A New Genus and Species of Boxfish (Tetraodontiformes: Ostraciidae) from the Oligocene of Moravia, the Second Fossil Representative of the Family

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ABSTRACT

Tyler, James C., and Růžena Gregorová. A New Genus and Species of Boxfish (Tetraodontiformes: Ostraciidae) from the Oligocene of Moravia, the Second Fossil Representative of the Family. *Smithsonian Contributions to Paleobiology,* number 71, 20 pages, 8 figures, 1 table, 1991.—A new genus and species of boxfish (Ostraciidae) is described on the basis of five specimens from the Menilitic Formation of the Lower Rupelian part of the middle Oligocene (ca. 35 MYA) of Moravia, Czechoslovakia. A sixth but incomplete specimen is recorded from the Menilitic Formation of southern Poland. The fossil record of the family previously was based only on *Eolactoria sorbinii* from the lower Eocene of Monte Bolca, Italy, and on isolated carapace scale plates also dating back to the Eocene. The new genus differs most significantly from all other Recent and fossil ostraciids in the greater posterior extension of the carapace onto the caudal peduncle; the lesser number of anteroposteriorly compressed centra of the vertebrae of the caudal peduncle; the greater length of the caudal fin in relatively small specimens; and perhaps by having a reduced number of caudal rays (nine rather than 10).

The new species is a typical member of the in-shore benthic Ostraciidae, but the other fishes with which it is associated in the Menilitic Formation are nearly all more off-shore mesopelagic species of Myctophidae and Gonostomatidae. To account for this, we propose that the new species represents the oceanic, pelagic, pre-settlement stage of this genus, as in the Recent *Lactoria,* some species of which, especially *L. diaphana,* remain pelagic to sizes of over 100 mm SL and can be sexually mature while pelagic before settling into their conclusive benthic state.

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of Boxfish (Tetraodontiformes: Ostraciidae) from the Oligocene of Moravia, the Second Fossil Representative of the Family

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Introduction

The superfamily Ostracioidea of the tetraodontiform suborder Balistoidei is comprised of two families: the more anatomically generalized Aracanidae, and the derived Ostraciidae. There are about 20 internal osteological characteristics that are differentially diagnostic for these two families (Tyler, 1980:185, 211; Winterbottom and Tyler, 1983:908). Most of these features usually cannot be seen in fossil ostracioids because of a combination of highly compressed, nearly two-dimensional preservation and the obscuring of internal features by the relatively intact covering of enlarged and thickened carapace scale plates. However, several features of the usually well-preserved carapace are diagnostic for one family or the other, and fossil specimens that are relatively complete can be assigned with confidence to a particular family on the basis of these carapace characteristics, as well as from osteological features that occasionally are exposed.

The fossil records of both families of ostracioids begin with relatively well-preserved whole skeletons from the Eocene of Monte Bolca, Italy (upper portion of lower Eocene, ca. 50 MYA). That of the Aracanidae is based on the holotype of *Proaracana dubia* (Blainville, 1818:337; redescribed by Agassiz, illustration in 1839, pl. 74, text in 1844:263; and by Le Danois, 1961:314–315) and two additional specimens described by Tyler (1973:114). That of the Ostraciidae has been based only on the holotype of *Eolactoria sorbinii* Tyler

(1973:106). Three additional specimens of *E. sorbinii* and one incomplete but anatomically informative skeleton of *Proaracana dubia* have been found more recently by Lorenzo Sorbini among the Monte Bolca collections at the Museo Civico di Storia Naturale di Verona. Examination of these new materials and all previously available specimens reinforce the previously proposed carapace distinctions between the fossils of these two families, substantiating our referral of the new Oligocene genus to the Ostraciidae.

Isolated scale plates believed to be from the carapace of ostracioids have been described under several names: *Ostracion meretrix* Daimeries (1891:lxxv) from the Eocene of Belgium, with Leriche (1905:167; 1906:263) recording additional plates from the Eocene of Belgium, as well as from the Eocene of Virginia, USA (Leriche, 1942:42); *Ostracion* sp. (e.g., Krejci-Graf and Weiler (1928:75) for two types of plates with distinctly different ornamentation from the Oligocene of Romania); *Ostracion clavatus* Casier (1946:181) from the Eocene of Belgium; and *Ostracion macropunctatus* Nolf (1970:120) from the Eocene of Belgium. The plates described as *O. clavatus* and *O. macropunctatus* were said to differ from those originally described as *O. meretrix* only by the relative size and number of the knob-like tubercles present on the external surface of the plates.

Intra- and interspecific variation in the relative size of the tubercular ornamentation of the scale plates in ostracioids is poorly known. Tyler (1965b:265–268, fig. 14) compared the number of tubercles present at various specimen sizes in the four species of the Recent genus *Acanthostracion*. He showed that definite differences were present in the number of tubercles

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(granulations) on *A. polygonius* and *A. notacanthus* versus *A. quadricornis* and *A. guineensis*, but that these differences only became marked in large specimens. Based on a comparison with *Acanthostracion*, Krejci-Graf and Weiler (1928:75–77) believed that the two kinds of tubercules in their Oligocene materials of *Ostracion* sp. were attributable to the plates having come from the upper and lower surfaces of the carapace.

There is not yet available in collections an adequate sample of isolated fossil scale plates (much less of intact carapaces) of various sizes to permit statistical analyses of variation in ornamentation, which would allow us to establish if these fossil plates are from more than one species. In describing *O. clavatus*, Casier (1946:181–182) reported two varieties of plates among his collection of 32 (which is by far the largest single sample available). He thought that one variety with a large central spiny tubercle and convex upper and lower plate surfaces was similar to dermal plates found in some skates (Rajidae). The other variety had more numerous (4 to 33), regularly arranged tubercles, similar to *O. meretrix* but in Casier's opinion sufficiently different to merit specific recognition. It should be noted that the original description of *O. meretrix* Daimeries (1891:lxxv) did not distinguish those isolated scale plates from the plates in the intact carapace of the previously described *Proaracana dubia* (Blainville, 1818:337).

Also, the subsequent descriptions by Leriche (1905:167; 1906:263) simply say that in *O. meretrix* the tubercles radiating out from the center of the scale plate are larger than in "*Ostracion micrurus* Agassiz" (= *Proaracana dubia*).

In his work on the fishes of the Eocene of the London Clay, Casier (1966:374–375) stated that *Ostracion*-like isolated carapace scale plates were absent from this formation (they actually are present, see "Material Examined" in this paper) but offered his revised opinion about both *O. meretrix* and his own *O. clavatus*, concluding that the plates were all probably from a hypolophid stingray (Dasyatidae).

Based on our examination of a limited number of isolated fossil carapace scale plates identified in museum collections as *Ostracion*, we believe that those of relatively hexagonal shape with small denticulations along the edges for articulation with apposed plates and with relatively flat upper and lower surfaces (except for crested plates from the major ridges or angles of the carapace) and tubercles of small to moderate size and of moderate to large number depending on specimen (plate) size could well be from ostracioids. Plates much abraded on the edges, and rounded with convex surfaces, are especially difficult to identify and are not necessarily from ostracioids.

It cannot be established at present with any confidence whether those few isolated scale plates that are from ostracioids represent one or several species. Because the structure of the scale plates is similar in the Aracanidae and Ostraciidae, the isolated fossil plates cannot be assigned with certainty to either family (Tyler, 1973:103). Thus, the isolated plates are uninformative about anatomical diversity and phylogenetic relationships.

Although it is likely that more than a single species of each of the two families of ostracioids occurred in Eocene seas, at present we can be confident only of *Proaracana dubia* of the Aracanidae and *Eolactoria sorbinii* of the Ostraciidae. Therefore, the new genus and species of boxfish described below from the Oligocene represents only the third valid fossil species of the Ostracioidea, the second of the Ostraciidae, and the first occurrence of a fossil of this superfamily from more recently than the Eocene.

METHODS

Standard length (SL) in millimeters (mm) is from the anterior end of the jaws and teeth to the posterior edge of the hypural plate. The length of the preorbital and preanal carapace spines is measured as in Tyler (1965b:270, fig. 13, as shown for Recent species; and 1973, fig. 2, as applied to both Recent and fossil species): that is, from the peripheral base of the scale plate bearing the spine, not just the length of the spine that protrudes from the basal plate. Body depth is the greatest vertical distance of the carapace, even if exaggerated by compression. Predorsal length of the carapace is measured from the tip of the snout to the origin of the dorsal fin. Caudal-fin length is measured from the posterior edge of the hypural plate to the distal edge of the fin. Scale-plate diameter is the greatest width.

ABBREVIATIONS

BM(NH)   British Museum (Natural History), now the Natural History Museum, London
MCSN   Museo Civico di Stora Naturale, Verona
MM   Moravske Muzeum, Brno, Czechoslovakia
MNHN   Muséum National d'Histoire Naturelle, Paris
USNM   former collections of the United States National Museum now deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZPAL   Zoological Institute (Paleozoology) of Wroclaw University, Poland

MATERIAL EXAMINED

Ostraciidae

Oligolactoria bubiki, new species. Holotype: Moravske Muzeum (MM), Brno, Ge 26 828 (original numbers IV/324, head to right, and IV/326, head to left), 54.8 mm SL.

Paratypes: MM Ge 26 829 (orig. no. IV/458), 42.5 mm SL; MM Ge 26 830 (orig. no. IV/449), 39.5 mm SL; MM Ge 26 831 (orig. no. IV/450), 33.3 mm SL; MM Ge 26 832 (orig. no. IV/303), 25.5 mm SL. All of these specimens are complete and in paired plates (part and counterpart) and all of them are from the Menilitic Formation, Zone IPM 3, lower part of the middle

Oligocene (Rupelian) of Moravia, Czechoslovakia. We presume that an isolated hexagonal flat scale plate from this same gisement is likely to have been from the carapace of *O. bubiki*, as it has similar ornamentation, but we do not include it among the type specimens: MM Ge 26 833 (orig. no. IV/565), 2.3 mm greatest dimension.

We designate as a paratype an incomplete specimen (most of head missing) in paired plates from the collections of the Paleozoological Department of the Zoological Institute of Wroclaw University, Poland, ZPAL Wr./Os. 397, 22 mm length from rear of head to base of caudal fin, from the Menilitic Formation of the Carpathians in southeastern Poland at Kniazyce, near Przemysl, Skole Unit, Zone IPM 4, several million years younger in age than the materials from Moravia in Zone IPM 3. Although this specimen was not used as a basis for our description, we believe it to be conspecific with the other type materials. Both Zone IPM 3 and 4 are characterized by a predominance of mesopelagic fishes (Kotlarczyk and Jerzmańska, 1988:349).

