

An extraordinary pipefish (Teleostei, Syngnathidae) with fully developed anal fin from the Oligocene of the North Caucasus (SW Russia)

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KEYWORDS - *Syngnathiformes*, *Syngnathidae*, *Pshekhagnathinae* n. subfam., *Pshekhagnathus polypterus* n. gen. n. sp., *Oligocene*, *early Rupelian*, *North Caucasus*.

ABSTRACT - A new genus and species of pipefishes (*Syngnathiformes*, *Syngnathidae*), *Pshekhagnathus polypterus* n. gen. n. sp. is described from the Lower Oligocene (*Planorbella* Beds, *Lower Maikopian Series*) of the North Caucasus, Russia. Unlike all the other extant and fossil *syngnathids* known to date, which are characterized by a very small anal fin with two to six anal-fin rays, the new pipefish described herein has a fully developed anal fin as equally almost identical to its opposite dorsal fin. This remarkable morphological feature justifies the creation of a new pipefish subfamily - *Pshekhagnathinae* n. subfam. - to accommodate this early Oligocene form.

RIASSUNTO - [Un nuovo straordinario pesce ago (Teleostei, Syngnathidae) con una pinna anale completamente sviluppata proveniente dall'Oligocene del Caucaso Settentrionale] - *Pshekhagnathus polypterus* n. gen. n. sp., un nuovo pesce ago proveniente dai depositi dell'Oligocene Inferiore (letti a *Planorbella*, Serie del Maikopiano inferiore, Rupeliano inferiore, circa 32 Ma) affioranti lungo le sponde dei fiumi *Pshekha* e *Belaya*, nel Caucaso settentrionale, Russia, viene descritto sulla base di 11 reperti in ottimo stato di conservazione. A differenza di tutti gli altri membri della famiglia *Syngnathidae*, sia viventi sia fossili, il nuovo pesce ago descritto in questa sede presenta una pinna anale completamente sviluppata e quasi identica alla pinna dorsale ad essa opposta. Questo carattere risulta estremamente rilevante per definire la posizione tassonomica del pesce ago oligocenico in questione e giustifica la creazione della nuova sottofamiglia *Pshekhagnathinae* n. subfam.

INTRODUCTION

The pipefishes (*Syngnathiformes*, *Syngnathidae*) are predominantly marine inshore fishes very peculiar morphologically (Jungersen, 1910; Duncker, 1915; Rauther, 1925; Fritzsche, 1980; Dawson, 1985). They have an elongate and slender body completely encased in a series of bony rings, and a pore-like gill opening. The snout is tubular and terminates anteriorly with a small edentulous mouth. Ribs and supracleithra are absent. The dorsal fin, when present, is single, whereas the pelvic fins are always absent. When the caudal fin is absent, the tail is usually prehensile. The anal fin, when present, is very small representing a sort of “vestigial” structure that contains two to six rays.

Syngnathids are characterized by the frequent occurrence of sex-role reversals (female-female competition for mates), and remarkable adaptations for paternal care. During mating, the female deposits eggs directly on a specialized brooding area or into a pouch located in the abdominal or caudal area of the male, where the embryos are protected, nourished, aerated and osmoregulated by special structures (Breder & Rosen, 1966).

Both morphological and molecular studies concur to recover the ghost pipefishes family *Solenostomidae* as the sister group of the *Syngnathidae* (e.g., Pietsch, 1978; Orr, 1995; Keivany & Nelson, 2006; Kawahara et al., 2008; Song et al., 2014). The family *Syngnathidae* includes the pipefishes, pipehorses, seadragons and seahorses comprising slightly less than 300 extant species arranged

in about 57 genera, many of which are monotypic (Wilson & Orr, 2011). The family is usually (e.g., Nelson et al., 2016) divided into two subfamilies: *Hippocampinae*, or seahorses (upright posture with curved trunk, ventrally bent head and prehensile tail), and *Syngnathinae*, or pipefishes (tail predominantly not prehensile and head in line with the main body axis). The brooding structures are widely diverse and vary in complexity (a simple unprotected ventral area for gluing eggs; individual membranous egg compartments; protection of eggs in a pouch with pouch plates; bilateral pouch folds that grow together into a closed pouch; the completely enclosed brooding pouch of seahorse), and the brooding may occur on the abdomen, in the so-called *Gastrophori*, or on the tail, in the so-called *Urophori* (e.g., Herald, 1959). *Gastrophori* and *Urophori* therefore represent two informal groups into which the family *Syngnathidae* is subdivided (Duncker, 1915; Herald, 1959).

There are 56 extant genera of *syngnathines* (Nelson et al., 2016) and a single genus of seahorses, *Hippocampus*, with about 54 species. The ancestral morphotype for the *syngnathids* is that of pipefishes characterized by a horizontal body posture with a relatively stiffened tail and a well-developed caudal fin. However, the earliest phases of the evolutionary history of these fishes are elusive and their fossil record is relatively scarce and inadequately investigated. Most fossil pipefishes have been assigned to the extant genus *Syngnathus*, and this attribution should be verified in many cases. The earliest pipefishes, “*Syngnathus*” *heckeli* de Zigno, 1874a and “*S.*” *bolcensis*

de Zigno, 1874b have been reported from the upper Ypresian (Lower Eocene) of Monte Bolca in northern Italy (de Zigno, 1874a, b). *Prosolenostomus lessinii* Blot, 1980 was described from the same locality as a putative solenostomid (Blot, 1980), and subsequently transferred to the Syngnathidae (Bannikov, 2014; Carnevale et al., 2014).

