A new look at the Cretaceous Lamprey *Mesomyzon* Chang, Zhang & Miao, 2006 from the Jehol Biota
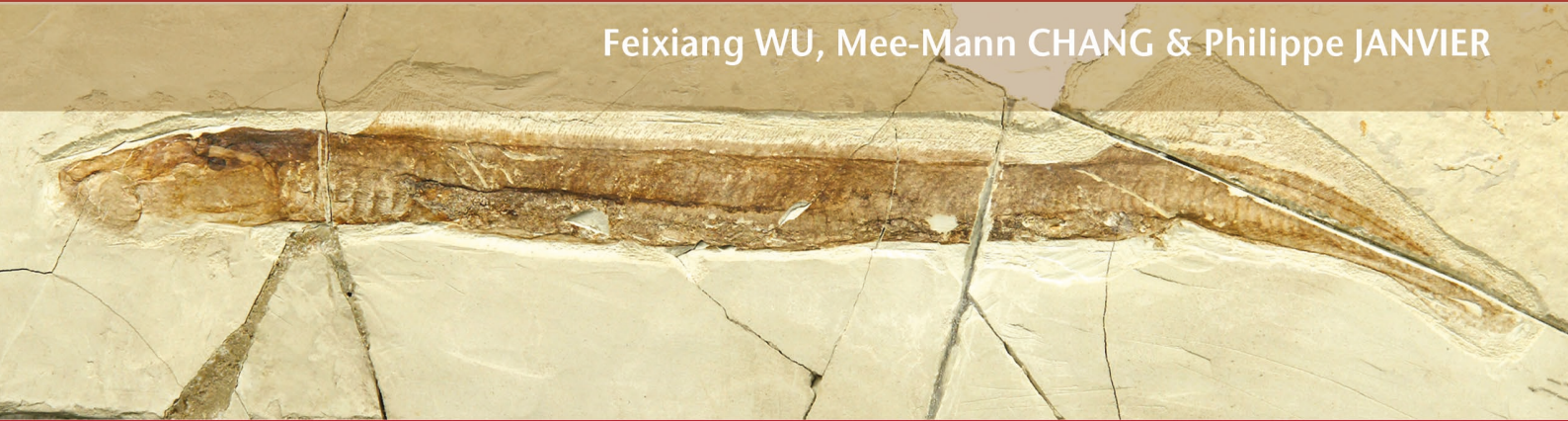
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ABSTRACT

Lampreys, one of the remaining two living jawless vertebrates, carry great weight in the study of vertebrate evolution. They have a long history dating back to the Devonian but left a scarce fossil record. So far, only five unequivocal fossil lampreys have been described, of which four are Paleozoic. *Mesomyzon* Chang, Zhang & Miao, 2006, the only known Mesozoic lamprey bridging the Paleozoic and extant relatives, was originally considered similar in morphology and life history to modern forms. Although being repeatedly referred to in early vertebrate phylogeny, the morphology of *Mesomyzon* is far from adequately known. Based on extensive investigations on numerous new and well-preserved specimens, we present herein more details of the morphology of this fossil lamprey, thereby releasing a package of new information of the cranial nerves, some associated structures of the oral disc, and the naso-hypophysial complex, which are barely preserved in previously known fossil lampreys. *Mesomyzon* shows peculiarities in having an extremely long anterior dorsal fin and a ribbon-like preanal skin fold, and hence being restored in a distinct profile from the formerly claimed look. Additionally, it shares with some Southern Hemispheric species the widely separated dorsal fins, posteriorly positioned cloaca and enlarged oral papillae. In the light of these new data, the feeding ecology of *Mesomyzon* was tentatively discussed and this fossil lamprey was considered a likely blood feeder, judging from the reinforcement of the attachment and sensory structures on the periphery of the oral disc.

RÉSUMÉ

Un nouveau regard sur la lamproie Mesomyzon Chang, Zhang & Miao, 2006, du Crétacé du Biote de Jehol.
Les lamproies, l'un des deux groupes actuels de vertébrés sans mâchoires, jouent un rôle important dans l'étude de l'évolution des vertébrés. Elles ont une longue histoire qui a débuté au Dévonien, mais, dépourvues de squelette minéralisé, elles n'ont laissé qu'un maigre registre fossile. Jusqu'alors, seules cinq incontestables lamproies fossiles ont été décrites, dont quatre sont paléozoïques. *Mesomyzon* Chang, Zhang & Miao, 2006, la seule lamproie mésozoïque, assurant le lien entre ses parents paléozoïques et actuels, a été à l'origine considérée comme semblable aux formes modernes, tant par sa morphologie que par son histoire de vie. Bien que fréquemment citée dans la littérature sur les premiers vertébrés, la morphologie de *Mesomyzon* est loin d'être connue en détail. Nous appuyant sur du nouveau matériel mieux conservé, nous présentons ici une description plus détaillée de cette lamproie fossile, fournissant un ensemble d'informations nouvelles sur les nerfs crâniens et certaines structures associées à la ventouse orale et le complexe naso-hypophysaire, qui sont généralement mal conservées chez les lamproies fossiles décrites auparavant. *Mesomyzon* montre des caractères uniques, notamment une nageoire dorsale antérieure extrêmement longue et un repli cutané pré-anal rubané, ce qui lui confère un profil différent de celui des précédentes reconstitutions. De plus, elle partage avec quelques espèces actuelles de l'hémisphère sud des nageoires dorsales largement séparées, un cloaque situé très postérieurement et de très grandes papilles orales. À la lumière de ces nouvelles données, l'écologie et le comportement alimentaire de *Mesomyzon* sont discutés et les structures sensorielles associées au disque oral suggèrent qu'elle ait été hématophage.

MOTS CLÉS
Lamproies fossiles,
Mesomyzon,
anatomie,
phylogénie,
hématophagie.

INTRODUCTION

Cyclostomes, the only extant jawless vertebrates (agnathans) consisting of lampreys and hagfishes, are generally considered as the most primitive lineage of vertebrates (Janvier 1996, 2008, 2015; Oisi *et al.* 2013). Despite the long-standing morphology-molecular conflict on the phylogeny of this group (Miyashita *et al.* 2019), these animals are vitally important in understanding the early evolution of jawed vertebrates (gnathostomes) (Janvier 2008, 2015; Miyashita *et al.* 2019). Compared to the hagfishes, the lampreys seem to bear greater resemblance with jawed vertebrates and deeper fossil record dating back to the Late Devonian (Hardisty 1979; Gess *et al.* 2006; Janvier 2008). However, their fossil record is poor. Only five unequivocal lamprey taxa and a few other enigmatic candidates are known in the fossil record, which are all Paleozoic with the sole exception of *Mesomyzon* from the Cretaceous of China (Janvier 2008; Miyashita *et al.* 2021). Albeit so ancient a lineage, the crown group is considered generally conservative in anatomy (Janvier 2006; Chang *et al.* 2014). The Paleozoic stem lampreys already have the characteristic crown lamprey morphology, including a long eel-like body, an oral disc, non-mineralized (presumed to be keratinous) teeth, while lacking paired fins (Bardack & Zangerl 1968; Janvier & Lund 1983; Gess *et al.* 2006; Sallan *et al.* 2017). Despite this, they still have some features, e.g., the extremely small body equipped with a teeth-bearing oral disc and prominent eyes, which suggest an ancestral life history pattern without the larval stages and hence distinct from that of their living counterparts (Miyashita *et al.* 2021). *Mesomyzon*, the only Mesozoic representative of this group, reduces the gap between the Paleozoic and modern lampreys (Chang *et al.* 2006). It shows not only a fairly modern look in external morphology, but also a three-phased (larva, metamorphosis and adult) life cycle interposed with a stage of radical metamorphosis (Chang *et al.* 2006, 2014), a particular adaptive strategy well known in living lampreys (Hardisty 1979). However, since only a young adult specimen was used in the original description of *Mesomyzon* (Chang *et al.* 2006) and the subsequent study merely focused on the larvae and transformers (Chang *et al.* 2014), the knowledge of the morphology of this fossil lamprey is still limited. Inspired by the collection during the past ten years of dozens of exquisitely-preserved specimens, we present here an extensive morphological investigation of *Mesomyzon*. In comparison with the organic decay process of a modern lamprey (Sansom *et al.* 2013), these fossilized animals were preserved in a superb state, affected little by the decay process. Consequently, they expose delicate anatomical details of the naso-hypophysial complex, oral fimbriae and papillae, cranial nerves, as well as some unique features of the fins, which have never been clearly preserved or documented in the lamprey stem. With this wealth of new information, some previous descriptions are also revised. New data are synthesized and compared among fossil and living lampreys (Fig. 1) to tentatively restore the feeding habit of *Mesomyzon*. Therefore, this study has no doubt refined the existing knowledge of the morphology and ecology of this fossil lamprey and paved the way for the updated phylogenetic analyses to test its systematic status.