Eolactoria sorbinii Tyler (1973:106). Holotype: Museo Civico di Storia Naturale, Verona, MCSN T6-T7, 15.5 mm SL, in counterpart. Additional specimens recently examined: MCSN T408, 13.2 mm SL, single plate, head to right; MCSN T394, 8.1 mm SL, single plate, head to right(?); MCSN IG132593, 13.5 mm SL, single plate, head to right. All from the upper part of the lower Eocene of Monte Bolca, Italy.

Aracanidae

Proaracana dubia (Blainville, 1818:337). Holotype: Muséum National d'Histoire Naturelle, Paris, MNHN 10974-10975, 54.5 mm SL, in counterpart. Additional specimens described by Tyler (1973:116–117): MCSN T8–T63, 31.5 mm SL, in counterpart; MCSN IG uncataloged, ~52 mm SL, single plate, head to left. Additional specimen recently examined: MCSN IG23607, rear half of body only, about 26 mm length along remains of caudal portion of vertebral column, with excellent preservation of divergent basal pterygiophores of anterior region of anal fin, peduncular vertebrae (of which none are compressed), carapace scale plates and medial fins. All from the upper part of the lower Eocene of Monte Bolca, Italy.

Family Incertae Sedis

Isolated scale plates identified in collections under the following names: *Ostracion meretrix* Daimeries (1891: lxxv). National Museum of Natural History, Smithsonian Institution, USNM 351461, single scale plate of 11.0 mm greatest dimension, Aquia Formation of Aquia Creek, Virginia, USA, Eocene, described by Leriche (1942:42, pl. 6: fig. 19); British Museum (Natural History), BM(NH) P15194, five scale plates, 2.2–6.0 mm greatest dimension, Barton, Hants, Eocene, H. Eliot Walton Coll.

Ostracion. BM(NH) P28299, single plate, 5.3 mm greatest dimension, Southampton, Lutetian, Eocene, J.G. Turner Coll.; BM(NH) P25788, single plate, 4.8 mm greatest dimension, King George V Dock, Millbrook, Southampton, Hants, Lutetian, Eocene, E.M. Venables Coll.; BM(NH) P50856, single plate, 1.1 mm greatest dimension, Bracklesham Beds, Shore Road Bed, East Wibtering, Sussex, Eocene, R. Fowler Coll.; BM(NH) P28081, single plate, 5.2 mm greatest dimension, Blackheath Beds, Abbey Wood, Kent, Sparnacian, Eocene, J.G. Turner Coll.; BM(NH) P30192, single plate, 7.3 mm greatest dimension, Clark County, Alabama, USA, Eocene, Enniskillen Coll., mentioned by White (1956:146, 147).

Order TETRAODONTIFORMES Berg (1940)

Superfamily OSTRACIOIDEA (sensu Tyler, 1980)

Family OSTRACIIDAE (sensu Tyler, 1980)

Oligolactoria, new genus

TYPE SPECIES.—*Oligolactoria bubiki*, new species, by monotypy.

ETYMOLOGY.—The specific epithet is from *Oligo* (for the Oligocene age) plus *lactoria* (for its resemblance to the Recent *Lactoria*).

DIAGNOSIS

Oligolactoria, new genus, differs from all other genera of the family Ostraciidae by the following: carapace extending far posteriorly, about to level of penultimate vertebral centrum, with only one or two peduncular vertebrae posterior to posterior edge of carapace; a single peduncular vertebra (PU_2) compressed anteroposteriorly; caudal fin extremely long (45% to 56% SL) at relatively small specimen size, and perhaps with only nine rays; exceptionally deep grooves on preorbital and preanal carapace spines.

COMMENTS ON DIAGNOSTIC FEATURES

POSTERIOR EXTENT OF CARAPACE.—In the Aracanidae, the carapace is open posterior to the dorsal and anal fins and does not extend posteriorly much, if at all, beyond the obliquely vertical line through the rear ends of the bases of these fins, and a mid-ventral carapace ridge is more or less developed (well developed in most genera, but weak in *Kentrocapros* and essentially absent in *Polyplacapros*). By contrast, the carapace in the Ostraciidae is always fully closed behind the dorsal and anal fins and extends posteriorly well beyond their bases, except in one Recent species (*Lactophrys trigonus*), in which it is only partially closed behind the dorsal fin, whereas a ventral carapace ridge is never developed (Fraser-Brunner, 1935:315, 316; Tyler, 1973:104; 1980:185, 211; Matsuura and Yamakawa, 1982:39; Winterbottom and Tyler, 1983:911–913). *Oligolactoria* has the typical ostraciid condition of the carapace broadly closed behind the dorsal and anal fins and no mid-ventral ridge (Figure 1).

The degree of development of the carapace posteriorly on the caudal peduncle is best expressed in relation to the number of posterior vertebrae behind the level of the rear edge of the carapace. There is significant overlap in this number between the two families of ostracioids.

In the Recent Aracanidae, four or five vertebrae lie posterior to the rear edge of the carapace. Of the four available specimens of the Eocene aracanid *Proaracana*, the carapace ends over the centrum of the fifth from last vertebra in two specimens and over the sixth from last in the other two. In all of the Recent and

fossil Ostraciidae except *Oligolactoria* there are three to five vertebrae posterior to the posterior edge of the carapace. In the four available specimens of the Eocene ostraciid *Eolactoria*, this region is relatively well exposed only in the holotype, in which there is, however, a vertical fracture in the matrix just at the posterior end of the carapace, but with three vertebral centra fully behind the fracture without the presence of overlying carapace plates. In *Oligolactoria* the carapace extends even farther posteriorly than in the other ostraciids, leaving uncovered only the hypural plate and, in some specimens, part or all of the penultimate vertebra. In three (Ge 26 829, 26 830, 26 831) of the specimens of *Oligolactoria* the carapace extends posteriorly over most of the penultimate centrum, almost to the anterior edge of the centrum of the last vertebra (the fused urostylar centrum and hypural plate); in another (Ge 26 832) the carapace extends to about the front of the penultimate centrum; and in one (Ge 26 828) to about two-thirds the distance posteriorly over the antipenultimate centrum (Figures 6, 7). Thus, there are only one or two peduncular vertebrae posterior to the posterior edge of the carapace in *Oligolactoria*. This is one to three fewer vertebrae than in other ostraciids (see illustrations in Tyler, 1963:172, 175, 178, 180; 1980:221, 226, 230–233, for the number of vertebrae posterior to the carapace in ostraciids, which is the same as the number of unsutured vertebrae posterior to the vertebra whose haemal spine supports the last few anal-fin basal pterygiophores).

COMPRESSION OF CAUDAL PEDUNCLE VERTEBRAE.—Lateral flexibility of the tail in *Oligolactoria* apparently was restricted to the last two segments of the vertebral column, whereas at least the last three segments are flexible in other ostraciids. Presumedly associated with this reduced flexibility of the caudal peduncle in *Oligolactoria* is a less-pronounced compression of the centra of the more posterior vertebrae. In the Aracanidae (including the Eocene *Proaracana*) the centra of the penultimate and antipenultimate vertebrae are slightly shorter or more anteroposteriorly compressed than in those elements preceding them, but in the Recent Ostraciidae the centra of these two vertebrae (PU_2 and PU_3) are always highly compressed. In some Recent ostraciids one or two additional vertebrae anterior to PU_2 and PU_3 also may be much foreshortened, with compression of all the vertebrae between the last vertebra whose haemal spine supports the more posterior of the anal-fin basal pterygiophores and the last or hypural centrum. In *Oligolactoria* only the centrum of the penultimate vertebra (PU_2) is anteroposteriorly foreshortened, with the centrum of the antipenultimate vertebra being of a length about equal to those preceding it. This restriction of the foreshortened centra to a single vertebra in *Oligolactoria* is understandable functionally because this is the only vertebra (other than the large hypural plate) either at or just behind the rear edge of the carapace. Thus, the penultimate vertebra in *Oligolactoria* is the pivot vertebra on which the caudal peduncle is flexed.

CAUDAL-FIN LENGTH.—*Oligolactoria* has a longer caudal

fin at a smaller specimen size than in any other ostracioid. In the Aracanidae and in all but one species of the Ostraciidae, the caudal fin is of moderate length, usually about 15 to 35 percent SL, and it does not increase much in proportional length with increasing specimen size (see Tyler, 1965b:287, fig. 20, for caudal-fin length at various sizes in the four species of *Acanthostracion*, about the norm for most ostracioids). In the Recent genus *Lactoria*, two of the three species have caudal fins of moderate length, about 17 to 33 percent SL in *L. diaphana*, a relatively large species (largest examined in this study 245 mm SL and 304 mm total length, with literature records of about 190 mm SL and 300 mm total length: Matsuura, 1984:362; Hutchins and Swainston, 1986:112; Shirai, 1986:305–306), and about 19 to 30 percent SL in *L. fornasini*, a smaller species (largest examined in this study 112 mm SL and 137 mm total length, with literature records of about 100 mm SL and 150 mm total length: loc. cit.). In neither of these two species does the caudal fin increase much proportionally in length with increasing specimen size. However, in *L. cornuta*, which is the largest species of the genus (largest examined in this study 289 mm SL and 476 mm total length, with literature records of about 300 mm SL and 500 mm total length: loc. cit.), the caudal fin becomes remarkably elongate with increasing specimen size, routinely achieving lengths of 50 percent SL and greater at sizes of about 85 mm SL and longer, with one of the larger specimens of *L. cornuta* examined in this study, 202 mm SL, having a caudal fin of 80 percent SL (Figure 8).

The caudal fin is well-enough preserved to be measured in two of the five specimens of *Oligolactoria*, ranging from 44.7 to 55.9 percent SL in the specimens of, respectively, 33.3 and 39.5 mm SL. This is a longer caudal fin (Figures 2, 6, 7) than in any other species of ostracioid except *L. cornuta*. In *L. cornuta*, a caudal-fin length of 45 to 56 percent SL is not achieved until sizes of about 90 to 140 mm SL. Moreover, *L. cornuta* has a relatively longer caudal fin than the 60 percent SL or greater of *Oligolactoria* only at sizes of at least 95 mm SL and usually only at sizes of about 130 mm SL and larger. When larger specimens of *Oligolactoria* become available, it will be intriguing to learn whether the caudal fin is proportionally even longer than in the present specimens.