Oligocene *Syngnathus* were recorded from the North Caucasus (*S. incertus* Daniltshenko, 1960), Romania, Poland, and Germany (*S. incompletus* Cosmovici, 1887) (see, e.g., Danil'chenko, 1960; Jerzmańska, 1968; Ciobanu, 1977; Bannikov, 2010). The Miocene species referred to *Syngnathus* were described from the North Caucasus, Crimea, Azerbaijan and Turkey (*S. altus* Daniltshenko, 1960; Danil'chenko, 1960; Bannikov, 2010), Croatia (*S. affinis* Kramberger, 1891 and *S. helmsii* Steindachner, 1860), Moravia (*S. incompletus*; Kalabis, 1957), Turkey (*S. faruki* Rückert-Ülkümen, 1991; Rückert-Ülkümen, 1991), Greece (Crete) (*S. heraklionis* Bachmayer, Kähsbauer & Symeonidis, 1984 and *S. kaehsbaueri* Bachmayer & Symeonidis, 1978; Bachmayer & Symeonidis, 1978; Bachmayer et al., 1984), Italy and Algeria (*S. albyi* Sauvage, 1870; e.g., Arambourg, 1927; Carnevale, 2007), and California (*S. avus* Jordan & Gilbert, 1919 and *S. emeritus* Fritzsche, 1980; Fritzsche, 1980). Moreover, the extant *S. acus* Linnaeus, 1758 and an undescribed syngnathid species were reported from the Pliocene of Italy (Sorbini, 1988). An indeterminate syngnathid species was reported from the Middle Miocene of North Caucasus (Carnevale et al., 2006). The Early Miocene *S. faruki* from Turkey (Rückert-Ülkümen, 1991) was regarded as a possible synonym of *S. altus* by Bannikov (2010).

The extant syngnathine genera *Doryrhamphus*, *Microphis* and *Nerophis* were recorded in the Lower Oligocene - *D. incolumis* (Daniltshenko, 1960) and *D. squalidus* (Daniltshenko, 1960) - of the North Caucasus (Danil'chenko, 1960), Lower Oligocene - *D. sp.* and *M. sp.* - of Germany (e.g., Micklich & Parin, 1996), Lower Miocene - *N. gracilis* Sergienko, 1971 - of Azerbaijan (e.g., Bannikov, 2010), and Middle Miocene - *N. zapfei* Bachmayer, 1980 - of Austria and Moldova (e.g., Bachmayer, 1980; Popov, 2017). Seahorses of the extant genus *Hippocampus* are known from the Middle Miocene of Slovenia (*H. sarmaticus* Žalohar, Hitij & Križnar, 2009 and *H. slovenicus* Žalohar, Hitij & Križnar, 2009; Žalohar et al., 2009). The extant species *H. ramulosus* (Leach, 1814) has been reported from the Pliocene of Italy (Sorbini, 1988).

Two Early Oligocene syngnathine genera were established based on material from the North Caucasus (*Maroubriichthys serratus* Parin, 1992; Parin, 1992) and France (*Nepigastrosyngnathus*; Pharissat, 1993). Finally, the peculiar fossil genus *Hipposyngnathus* Daniltshenko, 1960 is known to contain three species: the Oligocene, *H. convexus* Daniltshenko, 1960 from the North Caucasus and *H. neriticus* Jerzmańska, 1968 from the Polish Carpathians, and the Miocene *H. imporctor* Fritzsche, 1980 from California (Danil'chenko, 1960; Jerzmańska, 1968; Fritzsche, 1980; Prikryl et al., 2011). The subfamilial name Eogastrophinae or Hipposyngnathinae was proposed to accommodate this genus (Jerzmańska, 1968; Fritzsche, 1980).

Recently, a new syngnathid fish with peculiar morphology was discovered during the excavations of the Borisyak Paleontological Institute of the Russian Academy of Sciences (PIN) in the Lower Oligocene deposits outcropping along the Pshekha River in the Krasnodar Region and Belaya River in Republic Adygea (northwestern Caucasus). Unlike all the other syngnathids known to date, both extant and fossil, which are characterized by a considerably small anal fin with two to six anal-fin rays, the new Oligocene pipefish described herein exhibits a fully developed anal fin. In order to accommodate this new Oligocene taxon within the Syngnathidae, the creation of a new subfamily is necessary. Moreover, a slight emendation of the family diagnosis would be desirable to include the unusual set of features observed in the new Oligocene pipefish described herein. This new extraordinary Oligocene pipefish is described below as a new genus and species, *Pshekhagnathus polypterus* n. gen. n. sp.

MATERIAL AND METHODS

The eleven available specimens from the PIN collection were collected from the two localities along the Pshekha and Belaya rivers. The specimens required matrix removal before examination in order to allow investigations of their skeletal structures in as much detail as possible; these were prepared using thin needles. The counterparts of two specimens were prepared through the transfer method following the procedure proposed by Kaiser & Micklich (1995). Standard length (SL) is used throughout. The fossils were studied using a stereomicroscope Leica M165C equipped with camera lucida drawing arm.

SYSTEMATIC PALEONTOLOGY

Order SYNGNATHIFORMES sensu Nelson, Grande & Wilson, 2016

Superfamily SYNGNATHOIDEA Bonaparte, 1831

Family SYNGNATHIDAE Bonaparte, 1831

Subfamily PSHEKHAGNATHINAE n. subfam.

Diagnosis - Pipefishes with horizontal body posture; caudal fin present; cleithrum bearing few antrorse spines emerging along its outer surface; anal fin extended, comprising more than ten anal-fin rays.

Composition - *Pshekhagnathus* n. gen. only.

Genus *Pshekhagnathus* n. gen.

Type species *Pshekhagnathus polypterus* n. gen. n. sp.

Diagnosis - A pipefish genus with a strongly elongated snout and body; five or six infraorbital bones present; pectoral, dorsal, anal and caudal fins well-developed; principal ridges of each ring of dermal bony plates with a prominent retrorse spine caudad, ridge margins otherwise entire.

Etymology - From the Pshekha River and the generic name *Syngnathus*.

Composition - The type species and, probably, *Acanthognathus* (= *Doryrhamphus*) *squalidus* Danil'chenko, 1960 from the Lower Oligocene of the North Caucasus (see Taxonomic Remarks below).

