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REVISION OF THE ATERINIFORM FISH GENERA
RHAMPANOGRATHUS AGASSIZ AND MESOGASTER
AGASSIZ (TELEOSTEI) FROM THE EOCENE OF BOLCA,
NORTHERN ITALY

ABSTRACT

Revision of the type and additional materials on Rhamphognathus paralepoides Agassiz, 1844 and Mesogaster sphyraenoides Agassiz, 1844, from the lower part of the Middle Eocene (Lutetian) of the Monte Bolca locality (Pesciara cave site, in northern Italy), indicates that two new families of atheriniform fishes, the Rhamphognathidae and Mesogasteridae, are required to accommodate these taxa. The validity of the genus Mesogaster Agassiz, 1844 is restored. A new genus and species of mesogasterid, Latellagnathus teruzzii gen. et sp. nov., is described based on ten skeletons from the Bolca locality. The paratype of L. teruzzii previously was erroneously attributed by Agassiz to both Rhamphognathus paralepoides and Mesogaster sphyraenoides.

Key words: Atheriniformes, Rhamphognathus, Mesogaster, new taxa, Eocene, northern Italy, Bolca locality.

INTRODUCTION

In his pioneering monograph on the Bolca fish fauna, Volta (1796) described and figured, among others, several fishes identified as Recent species of the genera Esox, Ammodytes and Silurus. Subsequently, two small specimens identified by Volta as Silurus cataphractus and S. ascita were named by Agassiz (1833-1844a) as Atherina macrocephala Ag., but not described. A very brief description of A. macrocephala appeared for the first time in the Descriptive Catalog of de Zigno (1874); Woodward (1901) did not cite this description when he described A. macrocephala as a new species. Larger specimens identified by
Volta (1796) as *Esox saurus*, *E. sphyraena*, *Ammodytes tobianus* and *Silurus bagre* were subsequently described by Agassiz (1833-1844b) as two new genera and species of the "famille Sphyrénoides", *Rhamphognathus paralepoides* and *Mesogaster sphyraenoides*. The identification of the specimen now housed in the Muséum d'Histoire Naturelle (Paris), collection number Bol 3 (10854), was confused by Agassiz. He attributed the figure of this specimen published by Volta (1796, pl. 24, fig. 3) to the synonymy of *Mesogaster sphyraenoides* (Agassiz, 1833-1844a, b), whereas he placed his own illustration of the specimen (Agassiz, 1833-1844b, pl. 38, fig. 2) under the name *Rhamphognathus paralepoides*. According to the description of Agassiz (1833-1844b: 104), he definitely used the specimen MNHN Bol 3 (10854) in addition to the lectotype (Agassiz, 1833-1844b, pl. 38, fig. 1) in his diagnosis of *R. paralepoides*, as also did subsequent describers (de Zigno, 1874; Bassani, 1876).

Both de Zigno (1874) and Bassani (1876) followed Agassiz and placed *Rhamphognathus* and *Mesogaster* in the “Sphyraenoides”. Woodward (1901) regarded *Mesogaster* as a synonym of *Rhamphognathus*, and in the XX century other authors did likewise (Eastman, 1905; Leriche, 1906; Danil’chenko, 1964; Blot, 1980). Woodward (1901) first attributed *Rhamphognathus* in the Atherinidae, and subsequent authors accepted this point of view, until Blot (1980) regarded *Rhamphognathus* as being *incertae sedis* in the Acanthopterygii.

Our observations on the type material on *Rhamphognathus paralepoides* and *Mesogaster sphyraenoides* and additional materials identified as these species indicates that the two species are very different at the generic level and, furthermore, at the familial level. Both *Rhamphognathus* and *Mesogaster* can be accommodated in the suborder Atherinoidei of the order Atheriniformes, as defined by Nelson (1994, 2006). The syntype of *Rhamphognathus paralepoides*, MNHN Bol 3 (10854), was attributed in confusion to *Mesogaster sphyraenoides* by Agassiz (1833-1844a, b), Woodward (1901) and Eastman (1905), but actually represents a new taxon distinct from both *Rhamphognathus* and *Mesogaster*. This new genus and species is represented by at least 10 specimens in the museums of Paris, Milan and Verona. Since it is more closely related to *Mesogaster*, *Latellagnathus teruzzii* gen. et sp. nov. is described below in the family Mesogasteridae fam. nov.

**METHODS**

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

Abbreviations are as follows: **Institutional**: IGUP – Istituto di Geologia della Università di Padova; MCSNM - Museo Civico di Storia Naturale di Milano; MCSNV - Museo Civico di Storia Naturale di Verona; MFB – Museo dei Fossili di Bolca (VR); MNHN - Muséum National d’Histoire Naturelle, Paris; **Anatomical**: PU - preural vertebra; SL - standard length; sp – spur; U - ural vertebra.

**SYSTEMATIC DESCRIPTION**

Order Atheriniformes  
Suborder Atherinoidei  
Family Rhamphognathidae fam. nov.


**Diagnosis.** Body strongly elongated, with very slender caudal peduncle. Head depressed dorso-ventrally. Snout with long and tapered rostrum. 56 vertebrae. Abdominal vertebrae with broad transversal processes. Vertebral spines short and expanded medially. Intermuscular bones strongly developed. Short first dorsal fin with 4 spines, first longest. Anterior dorsal pterygiophore a long and slender rod. Interdorsal bones (rayless pterygiophores) between dorsal fins attached to one another. Anal fin originates in front of second dorsal; posterior pterygiophore of both fins bears long caudally directed spur. Pelvic fins abdominal, situated well before first dorsal fin. Caudal fin relatively small, with lower lobe somewhat longer than upper lobe. Scales small and thin.