NUMBER OF CAUDAL-FIN RAYS.—All of the Recent Aracanidae normally have 11 caudal-fin rays, but the Eocene *Proaracana* has only 10 rays (Tyler, 1973:104; 1980:205) and two of the Recent species sometimes have 10 rays in a minority of specimens (Matsuura and Yamakawa, 1982:33, 35). In the Ostraciidae all Recent species have 10 caudal-fin rays, and the caudal fin is not sufficiently preserved in the specimens of the Eocene *Eolactoria* for the number of rays to be known with certainty. The rays of the caudal fin of *Oligolactoria* are not adequately preserved in any of the specimens for us to confidently count either them or their impressions consistently (some are slightly misplaced and squeezed together basally along the edge of the hypural plate). Our interpretation of the

number of caudal-fin rays has vacillated between nine and 10. It remains possible that, just as the Eocene *Proaracana* has one less ray in the caudal fin than is typical of the Recent species of the Aracanidae, *Oligolactoria* has nine rather than the 10 caudal rays found in all of the Recent Ostraciidae.

DEPTH OF GROOVES ON CARAPACE SPINES.—The well-developed preorbital and preanal carapace spines of *Oligolactoria* are unique among ostracioids in the great depth of the longitudinal grooves present from the distal tip to just above the expanded basal plate. In the two Recent genera (*Acanthostracion* and *Lactoria*) with preorbital and preanal carapace spines, these grooves are much shallower and more numerous than in *Oligolactoria*. We believe this difference is best seen by comparing the photograph (Figure 4) of the impression in the matrix of one of the preorbital spines in a specimen of *Oligolactoria*, where the bony material of the spine is in the counterpart, with a photograph (Figure 5) of an impression we have made in clay of the preorbital spine of a specimen of *Lactoria cornuta* of comparable size. The preorbital and preanal spines in *Oligolactoria*, *Lactoria*, and *Acanthostracion* lack the surface serrations found in *Eolactoria* (see Tyler, 1973, pl. 3).

Oligolactoria bubiki, new species

FIGURES 1–7

HOLOTYPE.—A relatively complete skeleton, part and counterpart, MM Ge 26 828, 54.8 mm SL.

TYPE LOCALITY AND HORIZON.—Bystřice/Olší, N.E. Moravia, Czechoslovakia; Menilitic Formation, Šitbořice Beds, NP 23, Middle Oligocene (Rupelian).

DIAGNOSIS.—As for the monotypic genus.

ETYMOLOGY.—The specific epithet *bubiki* is in honor of Mr. Miroslav Bubik of the Brno office of the Czechoslovakian Geological Survey. Mr. Bubik was responsible for collecting most of the type specimens of *Oligolactoria* and many other interesting materials from the Menilitic Formation in Moravia.

DESCRIPTION

Each of the five relatively complete skeletons of *Oligolactoria* consists of a composite of bony material, scale plates, and impressions of missing parts in the matrix. The remains of the carapace plates obscure most of the phylogenetically informative osteological features, as is the case with the Eocene *Proaracana* and *Eolactoria*. The specimens of *Oligolactoria* are all highly compressed laterally, except for one (Ge 26 831, Figure 2), which is compressed dorsoventrally. All five entire specimens are slightly distorted and incomplete. Nevertheless, with this many specimens available we can describe *Oligolactoria* with the same degree of precision as the individually better-preserved remains of *Proaracana* and *Eolactoria* from Monte Bolca, Italy, and render a reasonably accurate reconstruction (Figure 1).
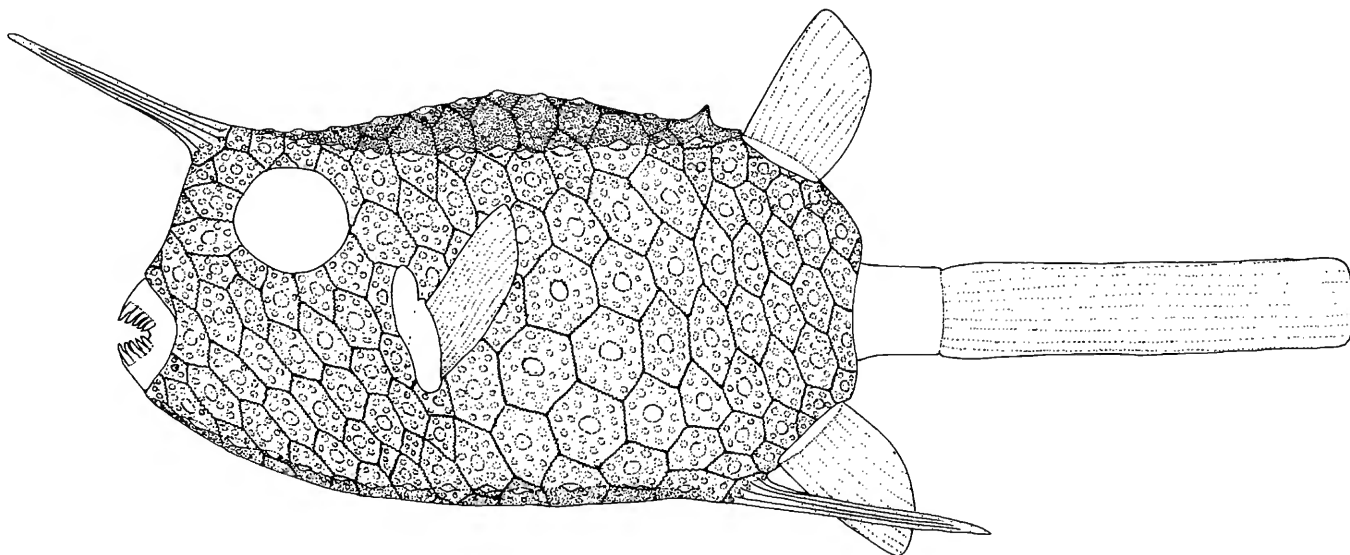
FIGURE 1.—Reconstruction of *Oligolactoria bubiki,* new species, composite based on all five of the entire type specimens (depth of body speculative, as discussed under "Measurements").

TABLE 1.—Measurements in mm of the five entire type specimens of *Oligolactoria bubiki,* new species (numbers in parentheses are values in percent SL (standard length); dashes indicate measurements that were unable to be obtained from specimens).

Character	Ge 26 828 holotype	Ge 26 829 paratype	Ge 26 830 paratype	Ge 26 831 paratype	Ge 26 832 paratype	Average value in percent SL
SL	54.8	42.5	39.5	33.3	25.5	
Body depth	38.8 (70.8)		–			70.8
Predorsal length		32.5 (76.5)		26.0 (78.1)		77.3
Caudal-fin length			21.1 (55.9)	14.9 (44.7)		50.3
Preorbital-spine length	16.0 (29.2)			10.9 (32.7)	6.9 (27.1)	29.7
Preanal-spine length	15.1 (27.6)	14.1 (33.2)	14.3 (36.2)	11.6 (34.8)		33.0
Scale-plate diameter	4.8 (8.8)	5.6 (13.2)	3.9 (9.9)	3.3 (9.9)	2.7 (10.6)	10.5

MEASUREMENTS.—Measurements for the five relatively complete type specimens are given in Table 1. Only one of these (Ge 26 828) has the carapace sufficiently preserved for an accurate measurement of body depth. We believe that our figure of 70.8 percent SL is higher than natural because of flattening and dorsoventral expansion. In our reconstruction of *Oligolactoria* we show the carapace depth as being about 50 percent SL. This is typical of other species of ostraciids with a similar body shape (those with a carapace having a rectangular to pentagonal cross-section). Not included in the table is the length of the pectoral fin, which could be measured in only one specimen (Ge 26 831), 22.2 percent SL.

FIN-RAY COUNTS.—The dorsal-fin rays are relatively intact and well preserved in only one specimen (Ge 26 829), in which we estimate 10 rays. A full complement of anal-fin rays is not preserved in any of the specimens, even though the position of the fin is clear from the remains of the anal-fin basal pterygiophores. In one specimen (Ge 26 829) the displaced remains of between four and six anal-fin rays can be seen. We believe that to be an incomplete number because the number of

FIGURE 2.—Photograph of *Oligolactoria bubiki*, new species, Ge 26 831, 33.3 mm SL, exposed in dorsoventral view (anterior to left) with periphery outlined in ink: front of left side of head and left preorbital carapace spine missing (dashed lines); left pectoral fin (below) present but only base of right pectoral fin indicated; right preorbital and both preanal carapace spines and caudal fin especially distinct; snout region with dentary and lower jaw teeth exposed.

dorsal and anal rays is similar in all Recent species of the family. Remains of pectoral-fin rays can be seen in two specimens (Ge 26 829 and Ge 26 831) but the number of rays cannot be determined.

TEETH.—There are five teeth on each dentary and premaxillary. We can count the teeth and impressions in two (Ge 26 828 and Ge 26 830) of the four specimens exposed in lateral view, and especially clearly in the lower jaw of the specimen (Ge 26 831) exposed in dorsoventral view. The teeth have smooth surfaces and are conical and somewhat laterally compressed at the base. They are constricted and slightly inwardly curved distally. The distal tapering part of the tooth is darker than the base. The teeth in *Oligolactoria* are similar to those described by Tyler (1973:108–112) for the Eocene *Eolactoria* and *Proaracana*. The teeth are probably slightly larger and more constricted distally than in the Recent ostracioids, and perhaps

more like those of the balistoid tetraodontiforms from which the ostracioids are thought to have been derived (Winterbottom, 1974:93; Tyler, 1980:208). In one specimen (Ge 26 829) a pocket of small, conical pharyngeal teeth is evident anteroventral to the orbit.

INTERNAL OSTEOLOGICAL FEATURES.—The carapace is sufficiently incomplete and fractured in places to reveal limited aspects of the internal osteological structure in a fragmentary fashion in most of the specimens.

