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Eocene ghost pipefishes (Teleostei, Solenostomidae) from Monte Bolca, Italy

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KEYWORDS - Syngnathiformes, stem-Solenostomidae, †Solenorhynchinae n. subfam., Eocene, Monte Bolca.

*ABSTRACT - Ghost pipefishes of the family Solenostomidae (Teleostei, Syngnathiformes) are shallow tropical syngnathiforms found today exclusively in the Indo-Pacific where they live associated with seagrass beds and reefs. Presented herein is a revision of the Eocene fishes from Monte Bolca, northern Italy, assigned to the family Solenostomidae. The genus †*Prosolenostomus *Blot, 1980 is excluded from the Solenostomidae and is regarded as aligned to the pipefish family Syngnathidae. The stem-Solenostomidae †*Calamostoma *Agassiz, 1833 and †*Solenorhynchus *Heckel, 1854 are accommodated in the separate subfamily †Solenorhynchinae n. subfam., representing the sister taxon of the extant genus* Solenostomus *Lacèpede, 1803. It is demonstrated that the correct name of the type and only species of †*Calamostoma *should be †*C. lesiniforme *(Volta, 1796) rather than †*C. breviculum *(Blainville, 1818). The diagnosis of the family Solenostomidae is emended to accommodate the fossil ghost pipefish genera.*

RIASSUNTO - [I pesci pipa fantasma (Teleostei, Solenostomidae) eocenici di Monte Bolca, Italia] - *I pesci pipa fantasma della famiglia Solenostomidae (Teleostei, Syngnathiformes) sono singnatiformi tipici delle acque costiere tropicali dove vivono associati principalmente a praterie a fanerogame e barriere coralline. Viene presentata una revisione dei taxa attribuiti alla famiglia Solenostomidae provenienti dai depositi eocenici di Monte Bolca. Il genere †*Prosolenostomus *Blot, 1980 viene escluso dalla famiglia Solenostomidae e considerato un membro della famiglia Syngnathidae. Gli stem-Solenostomidae †*Calamostoma *Agassiz, 1833 and †*Solenorhynchus *Heckel, 1854 vengono attribuiti alla nuova sottofamiglia †Solenorhynchinae, interpretata come il sister taxon del genere attuale* Solenostomus *Lacèpede, 1803. Il nome della specie tipo del genere monotipico †*Calamostoma *risulta essere †*C. lesiniforme *(Volta, 1796) piuttosto che †*C. breviculum *(Blainville, 1818). La diagnosi della famiglia Solenostomidae viene emendata per consentire l'inclusione dei generi estinti di pesci pipa fantasma.*

INTRODUCTION

Fishes of the family Solenostomidae (Teleostei, Syngnathiformes), commonly known as ghost pipefishes, are today restricted to the shallow tropical waters of the Indo-Pacific where they live associated with rocky substrates, coral reefs and seagrass beds. The Solenostomidae is a small family comprising four extant species within the genus *Solenostomus* Lacepède, 1803 (Orr & Fritzsche, 1993; Orr et al., 2002). As pointed out by Orr & Fritzsche (1993, p. 168), "…although characterized by the typical elongate snout of syngnathoid fishes, the morphology of the solenostomids is striking even for this highly specialized suborder…". The ghost pipefishes are characterized by a relatively short and compressed body covered with large stellate bony plates; two separate dorsal fins, each on a raised base; anal fin opposite to soft dorsal; pelvic fins relatively large, approximately opposite to spinous dorsal fin; females with brood pouch formed by the pelvic fins; relatively large caudal fin; 32-34 vertebrae (Jurgersen, 1910; Orr & Fritzsche, 1993; Nelson et al., 2016).

Three monotypic fossil ghost pipefish genera have been reported in the Eocene fish fauna of Monte Bolca (northern Italy) (Blot, 1980), †*Calamostoma* Agassiz, 1833, *Prosolenostomus* Blot, 1980 and *Solenorhynchus* Heckel, 1854. Each of these is known based on either a single (†*Prosolenostomus* and †*Solenorhynchus*) specimen or only a few (†*Calamostoma*) specimens. Our revisionary study of the fossil material has revealed that only two of above listed genera can be aligned with the family Solenostomidae, requiring a considerable emendation of the limits and diagnosis of the family. The genus †*Prosolenostomus* is characterized by a strongly elongated body completely encased in a series of bony rings (rather than stellate bony plates), a small head with a short tube-shaped snout and apparent absence of the dorsal, anal and pelvic fins, thereby implying that it cannot be assigned to the ghost pipefishes as formerly proposed by Blot (1980). The overall morphology of †*Prosolenostomus* is clearly consistent with that of pipefishes of the family Syngnathidae (see Orr, 1995; Bannikov, 2014; Carnevale et al., 2014). Its type species, †*P. lessinii* Blot, 1980, was described based on a single partially complete specimen in the collections of the Museo Civico di Storia Naturale, Verona (Blot, 1980, p. 365; pl. VI, fig. 3). Subsequently, an additional incomplete specimen housed in the Carnegie Museum of Natural History, Pittsburgh, was referred to †*P. lessinii* and figured by Frickhinger (1991); however, this specimen lacks the characteristic cranial horn emerging just above the orbit considered diagnostic by Blot (1980) (see Fig. 1).

The genus †*Solenorhynchus* exhibits a number of features regarded as diagnostic of the extant members of the family Solenostomidae (body covered with stellate bony plates; two separate dorsal fins, each on a raised base; anal fin opposite to the soft dorsal fin; pelvic fins relatively large; long caudal fin); however, it has a strongly elongate body, exceptionally elongate caudal-fin rays, and a higher number of vertebrae. The genus †*Calamostoma*

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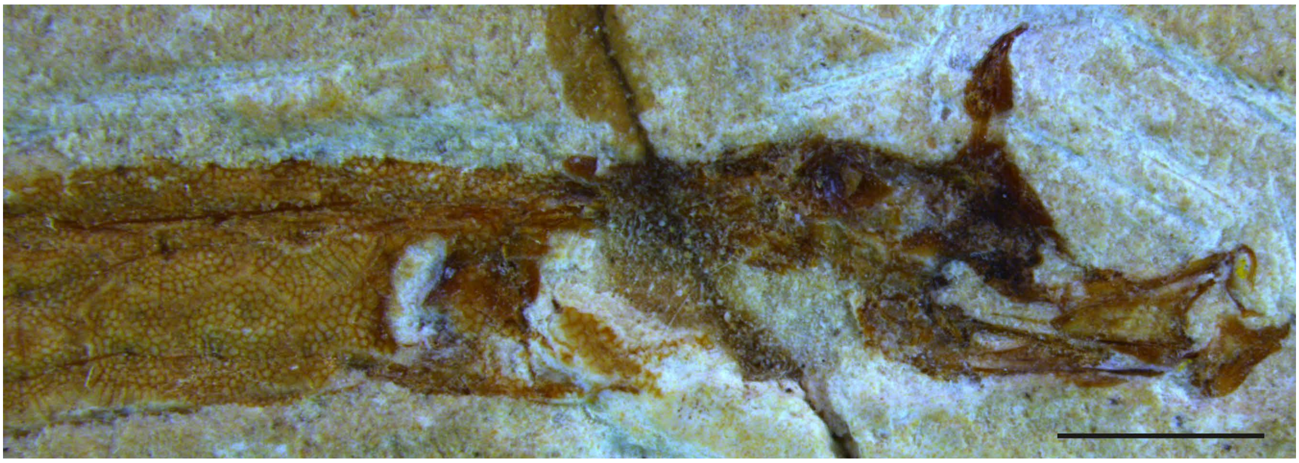