Pshekhagnathus polypterus n. sp.
(Figs 1-7)

Diagnosis - As for the genus.

Holotype - PIN 5419/2, complete part and somewhat incomplete posteriorly (transfer prepared) counterpart, articulated skeleton, 82 mm SL (Figs 1a, 2a, 3).

Paratypes - PIN 5419/3, incomplete posteriorly part and incomplete anteriorly (transfer prepared) counterpart, articulated skeleton, ca. 72 mm SL (Fig. 4); PIN 5419/4, complete part and incomplete posteriorly counterpart, articulated but partly distorted skeleton, 61 mm SL; both from the type locality.

Referred specimens - PIN 5419/5, complete articulated skeleton, in part and counterpart, ca. 36 mm SL (Fig. 5); PIN 5419/6, complete articulated skeleton with anteriorly

incomplete counterpart, 111 mm SL; PIN 5419/7, articulated skeleton slightly incomplete posteriorly, in part and counterpart, > 70 mm SL; PIN 5419/8, articulated skeleton slightly incomplete posteriorly, > 65 mm SL (Fig. 1b); PIN 5419/9, articulated skeleton slightly incomplete posteriorly with partially complete counterpart, > 90 mm SL (Figs 1c, 2b); PIN 5419/10, posterior portion of the skeleton, measuring about 47 mm; PIN 5419/11, almost complete articulated skeleton, ca. 58 mm SL; all from the type locality; PIN 3363/181, complete articulated skeleton plus counterpart of the head, 48 mm SL; right bank of the Belaya River upstream from the Abadzekhskaya settlement, Adygea Republic, SW Russia; lower Rupelian, Lower Maikopian Series, Pshekhha regional stage, *Planorbella* Beds.

Type locality and horizon - Near the farmstead of Gorny Luch, right bank of the Pshekhha River, Apsheronsk District, Krasnodar Region, SW Russia (N44.33303, E39.80817); lower Rupelian, Lower Maikopian Series, Pshekhha regional stage, *Planorbella* Beds, around 32 Ma (see Leonov et al., 1998).

Etymology - From the Greek words πολύ for many and πτερόν for feather, in reference to the considerable number of anal-fin rays.

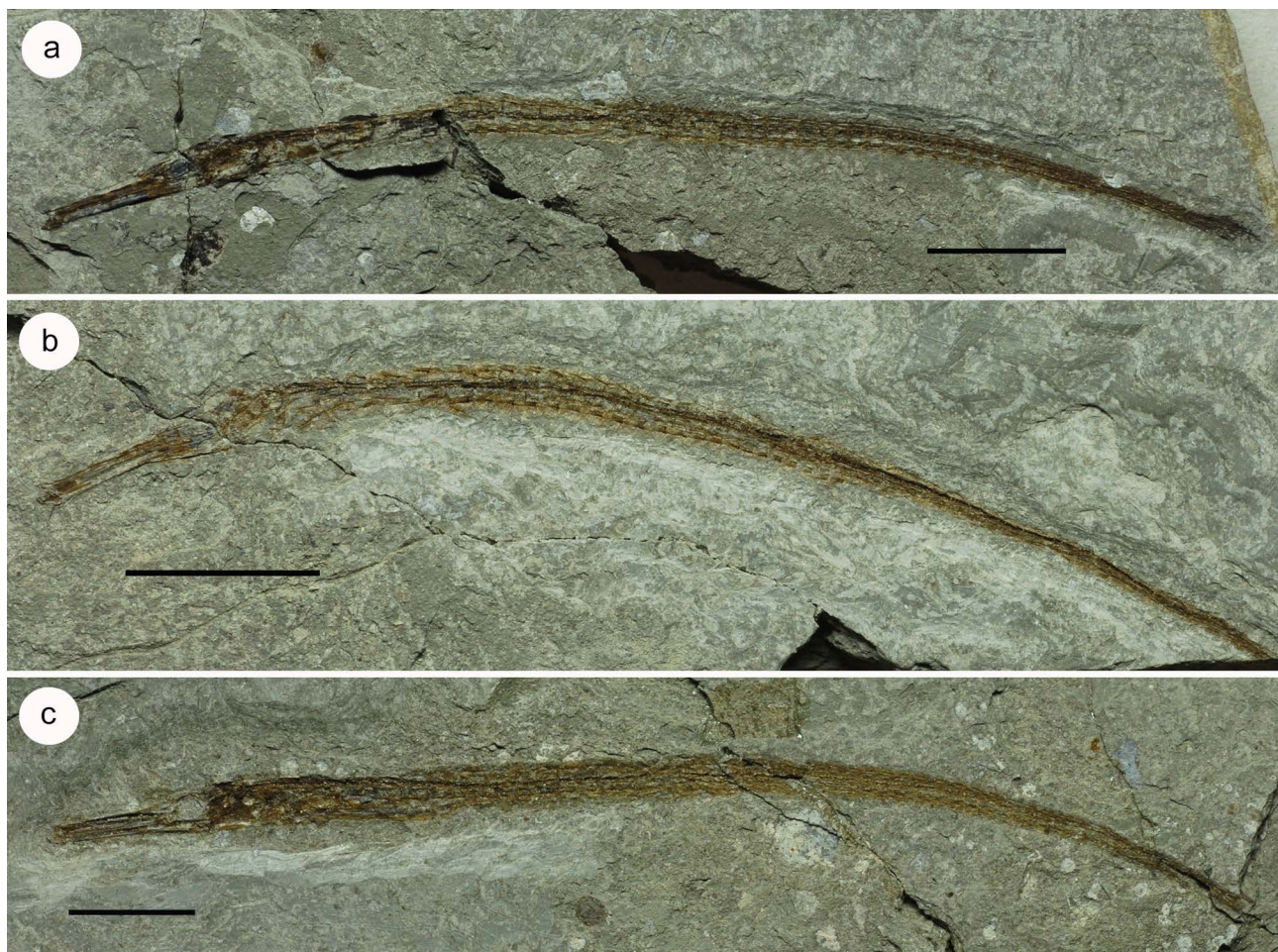


Fig. 1 - (Color online) *Pshekhagnathus polypterus* n. gen. n. sp. from the Lower Oligocene of Pshekhha River, North Caucasus, left lateral view. a) Holotype, PIN 5419/2. b) PIN 5419/8. c) PIN 5419/9. Scale bars correspond to 10 mm.

