

A new genus and species of lutjanid fish (Perciformes) from the Eocene of Bolca, Northern Italy

ALEXANDRE F. BANNIKOV* - ROBERTO ZORZIN**

(*Borisjak Paleontological Institute of the Russian Academy of Sciences, Moscow)

(**Museo Civico di Storia Naturale, Verona)

ABSTRACT

A new genus and species of lutjanid fish (Perciformes, Percoidei), *Lessinia horrenda*, is described based on a single skeleton from the Eocene locality of Bolca in northern Italy. An additional specimen from the same locality is identified as *Lessinia* sp. In comparison with other lutjanids from Bolca, the new genus has a smaller mouth and weaker dentition. The new taxon extends the list of Bolca snappers known to date to five or six species and four genera.

Key words: Perciformes, Lutjanidae, Eocene, northern Italy, Bolca locality.

RIASSUNTO

Un nuovo genere e specie di lutjanide (Perciformes, Percoidei), *Lessinia horrenda*, è descritto sulla base di un unico scheletro proveniente dall'Eocene di Bolca (Italia settentrionale). Un ulteriore esemplare, della stessa località, è identificato come *Lessinia* sp. Dal confronto con altri lutjanidi di Bolca, il nuovo genere ha una bocca più piccola e una dentatura più debole. Il nuovo taxon estende l'elenco dei dentici di Bolca noti fino ad oggi a cinque o sei specie e quattro generi.

Parole chiave: Perciformi, Lutjanidae, Eocene, Italia settentrionale, Bolca.

INTRODUCTION

The fauna of the famous Monte Bolca locality, to the north of Verona in northern Italy, is exceptionally rich in marine Eocene fishes, especially of acanthopterygians. However, in his systematic catalog of Bolca fishes Blot (1980) did not indicate any lutjanid fish from there. Lutjanids, or snappers, are mostly reef-dwelling fishes presently widely distributed in tropical and subtropical marine waters. There are 17 genera and about 105 species of lutjanids in the Recent fauna (Allen, 1985; Nelson, 2006).

It has recently been shown (Bannikov, 2006) that the family Lutjanidae is represented in the Bolca fauna by at least four species in three genera (*Ottaviana* Sorbini, 1983, *Goujetia* Bannikov, 2006 and *Veranichthys* Bannikov, 2006). *Ottaviana mariaae* was briefly described by Sorbini (1983) as a perciform fish of uncertain relationships, but it was subsequently redescribed by Bannikov and Zorzin (2004) in detail as a lutjanid perhaps related to the subfamily Etelinae. The species long known as the sparid *Dentex leptacanthus* (Agassiz, 1833-1844; de Zigno, 1874) was shown by Bannikov (2006) to be a second species of *Ottaviana*. Similarly, *Dentex crassispinus* Agassiz, 1839 was redescribed as a lutjanid

by Bannikov (2006) and attributed to the new genus *Goujetia*. Finally, Bannikov (2006) showed that the species known as the serranid *Serranus ventralis* (Agassiz, 1833-1844; de Zigno, 1874) actually represents a snapper of the new genus *Veranichthys*, of which *Serranus rugosus* Heckel, 1854 must be regarded as its junior synonym. In addition to the true lutjanids, there is also an *incertae sedis* percoid in the Bolca fish fauna which is probably related to the Lutjanidae: *Parapelates quindecimalis* (Agassiz, 1836), as suggested by Bannikov (2008).

The field excavations executed in 2005-2011 by the second listed author and his colleagues about 25 meters higher up the steep hillside from the entrance to the classic Pesciara cave site of the Monte Bolca locality yielded many interesting materials, including new species of fishes and additional specimens of some fish taxa that had previously been known only on the basis of holotypes collected at the old Pesciara site during the nineteenth century. Among the materials collected at the new Pesciara site in 2007 is a single specimen of lutjanid fish that can be attributed to the new genus and species described below. A poorly preserved specimen (IG 126422/126423) in the collection of the Museo Civico di Storia Naturale di Verona also belongs to this new genus, but it probably represents a different spe-

cies; however, we prefer to wait for a better preserved specimen to be obtained before describing it.

Thus, the list of the Bolca snappers known to date can be extended to five or six species and four genera. Even though they are relatively diverse taxonomically, the lutjanids are not commonly collected at the Bolca locality; each of their species is represented to date by only one to a few specimens in the collections of the world's museums.

METHODS

Some details of the specimens examined were best seen when the specimens were moistened with alcohol during microscopic examination.

Interneural and interhaemal spaces are numbered based on the vertebra whose neural or haemal spine forms the anterior border of the space, with the first space being between the first and second neural or haemal spines (following Baldwin and Johnson, 1993; Bannikov and Tyler, 1995; Tyler and Bannikov, 1997; etc.).

