General palaeontology, systematics and evolution (Vertebrate palaeontology)

New information about the anatomy of a peculiar fish of the genus *Hipposyngnathus* Daniltshenko, 1960

Nouvelle information à propos de l'anatomie d'un poisson particulier du genre Hipposyngnathus Daniltshenko, 1960

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ABSTRACT

An extraordinary pipefish genus *Hipposyngnathus* has been described from Paleogene and Neogene sediments from several localities in the world. This fish is clearly recognizable by its unpaired abdominal ventral ledge, but, unfortunately, no authors have been able to provide a detailed description of the skull until today. The newly discovered specimen from the Oligocene locality Hermanowa (Poland) is sufficiently preserved and allow for the first time the description and reconstruction of the skull morphology in detail. The skull shows a typical elongation of the preorbital area, tiny terminal jaws, a reduced number of circumorbital bones and a typical syngnathid cranial architecture. The snout is relatively short, but low. Separate skull bones have been identified.

RÉSUMÉ

Un extraordinaire syngnathe du genre *Hipposyngnathus* a été décrit dans des sédiments paléogènes et néogènes de différentes localités dans le monde. Ce poisson est facilement reconnaissable par sa bosse abdominale ventrale unique, mais malheureusement, aucun auteur n'a été capable, jusqu'à présent, de fournir une description détaillée du crâne. Le spécimen récemment découvert dans la localité oligocène d'Hermanowa (Pologne) est suffisamment bien conservé pour permettre la description et la reconstitution de la morphologie crânienne en détail. Le crâne présente une élongation typique de la zone préorbitale, des mâchoires terminales minuscules, un nombre réduit d'os circum-orbitaux et une architecture crânienne syngnatide typique. Le museau est relativement court, mais bas. Des os crâniens séparés ont été identifiés.

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1. Introduction

The family Syngnathidae is represented by pipefishes and seahorses (Nelson, 2006) which are recognizable, among others, by the elongated snout and dermal armour. Such morphological features allow us to recognize this group also in the fossil record: the oldest pipefishes are known from the Eocene (Patterson, 1993) and seahorses from Middle Miocene (Žalohar et al., 2009).

On the other hand, not only morphological, but also ecological features are characteristic for the recent representatives of the group. One of them, and probably the most characteristic, is the care of fertilized eggs by the male individuals ("male pregnancy") on the surface of their body (e.g., Wilson et al., 2001; Nelson, 2006). The concept of actuopaleontology (e.g., Kowalewski, 1999) allows us to suppose that similar features were also present in fossil representatives.

It is important to say that such a behavior induces the origin of specific anatomical adaptations on the body of male syngnathids. The position of this morphological structure, i.e., the brooding area (brood pouch), allows us to separate all members of the family into two morphological groups (e.g., Duncker, 1915; Herald, 1959): Gastrophori (the brood pouch is situated below the trunk) and Urophori (the brood pouch is located below the postanal part of the body). Although soft bodied breeding tissue is rarely fossilized, it is possible to suppose such an area in some fossil representatives on the basis of the skeletal elements, which supported a brood pouch. An extremely well developed ventral abdominal ledge was described and interpreted as supporting a brood pouch in the genus *Hipposyngnathus* (Daniltshenko, 1960; Jerzmańska, 1968; Fritzsche, 1980).

This genus is a specialized type of pipefish, easily distinguishable on the basis of an unpaired ventral abdominal ledge. Three species of the genus were described from Oligocene and Miocene sediments from different parts of the world. *Hipposyngnathus convexus* was originally described by Daniltshenko (1960) from the Oligocene of the Caucasus, but his specimens were lacking the postanal portions of their bodies. Later, the subfamily Eogastrophinae was erected and the new species *H. neriticus* was described from the Oligocene of Jamna Dolna by Jerzmańska (1968). The same author provided a more detailed description, and she also suggested the presence of a bilateral soft tissue brood pouch, which was medially divided by an unpaired ventral ledge. Fritzsche (1980) published a revision of the eastern Pacific syngnathids and, additionally, described a new species *H. imporcitor* from Californian Miocene sediments (Modelo Fm.). The same author also for the first time recognized the presence of a scutellum in the dermal armour of *Hipposyngnathus*, and presented an alternative hypothesis concerning the attachment of the fertilized eggs on the surface of the ventral ledge without any covering of the brood pouch by tissue flaps, similar to that in the genus *Maroubra* Whitley, 1948.

