A revision of *"Gobius" microcephalus* Ag. (Teleostei) from the early Eocene locality of Monte Bolca (Pesciara site, northern Italy)

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Abstract

A new genus, *Guus* gen. nov., is established for the poorly known species *Gobius microcephalus* Agassiz, 1839 from the Eocene (upper Ypresian) of the Pesciara site of the Monte Bolca locality, northern Italy. This species is characterized by a single dorsal fin and three supraneurals, and, therefore, it cannot be attributed to either genus *Gobius* or to the gobioids in general. *Guus* gen. nov. has significant similarities to the genus *Tortonesia* Sorbini, 1983, from the same locality, and *Guus* is attributed to the family Tortonesidae. This pharyngognath family was originally postulated as having labroid affinities, and it is placed herein as *incertae sedis* within the order Perciformes.

Key words: Teleostei, Perciformes *incertae sedis*, family Tortonesidae, *Guus microcephalus* (Agassiz, 1839), Eocene, Ypresian, Monte Bolca, Pesciara.

Riassunto

Il nuovo genere *Guus* gen. nov. è descritto per la specie, fino ad ora poco conosciuta, *Gobius microcephalus* Agassiz, 1839 dell'Eocene (Ypresiano superiore) della Pesciara di Bolca, Italia settentrionale. Questa specie è caratterizzata dalla pinna dorsale singola e dall'avere tre supraneurali, caratteri che non permettono di attribuirla né al genere *Gobius* né ai gobioidei in senso lato. *Guus* gen. nov. presenta somiglianze significative con il genere *Tortonesia* Sorbini, 1983 della stessa località ed è attribuito alla famiglia Tortonesidae. Questa famiglia di faringognati non ha necessariamente affinità con i labroidei, come originariamente suggerito e viene situata come *incertae sedis* all'interno dell'ordine Perciformes.

Parole chiave: Teleostei, Perciformes *incertae sedis*, famiglia Tortonesidae, *Guus microcephalus* (Agassiz, 1839), Eocene, Ypresiano, Bolca, Pesciara.

Introduction

The early Eocene marine fishes from Monte Bolca (northern Italy) have been known since the mid-sixteenth century for their extraordinary preservation. When Agassiz (1833-1844) published his monumental treatise on comparative palaeoichthyology, it was largely based on materials from Monte Bolca. Since that time, a huge number of papers have been devoted to the Monte Bolca fish fauna based on the thousands of specimens extracted from this locality and now disseminated in museums and research institutes around the World. The latest lists of the Monte Bolca fishes (Bannikov, 2014; Carnevale *et al.*, 2014) include 238 taxa, among which 222 taxa represent actinopterygians. Monte Bolca marks the first fossil record of many groups of fishes found on modern coral reefs (Bellwood, 1996). Some groups of Recent coral reef fishes (e.g., butterflyfishes and gobies) first appeared only in the Oligocene or later

in the Eocene; these were represented in the Bolca assemblage by their extinct ecological analogues (Bannikov, 2004a, b).

True gobioids are represented in the Bolca fish fauna only by a single specimen of a diminutive species (Bannikov and Carnevale, 2016), whereas the only previous gobioid record from there is highly questionable (Bannikov, 2014; Bannikov and Carnevale, 2016). Agassiz (1833-1844) described the doubtful goby *Gobius microcephalus* Agassiz, 1839 based on a single skeleton of the small fish from the collection of Dr. Hartmann (Goeppingen). Woodward (1901: 588) indicated the "typical" specimen of *G. microcephalus* as being in the NHMUK collection, no. 44873, whereas Blot (1980) referred MNHN 11067/11068 (Bol 422/Bol 423) as the type of the species. Eastman (1905, pl. II, fig. 3) figured the Paris specimen and stated that it is not the type

described by AGASSIZ, and that the indentation of the dorsal fin noted by AGASSIZ is actually absent. Both NHMUK 44873a/44873b and MNHN Bol 422/Bol 423, although almost equally small in size, are definitely not identical to the figure of AGASSIZ (1833-1844, pl. 34, fig. 2) and, therefore, neither of these two specimens can be regarded as the holotype of *Gobius microcephalus*. However, it seems likely that all of them belong to the same species. In addition to NHMUK 44873 and MNHN Bol 422/Bol 423, there are additional specimens from the MNHN (Bol 430/Bol 432) and NHMUK (16755) collections as well as several specimens from the MCSNV collection which can be confidently attributed to *Gobius microcephalus*. All of them have a single dorsal fin and three supraneurals, and, therefore, they cannot be attributed to either the genus *Gobius* or to the gobioids in general. The revision of "*Gobius*" *microcephalus* Ag. is the goal of the present paper.

All the fossil fish materials of "*Gobius*" *microcephalus* from Monte Bolca were collected at the Pesciara cave site rather than at the Monte Postale site. The quantitative and taphonomic analyses of the Pesciara and Monte Postale fish assemblages performed recently (MARRAMÀ *et al.*, 2016) clearly defined two distinctive palaeocommunities and two different depositional settings. Since the holotype of "*Gobius*" *microcephalus* indicated by AGASSIZ (1833-1844) as present in the collection of Dr. Hartmann (Goeppingen) was subsequently apparently lost, a neotype from the type locality is proposed herein.

MATERIAL AND METHODS

Specimens were examined using a WILD Heerbrugg stereomicroscope with an attached camera lucida drawing arm. Some details of the specimens examined were best seen when the specimens were moistened with alcohol. The specimens were prepared by needle. Measurements were taken with a dial caliper, to the nearest 0.1 mm.