Abbreviations are as follows: *Institutional*: MCS-NV – Museo Civico di Storia Naturale di Verona; *Anatomical*: E – epural; H – hypural; HL – head length; HPU – haemal spine of preural vertebra; Mx – maxilla; NPU – neural spine of preural vertebra; Pal – palatine; Ph – parhypural; Pmx – premaxilla; PU – preural vertebra; SL – standard length; U – ural vertebra; Un – uroneural.

SYSTEMATIC DESCRIPTION

Order Perciformes
Suborder Percoidei
Family Lutjanidae Gill, 1884

Genus *Lessinia* gen. nov.

Type species

Lessinia horrenda sp. nov., by monotypy and designation herein.

Diagnosis

Dorsal profile of body somewhat more convex than ventral profile. Head relatively small. Maximum body depth exceeds head length. Supraoccipital crest prominent. Mouth small; lower jaw articulation under anterior half of orbit. Jaws with an outer row of small blunt conical teeth and an inner band of minute sharp villiform teeth. One or a few anterior premaxillary teeth canine-like. Preopercle finely serrated. 10+14 vertebrae. Hypurals 1-2 and 3-4 fused into two plates. Three strong supraneurals. Dorsal fin continuous, with 10 slender spines and 11 soft rays. Anal fin with 3 graduated slender spines and 8 rays. Pelvic fins inserted behind pectorals. Outer pelvic-fin ray not elongated. Pectoral fins moderately long. Caudal fin deeply forked. Scales moderately large and cycloid, each scale with numerous radii basally. Lateral line complete, passes relatively low on flank.

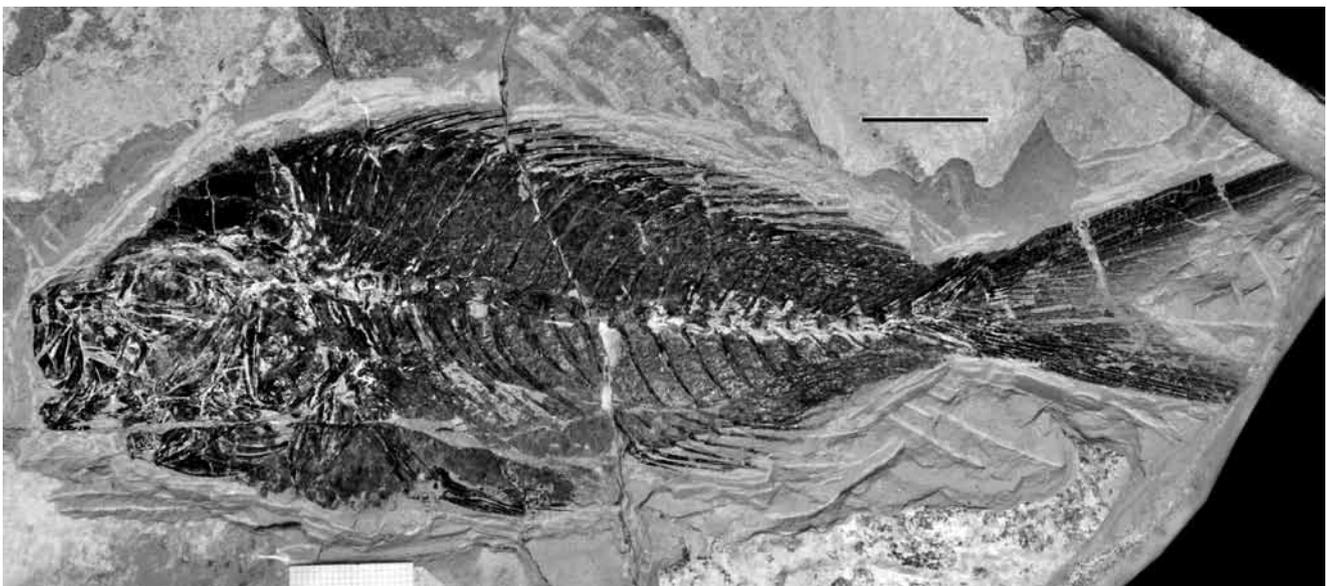


Fig. 1 – *Lessinia horrenda* sp. nov., photograph of holotype MCSNV IGVR 71613, 152 mm SL; uppermost Lower Eocene, Monte Bolca locality in northern Italy, Pesciara site. Scale bar = 2 cm.