SYSTEMATIC PALEONTOLOGY

Class CYCLOSTOMI Duméril, 1806
Order PETROMYZONTIFORMES Berg, 1940
Genus *Mesomyzon* Chang, Zhang & Miao, 2006

Mesomyzon mengae Chang, Zhang & Miao, 2006
(Figs 2-4)

HOLOTYPE. — IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) collection number V14719,

a nearly complete adult specimen, without preservation of the tail (Chang *et al.* 2006: fig. 1a).

REFERRED MATERIAL. — IVPP V14718A, B (a metamorphosed individual), V14981A, B, V15027A, B, V15450.3, V15448A, B, V15449.

HORIZON AND LOCALITY. — Yixian Formation, Lower Cretaceous (*c.* 125 Ma) (Zhou 2014; Zhou & Wang 2017); Ningcheng, Inner Mongolia and Yongyin County, Hebei Province, China.

AMENDED DIAGNOSIS. — A fossil lamprey with elongated and eel-shaped body, body length 12 times the maximum body depth, 4 times the head length; first gill pouch posteroventral to otic capsule; prebranchial region long, twice the maximum head height and 1.3-1.8 times the branchial length; oral papillae large and triangular (conical); oral fimbriae numerous, maximum number presumably no less than 80; circumoral teeth series incomplete and lacking the posterior section; supraoral lamina large and bicuspid; two dorsal fins widely separated, anterior dorsal fin long and commencing above 4th gill pouch; ribbon-like preanal skin fold long and extending to anterior branchial region; anal fin fold present; 70-80 preanal muscular segments; preanal myomeres Z-shaped and caudal ones W-shaped; tail hypocercal.

DESCRIPTION

General appearance

As described by Chang *et al.* (2006), *Mesomyzon* has an eel-like body and lacks paired fins. The adult individuals described here are larger than the holotype (Table 1). They have a well-developed oral disc and a long prebranchial region. The new materials here show that the anterior dorsal fin is very long and the ventral midline of the trunk is fringed with a ribbon-like preanal skin fold. The tail is hypocercal (Fig. 2).

Head

The cranial cartilages are preserved in imprints in some specimens. Here we follow Hardisty & Potter (1981) and De Iluiis & Pulerà (2011) for the terminology of the cranial cartilages referred below. The main parts of the anterior and posterior dorsal cartilages, and the anterior lateral cartilage can be delineated (Figs 3A-D; 4A-C). The anterior lateral cartilage is situated ventrolaterally to the front part of the anterior dorsal cartilage and is tapering in the ventral part. The anterior dorsal cartilage is wider in the hind part than in the front, whose lateral margin is flared backward into a posterolateral angle. The posterior limit of the anterior dorsal cartilage terminates at the level very close to the external narial opening. The posterior dorsal cartilage is wider than the anterior dorsal cartilage and overlaps the latter posteriorly as in living lampreys (Fig. 1B) (Hardisty & Potter 1981: fig. 4; Marinelli & Strenger, 1954: (figs 24, 51a). There is a joint occasionally preserved in the fossils along the dorsal edge of the snout region (some distance in front of the eyes) (Figs 3B, C; 4A) which might indicate the differentiation of the anterior dorsal and posterior cartilages.

To the rear of the posterior dorsal cartilage there is a notable dark imprint which is nearly vertically arranged immediately in front of the eye (Figs 3A, B; 4A). This may represent the anterior pillar of the subocular arch (Figs 3B; 4A) to form the anterior part of the orbital cavity as in living lampreys (Johnels 1948: fig. 57; Hardisty & Potter 1981: fig. 4; Janvier 1993: fig. 4.4).

The imprints of the styliform cartilage is preserved posteroventral to the otic capsule (Figs 3A-D; 4A). It extends posteroventrally towards the pharynx as its counterpart in living forms (Hardisty & Potter 1981: fig. 4). It is linked to the velar skeleton by small muscles in modern lampreys (Janvier 1993). The structures of the naso-hypophysial complex is well-preserved in IVPP V 15449 and V 15450.3, with the olfactory organ's left side exposed in the former and the dorsal aspect in the latter (Figs 3C-F; 4B, F). It is enclosed within the imprints of the nasal sac, which is located in the midline and just anterodorsally to the eyes and likely independent from the cranial cartilages. The olfactory organ is preserved in a way that it partly overlaps the naso-hypophysial atrium in IVPP V 15449 (Figs 3C, D; 4B). The preserved part of this organ bears eight folds in IVPP V 15449 (dorsolateral view) (Figs 3C, D; 4B) and six parallel and evenly arranged folds in IVPP V 15450.3 (dorsal view) (Figs 3E, F; 4F). The naso-hypophysial duct extends anterodorsally for a length that approximates that of the short axis of the eye to the naris, which is dorsally positioned without a depression surrounding itself as in living lampreys (Janvier 1974). The hypophysial pouch (tube) (Figs 3C, D; 4B), a blind-ending structure serving to pump water into and out of the naso-hypophysial atrium (Janvier 1974), extends posteroventrally from the bottom of the olfactory organtowards the pharynx, and bends downward abruptly when it approaches the branchial apparatus. It must have extended more posteriorly, as its rear is covered by the gill structures in IVPP V 15449. The region of the pineal organ cannot be clearly distinguished as it is blurred by a patch of dark matter above the olfactory organ.

Brain and cranial nerves

(IVPP V15450.3): The remnants of the brain are represented by a patch of coarse sediments in IVPP V 15450.3 (Figs 3E, F; 4F). Based on the position of the roots of some cranial nerves and their arrangement in living lamprey (Fig. 1C), the major divisions of the brain can be roughly recognized. The paired olfactory nerves can be roughly discerned, which contact anteriorly with the hind part of the nasal sac. The posterior part of the telencephalon is rounded and terminated at the level of the posterior rim of the eyes. After exiting from the braincase, the trigeminus ophthalmicus profundus (V_1) extends above the eyes and branches off to innervate the annular muscles of the oral disc. The buccal ramus of the facial nerve (VII.buc) exits below the eyes and extends anteriorly to be convergent with the V_1 toward the oral disc. The recurrent rami of the facial nerve are well preserved *in situ*, and originally surround the otic capsules. The labyrinth membrane cannot be detected in our materials. The glossophyngeus (IX) and vagus (X) nerves are also arranged in a pattern that is almost identical to that in living lampreys (Fig. 1C) (Marinelli & Strenger 1954: figs 51, 52).

Oral disc

The oral disc and other associated structures are detected based on the pattern in living lamprey (Fig. 1D). In larger individuals, the oral disc is well developed, with the anterior fieldwider

than the lateral and posterior ones. In IVPP V 15449, where the oral disc is best preserved, the oral disc occupies 6.64% of the total body length. In the same specimen, the impressions of a dozen of oral fimbriae (right side) are preserved in the perimeter of the oral disc (Fig. 3C, D). They are small, rod-like, and so closely arranged that they form together a comb-like pattern. This morphology is reminiscent of the oral fimbriae in living lampreys (Renaud 2011) and the ridges along the periphery of the oral disc of fossil lamprey *Priscomyzon* (Miyashita *et al.* 2021) Based on the arrangement of these structures, and the proportion of the length with the fimbriae preserved, at least 80 oral fimbriae might be present around the oral disc in IVPP V 15449.

The oral papillae are partly preserved in IVPP V 15027 and 15449 (larger individuals) (Figs 3A-D; 4C). They fringe the outer rim of the oral disc. The papillae are fairly large in relative to the oral disc size and triangular in shape (possibly conical as in living lampreys when the animals were alive, Renaud 2011: 5, fig. 20). They are connected to each other at the base, so that they must have entirely surrounded the oral disc. Judging from their size and arrangement, there could be no more than 30 oral papillae in the material at hand.

Annular cartilage

This is the structure that supports the supraoral and infraoral laminae (Renaud 2011). The remains of the annular cartilage are seen in some specimens, which are demonstrated either as a horseshoe-like impression (smaller individuals) or a nearly complete circle (larger individuals) (Figs 3A-F; 4A, C). When complete, its anterior part appears to be somehow broader than the posterior part. Interestingly, in the specimen (IVPP V 15450.3) with a horseshoe-like impression of the annular cartilage, no traces of the posterior part of the cartilage are discernable although the remainder of this cartilage (element) is very well-preserved.