**Type genus.** *Rhamphognathus* Agassiz, 1844.

**Composition.** Type genus only.

Genus *Rhamphognathus* Agassiz, 1844


**Diagnosis.** Body depth is 13-14 times in SL; head length 2.9 times in SL; teeth moderate, conical; 56 vertebrae; 2 epurals; epaxial hypurals unfused; distance between dorsal fins exceeds distance between second dorsal and caudal fin; 12 to 13 interdorsal bones between dorsal fins; a spine and 7 or 8 soft rays in second dorsal fin; a spine and 9 or 10 soft rays in anal fin; second dorsal fin originates not less than 2 vertebrae behind anal-fin origin; pectoral fins short, with 13 or 14 rays; 6-rayed pelvic fins moderate, situated about 4 vertebrae anterior to first dorsal-fin origin; pectoral to pelvic fin distance less than pelvic to anal fin distance.

**Type species.** *Rhamphognathus paralepoides* Agassiz, 1844, by monotypy and designation of Woodward (1901).

*Rhamphognathus paralepoides* Agassiz, 1844

Figures 1-3

*Esox sphyraena* L. (part.): Volta, 1796: 107, pl. 24, fig. 2 (*nec* fig. 1, 3).
*Rhamphognathus paralepoides* (part.): Agassiz, 1835; 292 (nom. nud.); 1833-1844b: 104, pl. 38, fig. 1 (as *R. pompilius*; *nec* fig. 2); de Zigno, 1874: 135; Bassani, 1876: 186; Woodward, 1901: 361; Eastman, 1911: 359 (?).

**Diagnosis.** As for the genus.

**Lectotype.** MNHN Bol 10 (10874), single plate, complete skeleton, 198 mm SL; lower part of the Middle Eocene, Lutetian, zone *Discoaster sublodoensis*; Monte Bolca locality, Pesciara cave site.

**Referred specimens.** MCSNM V263, single plate, complete skeleton; MCSNV VII.C.24, single plate, complete skeleton; MCSNV VII.C.25, single plate, postcranial skeleton, to which is added the skull from a different fish; MCSNV VII.C.36, single plate, skeleton with skull
incomplete anteriorly; MCSNV S.41, single plate, skeleton without skull; all from the type locality.

Description. The body is strongly elongate and fusiform, with a long and very slender caudal peduncle. The caudal peduncle depth is 0.20 to 0.25 of the body depth. The head is long; its length (tip of snout to posterior edge of opercle) is contained 2.9 times in SL.

- Head. The head is depressed and arrowhead-shaped in dorsal view, with a long and tapered snout. The width of the head is contained 3.3-3.9 times in its length. The orbit is relatively small. The snout length is 0.63-0.64 of the head length. The mouth is wide, with the lower jaw articulation situated approximately under the anterior border of the orbit. The neurocranium is elongate, with a long ethmoid region. The frontals appear to form most of the cranial roof, whereas the supraoccipital seems to be small. The frontals bear a longitudinal canal of the lateral line system; the frontals are tapered rostrally, with their width above the orbit only slightly less than the post-orbital width. The upper surface of the frontals is ornamented by small pits and grooves. Since the jaws are always preserved in a largely dorso-ventral projection among the material available, details of their structure and relative length are scarcely recognizable. The jaw teeth are moderately small and conical. The suspensorium, hyoid and branchial arches bones are not recognizable. The opercular bones have even margins. The opercle is broad and rounded posteriorly.

- Axial skeleton. There are 56 vertebrae, about 24 of these are caudal, including the urostyle. The vertebral centra are almost rectangular in the lateral view. All the vertebral spines are short. The approximately 20 anteriormost neural spines are strongly expanded medially, blunt and moderately inclined posteriorly; their upper border is concurrent.
with the dorsal profile of the body. Caudally, the neural spines become narrower, pointed and more strongly inclined, until they are very short and slender under the origin of the second dorsal fin. The neural spines in the caudal peduncle at first become longer, blunt and more expanded again, and then they become shorter and posteriorly directed, overhanging the succeeding centra. The haemal spines of the anterior caudal vertebrae are short, slender, pointed and strongly inclined, whereas on the caudal peduncle the haemal spines are similar to the opposite neural spines in shape and size. All the abdominal vertebrae bear strong and wide transverse processes indented apically. Each transverse process bears both a pleural rib and intermuscular bone (epineural), which are almost equally long and posteriorly directed. The ribs are only slightly stronger than the epineurals.

- Pectoral fin and girdle. The pectoral girdle is not clear in any of the specimens, but a large scapular foramen is evident in MCSNV VII.C.24 and VII.C.36. The pectoral fin is relatively short and consists of about 13 rays. The base of the pectoral fin is situated opposite the fifth vertebra. The first two pectoral-fin rays are simple (unsegmented and unbranched); the first of these is rudimentary while the second is strong. The length of the pectoral fin corresponds to the length of five opposite vertebrae.

- Pelvic fin and girdle. The pelvic bones are rather short; each consists of a wedge-shaped main body and strong postero-medial process for articulation with its opposite member. The pelvic fin contains six soft rays. The outer pelvic-fin ray is simple, whereas the others are branched. The pelvic fin is moderately long; it is inserted at the length of at least four vertebrae anterior to the origin of the first dorsal fin.

