Fishes from the Eocene of Bolca, northern Italy, previously classified in the Sparidae, Serranidae and Haemulidae (Perciformes)

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ABSTRACT

A revision of the type specimens of the Eocene fish species described by Agassiz from Bolca (Italy) and deposited in the Muséum national d'Histoire naturelle, Paris, revealed that the putative Eocene sparids include the monotypic genera *Abromasta* (with the species *A. microdon* (Agassiz, 1839)), *Pseudosparnodus* (with the species *P. microstomus* (Agassiz, 1839)), and less definitely *Ellaserrata* (with the species *E. monksi* Day, 2003), in addition to the genus *Sparnodus* with two species, *S. vulgaris* (Blainville, 1818) and *S. elongatus* Agassiz, 1839. The validity of the latter is restored. *Dentex leptacanthus* Agassiz, 1839 and *D. crassispinus* Agassiz, 1839 are redescribed in detail and recognized as lutjanids rather than sparids, with the new species combinations *Ottaviania leptacanthus* n. comb. and *Goujetia crassispina* n. comb. respectively. *Dentex ventralis* Agassiz, 1839 is regarded as a *nomen dubium*. *Serranus ventralis* Agassiz, 1839, previously thought to be a synonym of *Sparnodus elongatus*, is described as the lutjanid *Veranichthys ventralis* n. comb.; the species name *Serranus rugosus* Heckel, 1854, usually regarded as valid, is actually its junior synonym. Thus, the genus *Serranus* is absent in the Bolca fauna. The family Lutjanidae is represented in the Bolca fish assemblage by at least four species in three genera (*Ottaviania* Sorbini, 1983, *Goujetia* n. gen. and *Veranichthys* n. gen.). It is shown that the "haemulid" *Pomadasys furcatus* (Agassiz, 1839) is actually a synonym of *Sparnodus elongatus* Agassiz, 1839, and that haemulids are absent from the Eocene fauna of Bolca. *Odonteobolca sparoides* (Agassiz, 1839) is probably a synonym of the "sparid" *Pseudosparnodus microstomus* (Agassiz, 1839). If it can be confirmed, the generic name *Odonteobolca* Krell, 1991 will have priority over the name *Pseudosparnodus* Day, 2003.

KEY WORDS
Perciformes,
Percoidei,
Sparidae,
Lutjanidae,
Goujetia n. gen.,
Veranichthys n. gen.,
Eocene,
Bolca,
Italy,
new genera.

RÉSUMÉ

Les poissons éocènes de Monte Bolca, Italie septentrionale, classés jusqu'à présent dans des Sparidae, Serranidae et Haemulidae (Perciformes).

Une révision des spécimens types de Perciformes de l'Éocène du Monte Bolca jadis décrits par Agassiz et conservés dans les collections du Muséum national d'Histoire naturelle, Paris, a permis d'inclure dans les Sparidae : *Abromasta* (avec l'espèce *A. microdon* (Agassiz, 1839)), *Pseudosparnodus* (avec l'espèce *P. microstomus* (Agassiz, 1839)), ainsi qu'*Ellaserrata* (avec l'espèce *E. monksi* Day, 2003), en plus du genre *Sparnodus* avec deux espèces *S. vulgaris* (Blainville, 1818) et *S. elongatus* Agassiz, 1839. *Dentex leptacanthus* Agassiz, 1839 et *D. crassispinus* Agassiz, 1839 sont redécrits et rapportés aux lutjanidés plutôt qu'aux sparidés, les nouvelles combinaisons nomenclaturales *Ottaviania leptacanthus* n. comb. et *Goujetia crassispina* n. comb. sont proposées. *Dentex ventralis* Agassiz, 1839 est considéré comme un *nomen dubium*. *Serranus ventralis* Agassiz, 1839, que l'on pensait être un synonyme de *Sparnodus elongatus* est redécrit et lui aussi rapporté aux lutjanidés sous la nouvelle combinaison nomenclaturale *Veranichthys ventralis* n. comb. *Serranodus elongatus* Heckel, 1854, considéré comme une espèce valide, en est un synonyme plus récent. Ainsi le genre *Serranodus* serait absent de la faune du Monte Bolca et la famille Lutjanidae connue par quatre espèces rapportées à trois genres (*Ottaviania* Sorbini, 1983, *Goujetia* n. gen. et *Veranichthys* n. gen.). Nous considérons que l'« haemulid » *Pomadasys furcatus* (Agassiz, 1839) et plus généralement les haemulides sont absents de la faune du Monte Bolca. *Odonteobolca sparoides* (Agassiz, 1839) est probablement un synonyme du sparidé *Pseudosparnodus microstomus* (Agassiz, 1839). Si ceci peut être démontré, le genre *Odonteobolca* Krell, 1991 devra avoir la priorité sur le nom *Pseudosparnodus* Day, 2003.

MOTS CLÉS
Perciformes,
Percoidei,
Sparidae,
Lutjanidae,
Goujetia n. gen.,
Veranichthys n. gen.,
Éocène,
Bolca,
Italie,
nouveaux genres.

INTRODUCTION

Sparid fishes are common and conspicuous components of marine hard-bottom demersal neritic extant fish communities. Traditionally the family Sparidae has been placed centrally among the numerous families of percoid fishes (Nelson 1994; Eschmeyer 1998). Johnson (1980) recognized the superfamily Sparoidea, comprising the Sparidae, Lethrinidae, Nemipteridae, and Centracanthidae. The first three of these families comprise the "spariform" fishes of Akazaki (1962). Carpenter & Johnson (2002) attempted a cladistic analysis of sparoid fish evolutionary relationships using 54 osteological, ligament, and squamation characters, without a rigorous treatment of generic relationships within any of the families. Simultaneously, Day (2002) published a phylogenetic analysis of the majority of sparid genera and representatives of other sparoid families using 87 predominantely osteological characters. In both analyses the centracanthids nested within the Sparidae. Carpenter & Johnson (2002) revealed the phyletic sequence (Nemipteridae (Lethrinidae + Sparidae)), whereas the interrelationships of these three families were unresolved in the cladogram of Day (2002). A monophyletic Sparidae + Centracanthidae is supported by four synapomorphies in each analysis, but only two of these characters concur: three openings in the lateral wall of pars jugularis and a specialized premaxilla/maxilla articulation. The Haemulidae are the sister group of the Sparoidea in the analyses of both Day (2002) and Carpenter & Johnson (2002).

Sparid fishes are common components in the Eocene marine assemblage of the famous locality of Bolca in northern Italy. Volta (1796) attributed sparids from Bolca to a variety of Recent taxa. Agassiz (1833-1844) described 11 fossil species of Sparidae from Bolca: five in the fossil genus *Sparnodus* Agassiz, 1838, five in *Dentex* Cuvier, 1814, and one in *Pagellus* Valenciennes in Cuvier & Valenciennes, 1830. Three other species were described by Agassiz (1833-1844) in the serranid genus *Serranus* Cuvier, 1816: *S. ventralis* Agassiz, 1839, *S. microstomus* Agassiz, 1839, and *S. occipitalis* Agassiz, 1839 (precise date of publication of the livraison with the species descriptions is taken from Brown 1890). All these species were subsequently (Woodward 1901) considered as synonyms of species of *Sparnodus*. Szajnocha (1886) added one more species of *Sparnodus* to the list of the Sparidae from Bolca. Woodward (1901) reduced the number of Bolca sparids: he recognized three species of *Sparnodus* (*S. macrophthalmus* Agassiz, 1839, *S. elongatus* Agassiz, 1839 and *S. microstomus* Agassiz, 1839), four species of *Dentex* (*D. crassispinus* Agassiz, 1839, *D. leptacanthus* Agassiz, 1839, *D. microdon* Agassiz, 1839 and *D. ventralis* Agassiz, 1839), and *Pagellus microdon* Agassiz, 1839. Eastman (1905) recognized the types of certain sparid species described by Agassiz (1833-1844) (those deposited in MNHN); he stated that the species name *Sparus vulgaris* of de Blainville (1818) has priority over the name *Sparnodus macrophthalmus* of Agassiz (1833-1844); this was accepted by Blot (1980).

Recently, Day (2003) revised some of the Bolca Sparidae. She did not take into consideration any of Agassiz's species of *Dentex*, and mostly revised the genus *Sparnodus* sensu Woodward (1901). Day (2003) also recognized the new genus *Abromasta* for *Pagellus microdon* Agassiz, 1839. Day (2003) left only the type species *S. vulgaris* in the genus *Sparnodus*, regarding *S. elongatus* as its junior synonym. *Sparnodus microstomus* (Agassiz, 1839) was transferred by Day (2003) to the new genus *Pseudosparnodus*. Finally, a new genus and species, *Ellaserrata monksi*, "distinguished by a serrated preoperculum" (Day 2003: 339) was described. Day (2003) incorporated the four studied taxa from Bolca together with *Sciaenurus bowerbanki* Agassiz, 1845 from the lower Eocene of England, into her cladistic analysis of the Recent Sparidae.

A study of the type specimens of Agassiz's sparids deposited in the Muséum national d'Histoire naturelle, Paris, allows for a better understanding of the real biodiversity of sparoid fishes in the Tethys Ocean in early Lutetian time. The type specimens of Bolca fishes originally classified with *Serranus* (Serranidae) and *Pomadasys* (Haemulidae) are also deposited in the Paris Muséum. The present research indicates that these genera are absent in the fish assemblage of Bolca.

METHODS

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

Each MNHN specimen usually has two collection numbers: the ancient one (e.g., 10799), and a new one (e.g., Bol 280). In the figure captions of the paper of Day (2003), the latter numbers were erroneously indicated with the abbreviation MCSNV rather than "Bol".

ABBREVIATIONS

Institutional

BMNH	The Natural History Museum, London;
MCSNV	Museo Civico di Storia Naturale di Verona;
MNHN	Muséum national d'Histoire naturelle, Paris.

Anatomical

HL	head length;
PU	preural vertebra;
SL	standard length;
U	ural vertebra.

COMMENTS ON *SPARNODUS*, *ELLASERRATA* AND *PSEUDOSPARNODUS*

Direct observations on the type specimens of Agassiz's sparids and non-type materials deposited in the MNHN lead us to question some features indicated by Day (2003) as diagnostic for the genera of Eocene sparids. Day (2003) also erroneously indicated

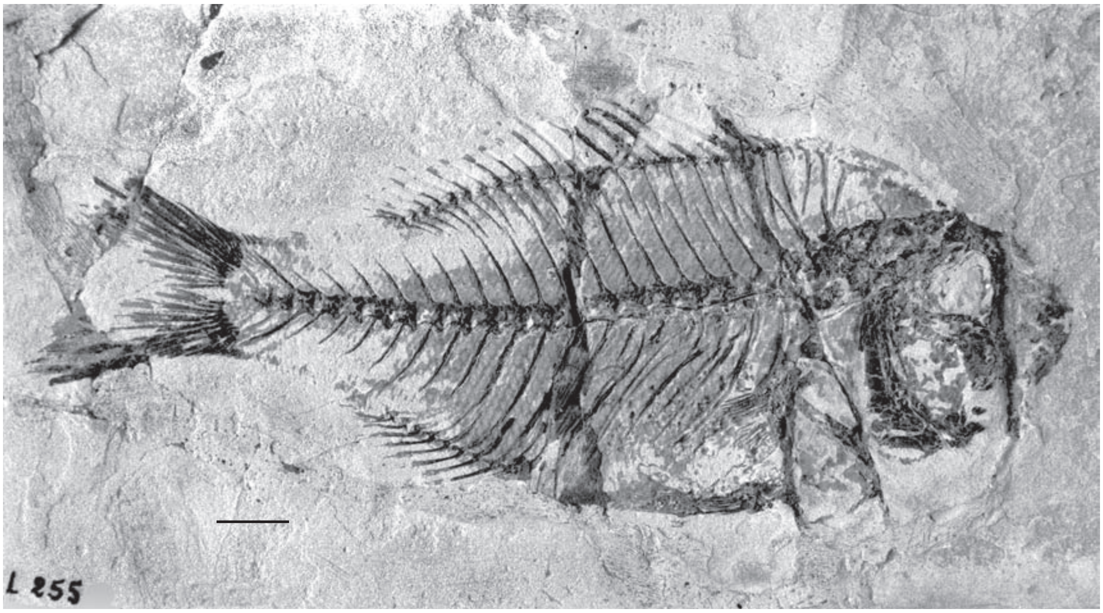

Fig. 1. — *Pseudosparnodus microstomus* (Agassiz, 1839), MNHN Bol 255 (10726, lectotype of *Serranus microstomus* Agassiz, 1839 as designated by Eastman [1905]). Middle Eocene of Bolca, northern Italy. Scale bar: 10 mm.