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

Abbreviations are as follows: *Institutional*: MCSNM – Museo Civico di Storia Naturale di Milano, MCSNV – Museo Civico di Storia Naturale di Verona, MNHN – Muséum national d'Histoire naturelle, Paris, NHMUK – Natural History Museum, London; *Anatomical*: HL – head length; PU – preural vertebra; SL – standard length; U – ural vertebra.

SYSTEMATIC PALAEONTOLOGY

Subdivision TELEOSTEI *sensu* PATTERSON and ROSEN, 1977
Order PERCIFORMES *sensu* JOHNSON and PATTERSON, 1993
Family TORTONESIDAE SORBINI, BOSCAINI et BANNIKOV, 1991
Tortonesidae: SORBINI *et al.*: 116.

Emended diagnosis
Moderately elongate fishes with relatively long caudal peduncle; relatively small head; jaws with moderately small conical teeth; preopercle smooth; about six branchiostegal rays; lower pharyngeal ankylosed; vertebral column containing 25 to 26 (11 to 12 + 14) vertebrae; hypurals not fused; haemal spine of PU2 autogenous; dorsal fin continuous, with five slender spines and up to 14 rays; short-based anal fin with one or two spines and up to 9 rays; four anterior anal-fin pterygiophores inserted anterior to first haemal spine; pelvic fins below or behind pectorals; caudal fin rounded, with 15 (8+7) principal rays, uppermost branched ray filamentous or not; caudal fin moderate or long; body covered with large ctenoid scales.

Type genus
Tortonesia SORBINI, 1983, late Ypresian of Italy.

Composition
Type genus and *Guus* gen. nov., late Ypresian of Italy.

Genus *Guus* gen. nov.

Diagnosis
Tortonesid of relatively small size; vertebral column with 25 (11 + 14) vertebrae; dorsal fin continuous, with 14 (rarely 13 or 15) soft rays; anal fin with one spine and 9 (rarely 8) rays; caudal fin moderate and only slightly convex posteriorly, with uppermost branched ray not filamentous.
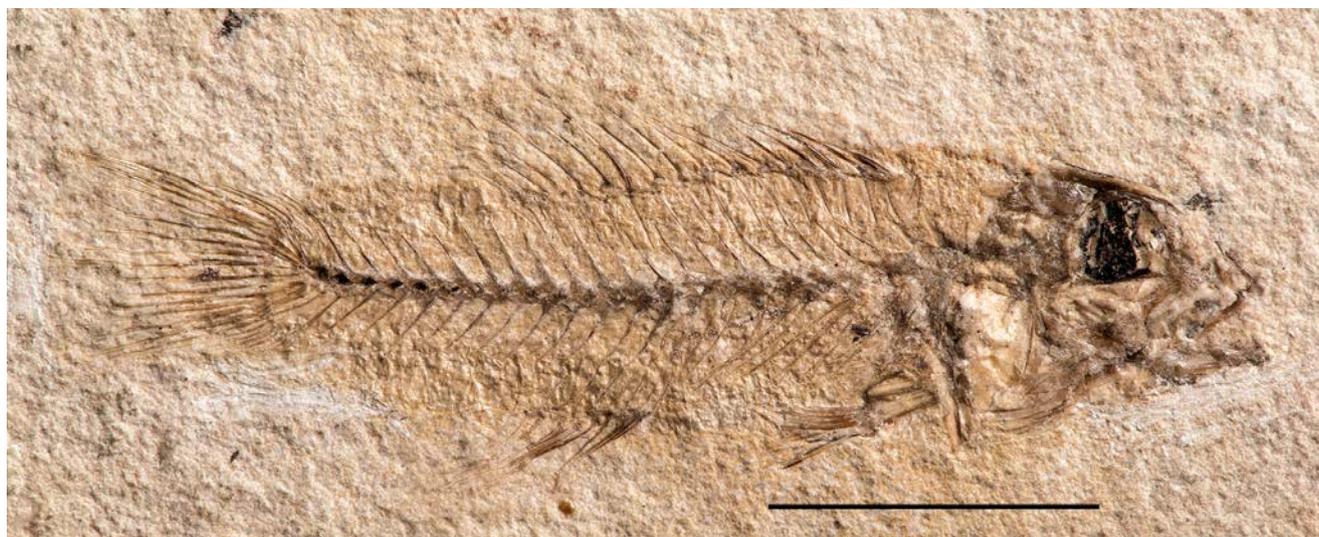
Fig. 1 – *Guus microcephalus* (AGASSIZ, 1839), neotype MCSNV T1044, general view; Lower Eocene of Bolca in northern Italy, Pesciara. Scale bar: 10 mm

Type species
Gobius microcephalus AGASSIZ, 1839, by monotypy and designation herein.

Etymology
Generic epithet is composed by arbitrary combination of letters; gender masculine.

Composition
Type species only.

Guus microcephalus (AGASSIZ, 1839)
Figures 1–6
Gobius microcephalus AGASSIZ: AGASSIZ, 1833-1844: 204, pl. XXXIV, fig. 2; DE ZIGNO, 1874: 104; WOODWARD, 1901: 588; EASTMAN, 1905, Pl. II, fig. 3.
Tortonesia esilis SORBINI: SORBINI *et al.*, 1991, Pl. III, fig. 2.

Diagnosis
As for the genus.

Neotype
MCSNV T1044, single plate, complete skeleton, 30.5 mm SL, laterally compressed (Fig. 1).

