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A new genus and species of percomorph fish ("stem pleuronectiform") from the Eocene of Bolca in northern Italy

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ABSTRACT

A new genus and species of relatively deep-bodied percomorph fish, †*Anorevus lorenzonii*, is described based on a single skeleton from the Eocene locality of Bolca (Pesciara cave site) in northern Italy. This taxon cannot be accommodated in any known family, and it is placed in the Percomorpha inc. sed. †*Anorevus lorenzonii* gen. et sp. nov. could be regarded as a "stem pleuronectiform" percomorph, as indicated by both its initial cranial asymmetry and initial anterior shift of the dorsal-fin origin. The new taxon is characterized by an unusual vertebral formula (11+12), as few as 13 anal-fin soft rays and wide oblique mouth.

Key words: Percomorpha, new genus and species, Eocene, northern Italy, Bolca locality.

RIASSUNTO

†*Anorevus lorenzonii*, un nuovo genere e specie di pesce percomorfo con corpo relativamente alto, viene descritto sulla base di un singolo scheletro proveniente dalla località eocenica di Bolca (Pesciara), Italia settentrionale. Questo taxon non può essere allocato in nessuna famiglia nota ed è inserito nei Percomorpha inc. sed. †*Anorevus lorenzonii* potrebbe rappresentare uno stem-pleuronettiforme con asimmetria cranica ad uno stadio iniziale e spostamento anteriore dell'origine della pinna dorsale. Il nuovo taxon è caratterizzato da un'insolita formula vertebrale (11+12), 13 raggi della pinna anale e ampia apertura boccale con andamento obliquo.

Parole chiave: Percomorpha, Percoidei, nuovo genere e nuova specie, Eocene, Italia settentrionale, Bolca.

INTRODUCTION

The Eocene marine fishes from the Bolca locality in northern Italy have been known since the mid-sixteenth century (SORBINI, 1981). This locality is exceptionally rich in bony fishes, especially the acanthomorphs (BANNIKOV, 2014; CARNEVALE *et al.*, 2014; BANNIKOV and ZORZIN, 2019). Bolca marks the first fossil record of many groups of fishes found on modern coral reefs (BELLWOOD, 1996). Fish remains have been collected in the fossiliferous layers of the Pesciara and Monte Postale sites of the Bolca locality. These two coeval sites have different fish assemblages and different depositional contexts (MARRAMÀ *et al.*, 2016). The fossiliferous sediment of the Pesciara was deposited in a relatively shallow basin with persistent dysoxic or anoxic conditions at the bottom, corroborating the hypothesis of a stagnation deposit with low hydrodynamic energy. The Monte Postale sediments were deposited close to an emerged coastal area, in a setting characterized by seagrass beds, mangroves and coral reefs; fish specimens from the Monte Postale site are less well preserved than those from the Pesciara site.

The Bolca locality marks one of the earliest fossil records of the flatfish order Pleuronectiformes, represented by both the unquestionable pleuronectiform †*Eobothus minimus* (AGASSIZ, 1839) and two "stem flatfish taxa with incomplete orbital migration" (FRIEDMAN, 2008, 2012), these being †*Amphistium paradoxum* AGASSIZ, 1844 and †*Heteronectes chaneti* FRIEDMAN, 2008, whose attribution to the pleuronectiforms is not unequivocal (see CHANET, 1999). One additional taxon, †*Quasinectes durello* BANNIKOV and ZORZIN, 2019, superficially resembles flatfishes in its ovoid body with a deep caudal peduncle and the rounded caudal fin but lacks evidence of pleuronectiform synapomorphies, and it was classified as a perciform of uncertain relationships (Bannikov and Zorzin, 2019). Another a specimen of an as yet undescribed percomorph fish from Bolca housed in the Museo Civico di Storia Naturale di Verona collection also exhibits an ovoid body and certain initial cranial asymmetries that parallel those of flatfishes; it is described below as †*Anorevus lorenzonii* gen. et sp. nov. The new taxon belongs to the Pesciara assemblage, as do †*Eobothus* and †*Amphistium*, whereas †*Heteronectes* and †*Quasinectes* represent the Monte Postale assemblage.