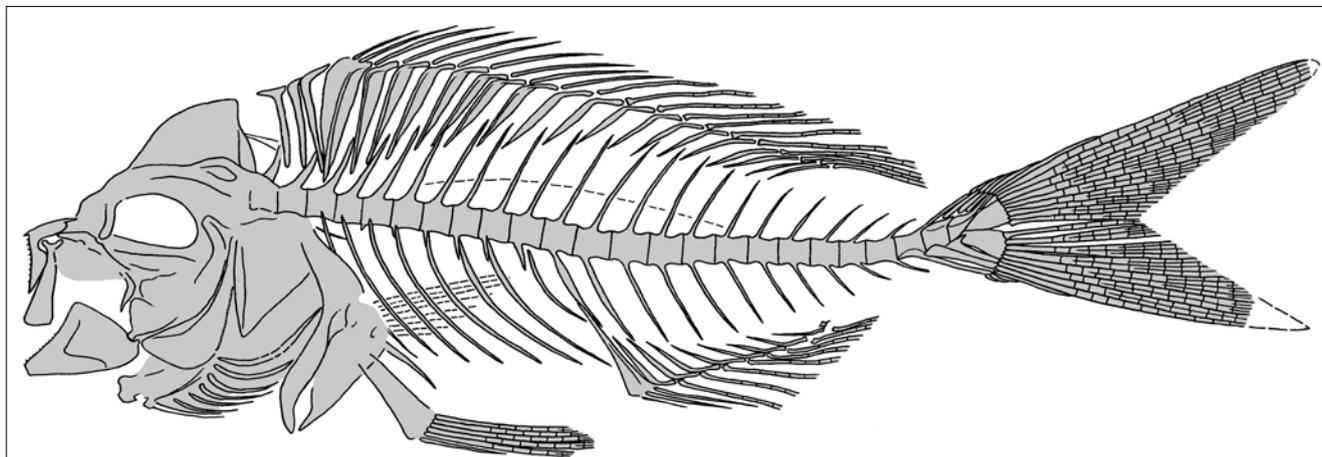


Fig. 2 – *Lessinia horrenda* sp. nov., reconstruction of entire skeleton based upon holotype MCSNV IGVR 71613; scales omitted.

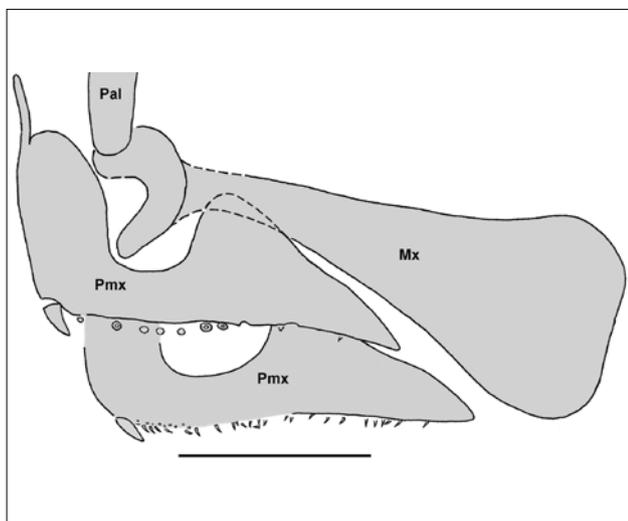


Fig. 3 – *Lessinia horrenda* sp. nov., drawing of upper jaws of holotype MCSNV IGVR 71613. Scale bar = 5 mm.

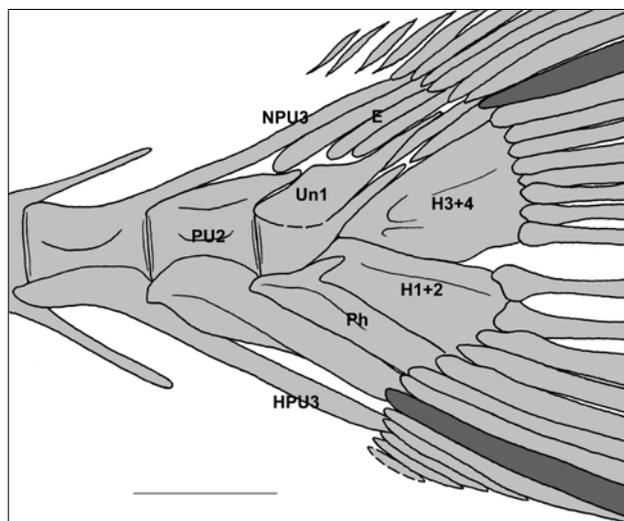


Fig. 4 – *Lessinia horrenda* sp. nov., reconstruction of caudal skeleton based upon holotype MCSNV IGVR 71613; dark coloration marks outermost principal caudal-fin rays. Scale bar = 4 mm.

Etymology

Named after the natural park Lessinia to the north of Verona; gender feminine.

Referred species

Type species and *Lessinia* sp. from the same locality.

Lessinia horrenda sp. nov.

Figures 1 – 4

Diagnosis

As for the genus.