Fig. 1 - †*Prosolenostomus lessinii* Blot, 1980 from the Eocene of Monte Bolca, Italy; holotype, MCSNV IG37597, head and anterior portion of the body. Scale bar corresponds to 2 mm.

appears in some ways more similar morphologically to the extant genus *Solenostomus* than to †*Solenorhynchus*. However, the two Eocene genera from Monte Bolca share a unique set of features not observed in *Solenostomus*, including a relatively short dorsal spinous fin, pelvic-fin insertion anterior to the first dorsal-fin insertion, more than four complete pretrunk rings of stellate bony plates, and a low number of dorsal- and anal-fin rays. Therefore, an attribution of †*Solenorhynchus* and †*Calamostoma* to the Solenostomidae necessarily requires an emendation of the diagnosis of the family, as well as the creation of a new ghost pipefish subfamily to accommodate these two extinct genera.

The goal of this paper is to redescribe the Eocene ghost pipefishes from Monte Bolca and to briefly discuss their affinities.

MATERIALS AND METHODS

The present study is based on seven specimens housed in the collections of the Museo Civico di Storia Naturale, Verona (MCSNV), Muséum National d'Histoire Naturelle, Paris (MNHN), Natural History Museum, London (NHMUK), and Naturhistorisches Museum, Wien (NHMW). Extant comparative material derives from the collection of the National Museum of Natural History, Smithsonian Institution, Washington (USNM). The specimens were studied using stereomicroscopes WILD Heerbrugg, Leica MZ6, and Leica M80 with attached camera lucida drawing arms. During examination, the specimens were moistened with alcohol to enhance some details of their skeletal anatomy. Measurements were taken with a dial caliper to the nearest 0.1 mm. Counts and measurements mostly follow Orr & Fritzsche (1993) and Orr et al. (2002), except for pretrunk and trunk length. Pretrunk length is defined herein as the greatest distance between the posterior edge of the opercle and pretrunk ring that lies just anterior to the first dorsal fin; trunk length is defined herein as the greatest distance between the posterior pretrunk ring and the caudal-fin base. Standard length (SL) is used throughout. Extinct taxa are marked with a dagger (†) preceding their name.

SYSTEMATICS

Order Syngnathiformes Berg, 1940
Family Solenostomidae Lacepède, 1803

Emended diagnosis - Body short to considerably elongated, covered with large stellate bony plates; two separate dorsal fins, the first containing five thin pseudospines, and the second with 14-22 unbranched soft rays; both the second dorsal and anal fins on a raised base and opposite to each other; anal fin with 13-22 unbranched soft rays; pelvic fins relatively large, with a single pseudospine plus six soft branched rays, anterior or opposite to the first dorsal fin; females with brood pouch formed by the pelvic fins; infraorbital bones absent; postcleithrum absent; caudal fin relatively large, with 12-16 rays; 27-40 vertebrae.

Type Genus - *Solenostomus* Lacepède, 1803, extant.

Composition - Three genera, the extant *Solenostomus* (with four species), and the Eocene †*Calamostoma* and †*Solenorhynchus*; the Eocene genera are grouped together within the subfamily †Solenorhynchinae.

Subfamily †Solenorhynchinae n. subfam.

Diagnosis - Head length comprised between 2.5 and 3.7 times in SL; first dorsal fin relatively short, its length contained about 11 to 14 times in SL; pelvic-fin insertion located anterior to the first dorsal-fin insertion; pretrunk length contained between 2.7 and 2.9 times in SL; complete pretrunk rings more than four; second dorsal fin with 14(15) soft rays; anal fin with 13-14(15) soft rays.

Type Genus - †*Solenorhynchus* Heckel, 1854.

Composition - Two genera, †*Calamostoma* and †*Solenorhynchus*, from the Eocene of Monte Bolca.

Remarks - The genera †*Calamostoma* and †*Solenorhynchus* exhibit a number of diagnostic features that support their assignment to the ghost pipefish family Solenostomidae, including: body covered with stellate plates; nasal capsule triangular; pseudospines in the first dorsal and pelvic fins; four anterior abdominal vertebrae elongated; two widely separated dorsal fins; pelvic fins expanded and elongate, forming a brood pouch in females; metapterygoid, zygapophyses, and epineurals absent (Pietsch, 1978; Johnson & Patterson, 1993; Orr & Fritzsche, 1993; Orr, 1995). Moreover, these Eocene genera share a unique set of features (head length ranging between 26.4 and 36.5% SL; spinous dorsal-fin length between 7 and 8.6% SL; pelvic-fin insertion located anterior to the first dorsal-fin insertion; more than four complete pretrunk rings; pretrunk length between 30.1 and 36.3% SL; second dorsal and anal fin containing less than 16 rays) not observed in *Solenostomus* and that provides a clear evidence of their separate status within the expanded limits of the family Solenostomidae.

Genus †*Calamostoma* Agassiz, 1833

1833 *Calamostoma* AGASSIZ, p. 18.
1874b *Calamostoma* Agassiz - DE ZIGNO, p. 40.
1901 *Calamostoma* Agassiz - WOODWARD, p. 383.

Diagnosis - Body depth comprised between 5.0 to 7.7 times in SL; head length comprised 2.5 to 2.7 times in SL; seven pretrunk, 11 trunk, and eight tail complete rings of four-rooted stellate bony plates; total number of body rings 26 or 27, all complete; first dorsal fin situated 1.3-1.6 times closer to soft dorsal fin than to skull; caudal-fin rays moderately developed; caudal-fin length much shorter than head length; about 27 vertebrae, anterior four considerably elongated; strong ossified tendon inserting on the occiput; snout tubular; mesethmoid and preopercle bearing downward projecting spines; neural and haemal spines of the second preural vertebra posteriorly oriented.

Type species - *Syngnathus breviculus* Blainville, 1818 (= *Pegasus lesiniformis* Volta, 1796; syn. nov.), by monotypy and designation of Woodward (1901).

Remarks - The type species of †*Calamostoma* is †*C. breviculum* (Blainville, 1818) (Agassiz, 1833-1844; de Zigno, 1874b; Woodward, 1901; Eastman, 1905; Blot, 1980). This species was created based on a specimen erroneously assigned by Volta (1796) to the extant *Pegasus natans* Linnaeus (synonym of *P. volitans* Linnaeus), and subsequently referred by Blainville (1818) to †*Syngnathus breviculus*. Moreover, Volta (1796) described another specimen from Monte Bolca as †*Pegasus lesiniformis* and noted its similarity with the specimen referred to as "*P. natans*". The holotype of †*Pegasus lesiniformis* consists of a nearly complete skeleton with poorly preserved or falsified snout, which was figured in the lithograph (Fig. 2;