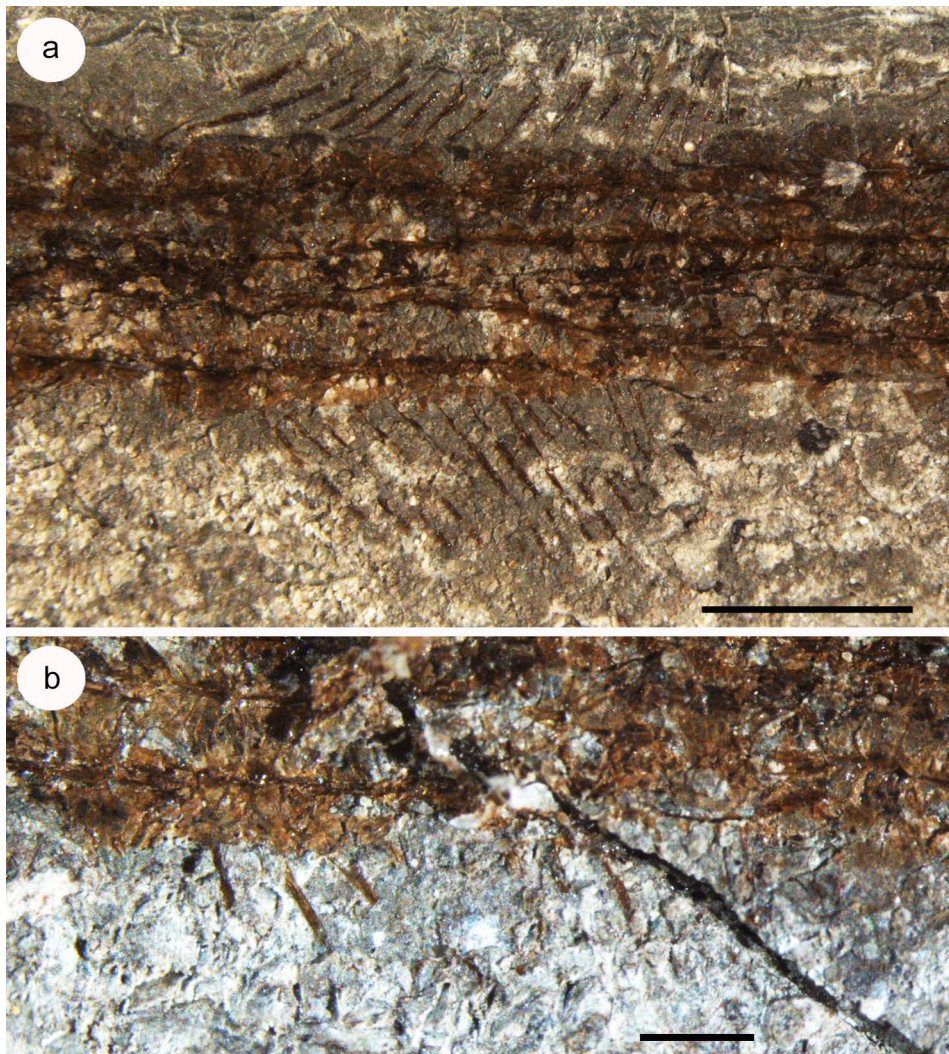


Fig. 2 - (Color online) *Pshekhagnathus polypterus* n. gen. n. sp. from the Lower Oligocene of Pshekha River, North Caucasus, left lateral view, details. a) Holotype, PIN 5419/2, dorsal and anal fins. b) PIN 5419/9, anal fin. Scale bars correspond to 2 mm.

Description - The body is very slender and elongate; its depth is contained approximately 24 times in SL. In adult specimens, the head length (HL) is contained approximately 5.4 times in SL and is about 4.4-4.5 times greater than the body depth.

The body is encased in a series of bony rings; the tail is not prehensile. There are 20 trunk rings (including the anal ring) and 32 tail rings, excluding the terminal element bearing the caudal fin. The number of total ring is 52. The principal body ridges are distinct, including the lateral trunk ridge. The body seems to be not laterally compressed, since no one of the available specimens is exposed in perfect lateral view. However, such kind of preservation makes it difficult to identify the exact lateral pattern of ridge configuration (e.g., Dawson, 1985). We tentatively interpret the inferior trunk and tail ridges as continuous, and lateral trunk ridge as confluent with lateral and superior tail ridge (Fig. 7). The principal ridge of each dermal bony plate is elevated and bears a prominent retrorse spine emerging in its posterior portion; otherwise ridge margins are always entire. The surface of the dermal bony plates is sculptured by the multiple grooves radiating

transversely from the principal ridge. The scutellae usually are not evident, except for a few in PIN 5419/6.