- Dorsal fins. No supraneurals are present anterior to the first dorsal fin. The first dorsal fin is small and short at the base. There are four slender and flexible dorsal-fin spines. The first spine is longest; the other spines decrease in length posteriorly in the series. The dorsal-fin spines are serially associated with the pterygiophores. The first dorsal-fin pterygiophore is large, it forms a long and slender rod extending rostrad along the dorsal profile of the body and ends anterior to the pelvic-fin origin. Three other pterygiophores of the dorsal fin are small, strongly inclined and closely adjoin each other. There is a continuous series of 12 or 13 pterygiophore-like interdorsal bones between the dorsal fins. The interdorsal bones are larger than the second to fourth dorsal-fin pterygiophores and usually elongate-rhomboïd in shape; adjacent interdorsal bones adjoin one another along the dorsal profile of the body.

The second dorsal fin originates over the 40th vertebra, it consists of a short spine and seven or eight soft rays. The first soft ray is unbranched, whereas the other rays are branched. The height of the second dorsal fin exceeds the length of its base. The rays of the second dorsal fin rapidly decrease in length posteriorly in the series. The pterygiophores of the second dorsal fin closely adjoin one another and decrease in length posteriorly in the series. The last pterygiophore bears both the last soft ray and a spur (a slender bony rod directed posteriorly along the dorsal profile of the body and divided to the end).

- Anal fin. The anal fin originates anterior to the origin of the second dorsal fin at the length of not less than two opposite vertebrae. This fin has a short spine and nine or ten soft rays. The anal-fin spine is supernumerary. The anal fin is similar to the second dorsal fin in shape and size. The first anal-fin pterygiophore is large, sturdy, and expanded in the middle; its shaft is strongly inclined anteriorly. The succeeding pterygiophores rapidly decrease in length posteriorly in the series. The last anal-fin pterygiophore bears both the last soft anal-fin ray and a spur, similar to that of the second dorsal fin (Fig. 2A).
- Caudal fin and skeleton. The terminal centrum is composed of the fusion of PU1, U1 and U2. Hypurals 3-5 and the parhypural are autogenous, whereas the first and second hypurals are fused (Fig. 2B). The haemal spines of PU2 and PU3 seem to be fused with their centra. There is a narrow hypural 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 evidently is absent. Two slender epurals are recognizable; the first is longer than the second. A uroneural seems to be at least partly fused with the urostyle. The caudal fin is relatively small and forked, its lower lobe is longer than upper lobe. There are 17 principal rays in the caudal fin (1.8-7.1), eight procurrent rays above and seven or eight rays below. The procurrent rays are not spiny.

- Squamation. Small and thin scales cover the entire body. The scales appear to be cycloid. The lateral line is absent.

- Measurements. The largest complete specimen examined (MCSNV VII.C.24) is 220 mm SL. Incomplete specimen MCSNV VII.C.25 is 1.25 times larger. Measurements of the lectotype MNHN Bol 10 (10874) and MCSNV VII.C.24 (in parentheses) in percent of SL are as follows:
  - Head length from tip of snout to posterior border of opercle: 34 (34)
  - Maximum body depth: ~7.5 (~7)
  - Depth of caudal peduncle: 1.5 (1.4)
  - Distance between tip of snout and first dorsal fin: 58 (?)
  - Distance between tip of snout and second dorsal fin: 80 (80)
  - Distance between tip of snout and anal fin: 77 (78)
  - Distance between tip of snout and pelvic fin: 53 (55)
  - Distance between pelvic fin and anal fin: 23 (22)
  - Distance between pectoral fin and pelvic fin: 17 (19)
  - Length of longest ray of caudal fin: 8 (?)

Family Mesogasteridae fam. nov.

**Diagnosis.** Body elongated, with moderately slender caudal peduncle. Head not depressed dorso-ventrally. Snout moderate to long, not forming tapered rostrum. 39-41 vertebrae. Parapophyses present on posterior abdominal vertebrae. Vertebral spines short and slender except for a few anterior neural spines that are expanded antero-posteriorly. Intermuscular bones moderately developed. First dorsal fin with 6 to 7 (rarely 5) spines, second or third longest. Anterior dorsal pterygiophore expanded and lamellar. Interdorsal bones between dorsal fins usually not attached to one another. Anal fin originates under or in front of second dorsal; posterior pterygiophore of both fins not bearing long spur. Pectoral fins situated low on body; pelvics abdominal, situated anterior to first dorsal fin. Caudal fin moderate to rather large, deeply notched; with lower lobe longer than upper lobe. Scales moderately small.

**Type genus.** *Mesogaster* Agassiz, 1844.
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COMPOSITION. Type genus and *Latellagnathus* gen. nov.

Genus *Latellagnathus* gen. nov.

*Rhamphognathus* (part.): Agassiz, 1833-1844b: 9, 104; de Zigno, 1874: 32; Woodward, 1901: 361.

**Diagnosis.** Body depth is 6-8 times in SL; head length 2.7-2.9 times in SL; snout length not less than half of head length; upper jaw protrudes; relatively strong conical teeth in jaws in addition to marginal series of minute teeth; 39-40 vertebrae; third hypural autogenous; distance between dorsal fins exceeds distance between second dorsal and caudal fin; 8 to 9 interdorsal bones between dorsal fins; 6 spines in first dorsal fin; a spine and 8 soft rays in second dorsal fin; a spine and 9 soft rays in anal fin; second dorsal fin originates above anal-fin origin or slightly behind it; pectoral fins moderate; 6-rayed pelvic fins situated slightly before first dorsal-fin origin; pectoral to pelvic fin distance less than pelvic to anal fin distance.

**Type species.** *Latellagnathus teruzzii* sp. nov., by monotypy and designation herein.

**Etymology.** Named in honour of my friend Dr. Leonardo Latella, Editor of the serial issues “Studi e Ricerche sui Giacimenti Terziari di Bolca” (*Latella*, plus ending of the generic name *Rhamphognathus*).

*Latellagnathus teruzzii* sp. nov.