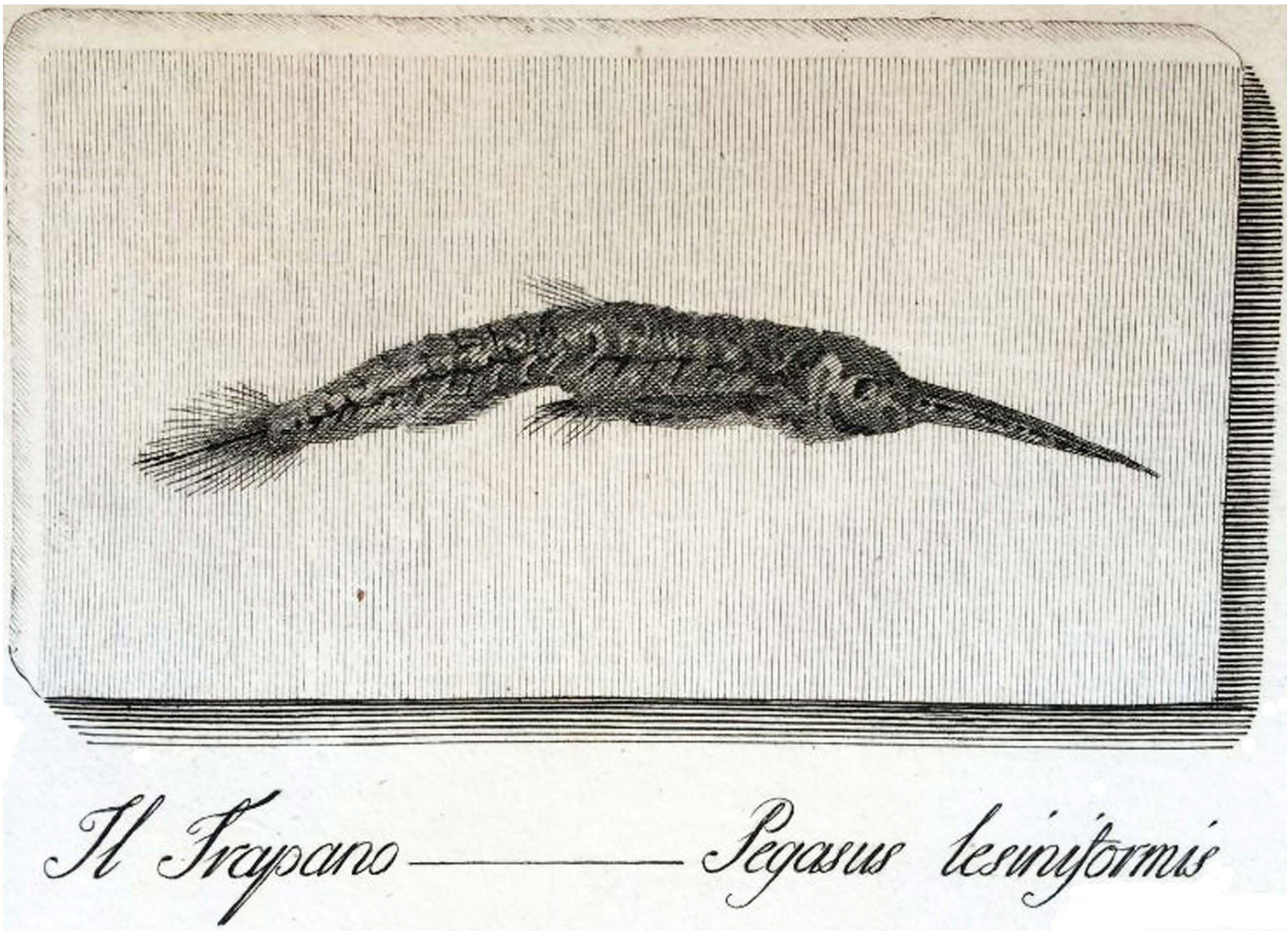

Fig. 2 - †*Calamostoma lesiniforme* (Volta, 1796), holotype figured on lithograph in Volta (1796: pl. 39, fig. 1) as †*Pegasus lesiniformis*.

Volta, 1796: pl. 39, fig. 1) as a long and pointed rostrum. This apparent artifact of preservation led Agassiz (1835) to assign this specimen to †*Rhinellus nasalis*, although the species name created by Volta (1796) unquestionably has priority. Almost 150 years later, Blot (1980) considered †*Rhinellus nasalis* as a synonym of †*Calamostoma breviculum*. Consequently, the correct name of this species must be †*Calamostoma lesiniforme* (Volta, 1796).

Composition - Type species only.

†*Calamostoma lesiniforme* (Volta, 1796)
(Figs 2-5, 7a)

1796 *Pegasus natans* (non Linnaeus, 1766) - Volta, p. 21, Pl. 5, fig. 3.
1796 *Pegasus lesiniformis* Volta, p. 159, Pl. 39, fig. 1.
1818 *Syngnathus breviculus* Blainville, p. 339.
1833 *Calamostoma breviculum* (Blainville) - Agassiz, p. 18, 276, Pl. 74, fig. 1.
1835 *Rhinellus nasalis* Agassiz, p. 291.
1874b *Calamostoma breviculum* (Blainville) - De Zigno, p. 167.
1901 *Calamostoma breviculum* (Blainville) - Woodward, p. 383.
1991 *Calamostoma breviculum* (Blainville) - Frickhinger, fig. on p. 768.

Diagnosis - As for the genus.

Holotype - The specimen figured by Volta (1796: pl. 39, fig. 1), complete skeleton with either poorly prepared or falsified snout; formerly housed in the Gazola Museum, present location unknown (Fig. 2).

Referred specimens - MNHN Bol50 (10982), nearly complete articulated skeleton, 58 mm SL, figured by Volta (1796: pl. 5, fig. 3) and Agassiz (1833-1844: pl. 74, fig. 1), holotype of *Calamostoma breviculum* (Fig. 3a); MCSNV IG60/IG61, nearly complete articulated skeleton, 93 mm SL, in part and counterpart (Fig. 3b-c); MCSNV VIIC9/VIIC10, nearly complete articulated skeleton, 40.5 mm SL, in part and counterpart (Fig. 3d-e); MCSNV IG59, partially complete articulated skeleton lacking the snout (Fig. 4b); MCSNV IM62, partially complete and disarticulated skeleton (Fig. 4a); NHMUK P.9430, partially complete articulated skeleton, dorsal (both spinous and soft) and anal fins not recognizable, 54.1 mm SL; all from the upper Ypresian, SBZ 11, *Alveolina dainelli* Zone (Papazzoni & Trevisani, 2006); Monte Bolca locality, Pesciara site.

Description - Measurements are summarized in Tab. 1.

The location of the holotype of †*Calamostoma lesiniforme* is unknown; perhaps it was lost. Based on the drawing provided by Volta (1796, pl. 39, fig. 1; Fig. 2), the holotype consists of an almost complete articulated skeleton with a poorly prepared or falsified snout; the latter resembles a long and pointed rostrum rather than the typical tube-shaped structure with a terminal mouth, clearly recognizable in the other specimens.

In general, the osteological structure is only partially recognizable since most of the postcranial skeleton is not exposed, being hidden by the strong stellate bony plates (Figs 3-4, 7). For this reason, although the general outline of the body is usually properly recognizable, very few of the internal osteological characters are clearly exposed. The body is elongated, laterally compressed and with a short caudal peduncle. The body depth is contained between 5.0 to 7.7 times in SL. The caudal peduncle depth is up to three times less than the body depth. The head is relatively large; the head length is contained between 2.5 to 2.7 times in SL. The body reaches its maximum depth just anterior to the pelvic-fin insertion.