Although all of these authors provided selected morphometric characters of each species in the genus, and also a general description of the body, the cranial anatomy is still poorly known. Jerzmańska (1968) published a figure and a short description of the skull in which she identified the following elements: opercle, preopercle, quadrate, ectopterygoid, premaxilla, maxilla and dentary. Other authors (Daniltshenko, 1960; Fritzsche, 1980) did not provide any details about the cranial anatomy of the genus *Hipposyngnathus*.

The cranial anatomy of recent syngnathids has been described in detail in many works, e.g., Jungersen (1910), Kadam (1961), Leysen et al. (2010). Several important questions were still unclear, especially concerning the presence or absence of a metapterygoid, and were discussed for a long period of time (e.g., Jungersen, 1910; Azzarello, 1989), although, today, the presence of such an element is the generally accepted point of view (e.g., Azzarello, 1989; Leysen et al., 2010).

The main goal of this paper is (1) to describe and to discuss new information about the skull anatomy and (2) to get a general idea concerning of the feeding habits of the genus *Hipposyngnathus*.

2. Material and methods

The newly studied fossils were found in the locality of Hermanowa, south of the city of Rzeszów (South-East Poland). The common occurrence of the genera *Hipposyngnathus* and *Trachinus* in the sediments allows the classification of the appropriate strata into the IPM 2 zone (Kotlarczyk and Jerzmańska, 1976; Kotlarczyk et al., 2006). According to Kotlarczyk et al. (2006) the locality belongs to Paleogene Flysh strata which are older than the Menilite Formation. Other stratigraphic data are lacking.

The fossils are preserved as natural moulds at the surface of the light brown to grey "diatomite shales". The character of the fossils and the sediment (density and fragility) does not allow any detailed preparation.

Specimen Pi-F/MP/4a/1572/10 (counterpart Pi-F/MP/4b/1572/10) shows the skull and the preanal part of the body, with proximal parts of several dorsal fin rays; the second fossil Pi-F/MP/5a/1572/10 (counterpart Pi-F/MP/5b/1572/10) represents the abdomen without the skull and fins.

The studied specimens were compared with two specimens of *H. neriticus* (Pi-F/MP/1/1572/10 and Pi-F/MP/2/1572/10) from the Jamna Dolna locality and with data from the literature.

Morphometric data (Table 1) were measured with an accuracy to one tenth of a millimeter. A schematic illustration of the measured morphometric features and position of body ridges is given in Fig. 1.

It is impossible to recognize the actual number of the abdominal and tail rings because the anal fin is missing and, furthermore, because of the slightly displaced dermal armour and its unclear interpretation. On the other hand, Fritzsche (1980) suggested that the number of abdominal rings is same as the number of the rings with the developed unpaired ventral ledge (enlarged median ventral trunk ridge).

Table 1

Comparison of selected morphometric features of the genus *Hipposyngnathus* from different localities.

Tableau 1

Comparaison des caractéristiques morphométriques sélectionnées pour le genre *Hipposyngnathus* de différentes localités.