The head is elongated; its depth is contained 3.9-4.4 times in HL. The orbit is relatively small, rounded and placed in the upper half of the head. The horizontal diameter of the orbit is 12.5-16% HL. The snout is long and tubular; its length is 55-60% HL and 1.8-2.2 times longer than the postorbital distance. The snout depth is 2.5-3.4 times less than the head depth. The edentulous mouth is small and obliquely oriented, with the lower jaw length contained about 8-10 times in HL. The head ridges are not evident. Only a few of the specimens have the head preserved in lateral view; in many specimens the skull is oriented more or less obliquely, and in PIN 5419/6, PIN 5419/7 and PIN 5419/11 the neurocranium is almost dorso-ventrally exposed. The neurocranium seems to be wider than deep. Based on the specimen PIN 5419/6, the neurocranium width is about 20-21.5% HL, and the interorbital width is 3.4-3.8 times less than the neurocranium width measured just behind the orbits (at the level of the sphenotics). The limits of the neurocranial bones are unclear. The frontals occupy most of the

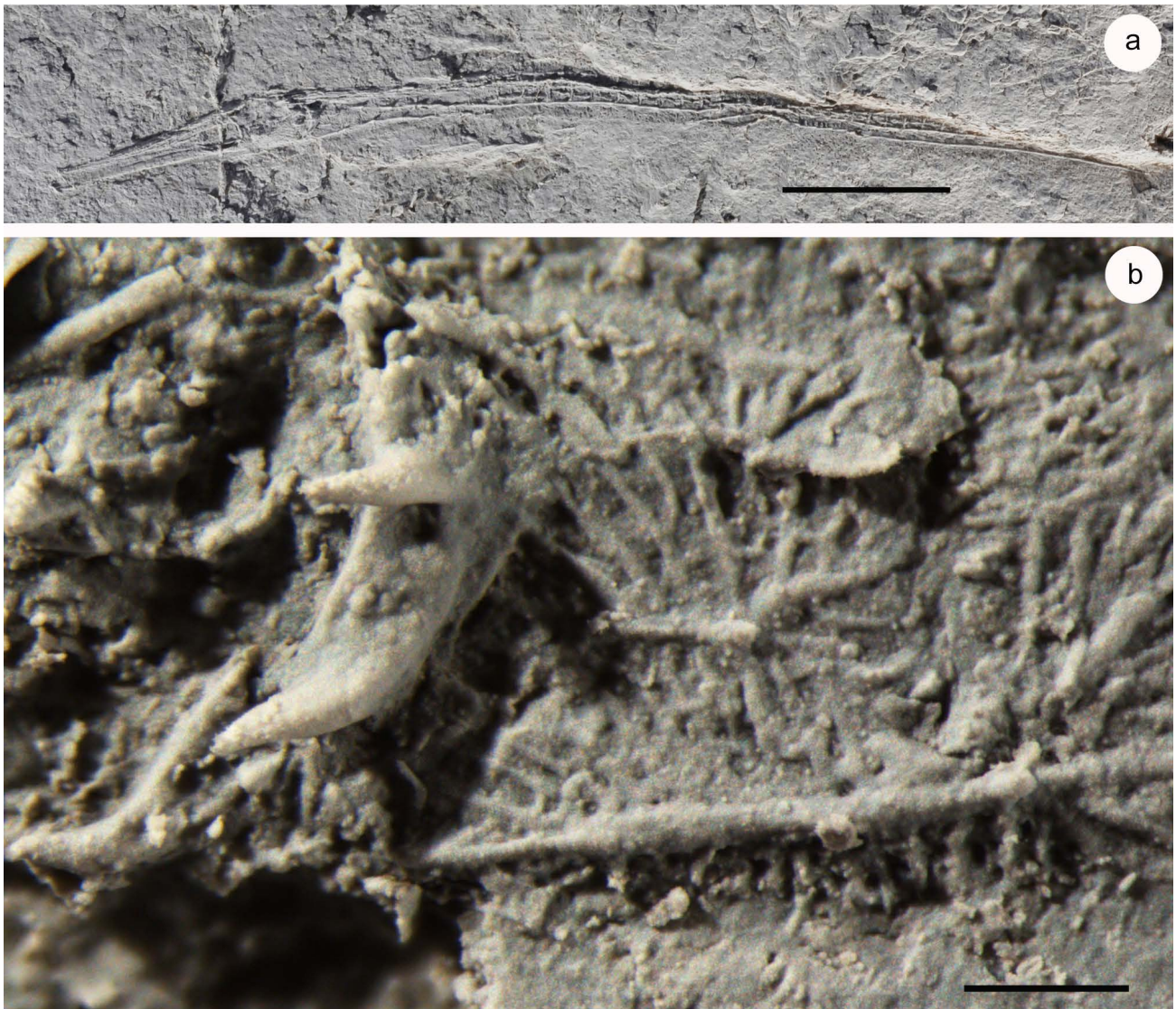


Fig. 3 - (Color online) *Pshekhagnathus polypterus* n. gen. n. sp. from the Lower Oligocene of Pshekha River, North Caucasus, left lateral view of the holotype, PIN 5419/2, transfer-prepared counterpart. a) General view; scale bar corresponds to 10 mm. b) Details of cleithrum and anterior dermal bony plates; scale bar corresponds to 0.5 mm.