"Teeth"

In all large adult individuals with the well-preserved impression of the oral disc and annular cartilage, some non-mineralized, presumably keratinous teeth are already in place, though being developed to a lesser extent than in extant lampreys (Marinelli & Strenger 1954; Renaud 2011). Although the arrangement of the keratinous teeth varies among living lampreys, e.g., *Geotria australis* Gray, 1851 has few teeth in the posterior field of the oral disc, *Lampetra fluviatilis* (Linnaeus, 1758) lacks anterior and posterior circumoral teeth (Potter & Hilliard 1987), as a whole they all have more teeth on the oral disc than *Mesomyzon*. In *Mesomyzon*, there are no teeth preserved on the anterior, lateral and posterior fields (see Hubbs & Potter 1971; Renaud 2011 and Fig. 1D for delineation) of the oral disc outside of the circumoral teeth. Given the good preservation of the circumoral teeth under the same taphonomic condition, teeth might be absent, or at least very weakly developed on those fields. The series of the circumoral teeth is incomplete, only the anterior and lateral rows are prominent. These triangular teeth are relatively loosely arranged and similar in size. The teeth on the

supraoral lamina are strong and bicuspid (Figs 3A, B, E, F; 4A, C). Those on the infraoral lamina are occasionally seen, and are also roughly triangular in shape (Figs 3A, B; 4A, C). Although their detailed structure of the transversal and longitudinal lingual laminae can be recognized, some dark matter preserved roughly at the anterior end of the piston cartilage might suggest their presence (Figs 3B-D; 4A).

Lingual (piston) cartilage

The piston cartilage is usually preserved as a slender longitudinal band extending along the ventral part of the pharynx from the mouth and posteriorly towards the branchial region (Fig. 3B-D). In IVPP V 15035A (Figs 3B; 4A), IVPP V 15449 (Fig. 3C, D), the anterior end of the piston cartilage, or apical cartilage, can be roughly recognized. It is continuous with the remaining part of this cartilage. This part is obviously darker in color than other part of the cartilage, possibly suggesting the fairly thick and complex structure (e.g., the apicalis cartilage) as in living lampreys (Marinelli & Strenger 1954: figs 19-21; Janvier 1993: fig. 4.4).

Velar skeleton

Immediately in front of the branchial apparatus, there is a prominent dark impression with an irregular profile (Figs 3B; 4A) which points to velar skeleton on the basis of the comparison to its homologue in extant lampreys (in Fig. 1A and Marinelli & Strenger 1954: figs 64, 65; Janvier 1993: fig. 4.4). More dorsally, there is a band-like impression extending anterodorsally toward the cranium, which is likely the imprinted styliform cartilage. This cartilage is linked to the velar skeleton by some muscles in modern lampreys (Janvier 1993).

Branchial apparatus

The distance between the eye and the branchial apparatus roughly equals the interval of four branchial openings. Seven gill pouches are seen, slightly slanting posteriorly, and of which the foremost one is triangular and much smaller than the remaining ones (Figs 2C; 3A-D). The branchial basket is partially preserved in IVPP V 15027A and 15449, where the impressions of the ventral part of branchial basket is well exposed. In the anteriormost part, some relics of the extra hyal arch can be detected (Figs 3C, D; 4D, E). More posteriorly, each of the branchial units shows a reversed Y-shaped profile in lateral view, which is connected ventrally with the longitudinal hypobranchial bar (Figs 3A, C, D; 4D, E). Based on the position relative to the external gill openings, this fork must be positioned below the hypotrematic bar, by comparison to the arrangement of gill basket in living lampreys (Fig. 1B) (Marinelli & Strenger 1954). This is different from the living lampreys in lacking the slanting rods above the junction of this bar and each extrabranchial arch as the attachment area of some external branchial constrictor muscles (Marinelli & Strenger 1954: figs 13, 14). Although we cannot say with certainty that this suggests difference in the configuration of the branchial muscles, the available information indeed reflects some structural variations of the gill-supporting architecture between *Mesomyzon* and
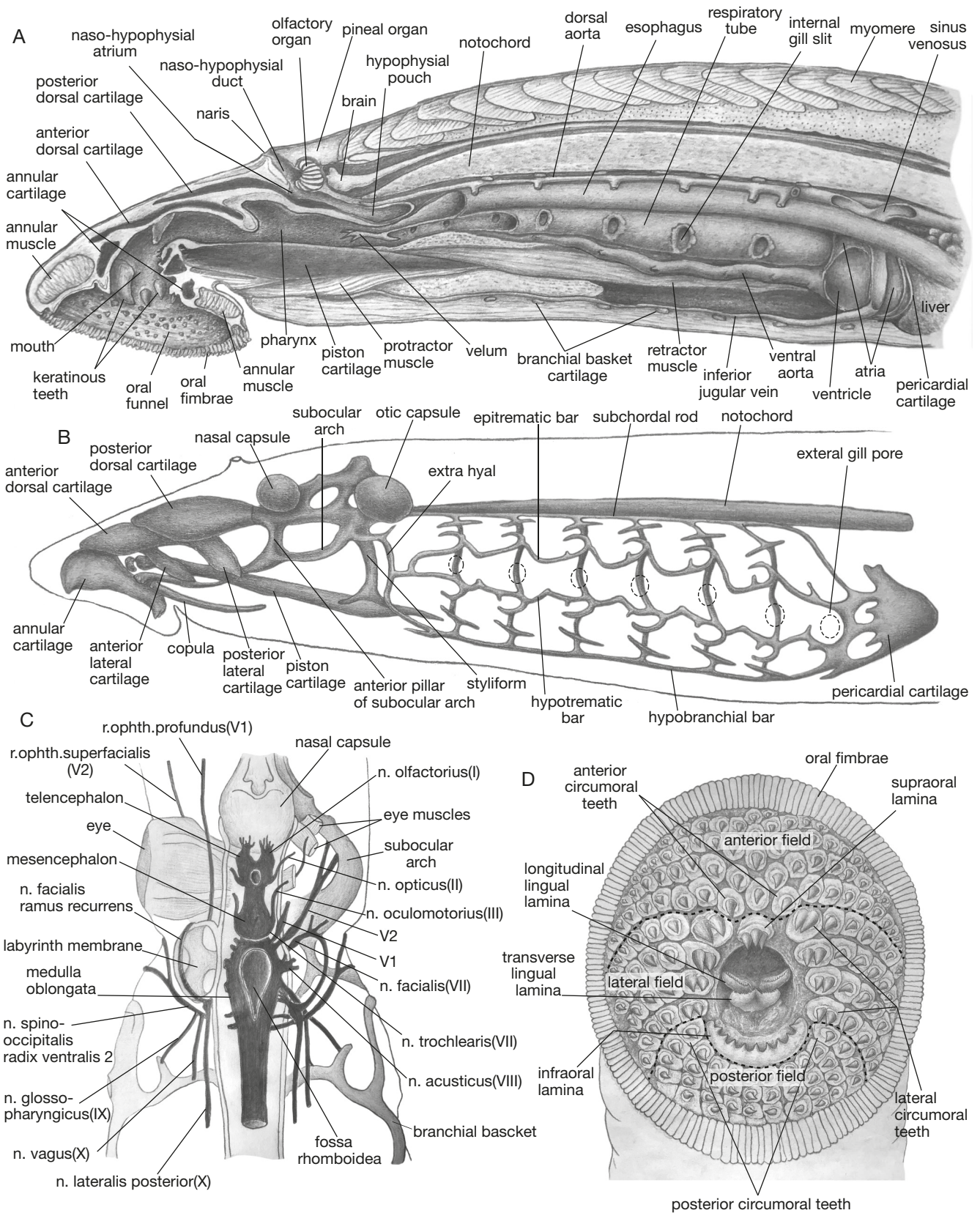
FIG. 1. — Generalized anatomy of living lampreys: **A**, schematic sagittal section through head and pharyngeal region; the vessels, esophagus, respiratory tube, and parts of the heart are shown with portions cut away, rather than in sagittal section; redrawn after De Iuliis & Pulerà 2011, with the structures of the naso-hypophysial complex labelled after Janvier 1974; **B**, the cranial skeleton of an adult lamprey, redrawn after Hardisty & Potter 1981; **C**, arrangement pattern of the cranial nerves, redrawn after Marinelli & Strenger 1954; **D**, oral disc of an adult lamprey showing the keratinous teeth and other associated structures. The dotted lines delineate the various fields. Redrawn after Renaud 2011.