Dimension	Measurement (%SL)
Standard length	40.5 mm
Maximum body depth	14.3
Head length	36.5
Orbit length	3.3
Snout length	26.0
Greatest snout depth	5.7
Least snout depth	4.2
Mandible length	6.1
Caudal peduncle length	8.1
Caudal peduncle depth	7.0
Predorsal (1st dorsal) length	66.6
Predorsal (2nd dorsal) length	86.4
Preanal length	85.9
Prepelvic length	60.8
Distance between pelvic and anal fins	21.4
Spinous dorsal-fin length	8.6
Pelvic-fin length	14.9
Caudal-fin length	17.4

Tab. 1 - Measurements of †*Calamostoma lesiniforme* (Volta, 1796), MCSNV VIIC9/VIIC10. Standard length in mm. All other measurements are expressed as a percentage of SL.

There are seven complete pretrunk rings of large four-rooted stellate bony plates; the subsequent plates are comparatively smaller. The total number of body rings is 26 or 27, with eight tail rings of which five are restricted to the caudal peduncle; all of them are complete. The anterior five rings consist of the dorsal, ventral and three transverse lateral plates each. In the succeeding rings unpaired (dorsal and ventral) ossifications seem to be absent, while each of the paired transverse lateral rows consists of four bony plates. Thus, there are four more or less regular longitudinal rows of bony plates behind the pelvic-fin insertion. Apparently, there are at least loose connections between the neighboring stellate bony plates in both transverse and longitudinal rows. The stellate ossifications bear a short central upright spine.

The head is elongated; its depth is contained 2.7-2.9 times in head length (Fig. 5). The regularly tubular snout is long, relatively narrow, and laterally compressed. The orbit is small; its length represents 9 to 17% of head length. The neurocranial bones are superficial in position (Fig. 5). There are few small spines along the dorsal midline

Fig. 3 - †*Calamostoma lesiniforme* (Volta, 1796) from the Eocene of Monte Bolca, Italy. a) MNHN Bol50 (10982), holotype of *Calamostoma breviculum* (Blainville, 1818), right lateral view. b) MCSNV IG60, left lateral view. c) MCSNV IG61 (counterpart of specimen in b), right lateral view. d) MCSNV VIIC10, left lateral view. e) MCSNV VIIC9 (counterpart of specimen in d), right lateral view. Scale bars correspond to 10 mm.

of the neurocranium, emerging anterior to the orbit on the frontals and the mesethmoid; these are well exposed in the specimen MCSNV IG60/IG61. The braincase is compact and only moderately preserved; its osteological

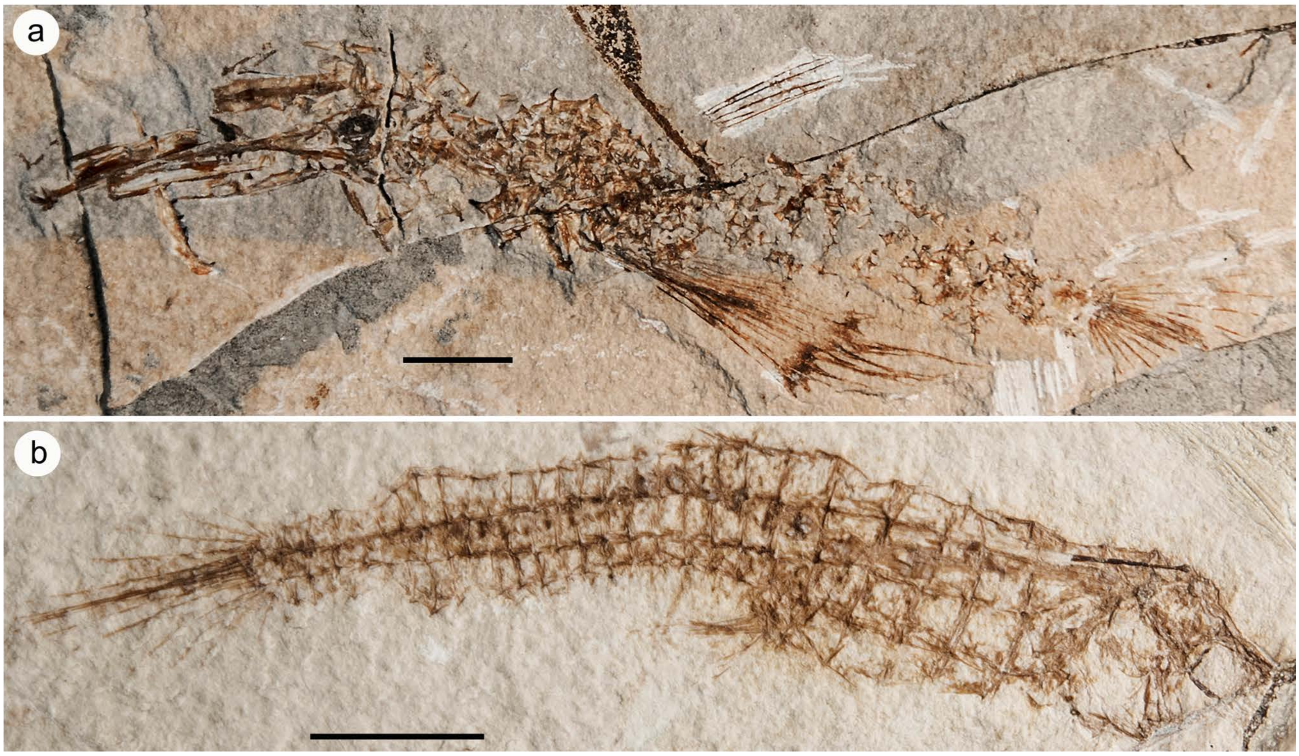

Fig. 4 - †*Calamostoma lesiniforme* (Volta, 1796) from the Eocene of Monte Bolca, Italy. a) MCSNV IM62, left lateral view. b) MCSNV IG59, right lateral view. Scale bars correspond to 10 mm.

architecture is unclear due to the problematic evaluation of the limits of most of its bones. The frontals are elongate and irregular in outline. The laterosensory canals seem to be absent. The supraoccipital appears to be almost triangular. The parasphenoid borders the lowermost portion of the orbit as a relatively slender shaft with convex ventral margin. The relatively small quadrangular lateral ethmoids constitute the anterior wall of the orbit and posterior border of the large and triangular nasal (=olfactory) capsule (Fig. 5). The very long and narrow mesethmoid embraces most of the nasal capsule and forms the roof of most of the tubular snout. The mesethmoid bears several strong and downward projected spines that are visible in the specimens MCSNV IG60/IG61 and MCSNV IM62. There is no evidence of the nasal and metapterygoid. The hyomandibula seems to be small and oblique. The quadrate seems to be more extended than the symplectic (unlike in *Solenostomus*; see Jurgersen, 1910). The anterior margin of the quadrate is nearly vertical and articulates with the narrow ectopterygoid. The edentulous upper jaw is clearly visible in the specimen MCSNV IG60/IG61 (Figs 3b-c, 5, 7); the premaxilla is small and narrow and bears a very short ascending process. The maxilla is expanded distally and has a prominent articular head. The lower jaw is relatively deep, but with a low and oblique symphysis; the dentary seems to be larger than the angulo-articular. The opercle is moderately large with a nearly rounded posterior profile; three radiating crests on the opercle are recognizable in the specimen MCSNV IG60/IG61 (Figs 3b-c, 5, 7). The preopercle has a short and slightly oblique ascending arm and a long and tapering horizontal arm that terminates approximately at the midlength of the snout. The lower border of the preopercle bears several strong but short spines. There are vertical striations on the lateral surface of the preopercle in the specimen MCSNV IG60/IG61 (Figs 3b-c, 5, 7). The distal portion of the hyoid bar is exposed in the specimen MCSNV IG60/IG61 (Figs 3b-c, 5, 7); the limits of its individual bones are unclear. The urohyal is narrow but relatively strong proximally. There are two branchiostegal rays (apparently right and left) which seem to divide distally.