Species	*H. neriticus*						*H. convexus*	
Locality	Hermanowa		Jamna Dolna				Maikop	
Specimen number	Pi-F/MP/4a/1572/10		Pi-F/MP/1/1572/10		Pi-F/MP/2/1572/10		(according to Daniltshenko, 1960, specimen numbers unknown)	
	mm	% of head length	mm	% of head length	mm	% of head length	mm	% of head length
Head length	10.1	–	8.6	–	10.9	–	24–27	–
Preorbital length	5.2	51.5	4.9	57.0	5.7	52.3		50–53
Diameter of orbit	1.7	16.8	1.4	16.3	1.6	14.7		20–22
Head depth (directly after head lenth)	2.7	26.7	2.9	33.7	3.3	30.3		32–35
Maximum body depth	7.0	69.3	8.3	96.5	10.7	98.2		70–74
Maximum ventral cristae depth	2.9	28.7	3.2	37.2	4.3	39.4		?
Abdominal length	17.0	–	12.8	–	18.9	–		–

All fossil specimens are housed in the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow.

3. Abbreviations

Anatomical abbreviations: ar: anguloarticular; cl: cleithrum; dt: dentary; ect: ectopterygoid; fr: frontal; io: infraorbital; L: left side; lac: antorbitolacrimal; leth: lateral ethmoid; meth: mesethmoid; mx: maxilla; n: naris; op: opercle; pa: palatine; pmx: premaxilla; pop: preopercle; psph: parasphenoid; q: quadrate; soc: supraoccipital; sph: sphenoid; spop: suprapreopercular; v: vertebra; vm: vomer.
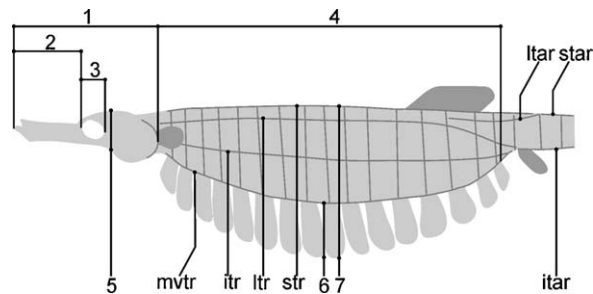
Body ridges (Fig. 1): itar: inferior tail ridge; itr: inferior trunk ridge; ltar: lateral tail ridge; ltr: lateral trunk ridge; mvtr: median ventral trunk ridge; star: superior tail ridge; str: superior trunk ridge.

Fig. 1. Selected morphometric features of genus *Hipposyngnathus*. Caudal part is not figured. 1. Head length. 2. Preorbital length. 3. Eye diameter. 4. Abdominal length. 5. Head depth at the level of the anterior edge of the operculum. 6. Maximal depth of ventral unpaired cristae. 7. Maximal abdominal depth. Body ridges: itar: inferior tail ridge; itr: inferior trunk ridge; ltar: lateral tail ridge; ltr: lateral trunk ridge; mvtr: median ventral trunk ridge; star: superior tail ridge; str: superior trunk ridge. The grey shadow represents body area.

Fig. 1. Caractéristiques morphométriques sélectionnées du genre *Hipposyngnathus*. La partie caudale n'est pas figurée. 1. Longueur de la tête. 2. Longueur pré-orbitale. 3. Diamètre de l'oeil. 4. Longueur abdominale. 5. Épaisseur de la tête au niveau du bord antérieur de l'opercule. 6. Épaisseur maximum des cristae ventrales uniques. 7. Épaisseur abdominale maximale. Stries sur le corps : itar : strie inférieure de la queue ; itr : strie inférieure du tronc ; ltr : strie latérale de la queue ; ltr : strie latérale du tronc ; mvtr : strie médioventrale du tronc ; star : strie supérieure de la queue ; str : strie supérieure du tronc. La partie ombrée en gris représente la zone corporelle.

4. Systematic part and description

Eogastrophinae Jerzmańska, 1968 (Hipposyngnathinae *sensu* Fritzsche, 1980)
Hipposyngnathus Daniltshenko, 1960
Hipposyngnathus neriticus Jerzmańska, 1968

The right side of the fossil (specimen Pi-F/MP/4a/1572/10) is preserved in lateral view (Fig. 2A). The skull is in articulation with the abdomen, but the tail is missing (it is broken off at the level of the sixth caudal ring).