Figures 4-6

_Esox sphyraena_ L. (part.): Volta, 1796: 107, pl. 24, fig. 3 (*nec* figs. 1, 2).
_Esox saurus_ Walbaum: Volta, 1796: 206, pl. 50, fig. 2.
_Ammodytes tobianus_ L.: Volta, 1796: 220, pl. 53, fig. 3.
“_Ammodytes tobianus_”: Blainville, 1818: 360.
*Rhamphognathus paralepoides* (part.): Agassiz, 1835: 292 (nom. nud.); 1833-1844b: 104, pl. 38, fig. 2 (as *R. pompilius*; *nec* fig. 1); de Zigno, 1874: 135; Bassani, 1876: 186; 1898: 81, pl. 9, fig. 3 (?); Woodward, 1901: 361.

**Diagnosis.** As for the genus.

**Holotype.** MCSNM V6060a/b, part and counterpart, complete skeleton, 205 mm SL; lower part of the Middle Eocene, Lutetian, zone *Discoaster sublodoensis*; Monte Bolca locality, Pesciara cave site.

**Paratype.** MNHN Bol 3 (10854), single plate, complete skeleton, 145 mm SL [syntype of *Rhamphognathus paralepoides*, figured by Volta (1796, pl. 24, fig. 3) and Agassiz (1833-1844, pl. 38, fig. 2)]; from the type locality.

**Referred specimens.** MCSNM V162, single plate, complete skeleton; MCSNM V192, single plate, complete skeleton; MCSNM V260/293, part and counterpart, complete skeleton; MCSNM V266, single plate, complete skeleton; MCSNM V272/286, part and counterpart, complete skeleton; MCSNM V284, single plate, complete skeleton; MCSNM V316, single plate, complete skeleton; MCSNV S. 195, single plate, almost complete skeleton; all from the type locality.
**ETYMOLOGY.** Named in honour of my friend Dr. Giorgio Teruzzi, paleontologist at the MCSNM, in recognition of his constant assistance with the examination of the specimens in his care.

**DESCRIPTION.** The body is elongate, with a relatively long caudal peduncle. The body depth is contained 6-8 times in SL. The caudal peduncle depth is 0.41 to 0.47 of the body depth. The head is large; its length 2.1-2.7 times exceeds the body depth. The head length is contained 2.7-2.9 times in SL.

- Head. The head is elongate; its dorsal profile is less convex than the ventral profile. The orbit is relatively small and placed close to the dorsal profile of the head. The snout length forms not less than half of the head length. The postorbital distance significantly exceeds the orbit diameter. The mouth is large. The lower jaw articulation is situated under the posterior margin of the orbit. No infraorbital bones are recognizable. The neurocranium is low; the ethmoid region is long. The supraoccipital crest is not evident. The parasphenoid is straight; it is exposed in the lower part of the orbit. The upper jaw strongly protrudes in relation to the lower jaw. The premaxillary ascending process is evidently poorly developed (if present at all). The premaxilla is ornamented by shallow longitudinal grooves. The premaxilla bears a marginal series of minute teeth and strong conical teeth lingually to this series. The lower jaw is rather shallow. There is no ventral projection near the mandibular symphysis. The mandibular dentition is the same as that of the premaxilla. The hyomandibular shaft is very slightly inclined. The quadrate appears

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Figure 4 - *Latellagnathus teruzzii* gen. et sp. nov. **A** - holotype MCSNM V6060b; **B** – paratype MNHN Bol 3 (10854), specimen wet with alcohol to improve contrast (×0.85); Middle Eocene (Lutetian), Monte Bolca locality in northern Italy, Pesciara. Scale bar = 1 cm.
to be triangular. None of the pterygoid bones is well-enough preserved to be described. The opercular bones have even margins. The preopercle is slightly concave anteriorly, its greatest width is along the lower margin. The opercle is a relatively wide flat bone. Neither the hyoid arch nor the branchial bones are recognizable except for faint remains of a few branchiostegals.

- Axial skeleton. There are 39 to 40 vertebrae, 19 of which are caudal. The vertebral centra are almost rectangular in lateral view. The length of the abdominal portion of the vertebral column is 1.2 times greater than the length of the caudal portion of the vertebral column. The vertebral spines are short and almost straight; most of them are slender. The spines of several preural vertebrae are stouter than those of preceding vertebrae. The neural spines of about five anterior vertebrae are expanded antero-posteriorly. The neural spines arise from the posterior half of the centra, whereas the anterior haemal spines arise from the anterior half of the centra. The haemal spines of two anterior caudal vertebrae are curved. Parapophyses are evident in about the last six abdominal vertebrae (in more anterior vertebrae the parapophyses are perhaps directed transversely and thus cannot be recognized in laterally compressed fossils). The pleural ribs are relatively short and slender; these are inclined posteriorly and decrease in length caudad. Some slender epineurals are recognizable below the centra of the abdominal vertebrae; most of the epineurals are probably obscured by the centra.

- Pectoral fin and girdle. Faint remains of the elongate posttemporal and the supracleithrum are sometimes recognizable. The cleithrum is relatively large and elongate; its posterodorsal part is curved. The ventral postcleithrum is relatively short and rib-like. The coracoid and scapula are rather poorly preserved, but a large scapular foramen is recognizable in the holotype. The moderately large pectoral fin is rather narrow at its base and has about 10 rays; the first ray is simple. The base of the pectoral fin is situated under the fourth to sixth vertebra relatively low on the flank.

- Pelvic fin and girdle. The pelvic bones are relatively large; each consists of a wedge-shaped main body and a strong postero-medial process for the articulation with its opposite member. The pelvic fin contains six soft rays. The outer pelvic-fin ray is simple, whereas the others are branched. The pelvic fin is moderately long; it is inserted at the length of about two vertebrae anterior to the origin of the first dorsal fin.