Vertebral Column: The elements of the hypural plate appear to be fused to one another and to the ural centrum, forming a squarish plate supporting the caudal-fin rays. There seems to be an indentation on the middle of the posterior edge of the hypural plate and a shallow groove along the side of the plate just in front of the indentation, typical for ostracioids. In one specimen (Ge 26 829) the remains of about the last 10
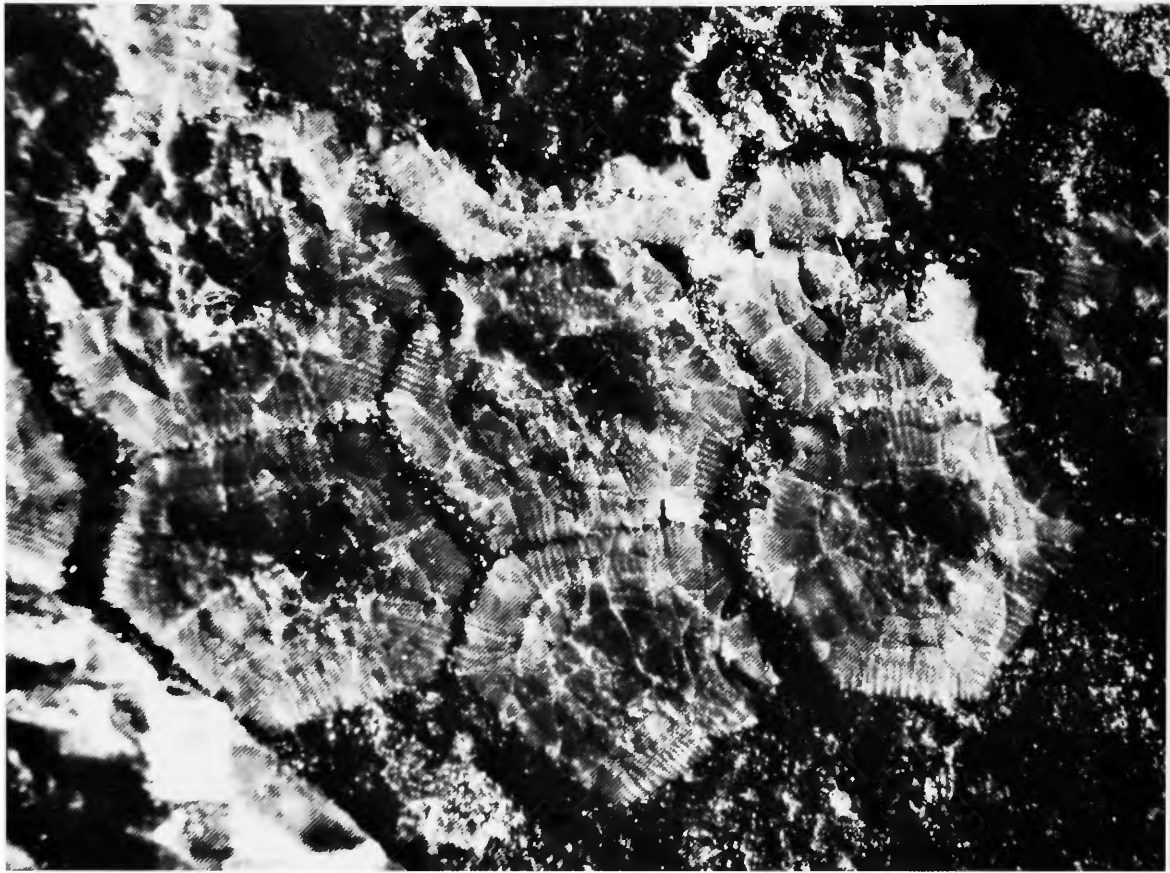
FIGURE 3.—Photograph of carapace scale plates of *Oligolactoria bubiki*, new species, Ge 26 830, 39.5 mm SL; greatest dimension of largest scale plates 3.9 mm (9.9 percent SL).

vertebrae can be seen, but we cannot obtain a total vertebral count because the carapace obscures most of the abdominal vertebrae. The haemal spine of the penultimate vertebra (PU_2) is relatively small and poorly developed, as in ostraciids and in contrast to the larger one in aracanids.

The Recent species of ostracioids have 18 vertebrae (except for one with 19), half of which are abdominal (Tyler, 1980: 415–416). We cannot see the more anterior abdominal vertebrae in the specimens of *Oligolactoria* to determine how many vertebrae were of smaller size and greater anteroposterior compression than the others. In the Recent species there are two such vertebrae in the Aracanidae and four to five such vertebrae in the Ostraciidae. Unfortunately, the anterior vertebral column also cannot be seen in the Eocene *Eolactoria* and *Proaracana*. As a consequence we cannot determine whether the Eocene and Oligocene fossils demonstrate the unique reduction in size and fusion of the more anterior abdominal vertebrae to each other and to the cranium typical of Recent ostracioids.

Anal-fin Basal Pterygiophores: Ostracioids are unique among fishes in the divergent non-sagittal placement of most of the more anterior anal-fin basal pterygiophores. The anterior four or five basal pterygiophores are crowded together distally in the midline just below the base of the anal fin but diverge to the right or left of the sagittal plane proximally where they fan out into a muscle mass at the rear of the abdominal cavity (Tyler, 1963:171–174; 1980:225, fig. 156; Winterbottom, 1974:43, 174, fig. 133). This is true in all Recent species of ostracioids and in the Eocene *Proaracana* (in the additional specimen of the latter recently examined for this work, MCSN IG23607, the compressed and apparently divergent condition of the anterior pterygiophores of the anal fin is especially well exposed and more obvious than in the holotype). The condition of these basal pterygiophores in the Eocene *Eolactoria* is unknown because of lack of preservation or exposure in the four available specimens. In two (Ge 26 830 and 26 832) of the five entire specimens of *Oligolactoria*, the anterior basal pterygiophores are well exposed and can be seen to be crowded together in the manner typical of other ostracioids (Figure 7), and we presume that they were proximally divergent from the midline.

Coracoid-Cleithral and Hyomandibular-Preopercular Complexes: In both the Aracanidae and the Ostraciidae, the

FIGURE 4.—Photograph of stone matrix impression of basal portion of preorbital carapace spine of *Oligolactoria bubiki,* new species, Ge 26 828, 54.9 mm SL, spine length 16.0 mm (29.2 percent SL), to show great depth of longitudinal grooves: base of spine, below, fragmented; spine impression incomplete distally; left preorbital spine, to left, most prominent, but remains of basal plate and impression of spiny process of right preorbital spine, to right, also apparent. Compare with Figure 7.

coracoid and cleithrum are especially large relative to other tetraodontiforms. The postcleithrum is a relatively flat plate just under the carapace in both families, but is greatly enlarged posteriorly only in the Aracanidae (see illustrations in Tyler, 1980:196, 200-202; for polarity of character states, see Winterbottom and Tyler, 1983:906). The hyomandibular in ostracioids also is an especially large and thick element firmly bound to the posterior end of the preoperculum. In one of the specimens (Ge 26 829) of *Oligolactoria,* this region of the skeleton is relatively well exposed beneath the fractured carapace. It is clear that the coracoid, cleithrum, and hyomandi-

bular of *Oligolactoria* have the large size typical of all ostracioids. The postcleithrum in *Oligolactoria* appears to be a relatively narrow, flat plate directed posteriorly from the pectoral girdle just above the region of the remains of the pectoral fin, the condition in ostraciids. This condition contrasts with the distally greatly expanded postcleithrum of aracanids.