Methods

The specimen of †*Anorevus lorenzonii* gen. et sp. nov. was examined using a WILD Heerbrugg stereomicroscope equipped with a camera lucida drawing arm and measurements were taken with a dial caliper to the nearest 0.1 mm. Some details of the specimen were best seen when the specimen was moistened with alcohol during microscopic examination. The specimen was prepared by needle, and subsequently the counterpart was prepared with the acid-transfer method (following Toombs, 1948; Toombs and Rixon, 1959).

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*: MCSNV – Museo Civico di Storia Naturale di Verona; *Anatomical*: HL – head length; PU – preural vertebra; SL – standard length; U – ural vertebra.

The dagger symbol (†) indicates extinct taxa.

Systematic description

Series PERCOMORPHA

Percomorpha *incertae sedis*

Genus †*Anorevus* gen.nov.

Diagnosis

Body relatively deep, its length 2.4 times greater than its depth. Head length less than body depth. Eye relatively small; orbit diameter almost as long as snout length. Mouth large, oblique and terminal. Ascending premaxillary process moderately long. Jaw teeth sharp and conical. Lower jaw articulation under posterior border of orbit. Opercular region moderately wide. Vertebrae 23 (11+12); parapophyses developed on about five posterior abdominal vertebrae. Pleural ribs short and slender. Hypurals unfused. Two supraneurals. Dorsal fin single, long-based; soft portion much longer than spinous portion. Dorsal fin with five slender flexible graduated spines and about 25 very long soft rays; it originates above occiput. Anal fin with three relatively strong graduated spines and about 13 long soft rays. Anal fin with moderately extended base. Two anal pterygiophores precede first haemal spine, and five pterygiophores precede second haemal spine. Pelvic fins long, situated anterior to the pectorals. Caudal fin rounded, fan-shaped, with 17 principal rays. Scales small, densely covering whole body, head and bases of unpaired fins. Lateral line not traceable.

Type species

†*Anorevus lorenzonii* sp. nov., by monotypy and designation herein.

Composition

Type species only.

Etymology

After Verona, written backward – anagram *anorev*; gender masculine.

†*Anorevus lorenzonii* sp. nov.

Figures 1-3

Diagnosis

As for the genus.

Holotype

MCSNV IG 43390, complete articulated specimen, and somewhat incomplete counterpart MCSNV IG 43391 prepared with acid-transfer method, ca. 34.5 mm SL; collected in 1982.

Type Locality and Horizon

North-eastern Italy, Bolca locality, Pesciara site; late early Eocene, late Ypresian, about 50 Ma (Papazzoni *et al.*, 2014).

Referred specimens

None.

Fig. 1 – †*Anorevus lorenzonii* gen. et sp. nov., holotype MCSNV IG 43390, ca. 34.5 mm SL; uppermost Lower Eocene, Monte Bolca locality in northern Italy, Pesciara: **A** – general view; **B** – specimen moistened with alcohol. Scale bar: 0.5 cm

Etymology

The species is named in honour of Mr. Aldo Lorenzoni, Director of the Consorzio Tutela Vini Soave, who recognizes the international importance of the Eocene fossils from the Alpone Valley, with particular reference to the Bolca locality.

Description

The body is relatively deep and ovoid, evidently compressed laterally, with a short and deep caudal peduncle. The caudal peduncle depth is 3.5 times less than the maximum body depth. The head is relatively large; its length (tip of snout to posterior