"holotypes" for Agassiz's sparids. The specimen MNHN Bol 265 (10796) indicated as the holotype of *Sparnodus vulgaris* (Day 2003: fig. 1a) is actually its lectotype, as well as the lectotype of *Sparnodus ovalis* Agassiz, 1839; MNHN Bol 268 (10804) indicated as the holotype of *Sparnodus elongatus* (Day 2003: fig. 2) is actually the lectotype of that species; MNHN Bol 260 (10730) indicated as the holotype of *Pseudosparnodus microstomus* (Day 2003: fig. 3a) is actually the lectotype of *Serranus occipitalis* Agassiz, 1839. The figure of the type of *Serranus microstomus*, announced in Agassiz (1833-1844: pl. XXIII*a*), was not actually published; Eastman (1905) proposed MNHN Bol 255 (10726) (Fig. 1) as the lectotype of *S. microstomus*. The specimen shown by Day (2003) in her figure 3a is not the specimen MNHN Bol 260 (10730) (as indicated in the figure caption) but, rather, its counterpart MNHN Bol 254 (10729) with reversed image.

The type series of *Ellaserrata monksi* Day, 2003 includes three specimens identified by Woodward (1901: 526) as *Sparnodus elongatus* Agassiz, 1839. According to Day (2003), the principal generic feature of *Ellaserrata* is a serrated preopercle. She also indicated the formula of the dorsal fin of *Ellaserrata* as X + 10, whereas in her diagnoses of the genera *Sparnodus* and *Pseudosparnodus* that formula is XII + 9 in both cases. However, Day (2003) indicated 10 dorsal fin spines in the description of the type species of *Sparnodus*, *S. vulgaris*. Our observations show that all sparid specimens from Bolca deposited in the MNHN have 10 dorsal fin spines, except for the holotype of *Abromasta microdon* (Agassiz, 1839), which has 12 dorsal fin spines. Also, when the soft dorsal fin is completely preserved, not less than 10 soft dorsal fin rays are evident in any of the specimens. Serrations on the peripheral border of the preopercle are evident on numerous specimens, including the types of Agassiz's *Sparnodus macrophthalmus* (MNHN Bol 256 (10793)); *S. micracanthus* (MNHN Bol 266 (10797)); *S. altivelis* (MNHN Bol 263 (10789)); *Serranus occipitalis* (MNHN Bol 269 (10730a), MNHN Bol 254 (10729)) and *S. ventralis* (MNHN Bol 24 (10723), MNHN Bol 275 (10724)). Agassiz (1833-1844) indicated a serrated preopercle in his

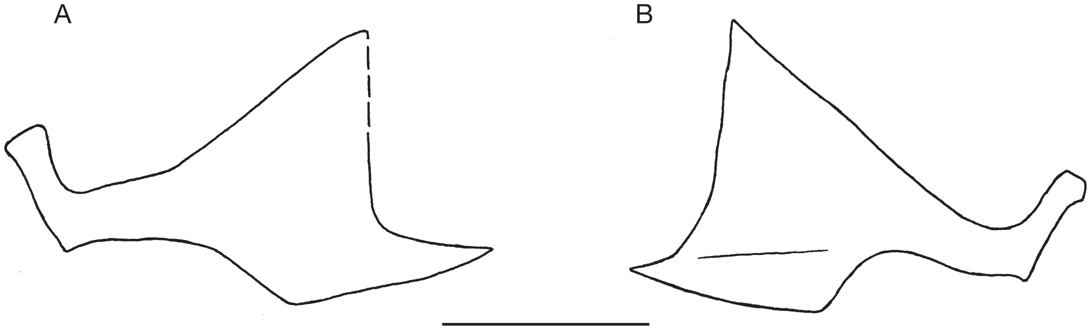

FIG. 2. — The urohyal of *Pseudosparnodus microstomus* (Agassiz, 1839): **A**, MNHN Bol 252 (10795), *c.* 118 mm SL; **B**, MNHN Bol 269 (10730a), 109 mm SL. Middle Eocene of Bolca, northern Italy. Scale bar: 5 mm.

descriptions of *Serranus occipitalis*, *S. microstomus* and *Sparnodus altivelis*; this feature is diagnostic for *Sparnodus* according to Woodward (1901). The latter author specifically stated that BMNH 44867 "displays the fine serrations of the preoperculum" (Woodward 1901: 525). This specimen has been acid prepared subsequently and it forms the basis of the description of *Sparnodus vulgaris* by Day (2003), who mentioned ridges along the posterior margin of the preopercle, but did not describe the serrations.

Thus, based on both serrated preopercle and the formula of the dorsal fin, *Ellaserrata* cannot be distinguished from *Sparnodus*. Day (2003) incorrectly indicated the dorsal fin formula of *Pseudosparnodus* as XII+9, and anal fin formula as III+9. Our observations on the material of *P. microstomus* confirm the data of Woodward (1901), who indicated 10 dorsal fin spines, 12 dorsal fin soft rays, and 10 anal fin soft rays in this species. We suppose that the greater number of soft dorsal and anal fin soft rays justifies the recognition of the monotypic genus *Pseudosparnodus* for *P. microstomus*, as do also the consolidated hypurals (see below).

Woodward (1901) indicated that the genus *Sparnodus* has uniserial, stout, obtusely-conical teeth in the jaws, with a few irregular, minute, obtusely-conical teeth within. Day (2003) described in *S. vulgaris* a single row of conical teeth in the jaws, without mention of medial minute teeth. In the jaws of *Ellaserrata monksi*, Day (2003) described both a single row of caniniform teeth and villiform teeth medially. In the present work, villiform teeth were not found in the jaws of any of the sparid specimens deposited in the MNHN and labeled as "*Sparnodus*", except for the two type specimens of "*Serranus ventralis*" Agassiz, 1839 (a synonym of *Sparnodus elongatus* according to Woodward 1901). The latter species is described below as a lutjanid rather than sparid. Most of the specimens deposited in the MNHN and labeled as "*Sparnodus*" display stout, obtusely-conical teeth in the jaws only, whereas in certain specimens (e.g., MNHN Bol 261 (10805), Bol 263/264 (10789/10790), Bol 284 (11074), Bol 265/266 (10796/10797), Bol 276/277 (10781/10788), Bol 282 (11076)) at least a few minute, obtusely-conical teeth are also visible. Apparently in some specimens these minute teeth are obscured by matrix, but they should be visible in acid prepared specimens. However, in such an acid prepared specimen of *Sparnodus vulgaris* minute teeth were not revealed by Day (2003). If, indeed, two different types of dentition exist amongst specimens that otherwise are not distinguishable, then more than one species of *S. vulgaris* has to be recognized. Since MNHN Bol 265/266 (10796/10797) should be regarded as the lectotype of *Sparus vulgaris* Blainville, 1818, and it has minute, obtusely-conical teeth in addition to stout teeth, we tentatively restore the validity of *Sparnodus elongatus* Agassiz, 1839. The lectotype of the latter species (MNHN Bol 259/268 (10803/10804)) lacks minute teeth. Thus, we presume that the acid prepared specimen BMNH 44867 described and figured by Day (2003: 335, fig. 1b, c) as *Sparnodus vulgaris* is actually *Sparnodus elongatus*.

Day (2003) indicated separate hypurals in *Sparnodus* and fused hypural plates 1-2 and 3-4 in *Ellaserrata* and *Abromasta*. She did not specify the condition of the hypurals in *Pseudosparnodus*. Our observations show that in all cases when the hypurals are adequately preserved in specimens of *P. microstomus* (MNHN Bol 252 (10795), Bol 254 (10729) and Bol 271 (11083)), these are fused in two plates, epaxial and hypaxial. *Pseudosparnodus* has a peculiar structure of the urohyal, with a long slender dorsal process ascending from the anterior end of the bone (Fig. 2). A somewhat similar condition is recorded for the girellid *Girella punctata* Gray, 1835 and the labrid *Iniistius pavo* (Valenciennes in Cuvier & Valenciennes, 1840) (Kusaka 1974). A long antero-dorsal process of the urohyal is definitely an autapomorphy of *Pseudosparnodus*.

The four Eocene genera from Bolca treated as sparids by Day (2003) can be regarded as representing the Sparidae only putatively, since most sparid autapomorphies listed by Carpenter & Johnson (2002) and Day (2002) cannot be determined on the fossils because of poor preservation of the material. These characters are: three openings in the lateral wall of the pars jugularis; a specialized premaxilla/maxilla articulation (Day [2003] found this articulation in the acid prepared specimen of *Sparnodus vulgaris*); infraorbitals I and II deeper than wide; proximal tips of the first hypural and parhypural broadly overlap the urostyle; apical pores in the lateral line scales. Such sparid characters of Day (2002) as a reduced or absent postpelvic processes appear to be present in the Eocene genera from Bolca. A monophyletic Sparoidea is supported by seven unambiguous synapomorphies in the analysis of Day (2002), and three non-homoplasious characters in the analysis of Carpenter & Johnson (2002); two of these characters concur in both analyses: symplectic with dorsal and ventral laminar extensions and broad articulation between hyomandibular and metapterygoid (see Johnson 1980: figs 25-27). Whereas the symplectic is not well enough preserved in any of the specimens labeled as *Sparnodus* in the MNHN, a broad articulation between the hyomandibular and metapterygoid is evident in MNHN Bol 242/243 (B009/B010), with a detached suspensorium. The (Lethrinidae (Sparidae + Centracanthidae)) node of Carpenter & Johnson (2002) is supported by a number of non-homoplasious characters, most of which cannot be recognized in fossil material (e.g., absence of intercalar, suborbital shelf origin), but two of them are definitely absent in the Eocene sparids: preopercle not serrated and continuous fusion of the articular and ascending processes of premaxilla. Day (2003) stated that the articular and ascending processes of the premaxilla are fused in *Sparnodus vulgaris*, *Pseudosparnodus microstomus* and *Abromasta microdon*, but the material of these species deposited in the MNHN clearly shows articular and ascending process distinct from each other. The postmaxillary process is evident in the premaxilla of the holotype of *A. microdon* (MNHN Bol 46 (10784)), whereas it is absent in extant Lethrinidae and Sparidae (Johnson 1980; Carpenter & Johnson 2002).

In her descriptions of *Sparnodus vulgaris*, *Pseudosparnodus microstomus* and *Ellaserrata monksi*, Day (2003) stated that infraorbitals I and II are deeper than wide in these species. Deep anterior infraorbitals are observable in the Eocene specimens from the MNHN only occasionally (e.g., in Bol 260 (10730), syntype of *Serranus occipitalis*, and Bol 263 (10789), holotype of *Sparnodus altivelis*), but even in these specimens it is hardly recognizable whether these bones represent infraorbitals I and II (a specialization of the Sparoidea: Johnson 1980: table 1) or, rather, a single lachrymal (as in Lutjanoidea and Haemuloidea: Johnson 1980: table 1). In a single specimen of *Sparnodus vulgaris* (MNHN Bol 279 (11073)) small villiform teeth are observable posterodorsally from the maxilla. Judging from their position, these are teeth of either the ectopterygoid or the palatine. The palatine is edentulous in extant Haemuloidea and Sparoidea, whereas it is dentigerous in Lutjanoidea. The lutjanid genera *Ocyurus* Gill, 1862 and *Rhomboplites* Gill, 1862 also have villiform teeth in the ectopterygoid (Johnson 1980; Allen 1985).