A pair of large, robust and flattened ossified tendons articulates with the dorsal portion of the occipital region (on the epioccipitals or exoccipitals) of the neurocranium, extending posteriorly at least up to the third or fourth pretrunk ring of stellate bony plates.

The vertebrae are usually scarcely recognizable both because of poor preservation and because these are hidden by the strong stellate bony plates (Fig. 7). Twenty-seven vertebrae are recognizable. The vertebral centra are usually elongated and without zygapophyses, with the anterior four being much longer than the subsequent centra. The vertebral spines are obscured and not recognizable (perhaps they are weakly ossified). Ribs and epineurals are absent.

The caudal fin has a relatively deep base and is only moderately long; its longest medial rays do not exceed one half of the head length. There are 16 caudal-fin rays; the rays are segmented distally but unbranched. The structure of the caudal skeleton is partially recognizable in the specimen MCSNV IM62. The terminal vertebra is evidently formed by the fusion of the first preural centrum with the ural centra and the fan-shaped plate formed by the parhypural and hypurals. The second preural centrum appears to be fused with its expanded neural and haemal spines. Both the neural and haemal

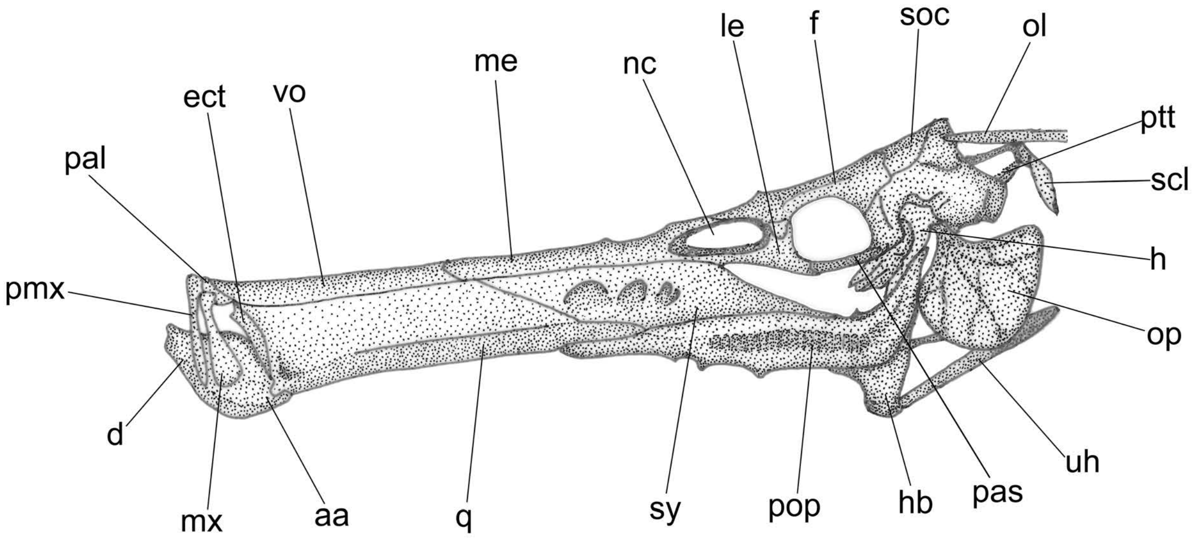

Fig. 5 - †*Calamostoma lesiniforme* (Volta, 1796) from the Eocene of Monte Bolca, Italy. Reconstruction of the head based on the specimens MCSNV IG59, MCSNV VIIC9/VIIC10 and MCSNV IG60/IG61, left lateral view. Abbreviations: aa: angulo-articular; d: dentary; ect: ectopterygoid; f: frontal; h: hyomandibula; hb: hyoid bar; le: lateral ethmoid; me: mesethmoid; mx: maxilla; nc: nasal capsule; ol: ossified ligament; op: opercle; pal: palatine; pas: parasphenoid; pmx: premaxilla; pop: preopercle; ptt: posttemporal; q: quadrate; scl: supracleithrum; soc: supraoccipital; sy: symplectic; uh: urohyal; vo: vomer.

spines are inclined posteriorly, unlike in certain species of the extant *Solenostomus*, in which the spines are inclined anteriorly (see Jurgensen, 1910; Fujita, 1990); according to Orr (1995), the second preural centrum of *Solenostomus paradoxus* Bleeker, 1854 lacks a haemal spine and bears a reduced neural arch, whereas that of *Solenostomus cyanopterus* (Pallas, 1770) has broadly expanded neural and haemal spines.

The first (spinous) dorsal fin is short-based and located behind the seventh pretrunk ring; it originates in the posterior portion of the anterior half of the axial body. It consists of five slender and relatively short pseudospines.

The second (soft) dorsal fin is relatively short-based; it is placed much closer to the caudal than to the spinous dorsal fin. There are about 11 trunk rings between the two dorsal fins. The somewhat raised base of the soft dorsal fin corresponds to three trunk rings. The soft dorsal fin is not completely preserved in any of the available specimens; about 14 soft rays appear to be present. The second dorsal-fin pterygiophores are difficult to recognize.

The anal fin is opposite to the soft dorsal fin and greatly resembles it in shape and size. The anal-fin base is also somewhat raised and extends for the length of three trunk rings. The anal fin is not completely preserved in any of the available specimens and appears to contain about 13 rays. The anal-fin pterygiophores are difficult to recognize.

The pectoral fin is poorly preserved. Of the pectoral girdle, the posttemporal, supracleithrum and cleithrum are partially recognizable. The posttemporal is bifurcated anteriorly and appears to be tightly sutured to the neurocranium. The cleithrum bears at least two spiny processes emerging along its posterior margin. There is no evidence of a postcleithrum.

The pelvic fins are located somewhat anterior to the spinous dorsal fin; there are two trunk rings between these fins. The pelvic fin seems to consist of a slender pseudospine plus six bifurcated rays. The pelvic-fin base is almost vertical in position. In all the examined specimens, except for MCSNV IM62, the pelvic fins are only moderately developed. The pelvic fins of MCSNV IM62 are especially long, being at least 2.7 times longer than the spinous dorsal fin (Fig. 4a). It is likely that this is a female specimen, and that its pelvic fins form the specialized brood pouch typical of ghost pipefishes. The basipterygium is not completely recognizable in any of the available specimens.

Traces of the original pigmentation pattern are preserved in the specimen MCSNV IM62 and document the presence of two transverse dark bands on the pelvic fins and of a medial longitudinal band on the caudal fin (Fig. 4a).

Genus †*Solenorhynchus* Heckel, 1854

1854 *Solenorhynchus* HECKEL, p. 126.
1863 *Solenorhynchus* Heckel - KNER & STEINDACHNER, p. 30.
1874a *Solenorhynchus* Heckel - DE ZIGNO, p. 296.
1874b *Solenorhynchus* Heckel - DE ZIGNO, p. 40.
1901 *Solenorhynchus* Heckel - WOODWARD, p. 380.