Referred specimens
MNHN Bol 422/Bol 423, part and counterpart, 27.5 mm SL; MNHN Bol 430/Bol 432, part and counterpart, 21.5 mm SL; NHMUK 44873a/44873b, part and counterpart, 37 mm SL (Fig. 2); NHMUK 16755, single plate, 42.5 mm SL; MCSNV T255/T256, part and counterpart, 25 mm SL; MCSNV T241/T242, part and counterpart, 22.5 mm SL; MCSNV S192/S193, part and counterpart, 33.5 mm SL; MCSNV T1043, single plate, 32 mm SL; MCSNV T61, single plate, lacking head; MCSNV 449, single plate, 23 mm SL (Fig. 3A); MCSNV 450, single plate, head disarticulated (Fig. 3B); MCSNM V349, single plate, 26.5 mm SL (erroneously identified as *Tortonesia esilis* by SORBINI *et al.*, 1991).

Type locality and horizon
Monte Bolca locality, Pesciara cave site; Early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina dainelli* Zone (see PAPAZZONI and Trevisani, 2006).

Description
The body is relatively elongate, with a moderately deep and rather long caudal peduncle. The caudal peduncle depth is 0.45–0.5 of the body depth. The maximum body depth is at the origin of the dorsal fin. The head is moderately large; its length exceeds the body depth. The head length is contained 3.2–3.6 times in SL. The dorsal and ventral profiles of the body are almost equally convex.

Head. The head is relatively deep, with its depth only slightly less than its length. The orbit is relatively big and situated in the upper portion of the head. The orbits usually are marked by extensive dark pigment; there are sclerotic ossifications in the
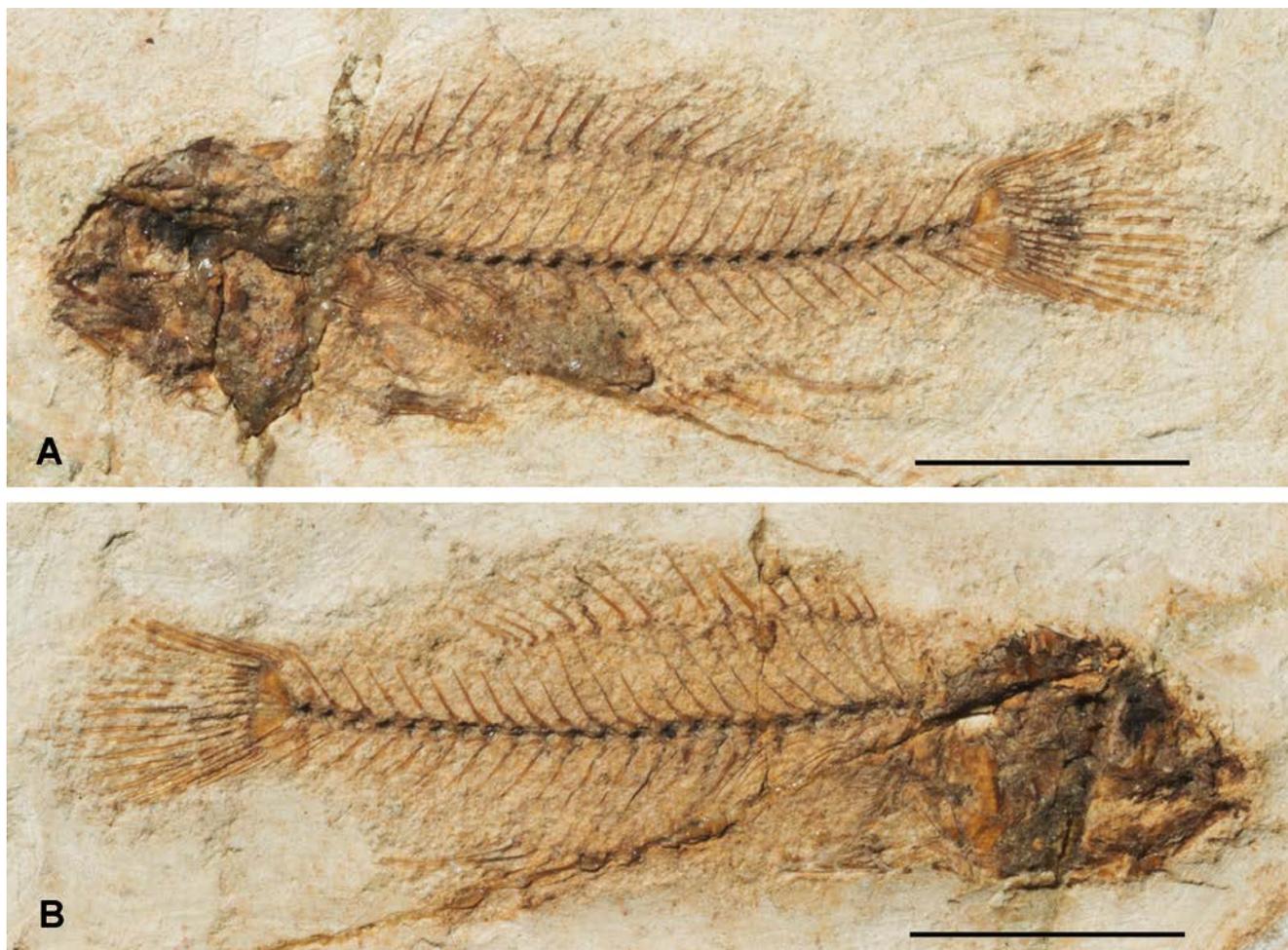
Fig. 2 – *Guus microcephalus* (AGASSIZ, 1839), referred specimen, part and counterpart; Lower Eocene of Bolca in northern Italy, Pesciara: **A** – NHMUK 44873a, **B** – NHMUK 44873b. Scale bar: 10 mm