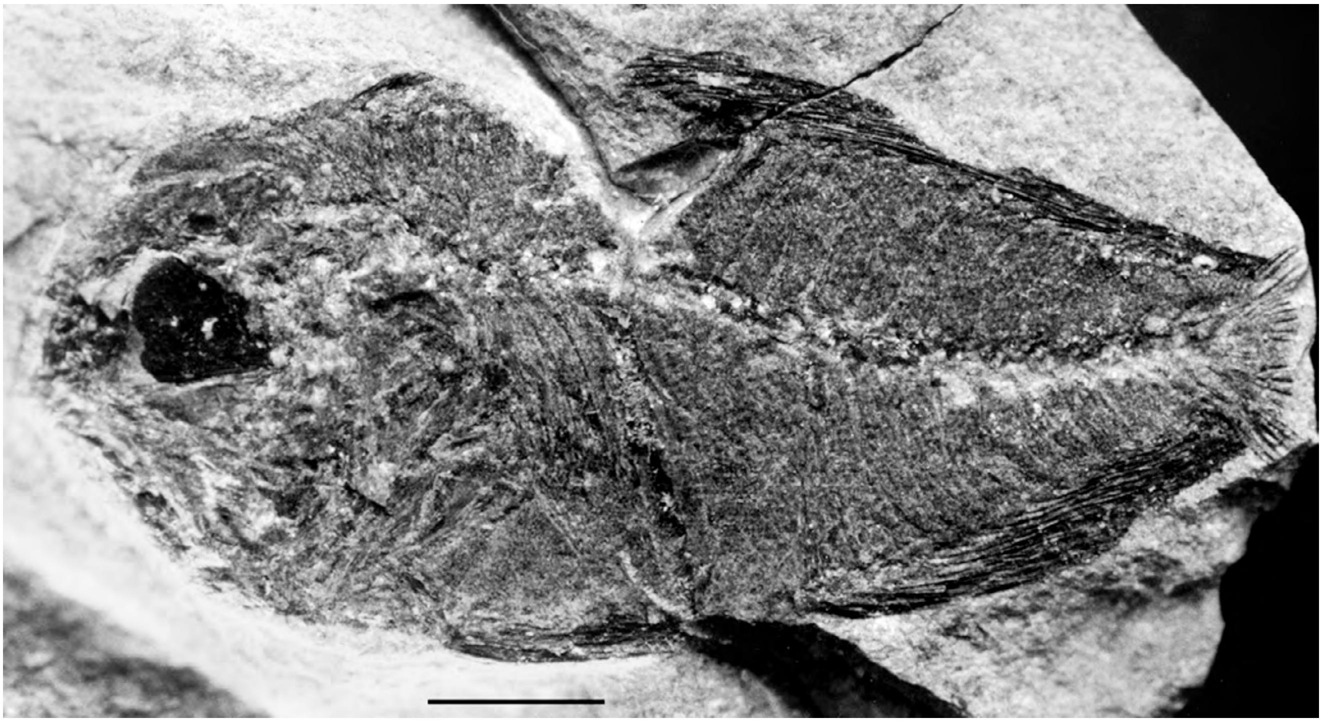

Fig. 2 – †*Anorevus lorenzonii* gen. et sp. nov., holotypic counterpart MCSNV IG 43391 prior to acid preparing; uppermost Lower Eocene, Monte Bolca locality in northern Italy, Pesciara. Scale bar: 0.5 cm

edge of the opercular region) is somewhat smaller than the maximum body depth. The head length is 2.7 times as long as SL. The ventral profile of the body is almost as convex as the dorsal profile of the body. The dense scale cover and strong pigmentation throughout the body, in addition to the poor coloration of the bony substance itself, make it difficult to recognize unambiguously some morphological characters.

Head. The head is relatively deep, with its depth almost equal to its length. The orbit is rather small and placed above the middle of the head depth. The orbit diameter almost equals the snout length. The neurocranium is relatively deep; the limits of most of its bones are scarcely distinguishable. The orbital region of the braincase of the acid-prepared counterpart shows slight cranial asymmetry based on the position of the frontals (as a dextral morph) (unless this is from taphonomic distortion). However, the strong and almost straight parasphenoid borders the right orbit from below, rather than passes through the middle of the orbit, as shown for the "stem pleuronectiform" from Bolca, †*Heteronectes chaneti* (Friedman, 2012, Figs. 1B, 3A, 4A, 6A, 7A). A supraoccipital crest seems to be poorly developed, and the posterior border of the braincase is oblique. There is a posterior depression of the braincase probably composed by both the pterotic and epiotic. The ethmoid region is short. None of the infraorbital bones are preserved. The mouth is large, oblique and terminal; the lower jaw articulation is situated at a level below the posterior border of the orbit. The premaxillary ascending process is moderately long and distinct from the massive articular process. The presence or absence of a postmaxillary process is unknown. The upper jaw teeth are strong, curved and conical. The jaw dentition is probably uniserial. The maxilla is long, narrow, and slightly expanded distally. A supramaxilla is not evident. The mandible is large but shallow at the symphysis; its length is 72% of HL. The dentary is deeply forked posteriorly. The retroarticular process is short but deep. The outer surface of the angulo-articular bears a distinct ridge extending rostrad from the articular facet. The lower jaw dentition is similar to that of the upper jaw, with curved, conical and probably uniserial teeth. The hyomandibular shaft is oriented close to the vertical. The limits of most of the pterygoid bones are scarcely distinguishable; however, it is evident that the endopterygoid (mesopterygoid)

