

On the osteology and relationships of the genus †*Callipteryx* Agassiz (Perciformes s.l.) from the Eocene of Bolca in northern Italy

ALEXANDRE F. BANNIKOV* - ROBERTO ZORZIN**

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

(***Museo Civico di Storia Naturale, Verona*)

ABSTRACT

The percomorph fish genus †*Callipteryx* Agassiz has long been known from the Pesciara site of the Eocene locality Bolca in northern Italy, but its systematics has not been revised since the publication of Woodward (1901). †*Callipteryx* has been usually placed in the suborder Trachinoidei (Perciformes s.l.). An analysis of the osteological features of †*Callipteryx* clearly indicates that it cannot be confidently assigned to any of the perciform suborders except for the inadequately defined and possibly non-monophyletic Percoidei. Agassiz (1833–1844) defined two species of †*Callipteryx*, †*C. speciosus* Ag. and †*C. recticaudus* Ag. However, some differences in size and proportions between the two species are likely not related to interspecific variability, but reflect ontogenetic, sexual or individual variations (intraspecific variability) and are partly artefact of preservation. Therefore, †*C. recticaudus* is placed herein into the synonymy of †*C. speciosus*.

Key words: Perciformes, Percoidei, †*Callipteryx* Agassiz, osteology, Eocene, northern Italy, Bolca locality, Pesciara site.

RIASSUNTO

Il pesce percomorfo del genere †*Callipteryx* Agassiz proveniente dal sito della Pesciara, località eocenica di Bolca dell'Italia settentrionale, è stato descritto molto tempo fa ma la sua sistematica non è stata rivista dopo la pubblicazione di Woodward (1901). †*Callipteryx* è stato tradizionalmente assegnato al sottordine Trachinoidei (Perciformes s.l.). Un'analisi delle caratteristiche osteologiche di †*Callipteryx* indica chiaramente che non può essere assegnato con certezza a nessuno dei sottordini di Perciformi ad eccezione dei Percoidei, un gruppo inadeguatamente definito e forse non monofiletico. Agassiz (1833–1844) definì due specie di †*Callipteryx*: †*C. speciosus* Ag. e *C. recticaudus* Ag. Tuttavia, alcune differenze nelle dimensioni e nelle proporzioni tra le due specie non sono probabilmente correlate a variabilità interspecifica, ma riflettono variazioni ontogenetiche, sessuali o individuali (variabilità intraspecifica) e sono in parte artefatti di preservazione. Pertanto, †*C. recticaudus* viene qui considerato sinonimo di †*C. speciosus*.

Parole chiave: Perciformes, Percoidei, †*Callipteryx* Agassiz, osteologia, Eocene, Italia settentrionale, località di Bolca, sito della Pesciara.

INTRODUCTION

The Early Eocene fish fauna of the famous locality Bolca, to the north of Verona in northern Italy, has been known since the mid-sixteenth century (Eastman, 1904; Sorbini, 1981; Romano and Carnevale, 2023). It is exceptionally rich in marine fishes, especially of the acanthomorphs (Bannikov, 2014;

Carnevale *et al.*, 2014; Friedman and Carnevale, 2018, etc.). Agassiz (1833–1844) in his monumental palaeoichthyological milestone, “Recherches sur les Poissons Fossiles”, which was largely based on the materials from Bolca, described in the “famille des Cottoïdes” a new genus †*Callipteryx* with two species, †*C. speciosus* Ag. and †*C. recticaudus* Ag., the latter being based on a single specimen from the

Bolca locality. †*C. speciosus* was based on the specimen housed in the Paris Museum and on the specimen figured by Volta (1796: Pl. XV) as *Gadus merluccius* (now it is exhibited in the Museo Civico di Storia Naturale di Verona). According to Agassiz, the two species are very similar, but †*C. recticaudus* is smaller, more slender, and its caudal fin is truncated rather than rounded.

Woodward (1901) re-defined the genus †*Callipteryx* in the family Trachinidae, and he regarded its rounded caudal fin among the generic diagnostic features. Thus, according to Woodward (1901: 589), †*C. recticaudus* is “a smaller and more slender species than the type”. Woodward indicated in addition to the type specimen of †*C. recticaudus* one more specimen from the British Museum of Natural History, with a crushed and imperfect head. Unfortunately, all the †*Callipteryx* specimens we know have imperfect heads; therefore, cranial osteology of this genus is not easily restorable. However, the postcranium of several specimens of †*Callipteryx* is relatively well preserved (e.g., Fig. 1C, 2).