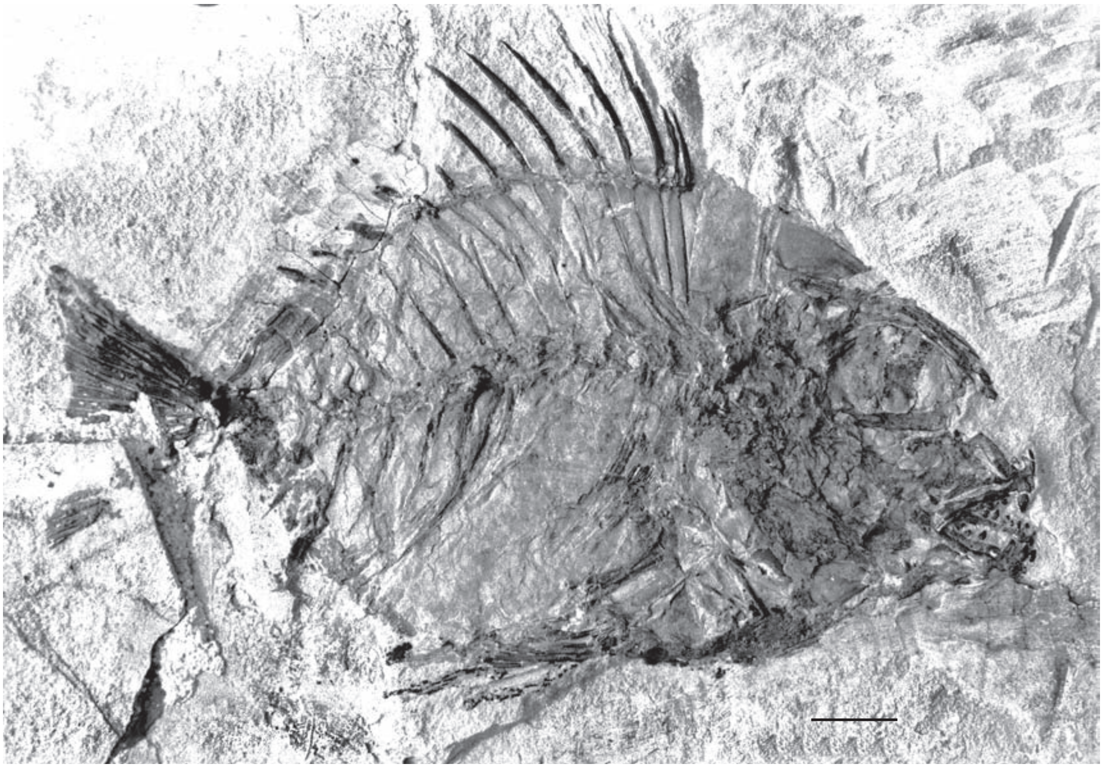

FIG. 3. — *Pseudosparnodus microstomus* (Agassiz, 1839), MNHN Bol 49 (10752b, holotype of *Odonteus sparoides* Agassiz, 1839). Middle Eocene of Bolca, northern Italy. Scale bar: 10 mm.

COMMENTS ON *ODONTEUS SPAROIDES* AND *PRISTIPOMA FURCATUM*

Agassiz (1833-1844) described a new genus and species of Bolca sciaenid *Odonteus sparoides* Agassiz, 1839, based on a single specimen in counterpart from the MNHN collection. Krell (1991) renamed this genus *Odonteobolca* since the original generic name was preoccupied. After Agassiz's work, the affiliation of *Odonteus* remained unchanged for a long time (Zigno 1874b; Bassani 1876), but most authors who mentioned *O. sparoides* in the 20th century (Woodward 1901; Eastman 1905; Blot 1980) regarded it as a pomacentrid until Bellwood (Bellwood & Sorbini 1996; Bellwood 1999) confirmed the suggestion of Arambourg (1927) that this taxon is not related to the Pomacentridae. Zigno (1874a) described from Bolca the new species *Odonteus pygmaeus* based on a specimen of diminutive size. Subsequently, it was shown that *O. pygmaeus* represents a juvenile of *Acanthonemus subaureus*, an acanthuroid fish (Blot 1988; Bannikov 1991). Bassani (1898) described a new variety (subspecies), *Odonteus sparoides* var. *depressus*, from the same locality of Bolca.

After the publication of Agassiz's (1833-1844) monograph no specimens have been confidently identified as *Odonteus sparoides*. Specimens designated by Eastman (1911: pl. XCVII, fig. 1; 1914: pl. XLVII, fig. 1) as *O. sparoides* are, as a matter of fact, "*O. pygmaeus*" (= *Acanthonemus subaureus*). *Odonteus sparoides* var. *depressus* Bassani, 1898, as it was described and figured, is definitely different from the type species of *Odonteus* at the generic (or even family) level.

When he defined the genus *Odonteus*, Agassiz (1833-1844) mentioned its similarity to the genus *Sparnodus* in the dentition and serrated preopercle;

however, he attributed *Odonteus* to the "sciénoïdes" based on the cavernous nature of the cranial roof bones. He also noted that the posterior part of the holotype is missing and restored with heterogenous pieces. Our examination of the holotype of *Odonteus sparoides* (MNHN Bol 48/49 (10752a/10752b)) does not reveal any particular cavernosity of its cranial roof bones, and the dentition of the holotype is identical to that of the genus *Pseudosparnodus* and those specimens of *Sparnodus* which lack minute teeth in the jaws (i.e. *S. elongatus*). "*Odonteus sparoides*" has uniserial, stout, obtusely-conical teeth with larger teeth situated anteriorly in the jaws (Fig. 3). In addition to its incompleteness posteriorly, MNHN Bol 48/49 (10752a/10752b) is slightly disarticulated, and all its three supraneurals are shifted anteriorly from their natural position close-set to the posterior border of the supraoccipital crest. The dorsal fin spines of "*Odonteus sparoides*" in relation to the maximum body depth seem to be slightly longer than in *Pseudosparnodus microstomus*, but otherwise these two taxa are identical in the characters available for the comparison. Therefore, we tentatively place herein the species name *sparoides* into the synonymy of *Pseudosparnodus microstomus* (although the possibility that "*Odonteus sparoides*" and *Sparnodus elongatus* are the same species cannot be currently excluded). If it can be confirmed, the generic name *Odonteobolca* Krell, 1991 will have priority over *Pseudosparnodus* Day, 2003, and the valid combination for the species name would be *Odonteobolca microstoma* (Agassiz, 1839). The holotype of "*Odonteus sparoides*" belongs to a moderately large fish: its head length is 39 mm, which corresponds to the estimated SL of *c.* 130 mm.

In the same chapter with *Odonteus sparoides*, Agassiz (1833-1844) described a new species from Bolca, *Pristipoma furcatum* Agassiz, 1839, based on a single specimen (MNHN Bol 68/69 (10753/10754)). It also was regarded as a sciaenid, although subsequently the genus *Pristipoma* Quoy & Gaimard, 1824 (junior synonym of *Pristipomus* Oken, 1817) was always affiliated with the Haemulidae (= Pomadasyidae). According to Eschmeyer (1998), the generic name *Pristipoma* is a junior synonym of the genus *Pomadasys* Lacepède, 1802. "*Pomadasys*" *furcatus*, as well as "*Odonteus sparoides*", reveals remarkable similarity with *Pseudosparnodus* (= *Odonteobolca*?) and *Sparnodus* in overall appearance, dentition and meristic counts. "*Pomadasys*" *furcatus* has uniserial, stout, obtusely-conical teeth on the margin of the jaws, longest at the symphysis, gradually becoming very short behind (Fig. 4). No medial minute teeth are evident. The counterpart MNHN Bol 69 (10754) has unfused hypurals, unlike *Pseudosparnodus microstomus*. The fin ray counts of "*Pomadasys*" *furcatus* (D X, 10; A III, 8) concur to those of *Sparnodus* rather than *Pseudosparnodus* (Agassiz [1833-1844] erroneously indicated 12 soft dorsal fin rays in *Pristipoma furcatum*). The holotype of "*Pomadasys*" *furcatus* has the body equal in depth to those of the most deep-bodied specimens of *Sparnodus* ever recorded (SL/maximum body depth ratio is 2.1). "*Pomadasys*" *furcatus* can be easily differentiated from the Haemulidae by the presence of 10+14 vertebrae, whereas in the Haemulidae there are 10-11+16 vertebrae (Johnson 1980, 1984). Moreover, extant haemulids have cardiform teeth in bands and not less than 11 soft dorsal fin rays. The predorsal configuration (Johnson 1980, 1984) of "*Pomadasys*" *furcatus* is 0/0/0+2/1+1/, whereas it is 0/0+0/2+1/1/ in Haemulidae (Johnson 1980; Carpenter & Johnson 2002).

It is clear from above that "*Pomadasys*" *furcatus* must be placed in the genus *Sparnodus*. Since based on the characters available it cannot be unambiguously differentiated from those *Sparnodus* which lack medial minute teeth (i.e. *Sparnodus elongatus*), we regard herein the species name *furcatus* as a synonym of *Sparnodus elongatus*.

COMMENTS ON "*SERRANUS*" AND "*DENTEX*" FROM BOLCA

Agassiz (1833-1844) described three new species of *Serranus* (Serranidae) from the Eocene of Bolca: *S. microstomus*, *S. occipitalis* and *S. ventralis*. Heckel (1854) established a fourth species, *S. rugosus*, based on one of the two syntypes of *S. ventralis*. Woodward (1901) and subsequent authors (Eastman 1905; Blot 1980) placed the species of Agassiz in the genus *Sparnodus* (*Serranus microstomus* and *S. occipitalis* as synonyms of *Sparnodus microstomus*,

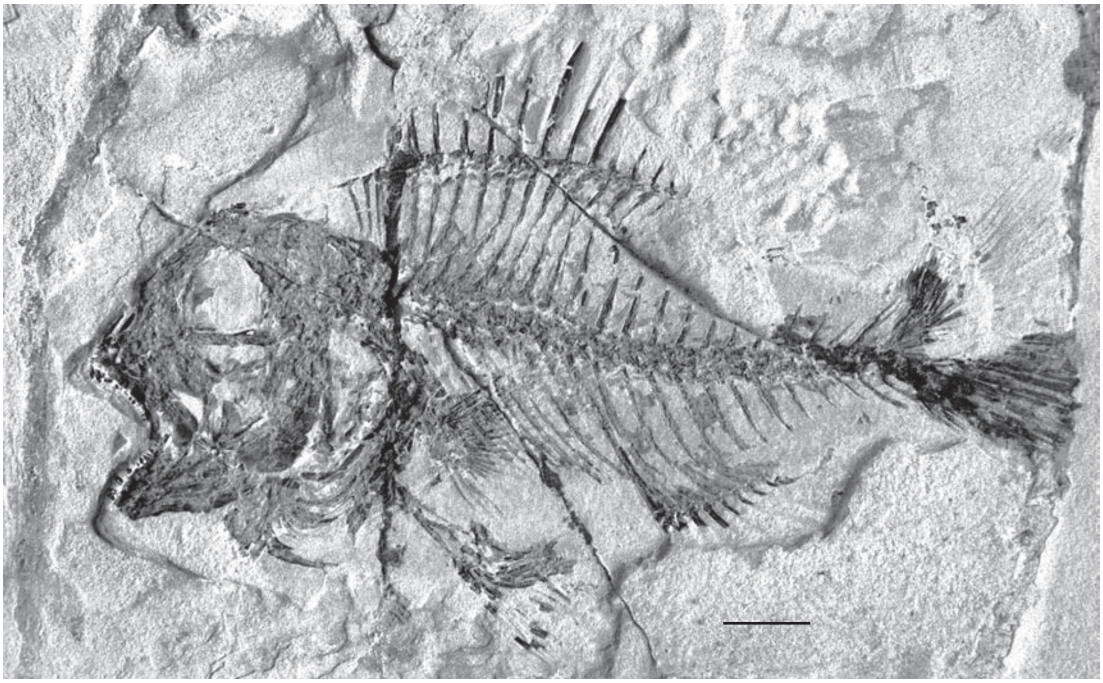

FIG. 4. — *Sparnodus elongatus* Agassiz, 1839, MNHN Bol 69 (10754, holotype of *Pristipoma furcatum* Agassiz, 1839). Middle Eocene of Bolca, northern Italy. Scale bar: 10 mm.