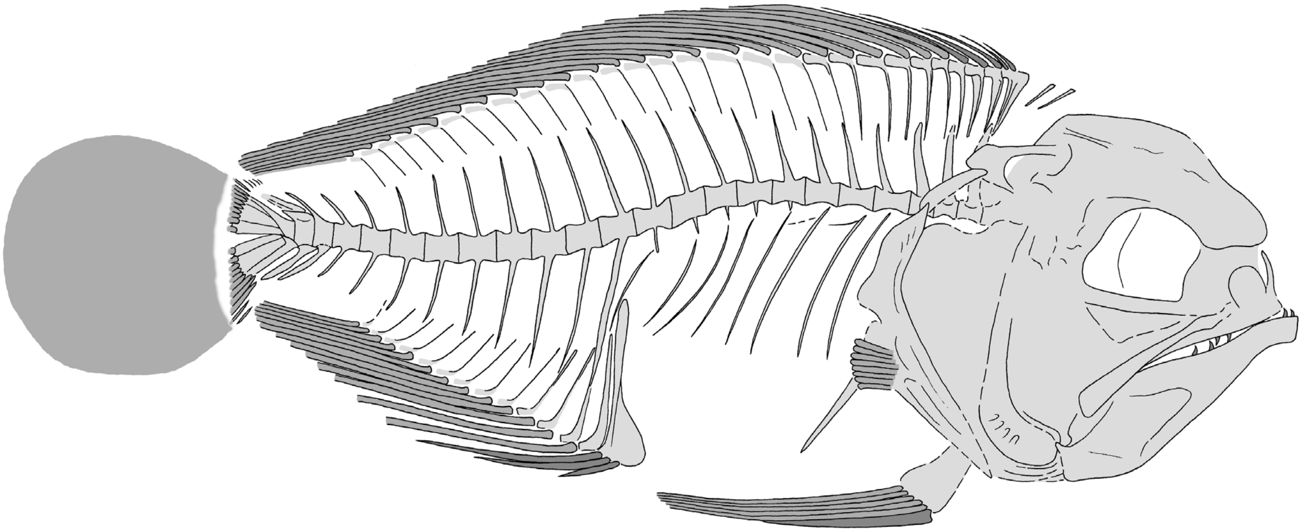

Fig. 3 – †*Anorevus lorenzonii* gen. et sp. nov., reconstruction of the skeleton based on the holotype MCSNV IG 43390/43391; scales omitted

is flat and extended, being situated just below the parasphenoid. The quadrate is relatively small, with distinct articular condyle. The opercular region is relatively narrow. The preopercle is narrow, almost straight dorsally, and broader and moderately curved ventrally; no serrations are evident along its border. The lower portion of the preopercle bears pores of the lateral line sensory canal. The opercle is flat, rather broad, and without evident spines. The bones of the hyoid bar are very incompletely preserved, and the total complement of branchiostegal rays is unknown; the few visible branchiostegal rays are short and sabre-like. The pharyngeal dentition is unknown.