orbit. The horizontal diameter of the orbit is 30–37% HL. The snout is moderately long; its length is 26–32% HL. The mouth is relatively small and terminal, somewhat oblique. The lower jaw articulation is situated under the anterior rim of the orbit or slightly behind. No infraorbital bones are recognizable. The neurocranium is moderately deep, with the supraoccipital crest relatively poorly developed. The frontals occupy most of the braincase roof above the orbit. The parasphenoid is relatively slender and almost straight. The ethmoid region is rather short. The premaxilla has a long and well-developed ascending process coalescent with the articular process. The premaxillary alveolar process appears to be longer than the ascending process. The premaxilla bears moderately large curved conical teeth, which are slightly blunt and usually marked with dark pigment apically (Fig. 4A). The maxilla is massive, elongate

and almost straight. The lower jaw is only moderately deep, and its length is 2–2.3 times shorter than HL. The dentary is V-shaped and has a deep indentation for the insertion of the angulo-articular. The symphysis of the dentaries is relatively low. The oral border of the dentary bears relatively moderately large curved and apically blunt conical teeth, which are usually marked with dark pigment distally. The angulo-articular is an elongate and tapered anteriorly; its retroarticular process is relatively long and deep. The bones of the suspensorium are only fragmentarily preserved. The shaft of the hyomandibula appears to be only slightly obliquely oriented. The quadrate is subtriangular in outline and very wide, it is thickened from the condyle along the postero-ventral margin. The ectopterygoid seems to be narrow and elongate. The opercular bones are usually not clearly recognizable. The preopercle appears to be
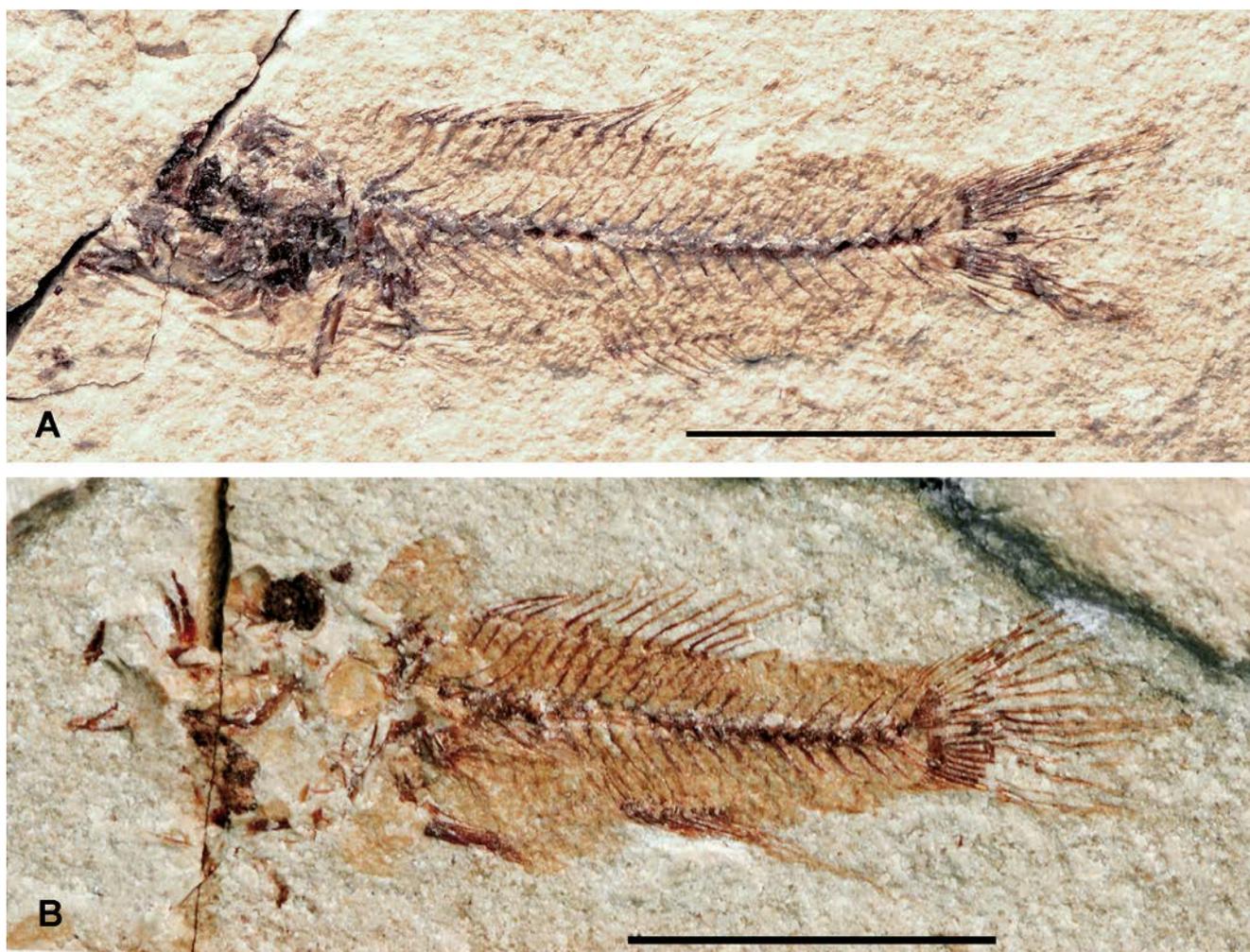
Fig. 3 – *Guus microcephalus* (Agassiz, 1839), referred specimens; Lower Eocene of Bolca in northern Italy, Pesciara: **A** – MCSNV 449, **B** – MCSNV 450. Scale bar: 10 mm

slightly curved; it is even along the posterior margin. The opercle is wide and rounded ventrally. The hyoid bar is relatively short and deep; the glossohyal is small, slender and elongate. The total complement of branchiostegal rays is difficult to calculate; about six sabre-like branchiostegals are recognizable, which become longer posteriorly in the series. The first branchiostegal ray is short and slender. Most of the branchial skeleton is badly preserved and the elements are difficult to recognize. The pharyngeal jaws are certainly hypertrophied, and the lower pharyngeal jaws (fifth ceratobranchials) are definitely fused. The lower pharyngeal jaw probably had some form of physical contact with the cleithrum, as evidenced in MCSNV S192/S193. The pharyngeal teeth are relatively large; there are both rounded molariform and blunt conical pharyngeal teeth.