and *Serranus ventralis* as a synonym of *Sparnodus elongatus*), whereas they retained *S. rugosus* in the genus *Serranus*. Our examination of the types of the species allocated by Agassiz to "*Serranus*" deposited in MNHN confirms that "*Serranus*" *microstomus* represents a species of *Pseudosparnodus* (= *Odonteobolca*?), and "*Serranus*" *occipitalis* is its synonym. However, "*Serranus*" *ventralis* is definitely different from *Sparnodus elongatus*, and we find no grounds to recognize "*Serranus*" *rugosus* as valid. Both syntypes of "*S.*" *ventralis* have the same pattern of dentition, meristic counts and cycloid (rather than ctenoid as in *Sparnodus*) scales. It was indicated (Heckel 1854; Zigno 1874b) that *Serranus rugosus* lacks canines and has larger head and deeper body than in *S. ventralis*. MNHN Bol 24 (10723) (type of "*S.*" *rugosus*) is more poorly preserved in some respects than MNHN Bol 275 (10724) (type of "*S.*" *ventralis*), but MNHN Bol 24 has a canine at the premaxillary symphysis. The relative body depth of MNHN Bol 24 (10723) is only slightly exceeding that of MNHN Bol 275 (10724), and the head is actually even smaller proportionally. MNHN Bol 24 (10723) has an expanded infraorbital. Although this bone is fractured, it seems likely that it was originally a single bone (as in Lutjanoidea and Haemuloidea) rather than a combination of two anterior infraorbitals, as in Sparoidea. The dentition pattern, vertebral and fin ray counts of "*Serranus*" *ventralis* are quite typical for the Lutjanidae; therefore, we describe this taxon below as a lutjanid. All of the above indications show that the genus *Serranus* is absent from the Eocene fauna of Bolca.

Agassiz (1833-1844) described five new species of *Dentex* (Sparidae) from the Eocene of Bolca: *D. crassispinus*, *D. leptacanthus*, *D. microdon*, *D. breviceps* and *D. ventralis*. Woodward (1901) and subsequent authors (Eastman 1905; Blot 1980) regarded *D. breviceps* as a synonym of *Sparnodus microstomus*. The figures of the types of *D. ventralis* and *D. crassispinus*, announced in Agassiz (1833-

1844: pl. XXIV), were not actually published. The former type was indicated by Agassiz as belonging to the collection of Dr. Hibbert, but it cannot be located (Blot 1980). Therefore, *D. ventralis* should be regarded as a *nomen dubium*. Eastman (1905) proposed MNHN Bol 8/9 (10811/10810) as the holotype of *D. crassispinus*. The type of *D. microdon* is deposited in the Paleontological Museum of Munich (Woodward 1901) and it was not studied for this work. Finally, the holotype of *D. leptacanthus* is deposited in the MNHN with the collection number Bol 14a/14b (10809a/10809b).

Our examination of these holotypes indicates that neither *D. leptacanthus* nor *D. crassispinus* can actually belong to the extant sparid genus *Dentex*. Both lack especially strong anterior premaxillary canines that are typical for *Dentex*, have as few as 10 dorsal fin spines (less than in *Dentex*) and weaker anal fin spines. *Dentex leptacanthus* is remarkably similar to *Ottaviania mariae* Sorbini, 1983. This fish was originally described as a perciform of uncertain relationships (Sorbini 1983), and subsequently referred to the Lutjanidae (Bannikov & Zorzin 2004). "*Dentex*" *crassispinus* also can be attributed to the Lutjanidae rather than to the Sparidae (see below).

SYSTEMATICS

Order PERCIFORMES
Suborder PERCOIDEI
Family LUTJANIDAE Gill, 1884
Genus *Ottaviania* Sorbini, 1983

Ottaviania leptacanthus

(Agassiz, 1839) n. comb.
(Figs 5; 6)

Lutjanus lutjanus Bloch, 1790 – Volta 1796: 222, pl. LIV. — Blainville 1818: 348.

Dentex leptacanthus Agassiz, 1839: 144, pl. XXVI. — Zigno 1874b: 65.

HOLOTYPE. — MNHN Bol 14a/14b (10809a/10809b), part and counterpart, complete skeleton, 261 mm SL; lower part of the middle Eocene, Lutetian, zone *Discoaster sublodoensis*; Monte Bolca locality, Pesciara cave site, northern Italy.

REFERRED SPECIMENS. — None.

DIAGNOSIS. — Head length 3.03 in SL. Maximum body depth 3.26 in SL. Lower jaw articulation under anterior border of orbit. Jaws with an outer row of strong conical teeth and an inner band of villiform teeth. Ventral postcleithrum wide. 11(?) + 13 vertebrae. Last pair of ribs slender. Three supraneurals. Dorsal fin continuous, with 10 flexible spines and 11 soft rays. Anal fin with 3 graduated flexible spines and 8 rays. Pelvic fins inserted under pectorals. Caudal fin deeply forked. Scales moderately large and cycloid, each scale with 7-14 radii basally. Lateral line complete, gently arched anteriorly.

DESCRIPTION

The body is relatively elongate, with a moderately slender caudal peduncle. The caudal peduncle depth is 0.39 of the body depth. The head is moderately large, its length (tip of snout to anterior edge of upper part of pectoral girdle) 1.08 times larger than the body depth. The head length is contained 3.03 times in SL. The dorsal and ventral profiles of the body are almost equally convex.

Head

The head is relatively deep, with its depth about 1.1 times less than its length. The orbit is small and placed close to the dorsal profile of the head. The horizontal diameter of the orbit is about 22% HL. The snout is pointed and relatively long; its length is about 44% HL. The mouth is moderately large and terminal. The lower jaw articulation is situated approximately under the anterior border of the orbit. No infraorbital bones are recognizable except for the remains of the lachrymal, which is definitely very long and deep. The neurocranium is relatively low, with the supraoccipital crest evidently poorly developed. The ethmoid region is rather long. The parasphenoid is rather robust and almost straight; it is exposed along the lower border of the orbit. The premaxilla is poorly preserved; its ascending process is relatively short. Multiserial minute villiform premaxillary teeth are evident in MNHN Bol 14a (10809a); larger conical teeth are not preserved. The maxillae are too fragmentary and poorly preserved to be described. No supramaxilla is evident. The lower jaw is moderately deep; its length is about

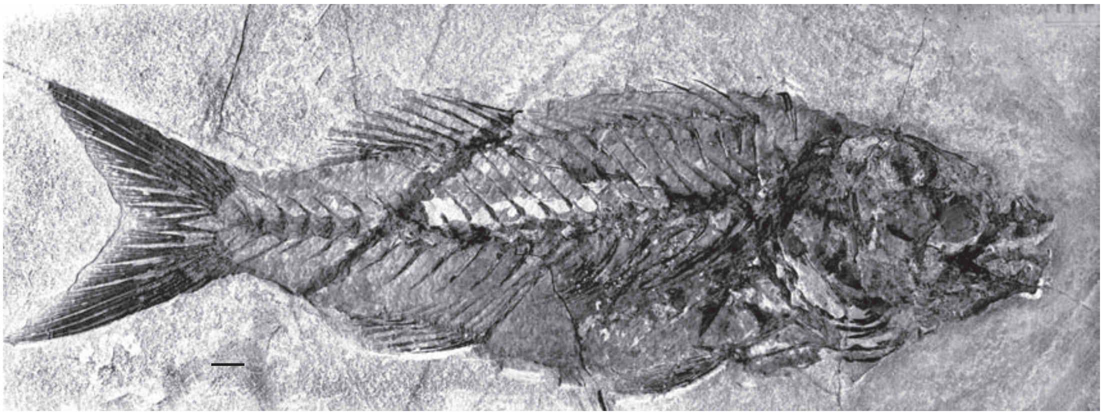

FIG. 5. — *Ottaviania leptacanthus* (Agassiz, 1839) n. comb., holotype, MNHN Bol 14b (10809b). Middle Eocene of Bolca, northern Italy. Scale bar: 10 mm.

50% HL. The dentary projects ventrally near the symphysis. The oral border of the dentary bears an outer row of large conical teeth, and an inner band of minute villiform teeth. The anterior canines appear to be slightly larger than those in the middle of the series. The hyomandibular shaft is slightly inclined anteroventrally. The quadrate is moderately large and triangular. The metapterygoid and endopterygoid (mesopterygoid) are only partially preserved. The ectopterygoid is narrow and slightly curved; it lacks a posterior extension. The opercular region is relatively narrow. The preopercle is only slightly curved. The opercular bones are only preserved as fragments. There are about seven sabre-like branchiostegal rays. The branchial bones are indistinct: MNHN Bol 14a (10809a) has small and minute pharyngeal teeth; these are slender, conical and sharp. Gill filaments are partly preserved.

Axial skeleton

There are most probably 24 vertebrae, including the urostyle; the first vertebra is not preserved, and its presence is indicated by faint remains in the matrix of MNHN Bol 14b (10809b). Thirteen caudal vertebrae can be seen confidently; however, if the upper tip of the first interhaemal was slightly displaced posteriorly *post-mortem*, the total number of caudal vertebrae could well be 14, as in all other lutjanids. The axis of the vertebral column is slightly elevated anteriorly. The vertebral centra are almost rectangular in lateral view. The length of the caudal portion of the vertebral column (13 posteriormost vertebrae) is about 1.4 times greater than the length of the abdominal portion of the vertebral column. The vertebral spines are relatively short, straight or slightly curved, and rather strong. The neural spines of the five anterior vertebrae are more strongly expanded than those of the succeeding vertebrae. The haemal spines of the anterior caudal vertebrae are usually slightly longer than the opposite neural spines, and most of the neural spines arise from the middle of the centra, whereas the anterior haemal spines arise from the anterior half of the centra. Parapophyses are scarcely recognizable in the abdominal vertebrae except for the long and curved parapophysis of the vertebra which seems to be the last abdominal (11th?). The pleural ribs are slender and moderately long; these are strongly inclined posteroventrally. The last pair of ribs is not expanded. Slender epineurals are scarcely recognizable in the anterior part of the abdominal cavity at the level of the vertebral column.

Pectoral fin and girdle.

The posttemporal is forked. Only the ventral part of the supracleithrum is recognizable. The cleithrum is large and elongate, oriented obliquely; its upper part is curved anteriorly and situated under the second vertebra. The ventral postcleithrum is moderately long, expanded proximally and tapered distally; it is directed posteroventrally. The coracoid is relatively narrow. Both the scapula and pectoral radials are scarcely recognizable. Only the basal parts of a few pectoral fin rays are preserved in MNHN Bol 14a (10809a). These indicate that the base of the pectoral fin is situated under the fifth to sixth vertebrae, near the midpoint between the vertebral column and the ventral profile of the body.

Pelvic fin and girdle

The pelvic bone is wedge-shaped in lateral view, with a well developed postpelvic (ischial) process. The pelvic fin contains a spine and five soft branched rays; it is inserted under the pectoral fin base. The pelvic fin is only moderately long; the pelvic fin spine is slender and longer than the longest (third) anal fin spine.