The specimen described by Volta (1796: 193, pl. XLVIII, fig. 1) as *Ophicephalus striatus* and regarded usually as a synonym of the scombrid †*Auxides propterygius* (e.g., Woodward, 1901: 464), and presently housed in the Museum of Le Mans, is composed of the skeletons of at least two different species; most of the skeleton belongs to †*Callipteryx*, whereas its anterior portion is of *Sphyræna* (Bannikov, 2014).

Eastman (1905, 1911) followed Woodward (1901) in attribution of †*Callipteryx* to the Trachinidae and identified in the Bolca collection of the Carnegie Museum of Natural History (CMNH) two more specimens of †*C. speciosus* and three more specimens of †*C. recticaudus* (Eastman, 1911). However, the specimen CMNH 4404 figured by Eastman (1911, Pl. CI, Fig. 1) as †*C. speciosus* is actually †*Eocottus veronensis* (Volta) (see Bannikov, 2004). Our observations in the collections of the Carnegie Museum in 2015 have revealed that †*Callipteryx* species actually are absent there except for CMNH 4207, and CMNH 4313, CMNH 4403, CMNH 5244 also represent †*Eocottus veronensis*.

The special family †Callipterygidae was established for †*Callipteryx* by Jordan (1905). Blot (1980) regarded †Callipterygidae as a synonym of Trachinidae, which was not supported subsequently (Bannikov, 2014; Carnevale *et al.*, 2014). In such characters as elongated body with extended soft dorsal and anal fins, relatively short caudal peduncle and rounded

caudal fin the genus †*Callipteryx* is similar to the fishes traditionally placed to the perciform suborder Trachinoidei (Pietsch, 1989; Nelson, 2006, etc.) (or “superfamily Trachinoidea of suborder Blennioidei”: Gosline, 1968; “blennioid infraorder Trachinoidea”: Watson *et al.*, 1984). However, extant trachinoids are generally small, whereas all known †*Callipteryx* specimens are relatively large, 25 to 70 cm in body length. Moreover, †*Callipteryx* has a primitive “basal number” (Gosline, 1968) of vertebrae (24), whereas the vertebrae of trachinoids are more numerous (Watson *et al.*, 1984: Table 138). Therefore, the similarity mentioned above could be superficial and not reflect true relationships.

The order Perciformes has traditionally been considered (Berg, 1940; Greenwood *et al.*, 1966; Nelson, 2006; etc.) the most diverse order of evolutionarily advanced bony fishes, the largest of the orders not only of fishes, but vertebrates in general. Recently, however, the traditional classification of organisms is often replaced by a formal cladistic systematics, built on computer processing of molecular data and often contradicting morphological evidence. In cladistic taxonomy, the order Perciformes is divided into numerous orders, bizarrely grouped into the taxa of higher rank (e.g., Wiley and Johnson, 2010; Near *et al.*, 2013; Nelson *et al.*, 2016; Betancur-R. *et al.*, 2017; Hughes *et al.*, 2018; etc.). The order Trachiniformes *sensu* Nelson *et al.* (2016) is apparently paraphyletic (Wiley and Johnson, 2010; Betancur-R. *et al.*, 2017). The higher taxa of the cladistic hierarchy are morphologically heterogeneous, which is recognized by the cladists themselves (Miya *et al.*, 2013); usually these taxa cannot be diagnosed by morphological features. In molecular taxonomy, many percomorph families and genera do not have a fixed position and transfer from one to another clade (or to the *incertae sedis* position) in different publications. This encourages us to use traditional, natural taxonomy herein, with the order Perciformes *sensu lato*, as did Heemstra *et al.* (2022) in their recently published books.

Since the time of Woodward (1901), the genus †*Callipteryx* has not been revised. Now it is obvious that it is represented by a very small number of specimens in different international museums. The characters by which the two species of this genus were distinguished are most likely not species differences, but ontogenetic changes that are intraspecific (see Discussion below).

MATERIAL

All the †*Callipteryx* specimens available have imperfect heads. The large size of the specimens does not require the use of a stereomicroscope for their study. Measurements were taken with a ruler, to the nearest 1.0 mm.