Axial skeleton. There are 25 vertebrae, including the urostyle: eleven abdominal and fourteen caudal. The axis of the vertebral column is very slightly curved, being elevated anteriorly. The vertebral centra are either square or slightly longer than high in lateral view. The first two vertebrae are shorter than the succeeding vertebrae. The length of the caudal portion of the vertebral column is 1.35 to 1.5 times greater than the length of the abdominal portion of the vertebral column. The vertebral spines are relatively short, straight or slightly curved, and very slender. The neural spines of the three anterior vertebrae are somewhat broadened. The neural spine of the first vertebra is strongly reduced. The haemal spines of the anterior caudal vertebrae are slightly longer than the opposite neural spines. Zygapophyses are usually scarcely distinguishable. The parap-
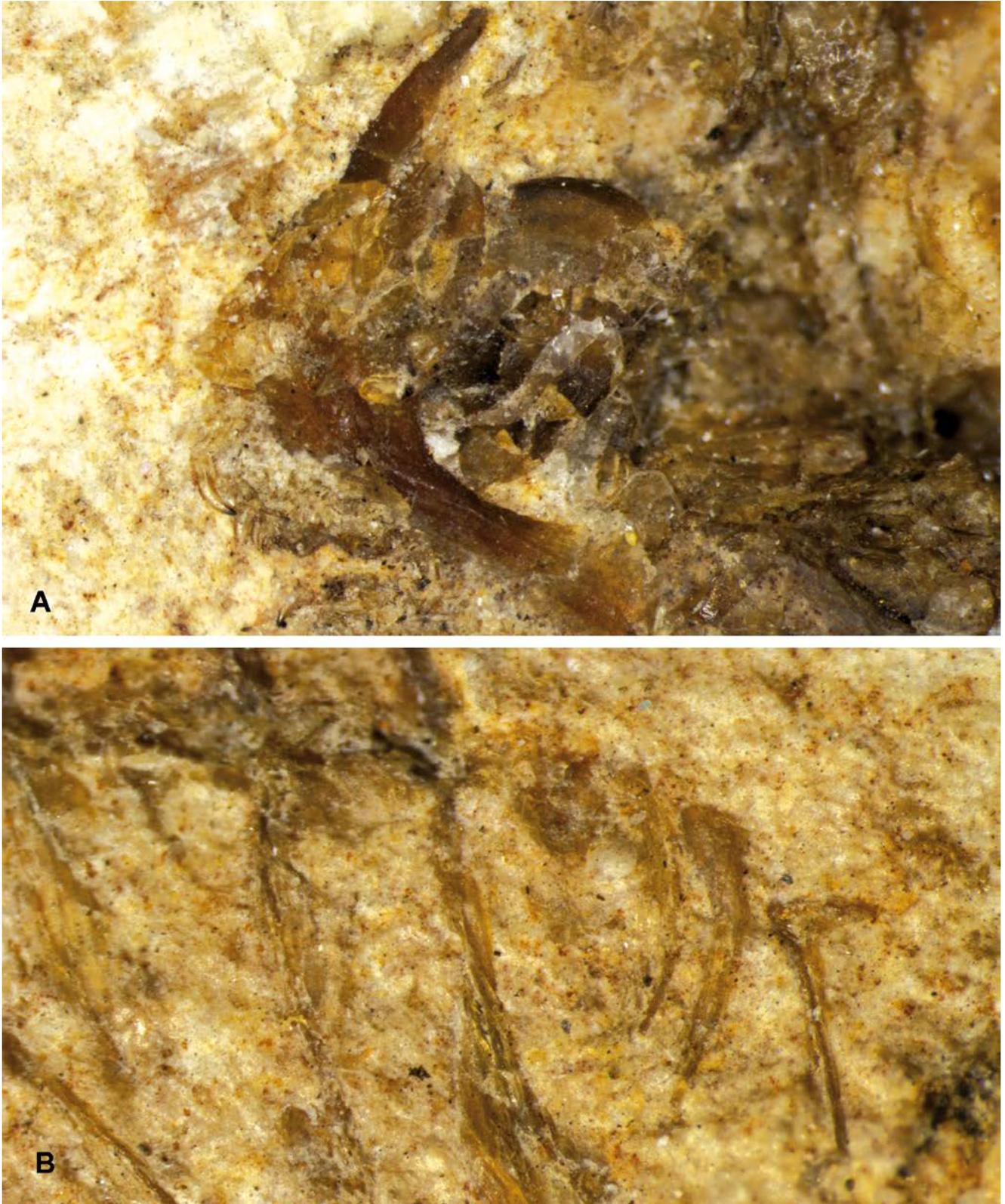
Fig. 4 – *Guus microcephalus* (Aɢᴀssɪᴢ, 1839), details of referred specimen, part and counterpart; Lower Eocene of Bolca in northern Italy, Pesciara: **A** – NHMUK 44873a, upper jaw and teeth; **B** – NHMUK 44873b, supraneurals and anterior portion of dorsal fin.