Supraneurals and dorsal fin

There are three short and slender supraneurals. The supraneurals are displaced from their natural position, being close-set to each other and shifted above the dorsal profile of the body. The dorsal fin is relatively long-based and continuous; it originates over the third vertebra and ends over the 19th vertebra. There are 10 dorsal fin spines and 11 soft segmented rays. The dorsal fin spines are very slender and evidently were flexible. The spines gradually increase in length from the first to the fifth; the succeeding spines have roughly the same length, with the last spine probably being the longest, 1.6 times longer than the second spine and 3.4 times longer than the first spine. The first two dorsal fin spines are supernumerary on the first dorsal fin pterygiophore; these are closely spaced. The first two soft dorsal fin rays are segmented but unbranched, whereas all the others are branched. The longest soft ray of the dorsal fin is only slightly shorter than the last dorsal fin spine. The length of the base of the soft portion of the dorsal fin is 1.26 times shorter than the base length of the spiny portion of the dorsal fin. There are a total of 19 dorsal fin pterygiophores. The first pterygiophore is large and sturdy, expanded anteroposteriorly, and bears a longitudinal strengthening ridge; the succeeding pterygiophores gradually become narrower. The ventral shafts of the first two dorsal fin pterygiophores are only slightly inclined. Posteriorly in the series the pterygiophores become more strongly inclined and of decreased length. Several posterior pterygiophores are evidently trisegmental. The interneural spaces below the dorsal fin have the ventral shafts of one (usually) or two pterygiophores present. There may be a slight displacement of the anterior dorsal fin pterygiophores in relation to the neural spines, because the third neural spine is crossed by three anteriormost pterygiophores in the holotype.

Anal fin

The anal fin originates under the level of the front of the 15th vertebra and ends under the end of the dorsal fin. There are three spines and eight soft segmented rays in the anal fin; all of these are branched. The anal fin spines are very slender and closely spaced, with the third spine 1.2 times longer than the second and 3.4 times longer than the first. The first two spines are supernumerary. The longest anal fin soft rays are slightly shorter than the longest dorsal fin soft rays. The first anal fin pterygiophore is long and sturdy, but relatively narrow; it is inclined at an angle about 45° to the body axis. The succeeding anal fin pterygiophores are slender and relatively strongly inclined; these decrease in length posteriorly in the series. The last pterygiophore is almost horizontally oriented.

Caudal fin and skeleton

The terminal centrum is composed of the fusion of PU1, U1 and U2. The parhypural, haemal spines of PU2 and (perhaps) PU3 are autogenous. Hypurals 1-2 and 3-4 are fused into two plates, whereas hypural 5 is autogenous. There is a small hypural diastema between the epaxial and hypaxial hypural plates. The neural and haemal spines of PU3 are longer and stouter than those of the preceding vertebra. The neural spine of PU2 is evidently a short crest extending caudad above the stegural. There are three epurals; the first is longest. The caudal fin is large and deeply forked. There are 17 principal rays in the caudal fin (I,8-7,I); procurrent rays are

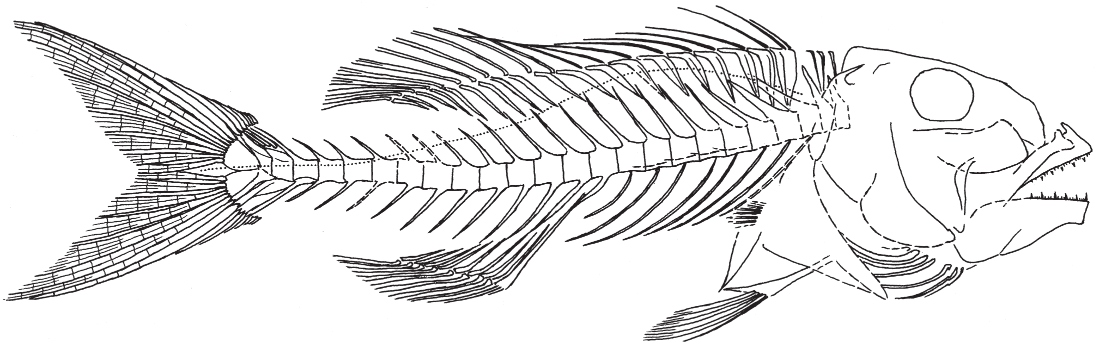

FIG. 6. — *Ottaviania leptacanthus* (Agassiz, 1839) n. comb., reconstruction of the skeleton based on the holotype (position of supraneurals changed, see text); scales omitted.

numerous, but their precise number is unknown. The upper lobe of the caudal fin is not longer than the lower lobe.

Squamation
Moderately large scales cover the entire body and the caudal fin base. Each scale bears seven to 14 radii in the basal field and tubercles in the posterior field. Ctenii are not evident. The lateral line is slightly arched anteriorly, being in close proximity to the dorsal profile of the body below the sixth to eighth dorsal fin spines; it descends to the level of the vertebral column near the 20th vertebra and extends onto the caudal fin base.

Measurements
See Table 1 (Appendix).

DISCUSSION
Ottaviania leptacanthus n. comb. greatly resembles *O. mariae* from the same locality in the overall shape of the body, the similar fin ray counts and dentition, and slenderness of the fin spines (see Bannikov & Zorzin 2004). However, the latter cannot be regarded as a synonym of the former, since these two species differ from one another considerably in certain respects. Whereas some differences in body proportions (e.g., relatively smaller orbit, shorter mandible, longer snout of *O. leptacanthus* n. comb.) can be explained by either ontogenetic changes (the holotype of *O. leptacanthus* n. comb. is 2.4 times bigger than the holotype of *O. mariae*) or intraspecific variations, certain quantitative differences indicate that both species are valid. *Ottaviania leptacanthus* n. comb. has cycloid scales (vs. feebly ctenoid in *O. mariae*), two unbranched dorsal fin soft rays (vs. one ray in *O. mariae*), slender last pair of ribs (vs. broadly flanged ribs in *O. mariae*), broader postcleithrum (vs. narrower postcleithrum in *O. mariae*), two equally long lobes of the caudal fin (vs. upper caudal fin lobe longer in *O. mariae*). The difference in vertebral formula (11 + 13 in *O. leptacanthus* n. comb. vs. 10 + 14 in *O. mariae*) could be caused by slight post-mortal posterior displacement of the upper tip of the first anal pterygiophore in the holotype of *O. leptacanthus* n. comb.

Both species of *Ottaviania* can be easily accommodated in the family Lutjanidae, since none of their characters contradicts that attribution, except for the cycloid scales of *O. leptacanthus* n. comb. Extant lutjanids are characterized by ctenoid scales (Johnson 1980; Allen 1985). Although *O. leptacanthus* n. comb. has granulations on the posterior field of the scales that are characteristic for ctenoid scales, it lacks true ctenii. A number of percoid families have both ctenoid and cycloid scales; the combination of these two types of scales can be observed even in a single specimen (e.g., some sciaenids). Therefore, we find no reason for the exclusion of *O. leptacanthus* n. comb. from the lutjanids based only on its possession of cycloid

FIG. 7. — *Goujetia crassispina* (Agassiz, 1839) n. comb., holotype, MNHN Bol 8 (10811). Middle Eocene of Bolca, northern Italy. Scale bar: 10 mm.

scales. The family scale characteristic certainly can be slightly changed throughout the last 50 millions of years.

Genus *Goujetia* n. gen.

TYPE SPECIES. — *Dentex crassispinus* Agassiz, 1839, by monotypy and designation herein.

ETYMOLOGY. — Named in honour of Prof. Daniel Goujet, in recognition of his contributions to paleoichthyology and invaluable help to the author in arranging his visit to Paris in 2005; gender feminine.

REFERRED SPECIES. — Type species only.

DIAGNOSIS. — Dorsal profile of body more convex than ventral. Head relatively small. Maximum body depth exceeds head length. Lower jaw articulation under middle of orbit. Jaws with an outer row of blunt conical teeth and an inner band of villiform teeth. Preopercle serrated. 10(?)+14 vertebrae. Hypurals 1-2 and 3-4 fused in two plates. Three supraneurals. Dorsal fin continuous, with 10 strong spines and 11 soft rays. Anal fin with three graduated strong spines and 10 rays. Pelvics inserted behind pectorals. Caudal fin deeply forked. Scales moderately large and very feebly ctenoid, each scale with 5-8 radii basally. Lateral line complete, concurrent with dorsal profile.

Goujetia crassispina (Agassiz, 1839) n. comb. (Figs 7-9)

Dentex crassispinus Agassiz, 1839: 147. — Zigno 1874b: 67.

HOLOTYPE. — MNHN Bol 8/9 (10811/10810), part and counterpart, complete skeleton, 128 mm SL; lower part of the middle Eocene, Lutetian, zone *Discoaster sublodoensis*; Monte Bolca locality, Pesciara cave site, northern Italy.

REFERRED SPECIMENS. — None.

DIAGNOSIS. — As for the genus.

DESCRIPTION

The body is moderately elongate, with a relatively slender caudal peduncle. The caudal peduncle depth is 0.27 of the body depth. The head is relatively small, its length 1.17 times less than the body depth. The head length is contained 3.25 times in SL. The dorsal profile of the body is more convex than the ventral profile.

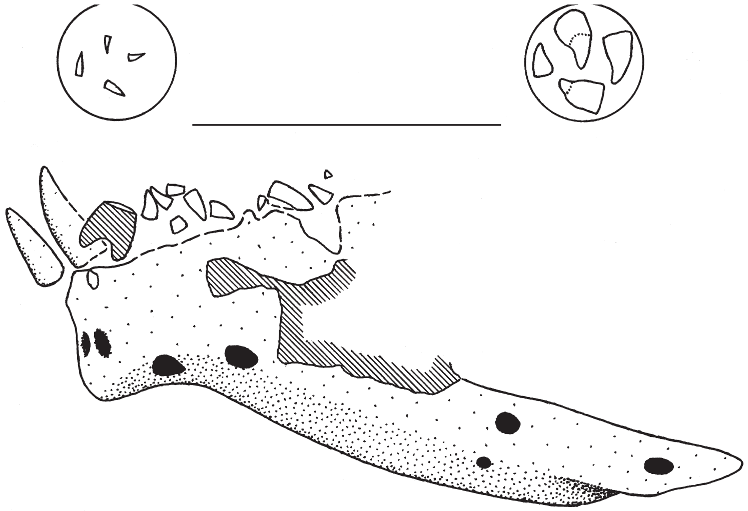

FIG. 8. — *Goujetia crassispina* (Agassiz, 1839) n. comb., holotype MNHN Bol 8 (10811); dentary, medial premaxillary teeth (upper left) and pharyngeal teeth (upper right). Middle Eocene of Bolca, northern Italy. Scale bar: 5 mm.

Head

The head is relatively deep, with its depth about 1.1 times greater than its length. The orbit is small and placed in the upper half of the head. The horizontal diameter of the orbit is about 21% HL. The snout is pointed and relatively long; its length is about 43% HL. The mouth is moderately large and terminal. The lower jaw articulation is situated approximately under the middle of the orbit. No infraorbital bones are recognizable except for faint remains of the lachrymal, which is definitely large. The neurocranium is relatively deep, with the supraoccipital crest prominent (which is evident from the impression on the matrix). The ethmoid region is moderately long. The parasphenoid is poorly preserved; it extends along the lower border of the orbit. The nasal is relatively short and trilobate proximally; it contains a longitudinal canal. The premaxilla has a well developed slender ascending process, and an articular process that is not fused to the former. Multiserial minute villiform premaxillary teeth are evident in MNHN Bol 8 (10811) (Fig. 8), whereas a few larger conical teeth are preserved in the counterpart MNHN Bol 9 (10810). The relatively long maxilla is preserved only as fragments. No supramaxilla is evident. The lower jaw is moderately deep; its length is about 46% HL. The dentary slightly projects ventrally near the symphysis. The oral border of the dentary bears an outer row of blunt conical teeth, and probably an inner band of minute villiform teeth. The conical teeth differ in size, with the anterior canines appearing to be larger than those from the middle region (Fig. 8). The hyomandibular shaft is very slightly inclined anteroventrally. The quadrate and pterygoids are imperfectly preserved. The opercular region is moderately narrow. The preopercle is only slightly curved; it bears serrations, at least at the angle. The opercular bones are very fragmentary. There are about seven sabre-like branchiostegal rays. The urohyal is elongate. The branchial bones are indistinct: MNHN Bol 8 (10811) reveals small and moderate pharyngeal teeth; these are slightly curved, conical and blunt, thickened at the base (Fig. 8).