Axial skeleton. There are definitely 12 caudal vertebrae (including the urostyle), and 11 abdominal vertebrae are recognizable. We cannot exclude the possibility of the presence of one more obscured vertebra anterior to the first recognizable vertebra, but this is quite ambiguous. The axis of the vertebral column is sigmoid and elevated anteriorly. Most of the vertebral centra are somewhat longer than high. The length of the caudal portion of the vertebral column is 1.17 times greater than the length of the abdominal portion of the vertebral column. Most of the neural and haemal spines are relatively stout and straight to slightly curved. None of the interneural spaces below the dorsal fin seems to be vacant. The neural spines of the middle portion of the vertebral column are longest. All the neural spines are inclined rather slightly posteriorly. The haemal spines are inclined even less than the corresponding neural spines. The haemal spines of the anterior caudal vertebrae are longer than the corresponding neural spines. The parapophyses are poorly developed. Pleural ribs are short and slender; these are moderately inclined posteriorly, thus occupying approximately the upper half of the abdominal cavity. Only a few of the short and slender epineurals are evident below the vertebral centra in the abdominal portion of the vertebral column.

Pectoral fin and girdle. The pectoral girdle is better recognizable in the acid-prepared counterpart MCSNV IG 43391. The posttemporal is forked, having two anterior processes, of which the upper one is longer. The supracleithrum is moderately large and elongate; it connects the posttemporal to the cleithrum. The cleithrum is a large and elongate bone, almost straight ventrally and in the middle, but with an anterior curvature of the dorsal portion; it has a flat and relatively narrow posterodorsal projection above the pectoral fin. The ventral postcleithrum is narrow, moderately long, and directed posteroventrally. The coracoid is narrow and relatively small. The scapula and pectoral radials are poorly recognizable, being hidden by the bases of the pectoral-fin rays. The pectoral fin of the holotype is folded anteriorly; it is narrow and contains at least 12 rays. The whole length of the pectoral fin is unknown. The pectoral-fin base is situated close to the midpoint between the vertebral column and the ventral profile of the body, below the fifth vertebra.

Pelvic fin and girdle. The pelvic bones are wedge-shaped and oriented posteroventrally. The pelvic fin is long; it has a strong spine and five soft rays. The pelvic-fin spine is much longer than the second anal-fin spine. The pelvic fin is inserted well anterior to the pectoral-fin base; it does not reach the origin of the anal fin.

Supraneurals and dorsal fin. There are two small straight and narrow supraneurals (predorsal bones); these are anteriorly inclined. The supraneurals are situated in the preneural space, above the occiput.

The dorsal fin is long-based and continuous, without indentation between the spiny and soft parts. The origin of the dorsal fin is anterior to a vertical level through the centrum of the first vertebra. The spiny portion of the dorsal fin consists of five very slender graduated spines, evidently flexible; the first spine is shortest, 3.8 times shorter than the fifth (longest) dorsal-fin spine. The length of the first spine is slightly shorter than the length of the base of the spiny dorsal fin. The first two spines are in non-serial secondary association (supernumerary) with the first dorsal-fin pterygiophore, which precedes the neural spine of the first vertebra. The soft dorsal fin is very extended and evidently high. However, the soft dorsal-fin rays of the holotype are depressed to the back, partly obscuring each other. Therefore, the precise length of the longest soft dorsal-fin rays is unknown, although it is quite clear that these are longer than the longest dorsal-fin spine. The peripheral border of the dorsal fin seems to be rounded. Based on the pterygiophores, there are about 25 soft dorsal-fin rays; when depressed, the dorsal fin reaches behind the caudal-fin base. The soft dorsal-fin rays are more widely spaced than the dorsal-fin spines. The first dorsal-fin pterygiophore seems to penetrate down into the preneural space, and the succeeding three pterygiophores occupy the first interneural space. The subsequent pterygiophores of the dorsal fin either terminate above the neural spines or penetrate slightly down into the interneural spaces, with all the interneural spaces below the soft dorsal fin base having the ventral shafts of one or two pterygiophores present. The proximal shafts of the few anterior pterygiophores are slightly inclined anteriorly, and the succeeding pterygiophores become at first oriented vertically and then are increasingly inclined posteriorly and gradually shorter. The first dorsal-fin pterygiophore is not the longest; it is expanded slightly medially and bears a longitudinal strengthening ridge but seems to lack a tapered projection directed anteriorly from the upper anterior part. The medial pterygiophores seem to be fused with the proximal pterygiophores.