- Dorsal fins. No supraneurals are present in front of the first dorsal fin. The first dorsal fin is small. There are six slender and flexible dorsal-fin spines. The second or third spine is longest; the third to sixth spines decrease in length posteriorly in the series. The dorsal-fin spines are serially associated with the pterygiophores. The first dorsal-fin pterygiophore is expanded and lamellar rostrad. The other pterygiophores of the dorsal fin are short and narrow, closely adjoining one another. There is a continuous series of eight or nine pterygiophore-like interdorsal bones between the dorsal fins. The interdorsal bones are narrow, longer posteriorly and shorter anteriorly; adjacent interdorsal bones are close together along the dorsal profile of the body, but do not adjoin one another.

The second dorsal fin originates approximately over the sixth caudal vertebra; it consists of a short spine and eight soft rays. The spine is serially associated with the first pterygiophore. The first soft ray is unbranched, whereas the other rays are branched. The height of the second dorsal fin exceeds the length of its base. The rays of the second dorsal fin rapidly decrease in length posteriorly in the series. The pterygiophores of the second dorsal fin are narrow, closely adjoining one another, and decrease in length posteriorly in
- Anal fin. The anal fin originates opposite the origin of the second dorsal fin or slightly anterior to it. There are a short spine and nine soft rays in the anal fin. The anal-fin spine is supernumerary. The anal fin is similar to the second dorsal fin in shape and size. The first anal-fin pterygiophore is longest and slightly expanded distally. The succeeding pterygiophores are narrow and decrease in length posteriorly in the series. Most of pterygiophores are trisegmental. There is a remnant of a rayless pterygiophore behind the last pterygiophore which bears last soft anal-fin ray.
Caudal fin and skeleton. The terminal centrum is composed of the fusion of PU1, U1 and U2. The third and fourth (and probably fifth) hypurals and parhypural are autogenous, whereas the first and second hypurals are fused (Fig. 5). The haemal spines of PU2 and PU3 seem to be fused with their centra. There is a narrow hypural diastema between the epaxial and hypaxial hypurals. The neural spine of PU2 is evidently absent. Two slender epurals are recognizable; the first is longer than the second and bears a longitudinal groove. A uroneural seems to be fused with the urostyle. The caudal fin is moderate and forked; its lower lobe is longer than the upper lobe. There are 17 principal rays in the caudal fin (18-7,1), ten or eleven procurrent rays above and seven to nine rays below. The procurrent rays are not spiny.

Squamation. Moderately small cycloid scales cover the entire body; there are not less than 75-80 transverse rows of scales. Each scale bears concentric striae; numerous (up to 10) radial basal grooves are recognizable on some scales. The lateral line is absent.

Measurements. The largest complete specimen examined (holotype) is 205 mm SL. Measurements of the holotype and paratype (in parentheses) in percent of SL are as follows:

- Head length from tip of snout to posterior border of opercle: 35 (35)
- Maximum body depth: 13 (17)
- Depth of caudal peduncle: 6 (7)
- Distance between tip of snout and first dorsal fin: 58 (57)
- Distance between tip of snout and second dorsal fin: 78 (77)
- Distance between tip of snout and anal fin: 77 (77)
- Distance between tip of snout and pelvic fin: 55 (56)
- Distance between pelvic fin and anal fin: 22 (22)
- Distance between pectoral fin and pelvic fin: 15 (18)
- Length of longest ray of caudal fin: ? (19)

Remarks. According to its description and figure, the fish described by Bassani (1898: 81, pl. 9, fig. 3) as *Rhamphognathus paralepoides* Agassiz could be different from *Latellagnathus teruzzii* sp. nov. Only direct examination of the material of Bassani (1898) will clarify its systematic position.

Genus *Mesogaster* Agassiz, 1844

*Mesogaster*: Agassiz, 1833-1844b: 9, 105; de Zigno, 1874: 32.
Diagnosis. Body depth is 6-7 times in SL; head length 3.6-3.7 times in SL; snout length 0.3-0.38 of head length; upper jaw slightly protrudes; jaw teeth multiserial, small and conical, those near premaxillary symphysis slightly larger; 40-41 vertebrae; third and fourth hypurals fused; distance between dorsal fins either exceeds or does not exceed distance between second dorsal and caudal fin; 7 to 8 interdorsal bones between dorsal fins; 5 to 7 spines in first dorsal fin; a spine and 9 soft rays in second dorsal fin; a spine and 9-11 soft rays in anal fin; second dorsal fin originates evidently behind anal-fin origin; pectoral fins rather short; 6-rayed pelvic fins situated evidently anterior to first dorsal-fin origin; pectoral to pelvic fin distance less than pelvic to anal fin distance.

Type species. *Mesogaster sphyraenoides* Agassiz, 1844, by monotypy.

*Mesogaster sphyraenoides* Agassiz, 1844

Figures 7-9

*Sylurus bagre* L.: Volta, 1796: 70, pl. 14, fig. 3.

“*Silurus bagre*”: Blainville, 1818: 343.

*Mesogaster sphyraenoides*: Agassiz, 1835: 292 (nom. nud.); 1833-1844b: 105, pl. 38, fig. 3; de Zigno, 1874: 136; Bassani, 1876: 187.


Diagnosis. As for the genus.

Lectotype. Specimen illustrated by Agassiz (1833-1844, pl. 38, fig. 3) as housed in MNHN (modern location of specimen unknown); lower part of the Middle Eocene, Lutetian, zone *Discaster sublodoensis*; Monte Bolca locality, Pesciara cave site.