CARAPACE CHARACTERISTICS.—The individual scale plates (Figure 3) are hexagonal, flat, and tuberculate on the outer surface, with the central tubercle tending to be larger and more elevated than the others. The edges of the plates are finely
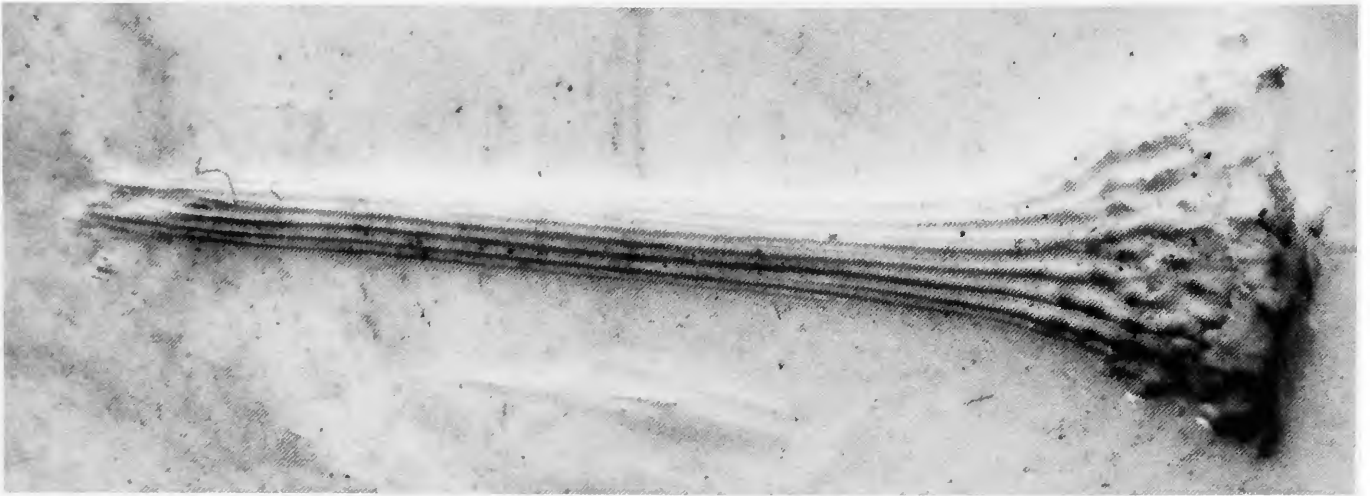
FIGURE 5.—Photograph of clay impression of preorbital carapace spine of *Lactoria cornuta*, USNM 135683, 45.0 mm SL, spine length 16.1 mm (35.8 percent SL) to show relative shallowness of longitudinal grooves of preorbital and preanal carapace spines in all of the Recent species of ostraciids.
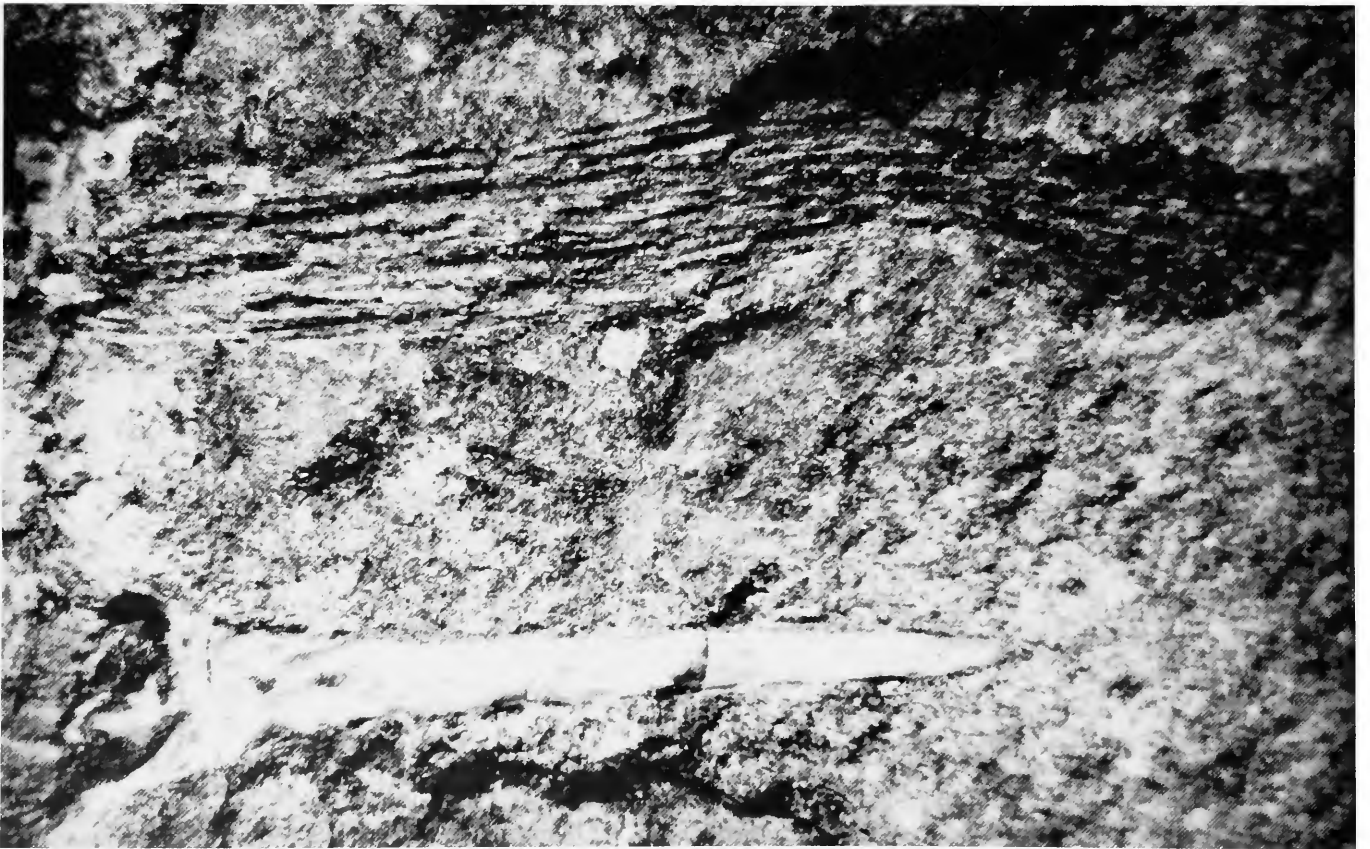
FIGURE 6.—Photograph of extreme posterior end of body of *Oligolactoria bubiki,* new species, Ge 26 831, 33.3 mm SL, to show the long narrow caudal fin above and the stout preanal carapace spine below (anterior to left).
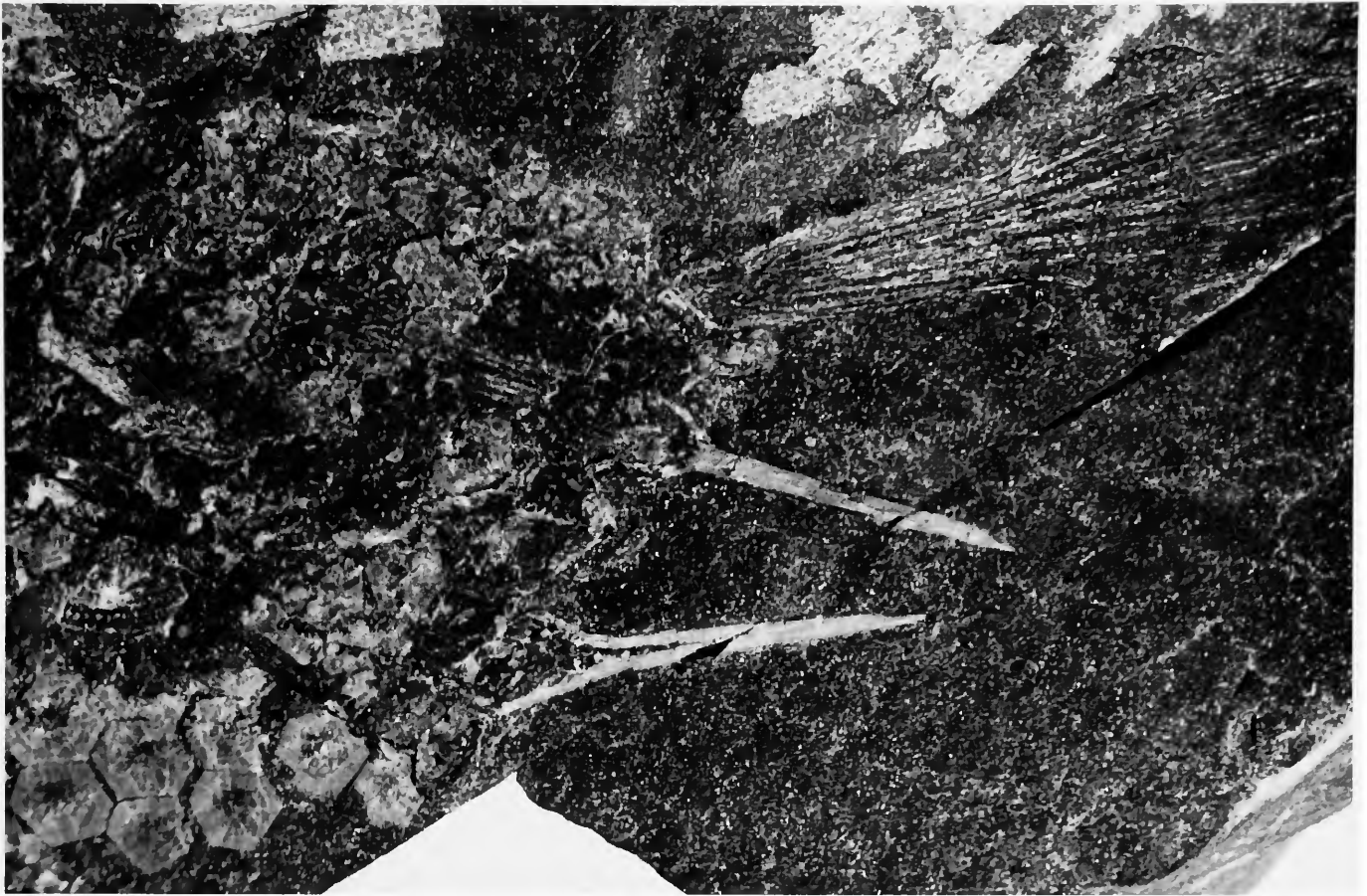
FIGURE 7.—Photograph of posterior half of body of *Oligolactoria bubiki,* new species, Ge 28 830, 39.5 mm SL, showing the caudal fin, preanal carapace spine from both sides, and the basal pterygiophores of the anal fin. The basal pterygiophores are indistinct and course obliquely anterodorsally from the region at the base of the more upwardly positioned of the two carapace spines.

denticulate for interdigitation with apposing plates to form a solid carapace. These features are typical of all ostracioids.

However, the carapace in *Oligolactoria* is broadly closed behind the dorsal and anal fins, extends far posteriorly, and lacks a well-developed mid-ventral carapace ridge. All of these are derived characteristics of the Ostraciidae.

The preorbital and preanal carapace spines of *Oligolactoria* are of about equal length, and vary from 27 to 36 percent SL. In comparison to the three species of the Recent *Lactoria,* the spine length in *Oligolactoria* is slightly longer than in *L. diaphana* and *L. fornasini* and slightly shorter than in *L. cornuta* (Tyler, 1973:107, fig. 2). The length of these spines in *Oligolactoria* is slightly greater than in the four species of the Recent *Acanthostracion* (Tyler, 1965b:287, fig. 21). The length of the spines in *Oligolactoria* is much less than in the Eocene ostraciid *Eolactoria,* which has the largest carapace spines by far among ostracioids, greater in length than the standard length of the body.

Although the carapace spines of *Oligolactoria* are fractured and displaced in most of the specimens, it is clear that the preorbital spines projected anterolaterally from the head (this is especially evident on the right side of Ge 26 831 exposed in dorsoventral view) and posterolaterally from the rear of the carapace (best seen in Ge 26 830 and Ge 26 831). Such well-developed preorbital and preanal carapace spines as found in *Oligolactoria* are present only in a few other species of Ostraciidae but not in the Aracanidae. In the Aracanidae many genera have spine-bearing dorsolateral or ventrolateral carapace ridges. In some of these taxa (e.g., *Capropygia* and *Caprichthys*) the ventral ridge terminates posteriorly in a posterolaterally directed spine similar to that in the ostraciid genera *Oligolactoria, Eolactoria, Lactoria,* and *Acanthostracion* (as well as in *Rhinesomus* and *Lactophrys,* in which some species have preanal but not preorbital carapace spines). Aracanids also may have a spine above the eye on the dorsolateral carapace ridge (e.g., in the genera *Aracana* and

Caprichthys), but this spine is always directed dorsally or posterodorsally, and is never in the position of the anterior or anterolaterally directed preorbital carapace spine found in *Oligolactoria, Eolactoria, Lactoria,* and *Acanthostracion.*

In one specimen (Ge 26 829) one of the mid-dorsal carapace scale plates in front of the dorsal fin has an especially high central conical process, which appears to be a medial carapace spine. The carapace scale plate bearing this dorsal spine is either slightly enlarged (as we show it in the reconstruction) or of more normal size with a much smaller plate between it and the slot in the carapace that accommodates the dorsal fin. In either case, this is a more posterior placement of the mid-dorsal carapace spine than in the Recent species of ostraciids with such a prominent spine. In the Recent ostraciids, the third or fourth carapace scale plate in front of the dorsal fin bears the spine (*Lactoria diaphana* and *L. fornasini*) rather than the first or second as in *Oligolactoria.*

Two specimens (Ge 26 829, Ge 26 830) show clear evidence of dorsolateral and ventrolateral carapace ridges. Thus, the carapace of *Oligolactoria* probably was at least partially rectangular in cross-section. However, even though the carapace is pressed into a single plane and is somewhat deformed into an unnaturally great depth of 70.8 percent SL in the only specimen whose depth we can measure, we believe that the presence of a predorsal medial carapace spine is evidence that the carapace was at least somewhat elevated into a crest dorsomedially between the head and the dorsal fin. Therefore, the carapace probably was pentangular in the middle of the body. The carapace evidently had a mid-dorsal crest of moderate height bearing a low spine in front of the dorsal fin. A dorsolateral carapace ridge was as well developed as the ventrolateral ridge. Thus, the side of the carapace below the mid-dorsal crest was vertical and the lower two-thirds of the carapace relatively rectangular.