Abbreviations are as follows: *Institutional*: CMNH – Carnegie Museum of Natural History, Pittsburg; MCSNM – Museo Civico di Storia Naturale di Milano; MCSNV – Museo Civico di Storia Naturale di Verona; MFB – Museo dei Fossili di Bolca; MGP – Museo di Geologia e Paleontologia dell'Università degli Studi di Padova; MNHN – Muséum National d'Histoire Naturelle, Paris; NHMUK – Natural History Museum, London; *Anatomical*: PU – preural vertebra; SL – standard length; U – ural vertebra.

The dagger symbol (†) indicates extinct taxa.

SYSTEMATIC DESCRIPTION

Order Perciformes sensu Nelson, 2006
Suborder Percoidei sensu Nelson, 2006 (?)
Family †Callipterygidae Jordan, 1905
Genus †Callipteryx Agassiz, 1838

†*Callipteryx*: Agassiz, 1833–1844, p. 12, 193; Woodward, 1909, p. 589.

†*Callipterix*: de Zigno, 1874, p. 21.

Diagnosis

Relatively elongate fish with a moderately short and deep caudal peduncle. Head relatively small. Maximum body depth 0.61–0.75 of head length. Supraoccipital crest low. Lower jaw articulation under middle of orbit. Jaws with multiserial small conical teeth and no fangs. Preopercular and opercular spines not evident. Branchiostegal rays 7. Vertebrae 24 (10+14); vertebral centra massive and spines short. Hypurals fused proximally to terminal centrum. Epurals 3. Haemal spine of PU3 fused to centrum. Ribs very slender and strongly inclined. No supraneurals. Dorsal fin long-based and continuous, shifted anteriorly, with 9 short spines and about 30 soft rays. First dorsal-fin spine shortest and supernumerary on first pterygiophore, which accommodates in first interneural space. Anal fin long-based, with 2 short spines (first minute) and 21 or 22 rays. First three anal-fin pterygiophores precede haemal spine of first caudal vertebra. Pelvics inserted opposite to pectoral-fin

base close to each other. Both pectoral and pelvic fins relatively short. Caudal fin truncate to rounded; composed of 17 principal rays. Scales and lateral line not evident.

Type Species

†*Callipteryx speciosus* Agassiz, 1838, by designation by Woodward (1901).

Composition

Type species from Pesciara di Bolca.

†*Callipteryx speciosus* Agassiz, 1838

Figures 1–4

Gadus merluccius: Volta, 1796, p. 72, pl. XV (error).
Trigla lyra: Volta, 1796, p. 131, pl. XXX; de Blainville, 1818, p. 345 (error).

†*Callipteryx speciosus*: Agassiz, 1833–1844, p. 12, 196, pl. XXX, fig. 1; Woodward, 1909, p. 589 (non Eastman, 1911, pl. CI, fig. 1: error); Brignon, 2019, fig. 24K.

†*Callipteryx recticaudus*: Agassiz, 1833–1844, p. 12, 198, pl. XXX, fig. 2; Woodward, 1909, p. 589; Brignon, 2019, fig. 23A.

†*Callipterix speciosus*: de Zigno, 1874, p. 75.

†*Callipterix recticaudus*: de Zigno, 1874, p. 76.

non †*Callipterys speciosus*: Frickhinger, 1991, Fig. on p. 882 (error).

Diagnosis

As for the genus.

Lectotype

MNHN 10822/10823a, part and counterpart, complete skeleton damaged by oblique fracturing of the matrix layer (Agassiz, 1833–1844, pl. XXX, fig. 1; Eastman, 1905; Blot, 1980).

Paralectotype

MCSNV T118, single plate, complete skeleton with anterior portion preserved dorsoventrally, ca. 50 cm SL (Fig. 1C).