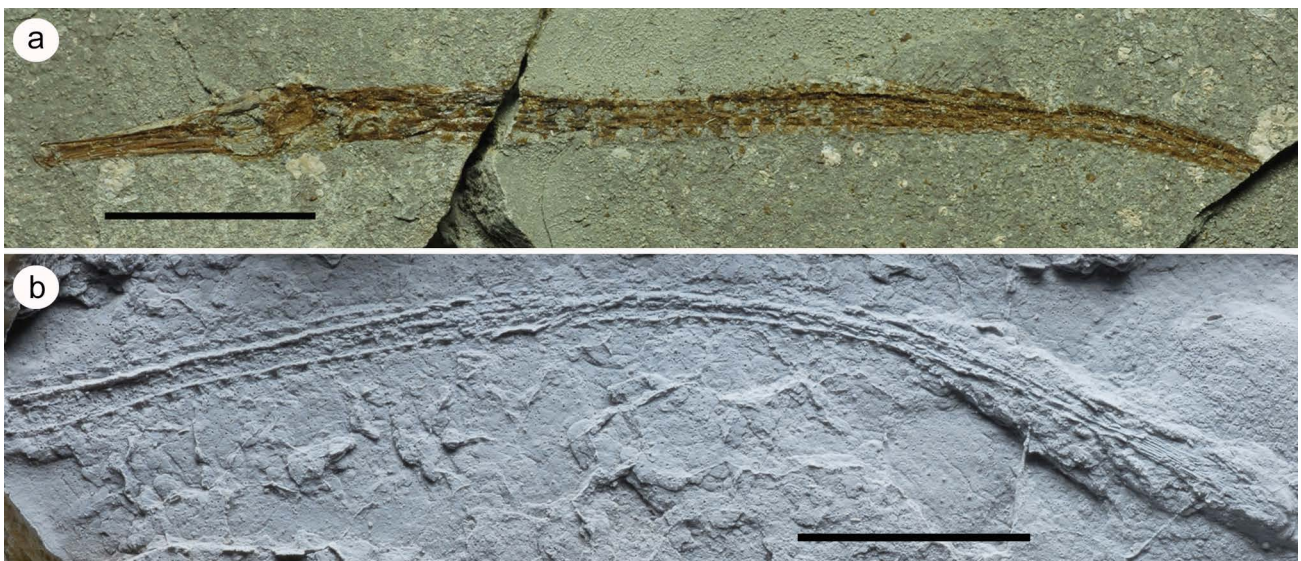


Fig. 4 - (Color online) *Pshekhagnathus polypterus* n. gen. n. sp. from the Lower Oligocene of Pshekha River, North Caucasus, left lateral view of the paratype, PIN 5419/3. a) General view. b) Transfer-prepared counterpart. Scale bars correspond to 10 mm.



Fig. 5 - (Color online) *Pshekhagnathus polypterus* n. gen. n. sp. from the Lower Oligocene of Pshekha River, North Caucasus, right lateral view of the head of PIN 5419/5. Scale bar corresponds to 1 mm.

braincase roof above the orbit and posteriorly (Fig. 6b). There is no evidence of the supraoccipital crest. The roof of the braincase is sculptured by the pits or furrows. The parasphenoid is slender and almost straight; it is exposed in the lower part of the orbit (Fig. 6b). The lateral ethmoid forms the anterior wall of the orbit and the posterior border of the nasal fossa (Fig. 6b). The very long and narrow mesethmoid embraces most of the nasal fossa and forms most of the roof of the tubular snout (Fig. 6b). The limits of most bones of the tubular snout are unclear, but it is evident that anterior portion of its ventral border is occupied by the quadrate (Fig. 6b). The infraorbital bones are represented by multiple (five or six) ossifications along the lateral surface of the tubular snout (well exposed in PIN 5419/4, Fig. 6), unlike in extant syngnathids that solely possess two or three infraorbitals (e.g., Jungersen, 1910; Leysen et al., 2010). Each of these ossifications is extensively sculptured by irregular ridges. The premaxilla is small and narrow; it is usually difficult to recognize. The maxilla is distally expanded (Fig. 6b). The lower jaw is relatively deep, with a low and oblique symphysis; the limits of the dentary and angulo-articular are not clear (Fig. 6b).

The opercle is relatively large (Fig. 6b); it is sculptured by pits arranged in multiple rows. The opercular ridge is moderately developed. The ascending arm of the preopercle is short, while the long horizontal branch is tapered and terminates at the midlength of the snout (Fig. 6b). The lateral surface of the preopercle has some vertical striations or furrows.

The limits of the bones of the hyoid bar are unclear. There are two very slender branchiostegal rays.

The vertebral column is usually hidden by the dermal bony plates. The vertebrae are elongate, but their precise number is unknown. However, the vertebral number likely corresponds to that of the bony rings (e.g., Neutens et al., 2017). There is a pair of ossified tendons along the vertebral column in the anterior portion of the body; these are particularly well exposed in the specimen PIN 5419/9.

The dorsal fin is relatively short-based; it originates in the first part of the posterior half of the body, closer to the caudal fin than to the tip of snout. The antero-dorsal distance is 53-61% SL. There are 17 to 18 soft unbranched dorsal-fin rays. The dorsal-fin base occupies one-half of a single trunk bony ring and at least five tail rings in the holotype. The length of the dorsal-fin base is greater than the height of the fin.

The anal fin originates slightly behind the dorsal-fin origin and is almost as equally high; the base of the anal fin is shorter than that of the dorsal fin. What appears to be the total complement of anal-fin rays is probably preserved only in the holotype, in which 14 or 15 rays are clearly recognizable (Fig. 2a).

The caudal fin is relatively small and consists of ten simple soft rays. The middle caudal-fin rays are longer than the outer ones. The structure of the caudal skeleton is not recognizable because it is hidden under dermal armor.

The pectoral fin is almost absent in the material examined, being preserved only as a few basal portions of rays in the holotype. Therefore, the total complement of the pectoral-fin rays is unknown. Most of the bones of the pectoral girdle are hidden by the dermal bony plates. The cleithrum is a strong slightly curved bone which borders the posterior margin of the opercle. The transfer-prepared counterpart of the holotype shows four strong antrorse spines projecting antero-laterally from the outer surface of the cleithrum (Figs 3b, 6b); these spines are remarkably well-exposed also in the specimen PIN 5419/6.

Unfortunately, the position and typology of the male brood area or pouch cannot be defined.

Ontogenetic variations - The SL of the examined specimens ranges from 36 mm to 111 mm. The smallest and presumably juvenile specimens (PIN 5419/5 and PIN 3363/181) exhibit a relatively larger head (4.6 to 4.8 times in SL) than the adults (5.4 times in SL). The specimen PIN 3363/181 also has a somewhat longer caudal fin with respect to SL. The tubular snout is somewhat conical rostrad in the adults, whereas in the juveniles it is homogeneously deep for most of its length (PIN 3363/181) or, at least, it becomes slightly thicker rostrad (PIN 5419/5; Fig. 5). In the largest specimen (PIN 5419/6) the retrorse spines are reduced in some of the principal ridges of the dermal bony plates in the anterior portion of the body.