Holotype

MCSNV IGVR 71613; complete skeleton, 152 mm SL,

single plate; upper part of the Lower Eocene, Ypresian, zone *Alveolina dainellii* (Papazzoni and Trevisani, 2006); Monte Bolca locality, Pesciara cave site.

Referred specimens

None.

Etymology

The species is named after the Latin word *horrendus* for marvelous, respectable.

Description

The body is moderately elongate, with a relatively short and rather slender caudal peduncle. The caudal peduncle depth is about 0.26 of the body depth. The head

is relatively small, its length (tip of snout to anterior edge of upper part of pectoral girdle) almost 1.25 times less than the body depth. The head length is contained about 3.28 times in SL. The dorsal profile of the body is slightly more convex than the ventral profile of the body.

- Head. The head is relatively deep, with its depth equals to its length. The orbit is moderate and situated in the upper half of the head. The horizontal diameter of the orbit is 26-27% HL. The snout is pointed and relatively short; its length is about 30% HL. The mouth is relatively small and terminal; the lower jaw articulation is situated approximately under the anterior half of the orbit. The infraorbital bones are badly damaged, but the lachrymal seems to be relatively deep. The neurocranium is relatively deep, with a high supraoccipital crest that is prominent and rounded anterodorsally. The ethmoid region is short. The narrow lateral ethmoid is prominent laterally, forming the anterior border of the orbit. The parasphenoid is robust and almost straight; it extends along the lower border of the orbit. The premaxilla has a well-developed long and slender ascending process and a massive articular process. A high triangular postmaxillary process is present on the distal half of the premaxilla (Fig. 3). The alveolar ramus of the premaxilla bears an outer row of relatively small blunt conical teeth, and an inner band of minute sharp conical teeth. One anterior tooth is canine-like. The maxilla is relatively short and expanded towards its rounded distal end. The maxillary head is crescent-shaped. There are no supramaxillae. The mandible is relatively short and rather deep. The length of the mandible is about 39% HL. The dentary is notched posteriorly. The retroarticular process of the angulo-articular is massive and deep. The dentary dentition is similar to that of the premaxilla except that an anterior canine-like tooth is not evident. The hyomandibular shaft is significantly inclined anteroventrally. The quadrate is subtriangular and moderately large. The symplectic seems to be a simple strutlike bone. The ectopterygoid evidently lacks a posterior extension separating the endopterygoid from the quadrate. The limits of the endo- and metapterygoid are unclear. The opercular region is moderately wide. The preopercle is only slightly curved and moderately wide; its posterior edge is finely serrated. The opercle is wide and thickened along its anterior border. There are seven sabre-like branchiostegal rays; the branchiostegals become longer and wider posteriorly in the series. The hypohyals are much fragmented, and the ceratohyal is exposed only anteroventrally; it seems to lack a beryciform foramen. The urohyal seems to have a shape typical for lutjanids (Kusaka, 1974),

with its posterior border widely notched. The branchial bones and pharyngeal dentition are indistinct.

- Axial skeleton. There are 24 vertebrae, ten abdominal and fourteen caudal, including the urostyle. The axis of the vertebral column is almost straight. Most of the vertebral centra are either square or slightly elongate anteroposteriorly and constricted in the middle. The length of the caudal portion of the vertebral column is 1.6 times greater than the length of the abdominal portion of the vertebral column. The neural spines of the abdominal vertebrae increase in length posteriorly in the series; those of the first five vertebrae are somewhat thicker than the others. The neural and haemal spines of the caudal vertebrae are moderately slender and straight or slightly curved, and decrease in length posteriorly in the series. The first haemal spine is slightly expanded in the middle. The neural spines of the caudal vertebrae are similar to the corresponding haemal spines in length and in the angle of posterior inclination. Parapophyses were definitely present on at least the six posteriormost abdominal vertebrae, but most of them are not preserved. Pleural ribs are present on the third to tenth vertebrae, these are relatively long and slender. Epineurals are situated on a level of the vertebral column, and most of them are obscured by the centra.

- Pectoral girdle. Extrascapulars are absent. A post-temporal and supracleithrum are only partly recognizable. The cleithrum is an elongate, strong bone, and somewhat S-shaped. The upper part of the cleithrum is curved forward and situated below the third vertebra. The ventral postcleithrum is only moderately long and wedge-like in shape; it is directed posteroventrally. The coracoid is moderately narrow; there is a gape between the lowermost portions of the cleithrum and coracoid. The scapula and pectoral radials are scarcely recognizable. The pectoral fin is mostly hidden by scales and ribs; however, it is evident that the fin is moderately long. The total complement of pectoral-fin rays is unknown. The pectoral fin is inserted under the fifth vertebra just above the midpoint between the vertebral column and the ventral profile of the body.