Fig. 5 – *Guus microcephalus* (AGASSIZ, 1839), referred specimen NHMUK 44873a, caudal skeleton; Lower Eocene of Bolca in northern Italy, Pesciara

ophyses are recognizable in at least the four posterior abdominal vertebrae; these increase in length posteriorly in the series. The pleural ribs are slender and relatively long; these are rather strongly inclined posteriorly, thus occupying about two-thirds of the abdominal cavity. Very few of the slender epineurals are recognizable, these being those just below the anterior portion of the vertebral column.

Pectoral fin and girdle. The pectoral girdle is usually only scarcely preserved; it is best seen in the specimen MCSNV S192/S193. The posttemporal and supracleithrum are poorly recognizable; the former has a long upper branch. The upper portion of the cleithrum is located under the first and second vertebrae. The cleithrum is strong and elongate, almost straight; its upper part is slightly curved anteriorly. The posterodorsal projection of the cleithrum above the pectoral-fin base is wide, and the lower portion of the cleithrum is expanded. The ventral postcleithrum is straight and rib-like; it extends obliquely above the pelvic-fin base. The coracoid is narrow, with interosseous space between the coracoid and cleithrum. The scapula is difficult to recognize. The four pectoral radials are hourglass-shaped; they increase in length downward. The base of the pectoral fin is situated under the fifth vertebra, closer to the vertebral column than to the ventral profile of the body. The pectoral fin seems to be rounded and moderately long; the proximal parts of at least 12 rays are observable in several specimens.

Pelvic fin and girdle. The pelvic bones are relatively narrow; they usually are preserved dorso-ventrally, and the bones are oriented in parallel to the body axis or slightly oblique to it. The pelvic fin
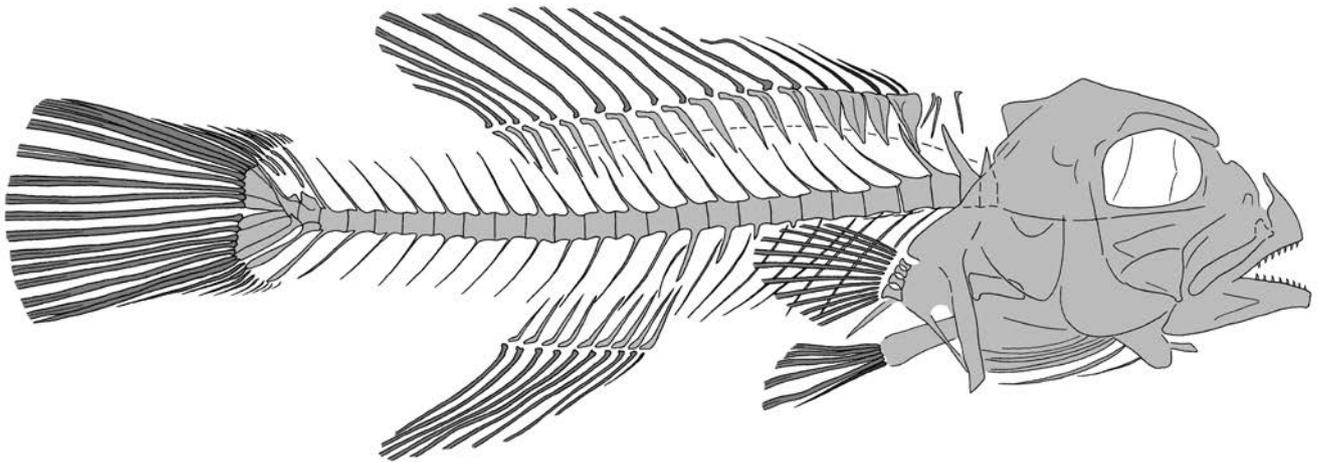
Fig. 6 – *Guus microcephalus* (Agassiz, 1839), reconstruction of the skeleton based on neotype and referred specimens, scales omitted

has a smooth spine and five soft rays. The pelvic-fin spine is as equally long as the longest dorsal-fin spine or only slightly shorter. The pelvic fin inserts at the same level as that of the pectoral fin insertion or somewhat posterior to it. The pelvic-fin rays are moderately long; these appear to be almost as equally long as the pectoral-fin rays.

Supraneurals and dorsal fin. There are three relatively small and narrow supraneurals (Fig. 4B). The first supraneural has a tapered projection directed anteriorly from the upper anterior part of the bone. The supraneurals are closely associated to each other and to the first dorsal-fin pterygiophore; depending on the preservation, the predorsal formula (see Ahlstrom *et al.*, 1976; Johnson, 1984) is either //0+0+0+2/1+1/ or /0/0+0+2/1+1/.