Referred Specimens

MNHN 10815/10816 (Bol 0120/0121), part and counterpart, complete skeleton damaged by fracturing of the matrix layer, ca. 19.4 cm SL (Fig. 1A,B) (holotype of †*Callipteryx recticaudus* Agassiz, 1838); MCSNM V262, single plate, complete skeleton, ca. 22 cm SL (Fig. 2A); MGP 12901, single plate, complete

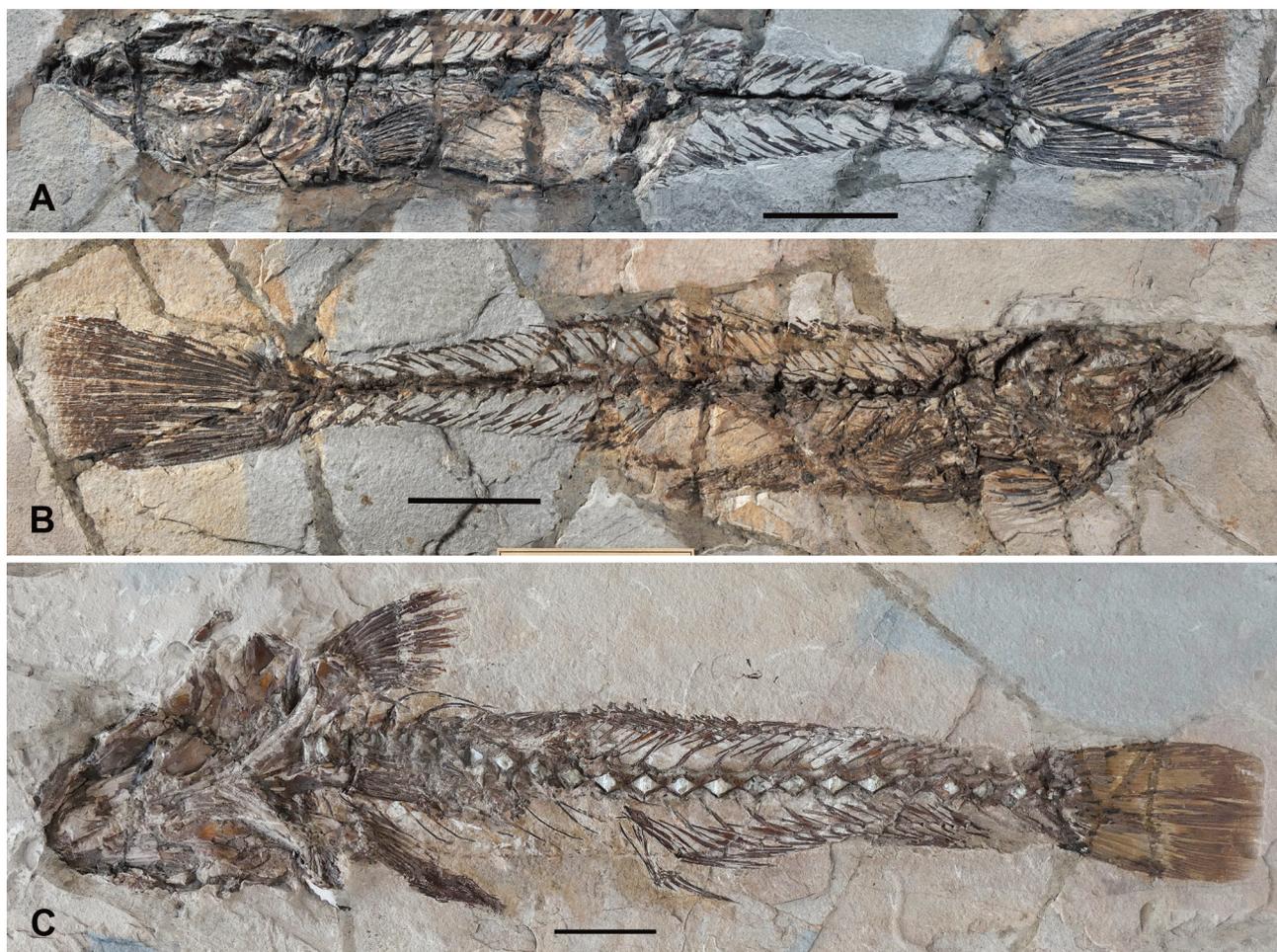


Fig. 1 – †*Callipteryx speciosus* Agassiz, 1838; Lower Eocene of Bolca in northern Italy, Pesciara: A, B – referred specimen MNHN 10815/10816 (Bol 0120/0121) (holotype of †*Callipteryx recticaudus* Agassiz, 1838), part and counterpart; C – paralectotype MCSNV T118. Scale bar: 5 cm.

skeleton, ca. 25.5 cm SL (Fig. 2B); NHMUK P.9477, part and counterpart (Woodward, 1901: 590); CMNH 4207, single plate, complete skeleton, ca. 45 cm SL (Eastman, 1911: 385). Moreover, there are two large (about 0.5 m long each) but poorly preserved complete skeletons in part and counterpart in MCSNV (IIB22/IIB23 and T19/IG23198). Perhaps huge (about 1.5 m long) but exceptionally poorly preserved skeleton in MFB (IG23208) and smaller, but terribly mutilated specimen in MNHN (Bol 0199) also represent †*Callipteryx speciosus*.