Description and interpretation of the skull (Fig. 3A, B):

The snout is elongated and relatively shallow. The preorbital area is predominantly formed by the mesethmoid, the antorbitolacrimal and the preopercle. Jerzmańska (1968: Fig. 16 C) also reconstructed another elongated bone – the quadrate. The amount of elongation of the quadrate is unknown, because its posterior part is overlaid by the preopercle and the antorbitolacrimal in the specimen from Hermanowa and the normal preservation of the specimens from Jamna Dolna locality does not allow a reconstruction of such details. The exposed medial surface of the left quadrate on the same specimen shows an elongation, but its extent is uncertain.

In the apical part of the snout it is possible to recognize tiny edentulous jaws. The premaxilla is a minute vertical bone with a concave shape, which is situated anterior to the maxilla (the articulation between both is not clear). The maxilla has an elongate triangular shape. The articular head is not preserved; the distal part of the body of the bone is faint and overlaps the dorsal surface of the dentary.
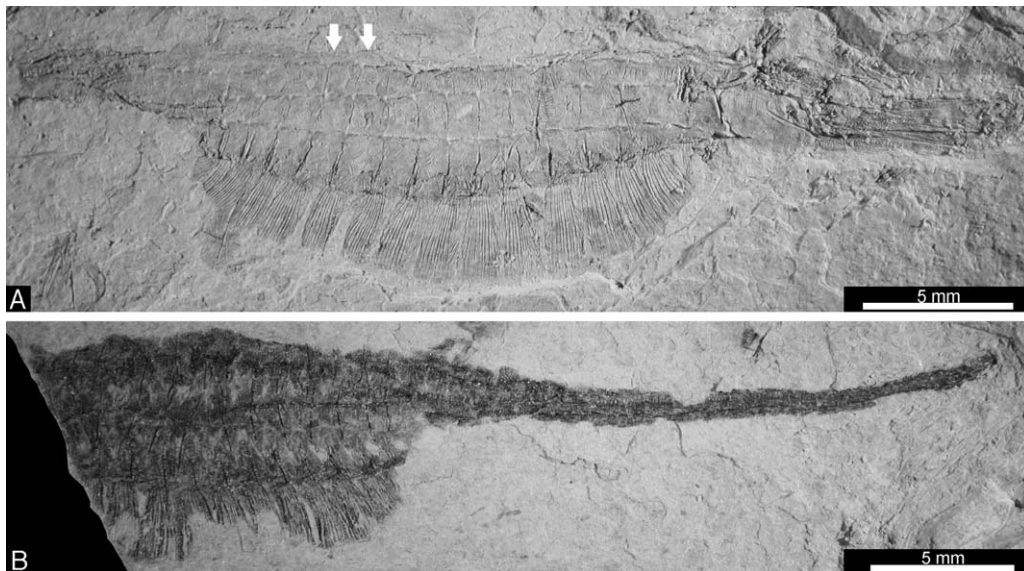
Fig. 2. *Hipposyngnathus neriticus*. Hermanowa locality, Oligocene. A. Specimen Pi-F/MP/4a/1572/10; the arrows show preserved remains of the dorsal fin. B. Specimen Pi-F/MP/5a/1572/10.
Fig. 2. *Hipposyngnathus neriticus*. Localité d'Hermanowa, Oligocène. A. Spécimen Pi-F/MP/4a/1572/10 ; les flèches indiquent les restes préservés de la nageoire dorsale. B. Spécimen Pi-/F/MP/5a/1572/10.

The dentary is a massive, cradle shaped bone with a longitudal notch (antero-posteriorly oriented, visible in the ventral third of the bone), which may represent a sensory canal, but this cannot be validated in the known specimens. Posteriorly, the dentary articulates with the anguloarticular which is short and deep, but insufficiently preserved.

The vomer is preserved in dorsal view and its anterior part is exposed; it projects between the mesethmoid and the antorbitolacrimal (its posterior border is not clearly distinguishable) and ventrally it is in contact with the presumed tiny palatine.