TABLE 1. — Meristic measurements of *Mesomyzon mengae* Chang, Zhang & Miao, 2006. Abbreviations and interpretations: **a**, cloacal slit length; **a-C**, tail length; **d**, oral disc length; **d-O**, preorbital length (from anteriormost internal edge of oral disc to anterior edge of eye); **d-B1**, prebranchial length or head length; **d-n**, snout length (narial opening not well-preserved, measured between anterior edge of naso-hypophysial organ to anteriormost internal edge of oral disc); B_1-B_2, interbranchial opening length; B_1-B_7, branchial length; B_7-a, trunk length; **Hh**, head height (measured at the level of posterior edge of eye); **I**, interocular length; **O**, eye length; **O-B₁**, postocular length; **TL**, total length.

	TL	B7-a	a-C	d-n	O	O-B1	B1-B2	Hh	d	d-O	d-B1	B1-B7	a
V14981	*c.* 150	74	37	?	?	?	2	?	?	?	20	13	2
V15448A	186	99	41	16.5	2.5	8	2.5	12	13	17	25.5	18	?
V15027	177	88	40	13	2	7.5	2	12.5	7.5	15.5	24	15	2
V15449	217	107	51	20	2.5	8	3	12.5	13	21.5	32	18	3

extant lampreys. We note that these muscle-supporting bars are not seen in lamprey larvae but exist later in adult forms (Hardisty 1981; Janvier 1993, 2008). The branchial basket is relatively well preserved in the Devonian lamprey *Priscomyzon* Gess, Coates & Rubidge, 2006 (Gess *et al.* 2006; Miyashita *et al.* 2021); however, its ventral part is also different from its analogue in *Mesomyzon*. There appears to be no bifurcation of the gill arch below the hypotrematic bar in *Priscomyzon* (Gess *et al.* 2006; Miyashista *et al.* 2021).

More dorsally, the longitudinal hypotrematic bar, the epitrematic bar and the sub-chordal rod of the branchial basket are either blurred by the gill tissues or not observable in available fossil materials.

The external openings of the branchial apparatus are arranged in a posteriorly slanting line (Figs 2C; 3B). Their posterior rims are usually more visible (darker) than the anterior rims, which might be resultant from the existence of the papillae in the posterior edge (Marinelli & Strenger 1954: figs 13-15, 37, 38, 40, 41).

Relative to the eyes, the branchial apparatus is more posteriorly positioned in *Mesomyzon* than in its Paleozoic relatives, whose branchial region extends forward nearly below the eyes (Bardack & Zangerl 1968; Janvier & Lund 1983; Lund & Janvier 1986; Janvier 2008) or even anterior to the eyes (Miyashita *et al.* 2021). The majority of living lampreys have a slightly more anteriorly located branchial region than in *Mesomyzon*, except for quite a few parasitic species, i.e., *Entosphenus minimus* (Bond & Kan, 1973), *Lampetra lanceolata* Kux & Steiner, 1972, which display a similar postocular length (the distance between the eyes and the first gill opening) to *Mesomyzon* (Renaud 2011).

The ratio of prebranchial length/ branchial length in *Mesomyzon* ranges from 1.4 to 1.8, a similar state as in Paleozoic lampreys (Bardack & Zangerl 1968; Janvier & Lund 1983; Lund & Janvier 1986; Gess *et al.* 2006; Janvier 2008). This ratio in six out of all 39 living lamprey species falls within this range or slightly exceeds it (see Appendices 1; 2). It is interesting that all these six species above except for *Lethenteron alaskenses* Vladykov & Kott, 1978 are parasitic (Renaud 2011). Among all living species, the non-parasitic species tend to have a smaller prebranchial length/ branchial length ratio than the parasitic ones (Renaud 2011). The prebranchial length was also assessed in another criterion. This region in *Mesomyzon* is no less than twice the maximal head depth. It is notably longer than that in *Mayomyzon* Bardack & Zangerl, 1968, *Hardistella*

Janvier & Lund, 1983 and *Pipiscius* Bardack & Richardson, 1977 (Bardack & Zangerl 1968; Bardack & Richardson 1977; Janvier & Lund 1983; Janvier 2008). *Priscomyzon* Gess *et al.*, 2006 displays a prebranchial length/maximal head depth ratio of *c.* 2, which actually results from the enlargement of the oral disc (Gess *et al.* 2006). This ratio in half of the living lampreys is smaller than that in *Mesomyzon*, whereas the remaining living species (21 out of 39 species) have a ratio approximating 2 or beyond (see Appendices 1; 2).

Pericardinal cartilage
The pericardial cartilage is connected to the rear of the branchial basket (Figs 3A-F; 4D), and shows a profile of an equilateral triangle with little difference from that in living lampreys (Fig. 1A, B and Marinelli & Strenger 1954: figs 59, 60; Hardisty & Potter 1981).

Intestine
The accurate morphology of the intestine cannot be determined; however, its position can be traced by the arrangement of the detrital gobbets occasionally preserved in some large adult specimens. Judging from the detritus preserved immediately behind the last gill pouch (Fig. 3C, D), the intestine is arranged in a similar pattern as in living adult lampreys (Fig. 1A and Marinelli & Strenger 1954). The preserved part of the detrital crumbs consists of coarse sand grains of variable sizes and their presence in the digestive tube possibly hints at the fossil lamprey's habit of attaching on stones or moving stones with their oral disc for nesting (Hardisty 1979; Renaud 2011), or alternatively the habit of burying themselves in the substrate when the mucus secreted by the oral fimbriae trapped the sand and silt, just like the case in some living lampreys (Khidir & Renaud 2003; Renaud 2011). In IVPP V 15449, there is a mass of detritus preserved between the buccal funnel and the pharyngeal cavity, which might locate the mouth (Fig. 3C, D). The ending of the intestine, the cloaca (anus) is located at the level of the peak of the "posterior dorsal fin".

The liver can be detected just behind the pericardial cartilage in several specimens (Fig. 3A, E, F). It shows a triangular profile and this part is always in a brightly red in color on the matrix (e.g., in IVPP V 15448A), which might be related with the oxidized iron ion (of the blood) originally concentrated in the liver organ. This is a similar preservation pattern interpreted in several agnathan fossils (Janvier 1996; Newman & Trewin 2001).

FIG. 2. — *Mesomyzon mengae* Chang, Zhang & Miao, 2006, new adult individuals and morphological restoration: **A**, photograph of IVPP V 15027; **B**, photograph of IVPP V 15449; **C**, photograph of IVPP V 14981B; **D**, restoration of the general appearance of *Mesomyzon*, dotted circle behind the eyes representing the otic capsule. Abbreviations: **adf**, anterior dorsal fin; **bp**, branchial pouches; **cf**, caudal fin; **cl**, cloaca; **e**, eye(s); **egp**, external gill pores; **od**, oral disc; **pdf**, posterior dorsal fin. Scale bars: 10 mm.

FINS

Dorsal and caudal fins

Here we hold the assumption proposed by Janvier (2008: 1051) that the so-called "posterior dorsal fin" in lampreys should represent the anterior part of the caudal epichordal lobe inserted on the markedly hypocercal tail and this issue will be referred to in the discussion section below. The anterior dorsal fin is so long that it extends anteriorly as far as to the level of the anterior edge of the fourth gill pouch. Its occupies 44%-48% of the total body length and the height occupies *c.* 50% of the maximal body depth. The fin changes little in height along its whole length, except that it is beveled smoothly at both ends. The anterior dorsal fin and the "posterior dorsal fin" are usually separated by a distance slightly smaller than the body depth in this position, except for one specimen (IVPP V 15448A), where the base of the "posterior

dorsal fin" extends anteriorly to touch the anterior dorsal fin and this connecting part lacks fin radials. This variation of "posterior dorsal fin" might be correlated with a sexual maturity or mating behavior, because this fin in living lampreys serves as a "brake" to present the male's tightly wound tail from gliding backward over the female's body during the mating act (Vladykov 197) and before the breeding season, the female (and sometimes the male) develops a swelling in the anterior edge of this fin (Janvier & Lund 1983: fig. 4f1). The chordal lobe of the tail is titled downwards at the position of the cloaca (anus). This feature is more marked than in extant lampreys (Renaud 2011). The "posterior dorsal fin" is mostly surmounted on the tail, roughly triangular in shape and notably higher than the anterior dorsal fin. More posteriorly, it is continuous with the posterior lobe of the caudal fin via a smoothly round notch. The posterior lobe is

spade-like in shape with the ventral lobe slightly longer than the dorsal one (Fig. 2).