Evidence for Inclusion of *Oligolactoria* in the Ostraciidae

The Ostraciidae has been defined on the basis of 20 autapomorphies of the skeleton and carapace and 16 autapomorphies of the muscles (Winterbottom and Tyler, 1983:908). We cannot determine myological features in the fossil taxa. In addition, the regions of the skeleton where 14 of the 20 osteological autapomorphies of ostraciids occur are either obscured by the enlarged scale plates of the carapace or not preserved. However, enough of the skeleton of *Oligolactoria* can be seen to determine that it has at least six of the autapomorphies of the Ostraciidae (polarizations discussed in Winterbottom and Tyler, 1983:908). These include: (1) the ventral postcleithrum is apomorphically small or absent, instead of enormously expanded (which condition also is apomorphic, as explained below) as in the Aracanidae; (2) at least one of the centra preceding the caudal plate is much compressed, versus none compressed in the Aracanidae; (3) the haemal spine of the second preural centrum is reduced, versus

large in the Aracanidae; (4) there usually are only 10 caudal-fin rays, versus 11 in the Aracanidae (except 10 in *Proaracana*) and 12 in balistoids (see "Note on *Proaracana*" for discussion of caudal-fin counts); (5) the carapace is closed behind the anal fin, versus open in the Aracanidae; and (6) the caudal peduncle lacks isolated scale plates, versus such plates present dorsally and laterally in the Aracanidae (and ventrally also, but such isolated plates ventrally could be considered as equivalent to the consolidated plates around the rear of the anal-fin base of ostraciids and therefore the same as the preceding character).

The Aracanidae has been defined on the basis of eight osteological autapomorphies (and eight myological ones not useful here) (Winterbottom and Tyler, 1983:906). For only one of these, the size of the ventral postcleithrum, is the skeleton of *Oligolactoria* both sufficiently preserved and exposed to allow us to determine the condition of the character. In *Oligolactoria* the ventral postcleithrum is reduced in size relative to the balistoids rather than greatly expanded as in the aracanids. Based on multiple outgroup comparisons, Winterbottom and Tyler assumed that both the reduced ostraciid condition and the expanded aracanid condition represent different apomorphies independently indicating monophyly of the two taxa respectively.

From all of the above, it is clear that *Oligolactoria* belongs to the ostraciid rather than aracanid lineage of boxfishes.

Systematic Position of *Oligolactoria* within the Ostraciidae

Tyler (1980:238–243) recognized two subfamilies of ostraciids on the basis of 10 character differences in meristics, osteology, and geographic distribution. These were the Ostraciinae (including *Lactoria, Ostracion, Rhynchostracion,* and *Tetrosomus*) and the Lactophrysinae (including *Acanthostracion, Lactophrys,* and *Rhinesomus*).

Although Tyler's work was not cladistic, half of the characters used in diagnosing the two subfamilies can be polarized relative to the generally less-specialized aracanid and balistoid outgroups. The differences in the modal numbers of dorsal-, anal-, and pectoral-fin rays between the lactophrysins and ostraciins are not phylogenetically useful because the broad range of these counts in the aracanids encompasses those of the ostraciids. In addition, the difference in geographic distribution, the variable pattern of autogeny versus fusion of the haemal spine of the penultimate vertebrae, and of a canal through that haemal spine, cannot be interpreted usefully for phylogenetic analysis.

However, five of the six osteological differences (Tyler, 1980:238) are indicative of phylogenetic relationship. The three characters thought to be uniquely derived for the four genera of Ostraciinae are: (1) two or more postdorsal caudal vertebrae with trifid neural spines (versus no vertebrae with divided neural spines in the Lactophrysinae and Aracanidae); (2) the last anal-fin basal pterygiophore laterally or anterolaterally expanded into a prominent flange for carapace support

(versus no such expansion for carapace support in the Lactophrysinae and Aracanidae); and (3) the last dorsal-fin basal pterygiophore moderately or greatly expanded laterally and posteriorly for carapace support (versus no such expansion for carapace support in the Lactophrysinae and Aracanidae). The two derived characters that unite the three genera of the Lactophrysinae are: (1) myodome essentially absent (versus small but distinct in the Ostraciinae and Aracanidae); and (2) five anterior abdominal vertebrae involved in the fusion complex at the rear of the skull (versus four in the Ostraciinae and two in the Aracanidae, except for one species of ostraciin, *Lactoria fornasini,* with five vertebrae involved, a situation most parsimoniously interpreted as an independent acquisition because *L. fornasini* has all three of the osteological autapomorphies that unite the ostraciins).

None of these five osteological features that distinguish the ostraciins from the lactophrysins are exposed in the specimens of *Oligolactoria.* Thus, because of the nature of the preservation of *Oligolactoria,* we must rely almost exclusively on carapace characteristics, or osteological features that can be seen outside of the carapace, in attempting to establish the probable relationships of *Oligolactoria* within the Ostraciidae. This is unfortunate because the osteological autapomorphies that define the subfamilies seem to us to be far more substantial characters than are those associated with the carapace and therefore are better phylogenetic indicators. Moreover, the morphology of the osteological region best seen in *Oligolactoria,* that of the caudal peduncle behind the carapace, although unique to the family, possesses only plesiomorphic conditions. The evidence from the paucity of exposed internal features is mostly in conflict with that derived from the carapace, as detailed below.

The relatively extensive development of the carapace posteriorly onto the caudal peduncle in *Oligolactoria* leaves only the penultimate vertebra as the pivot around which the fused ural-hypural plate supporting the caudal-fin rays is laterally flexed. Associated with this is the unique feature of *Oligolactoria* of a single vertebral centrum (the penultimate) greatly foreshortened by compression. In other ostraciids there are either two (*Lactophrys* and *Rhinesomus* in the Lactophrysinae, and *Lactoria* and *Tetrosomus* in the Ostraciinae), three (most species of *Acanthostracion* in the Lactophrysinae, and *Ostracion* and *Rhynchostracion* in the Ostraciinae), or four (*Acanthostracion quadricornis* only) vertebrae with highly compressed centra in the caudal peduncle involved in flexing the caudal fin (Tyler, 1963:171–182; 1970:19–20, 69–70, figs. 38–41; summarized in 1980:236).

Balistoids do not have anteroposteriorly compressed centra in the caudal peduncle, and those of aracanids, the outgroup of the ostraciids, are only slightly compressed in comparison to ostraciids (see Winterbottom and Tyler, 1983:905–908, for establishment of polarity and apomorphic diagnoses of outgroups). Therefore, the plesiomorphic condition in ostracioids is no compression of these centra, but within the ostraciids the compression of a single vertebra as found in *Oligolactoria* is plesiomorphic relative to two or more vertebrae being compressed.

Therefore, *Oligolactoria,* with one compressed peduncular vertebra, is the sister group of all other ostraciids, which have two or more such vertebrae. This is the only unequivocal evidence of the phylogenetic relationships of *Oligolactoria* that we have been able to find after study of both the fossil and Recent groups of ostracioids.

The only other evidence that we have found that bears on the relationships of *Oligolactoria* are characters of the carapace, and these seem to demonstrate a high level of homoplasy or to be in conflict with the meager osteological data. This more equivocal evidence is interesting but offers little help in resolving the relationships of *Oligolactoria* within the Ostraciidae.

For example, preorbital carapace spines are a striking feature of *Oligolactoria* and a few other ostraciids. These must be considered apomorphic because such spines are absent in all species of the aracanid outgroup and in most of the species of the ostraciid ingroup. In contrast, preanal spines are found even more widely in the Ostraciidae and may have a homologue in the spines along the ventrolateral carapace ridge of the Aracanidae; thus, their presence in ostraciids is not necessarily apomorphic.

The presence of preorbital carapace spines in the Oligocene *Oligolactoria* would seem to relate it among the Recent Ostraciidae to either *Acanthostracion,* with a triangular carapace, or to *Lactoria,* with a rectangular to pentagonal carapace (depending on the degree of development of the mid-dorsal ridge), or to a clade formed by those two genera.

In spite of their sharing the specialized feature of preorbital spines, Tyler (1980:238–241) did not think that *Lactoria* and *Acanthostracion* were particularly closely related; i.e., he believed the preorbital spines had been independently acquired. Tyler placed these two genera in different subfamilies on the basis of the 10 character differences, which here are translated into the five autapomorphies separating the two subfamilies.

These osteological autapomorphies that respectively unite *Lactoria* with the subfamily Ostraciinae and *Acanthostracion* with the subfamily Lactophrysinae are relatively complex in comparison to the single and relatively simple character of the enlargement of a carapace scale plate in front of the eye into a preorbital horn. Therefore, the presence of preorbital carapace spines in *Acanthostracion* and *Lactoria* is most parsimoniously interpreted as homoplastic. Furthermore, given the evidence from the peduncular vertebral compression that *Oligolactoria* is the sister group of all other ostraciids, it is consequently likely that the preorbital spines of *Oligolactoria* are homoplastic to those of *Acanthostracion* and *Lactoria.*

Another carapace character of interest is the presence of an upright medial carapace spine that is variously developed in front of the dorsal fin in *Oligolactoria* (weakly), *Lactoria* (well developed in *fornasini* and *diaphana;* present but weakly

developed in *cornuta*), and *Tetrosomus* (moderate). Such a mid-dorsal carapace spine otherwise is absent among ostraciids and all aracanids except the Eocene *Proaracana*, which has a high mid-dorsal and mid-ventral spine. Considering the presence of the mid-dorsal spine as a plesiomorphic feature in *Proaracana, Oligolactoria, Lactoria,* and *Tetrosomus* requires the unlikely independent loss of this spine in all aracanids except *Proaracana*, in all ostraciin ostraciids except *Lactoria* and *Tetrosomus*, and in all lactophrysin ostraciids. It is equally difficult to suppose that the mid-dorsal spine is an autapomorphy uniting the ostraciids *Oligolactoria, Lactoria,* and *Tetrosomus*, because this requires the independent acquisition of the spine in *Proaracana* and the reversal of the character state of the compression of the second vertebra (PU$_3$) in front of the hypural plate complex (PU$_1$).

With so much homoplasy in carapace characters we prefer to rely on what we believe is the firmer evidence from the caudal peduncle vertebrae, which simply places the Oligocene *Oligolactoria* as the sister group of all other ostraciids for which this character is known (the two Recent subfamilies; character state unknown in the Eocene *Eolactoria*).