DISCUSSION

Taxonomic comments

A detailed examination of the type materials of the Early Oligocene syngnathids described by Danil'chenko (1960, 1967) from the North Caucasus revealed the

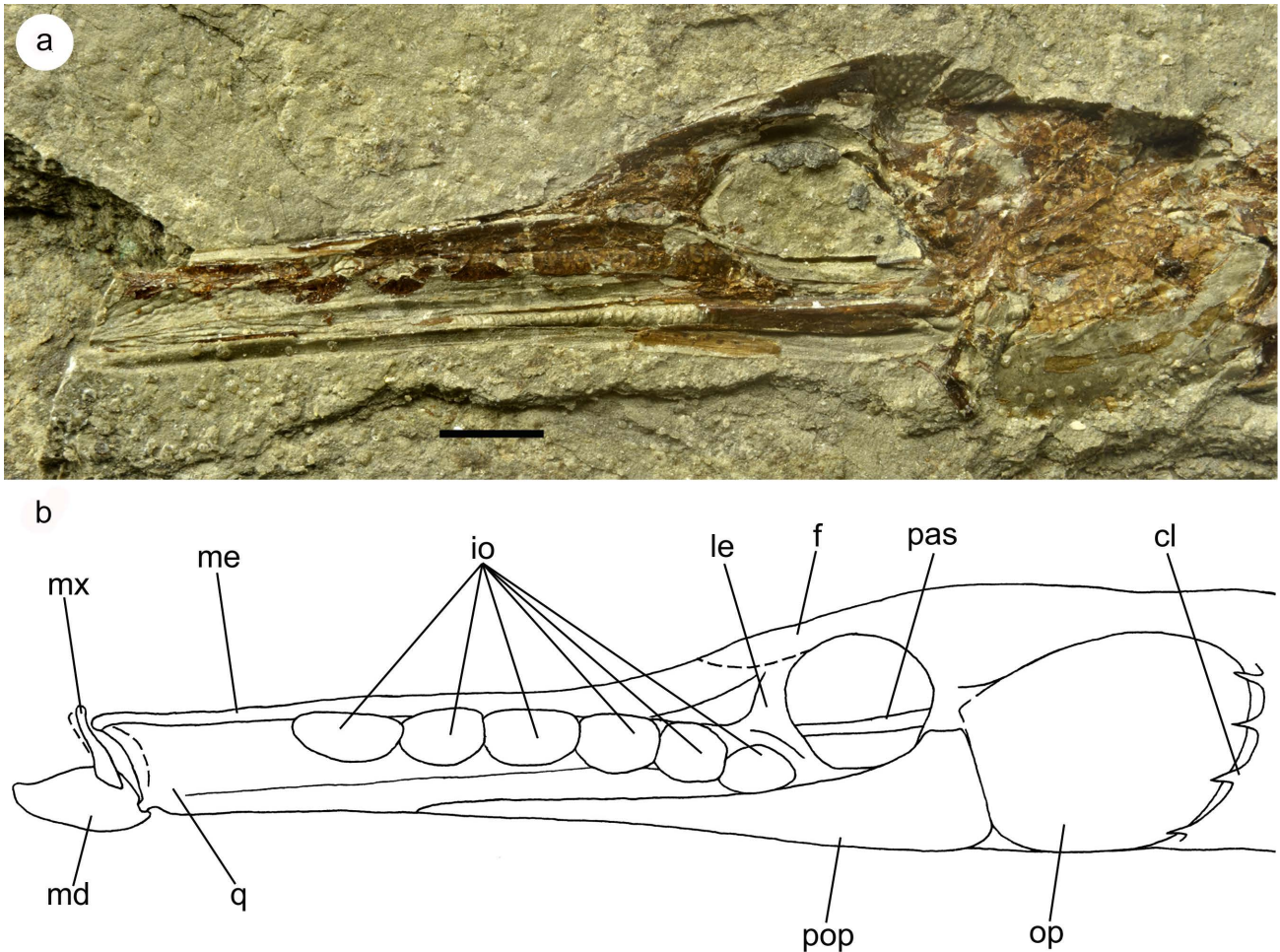


Fig. 6 - (Color online) *Pshekhagnathus polypterus* n. gen. n. sp. from the Lower Oligocene of Psekha River, North Caucasus, left lateral view of the head of the paratype, PIN 5419/4, showing the bones of the infraorbital series. a) General view; scale bar corresponds to 1 mm. b) Interpretative reconstruction. Abbreviations: cl, cleithrum; f, frontal; io, infraorbital bones; le, lateral ethmoid; md, mandible; me, mesethmoid; mx, maxilla; op, opercle; pas, parasphenoid; pop, preopercle; q, quadrate.

ambiguous systematic affiliation of *Acanthognathus* (= *Doryrhamphus*) *squalidus*. The holotype of this species was collected in the Republic of North Ossetia and figured by Danil'chenko (1960: pl. XXVIII, fig. 1) upside-down; it is possible that Danil'chenko (1960) regarded this orientation as correct, since he indicated the position of the dorsal fin. Actually, the dorsal fin is not preserved on the specimen, whereas the anal fin is preserved, although incompletely. Few anal-fin rays are present, including one of the anterior rays and four of the posterior ones; the gap between them implies that several additional anal-fin rays were lost either because of taphonomic reasons or during the preparing of the specimen. Thus,

most probably the species *squalidus* was characterized by the extended anal fin and therefore could not represent the genus *Doryrhamphus*. It is reasonable to hypothesize that this species should be regarded as belonging to the genus *Pshekhagnathus* n. gen. However, the inadequate preservation of the holotype of "*Pshekhagnathus*" *squalidus* n. comb. prevents a detailed comparative analysis of the taxonomic identity of this species and *P. polypterus* n. gen. n. sp.; the former seems to have less numerous bony rings and a relatively larger head, but many others of its characters are not recognizable.