Axial skeleton

There are probably 24 vertebrae, including the urostyle (the first vertebra is scarcely recognizable). The upper tip of the first interhaemal is situated just posterior to the haemal spine of the 11th vertebra. We interpret this as a *post-mortem* deformation of the specimen, and thus the reconstructed vertebral formula is 10+14, as in all other lutjanids. The axis of the vertebral column is almost straight. The vertebral centra are almost rectangular in lateral view. The length of the caudal portion of the vertebral column (14 posteriormost vertebrae) is about 1.6 times greater than the length of the abdominal portion of the vertebral column. The vertebral spines are relatively long, straight or slightly curved, and rather strong. Expansion of the neural spines of the anterior vertebrae is not evident. The haemal spines of the anterior caudal vertebrae are usually slightly longer than the opposite neural spines, and most of the neural spines arise from the middle of the centra, whereas the anterior haemal spines arise from the anterior half of the centra. Parapophyses are scarcely recognizable in the abdominal vertebrae, except for the last abdominal vertebra. Pleural ribs are slender and moderately long; these are strongly inclined posteroventrally. Faint remains of slender epineurals are barely recognizable in the abdominal part of the vertebral column at the lower border of the centra.

Pectoral fin and girdle

The pectoral girdle is very poorly preserved. The posttemporal is evidently forked. The anterior border of the cleithrum as preserved in MNHN Bol 9 (10810) indicates that this bone is large and elongate, oriented obliquely; its upper part is curved anteriorly and situated under the second to third vertebrae. The other pectoral girdle bones are not recognizable with confidence. The basal part of the pectoral fin is preserved in MNHN Bol 9 (10810). The pectoral fin consists of about 15 rays; its base is situated 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 elongate and wedge-shaped; they are tightly attached to one another along the midline. 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; the pelvic fin spine is slender and longer than the longest (third) anal fin spine.

Supraneurals and dorsal fin

There are three rather strong supraneurals. The supraneurals bear apical projections directed rostrad in the first supraneural and caudad in the second and third. The dorsal fin is relatively long-based and continuous; it originates over the third vertebra and ends over the 18th vertebra. There are 10 dorsal fin spines and 11 soft segmented rays. The dorsal fin spines are strong. The spines gradually increase in length from the first to the fourth; the succeeding spines very slightly decrease in length, with the last spine being 1.2 times shorter than the fourth spine. The fourth spine is 2.1 times longer than the first spine. The first two dorsal fin spines are supernumerary on the first dorsal fin pterygiophore; these are closely spaced. The longest soft ray of the dorsal fin is slightly longer than the longest dorsal fin spine. The length of the base of the soft portion of the dorsal fin is 1.25 times shorter than the base length of the spiny portion of the dorsal fin. There are a total of 19 dorsal fin pterygiophores. The first pterygiophore is large and sturdy, expanded anteroposteriorly, and bears a longitudinal strengthening ridge; the succeeding pterygiophores gradually become narrower. The ventral shaft of the first dorsal fin pterygiophore is only slightly inclined; one or two of the succeeding pterygiophores are displaced from their original position. Posteriorly in the series the pterygiophores become more strongly inclined and are of decreased length. Several posterior pterygiophores are evidently trisegmental. The interneural spaces below the dorsal fin have the ventral shafts of one or two pterygiophores present.

Anal fin

The anal fin originates under the 12th vertebra and ends under the 18th vertebra. There are three spines and 10 soft segmented and branched rays in the anal fin. The anal fin spines are relatively strong and closely spaced, with the third spine 1.3 times longer than the second and 2.8 times longer than the first. The first two spines are supernumerary. The longest anal fin soft rays are slightly shorter than the longest dorsal fin soft rays. The first anal fin pterygiophore is long and sturdy and wedge-like in shape; it is inclined at an angle about 75° to the

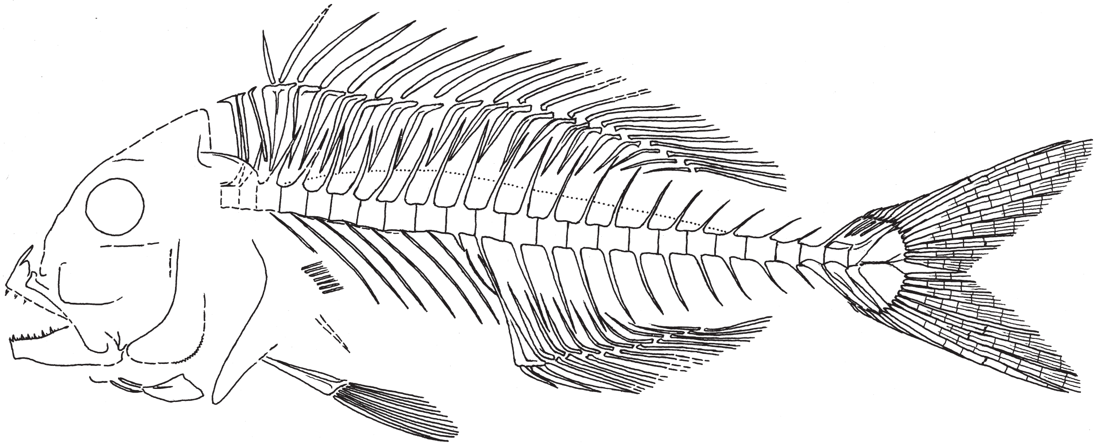

FIG. 9. — *Goujetia crassispina* (Agassiz, 1839) n. comb., reconstruction of the skeleton based on the holotype (deformations corrected); scales omitted.

body axis. The succeeding anal fin pterygiophores are slender and relatively strongly inclined; these decrease in length posteriorly in the series. The last pterygiophore is almost horizontally oriented.

Caudal fin and skeleton
The elements of the caudal skeleton are disarticulated and slightly displaced in the holotype (Fig. 7). The terminal centrum is composed of the fusion of PU1, U1 and U2. The parhypural and haemal spines of PU2 and PU3 are autogenous. Hypurals 1-2 and 3-4 are fused into two plates, whereas hypural 5 is probably autogenous. There appears to be a small hypural diastema between the epaxial and hypaxial hypural plates. The neural and haemal spines of PU3 are longer and stouter than those of the preceding vertebra. The neural spine of PU2 is evidently a short crest. There is a stegural and perhaps three epurals, although the epurals can be easily confused with the basal parts of the caudal fin rays. The caudal fin is moderately large and deeply forked. There are 17 principal rays in the caudal fin (I,8-7,I); the number of procurrent rays is unknown.

Squamation
Moderately large scales cover the entire body. Each scale bears five to eight radii in the basal field and tubercles in the posterior field. Ctenii are scarcely recognizable. The lateral line is very slightly convex anteriorly, while most of the lateral line is almost straight and parallel to the dorsal profile of the body; it descends to the level of the vertebral column near the 20th vertebra.

Measurements
See Table 2 (Appendix).

DISCUSSION
Goujetia n. gen. lacks the synapomorphies that define both the Sparoidea and Haemuloidea. However, none of its characters contradicts the accommodation of the new genus in the family Lutjanidae. The strong spines of the unpaired fins, larger supraneurals and greater number of the anal fin soft rays easily distinguish *Goujetia* n. gen. from the Eocene genus *Ottaviania* Sorbini, 1983. Modern lutjanids were subdivided by Johnson (1980) into four subfamilies: Etelinae, Apsilinae, Paradicichthyinae, and Lutjaninae. Subsequently, Johnson (1993) recommended treating the Caesionidae as an additional subfamily of the Lutjanidae. *Goujetia* n. gen. cannot be allocated to any of the lutjanid subfamilies (*sensu* Johnson 1980; Allen 1985) without the emendation of their diagnoses. Hypurals 1-2 and 3-4 of the new

genus are fused, as in the Etelinae, in contrast to the three other subfamilies. Ten anal fin soft rays distinguish *Goujetia* n. gen. from both the Etelinae and Apsilinae, which have only eight soft rays in the anal fin (nine rays in the eteline *Randallichthys* Anderson, Kami & Johnson, 1977) (Johnson 1980; Allen 1985). Unlike the Etelinae and Apsilinae with approximately equally convex dorsal and ventral profiles of the body, many paradicichthyines and lutjanines have the dorsal profile of the body more convex than the ventral profile, as in *Goujetia* n. gen. But most paradicichthyine and lutjanine genera have the caudal fin truncate to emarginate, and only the lutjanine *Ocyurus* has the caudal fin deeply forked with pointed lobes, just as in the new genus.

Genus *Veranichthys* n. gen.

TYPE SPECIES. — *Serranus ventralis* Agassiz, 1839, by monotypy and designation herein.

ETYMOLOGY. — Named in honour of Dr. Monette Véran, in recognition of her contributions to paleoichthyology and for her help to the author in arranging for a visit to the paleoichthyological collections of the MNHN, and the Greek word *ichthys* for fish; gender feminine.

REFERRED SPECIES. — Type species only.

DIAGNOSIS. — Dorsal profile of body more convex than ventral. Head relatively small. Maximum body depth exceeds head length. Lower jaw articulation under middle or anterior half of orbit. Jaws with an outer row of blunt conical teeth and an inner band of villiform teeth. Preopercle serrated. 10+14 vertebrae. Hypurals 1-2 and 3-4 not fused into two plates. Three supraneurals. Dorsal fin continuous, with 10 slender spines and 11 soft rays. Anal fin with three graduated slender spines and seven rays. Pelvic fins inserted under pectorals. Outer pelvic fin ray very elongate. Pectoral fins very long. Caudal fin forked. Scales moderately large and cycloid, each scale with 7-10 radii basally. Lateral line complete, concurrent with dorsal profile.

Veranichthys ventralis (Agassiz, 1839) n. comb.
(Figs 10; 11)

Sparus chromis Linnaeus, 1758 – Volta 1796: 138, pl. XXXII, fig. 1.

Serranus ventralis Agassiz, 1839: 104, pl. XXIII*b*. — Zigno 1874b: 53.

Serranus rugosus Heckel, 1854: 137. — Zigno: 1874b: 55 (*nec* Frickhinger 1991: fig. p. 801 [misidentification]).

LECTOTYPE. — MNHN Bol 275 (10724), single plate, complete skeleton, 175 mm SL; lower part of the middle Eocene, Lutetian, zone *Discoaster sublodoensis*; Monte Bolca locality, Pesciara cave site, northern Italy.

REFERRED SPECIMEN. — Paralectotype MNHN Bol 24 (10723), single plate, complete skeleton, 146 mm SL; from the type locality.

DIAGNOSIS. — As for the genus.

DESCRIPTION

The body is elongate, with a moderately slender caudal peduncle. The caudal peduncle depth is 0.32 of the body depth. The head is relatively small, its length 1.06-1.13 times less than the body depth. The head length is contained 2.9-3.3 times in SL. The dorsal profile of the body is more convex than its ventral profile.

Head

The head is relatively deep, with its depth almost equal to its length. The orbit is relatively small and placed close to the frontal profile of the head. The horizontal diameter of the orbit is 24-25% HL. The snout is pointed and relatively long; its length is 34-40% HL. The mouth is moderately large and terminal. The lower jaw articulation is situated under the middle or anterior half of the orbit. No infraorbital bones are recognizable except for the remains of the lachrymal, which is large and expanded. The neurocranium is moderately deep, with the supraoccipital crest probably moderately developed. The ethmoid region is not especially long. The parasphenoid is strong and straight; it extends along the lower border of the orbit. The nasal is steeply sloped. The premaxilla has a relatively long slender ascending process, and the articular process is not fused to the former. The oral border of the premaxilla bears an outer row of blunt conical teeth, and an inner band of minute villiform teeth. One or two of the anterior conical teeth are relatively strong canines. The maxillae are preserved only as fragments; their articular head is well developed.