- Pelvic fin and girdle. The pelvic bones are relatively strong and wedge-like. The anterior end of the basipterygium is oriented anterodorsally and attaches relatively high on the cleithrum. The pelvic fin has a spine and five soft branched rays; it is inserted behind the pectoral-fin base. The pelvic fin is moderately long.

- Supraneurals and dorsal fin. There are three very strong supraneurals (predorsal bones); the first supraneural bears a long apical process directed anteriorly, whereas the third supraneural bears a long apical pro-

cess directed posteriorly. The predorsal formula (Ahlfstrom et al., 1976) is /0+0/0+2/1+1/. Because in extant lutjanids the first supraneural away precedes the first neural spine (Johnson, 1980, 1984), one can assume that there was a slight post-mortem posterior displacement of the lower end of the first supraneural. The dorsal fin is relatively long-based and continuous; it originates over the fourth abdominal vertebra and terminates over the ninth caudal vertebra. There are ten dorsal-fin spines and eleven soft segmented rays; the last ray is not produced. The dorsal-fin spines are slender. The first two spines are supernumerary; these are closely spaced and shorter than the third to tenth spines, which are more or less equal in length. The first spine is 1.7 times shorter than the third. The first dorsal-fin soft ray is unbranched, whereas all the others are branched. The longest soft ray of the dorsal fin is somewhat longer than the last dorsal-fin spine. The length of the base of the soft portion of the dorsal fin is 1.17 times longer than the base length of the spiny portion of the dorsal fin. There are a total of 19 dorsal-fin pterygiophores. The ventral shafts of the two anterior dorsal-fin pterygiophores are only slightly inclined, whereas posteriorly in the series the pterygiophores become more strongly inclined, and the posteriormost pterygiophores are almost horizontally oriented. The pterygiophores of the dorsal-fin spines are expanded anteroposteriorly, and each bears a longitudinal strengthening ridge. The first pterygiophore is the largest; the succeeding pterygiophores become gradually shorter and narrower. At least the five posteriormost pterygiophores are trisegmental, with their medial segments unfused with the prox-

imal segments. The interneural spaces below the dorsal fin have the ventral shafts of one (usually) or two (the third, fifth, 11th, and 14th spaces) pterygiophores present.

- Anal fin. The anal fin originates under the third and ends under the ninth caudal vertebrae. There are three spines and eight soft segmented rays in the anal fin; all of the soft rays are branched. The spines are slender and very closely spaced; the third spine is at least 1.2 times longer than the second spine and 2.3 times longer than the first spine. The first two spines are supernumerary. The longest anal-fin soft ray is not longer than the third anal-fin spine, which is slightly shorter than the longest dorsal-fin spine. The first anal-fin pterygiophore is moderately long, sturdy, and wedge-like in shape; it is inclined at an angle of about 55° to the body axis. The succeeding anal-fin pterygiophores are slender and relatively strongly inclined; these gradually decrease in length posteriorly in the series. The last anal-fin pterygiophore is almost horizontally oriented. The six posteriormost pterygiophores are trisegmental. Most of the anal-fin pterygiophores are situated below the tips of the haemal spines, and thus they do not enter the interhaemal spaces.

- Caudal fin and skeleton. The terminal centrum is composed of the fusion of PU₁, U₁ and U₂ (Fig. 4). The neural spine of PU₂ is a short crest. The fifth hypural, parhypural, and haemal spines of PU₂ and PU₃ are autogenous. Hypurals 1-2 and 3-4 are fused into two plates. There are three epurals which decrease in length posteriorly in the series. There is a small hypural diastema (Monod, 1968). There are two uroneurals (the first as a stegural). The neural and haemal spines of PU₃ are