Diagnosis - Body considerably elongated and slender; body depth comprised more than 17 times in SL; about 20 rings of stellate bony plates present between the head and the first dorsal fin; head relatively small, its length comprised about 3.7 times in SL; first dorsal fin more than twice closer to the soft dorsal fin than to the skull; second dorsal fin with 14-15 rays; anal fin with 14-15 rays; caudal fin with 12 rays, narrow and about twice longer than skull; about 41 vertebrae.

Type Species - †*Solenorhynchus elegans* Heckel, 1854, by monotypy and designation of Woodward (1901).

Composition - Type species only.

†*Solenorhynchus elegans* Heckel, 1854
(Figs 6, 7b)

1854 *Solenorhynchus elegans* Heckel, p. 126.
1863 *Solenorhynchus elegans* Heckel - Kner & Steindachner, p. 31, Pl. 5, fig. 1.
1874a *Solenorhynchus elegans* Heckel - De Zigno, p. 297, Pl. 10, fig. 5.
1874b *Solenorhynchus elegans* Heckel - De Zigno, p. 168.
1901 *Solenorhynchus elegans* Heckel - Woodward, p. 380.

Diagnosis - As for the genus.

Holotype - NHMW 1853.XXVII.3, nearly complete articulated skeleton in a single plate, 57 mm SL (Fig. 6); upper part of the early Eocene, late Ypresian, about 50 Ma (Papazzoni et al., 2014); Monte Bolca locality, Monte Postale site.

Referred Specimens - None.

Description - Measurements are summarized in Tab. 2.

The holotype and only known specimen consists of a nearly complete but poorly preserved articulated skeleton. Although the general outline of the body is clearly recognizable, its osteological structure is largely unclear (Figs 6, 7b). The body is remarkably elongate, extremely slender and probably laterally compressed. The maximum body depth is contained 15.5 times in SL. The caudal peduncle is moderately elongate and slender, its depth is contained more than two times in the maximum body depth. The head is relatively small; its depth is equal to the maximum body depth, and its length is contained 3.7 times in SL.

Heckel (1854) calculated 36 rings of stellate bony plates on the trunk plus nine rings on the tail. Moreover, he restored the anteriormost plates as having the shape of "six-sided prisms" whereas the posterior plates resemble "four-sided prisms". Because of inadequate preservation, it is not possible to definitively confirm if the number of bony rings hypothesized by Heckel (1854; see also Kner & Steindachner, 1863) is correct, although it is certainly close to the actual. In addition, we are unable to recognize the outer morphology of the presumed six- and four-rooted plates. In any case, more than four pretrunk rings of stellate body plates are present. The stellate ossifications bear a short upright spine arising in their center.

Dimension	**Measurement (%SL)**
Standard length	57 mm
Maximum body depth	5.7
Head length	26.4
Orbit length	3.2
Snout length	18.0
Greatest snout depth	4.2
Least snout depth	2.6
Mandible length	4.1
Caudal peduncle length	17.6
Caudal peduncle depth	3.2
Predorsal (1st dorsal) length	62.5
Predorsal (2nd dorsal) length	78.2
Preanal length	77.7
Prepelvic length	54.2
Distance between pelvic and anal fins	20.4
Spinous dorsal-fin length	7
Pelvic-fin length	8.5
Caudal-fin length	66

Tab. 2 - Measurements of †*Solenorhynchus elegans* Heckel, 1854, holotype, NHMW 1853.XXVII.3. Standard length in mm. All other measurements are expressed as a percentage of SL.

The head is elongated, with its depth 3.9 times in head length. The middle portion of the snout is missing in the holotype. The orbit is small; its length is about 13% of head length. There seem to be two small spines along the dorsal surface of the neurocranium, one just above the orbit and another in the occipital region. The parasphenoid is exposed in the lowermost portion of the orbit as a slender and almost straight shaft. The posterior portion of the preopercle is relatively narrow and slightly curved. The anterior tip of the tubular snout mostly consists of the quadrate, with the dorsal portion probably formed by the vomer. Both the ectopterygoid and upper jaw are very tiny narrow bones, whereas the mandible is more robust, with an oblique symphysis. The mouth is edentulous.

Fig. 6 - †*Solenorhynchus elegans* Heckel, 1854 from the Eocene of Monte Bolca, Italy; holotype, NHMW 1853.XXVII.3. Scale bar corresponds to 10 mm.