We do not place phylogenetic significance in the fact that *Oligolactoria* has its closest phenetic resemblance to *Lactoria*. These shared resemblances include preorbital spines, preanal spines, mid-dorsal spines, a basically pentangular carapace, and a difference of only one in the number of compressed peduncular vertebrae. Similarly, we do not place phylogenetic significance on the phenetic dissimilarity between *Oligolactoria* and *Acanthostracion* (the latter lacks a mid-dorsal spine, has a triangular carapace, and two or three more compressed peduncular vertebrae). However, because *Oligolactoria* and *Lactoria* uniquely among ostraciids share a derived (not present in outgroups) ecological peculiarity in life-history stages discussed below, we remain open to the possibility that we have misinterpreted the anatomy of the peduncular region in *Oligolactoria*, or that the compression of the peduncular vertebrae is more homoplastic than presently known.

The Eocene *Eolactoria* is the only other described fossil ostraciid. Too little is known about the conditions in *Eolactoria* of meristic and skeletal features diagnostic of the Ostraciinae and Lactophrysinae for it to be placed with any confidence in either subfamily (Tyler, 1973:113; 1980:242), or to determine its relationships with the Oligocene *Oligolactoria*. We hypothesize that *Oligolactoria* and *Eolactoria* are not closely related, for *Eolactoria* possesses specializations (e.g., enormous length of preorbital and preanal carapace spines, with surface serrations) that would seem to be unlikely in an ancestral line leading to *Oligolactoria* (moderate preorbital and preanal carapace spines, without serrations). However, these features could be unique to *Eolactoria* and simply not present in the ancestor of it and *Oligolactoria*.

Discussion

The presence of a single compressed peduncular vertebra and the posterior position of the rear edge of the carapace at the level of this penultimate vertebra in *Oligolactoria* requires comment in light of some previous interpretations of the polarity states of these features.

Winterbottom and Tyler (1983:905–908) presented extensive evidence on the polarity of osteological, myological, and carapace characters in aracanids and ostraciids relative to the balistoid sister group. This was done to assist them in a proper interpretation of the relationships of the then recently described aracanid *Polyplacapros*, which is unique in having the caudal peduncle nearly completely covered with discrete bony scale plates and in having an almost fusiform body (low mid-ventral and mid-dorsal ridges). Other aracanids have fewer such scale plates, ranging from relatively many in *Kentrocapros*, to plates consolidated into several saddles in *Aracana* and *Strophiurichthys*, or into a ring in *Anoplocapros* and *Capropygia*, to only a few isolated scale plates in *Caprichthys*. In ostraciids there are no such isolated scale plates on the caudal peduncle (except in *Acanthostracion quadricornis*, which Tyler, 1965a:8–9, showed usually has one or two small scales present dorsally or ventrally; we believe this represents an independent acquisition in that species alone among the ostraciids).

Within the context of the more than 100 autapomorphies pertinent to hypotheses of phylogenetic relationships of the Balistidae, Aracanidae, and Ostraciidae, Winterbottom and Tyler (1983:911–913) concluded that the presence of numerous individual scale plates on the caudal peduncle, as in *Polyplacapros*, is plesiomorphic (present also in balistoids), and that within the aracanids there is a reduction and consolidation of scale plates in a sequential transformation series of increasing specialization from *Kentrocapros* to *Caprichthys*. The complete absence of peduncular scales in nearly all ostraciids is apomorphic, and obviously independent of the specialized reduction in an aracanid such as *Caprichthys*. It should be noted that the fossil ostracioids are in accord with that analysis, for the Eocene aracanid *Proaracana* has many isolated scale plates on the caudal peduncle (but fewer than in *Polyplacapros*), but there is no evidence of peduncular scales in either the Eocene ostraciid *Eolactoria* or in the Oligocene ostraciid *Oligolactoria*.

Winterbottom and Tyler (1983:908) noted that one of the 36 autapomorphies of ostraciids is the anteroposterior compression of at least two of the vertebrae preceding the hypural plate, versus the plesiomorphic condition of no such distinctive compression in aracanids. It is reasonable to assume that the compression of a single peduncular vertebra in *Oligolactoria* represents the most plesiomorphic condition yet known for this region of the ostraciid vertebral column, and that the compression of two or three, or in one case of four, peduncular vertebrae is an apomorphic sequential transformation series of increasing specialization.

There would seem to be little or no correlation in *Oligolactoria* between the plesiomorphic condition of a single compressed peduncular vertebra and the apomorphic condition of an especially well-developed posterior extension of the carapace onto the caudal peduncle. The posterior extension must be considered a specialization, because in all aracanids the carapace ends in the region below the bases of the dorsal and anal fins (and extends farthest posteriorly in the two genera, *Capropygia* and *Caprichthys,* considered the most specialized on the basis of osteological features as well), whereas in all ostraciids it extends behind the bases of these fins to varying degrees (e.g., slightly in *Lactophrys,* moderately in *Lactoria* and *Tetrosomus,* most extensively in *Oligolactoria*). Thus, *Oligolactoria* has a uniquely derived condition of posterior carapace extension among ostraciids, but the most primitive condition of compression of the peduncular vertebrae.

One might have expected these two features to be positively linked, but in *Oligolactoria* they are inversely correlated. It is understandable functionally for the species with the greatest posterior carapace extension to have the least number of compressed vertebrae because it is only those few centra behind the carapace that are involved in flexing the tail and in which vertebral compression is advantageous. Conversely, the mosaic of an apomorphic carapace over a plesiomorphic peduncle seems contrary to the proposed sequential transformation series of increasing specialization from one (*Oligolactoria*) to between two to four (all other ostraciids) compressed vertebrae. This apparent conflict between our interpretation of functional and phylogenetic reasonableness is not resolved here. We hope that the description of additional new species, especially of fossils, and better exposure of osteological features in additional specimens of the three presently known fossil species of ostracioids will, in the future, clarify the situation.

Note on *Proaracana*

Winterbottom and Tyler (1983:911) noted that the Eocene *Proaracana* had been placed by Tyler (1973:114–117, 1980:204–205) in the Aracanidae exclusively on the basis of primitive characters (especially the short carapace, deep ventral keel, and numerous isolated peduncular scale plates) but that *Proaracana* had 10 caudal-fin rays like ostraciids rather than 11 as in other aracanids (10 being apomorphic and 11 plesiomorphic as the ancestral balistid sister group has 12). On that basis alone they suggested that *Proaracana* should be placed in the Ostraciidae rather than the Aracanidae.

Winterbottom and Tyler (1983:911) mentioned that the reasonableness of that reallocation would be decreased by the then pending description of Matsuura and Yamakawa (1982:33, 35) of variation in the number of caudal-fin rays in *Kentrocapros,* in which the rays are sometimes 10 rather than 11 in *K. flavofasciatus* and *K. rosapinto.* Keiichi Matsuura (pers. comm.) also has found this to be true in *K. aculeatus.* We believe that the case for reallocation also is weakened by the distinct possibility that *Oligolactoria* has nine rather than 10 caudal rays. There is more variability in caudal counts in ostracioids than had previously been known. The reduction by one in the number of caudal-fin rays is not associated with fin size, for the reduction occasionally found in *Kentrocapros* is in a short fin and the possible reduction in *Oligolactoria* is in an exceptionally long fin.

Additional specimens of *Proaracana* showing internal osteological features will probably allow a firmer foundation for its familial allocation. In the interim, *Proaracana* is not known to possess any of the 36 autapomorphies of the ostraciids other than in the variable caudal-fin count. We believe it more prudent to retain *Proaracana* in the Aracanidae, with which family it has its greatest overall similarity in countenance, rather than in the Ostraciidae, with which it does not share even superficial features.

Paleoecology

Both the microfauna and flora of the Bystřice/Olší Locality that yielded *Oligolactoria* have been used previously to determine the bathymetric deposition conditions of these fossiliferous strata. The taphocoenosis, or death assemblage, of these Šitbořice Beds of the Menilitic Formation is characterized by an admixture of fossils with various relatively different ecological requirements.

Based on the presence of calcareous nannoplankton and planktonic foraminifera, Bubik (1987a:52–56) postulated an open sea environment for these strata. Benthic foraminifera also are found in these strata; some are bathyal marine genera but others are more typical of estuarine and lagoonal waters with very low salt content. Bubik proposed that the presence of the low salinity foraminifera resulted from the redeposition of sea margin deposits into deep sediments.

In relation to admixture, we must also emphasize the presence in these strata of both terrestrial and marine plants. In addition to marine brown algae, a mixture of mostly broadleafed evergreen angiosperms (Lauracea and Fagaceae) and conifers (*Taxodium, Pinus, Sequoia,* and *Tetraclinis*) have been reported by Kvaček and Bubik (1990:91–92). Those authors interpreted this mixture to be the result of terrestrial near-shore higher plants having been transported into deep marine sediments by wind and river flow. Similarly, H. Cappetta (pers. comm.) reported that, in the Golfe du Lions in the Mediterranean, leaf-bearing tree branches of various sizes are blown along the surface of the sea away from shore by the strong mistral winds, to sink to the bottom, often to depths of several hundred meters (based on their being trawled up in fishing nets).

The largest component (35 percent) of the ichthyofauna of these strata is photophore-bearing mesopelagic fishes of the families Gonostomatidae (*Kotlarczykia*), Photichthyidae (*Vinciguerria*), Sternoptychidae (*Argyropelecus*), and Myctophidae (genus undetermined) (Gregorová, 1989:95, and unpublished

data). Another prominent mesopelagic element (15 percent) is the family Trichiuridae (*Lepidopus*). Remains of several species of Clupeidae (cf. *"Clupea"*) also are abundant (15 percent, Gregorová, unpublished data). Clupeids also are represented by isolated scales that have been broadly referred to *"Clupea"* and *"Alosa"* (Szymczyzk, 1978:394-403). It is not known whether these clupeids were epipelagic or neritic. Several other taxa of teleosts (family undetermined) are present in these strata, and at least one species of perciform (cf. *"Serranus"*), but these are of unknown type of habitat. Three species of sharks are present in the formation: *Echinorhinus* cf. *riepli, Alopias* cf. *superciliosus,* and *Notorhynchus* sp. (Bubik, 1987b:48). The Recent species of *Echinorhinus* are deep-water (to 900 meters) benthic and epibenthic species of continental and insular shelves and slopes, whereas the monotypic *Notorhynchus* is benthic and neritic in shallower waters (surface to 46 meters) of continental shelves; by contrast, *Alopias* ranges widely in habitat from coastal to epipelagic and deep-water epibenthic, with some species more pelagic and others more benthic (Compagno, 1984:23, 25-27, 228-233). Therefore, like the clupeids, the presence of these three kinds of sharks ranging from shallow and deep water benthic to oceanic pelagic offers ambiguous data on habitat interpretation relative to *Oligolactoria.*

In a sedimentological study, Stránik et al. (1981:708) showed the Šitbořice Beds to be composed of bathyal sediments of the lower continental slope deposited in an anoxic bottom reducing environment, probably with only restricted communication with larger nearby bodies of water. The anoxic condition of the bottom during the deposition of the Bystřice/Olši strata also can be seen in the dark color of its pelite, the frequent occurrence of laminites, the well-preserved fish skeletons, and the presence of pyrites.