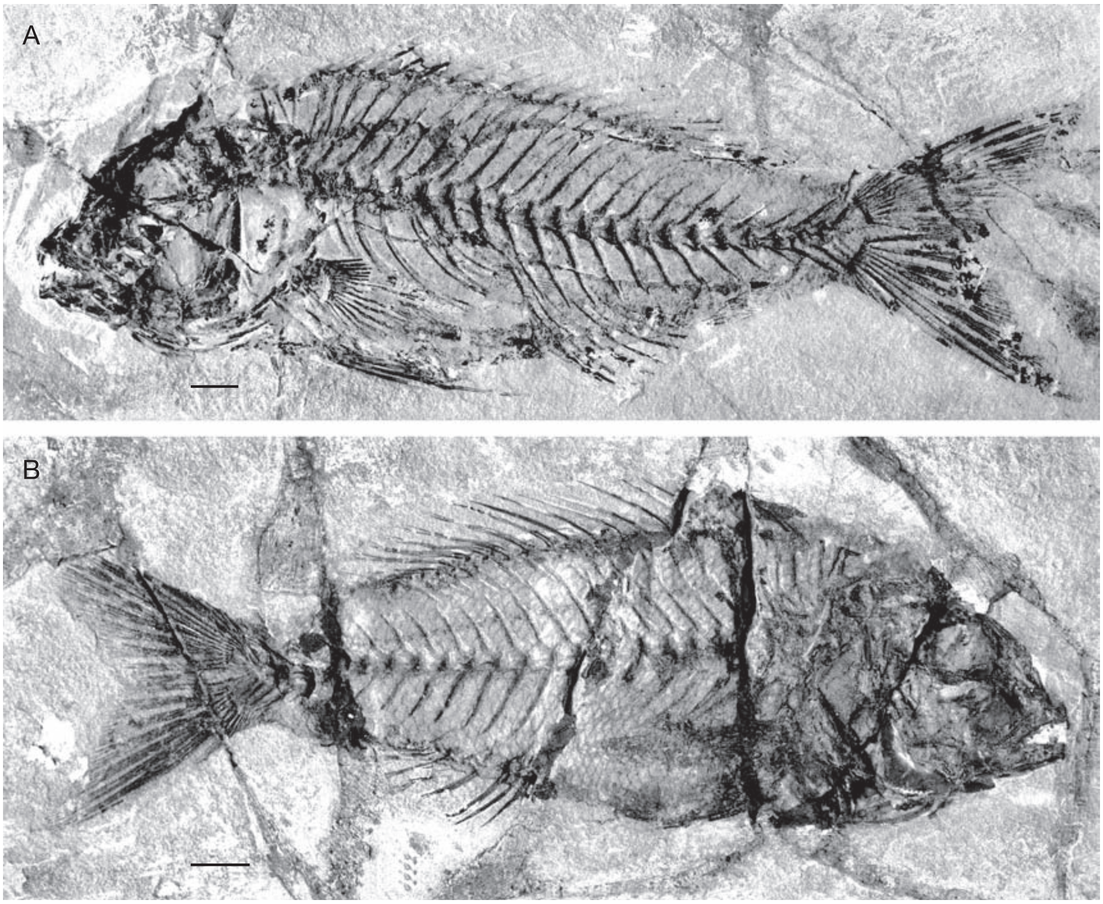

FIG. 10. — *Veranichthys ventralis* (Agassiz, 1839) n. comb.: **A**, lectotype, MNHN Bol 275 (10724); **B**, paralectotype, MNHN Bol 24 (10723) (lectotype of *Serranus rugosus* Heckel, 1854). Middle Eocene of Bolca, northern Italy. Scale bars: 10 mm.

No supramaxilla is evident. The lower jaw is moderately deep; its length is 46-47% HL. The dentary slightly projects ventrally near the symphysis. The oral border of the dentary bears an outer row of blunt conical teeth, and probably an inner band of minute villiform teeth. Anterior canines of the dentary appear to be somewhat smaller than those of the premaxilla. The hyomandibular shaft is very slightly inclined anteroventrally. The quadrate and pterygoids are imperfectly preserved. The opercular region is relatively narrow. The preopercle is moderately curved; it bears very fine serrations along the posterior border, and stronger serrations at the angle and ventrally. The opercle is relatively narrow. There are seven sabre-like branchiostegal rays. The branchial bones and pharyngeal teeth are indistinct; MNHN Bol 24 (10723) has densely arranged gill filaments.

Axial skeleton

There are 24 vertebrae, including the urostyle (the first two vertebrae are scarcely recognizable). The vertebral formula is 10+14. The axis of the vertebral column is almost straight, being only very slightly sygmoid. The vertebral centra are almost rectangular in lateral view. The length of the caudal portion of the vertebral column is 1.6-1.7 times greater than the length of the abdominal portion of the vertebral column. The vertebral spines are moderately long, straight or slightly curved, and rather strong. The neural spines of several anterior vertebrae appear to be more strongly expanded than those of the succeeding vertebrae. The haemal spines of the anterior caudal vertebrae are usually slightly longer than the opposite neural spines, and most of the neural spines arise from the middle of the centra, whereas the anterior haemal spines arise from the anterior half of the centra. At least two posterior abdominal vertebrae bear parapophyses. Pleural ribs are rather slender and moderately long; these are strongly inclined posteroventrally. Epineurals are not recognizable.

Pectoral fin and girdle

MNHN Bol 275 (10724) indicates a forked posttemporal with a rather broad posterior plate. An elongate and relatively narrow supracleithrum is evident in MNHN Bol 24 (10723); this bone extends somewhat obliquely from the vertical line between the posttemporal and cleithrum. The cleithrum is large and elongate, oriented obliquely; its upper part is curved anteriorly and situated under the second to third vertebrae. The other pectoral-girdle bones are not recognizable with confidence except for faint remains of the pectoral radials in MNHN Bol 275 (10724). The pectoral fin is better preserved in the lectotype; it consists of 15 rays, the uppermost of which are very strongly elongated: the apical tips of these definitely reach posteriorly beyond the anal fin origin. The base of the pectoral fin is situated under the fourth to fifth vertebra, in the midpoint between the vertebral column and the ventral profile of the body.

Pelvic fin and girdle

The pelvic bones are poorly preserved; these appear to be wedge-shaped. The pelvic fin has a slender and long (*c.* 16% SL) spine and five soft branched rays; it is inserted under the pectoral fin base. The outermost pelvic fin soft ray is strongly elongated, its distal tip reaches the anal fin origin or almost so.

Supraneurals and dorsal fin

There are three relatively strong supraneurals. The two posterior supraneurals have a nail-like expansion dorsally, and the first supraneural bears a long apical process directed rostrad. The dorsal fin is relatively long-based and continuous; it originates over the third vertebra and ends over the 18th or 19th vertebra. There are 10 dorsal fin spines and 11 soft segmented rays. The dorsal fin spines are slender. The several anterior spines gradually increase in length. The spines are not preserved in MNHN Bol 275 (10724), being represented there only by imprints in the matrix, but are mostly incomplete distally. In MNHN Bol 24 (10723) only the five posteriormost dorsal fin spines are completely preserved; therefore, it is not clear which spine is the longest. Whereas the five posteriormost dorsal fin spines are almost equal in length, the last spine seems to be slightly shorter than the penultimate spine. The penultimate spine is two times longer than the first spine. The first two dorsal fin spines are supernumerary on the first dorsal fin pterygiophore; these are closely spaced. The first soft dorsal fin ray is segmented but unbranched, whereas all the others are branched. The longest soft ray of the dorsal fin is almost as long as the longest dorsal fin spine. The length of the base of the soft portion of the dorsal fin is 1.29-1.34 times shorter than the base length of the spiny portion of the dorsal fin. There are a total of 19 dorsal fin pterygiophores. The first pterygiophore is large and sturdy, expanded anteroposteriorly, and bears a longitudinal strengthening ridge; the succeeding pterygiophores gradually become narrower. The ventral shaft of the first dorsal fin pterygiophore is almost vertical in MNHN Bol 24 (10723), slightly more inclined in MNHN Bol 275 (10724). Posteriorly in the series the pterygiophores become more strongly inclined and of decreased length. The interneural spaces below the dorsal fin have the ventral shafts of one or two pterygiophores present.

Anal fin

The anal fin originates under the 13th vertebra and ends under the 18th vertebra. There are three spines and seven segmented and branched rays in the anal fin. The anal fin spines are relatively slender and closely spaced; the first spine is not preserved in MNHN Bol 24 (10723) and is represented by

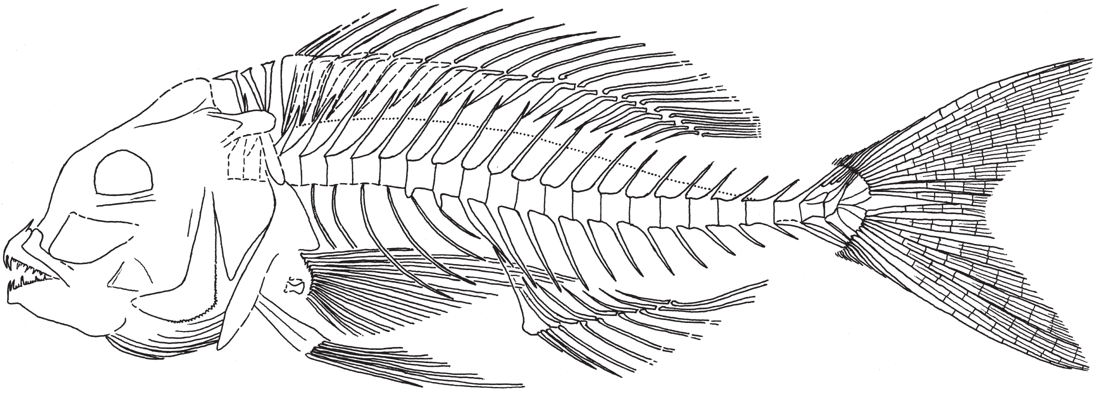

FIG. 11. — *Veranichthys ventralis* (Agassiz, 1839) n. comb., reconstruction of the skeleton based on two syntypes; scales omitted.

faint imprint in the matrix in MNHN Bol 275 (10724). The first two spines are supernumerary. The longest anal fin soft rays are shorter than the longest dorsal fin soft rays; in the lectotype the two posterior rays of the anal fin are elongate. Based on MNHN Bol 275 (10724), the first anal fin pterygiophore appears to be rather long, sturdy and wedge-like in shape; it is inclined at an angle about 65° to the body axis. The succeeding anal fin pterygiophores are slender and relatively strongly inclined; these decrease in length posteriorly in the series. The last pterygiophore is almost horizontally oriented. In MNHN Bol 24 (10723) the anal fin pterygiophores are slightly distorted, with the first one missing.

Caudal fin and skeleton

The caudal skeleton is best preserved in MNHN Bol 24 (10723). The terminal centrum is composed of the fusion of PU1, U1 and U2. The parhypural, hypurals, haemal spines of PU2 and perhaps PU3 are autogenous. There is a distinct diastema between the epaxial and hypaxial hypurals. The neural and haemal spines of PU3 are longer and stouter than those of the preceding vertebra. The neural spine of PU2 is evidently a short crest. There are two uroneurals (first as a stegural) and three epurals. The caudal fin is moderately large and forked. There are 17 principal rays in the caudal fin (I,8-7,I), and about 10 procurrent rays both above and below.

Squamation

Moderately large scales cover the entire body and bases of the unpaired fins. Each scale bears seven to 10 radii in the basal field and tubercles in the posterior field. Ctenii are not evident. The lateral line is very slightly convex anteriorly, but most of the lateral line is almost straight in parallel to the dorsal profile of the body; it descends to the level of the vertebral column near the 21st vertebra.

Measurements

See Table 3 (Appendix).

DISCUSSION

It is clear that *Veranichthys ventralis* (Agassiz, 1839) n. comb. cannot be regarded as either a serranid or a sparid, in which families it was previously classified. It lacks the serranid synapomorphies listed by Johnson (1983). Moreover, the new genus has a deeper lachrymal and stronger anterior canines in the jaws than recorded for the Serranidae. *Veranichthys* n. gen. lacks the synapomorphies of both the Sparoidea and Haemuloidea, but it can be accommodated in the family Lutjanidae. The new genus shares the same dorsal fin count as two other Eocene genera from Bolca, *Ottaviania* and *Goujetia* n. gen., and *Veranichthys* n. gen. unusually has fewer anal fin soft rays (seven vs. eight in *Ottaviania* and 10 in *Goujetia* n. gen.). Unlike *Goujetia* n. gen., the fin spines of *Veranichthys* n. gen. are slender, although not as extremely slender as in *Ottaviania*.