The fin "rays" (actually cartilaginous radials, see Marinelli & Strenger 1954; Janvier 2008; Miyashita *et al.* 2019 for interpretation for lampreys and other jawless vertebrates) are easily observable and closely arranged, with a density of about two rays per millimeter, which is more closely arranged than at least in the anal fin of a female *Petromyzon marinus* Linnaeus, 1758 (31 mm in length supported by 30 rays) (Vladykov 1973). There is a continuous dark band in the ventral part of the anterior and "posterior dorsal" fins (Figs 2; 3C, D), possibly reflecting the imprints of the radial muscles (Sansom *et al.* 2010: fig. 2a) and/or the adipose stratum (Marinelli & Strenger 1954: (figs 43, 44, 49). It is noticed that in IVPP V 15027A, there is a dorsal swelling of the body at the anterior base of the "posterior dorsal fin", which is not seen in other specimens (Fig. 2A). This fin is not completely preserved in the holotype and referred to as emerging above the posterior portion of the body (Chang *et al.* 2006).

Anal fin (fold)

The anal fin (fold) is present just behind the anus (cloaca), which is best preserved in IVPP V 15449 (Fig. 3G). It is shallow and elongate but separate from the ventral lobe of the caudal fin. It is more a skin fold than a "true" fin because no traces are detected as the supporting rays for this fin as in living form (Vladykov 1973).

Preanal skin fold

An unexpected finding is the long preanal skin fold that emerges immediately before the anus (cloaca) and extends on the ventral midline (Figs 2A, C; 3H). This structure is common in fossil lampreys from different localities of Jehol Biota. It reaches the level of the front end of the branchial apparatus (i.e., beyond the anterior termination of the anterior dorsal fin), at which point it becomes very shallow. This fold can be seen in IVPP V 14981B, 15027 and 15448, where it is much lighter in color than and clearly distinct in texture from the impressions of the trunk myomeres. Moreover, it is separated from the trunk myomere imprints by a clear black line delineating the ventral midline (Figs 2C; 3H). In contrast, there is no additional structure below the trunk myomeres in living lampreys as evidenced by the transverse section of the body (Marinelli & Strenger 1954: figs 42-44). In fossils at hand this fold is occasionally preserved in the way of wrinkling, suggestive a thin and soft nature, distinct from the stiff and straight ventral edge of the body. Additionally, its distal line is always clear rather than the obscure outline in decayed carcass (Sansom *et al.* 2013). According to current observable information, this fold is most likely median in position and lacks supporting radials.

Myomeres

The number of the trunk myomeres are counted in the range of 70-80. The trunk myomeres show a zig-zag profile (Figs 2; 3H) with the ventral section lacking the posteriorly-pointing apex of living forms (Sansom *et al.* 2010; Renaud 2011),

whereas those caudal myomeres show a typical W-shaped profile, with the median apex pointing anteriorly (Figs 2; 3G). The impressions the trunk muscular fibers are clearly observable and arranged in paralleling longitudinal direction as in living forms (Marinelli & Strenger 1954: fig. 6).

COMPARISONS AND DISCUSSION

Our study presents a set of characters not recorded in the original descriptions of *Mesomyzon* (Chang *et al.* 2006), and reveals additional traits shared with extant lampreys. The differentiation of the major cranial cartilages, i.e., the anterior lateral cartilage, the anterior and posterior dorsal cartilage, as well as the possible subocular arch, show no significant difference from those in living adult lampreys (Marinelli & Strenger 1954; Janvier 1993). The nasohypophysial organ displays many folds, indicating a pattern to increase of the surface area of the nasal epithelium, nearly identical with the modern counterpart in morphology (Marinelli & Strenger 1954). This organ was never preserved so well in other fossil lampreys (Bardack & Zangerl 1968; Bardack & Richardson 1977; Janvier & Lund 1983; Lund & Janvier 1986; Chang *et al.* 2006, 2014; Gess *et al.* 2006). Additionally, the general configuration of the naso-hypophysial duct and its external opening, and the hypophysial pouch closely resembles their counterparts in modern lampreys (Marinelli & Strenger 1954). Some cranial nerves, exemplified by the trigeminal and facial nerves, are also arranged in a modern pattern. The recurrent ramus of the facial nerve looping over the inner ear is characteristic in lampreys (Marinelli & Strenger 1954), and is not developed in living hagfishes (Marinelli & Strenger 1956; Oisi *et al.* 2013).

Despite resembling living forms in many aspects, *Mesomyzon* displays considerable peculiarities that distinguish itself from its modern and other fossil lamprey relatives. The anterior dorsal fin extends anteriorly above the middle branchial region, and is much longer than its counterpart in all living lampreys (Renaud 2011) and any other known fossil lampreys (Bardack & Zangerl 1968; Bardack & Richardson 1977; Janvier & Lund 1983; Lund & Janvier 1986; Chang *et al.* 2006, 2014; Gess *et al.* 2006), even with *Pipiscius* Bardack & Richardson, 1977 and *Gilpichthys* Bardack & Richardson, 1977 included in this group (Janvier 2008). Considering the similarly long dorsal fin fold of the larval and metamorphosing individuals (Chang *et al.* 2014) and the developmental process of the dorsal fins in modern lampreys (Potter *et al.* 1982; Richardson & Wright 2003), the long dorsal fin of adult *Mesomyzon* was likely inherited from the larval dorsal fin fold, with the addition of the later emergence of the supporting cartilaginous fin rays (radials). It should be kept in mind that the cartilaginous rays (radials) are deeply embedded in the dorsal portion of the body (Marinelli & Strenger 1954: figs 43, 44, 46).

Moreover, the anterior dorsal fin and "posterior dorsal fin" are widely separated in *Mesomyzon*. In other fossil lampreys with anterior dorsal fin developed, it is very close, if not in contact, to the "posterior dorsal fin" in *Hardistiella*
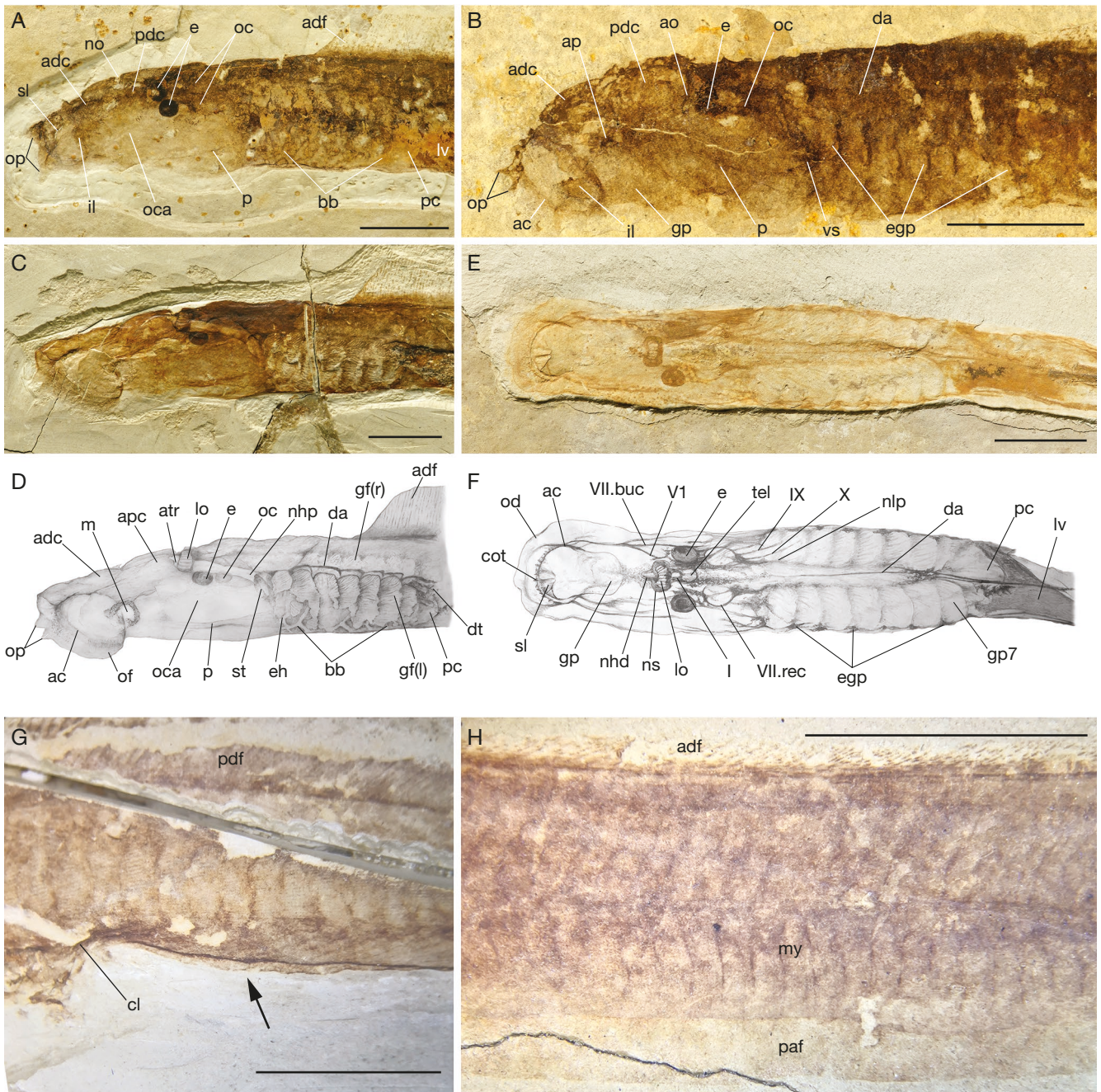
FIG. 3. — *Mesomyzon mengae* Chang, Zhang & Miao, 2006, head, branchial region, and fins. Photographs of: **A**, IVPP V 15027A; **B**, IVPP V 15035A; photograph (**C**) and line drawing (**D**) of IVPP V 15449; photograph (**E**) and line drawing (**F**) of IVPP V 15450.3; **G**, photograph of the tail of IVPP V 15449, the arrow points to the anal fold; **H**, close-up of middle trunk of IVPP V 14981B. Abbreviations: **ac**, annular cartilage; **adc**, anterior dorsal cartilage; **adf**, anterior dorsal fin; **ao**, anterior pillar of subocular cartilage; **ap**, apicalis and the laminae it carries; **atr**, naso-hypophysial atrium; **ba**, imprints of brain; **bb**, branchial basket; **cot**, circumoral teeth; **da**, dorsal aorta; **dt**, detritus in intestine; **eh**, extra hyal arch; **m**, mouth; **gp1**, **gp7**, 1st and 7th gill pouch; **il**, infraoral lamina; **lv**, liver; **no**, external narial opening; **nhp**, hypophysial pouch; **gl**, gill filaments; **gf(l, r)**, gill filaments of left and right gills; **gp**, infillings of gular pouch; **lo**, olfactory organ; **my**, myomeres; **nlp**, posterior lateral nerve; **ns**, nasal sac; **oc**, otic capsule; **oca**, oral cavity; **op**, oral papillae; **of**, oral fimbriae; **p**, piston cartilage; **paf**, preanal skin fold; **pc**, pericardial cartilage; **pdc**, posterior dorsal cartilage; **sl**, supraoral lamina; **st**, styliform; **tel**, telencephalon; **vs**, velar skeleton; **I**, olfactory nerve or tract; **V1**, ophthalmic ramus of trigeminal nerve; **VII. uc**, buccal ramus of facial nerve; **VII.rec**, recurrent ramus of facial nerve surrounding labyrinth; **IX**, glossopharyngeus nerve; **X**, vagus nerve. See Figure 2 for other abbreviations. Anterior facing left in all figures. Scale bars: 10 mm.

