diodontids, and molids. In *Eospinus* the eye is of moderate size and placed in about the middle of the upper half of the head, as it is also in triacanthoids and most other tetraodontiforms. The eye is somewhat more elevated in some balistids and in most ostraciids, but these never have the eye so small and highly placed just under the spiny dorsal-fin origin as in spinacanthids, the latter size and placement being a synapomorphy of *Spinacanthus* and *Protobalistum*. In *Eospinus* the soft dorsal and anal fins are not preserved, but based on the space available for them, they obviously were short-based, as in triacanthodids (the most morphologically generalized tetraodontiforms), ostraciids, and most Tetraodontoidea (except moderate in the Eocene *Eoplectus* and secondarily elongate in *Chonerhinos* and *Xenopterus*). In triacanthids (including the Eocene protacanthodins) the soft dorsal fin is secondarily elongate, while in balistids both the soft dorsal and anal fin are apomorphically elongate.

Phylogenetic Conclusion

The structure of the spiny dorsal fin, pelvic fin, scale plates, and teeth in *Eospinus* are all phylogenetically informative but some of the evidence conflicts with the accepted phylogeny of the balistoids and leaves the exact relationships of *Eospinus* uncertain.

The presence of three dorsal spines relates *Eospinus* to balistids, while the lack of a locking mechanism excludes *Eospinus* from the balistids as presently defined and places it as the sister group of the balistids. The position of the spiny dorsal fin over the rear of the skull relates *Eospinus* to spinacanthids and balistids. The increased length of the dorsal spines relates *Eospinus* to spinacanthids. The presence of a relatively large rudimentary pelvic spine at the end of the pelvis without surrounding encasing scales relates *Eospinus* to balistoids as this is the presumed ancestral condition of reduction in that clade but, without the condition of the pelvic fin being known in spinacanthids, it is not possible to further use this character to establish relationships within the clade. The shape of the teeth (conical with distal constrictions) relates *Eospinus* to

balistoids but not to any particular family because such teeth are plesiomorphic for balistoids. The enlargement of the scale plates into a partial carapace either relates *Eospinus* to both spinacanthids and ostraciids or is primitive for balistoids.

Although we believe that the evidence presented here abundantly supports our contention that *Eospinus* is a balistoid, we cannot determine on the basis of its few external characters whether *Eospinus* is more closely related to balistids or to spinacanthids. Given the tenuousness of the evidence from *Eospinus* and the weakness of the cladogram at the spinacan-thid-balistid node, we prefer not to make a formal rearrangement of these taxonomic groupings in order to accommodate *Eospinus* either in an expanded concept of the balistids or as a categorically equivalent sister group of them or of spinacanthids or of both. Rather, we adopt a conservative course and simply place *Eospinus* incertae sedis with the spinacanthid-balistid clade of balistoids.

We are confident that the exposure of even a few internal osteological features in future specimens of *Eospinus* will allow for its precise placement among the balistoids.

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