Type Locality and Horizon

Bolca locality, Pesciara cave site; late Early Eocene, late Ypresian, about 50 ma (see Papazzoni *et al.*, 2014).

Description

The body is relatively elongate, with a moderately short and deep caudal peduncle. The caudal peduncle depth is about 0.44–0.48 of the body depth. The head is relatively small; its length (tip of snout to anterior edge of upper part of pectoral girdle) is 1.52–1.59 times exceeds the body depth. The head length is contained 4.0–4.3 times in SL. The dorsal profile of the body is almost as equally convex as the ventral profile of the body.

Head. In all the specimens available the skull is very poorly preserved, with most of its bones being fractured and scarcely recognizable. The head is relatively deep, with its depth usually only somewhat less than its length. The orbit is moderate and placed high in the head depth, as evidenced by MNHN



Fig. 2 – †*Callipteryx speciosus* Agassiz, 1838; 1838; Lower Eocene of Bolca in northern Italy, Pesciara: A – referred specimen MCSNM V262, B – referred specimen MGP 12901. Scale bar: 5 cm.

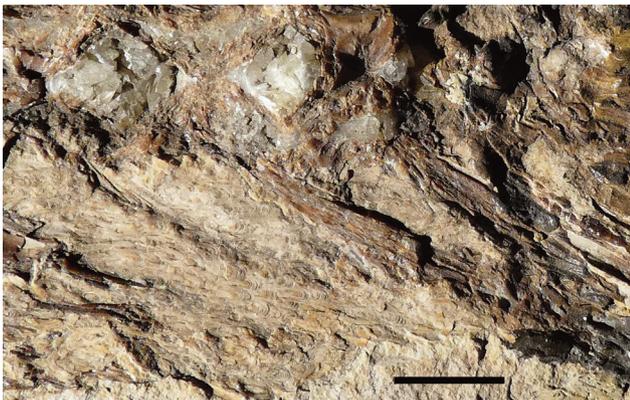


Fig. 3 – †*Callipteryx speciosus* Agassiz, 1838; paralectotype MCSNV T118, region of caudal peduncle; Lower Eocene of Bolca in northern Italy, Pesciara. Scale bar: 1 cm.

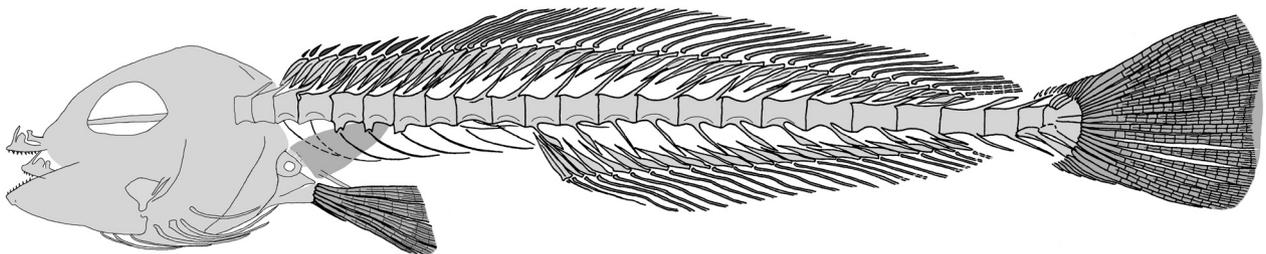


Fig. 4 – †*Callipteryx speciosus* Agassiz, 1838; reconstruction of the skeleton based mostly on MCSNM V262.