(Janvier & Lund 1983), whereas in *Mayomyzon*, there is even no differentiation of these fins (Bardack & Zangerl 1968). It is noted that the long dorsal fin in the original description of *Priscomyzon* (Gess *et al.* 2006) was recently . The disjunct pattern of these two fins are also distinct from their confluent status in most living lamprey species (Renaud 2011). Such a disjunction is only seen in the southern hemisphere species, *Geotria* Gray, 1851 and *Mordacia* Gray, 1851 (Renaud 2011).

The relative position of these two fins in most living lampreys is variable, except the southern hemisphere taxa *Geotria* Gray, 1851 and *Mordacia* Gray, 1851, whose the dorsal fins remain separate throughout the lifespan. Whereas in other species except for those with a single dorsal fin (e.g., *Ichthyomyzon* spp.) they progressively become closer to each other as the animal becomes sexually mature and eventually come into contact at the base (Renaud 2011). It cannot be determined for now whether this specimen with weak fin connection mentioned above fits this condition or not.

Another important feature refers to the unique ribbon-like preanal skin fold. This is not recorded in any other known lampreys (Bardack & Zangerl 1968; Bardack & Richardson 1977; Janvier & Lund 1983; Lund & Janvier 1986; Chang *et al.* 2006, 2014; Gess *et al.* 2006), nor in the original description of *Mesomyzon* (Chang *et al.* 2006). A preanal fold of such a dimension is also never developed among living lampreys except that a very short preanal fold is occasionally seen in a few living species, e.g., *Ichthyomyzon greeleyi* Hubbs & Trautman, 1937 (Renaud 2011). This preanal skin fold is also present in living and the recently reported fossil hagfishes (Miyashita *et al.* 2019, and personal communications with Miyashita) but arranged in a much more restricted extent (personal observations on living hagfish). It is worthy to note that the decay halo is occasionally seen in some cyclostome or other jawless vertebrate fossils (Newman & Trewin 2001; Miyashita 2020), which might raise the suspicion that the preanal skin fold here is just part of the decay halo, just like the case in the Carboniferous hagfish *Myxinikela siroka* Bardack, 1991 (Bardack 1991, 1998; Miyashita 2020). However, unlike the decay halo around the carcass, both along the ventral and dorsal edges of the body in *Myxinikela* (Miyashita 2020), there is no "decay halo" along the dorsal edge of the body in all *Mesomyzon*'s fossil materials with the preanal skin fold clearly observable. Therefore, it seems more possible that this fin fold in *Mesomyzon* is not a taphonomic artifact.

We also found a small distinct anal fin fold in *Mesomyzon*, which is again not seen in other fossil lampreys (Bardack & Zangerl 1968; Bardack & Richardson 1977; Lund & Janvier 1986; Gess *et al.* 2006) except for *Hardistiella*, which has a small anal fin (Janvier & Lund 1983; Janvier 2008). However, the anal fin in the latter is supported by radials, which are likely not present in this anal fold of *Mesomyzon*. A female sea lamprey (*Petromyzon marinus*) was reported to develop a true anal fin during the spawning time (Vladykov 1973). However, we think this might not be the case for *Mesomyzon*. This radial-free fin fold in *Mesomyzon* is present in several individuals of different sizes, and the individuals with this structure display few female secondary sexual features but instead some characters, e.g., the relatively long prebranchial length, oral disc and tail, which are regarded as male sexual features in living forms (Renaud 2011), were they related with the sexual maturity of *Mesomyzon*.

The tail is hypocercal in *Mesomyzon* (Fig. 2). The exact status of the tail of *Priscomyzon* is not clear as all known specimens of this taxon are preserved in dorsoventral compression (Miyashita *et al.* 2021), the feature of the caudal

fin in unclear either according to the restudy on this taxon (Miyashita *et al.* 2021). The tail is nearly straight in *Mayomyzon* (Bardack & Zangerl 1968; Janvier & Lund 1983; Janvier 2008) and in *Pipiscius* (Janvier 2008), whereas it is gently tilted downwards in *Hardistiella* (Janvier & Lund 1983), with a more marked inclination than in modern lampreys (Renaud 2011). The condition of the tail of *Mesomyzon* is therefore more similar to that in some other Paleozoic fossil jawless vertebrates, e.g., most "anaspids" and "thelodonts" (Janvier & Lund 1983; Janvier 2008) than in its modern and fossil lamprey allies.

The myomeres of the preanal trunk of *Mesomyzon* show a Z-shaped profile, and those in the tail region are typically W-shaped. The trunk myomeres in modern lampreys are W-shaped (Renaud 2011).

The oral fimbriae and papillae were never documented in previously known fossil lampreys (Bardack & Zangerl 1968; Bardack & Richardson 1977; Janvier & Lund 1983; Lund & Janvier 1986; Chang *et al.* 2006, 2014; Gess *et al.* 2006) except in the recently revisited Late Devonian lamprey *Priscomyzon*, where theoral fimbriae were recognized as the ridges along the edge of the oral funnel (Miyashita *et al.* 2021). These structures are relatively decay-resistant according to experimental taphonomy (Sansom *et al.* 2010, 2013). The development of oral fimbriae was documented in living lampreys by Lethbridge & Potter (1981). *Mesomyzon*'s oral fimbriae and papillae show some peculiarities in their shape and arrangement. The number of the oral fimbriae in *Mesomyzon* falls within the range exhibited by some living lampreys. The fimbriae are morphologically simpler in *Mesomyzon* than in their modern counterparts (Renaud 2011). The oral fimbriae are absent only in *Mordacia* which is currently confined to the southern hemisphere (Renaud 2011). The oral papillae of *Mesomyzon* are conspicuous in size and arrangement. In morphology, they are reminiscent of those of the Southern Hemispheric lamprey *Mordacia lapicida* (Gray, 1851) (Renaud 2011: fig. 20) but much larger in size than those in this species or other modern lampreys (Khidir & Renaud 2003; Renaud 2011). Additionally, they are more closely arranged and continuous at their base, and likely enclose the outer rim of the oral disc. The enlargement of the oral papillae was reported in another Southern Hemispheric taxon, *Geotira australis* Gray, 1851 (Potter 1980: fig. 4); however, only a pair of anterolateral papillae are involved in such a specialization and are proportionally much smaller than those in *Mesomyzon* described here.