The dorsal fin is moderately long at the base; its extension is 0.36 to 0.4 of the body length. The dorsal fin is continuous and originates just above the fourth vertebra. The proximal shaft of the anterior pterygiophore is located before the neural spines of the third vertebra, i.e., in the second interneural space. The dorsal fin has five slender spines and 14 soft rays, supported by 17 pterygiophores. (A single referred specimen, MCSNV 450, possesses 15 soft rays. Since the skeleton is very small and disarticulated anteriorly [Fig. 3B], it remains unresolved, whether this specimen represents intraspecific variation or whether it should be attributed to a different species). The first two spines are in non-serial secondary association (supernumerary) with the first dorsal-fin pterygiophore. The first dorsal-fin spine is the shortest; succeeding spines become gradually longer, with the last spine being the longest. The longest dorsal-fin spine is 2.4 to 2.8 times shorter than the maximum body depth. The length of the spiny portion of the dorsal fin is 3.6 to 4.3 times shorter than the length of the soft portion. The soft rays are segmented and at least those of the middle region are branched. The soft rays are longer than the dorsal-fin spines, and some specimens indicate that the soft dorsal fin forms a rounded profile, with a lobe posteriorly. The pterygiophores of the spiny portion of the dorsal fin are wedge-shaped, with a longitudinal strengthening ridge laterally; each of the second to fourth pterygiophores bears a spine in supernumerary association, and the fourth pterygiophore additionally bears a serially associated first soft ray. The pterygiophores of the soft portion of the dorsal fin are much narrower than those of the spiny portion of the dorsal fin. The interneural spaces below the dorsal fin have the ventral shafts of one (usually) or two pterygiophores (3rd, 13th and 14th interneural spaces) present. The dorsal fin terminates above the sixth or seventh caudal vertebra.

Anal fin. The anal fin is short-based; it originates under the boundary between the first and second caudal vertebrae and ends approximately under the end of the dorsal fin. The anal fin consists of a spine and nine soft rays, supported by nine pterygiophores; the first anal-fin spine is supernumerary. The anal-fin spine is much shorter than the longest

dorsal-fin spine. The anal-fin rays are longer than the anal-fin spine; some specimens indicate that the anal fin forms a rounded profile, with a lobe posteriorly which seems to be longer than that of the dorsal fin. The first anal-fin pterygiophore is almost as equally strong as the succeeding pterygiophores, which gradually decrease in length posteriorly in the series. The anterior four anal-fin pterygiophores are located before the haemal spine of the first caudal vertebra. The interhaemal spaces above the anal fin have the ventral shafts of one (first interhaemal space) or two pterygiophores (2nd and 3rd interhaemal spaces) present.

Caudal fin and skeleton. The caudal skeleton is of the generalized percoid type, with the fusion of PU1, U1, and U2 in the terminal centrum (Fig. 5). [The diural terminology is used because SCHULTZE and ARRATIA (2013) have shown that the two ural centra are not homologous in different Teleostei]. The neural spine of PU2 is a relatively low crest. All five hypurals, the parhypural, and the haemal spine of PU2 are autogenous, whereas the haemal spine of PU3 seems to be fused with the centrum. The neural and haemal spines of PU3 are somewhat longer and stouter than those of the preceding vertebra. There are three epurals, of which the first is much longer than the others. There is a stegural formed by the first uroneural. The caudal fin is moderately large and slightly convex posteriorly; there are no indications of any elongation of the uppermost branched ray. There are 15 principal rays in the caudal fin (I,7+6,I); nine or ten procurrent rays above and eight or nine procurrent rays below.

Squamation. Thin large scales cover the entire body. The scales are evidently ctenoid, although the individual scales are indistinguishable. There are indications of a low scaly sheath at the base of the medial fins. The lateral line runs high on the trunk, parallel to the dorsal profile of the body; it is interrupted under the posterior portion of the dorsal fin.

Coloration. There are no indication on any pigmentation along the body.

Measurements. Measurements as percentage of SL: head length = 28–31; maximum body depth = 24–27; snout length = 8–9.5; orbit diameter = 9–11; length of the mandible = 12.5–15; caudal peduncle depth = 11.5–13.5; predorsal length = 34–39; predorsal (soft dorsal) length = 45–48.5; preanal length = 62–64; prepelvic length = 39–42; distance between pelvic and anal fins = 22–24; base length of the dorsal fin = 36–40; base length of the spinous dorsal fin = 7–8; base length of the soft dorsal fin = 27–30;

base length of the anal fin = 12–14; length of the longest (last) dorsal-fin spine = 10–11; length of the longest dorsal-fin ray: 12–21; length of the longest anal-fin ray: 13–17; length of the longest pelvic-fin ray: 10–12.5; length of the longest caudal-fin ray: 18–26.

Remarks. Relatively poor preservation makes it difficult to recognize some characters in certain specimens. In cases when the dorsal-fin spines are incomplete distally, the more posterior of them could be confused with the anterior soft rays and vice versa. In the NHMUK 44873 specimen, the anterior dorsal-fin pterygiophore appears to have only one supernumerary dorsal-fin spine, unlike all the other specimens, which have two supernumerary spines. Apparently, the anteriormost dorsal-fin spine was originally present but is not preserved in the specimen. Also, the NHMUK 44873 specimen has an unusually deeply forked haemal spine of pu3 (Fig. 5), whereas in the other specimens this spine is thickened distally but not forked. The divided haemal spine of pu3 in the NHMUK 44873 specimen should be regarded as an individual variation rather than as a systematically valuable character.

DISCUSSION

"Gobius" microcephalus AGASSIZ, 1839 has a single dorsal fin and three supraneurals, and, therefore, it cannot be attributed to either the genus *Gobius* or to the gobioids in general. However, in most of its morphological characters *"Gobius" microcephalus* strongly resembles another acanthopterygian fish from the Monte Bolca fish fauna, *Tortonesia esilis* SORBINI, 1983, which justifies the establishment of the new genus, *Guus* gen. nov., to accommodate *"Gobius" microcephalus*.