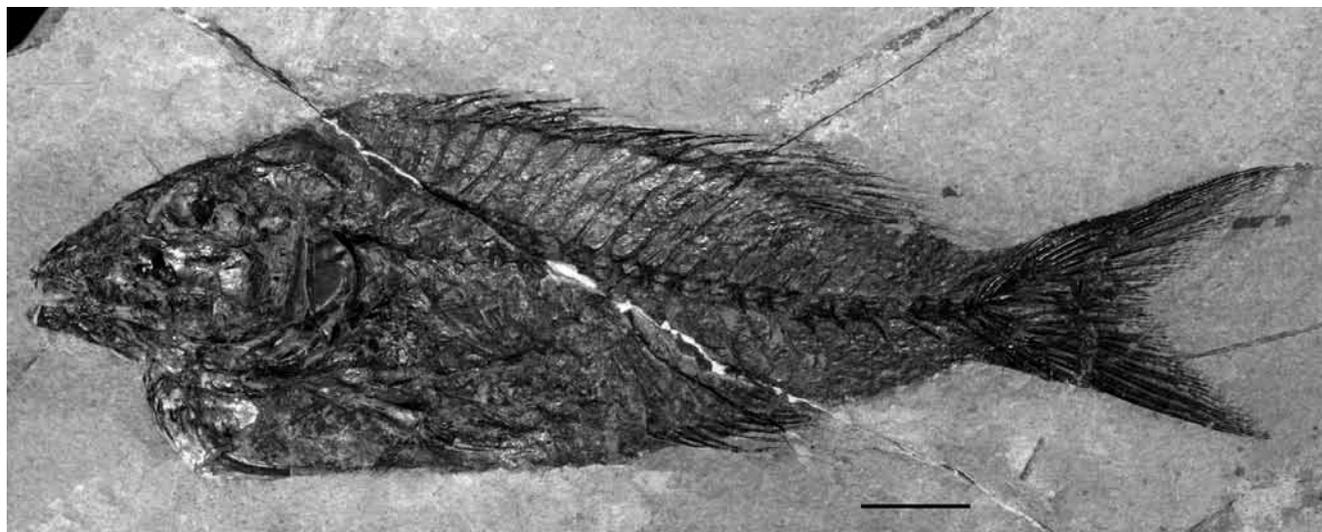


Fig. 5 – *Lessinia* sp., photograph of specimen MCSNV IG 126423, 179 mm SL; uppermost Lower Eocene, Monte Bolca locality in northern Italy, Pesciara site. Scale bar = 2 cm.

longer and stouter than those of the preceding vertebra. The caudal fin is large and forked; it has 17 principal rays, 15 of which are branched (I,8-7,I). The upper lobe of the caudal fin perhaps is slightly longer than the lower lobe. There are about 10 dorsal procurrent rays. The number of ventral procurrent rays is less precisely known because the several anteriormost elements are not preserved.

- Squamation. The scales are cycloid and moderately large; each scale bears numerous radii in the basal field. The number of radii varies from six (breast scales) to 11. The scales cover the body and cheek. The lateral line is very slightly arched and low in position; it descends to the level of the vertebral column near the 17th vertebra. Some scales bear minute spots of dark pigment.

- Measurements. The following measurements are presented as a percent of SL (152 mm) of the holotype, to the nearest half mm:

Head length from tip of snout to posterior border of opercle: 30.5

Maximum body depth: 38

Depth of caudal peduncle: 10

Distance between tip of snout and spiny dorsal fin: 37

Distance between tip of snout and soft dorsal fin: 59.5

Distance between tip of snout and anal fin: 64

Distance between pelvic fin and anal fin: 21

Length of base of spiny dorsal fin: 22

Length of base of soft dorsal fin: 25.5

Length of base of entire dorsal fin: 50

Length of base of anal fin: 21

Length of first spine of dorsal fin: 7.5

Length of longest spine of dorsal fin: 13

Length of longest soft ray of dorsal fin: 14

Length of third spine of anal fin: 10.5

Length of longest soft ray of anal fin: 10

Length of longest ray of pelvic fin: 17.5

Length of longest ray of caudal fin: ca. 35

Preorbital distance: 9

Horizontal diameter of orbit: 8.5

Length of lower jaw: 12

Remarks

Specimen MCSNV IG 126422/126423 (Fig. 5) is similar in many respects to the holotype of *Lessinia horrenda* sp. nov., and has to be attributed to the same genus. However, in certain morphological character states it is different from *L. horrenda* sp. nov., having a somewhat more elongate body, lower supraoccipital crest, longer ethmoid region, several canine-like teeth anteriorly on the premaxilla (vs. a single tooth in *L. horrenda* sp. nov.). Also, MCSNV IG 126422/126423 has the spiny portion of the dorsal fin longer at the base than

the soft portion, whereas in the holotype of *L. horrenda* sp. nov. the base length of the soft portion of the dorsal fin is longer. It is unlikely that these differences are caused by differing states of preservation, and it is difficult to explain them by possible sexual dimorphism; most likely the two specimens under consideration belong to two different species of the same genus. MCSNV IG 126422/126423 is somewhat less well preserved than the holotype of *L. horrenda* sp. nov., and some details of its structure are not clear. Therefore, until a better preserved specimen becomes available, we prefer to regard MCSNV IG 126422/126423 as *Lessinia* sp.

DISCUSSION

We attribute *Lessinia* gen. nov. quite confidently to the percoid family Lutjanidae. The new genus has a characteristic lutjanoid overall appearance, with a single dorsal fin, terminal mouth, high position of the orbit, seven branchiostegal rays, and supramaxilla absent, as well as the dentition typical for lutjanoids (Johnson, 1980): jaws with a canine, an outer row of larger conical teeth, and an inner band of smaller conical teeth. The dorsal (X, 11) and anal fin (III, 8) counts of *Lessinia* both are within the range recorded in the Lutjanidae.