Referred specimens, MNHN Bol 1/Bol 2 (10852/10853), part and counterpart, complete skeleton; MCSNM V73, single plate, complete skeleton; MCSNM V77, single plate, complete skeleton; MCSNM V96, single plate, complete skeleton; MCSNM V119, single plate, complete skeleton; MCSNM V268, single plate, complete skeleton; MCSNM V275, single plate, complete skeleton; MCSNM V276, single plate, complete skeleton; MCSNM V277, single plate, complete skeleton; MCSNM V291, single plate, complete skeleton; MCSNM V292, single plate, complete skeleton; MCSNM V295, single plate, complete skeleton; MCSNM VII.C.27/VII.C.28, part and counterpart, complete skeleton; MCSNM VII.C.29/VII.C.30, part and counterpart, complete skeleton; MCSNM VII.C.32, single plate, complete skeleton; MCSNM B.2, single plate, complete skeleton; MCSNV IG145070, single plate, complete skeleton; MFB IG145075, single plate, skeleton incomplete posteriorly; IGUP 8826, single plate, complete skeleton; IGUP uncatalogued, single plate, complete skeleton; all from the type locality.

Description. The body is elongate, with a relatively long caudal peduncle. The body depth is contained 6-7 times in SL. The caudal peduncle depth is 0.42 to 0.54 of the body depth. The head is relatively small; its length 1.7-2.0 times exceeds the body depth. The head length is contained 3.6-3.7 times in SL.

- Head. The head is conical, with approximately equally convex dorsal and ventral profiles. The orbit is moderate and placed close to the dorsal profile of the head. The snout length is 0.3-0.38 of the head length. The postorbital distance exceeds the orbit diameter. The mouth is moderate. The lower jaw articulation is situated under the anterior portion...
of the orbit. No infraorbital bones are recognizable. The neurocranium is low; the ethmoid region is moderately long. The frontals are relatively wide; their width above the orbit is only slightly less than the post-orbital width. The supraoccipital crest is not evident. The parasphenoid is slender and almost straight; it is exposed in the lower part of the orbit. The upper jaw usually slightly protrudes in relation to the lower jaw. The premaxillary ascending process is low and consolidated with the articular process. The premaxilla bears multiserial, small and conical teeth; those near the premaxillary symphysis are slightly larger. The maxilla is a narrow and almost straight bone with a relatively small head. The lower jaw is moderately shallow, without a distinct ventral projection near the mandibular symphysis. The mandibular dentition is similar to that of the premaxilla. The hyomandibular shaft is very slightly inclined. The quadrate appears to be elongate and subtriangular. None of the pterygoid bones is well-enough preserved to be described. The opercular bones have even margins. The preopercle is relatively strongly curved, with almost equally long upper

Figure 7 - *Mesogaster sphyraenoides* Agassiz, 1844: A - MCSNM V295; B – MCSNV IG 145070; C - MNHN Bol 2 (10853), specimen wet with alcohol to improve contrast (×1.3); Middle Eocene (Lutetian), Monte Bolca locality in northern Italy, Pesciara. Scale bar = 1 cm.
and lower branches. The opercle is a relatively wide flat bone. Neither the hyoid arch nor the branchial bones are clearly recognizable. The branchiostegal rays are definitely not numerous, although it is difficult to determine their exact number.

- Axial skeleton. There are 40 to 41 vertebrae, 22 of which are caudal. The vertebral centra are almost rectangular in lateral view. The length of the abdominal portion of the vertebral column is less than the length of the caudal portion of the vertebral column. The vertebral spines are short and usually almost straight; most of them are slender. The spines of several preural vertebrae are stouter than those of the preceding vertebrae. The neural spines of about five anterior vertebrae are expanded antero-posteriorly. The neural spines arise from the posterior half of the centra, whereas the anterior haemal spines arise from the anterior half of the centra. The haemal spines of two anterior caudal vertebrae usually precede the first anal-fin pterygiophore. Parapophyses are evident in the vertebrae of the posterior half of the abdominal section of the vertebral column (in more anterior vertebrae the parapophyses are perhaps directed transversely and thus cannot be recognized in laterally compressed fossils; there are indications of the presence of these anterior parapophyses in MCSNV VII.C.27/VII.C.28 and MCSNV VII.C.32). The pleural ribs are relatively short and slender; these are inclined posteriorly and decrease in length posteriorly in the series. Slender epineurals are seldom recognizable below the centra of the abdominal vertebrae; in most cases the epineurals are obscured by the centra.

  - Pectoral fin and girdle. Faint remains of the elongate posttemporal are sometimes recognizable. The cleithrum is relatively large and elongate; its posterodorsal part is curved. The ventral postcleithrum is relatively short and rib-like. The coracoid and scapula are rather poorly preserved, but a large scapular foramen is recognizable in some specimens. The relatively small pectoral fin is moderately narrow at the base and has about 12 rays; the first ray is simple. The base of the pectoral fin is situated under the fourth to fifth vertebra relatively low on the flank.

  - Pelvic fin and girdle. The pelvic bones are moderately large; each consists of a wedge-shaped main body and strong postero-medial process for the articulation with its opposite member. The pelvic fin contains six soft rays. The outer pelvic-fin ray is simple, whereas the others are branched. The pelvic fin is rather short; usually it is inserted at the length of about three vertebrae anterior to the origin of the first dorsal fin.