10815/10816. The horizontal diameter of the orbit seems to be not less than 25% HL. The snout is somewhat longer than the orbit diameter. The mouth is moderately wide and terminal. The lower jaw articulation is situated under the middle of the orbit, as evidenced by MNHN 10815/10816. The neurocranium is not deep, with the supraoccipital crest evidently poorly developed. The parasphenoid is moderately robust and almost straight; it is exposed close to the middle of the orbit in MNHN 10815/10816. The lower jaw slightly protrudes in relation to the upper jaw. The upper jaw bones are badly damaged; however, a relatively short and slender ascending premaxillary process and a robust articular process are distinguishable in MCSNM V262. The jaws bear apparently multi-serial small conical teeth and no fangs. The lower jaw is moderately deep. The dentary seems to not project ventrally near the moderately deep symphysis. The retroarticular process of MCSNM V262 is short but thick. Among the highly fragmented pterygoids and suspensorium bones only the quadrates are clearly recognizable (in paralectotype MCSNV T118, with the head visible from below). The quadrate is relatively small and wide, subtriangular in shape, and with the robust articulating condyle. The dorsal margin of the bone is convex. There is a process on the posterior margin of the quadrate divided by a notch from the dorsal margin of the bone. The rod-like symplectic occupies this notch. The opercular region is moderately narrow. The bones of the gill cover are highly fragmented, without evidence of the preopercular and opercular spines. Among the highly fragmented hyoid and branchial bones only the branchiostegal rays are clearly recognizable in MCSNM V262 and MNHN 10815/10816. The branchiostegal rays are long and sabre-like in shape; their number is most probably seven. The pharyngeal dentition is unknown.

Axial skeleton. There are 24 vertebrae, ten abdominal and fourteen caudal, including the urostyle. The axis of the vertebral column is almost straight. The vertebral centra are very strong and massive, with the anterior of them being almost rectangular in lateral view. Posterior abdominal and most of caudal vertebrae are elongated rostral-caudally. The length of the caudal portion of the vertebral column is 1.8 to 1.9 times greater than the length of the abdominal portion of the vertebral column. The vertebral spines are short and pointed, and are straight or slightly curved. The vertebral spines terminate rather far from the dorsal and ventral profiles of the body. Most of the neural and haemal spines are slender, but some of them are somewhat widened medially

in their middle portion. The haemal spines of the two anteriormost caudal vertebrae are always thickened in the middle. The longest neural spines are those of the anterior caudal vertebrae. The haemal spines of the caudal vertebrae are usually as equally long as the opposite neural spines. The first two anterior haemal spines are shorter and not as pointed as the succeeding spines. Most of the neural spines arise from the posterior half of the centra, whereas the anterior haemal spines arise either from the middle or from the anterior half of the centra. No parapophyses are recognizable in the abdominal vertebrae; however, these vertebrae apparently bear short lateral processes, as evidenced by the paralectotype MCSNV T118, with the anterior part of the vertebral column visible from below. The pleural ribs are very slender and strongly inclined posteriorly; they are only moderately long and occupy the upper half of the abdominal cavity. Slender epineurals are usually hidden by the vertebral centra, but are partly recognizable in several specimens.

Pectoral fin and girdle. The pectoral girdle is strongly damaged; its details are scarcely identifiable. The posttemporal is only partly preserved in two specimens and the supracleithrum is not recognizable at all. The cleithrum seems to be large and only moderately curved. The upper part of the cleithrum is located under the second and third vertebrae. The ventral postcleithrum is poorly recognizable as a straight rod only in MCSNM V262. The paralectotype MCSNV T118 reveals that the coracoid is relatively small, and the scapula is a rounded bone penetrated by the rather big foramen. The pectoral radials are poorly recognizable; these seem to be short. The pectoral fin is better preserved in the paralectotype MCSNV T118, where 17 pectoral-fin rays are evident. The first two pectoral-fin rays are not branched, whereas all other rays are both segmented and branched. The fifth ray is longest; its length equals the length of the four posteriormost abdominal vertebrae. The sixth and succeeding pectoral-fin rays rapidly decrease in length. The base of the pectoral fin is relatively wide and situated opposite to the third and fourth vertebrae relatively low on the flank.

Pelvic fin and girdle. The pelvic bones are incompletely preserved; these seem to be moderately long and relatively narrow. The paralectotype MCSNV T118 reveals that the pelvic fins are close together basally. Each pelvic fin seems to contain a spine and five soft segmented and branched rays. The pelvic fin is inserted approximately under the pectoral-fin base and roughly equals to it in length.