In his revision of extant lutjanoids, Johnson (1980) recognized the superfamily Lutjanoidea consisting of two families, Lutjanidae and Caesionidae. The Lutjanidae was subdivided by Johnson into four subfamilies, Etelinae, Apsilinae, Paradicichthyinae and Lutjaninae. Johnson's classification was accepted by succeeding authors (e.g., Allen, 1985; Carpenter, 1990), but subsequently Johnson (1993) recommended treating caesionines as a subfamily of the Lutjanidae, which was originally accepted by Nelson (1994). Later, Nelson (2006) changed back to treating the Caesionidae as a separate family. *Lessinia* gen. nov. is easily distinguishable from caesionines by its different dorsal-fin formula, absence of the separate ossification of the premaxillary ascending process that is characteristic for the caesionines, and a broad-based rather than finger-like postmaxillary process.

Among the morphological characters of *Lessinia* gen. nov., two have not previously been reported for the Recent lutjanids (Johnson, 1980, 1984): the predorsal configuration and cycloid scales. The first supraneural of extant snappers precedes the first neural spine, whereas it enters the first interneural space in *L. horrenda* sp. nov. (this character state is less clear in *Lessinia* sp.). However, as mentioned above, one can assume a slight post-mortem posterior displacement of the low-

er end of the first supraneural in the holotype of the new species. Concerning the cycloid scales, such scales have already been reported for one of the two species of the Eocene lutjanid genus *Ottaviana*, and for the genus *Veranichthys*, also from Bolca (Bannikov, 2006). The family-level scale characteristic certainly has slightly changed throughout the last 50 millions of years of lutjanid history.

In its dorsal and anal fin counts, deeply forked caudal fin and fused hypurals 1-2 and 3-4, *Lessinia* gen. nov. is closer to the lutjanid subfamilies Etelinae and Apsilinae than to the Paradicichthyinae and Lutjaninae (see Johnson, 1980). But the Eocene genus more closely resembles apsilines rather than etelines in a number of its character states. Unlike the Etelinae, *Lessinia* gen. nov. has the ultimate ray of the dorsal and anal fins equal to or shorter than the penultimate, and a relatively high supraoccipital crest (vs. low crest in the Etelinae). *Lessinia* gen. nov. differs from the Apsilinae in having somewhat shorter pectoral fins and slightly more numerous dorsal-fin soft rays (11 vs. 9 or 10 in the Apsilinae). The predorsal configuration of *Lessinia horrenda* sp. nov. (10+0/0+2/1+1/) is different from those of both the Etelinae (0/0+0/2/1+1/) and Apsilinae (0/0/0+2/1+1/). But the *Lessinia* condition could be more easily transformed into the predorsal configuration of the Apsilinae than into that of the Etelinae, just by the simple anterior shift of the first supraneural. Such character states of *Lessinia* gen. nov. as its relatively small head, relatively deep body and small mouth which differentiate this genus from the other Eocene lutjanids, have their analogues in some apsilines, especially in the genus *Paracaesio* Bleeker, 1875, some species of which also have a deeply forked caudal fin. The dentition of the new genus is much weaker than in the Eocene genera *Ottaviana* Sorbini, 1983, *Goujetia* Bannikov, 2006 and *Veranichthys* Bannikov, 2006 from Bolca, resembling that of the modern apsiline genus *Apsilus* Valenciennes, 1830 (Allen, 1985). Another extant apsiline genus, *Parapristipomoides* Kami, 1973, has dentition even weaker than in *Lessinia* gen. nov., because it has no canine-like teeth present (Johnson, 1980; Allen, 1985).

Thus, *Lessinia* gen. nov. represents a distinct genus of the Lutjanidae. It seems to be closer to the Apsilinae than to the other subfamilies of lutjanids and can be tentatively placed in that subfamily.

Other than in the Eocene of Monte Bolca where at least four of their genera are present, snappers are scarcely known at all in the fossil record. Patterson (1993) indicated that the late Eocene *Hypocephalus atlanticus* Swift et Ellwood from Florida was the oldest lutjanid based on osteological material; and it is possible

that the *incertae sedis* Oligocene percoid fish genus *Oliganodon* Bannikov from the Caucasus and Central Europe (Bannikov, 2010) may actually be attributable to the Lutjanidae. However, it is from Bolca that the fossil Lutjanidae are by far the best known.