During the mating activity of living lampreys, the male warps its tail around the female and slides posteriorly to approximate the female's urogenital region for fertilization (Johnson *et al.* 2015), and the female's "posterior dorsal fin" acts as a "brake" to hold a proper mating gesture of the male (Vladykov 1973). Therefore, it is interesting to note the position of the cloaca relative to the "posterior dorsal fin" among lampreys. The cloaca opens at the level of the peak of the "posterior dorsal fin" in *Mesomyzon*. It is more posteriorly positioned than in other fossil lampreys where the cloaca can be located. In *Hardistiella*, it is located slightly anterior to
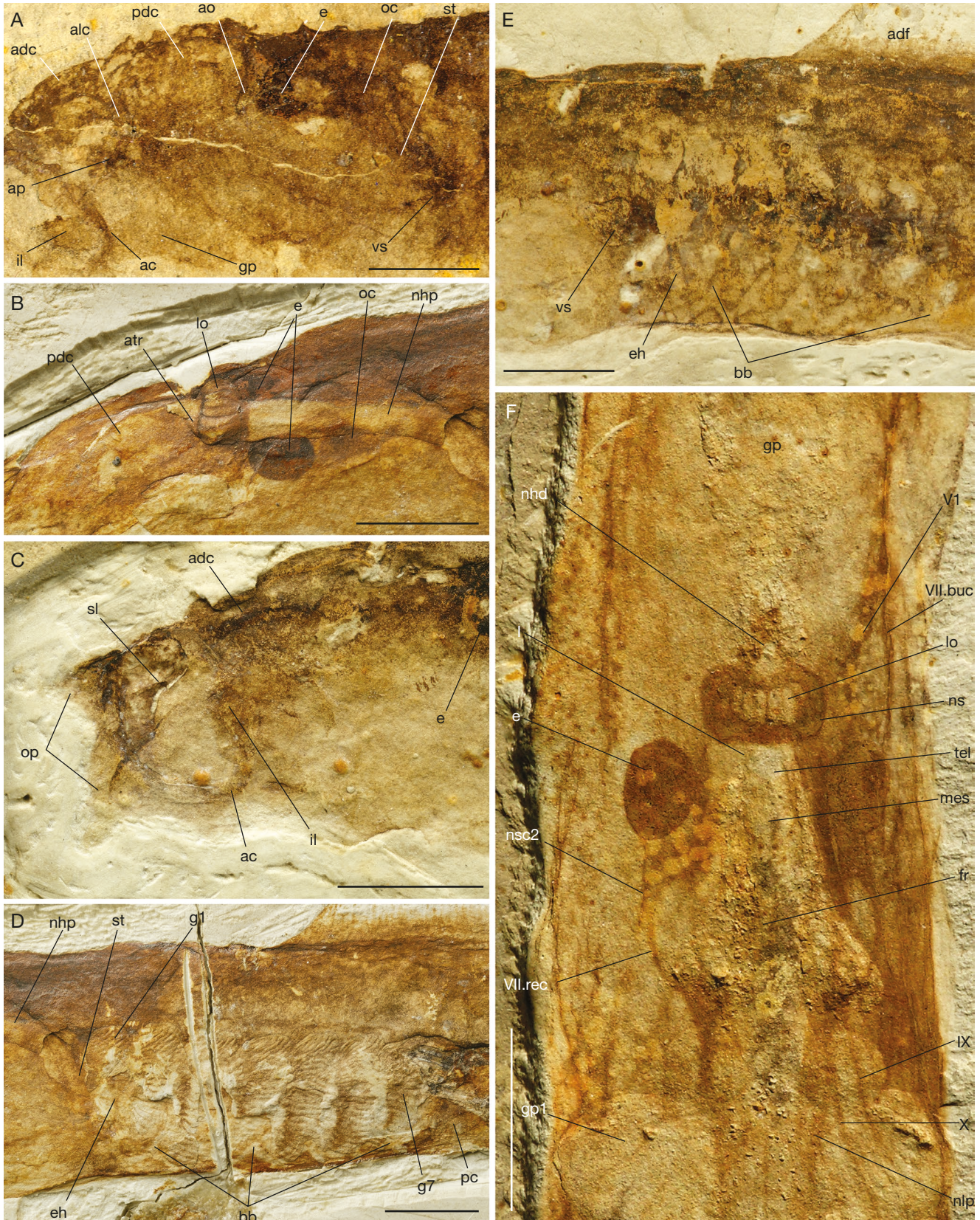
FIG. 4. — Close-up of some anatomical structures of *Mesomyzon* Chang, Zhang & Miao, 2006: **A**, head of IVPP V 15035A; **B**, naso-hypophysial complex and adjacent structures of IVPP V 15449; **C**, oral disc and associated structures of IVPP V 15027A; **D**, details of gills and branchial skeleton of IVPP V 15449; **E**, details of the branchial apparatus of IVPP V 15027A; **F**, imprints of the brain and some cranial nerves of IVPP V 15450.3. Abbreviations: **alc**, anterior lateral cartilage; **nhd**, naso-hypophysial duct; **fr**, presumed position of fossa rhomboidea; **g1**, gill filaments of the first gill; **nsc2**, ventral spino-occipital radix nerve. See Figures 1 and 2 for other abbreviations. Scale bars: 5 mm.

the base of the "posterior dorsal fin" (Janvier & Lund 1983), whereas in *Mayomyzon*, although not clearly preserved, judging from the position of the confluent anal fin, it must be positioned before the peak of the "posterior dorsal fin" (Bardack & Zangerl 1968; Janvier 2008). The situation is not clear in *Priscomyzon* where the fins cannot been clearly recognized (Miyashita *et al.* 2021). The cloaca of *Mesomyzon* opens more posteriorlythan in most living lampreys, where it is usually located at the level of the emergence of the "posterior dorsal fin". *Mesomyzon* resembles some Southern Hemispheric species (*Mordacia*), whose cloaca is positioned at a level slightly behind the peak of the "posterior dorsal fin" (Renaud 2011). Yet, *Lampetra lanceolate* Kux & Steiner, 1972 and some species of *Lethenteron* Greaser & Hubbs, 1922 also show a similarly posteriorly opened anus as in *Mesomyzon* (Renaud 2011). In is noteworthy that the taxonomic value of the position of anus (cloaca) relative to the posterior dorsal fin was highlighted for the classification of *Mordacia* by Renaud (2011).

The status of lamprey tail: the so-called posterior dorsal fin as a part of the hypocercal caudal fin

In the literature, lampreys are generally described as having two (one anterior and one posterior) dorsal fins (Hubbs & Potter 1971; Hardisty 1979, 1981; Potter *et al.* 1982, 2015; Renaud 2011). Actually, the so-called "posterior dorsal fin" is mostly inserted on the tail region (the part behind the cloaca) and its internal cartilaginous radials are continuous with those of the posterior lobe of the caudal fin in living lampreys (Marinelli & Strenger 1954: fig. 46; Renaud 2011). It is also the case in *Hardistiella*, whose "posterior dorsal fin" is completely confined in the tail region and there is even no mark between it and the more posterior part that was traditionally called "caudal fin" (Janvier & Lund 1983). The hypocercal tail of *Mesomyzon* here makes the arrangement more prominent. It is noted that in *Mayomyzon* the caudal fin is also mostly confined in the tail region (Bardack & Zangerl 1968; Janvier 2008), although no supporting radials are observable. According to a recent study, *Priscomyzon*'s fins cannot be discerned (Miyashista *et al.* 2021).

Additionally, the small rear pad of the caudal fin in lampreys practically prolongs the posterior tip of the notochord (Marinelli & Strenger 1954: fig. 46) as in hagfishes (Marinelli & Strenger 1956: fig. 109) and Devonian jawless fish *Euphanerops longaevus* Woodward, 1900 (Janvier & Arsenault 2007). Therefore, we insist on the presumption that lampreys' confluent "posterior dorsal fin" and the caudal fin should be the homolog of the markedly hypocercal tail in other fossil jawless fishes, e.g., euphaneropids and anaspids (Janvier 2008), which is compatible with the recognition of stem cyclostomes of these fossil forms (Miyashita *et al.* 2019). Namely, lampreys should have only one dorsal fin when present.