Dorsal fin. There are evidently no supraneurals (predorsal bones). The dorsal fin is long-based and continuous; it originates over the third / fourth vertebra transition and terminates over the 21th vertebra. There are nine dorsal-fin spines and 29 soft rays. The dorsal-fin spines are very short but rather robust, of increasing length posteriorly; the first spine is greatly reduced in size, being minute but evidently protruding to the exterior beyond the skin. The longest last spine is 2.2 times longer than the second spine and at least 3.0 times longer than the first spine. The first dorsal-fin spine is supernumerary on the first dorsal-fin pterygiophore. The longest soft ray of the dorsal fin is three times longer than the longest dorsal-fin spine. The length of the base of the soft portion of the dorsal fin of MCSNM V262 is 4.46 times longer than the base length of the spiny portion of the dorsal fin. The third and fourth dorsal-fin soft rays are longest; the succeeding rays gradually decrease in length posteriorly in the series; thereby, the fin is straight from above. The soft rays are segmented, but obviously unbranched. The last dorsal-fin rays do not reach the caudal-fin base. There are a total of 37 dorsal-fin pterygiophores in MCSNM V262. The first pterygiophore is not especially large; the succeeding pterygiophores of the dorsal-fin spines gradually increase in length, almost reaching the vertebral centra by their proximal ends. Most of the pterygiophores of the dorsal-fin soft rays are almost equal in length, but the posterior pterygiophores somewhat decrease in length. The dorsal-fin pterygiophores are pointed proximally, somewhat expanded anteroposteriorly, and bear a longitudinal strengthening ridge; these are rather strongly inclined posteriorly. The origin of the dorsal fin is poorly preserved in most of the specimens available, but the first dorsal-fin pterygiophore seems to insert into the first interneural space (between the first and second neural spine). The interneural spaces below the dorsal fin have the ventral shafts of two (rarely one or three) pterygiophores present. The pterygiophores have the proximal and medial elements fused.

Anal fin. The anal fin is long-based; it originates under the transition between the first and second caudal vertebrae and terminates under the eleventh caudal vertebra. There are two spines and 21 or 22 soft segmented rays in the anal fin. The anal-fin spines are very weak; the first spine is greatly reduced in size, being minute and evidently not protruding to the exterior beyond the skin. The first anal-fin spine is supernumerary. The shape of the soft part of the anal fin is similar to that of the soft

part of the dorsal fin. The first anal-fin pterygiophore is almost straight and narrow, moderately long; the second and succeeding anal-fin pterygiophores become slightly wider and are almost equal in length, but the posterior pterygiophores somewhat decrease in length. The first three anal-fin pterygiophores precede the haemal spine of the first caudal vertebra. The interhaemal spaces above the anal fin have the ventral shafts of two (rarely three) pterygiophores present. The anal-fin pterygiophores have the proximal and medial elements fused.

Caudal fin and skeleton. The caudal skeleton shows the fusion of PU1, U1, and U2 in the terminal centrum¹. The parhypural and haemal spine of PU2 are autogenous. A parhypurapophysis seems to be absent. Although the preservation of the material is only moderate, it seems that there is a fusion of the hypurals proximally with the terminal centrum, with their distal portions being divided by slits. The neural and haemal spines of PU3 are slightly longer than those of the preceding vertebra. The neural spine of PU2 is a low crest. There are three epurals; the condition of the uroneurals is unclear; perhaps these are fused with the terminal centrum. The caudal fin is moderately long, truncate to rounded. There are 17 principal rays in the caudal fin (I,8-7,D); there are up to 11 procurrent rays above and about seven rays below. There are no indications of the presence of a procurrent spur (Johnson, 1975). The inner principal rays of the caudal fin are segmented and intensively branched.

Squamation. Scales and lateral line are not evident in most of the specimens; however, in the caudal peduncle of the paralectotype MCSNV T118 exceptionally small and thin cycloid scales seem to be present (see Fig. 3).

Coloration. There are no unambiguous traces of the original pigmentation pattern preserved either on the body or on the fins.