The mesthmoid contacts the antorbitolacrimal ventrally. Its caudal edge is in contact with the lateral ethmoid (the actual shape of the lateral ethmoid is uncertain). The naris is bordered by the mesethmoid, the antorbitolacrimal and the lateral ethmoid.

The anteriormost point of the quadrate is the articular head for the anguloarticular. The anterior margin of the quadrate is in contact with the ectopterygoid and the posteroventral margin articulates with the preopercle. Dorsal and caudal parts of the quadrate are overlaid by the antorbitolacrimal, so it is impossible to identify the actual shape and size of the quadrate.

The ectopterygoid is almost triangular in shape; the vertical limb is in contact with the quadrate and it is more robust than the horizontal limb. Dorsally, it is in contact with a tiny ossified element, which we identify as probably being the palatine.

We are able to recognized just one circumorbital, i.e., the antorbitolacrimal. This antero-posteriorly elongate triangular bone has a smooth surface and there are no traces of a sensory canal. Its dorsal edge is in contact with the mesethmoid, and ventrally it abuts the preopercle.

On the other hand, another circumorbital bone (infraorbital) may be fused together with the preopercle as suggested by the shape of the preopercle. If this is correct, the original position of this circumorbital prior to the fusion was anterior to the orbit, dorsal to the preopercle.

The preopercle is L-shaped; the ramus horizontalis is about three times longer than the ramus verticalis. The dorsal edge of the ramus horizontalis is elevated in the preorbital area and probably represents the incorporation of one of the circumorbital bones. The outer surface of the preopercle is cracked in the suborbital region.

The dorsal edge of the orbit is formed by the frontal. The shape of its posterior part is uncertain, but it is wider than the anterior region. In the dorso-caudal portion of the skull is a small bone, presumably the supraoccipital crest. A small part of the sphenoid is preserved in the posterior part of the orbit, which anteriorly connects with the parasphenoid, and the two lie in the ventral third of the orbit. No ascending processes of the parasphenoid are visible.

The opercle is oval shaped with a small depression in its anterodorsal part. On the surface of the opercular a series of concentric circular structures is preserved. The small element between the preopercle and the opercle is probably a suprapreopercle. The tiny aperture behind the opercle represents the impression of the cleithrum.

The internal sides of the left preopercle, the quadrate and the ventral part of the ectopterygoid are partly exposed below the right preopercle.

The external surfaces of the preopercle, the mesethmoid, the vomer and a small area behind the orbit bear a reticular pattern; other bones appear to be smooth.

Body and dermal armour:

Ventral to the opercle lies the jugular plate–according to Jungersen's nomenclature (1910). Dorsal to the occipital
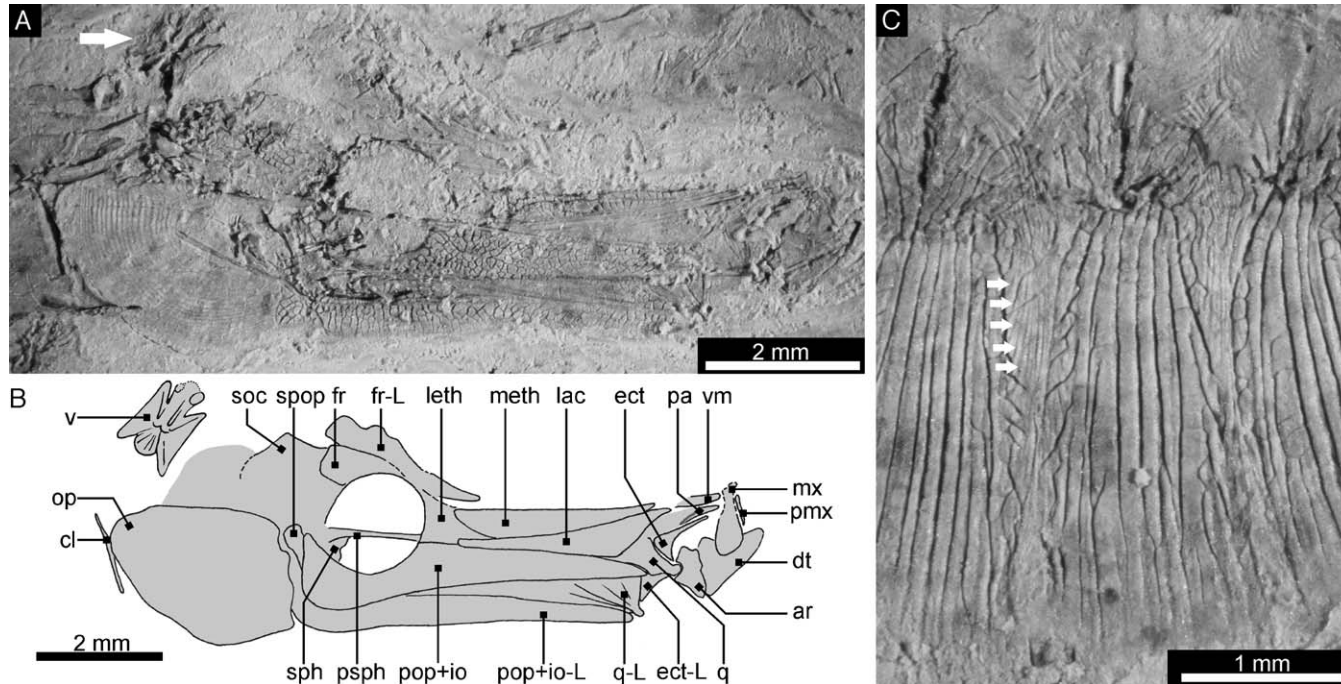
Fig. 3. *Hipposyngnathus neriticus*. Hermanowa locality, Oligocene. A. Detail of the skull (specimen Pi-F/MP/4a/1572/10); the arrow shows first vertebra. B. Interpretation of figure A. C. Detail of abdominal ridge, same specimen; the arrows show inserted filamentous elements. For abbreviations see section on materials and methods.

Fig. 3. *Hipposyngnathus neriticus*. Localité d'Hermanowa, Oligocène. A. Détail du crâne (spécimen Pi-F/MP/4a/1572/10) ; la flèche indique la première vertèbre. B. Interprétation de la figure A. C. Détail de strie abdominale, même spécimen ; les flèches indiquent les éléments filamenteux insérés. Pour les abréviations, voir la partie consacrée aux matériels et méthodes.

region lies the first vertebra that is preserved in ventral view (see arrow in Fig. 3A). It is possible to recognize large lateral projections and the prezygapophyses for the articulation with the occipital part of the skull. The second vertebra is preserved behind the head, but rotated from its natural anatomical position. Both disarticulated vertebrae are elongated antero-posteriorly, similar to that described and figured by Jungersen (1910: pl. IV, Fig. 3). Other vertebrae are not recognizable.

It is difficult to determine an accurate number of the abdominal and caudal armour rings because of the lack of an anal fin (see section material and methods). An unpaired ventral crista is present up to about the 17th ring. All rings are strengthened by scutellae. A few disarticulated scutellae also lie around the body.

The unpaired ventral ledge is formed by an enlarged median ventral trunk ridge on each abdominal ring. The space between surrounding ridges is filled by delicate filamentous elements (arrows in Fig. 3 C).

The proximal parts of seven dorsal fin rays are preserved in the posterior part of the body (see arrows in Fig. 2A). It is highly probable that this is not the total number of dorsal fin rays, but others are not preserved. Other fins are lacking.