ACKNOWLEDGEMENTS

We are very grateful to Dr. Giuseppe Minciotti, director of the Museo Civico di Storia Naturale di Verona, for providing funding for the travel of AFB in 2013 to Verona to engage in this and other studies. We also thank Dr. Anna Vaccari, collection manager, for her assistance, and Mrs. Bruna Burato for her aid with the literature on Bolca fishes. We are much indebted to Mr. Francesco Sorbini (Verona) for the photographs and Dr. James C. Tyler of the Smithsonian Institution for reviewing and correcting the English in the manuscript. The work of AFB was supported by the Russian Foundation for Basic Research, grant no. 14-04-00005.

LITERATURE CITED

- AGASSIZ L., 1833-1844. *Recherches sur les poissons fossiles*. Petitpierre, Neuchâtel: Tome IV: 296 pp.
- AHLSTROM E.H., BUTLER J.L., SUMIDA B.Y., 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. *Bulletin of Marine Science*, 26: 285-402.
- ALLEN G.R., 1985. FAO species catalogue. Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. *FAO Fisheries Synopsis*, (125) Vol. 6: 208 pp.
- BALDWIN C.C., JOHNSON G.D., 1993. Phylogeny of the Epinephelinae (Teleostei: Serranidae). *Bulletin of Marine Science*, 52 (1): 240-283.
- BANNIKOV A.F., 2006. Fishes from the Eocene of Bolca, northern Italy, previously classified in the Sparidae, Serranidae and Haemulidae (Perciformes). *Geodiversitas*, 28 (2): 249-275.
- BANNIKOV A.F., 2008. Redescription of "*Pelates*" *quindecimalis* Agassiz, 1836, percoid fish (Perciformes) from the Eocene of Bolca, Italy. *Miscellanea paleontologica n. 9. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 12: 57-64.
- BANNIKOV A.F., 2010. *Fossil Vertebrates of Russia and Adjacent Countries. Fossil Acanthopterygians Fishes (Teleostei, Acanthopterygii)*. GEOS, Moscow: LXI+244 pp. [In Russian].

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

BANNIKOV A.F., ZORZIN R. 2004. Redescription and affinities of the Eocene percoid fish *Ottaviania mariae* Sorbini, 1983 from Bolca, northern Italy. *Miscellanea paleontologica n. 7. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 10: 75-82.

BLOT J., 1980. La faune ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie). Catalogue systématique présentant l'état actuel des recherches concernant cette faune. *Bulletin du Muséum national d'Histoire naturelle (Paris), sér. 4, section C*, 2 (4): 339-396.

CARPENTER K.E., 1990. A phylogenetic analysis of the Caesionidae (Perciformes: Lutjanoidea). *Copeia*, 1990: 692-717.

JOHNSON G.D., 1980. The limits and relationships of the Lutjanidae and associated families. *Bulletin of the Scripps Institution of Oceanography*, 24: 1-114.

JOHNSON G.D., 1984. Percoidei: development and relationships. In: Moser H.G. et al. (Editors), Ontogeny and systematics of fishes. *American Society of Ichthyologists and Herpetologists*. Special Publication no.1: 464-498.

KUSAKA T., 1974. *The urohyal of fishes*. University of Tokyo Press, Tokyo: 320 pp.

MONOD T., 1968. Le complexe urophore des poissons téléostéens. *Mémoires de l'Institut Fondamental d'Afrique Noire*, 81: 1-705.

NELSON J.S., 1994. *Fishes of the World*. 3rd ed. John Wiley & Sons, New York, 600 pp.

NELSON J.S., 2006. *Fishes of the World*. 4th ed. John Wiley & Sons, Hoboken, New Jersey, 601 pp.

PAPAZZONI C.A., TREVISANI E., 2006. Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the "Pesciara di Bolca" (Verona, northern Italy): An early Eocene *Fossil-Lagerstätte*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242:21-35.

PATTERSON C., 1993. Osteichthyes: Teleostei: 621-656. In: Benton J.M. (Editor). *The fossil record 2*. Chapman and Hall, London.

SORBINI L., 1983. Le collezione Baja di pesci e piante fossili di Bolca. Museo Civico di Storia Naturale, Verona: 117 pp.

TYLER J.C., BANNIKOV A.F., 1997. Relationships of the fossil and Recent genera of rabbitfishes (Acanthuroidei: Siganidae). *Smithsonian Contributions to Paleobiology*, 84: 1-35.

ZIGNO A. DE, 1874. Catalogo ragionato dei pesci fossili del calcare eoceno di M. Bolca e M. Postale. *Atti dell'R. Istituto Veneto di Scienze, Lettere ed Arti*, ser. IV, 3: 1-215.

ADDRESSES OF THE AUTHORS

ALEXANDRE F. BANNIKOV

Borisyak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117997, Russia; e-mail: aban@paleo.ru

ROBERTO ZORZIN

Museo Civico di Storia Naturale di Verona, L.ge Porta Vittoria 9, Verona 37129, Italia; e-mail: roberto.zorzin@comune.verona.it