  - Dorsal fins. No supraneurals are present anterior to the first dorsal fin. The first dorsal fin is small. Usually there are six to seven slender and flexible dorsal-fin spines (MCSNV 145070 has only five spines). The second spine is longest, and the succeeding spines decrease in length posteriorly in the series. The first dorsal-fin spine is supernumerary (except in MCSNV 145070). The first dorsal-fin pterygiophore is expanded and lamellar rostrad. The other pterygiophores of the dorsal fin are short and narrow, closely adjoining one another. There is a continuous series of seven or eight pterygiophore-like interdorsal bones between the dorsal fins. The interdorsal bones are narrow, longer posteriorly and shorter anteriorly; adjacent interdorsal bones are close together along the dorsal profile of the body, but do not adjoin one another.

  The second dorsal fin originates over the seventh to ninth caudal vertebra; it consists of a short spine and nine soft rays. The spine is supernumerary on the first pterygiophore. The first soft ray is unbranched, whereas the other rays are branched. The height of the second dorsal fin exceeds the length of its base. The rays of the second dorsal fin rapidly decrease in length posteriorly in the series. The pterygiophores of the second dorsal fin are narrow, closely adjoin one another, and decrease in length posteriorly in the series.
The medial part of at least the posterior pterygiophores is not fused with the proximal part. There is a rayless pterygiophore behind the last pterygiophore which bears last soft dorsal-fin ray.

- Anal fin. The anal fin originates at the length of two to three vertebrae anterior to the origin of the second dorsal fin. There are a short spine and nine to eleven soft rays in the anal fin. The anal-fin spine is supernumerary. The anal fin is similar to the second dorsal fin in shape and size. The first anal-fin pterygiophore is longest and expanded distally. The succeeding pterygiophores are narrow and decrease in length posteriorly in the series. Most of pterygiophores are trisegmental. There is a rayless pterygiophore behind the last pterygiophore which bears the last soft anal-fin ray.

- Caudal fin and skeleton. The terminal centrum is composed of the fusion of PU1, U1 and U2. Hypurals 1-2 and 3-4 are fused into two plates, whereas the fifth hypural and parhypural are autogenous (Fig. 8). The haemal spines of PU2 and PU3 seem to be fused with their centra. There is a narrow hypural diastema between the epaxial and hypaxial hypurals. The neural spine of PU2 is evidently a short crest. There are two slender epurals; the first is much longer than the second. A uroneural seems to be fused with the urostyle. The caudal fin is large and forked; its lower lobe is longer than upper lobe. There are 17 principal rays in the caudal fin (I,8-7,1), about ten procurent rays above and about eight rays below. The procurent rays are not spiny.
- Squamation. Moderately small cycloid scales cover the entire body. Each scale bears concentric striations; radial basal grooves occasionally can be recognizable on some scales (e.g., in the caudal peduncle of MCSNM VII.C.27/VII.C.28). The lateral line is absent.
- Measurements. The largest complete specimen examined (MCSNM V295) is 131 mm SL. The following measurements taken from five specimens (MCSNM V295, MCSNM V119, MCSNV VII.C.32, MCSNV IG145070 and MNHN Bol 2) of 79-131 mm SL are presented as percent of SL:
  - Head length from tip of snout to posterior border of opercle: 27-28
  - Maximum body depth: 14-17
  - Depth of caudal peduncle: 6-8
  - Distance between tip of snout and first dorsal fin: 51-53
  - Distance between tip of snout and second dorsal fin: 72-76
  - Distance between tip of snout and anal fin: 68-70
  - Distance between tip of snout and pelvic fin: 46-48
  - Distance between pelvic fin and anal fin: 22-23
  - Distance between pectoral fin and pelvic fin: 12-14.5
  - Length of longest ray of caudal fin: 25-27

DISCUSSION

The Atherinomorpha, a group of eurypterigian teleost fishes, was first recognized and classified by Rosen (1964) as the order Atheriniformes. Superordinal rank was first attached to the atherinomorphs by Greenwood et al. (1966). Rosen and Parenti (1981) proposed 10 characters to support the monophyly of the Atherinomorpha. None of these can be determined in either the Rhamphognathidae fam. nov. or Mesogasteridae fam. nov. because some of them are unknown (characters of egg, embryo, spermatogonium formation), whereas others are not recognizable in fossils (characters of ethmoid ossification, infraorbital bones, rostral cartilage, upper-jaw protrusile mechanism, nasal capsule and dorsal gill arch skeleton). Stiassny (1990) and Parenti (1993) treated the absence of supraneural bones as an atherinomorph autapomorphy. Parenti (1993:183) also drew attention that in atherinomorphs “...a distinct rectangular plate extends anterior and posterior to the neural arches of each of the first or second through fifth or higher vertebrae”. Both of these two mentioned characters definitely are present in the Rhamphognathidae fam. nov. and Mesogasteridae fam. nov. Moreover, the combination of a number of characters clearly indicates the relationship of the two fossil families with the order Atheriniformes, as it is defined by Nelson (1994, 2006).

Figure 9 - Mesogaster sphyraenoides Agassiz, 1844, reconstruction of the skeleton based mostly on MCSNM V295, with some details from other specimens; scales omitted.
These characters are as follows: numerous vertebrae (39-56); abdominal position of pelvic fins; two dorsal fins, the first with flexible spines; the anal fin preceded by a spine; small number of branchiostegal rays; cycloid scales; absence of lateral line.

Among the 10 characters proposed by Dyer and Chernoff (1996) to support the monophyly of the Atheriniformes most are either non-applicable for fossils (larval and myological characters) or not recognizable in the Rhamphognathidae fam. nov. and Mesogasteridae fam. nov. (curvature of the vomer ventral face, number of the anterior infraorbitals, presence of the pelvis-rib ligamentous connection and the lateral band), whereas three characters definitely are present in the new families. These are characters 58, 66 and 74 of Dyer and Chernoff (1996): i.e., the pelvic medial plate short anteriorly, a single flexible spine in the second dorsal fin, and the body depth less than 20% of SL. Thus, we believe that the attribution of the Rhamphognathidae fam. nov. and Mesogasteridae fam. nov. to the order Atheriniformes is well justified.