•*Measurements* of the MCSNM V262, in percent of SL (ca. 22 cm) are as follows:

- Head length from tip of snout to anterior border of cleithrum: ca. 24
- Maximum body depth: ca. 17
- Depth of caudal peduncle: 7
- Distance between tip of snout and first dorsal-fin spine: 28
- Distance between tip of snout and first dorsal-fin soft ray: 40
- Distance between tip of snout and anal fin: 52

¹ The diurnal terminology is used. Schultze and Arratia (2013) have shown that the two ural centra are not homologous in different Teleostei.

- Distance between pelvic fin and anal fin: 27
- Length of base of dorsal fin: 62
- Length of base of spiny dorsal fin: 11.5
- Length of base of soft dorsal fin: 50
- Length of base of anal fin: 38
- Length of last spine of dorsal fin: 3.5
- Length of longest soft ray of dorsal fin: 10.5
- Length of second spine of anal fin: 2.5
- Length of longest soft ray of anal fin: 9.5
- Length of pelvic fin: 13
- Length of caudal fin: 17.5
- Length of lower jaw: ca. 12

DISCUSSION

The presence of true spines in the dorsal and anal fins definitely indicates that †*Callipteryx* belongs to a large and diverse clade of spiny-rayed bony fishes, the superorder Acanthopterygii (Greenwood et al., 1966) or “Series Percomorpha” (sensu Nelson, 2006). This taxon demonstrates anatomical evidence of its belonging to the order Perciformes (in its traditional sense) – in particular, the general configuration of its caudal skeleton, characterized by “five or less” hypurals and autogenous haemal processes of the second preural vertebrae (Johnson and Patterson, 1993). At the same time, the morphological peculiarity of the new genus – a combination of characters such as an elongate body with a “basal perciform number” of vertebrae (24), especially massive vertebral centra, a long-based single dorsal fin shifted anteriorly, three anal-fin pterygiophores preceding the first haemal spine, exceptionally small cycloid scales – makes it difficult to identify its close relatives and, accordingly, its position within the order Perciformes. We use traditional, natural taxonomy herein; with the order Perciformes *sensu lato* (see above).

Various authors have distinguished within the Perciformes a different number of suborders. †*Callipteryx* is usually brought together with the Trachinoidei (Woodward, 1901; Eastman, 1905, 1911; Blot, 1980; Bannikov, 2014; Carnevale *et al.*, 2014) based on its superficial similarity with trachinoids: elongated body with extended dorsal and anal fins and unforked caudal fin. Some other characters of †*Callipteryx* can be also found in any of the Trachinoidei (e.g., in *Trachinus* several anal-fin pterygiophores also precede the first haemal spine), however, a whole combination of characters of †*Callipteryx*, and first of all its few and especially massive vertebral centra differ this extinct genus greatly from the trachinoids.

The analysis of the osteological features of †*Callipteryx* clearly indicates that it cannot be confidently assigned to any of the perciform suborders except for the inadequately defined and possibly non-monophyletic Percoidei. This heterogeneous assemblage is currently defined by several plesiomorphic perciform features and in practice constitutes a convenient repository for those generalized perciform fishes, like †*Callipteryx* and many other taxa from Bolca (see Bannikov, 2014; Bannikov & Zorzin, 2020; etc.), that cannot obviously be placed elsewhere (Johnson, 1984). The morphological peculiarity of †*Callipteryx* clearly indicates that this genus deserves to be attributed to a special family Callipterygidae Jordan, 1905 within the suborder Percoidei. Currently, it is difficult to identify the closest relative of this family, although the largest †*Eocottus* (Eocottidae) have been confused with †*Callipteryx* by Eastman (1911) and Frickhinger (1991).

According to Agassiz (1833–1844), the two species of †*Callipteryx* are very similar, but †*C. recticaudus* is smaller, more slender, and its caudal fin is truncated rather than rounded. However, the paralectotype MCSNV T118 of †*C. speciosus* also has a truncated caudal fin and more slender body than the lectotype. Thus, for the moment we cannot find adequate characters for defining of two species of †*Callipteryx*. Some differences in size and proportions between the specimens available most probably are not of species level, but reflect ontogenetic, intraspecific changes, and partly caused from the stage of preservation. Therefore, †*C. recticaudus* is placed herein into the synonymy of †*C. speciosus*.

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ADDRESSES OF THE AUTHORS

ALEXANDRE F. BANNIKOV – Borisyak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117647, Russia; e-mail: aban@paleo.ru

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