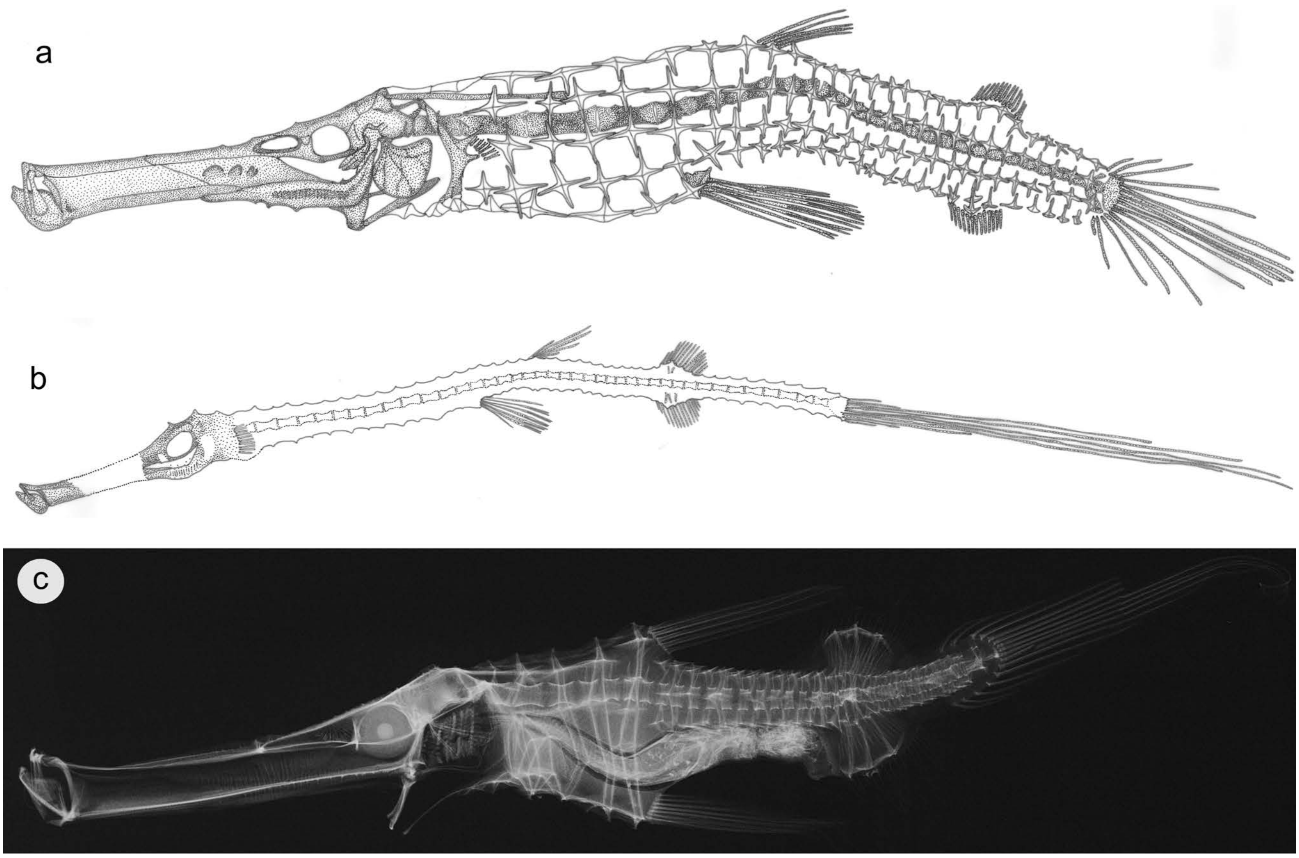

Fig. 7 - Representatives of fossil and extant ghost pipefish genera. a) †*Calamostoma lesiniforme* (Volta, 1796) from the Eocene of Monte Bolca, Italy; reconstruction of the skeleton based on specimens MCSNV IG59, MCSNV VIIC9/VIIC10 and MCSNV IG60/IG61, left lateral view. b) †*Solenorhynchus elegans* Heckel, 1854 from the Eocene of Monte Bolca, Italy; reconstruction of the skeleton based on the holotype NHMW 1853.XXVII.3; left lateral view. c) *Solenostomus cyanopterus* Bleeker, 1854, USNM 320114, radiograph, left lateral view; image courtesy of Sandra J. Raredon.

The vertebrae are scarcely recognizable because of the rather poor preservation of the holotype. Moreover, they are largely obscured by the stellate bony plates. Fourty-one vertebrae can be tentatively recognized. The vertebral centra are elongated, with the anterior three being somewhat longer than the succeeding centra. The posterior abdominal vertebrae seem to be the shortest in the series. The vertebral spines are not recognizable.

The first (spinous) dorsal fin has a short base; it is situated in the middle of the postcranial body length. The spinous dorsal fin contains five slender and relatively short, apparently feeble pseudospines. According to Heckel (1854), the first dorsal fin is located behind the 21st body ring.

The second (soft) dorsal fin is relatively short-based; it is placed slightly closer to the first dorsal than to the caudal fin. There are twelve trunk rings between the dorsal fins. The length of the somewhat raised base of the soft dorsal fin corresponds to three trunk rings. Heckel (1854) reported the presence of 17 rays in the soft dorsal fin; however, our examination of the specimen revealed not more than 14 or 15 rays. The rays are simple and short; their distal ends are incomplete. The dorsal-fin pterygiophores are not recognizable.

The anal fin is located opposite to the second dorsal and resembles it in shape and size. The anal fin also has a somewhat raised base corresponding to three trunk rings. About 14 or 15 simple rays are recognizable in the anal fin, and no anal-fin pterygiophores are visible.

The pectoral fins and their supports are not recognizable. Heckel (1854) supposed that the pectoral fins were characterized by numerous short rays, which are incompletely preserved.

The pelvic fins are located well anterior to the first dorsal fin (Figs 6, 7b); these two fins are separated by five trunk rings. The pelvic fin was formerly regarded as characterized by three rays bifurcated from their bases (Heckel, 1854) or multifurcated (Kner & Steindachner, 1863). We regard this fin as consisting of a slender spine plus six bifurcated rays, representing the typical condition of solenostomids. The pelvic fins are slightly longer than the first dorsal fin. As noted by Heckel (1854), the pelvic fins seem to be too small to form a brood pouch; however, it is likely that the single known specimen represents a male individual. The basipterygium is not recognizable.

The caudal fin is narrow and exceptionally long; its longest medial rays are two times longer than the head length and are as long as three quarters of the postcranial body length. There are not less than ten simple caudal-fin rays, most likely 12, as indicated by Heckel (1854). The structure of the caudal skeleton is not recognizable.

There is no evidence of the original pigmentation pattern of the fish.

DISCUSSION

Morphological and molecular evidences concur to suggest that the Solenostomidae forms the sister group to the Syngnathidae, the clade that comprises pipefishes, pipehorses, seahorses, seadragons, etc. (e.g., Pietsch, 1978; Orr, 1995; Keivany & Nelson, 2006; Kawahara et al., 2008; Song et al., 2014; Bannikov et al., 2017). These two families share several features (Orr, 1995), including prootics widely separated over the parasphenoid; branchiostegals one or two; three epibranchials; fourth pharyngobranchial toothplate absent; pectoral-fin radials remarkably hourglass-shaped; laterosensory canal absent; parental brooding reproductive mode. As far as concerns this latter synapomorphic feature, while ghost pipefishes are characterized by a typical female brooding of the eggs (Playfair & Günther, 1866; Orr & Fritzsche, 1993) using a brood pouch formed by expanded pelvic fins that are united to each other and to the abdomen along their dorsal margin, syngnathids exhibit a highly specialized male brooding with a variety of reproductive strategies (e.g., Herald, 1959; Wilson et al., 2003). Therefore, as also suggested by Wilson & Rouse (2010), a solenostomids plus syngnathids sister group arrangement necessarily implies a plesiomorphic acquisition of the specialized parental brooding that was established in the common ancestor of these lineages.

Orr (1995) suggested that †*Calamostoma* and †*Solenorhynchus* may represent intermediate forms between solenostomids and syngnathids (see also Wilson & Orr, 2011). Our study, however, indicates that both these Eocene genera must be regarded as genuine members of the family Solenostomidae due to the presence of a number of features exclusive of this family (e.g., body covered

	†*Calamostoma lesiniforme*	†*Solenorhynchus elegans*	*Solenostomus halimeda*	*Solenostomus cyanopterus*	*Solenostomus armatus*	*Solenostomus paradoxus*
Morphometrics (%SL)						
Head length (HL)	36.5	26.4	45.3-52.5	39.8-50.5	40.3-49.0	37.2-53.5
Snout length	26.0	18.0	30.1-36.7	21.4-34.3	26.1-35.1	25.8-38.6
Body depth	14.3	5.7	17.0-29.9	13.8-48.4	15.7-22.8	13.1-25.1
Pretrunk length	30.1	36.3	11.7-15.3	6.3-16.1	7.7-12.1	4.5-19.0
Trunk length	34.1	38.4	35.9-41.9	36.7-52.0	42.3-49.9	37.5-50.5
Caudal peduncle length	8.1	17.6	5.4-10.9	1.4-17.3	10.4-17.6	4.4-20.2
Caudal peduncle depth	7.0	3.2	3.5-4.4	3.2-10.4	2.9-3.7	2.3-8.0
Spinous dorsal-fin length	8.6	7	13.4-19.0	18.5-31.2	23.7-30.7	14.8-33.5
Pelvic-fin length	14.9	8.5	14.2-24.3	16.9-38.9	22.8-36.5	18.5-30.9
Caudal-fin length	17.4	66.0	16.0-22.6	30.3-44.9	33.3-45.6	15.9-35.1
Morphometrics (%HL)						
Mandible length	16.9	15.8	15.1-15.7	13.3-19.3	13.1-15.7	10.3-18.7
Greatest snout depth	15.7	16.0	9.9-12.6	9.0-23.2	9.1-10.9	7.4-16.0
Least snout depth	11.5	9.9	9.3-11.1	7.4-22.7	7.8-9.6	7.1-13.6
Orbit length	9.2	12.3	9.8-12.6	7.1-14.9	8.6-10.5	8.3-14.4
Meristics						
Vertebrae	27	41	32	32-33	34	32-33
Dorsal-fin rays	14?	14(15)	16-18	18-22	20-22	17-21
Anal-fin rays	13?	14(15)	17-19	17-21	20-22	18-22
Total rings	26-27	43?	27-29	27-35	27-35	31-35
Pretrunk rings	7 complete	? (more than 4)	4 complete	4 complete	4 complete	4 complete
Trunk rings	11 complete	?	11-13 (4-5 complete)	10-14 (4-8 complete)	12-15 (4-10 complete)	11-14 (4-8 complete)
Caudal peduncle rings	5	?	8-11	5-10	6-11	7-12
Tail rings	8 complete	?	16-18 (8-11 complete)	12-17 (5-9 complete)	15-18 (6-11 complete)	14-18 (5-11 complete)