Two remarkable characters of the new genus are its strongly elongated pectoral and pelvic fins. Whereas equally elongate pectoral fins are known in some of extant lutjanids, e.g., *Symphorichthys* Munro, 1967 and *Lipocheilus* Anderson, Talwar & Johnson, 1977 (Allen 1985), the very long ventral fins of *Veranichthys* n. gen. have no analogue amongst the Recent Lutjanidae. All the extant lutjanids are known to have the longest ray of the pelvic fin not reaching the anal fin origin, unlike in *Veranichthys* n. gen. Amongst extant lutjanids as few as seven anal fin soft rays are recorded only in some lutjanines (Johnson 1980; Allen 1985), although only as a variation of the known range of the anal fin count (Allen & Talbot 1985); representatives of three other lutjanid subfamilies have not less than eight rays in the anal fin. Whereas *Veranichthys ventralis* n. comb. has granulation on the posterior field of the scales characteristic for ctenoid scales, it lacks true ctenii and thus resembles *Ottaviania leptacanthus* n. comb.

CONCLUSIONS

A revision of the type specimens of the Eocene species from Bolca (Italy) from the MNHN, attributed by Agassiz (1833-1844) to the fossil genera *Sparnodus* and *Odonteus* (= *Odonteobolca*) in comparison to the extant genera of sparids *Dentex* and *Pagellus*, serranids *Serranus* and haemulids *Pristipoma* (= *Pomadasys*), resulted in the following conclusions.

The "haemulid" *Pomadasys furcatus* (Agassiz, 1839) is in fact a synonym of *Sparnodus elongatus* Agassiz, and haemulids are absent from the Eocene fauna of Bolca.

Odonteobolca sparoides (Agassiz, 1839), variously attributed to either the sciaenids or pomacentrids, is probably a synonym of the "sparid" *Pseudosparnodus* (= *Odonteobolca*?) *microstomus* (Agassiz, 1839). If it can be confirmed, the generic name *Odonteobolca* Krell, 1991 will have priority over *Pseudosparnodus* Day, 2003.

Those of Agassiz's species of *Dentex* whose type specimens are located in the MNHN, i.e. *D. leptacanthus* and *D. crassispinus*, must be regarded as lutjanids rather than sparids, with the following new species combinations: *Ottaviania leptacanthus* (Agassiz, 1839) n. comb. and *Goujetia crassispina* (Agassiz, 1839) n. comb., respectively. *Dentex ventralis* Agassiz, 1839 should be regarded as a *nomen dubium*.

We restore the validity of the species *Serranus ventralis* Agassiz, 1839 previously regarded as a synonym of *Sparnodus elongatus*. A new genus of the Lutjanidae, *Veranichthys* n. gen., is erected for this species. The species name *Serranus rugosus* Heckel, 1854, long regarded as valid, is actually a junior synonym of *Veranichthys ventralis* (Agassiz, 1839) n. comb. Thus, the genus *Serranus* is absent from the Bolca fauna. Because *Dules temnopterus* Agassiz, 1839 in fact does not belong to the serranid genus *Dules* (Bannikov & Carnevale in press), the family Serranidae is absent from the Bolca fauna.

The family Lutjanidae is represented in the Bolca fauna by at least four species in three genera (*Ottaviania* Sorbini, 1983, *Goujetia* n. gen. and *Veranichthys* n. gen.). Conversely, the number of sparids in the Bolca fauna should be reduced, and these taxa must be regarded as members of the Sparidae only putatively, since most sparid autapomorphies cannot be determined in the fossils. The Eocene "sparids" include the monotypic genera *Abromasta* (with the species *A. microdon* (Agassiz, 1839)), *Pseudosparnodus* (= *Odonteobolca*?) (with the species *P. microstomus* (Agassiz, 1839)), and less definitely *Ellaserrata* (with the species *E. monksi* Day, 2003), in addition to the genus *Sparnodus* with two species: *S. vulgaris* (Blainville, 1818) and *S. elongatus* Agassiz, 1839. The latter was recently regarded as a synonym of the former by Day (2003), and its validity is restored herein. Evolution of the ideas concerning the systematic position of the "sparoid" species from the Eocene of Monte Bolca is shown in Table 4 (Appendix).

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APPENDIX

TABLE 1. — Measurements of *Ottaviania leptacanthus* (Agassiz, 1839) n. comb., presented as a percent of SL (261 mm) of the holotype.

Head length from tip of snout to posterior border of opercle	33
Maximum body depth	31
Depth of caudal peduncle	12
Distance between tip of snout and spiny dorsal fin	36
Distance between tip of snout and soft dorsal fin	62
Distance between tip of snout and anal fin	69
Distance between pelvic fin and anal fin	27
Length of base of spiny dorsal fin	24
Length of base of soft dorsal fin	20
Length of base of entire dorsal fin	46
Length of base of anal fin	13
Length of longest spine of dorsal fin	13
Length of longest soft ray of dorsal fin	12
Length of third spine of anal fin	9
Length of longest soft ray of anal fin	10
Length of longest ray of pelvic fin	14
Length of longest ray of caudal fin	30
Preorbital distance	14
Horizontal diameter of orbit	7
Length of lower jaw	15

TABLE 2. — Measurements of *Goujetia crassispina* (Agassiz, 1839) n. comb., presented as a percent of SL (128 mm) of the holotype.

Head length from tip of snout to posterior border of opercle	30
Maximum body depth	35
Depth of caudal peduncle	9
Distance between tip of snout and spiny dorsal fin	38
Distance between tip of snout and soft dorsal fin	61
Distance between tip of snout and anal fin	60
Distance between pelvic fin and anal fin	18
Length of base of spiny dorsal fin	26
Length of base of soft dorsal fin	20
Length of base of entire dorsal fin	48
Length of base of anal fin	20
Length of longest spine of dorsal fin	13
Length of longest soft ray of dorsal fin	14
Length of third spine of anal fin	11
Length of longest soft ray of anal fin	12
Length of longest ray of pelvic fin	*c.* 15
Length of longest ray of caudal fin	25
Preorbital distance	12
Horizontal diameter of orbit	6
Length of lower jaw	*c.* 12.5

TABLE 3. — Measurements of *Veranichthys ventralis* (Agassiz, 1839) n. comb., presented as a percent of SL of the lectotype and paralectotype (in parentheses).

Head length from tip of snout to posterior border of opercle	32 (30)
Maximum body depth	34 (34)
Depth of caudal peduncle	11 (11)
Distance between tip of snout and spiny dorsal fin	40 (39)
Distance between tip of snout and soft dorsal fin	64 (63)
Distance between tip of snout and anal fin	62 (63)
Distance between pelvic fin and anal fin	24 (25)
Length of base of spiny dorsal fin	26 (27)
Length of base of soft dorsal fin	21 (20)
Length of base of entire dorsal fin	48 (48)
Length of base of anal fin	18 (16)
Length of longest spine of dorsal fin	14 (14)
Length of longest soft ray of dorsal fin	14? (14)
Length of third spine of anal fin	11 (10)
Length of longest soft ray of anal fin	12 (11?)
Length of longest ray of pelvic fin	≥ 25 (≥ 21)
Length of longest ray of pectoral fin	≥ 32 (?)
Length of longest ray of caudal fin	31 (30)
Preorbital distance	13 (10)
Horizontal diameter of orbit	8 (9)
Length of lower jaw	15 (14)

TABLE 4. — Evolution of the ideas concerning the systematic position of the “sparoid” species from the Eocene of Monte Bolca.

Agassiz 1833-1844; Heckel 1854; Szajnocha 1886	Woodward 1901	Eastman 1905; Blot 1980	Day 2003	Present study
Sparnodus macrophthalmus Agassiz, 1839	*Sparnodus macrophthalmus* Agassiz, 1839	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)
Sparnodus ovalis Agassiz, 1839	*Sparnodus macrophthalmus* Agassiz, 1839	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)
Sparnodus altivelis Agassiz, 1839	*Sparnodus macrophthalmus* Agassiz, 1839	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)
Sparnodus micracanthus Agassiz, 1839	*Sparnodus macrophthalmus* Agassiz, 1839	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)
Sparnodus elongatus Agassiz, 1839	*Sparnodus elongatus* Agassiz, 1839	*Sparnodus elongatus* Agassiz, 1839	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus elongatus* Agassiz, 1839
Sparnodus lethriniformis Szajnocha, 1886	*Sparnodus macrophthalmus* Agassiz, 1839	*Sparnodus vulgaris* or *Sparnodus lethriniformis*	*Sparnodus vulgaris* (Blainville, 1818)	*Sparnodus vulgaris* (Blainville, 1818)
Dentex crassispinus Agassiz, 1839	*Dentex crassispinus* Agassiz, 1839	*Dentex crassispinus* Agassiz, 1839	–	*Goujetia crassispina* (Agassiz, 1839) n. comb.
Dentex leptacanthus Agassiz, 1839	*Dentex leptacanthus* Agassiz, 1839	*Dentex leptacanthus* Agassiz, 1839	–	*Ottaviania leptacanthus* (Agassiz, 1839) n. comb.
Dentex microdon Agassiz, 1839	*Dentex microdon* Agassiz, 1839	*Dentex microdon* Agassiz, 1839	–	–
Dentex ventralis Agassiz, 1839	*Dentex ventralis* Agassiz, 1839	*Dentex ventralis* Agassiz, 1839	–	*nomen dubium*
Dentex breviceps Agassiz, 1839	*Sparnodus microstomus* (Agassiz, 1839)	*Sparnodus microstomus* (Agassiz, 1839)	*Pseudosparnodus microstomus* (Agassiz, 1839)	*Pseudosparnodus* (= Odonteobolca?) *microstomus* (Agassiz, 1839)
Pagellus microdon Agassiz, 1839	*Pagellus microdon* Agassiz, 1839	*Pagellus microdon* Agassiz, 1839	*Abromasta microdon* (Agassiz, 1839)	*Abromasta microdon* (Agassiz, 1839)
Serranus ventralis Agassiz, 1839	*Sparnodus elongatus* Agassiz, 1839	*Sparnodus elongatus* or *Serranus rugosus*	*Sparnodus vulgaris* (Blainville, 1818)	*Veranichthys ventralis* (Agassiz, 1839) n. comb.
Serranus microstomus Agassiz, 1839	*Sparnodus microstomus* (Agassiz, 1839)	*Sparnodus microstomus* (Agassiz, 1839)	*Pseudosparnodus microstomus* (Agassiz, 1839)	*Pseudosparnodus* (= Odonteobolca?) *microstomus* (Agassiz, 1839)
Serranus occipitalis Agassiz, 1839	*Sparnodus microstomus* (Agassiz, 1839)	*Sparnodus microstomus* (Agassiz, 1839)	*Pseudosparnodus microstomus* (Agassiz, 1839)	*Pseudosparnodus* (= Odonteobolca?) *microstomus* (Agassiz, 1839)
Serranus rugosus Heckel, 1854	*Serranus rugosus* Heckel, 1854	*Serranus rugosus* Heckel, 1854	–	*Veranichthys ventralis* (Agassiz, 1839) n. comb.
Pristipoma furcatum Agassiz, 1839	*Pristipoma furcatum* Agassiz, 1839	*Pomadasys furcatus* (Agassiz, 1839)	–	*Sparnodus elongatus* Agassiz, 1839
Odonteus sparoides Agassiz, 1839	*Odonteus sparoides* Agassiz, 1839	*Odonteus sparoides* Agassiz, 1839	–	*Pseudosparnodus* (= Odonteobolca?) *microstomus* (Agassiz, 1839)
–	–	–	*Ellaserrata monksi* Day, 2003	“*Ellaserrata monksi*” Day, 2003