The new families lack obvious synapomorphies of the extant atheriniform families sensu Dyer and Chernoff (1996), Dyer (1998) and Nelson (2006), such as: three to ten ribs posterior to the anal-fin origin for the Atherinopsidae, a single epural and long dorsolateral spur of the pelvic bone for the Notocherididae (Isonidae), a relatively deep body, three or more ribs posterior to the first anal pterygiophore and absence of a flexible spine in the second dorsal fin for the Melanotaeniidae sensu lato (sensu Dyer and Chernoff, 1996), small-sized adults and modified or absent pelvic fins for the Phallostethidae, spinules in rows on the head and denticles covering outer surfaces of the premaxilla and dentary for the Atherionidae, and a ventral pelvic spine for the Atherinidae sensu stricto (Dyer and Chernoff, 1996). Parenti (1993) interpreted the relatively weakly divided dorsal fins of Bedotia (Bedotiidae, or Melanotaeniidae sensu Dyer and Chernoff, 1996) as reduced from a single spinous dorsal fin by loss of two fin rays. One can assume that equally weakly divided dorsal fins would be expected in most ancient atheriniforms (the first otolith-based fossil record of atheriniforms is dated as the Ypresian: Patterson, 1993). However, the early Lutetian Rhamphognathidae fam. nov. and Mesogasteridae fam. nov. have as equally widely divided dorsal fins as in most of the extant atheriniforms or even wider, with 7 to 13 interdorsal bones between the dorsal fins.

The Rhamphognathidae fam. nov. differs greatly from all of the other known atheriniform families in its snout, which forms a long and tapered rostrum, in parallel to the Belonidae, which family belongs to the Beloniformes (second order of the Atherinomorpha). The other autapomorphies of the Rhamphognathidae fam. nov. are as follows: the abdominal vertebrae with strong transverse processes; numerous (about 20) anterior most neural spines strongly expanded antero-posteriorly; the first dorsal-fin pterygiophore forming a long and slender rod; the posteriormost pterygiophore of both the second dorsal and anal fins bearing a long caudally directed spur (fig. 2A). The Mesogasteridae fam. nov. is much more generalized that the Rhamphognathidae fam. nov. Only a few anterior most abdominal vertebrae of Latellagnathus teruzzii gen. et sp. nov. and Mesogaster sphyraenoides have antero-posteriorly expanded neural spines, while the other neural spines are slender. The first dorsal-fin pterygiophore of these fishes is expanded anteriorly in a similar way to that of Bedotia (Parenti, 1993: fig. 8B) rather than forming a long and slender rod as in Rhamphognatus. The posterior pterygiophore of both the second dorsal and anal fins of the Mesogasteridae fam. nov. does not bear a long spur, but, rather, a rayless pterygiophore is present behind the last pterygiophore which bears the last soft dorsal- or anal-fin ray.
Latellagnathus gen. nov. and Mesogaster Agassiz, 1844 have a rather similar postcranial skeleton but differ greatly from each other in their cranial skeleton and dentition. Mesogaster has a relatively small head, moderately wide mouth and moderately long snout, whereas the head of Latellagnathus gen. nov. is proportionally larger than in any of the other atheriniforms except for Rhamphognatus, the mouth is wide and the snout is long. The premaxilla of Latellagnathus gen. nov. strongly protrudes anteriorly and its ascending process is not evident, whereas in Mesogaster the premaxilla only slightly protrudes and its ascending process is developed, although short. Latellagnathus teruzzii gen. et sp. nov. has a marginal series of minute teeth in the jaws and strong conical teeth lingually to this series. In contrast, the jaw teeth of Mesogaster sphyraenoides are multiserial, small and conical, and those near the symphysis are slightly larger. The caudal fin of Mesogaster sphyraenoides is proportionally larger than that of Latellagnathus teruzzii gen. et sp. nov.

Thus, atheriniform fishes were quite common in the Bolca fish fauna, being represented there by at least four species (“Atherina” macrocephala, Rhamphognatus paralepoides, Latellagnathus teruzzii gen. et sp. nov., and Mesogaster sphyraenoides) belonging to four genera and three families.

ACKNOWLEDGEMENTS

I am grateful to Dr. Alessandra Aspes, Director of the Museo Civico di Storia Naturale di Verona, for providing funding for my travel in 2006 to Verona to engage in this and other studies. I also thank Dr. Roberto Zorzin and Dr. Anna Vaccari at the MCSNV for their continuing help in facilitating my research on the fishes of Monte Bolca; Dr. Leonardo Latella for editorial processing of the manuscript; and Mrs. Bruna Burato for her aid with the literature on Bolca fishes. I am much indebted to Prof. Daniel Goujet, Muséum National d’Histoire Naturelle, Paris, whose efforts resulted in a Grant of Invited Professorship, allowing the author to visit the MNHN in 2005 to engage in this and other studies. Dr. Monette Véran helped arrange for this visit to the paleoichthyological collections of the MNHN. This work was initiated in Paris in 2004 under a NATO Life Science and Technology collaborative linkage grant (LST. CLG. 978836). Dr. Raoul Mutter, Edmonton, Canada, kindly made the photographs of the specimens in the MNHN. I thank Dr. Giorgio Teruzzi at the MCSNM for loan the specimens in his care. Dr. James C. Tyler of the Smithsonian Institution kindly revised the manuscript and improved the English, and Dr. Chiara Sorbini of the University of Pisa translated the Abstract into Italian.

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