Anal fin. The anal fin originates under the level of the centrum of the first caudal vertebra. There are three moderately strong, smooth, graduated spines and 13 soft rays in the anal fin. The first two spines are supernumerary on the first anal-fin pterygiophore. The anal-fin soft rays of the holotype are depressed to the back, partly obscuring each other. Therefore, the precise length of the longest soft anal-fin rays is unknown, although it seems to be that these are longer than the longest dorsal-fin spine. The peripheral border of the anal fin appears to be rounded; when depressed, the anal fin reaches behind the caudal-fin base. Two anal-fin pterygiophores insert anterior to the first haemal spine, and five pterygiophores precede the second haemal spine. The first anal-fin pterygiophore is stout, straight and long; its distal portion has a lamellar expansion anteroventrally. The first anal-fin pterygiophore is almost vertically oriented. The second and succeeding anal-fin pterygiophores are much shorter and decrease in length posteriorly in the series, being increasingly inclined posteriorly. The second and succeeding interhaemal spaces accommodate the proximal shafts of one or two anal-fin pterygiophores.

Caudal fin and skeleton. The caudal skeleton is of the generalized percoid type, showing the fusion of PU1, U1, and U2 in the terminal centrum[1]. All five hypurals, the parhypural, and the haemal spine of PU2 are autogenous. There seems to be two uroneurals. Because the dense scale cover, it is unclear if there are three or two epurals and if the haemal spine of PU3 is autogenous or not. The neural spine of PU2 forms a relatively low crest. The neural and haemal spines of PU3 are only slightly stronger than those of the preceding vertebra. The caudal fin is incomplete posterodorsally; it has 17 principal rays, with 15 branched (I,8-7,I). There are at least eight procurrent rays above and more than four rays below; the presence of a procurrent spur (Johnson, 1975, 1984; Johnson and Patterson, 1993)

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

is uncertain. The caudal fin appears to be rounded and fan-shaped.

Squamation. The scales are small and densely cover the whole body, head and bases of the unpaired fins. The limits of individual scales are scarcely recognizable; therefore the number of the scale rows on the body is unknown. Neither ctenii nor radiating basal grooves are recognizable in the scales. There are circular striations on the scale surface. The lateral line is not distinguishable.

Coloration. Traces of the original pigmentation pattern are preserved throughout the whole body, dorsal and anal fins: these represent numerous minute dark spots arranged densely.

Measurements of the holotype, in percent of SL (ca. 34.5 mm), are as follows:

- Head length from tip of snout to posterior border of opercle: 36.5
- Maximum body depth: 42.5
- Depth of caudal peduncle: 12
- Distance between tip of snout and first dorsal-fin spine: 34
- Distance between tip of snout and first dorsal-fin soft ray: 39.5
- Distance between tip of snout and anal fin: 65
- Distance between pelvic fin and anal fin: 27
- Length of base of dorsal fin: 64
- Length of base of anal fin: 29
- Length of first spine of dorsal fin: 5
- Length of longest (last) spine of dorsal fin: 18
- Length of spine of pelvic fin: 18
- Length of longest soft ray of pelvic fin: 25
- Preorbital distance: 9.5
- Horizontal diameter of orbit: 10
- Length of lower jaw: 26

Discussion

The presence of true spines in the dorsal and anal fins definitely indicates that †*Anorevus* gen. nov. 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). The new 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 and (perhaps) third preural vertebrae (Johnson and Patterson, 1993). At the same time, the morphological peculiarity of the new genus – a combination of characters such as a relatively deep body with a decreased number of vertebrae (the "basal number" of vertebrae in perciforms is 24-25: Gosline, 1971), a long-based single dorsal fin originated above the occiput, two anal-fin pterygiophores preceding the first haemal spine, small cycloid scales – makes it difficult to identify its close relatives and, accordingly, its position within the order Perciformes. The order of perch-like fishes (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 of vertebrates in general. Various authors have distinguished within the Perciformes a different number of suborders. 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 subdivided into numerous orders, bizarrely grouped into taxa of higher rank (Wiley and Johnson, 2010; Near *et al.*, 2012, 2013; Betancur-R. *et al.*, 2013, 2017; Nelson *et al.*, 2016; etc.). 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. This encourages us to use traditional, natural taxonomy herein, also because molecular systematics are not stabilized yet and sometimes contradict each other.