Only ten specimens from the type locality and a single specimen from the coeval strata outcropped along the

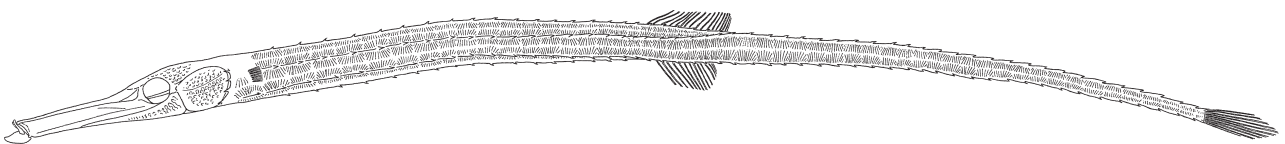


Fig. 7 - *Pshekhagnathus polypterus* n. gen. n. sp. from the Lower Oligocene of Psekha River, North Caucasus, reconstruction of the body, left lateral view.

Belaya River, Adygea Republic, 32 km from the type locality, are referred herein to *Pshekhagnathus polypterus* n. gen. n. sp. However, there are several more specimens in the PIN collection which perhaps could also belong to this species. These specimens were collected both in the type locality and along the Belaya River bank. However, these additional specimens could not be attributed confidently to the new taxon since the diagnostic features (particularly the extended anal fin) are not evident in them, mostly because of their inadequate preservation.

The extinct pipefish *Maroubriichthys serratus* was described based on a single specimen collected from lower Rupelian deposits exposed along the right bank of the Belaya River, Adygea Republic, North Caucasus (Parin, 1992), coeval of those of the type locality of *Pshekhagnathus polypterus* n. gen. n. sp. The holotype of *Maroubriichthys serratus* consists of a well-preserved relatively small individual (55 mm SL) similar to *Pshekhagnathus polypterus* n. gen. n. sp. in its proportions and possession of the spines on the dermal bony plates. However, none of the diagnostic features of *Pshekhagnathus polypterus* n. gen. n. sp., including the well-developed anal fin, are recognizable on the holotype of *Maroubriichthys serratus*, although the latter is almost perfectly exposed in lateral view (Parin, 1992: fig. 2; Bannikov, 2010: pl. IV, fig. 4).

Concluding remarks

As discussed above, the presence of a fully developed anal fin is the most striking morphological feature that characterizes the new Oligocene pipefish described herein. This feature unquestionably contributes to distinguish *Pshekhagnathus polypterus* n. gen. n. sp. from all the other syngnathids known to date, both extant and fossils. The interpretation of the evolutionary significance of this feature is problematic considering the lack of a comprehensive phylogenetic study of the Syngnathidae based on morphological features. In the absence of an unambiguous interpretation of the phylogenetic position of *Pshekhagnathus* n. gen., it is therefore impossible to define whether the presence of a fully developed anal fin in this Oligocene pipefish actually represents a genuine evidence of its primitive status within the Syngnathidae or the product of a phylogenetic character reversal (=taxic atavism; see Stiassny, 1992). It is interesting to note that *Pshekhagnathus* n. gen. exhibits an unusually high number of infraorbital bones (Fig. 6), representing an additional plesiomorphic condition that might provide further support to the hypothesis of its basal position within the Syngnathidae. In any case, it is our opinion that *Pshekhagnathus* n. gen. is characterized by a peculiar set of features that justify the creation of a new subfamily in order to accommodate it. Although the currently accepted higher classification divides the Syngnathidae into Syngnathinae and Hippocampinae (e.g., Nelson et al., 2016), there is a host of subfamily names that have been historically used. For example, Herald (1959) recognized six subfamilies (Doryrhamphinae, Hippocampinae, Nerophinae, Solenognathinae, Syngnathinae, Syngnathoidinae) and additional subfamilial groups (Acentronurinae, Haliichthyinae, Leptoichthyinae, Phyllopteryginae) were previously introduced by Whitley & Allan (1958). A recent molecular phylogenetic study (Wilson &

Rouse, 2010) demonstrated that the subdivision of the Syngnathidae into two subfamilial groups is untenable and that a number of well-defined subfamilial lineages (Doryrhamphinae, Haliichthyinae, Hippocampinae, Nerophinae, Phyllopteryginae, Solenognathinae, Syngnathinae, Syngnathoidinae) are clearly recognizable within the syngnathids. The rapid radiation of multiple syngnathid lineages during the earliest phases of their evolutionary history seems to be associated with a remarkable increase in morphological and functional complexity as indicated by both single-gene and total molecular evidence analyses (Wilson et al., 2001, 2003). Additional lineages that possibly originated during this initial radiation of syngnathids, such as the *Pshekhagnathinae* n. subfam. and *Eogastrophinae* (or *Hipposyngnathinae*), became extinct during the Cenozoic.

The earliest known pipefishes, from the Eocene of Monte Bolca, exhibit a reduced “vestigial” anal fin, fully consistent with that of all the other syngnathids, except for *Pshekhagnathus* n. gen. Although such an observation does not have any conclusive phylogenetic significance, at the same time it clearly indicates that the modern pipefish body plan was already in existence in the Early Eocene. Therefore, the ancient age of the modern pipefish body plan suggests that the functional role of the anal fin was lost early in the evolutionary history of these fishes. Pipefishes, and more generally all the members of the family Syngnathidae, are characterized by a type of swim with a slow speed and a high maneuverability, optimal for living in heterogeneous biotopes such as coral reefs and seagrass beds. These fishes use an amiiform mode of swimming, relying on rapid oscillations of their dorsal and pectoral fins for propulsion (Breder & Edgerton, 1942; Consi et al., 2001; Ashley-Ross, 2002). In pipefishes, swimming exclusively occurs through dorsal and pectoral fin movements, without any contribution of the anal fin and with a very limited use of the tail (e.g., Neutens et al., 2017). Therefore, also in this case, it is difficult to properly interpret whether the fully developed anal fin had a peculiar functional significance in the locomotion of *Pshekhagnathus* or solely represented a functionless atavistic structure resulting from the evolutionary re-expression of a plesiomorphic morphology.

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