The new genus lacks the synapomorhy of *Tortonesia* SORBINI, 1983 in the caudal fin structure; the uppermost branched caudal-fin ray of *T. esilis* is extremely elongated and filamentous, while the succeeding medial rays initially are shortened and subsequently increase in length, and the middle principal rays are very long. Thus, the posterior border of the caudal fin of *T. esilis* has a characteristic sigmoid shape (SORBINI *et al.*, 1991). Unlike *Tortonesia*, the caudal fin of *Guus* gen. nov. is only moderately long and slightly convex posteriorly, with the uppermost branched ray not being filamentous. The new genus shares most of the other morphological characters with *Tortonesia*: both genera have a similar body

shape, a relatively small head, similar dentition, smooth preopercle, ankylosed lower pharyngeal, 14 caudal vertebrae, caudal skeleton of generalized percoid type but with the haemal spine of pu3 fused to the centrum, continuous dorsal fin with five slender spines and 14 rays, short-based anal fin with one or two spines and nine rays, four anterior anal-fin pterygiophores inserted anterior to the first haemal spine. Both the dorsal and anal fin of *T. esilis* form a posterior lobe (Sorbini *et al.*, 1991). Such lobes are not recognizable in many of the specimens of *Guus microcephalus*, although sometimes these are visible in both the dorsal and anal fin (e.g., MCSNV S192/S193). Perhaps these lobes are not preserved in some of the smaller specimens of *G. microcephalus* because of taphonomic reasons.

One can suppose that the peculiar shape of the caudal fin of *Tortonesia*, that differs from that of *Guus* gen. nov., can be explained by the sexual dimorphism of a single taxon (males of certain bony fishes exhibit stronger development of fins than females; e.g., Nelson, 2006). However, we regard the difference in the caudal fin structure of *Tortonesia esilis* and *Guus microcephalus* as a systematically important character at the generic level, especially because it is not the only difference between these two taxa. A diagnostic character of *Tortonesia* is the possession of two anal-fin spines (Sorbini *et al.*, 1991), whereas *Guus* gen. nov. is characterized by only one spine in the anal fin. Additionally, *Tortonesia esilis* differs from *Guus microcephalus* by having 11 to 12 abdominal vertebrae (vs. always 11 abdominal vertebrae in *G. microcephalus*) and it is in general larger in size. It should be noted that, because of poor preservation, difficulties arise in the identification of some specimens. For example, the referred specimen of *G. microcephalus* MCSNM V349 was erroneously identified as *Tortonesia esilis* by Sorbini *et al.* (1991).

The strong resemblance of *Guus* gen. nov. and *Tortonesia* documented above necessarily implies their placement in the same family. The monotypic family Tortonesidae, based on the possession of a pharyngeal jaw, was originally placed in the suborder Labroidei of the order Perciformes as related to the Pomacentridae (Sorbini *et al.*, 1991).

Labroid fishes usually were regarded as a suborder in the order Perciformes based on a single complex of functionally related characters, mostly in the pharyngeal region. The limits and composition of this group have been relatively unstable. The Labroidei *sensu stricto* includes three families: Labridae,

Scaridae, and Odacidae (Nelson, 1984) (recently the latter two groups are usually regarded as tribes within the Labridae: Bellwood *et al.*, 2019), whereas in the Labroidei *sensu lato* three more families (Cichlidae, Embiotocidae, Pomacentridae) have been added (Kaufman and Liem, 1982; Stiassny and Jensen, 1987; Nelson, 2006; Wiley and Johnson, 2010). Although long recognized and diagnosed by a series of synapomorphic features, labroid monophyly has been recently reconsidered and extensively discussed by several authors pointing out that it is exclusively supported by a single complex of functionally related characters (e.g., Johnson, 1993; Mabuchi *et al.*, 2007; Wainwright *et al.*, 2012), none of which appears to be unique to labroids. Recent molecular evidence indicates that the Pharyngognathi and Labroidei *sensu lato* are not monophyletic and that the Labroidei *s.l.* incorporates at least two distinct lineages, the Labridae which remains in the Labroidei *sensu stricto*, and the Pomacentridae and Cichlidae (Miya *et al.*, 2003; Wainwright *et al.*, 2012; Near *et al.*, 2013), which have been moved to the "Subseries Ovalentaria" (Wainwright *et al.*, 2012). However, none of the molecular phylogenies agree in detail. In the latest publications, the Labroidei is regarded as the order Labriformes (Wiley and Johnson, 2010; Nelson *et al.*, 2016).

Given the growing evidence that the Labroidei is not monophyletic, Bannikov and Carnevale (2012) proposed that the labroid affinities of *Tortonesia* should be reconsidered, along with those of *Quasicichla* and *Sorbinia*, two other taxa from the Bolca fish fauna originally referred to the basal labroids (Bellwood, 1995; Bannikov, 2004b). Indeed, except for the possession of a pharyngeal jaw, there is nothing in common between the Tortonesidae and the Labroidei *sensu lato*. The relationships of the Tortonesidae are rather problematic. Having some superficial similarity with *Sorbinia caudopunctata* Bellwood, 1995 in general appearance (similar body shape, single dorsal fin, short-based anal fin) and possession of pharyngognathy, the tortonesids differ greatly by their possession of unfused hypurals, ctenoid scales, fewer caudal vertebrae, much fewer dorsal-fin spines, more dorsal- and anal-fin rays, and four anterior anal-fin pterygiophores inserted anterior to the first haemal spine. The last character is an autapomorphy of the Tortonesidae; it is rarely found in some of the acanthopterygians definitely not related to tortonesids (e.g., a few gobioids, stromateoids and trachinoids). The basic osteological configuration apparently does not provide any convincing

evidence that would relate the Tortonesidae to any of the known extinct or extant perciform (*sensu* NELSON, 2006) families or *incertae sedis* genera. Therefore, because of the evident difficulties to unambiguously identify the sister-group relationships of the Tortonesidae, it is reasonable to place this Eocene family *incertae sedis* within the order Perciformes.

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