Specimen Pi-F/MP/5a/1572/10 (Fig. 2B, main part) is preserved as a partial body missing the skull and the cranial part of the trunk. The fins are lacking. The dermal armour is well preserved, although slightly disarticulated (the rate of disarticulation is higher in the caudal region). Its general structure and extent of armour cristae appears to be the same as the one that described and figured by Jerzmańska (1968: Fig. 16D,A, respectively). The actual numbers of abdominal and caudal rings are not known. Each ring is supported by scutellae. Each scutellum (Fig. 4 C) has a horizontal and vertical ridge with the vertical one extending prominently into the dorsal apex. Web-like structures spread out from the ridges.

5. Discussion

5.1. Anatomy

The circumorbital bones in genus *Hipposyngnathus* are modified similar to those of other syngnathids (Branch, 1966; see discussion in Leysen et al., 2010, p. 265). According to Nelson (2006), the members of suborder Syngnathoidei usually have a lachrymal (antorbitolacrimal) present, whereas the other circumorbital bones are usually missing. Leysen et al. (2010) described the situation in *Syngnathus rostellatus*, in which at most two circumorbital bones can be found (in one specimen they found just one circumorbital, which appeared to be fused with the second one). We are not able to recognize the number of circumorbital bones in our specimens from Jamna Dolna, and neither Daniltshenko (1960) nor Jerzmańska (1968) described the number of circumorbitals. Fritzsche (1980) mentioned two infraorbitals for *H. importcitor* without giving a more precise description and position.

5.2. Paleoecology and feeding habits

Hipposyngnathus was probably a neritic (Jerzmańska and Kotlarczyk, 1968) or pelagic (Daniltshenko, 1960; Fritzsche, 1980) type of fish, similar to other syngnathids. The suggested living conditions are based on comparison with recent relatives and also on the basis of the association with shallow water fish (sublittoral *Trachinus minutus* (Jonet, 1958)) in the appropriate strata (Kotlarczyk et al., 2006). Furthermore, *Hipposyngnathus* fossils were found together with fossils of algae, sea grass and swimming crabs of the genus *Portunus* Weber, 1795 (Jerzmańska and Kotlarczyk, 1968), which is reminiscent of present-day assemblages associated with floating algae. We lack any other information about the paleoecology of this genus.

The whole body is elongate and relatively slim (reconstruction in Fig. 4A), the same as in other syngnathids, which represents an adaptation for living among sea grass. With our new restoration of the main parts of the skull (Fig. 4B), we are able to say that the snout of *Hipposyngnathus* comprises about 50% of head length (Table 1; Daniltshenko, 1960; Jerzmańska, 1968) and it was relatively shallow in contrast to the previous reconstruction by Jerzmańska (1968: Fig. 16C). The possibility of reconstructing the feeding ecology is connected with the knowledge of cranial architecture and its comparison with the same features in recent syngnathids.

Kendrick and Hyndes (2005) provided a functio-morphological analysis of different syngnathid species in regard to snout morphology correlated with feeding behavior. The study was based on specimens from the south-western Australian region. According to their results, syngnathids with long snouts feed on more mobile prey than the morphotypes with shorter snouts, and if we compare morphometric characters of the head of *Hipposyngnathus* (Table 1) with results summarized in Fig. 3 by Kendrick and Hyndes (2005), we can say that *Hipposyngnathus* belongs into the short-snout or transitional category. Analogous to the material described and discussed by Kendrick and Hyndes (2005, mainly Table 5), we can infer that prey of *Hipposyngnathus* was probably composed mainly of carid shrimps, amphipods, isopods, copepods, and mysids.

5.3. Generic character or sexual dimorphism?

It is interesting to note that preserved *Hipposyngnathus* specimens are generally classified as males. Females probably lacked the distinctive medial ventral rib (there is no necessity to support a brood pouch), so they can be confused with specimens of the genus *Syngnathus* Linnaeus, 1758, as was mentioned by Jerzmańska (1968: 439). Lack of female specimens can also be explained by different ecological demands. The latter possibility is represented by the fact that the ventral rib can be present in both sexes. In such a case the question remains, whether the ventral rib really represents a morphological structure associated with the process of reproduction.