The new genus described above resembles the flatfishes of the order Pleuronectiformes in its ovoid body with a deep and short caudal peduncle and the rounded caudal fin, insertion of the few anal-fin pterygiophores anterior to the first haemal spine, and in apparent initial cranial asymmetry. Chapleau (1993) identified three synapomorphies of living flatfishes, two of which are osteological: migration of one eye during ontogeny, resulting in profound cranial asymmetry; and an anterior insertion of dorsal fin that overlaps the neurocranium. Friedman (2008, 2012) added more characters supporting flatfish monophyly, including: absence of supraneurals; absence of well-developed membranous extensions on the shafts of most dorsal- and anal-fin proximal-middle radials; haemal arch and spine of the third preural vertebra fused to the centrum; a full neural spine on the second preural centrum; two or fewer epurals. None of the characters listed above (except for the initial cranial asymmetry) could be confidently recognized in the holotype of †*Anorevus lorenzonii* gen. et sp. nov., although perhaps partly because of its inadequate preservation. The latter prevents the exclusion of the possibility of the presence of two epurals and the fusion of the haemal spine of the third preural vertebra to the centrum. In any case, the presence of two supraneurals and the dorsal fin not overlapped the neurocranium confidently differentiate the new taxon from the Pleuronectiformes.

Betancur-R. *et al.* (2017) placed the order Pleuronectiformes in their "Series Carangaria" together with the orders Carangiformes and Istioforiformes and seven *incertae sedis* families. They mentioned the lack of morphological synapomorphies for the carangarians (indeed, it is difficult to find among the percomorphs as morphologically strongly different fishes as the flatfish and billfish!) but indicated "a strong molecular signal supporting their monophyly" (Betancur-R. *et al.*, 2017, p. 24).

Friedman (2008, 2012) regarded two Bolca taxa, †*Amphistium paradoxum* Agassiz, 1844 and †*Heteronectes chaneti* Friedman, 2008 as stem flatfishes with incomplete orbital migration. Specimens of †*Amphistium* include both dextral and sinistral morphs, as in the morphologically primitive living flatfish *Psettodes*, whereas †*Heteronectes* is known based on a single incomplete specimen. We have previously discussed the possible systematic position of †*Amphistium* and †*Heteronectes* (Bannikov and Zorzin, 2019) and suggested that, although Friedman (2008, 2012) regarded †*Heteronectes* as a stem flatfish which "occupies an exceptionally deep position on the pleuronectiform stem" (Friedman, 2012: 750), it is reasonable to accommodate this genus among the percomorphs outside of the order Pleuronectiformes. It was also stated that, apart from the cranial asymmetry, the presence of which cannot be unequivocally stated for †*Quasinectes durello* Bannikov and Zorzin, 2019, in the available characters for comparison this fish exhibits strong similarity to †*Heteronectes* from the same Monte Postale site (Bannikov and Zorzin, 2019). Paleontological data suggest that in the Eocene time, when the earliest true pleuronectiforms already existed (†*Eobothus* and some other genera: Chanet, 1997, 1999), some percomorphs also exhibited certain cranial asymmetry in parallel to flatfishes. In addition to †*Heteronectes* (and perhaps †*Amphistium* whose attribution to the pleuronectiforms is not unequivocal; see Chanet, 1999), there is also the discovery in the basal Eocene of the North Caucasus of an as yet undescribed deep-bodied percomorph with a somewhat asymmetrical cranium, and †*Anorevus lorenzonii* gen. et sp. nov. described herein.

Thus, †*Anorevus lorenzonii* gen. et sp. nov. could be regarded as a "stem pleuronectiform" percomorph (*sensu* Friedman, 2008, 2012) with both the initial cranial asymmetry and initial shift anteriorly of the dorsal-fin origin. †*Anorevus* also exhibits a wide oblique mouth (characteristic for many flatfishes except for the soleids and cynoglossids with a small mouth). On the other hand, the new genus reveals an apomorphic reduction of the number of the caudal vertebrae to 12, never observed in either "stem" or true pleuronectiforms. The relatively small number of anal-fin rays in †*Anorevus* is also quite unusual for flatfishes.

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