Tab. 3 - Summary of selected morphometric and meristic features of fossil and extant species of the family Solenostomidae. Includes new data and data from Heckel (1854), Orr & Fritzsche (1993), and Orr et al. (2002).

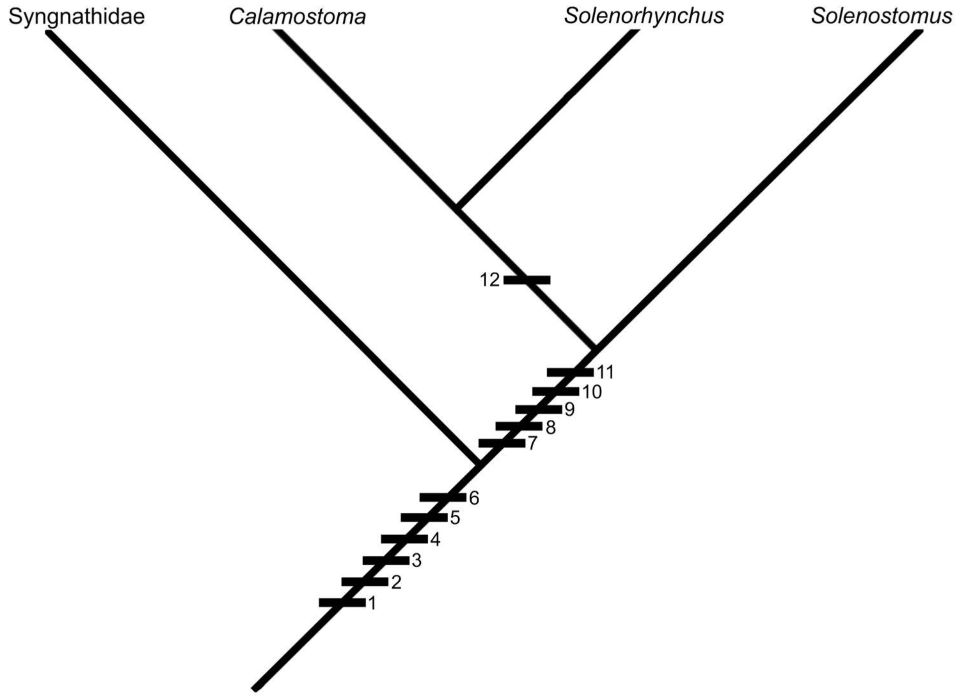

Fig. 8 - Cladogram showing hypothetical relationships of †*Calamostoma* and †*Solenorhynchus* within the Solenostomidae. Characters are: 1) branchiostegals one or two; 2) three epibranchials; 3) fourth pharyngobranchial toothplate absent; 4) laterosensory canals absent; 5) prootics widely separated over the parasphenoid; 6) parental brooding reproductive mode; 7) presence of pseudospines in the dorsal and pelvic fins; 8) pelvic fins with a single pseudospine plus six soft rays; 9) body covered with large stellate plates; 10) postcleithrum absent; 11) brood pouch formed by the pelvic fins; 12) pelvic-fin insertion located well anterior to the spinous dorsal-fin origin. Characters 1-6 from Orr (1995), 7 from Johnson & Patterson (1993), 9-11 from Pietsch (1978), Orr & Fritzsche (1993), and Orr (1995).

with stellate plates; nasal capsule triangular; pseudospines in the first dorsal and pelvic fins; four anterior abdominal vertebrae elongated; two widely separated dorsal fins; metapterygoid, zygapophyses, and epineurals absent). These two Eocene genera exhibit a series of morphometric and meristic features (Tab. 3) that clearly support their recognition as separate taxa within the Solenostomidae. Moreover, morphometric and meristic features seem to provide evidence of their sister-group relationships, even if some of these might represent the plesiomorphic condition for the family. For example, the overall elongation of the body, relative length of the head, and reduced development of pelvic-fin rays in male individuals are very similar to those of pipefishes and allies (e.g., Jurgensen, 1910; Dawson, 1985). A remarkable feature shared by the two Eocene stem-solenostomid genera is related to the relative position of the first (spinous) dorsal and pelvic fins with the insertion of the pelvic fin situated well anterior to the dorsal-fin origin. This condition is notably different from that typical of *Solenostomus* (see Fig. 7), in which the insertions of these fins are located approximately at the same level of the body (e.g., Jurgensen, 1910; Orr & Fritzsche, 1993; Orr et al., 2002). The interpretation of the polarity of this character is rather problematic because there is no evidence of the spinous dorsal and pelvic fins in syngnathids (as well as in many other syngnathiform families) and the condition within the highly specialized syngnathiforms is in many ways ambiguous. The insertion of the first dorsal fin is located well behind that of the pelvic fin in the shrimpfishes (Centriscidae), snipefishes (Macrorhamphosidae) and the Cretaceous *Gasterorhamphosus* (e.g., Sorbini, 1981; Bannikov & Carnevale, 2012), whereas it is located in front of that of the pelvic fin or approximately at the same level of the body in the trumpetfishes (Aulostomidae) and in the Eocene Aulorhamphidae (e.g., Jurgensen, 1910; Tyler, 2004). Considering the instability of the current understanding of syngnathiform evolution primarily due to the lack of a comprehensive phylogenetic analysis comprising both fossil and extant taxa and the variety of interpretations resulting from morphological and molecular studies (see Wilson & Orr, 2011), it is not possible to resolve conclusively the evolutionary significance of the mutual position of dorsal- and pelvic-fin insertions. For this reason, we tentatively interpret the condition shared by †*Calamostoma* and †*Solenorhynchus* as a feature supporting their sister-group relationship, thereby representing a synapomorphy of the †Solenorhynchinae (Fig. 8).

The monophyletic status of the subfamily †Solenorhynchinae hypothesized herein necessarily implies that the clade formed by the two Eocene stem-Solenostomidae †*Calamostoma* and †*Solenorhynchus* represents the sister group to the genus *Solenostomus*. Therefore, the Eocene occurrence of solenorhynchines implies that the *Solenostomus* lineage was already in existence at that time, thereby suggesting that ghost pipefishes experimented a considerable morphological disparity during the first part of the Paleogene. Such a hypothesis appears to be consistent with the very high values of morphological disparity exhibited by Eocene syngnathiforms, as revealed by a recent analysis of the general patterns of morphospace occupation and evolution of body shape variation of teleost fishes from the Eocene to the present (Marramà et al., 2016).

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