Although the specimens from Hermonowa display some differences in morphometric characters compared to the
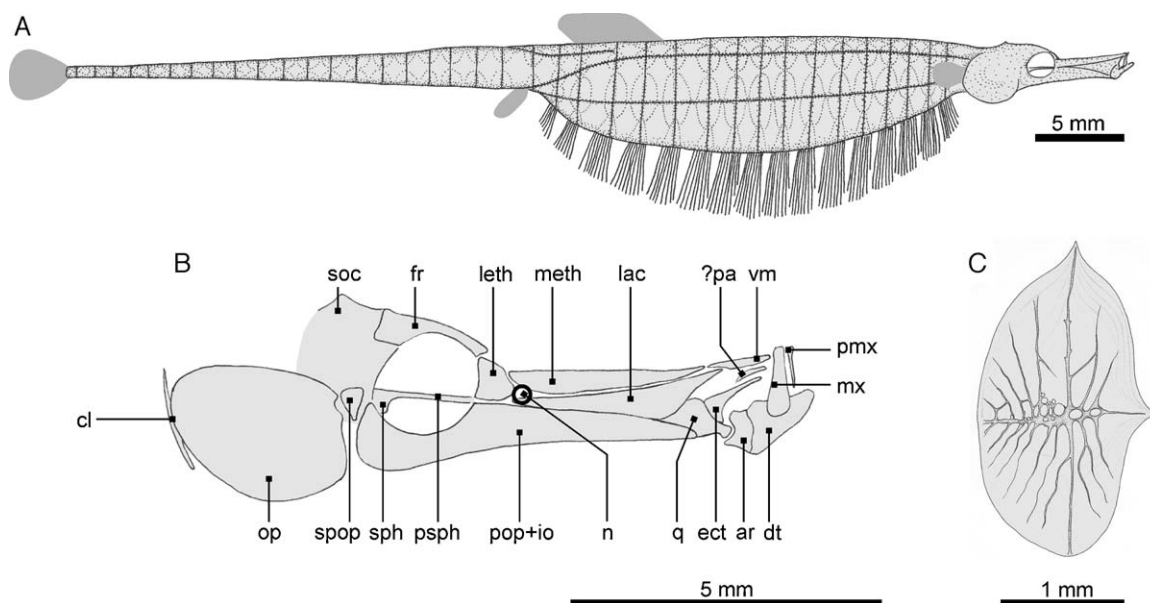
Fig. 4. *Hipposyngnathus neriticus*. Hermanowa locality, Oligocene. A. Reconstruction (assumed size and shape of the fins are indicated by grey shading). B. Reconstruction of the skull. C. Reconstruction of the scutellum. For abbreviations see section on materials and methods.
Fig. 4. *Hipposyngnathus neriticus*. Localité Hermanowa, Oligocène. A. Reconstitution (les taille et forme supposées des nageoires sont indiquées par les zones ombrées grises). B. Reconstitution du crâne. C. Reconstitution du scutellum. Pour les abréviations, voir la partie consacrée aux matériels et méthodes.

specimens from Jamna Dolna and to the Caucasian specimens (Table 1), these features are not sufficient for the erection of a new taxon. These differences are probably caused by different types of preservation and, maybe, by the ontogenetic stages of the specimens.

The specimens of *H. imporcitor* from the Californian Miocene were not investigated, so the detail comparison was not possible.

5.4. Taphonomic note

Beneath the ventral to the articulated elements of the right side of the skull, the same bones (more accurately the ectopterygoid, the quadrate and the preopercle, see Fig. 3A and B) from the left side are visible in medial view. A similar situation was figured for *Syngnathus avus* Jordan and Gilbert, 1919 from the Californian Miocene by David (1943: pl. 9, Fig. 6). This interesting taphonomic phenomenon is probably caused by a lack of stiff tissue in the floor of the buccal cavity. After dying, the soft tissue decomposes and the skull bones can be slightly displaced during the first phases of diageny.

Acknowledgements

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