Therefore, it is difficult at present to propose a consistent bathymetric interpretation of the deposition condition of the Šitbořice Beds at the Bystřice/Olší Locality that can account for the origin of all of its ecologically diverse elements.

One possibility is the redeposition of the shallow-water elements from the margins of the sea into the environment of the fossilization of the mesopelagic photophore-bearing fishes and of the deposition of the open ocean calcareous nannoplankton and planktonic foraminifera. For example, Arambourg (1927:247-248) proposed a mechanism similar to this to account for myctophids in the Gambeta locality of the Messinian of Oran, and considered such sediments to have been of bathypelagic origin.

Another possibility is the interpretation proposed by Kalabis (1938) and supported by Gaudant (1989:1163-1164) for the upper Miocene (Messinian) diatomites of southern Spain. They propose that the admixture of both mesopelagic and neritic fishes found in those strata is a result of the nycthemeral migration of the most common mesopelagic fishes (especially myctophids) and the occurrence of ascending water currents similar to upwellings.

In any case, the ichthyofauna of the Menilitic Formation is dominated by representatives of mesopelagic groups such as myctophiforms, stomiiforms, and trichiurid scombroid perciforms, and is composed almost exclusively of mesopelagic genera, with the possible exception of a few clupeids of unknown habitat (epipelagic or neritic?) and one or two sharks of varied habitats.

The presence of the armor-encased, heavy-bodied *Oligolactoria,* a representative of a family of typical in-shore, benthic, shallow-water fishes, would at first seem to call for the invocation of the admixture hypothesis. However, the occurrence of the boxfish *Oligolactoria* in this mesopelagic assemblage is perfectly explicable once one considers that our specimens represent the large, oceanic, pelagic, pre-settlement juvenile and young adult stages found in this species prior to it assuming its definitive benthic in-shore existence, by inference from *Lactoria diaphana* as discussed below.

Lactoria is unique among the extant ostraciids in containing a species (*diaphana*) that remains pelagic to the exceptionally large size of over 100 mm SL and obtains sexual maturity while pelagic before settlement. Moyer (1984:93) reported that *L. diaphana* arrives at Guam pelagically at sizes exceeding 150 mm total length (= ~120 mm SL, by extrapolation from Figure 8) and then settles to the bottom while still in this large and more transparent young adult stage. Leis and Moyer (1985:191, 200) considered *L. diaphana* a truly pelagic species for most of its life history, remaining pelagic to sizes of up to about 100 mm SL and reaching sexual maturity and spawning while pelagic, especially in the eastern Pacific populations; they recorded newly settled terminal adult stages of 102 and 131 mm SL. Myers (1989:264) reported that ripe females of *L. diaphana* of 20 to 35 mm SL are recovered from the stomachs of Guam gamefishes, evidence that *L. diaphana* can live and breed pelagically, and Fitch and Lavenberg (1975:93) and Thomson et al. (1979:238) also considered it as a pelagic species in the eastern Pacific. Ostraciids of undetermined species ranging in size up to 40 to 70 mm SL are important components of the stomach contents of Pacific scombroids (Moyer, 1979:157, and references therein). We suspect that many and probably most of these larger pelagic ostraciids are *L. diaphana,* whereas Fujita and Hattori (1976:138) have shown that smaller juvenile *L. fornasini* of about 13 to 17 mm SL are prominent in the stomach contents of Indo-Pacific *Alepisaurus* lancetfish.

Because *Oligolactoria* has at least phenetic similarity to *Lactoria,* and one of the three species of *Lactoria* alone among the ostraciids has a long duration, late-settling, large size (up to 120 mm SL), and sexually mature pelagic stage, we hypothesize that the specimens of 25 to 55 mm SL of *Oligolactoria* described here represent the late juvenile to young adult pelagic stage of *O. bubiki,* entirely comparable to the pelagic life cycle stages reported by Moyer (1984:93) and Leis and Moyer (1985:200) for *L. diaphana.*
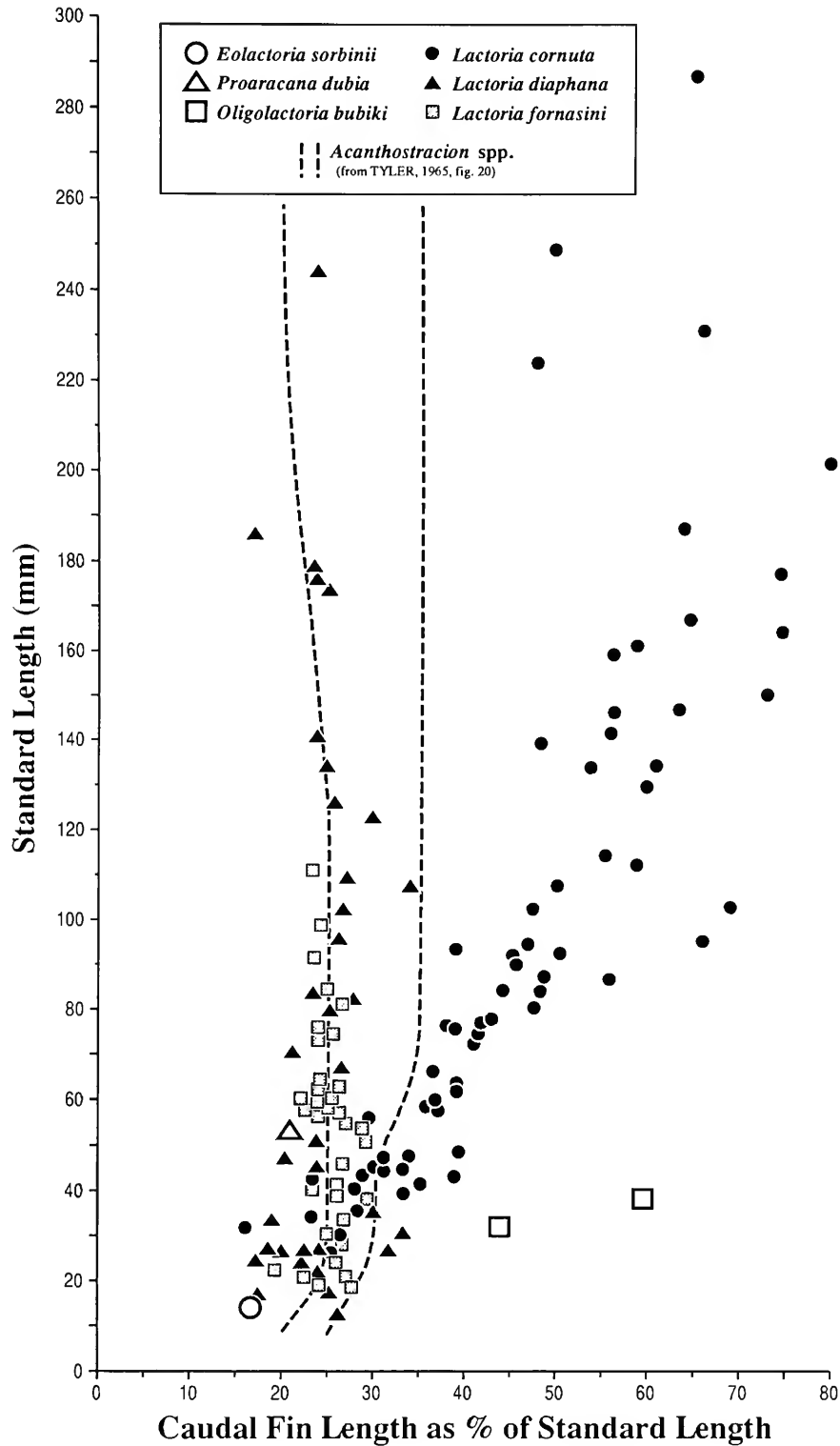
FIGURE 8.—Chart showing the relative length of the caudal fin in all of the fossil species and in representative Recent species of ostraciids. Most ostraciids have a caudal fin of 15 to 35 percent SL, not increasing much in proportional length in specimens of greater than about 25 mm SL, except in the single Recent species *Lactoria cornuta;* most ostraciids have a pattern similar to that shown in dashed lines for numerous specimens examined of the four species of *Acanthostracion,* as shown in more detail by Tyler (1965, fig. 20).

We believe that the presence of *Oligolactoria* in the Menilitic Formation along with a great variety of strictly off-shore mesopelagic fishes, such as myctophoids and stomiatoids, is evidence that the prolonged pelagic pre-settlement scenario for large juveniles and young breeding adults as found today in *Lactoria diaphana* was present in the phylogeny of the family at least as early as the Oligocene about 35 MYA.

Stratigraphy

All but one of the specimens of *Oligolactoria* are from the Bystřice/Olší Locality of the Menilitic Formation of the Subsilesian Unit of the Flysh Zone of the Western Carpathians in Northeastern Moravia. The fossiliferous strata bearing *Oligolactoria* belong to the sequence that terminated the sedimentation in the Menilitic Formation. With respect to their stratigraphic position, lithology, and paleontology, these strata are comparable to those of the Šitbořice Beds as described from the Ždánice Unit (Bubik, 1987b:56). With respect to their lithology, the Šitbořice Beds are composed of a pelitic facie (varying from dark calcareous claystones to marlstones) belonging to the nannoplankton zone of the middle Oligocene, NP 23 (Rupelian).

Based on the ichthyofaunal zonation of the Menilitic Formation in the Scole Unit of the Western Carpathians as proposed by Kotlarczyk and Jerzmańska (1976:57) and reaffirmed by Jerzmańska and Kotlarczyk (1981:64) and Kotlarczyk and Jerzmańska (1988:349), we can assign the Moravian strata bearing *Oligolactoria* to Zone IPM 3. The index species for this zone at the Bystřice/Olší Locality is *Kotlarczykia* sp. (Gregorová, 1989:91). This ichthyofaunal zonation at the Litenčice Locality, Ždánice Unit, is discussed by Gregorová (1988:87). The single specimen of *Oligolactoria* from Poland belongs to the Menilitic Zone IPM 4, slightly less old than the Moravian specimens of IPM 3.

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