A likely blood feeder?

When *Mesomyzon* was originally described (Chang *et al.* 2006), the possession of an oral disc with tooth plates did not warrant definitely a parasitic mode of life, as the holotype is relatively small, *c.* 8.4 cm in total length and no larger than some later transforming individuals and the other specimen is a metamorphosing individual (Chang *et al.* 2006, 2014). Additionally, the living non-parasitic species also retain oral disc and teeth (Renaud 2011).

The parasitic and non-parasitic lampreys show radically different modes of life in the post-metamorphosis period. The non-parasitic species no longer feed and shrink in size relative to their larval stages, whereas the parasitic species feed and naturally grow longer and larger than their larvae (Hardisty 1979; Potter *et al.* 1982; Renaud 2011). The individuals described here all display adult features in the oral disc, eyes, branchial apparatus and fins. Moreover, they are all much larger than the metamorphosing individuals and the young adult (the holotype) (Chang *et al.* 2014), which entails a post-metamorphic feeding habit and sufficient food ingestion. Therefore, it can be confirmed with confidence now that *Mesomyzon* is very likely a parasitic form.

The oral fimbriae and papillae are mucus-producing structures of the oral disc and closely associated with the feeding behavior of lampreys, or even linked to the variations of food types among the adults (Lethbridge & Potter 1981; Khidir & Renaud 2003; Clark & Uyeno 2019: 221). They secrete mucus that protect the oral disc from abrasion by sand particle and aid to ensure the sealing of the oral disc onto the body of the prey. More specifically, among the parasitic lampreys, the blood feeders (e.g., *Petromyzon marinus* Linnaeus, 1758) require an effective attachment of the oral disc more than do the flesh eaters (e.g., *Lampetra fluviatilis* (Linnaeus, 1758)), because they have to prevent any loss of the blood when they feed (Khidir & Renaud 2003). They also depend on these structures with possible sensory function (Lethbridge & Potter 1981) to sense the appropriate (i.e., more vascularized) site to feed on the prey (Khidir & Renaud 2003). In contrast, the flesh feeders (e.g., *Lampetra fluviatilis*) do not have such a strong requirement in these aspects (Khidir & Renaud 2003). *Mesomyzon* is well equipped with both the oral fimbriae and oral papillae, outstanding among all lampreys in the large and continuous series of oral papillae. This, as a natural consequence, endows the oral disc of *Mesomyzon* a considerable efficiency of attachment. With this in mind, we assume that *Mesomyzon* could be more a blood feeder than a flesh feeder. On the other side, the complete set of both oral fimbriae and papillae, as well as the enlargement of the latter, might merely be the compensation of the less well-developed teeth on the oral disc, which would be embedded in the host and prevent the slippage of the oral disc along the prey's body when the lamprey feeds (Clark & Uyeno 2019). Besides, the general feature of *Mesomyzon*'s oral disc is also compatible with the assumption of thr blood feeding habit, because the relative size of the oral disc (6.6% of total body length) falls in the range of that in some blood feeders (e.g., *Ichthyomyzon unicuspis* Hubbs & Trautman, 1937, *I. castaneus* Girard, 1858, *Mordacia mordax* (Richardson, 1846)) but is much larger than that of those typical flesh feeders (e.g., 4.5-5.5% of total body length in *Lampetra fluviatilis*) (Potter & Hilliard 1987; Khidir & Renaud 2003).

If *Mesomyzon* was indeed a land-locked predaceous lamprey (Chang *et al.* 2006), then it must have fed on some

local aquatic vertebrates. The aquatic vertebrates in the Jehol Biota include some swimming reptiles, amphibians, and fishes (Zhou 2014; Zhou & Wang 2017). Among them the fishes are potentially suitable hosts, e.g., the highly diversified acipenseriform fishes (sturgeons), as they are naked, with the integument delicate enough to penetrate for *Mesomyzon*, and they could grow to fairly large sizes, thereby facilitating the suctorial attachment of the lampreys (Jin 1995). The *Lycoptera* Müller, 1848 (a primitive bony-tongue) are also a potential food source for *Mesomyzon*, as they are abundant in that biota and their cycloid scales are relatively thin (Zhang *et al.* 1994). The abundant and naked salamanders (Zhou & Wang 2017) from this biota are also potential prey of lampreys. However, admittedly, no cases of bite marks on the skin by lampreys on these animals are documented yet. And moreover, the possibility of the anadromy cannot be excluded from the life history of *Mesomyzon*, as there might be some drainage links between region hosting the Jehol Biota and the nearby Bohai Bay from the Late Jurassic to early Early Cretaceous (Liu *et al.* 2015).

A LARGE ORAL CAVITY (PHARYNX) AND ITS FUNCTIONAL AND EVOLUTIONARY SIGNIFICANCE

The backward-shifted branchial apparatus and the resulting proportionally longer prebranchial region together make an enlargement of the pharynx (oral cavity) and hence more space for the development of the feeding structures in *Mesomyzon*. This recalls the expansion of the oral cavity from the larval to adult stages in modern lampreys (Potter *et al.* 1982: 155).

The oral cavity plays an important role in the feeding of living parasitic lampreys as they bite in the absence of moveable jaws (Clark & Uyeno 2019). It serves as the pump to generate volumetric fluctuations to facilitate the adhesive suction of the oral disc and rasping (incising) prey tissues of the teeth-bearing tongue (Clark & Uyeno 2019). It also actively expands to induce a vacuum to drag the fluid and food items into the mouth. In this sense, equipped with an enlarged oral cavity (pharynx), *Mesomyzon* would have reaped some selective advantage in feeding. Conversely, the anteriorly shifted branchial region in Paleozoic lampreys (Janvier 2008) squeezed out the room for the pharynx and hence the oral cavity, which had consequently caused a proportionally shorter piston cartilage (Hardisty 1979: 37). Although *Priscomyzon* has a relatively large prebranchial length (Gess *et al.* 2006); however, when leaving aside the question of the large oral disc, the length of the pharynx shows no significant difference from that in *Mayomyzon* and *Hardistiella* (Bardack & Zangerl 1968; Janvier & Lund 1983). This divergence should be partially related with the feeding efficiency between these Paleozoic forms and *Mesomyzon*, and in turn, accountable for in part the disparate body sizes of these lampreys, were they all parasitic.

Acknowledgements

REFERENCES

BARDACK D. 1991. — First fossil hagfish (Myxinoidea): a record from the Pennsylvanian of Illinois. *Science* 254 (5032): 701–703. https://doi.org/10.1126/science.254.5032.701

BARDACK D. 1998. — Relationships of living and fossil hagfishes *in* JØRGENSEN J. M., LOMHOLT J. P., WEBER R. E. & MALTE H. (eds), *The biology of hagfishes*. Springer, Dordrecht, the Netherlands: 3–14. https://doi.org/10.1007/978-94-011-5834-3_1

BARDACK D. & ZANGERL R. 1968. — First fossil lamprey: a record from the Pennsylvanian of Illinois. *Science* 162: 1265-1267. https://doi.org/10.1126/science.162.3859.126

BARDACK D. & RICHARDSON E. S. 1977. — New agnathous fishes from the Pennsylvanian of Illinois. *Fieldiana* (*Geology*) 33: 489-510. https://doi.org/10.5962/bhl.title.5167

CHANG M.-M., ZHANG J. Y. & MIAO D. S. 2006. — A lamprey from the Cretaceous Jehol biota of China. *Nature* 441: 972-974. https://doi.org/10.1038/nature04730

CHANG M.-M., WU F. X., MIAO D. S. & ZHANG J. Y. 2014. — Discovery of fossil lamprey larva from the Lower Cretaceous reveals its three-phased life cycle. *Proceedings of National Academy of Sciences*: 111:15486-15490. https://doi.org/10.1073/pnas.1415716111

CLARK A. J. & UYENO T. A. 2019. — Feeding in jawless fishes, *in* BELS V. & WHISHAW I. (eds), Feeding in Vertebrates. *Fascinating Life Sciences* Springer, Cham: 189-230. https://doi.org/10.1007/978-3-030-13739-7_7

DE IULIIS G. & PULERÀ D. 2011. — *The Dissection of Vertebrates: A Laboratory Manual*. Academic Press. https://doi.org/10.1016/C2009-0-00124-X

EVANS T. M., JANVIER P. & DOCKER M. F. 2018. — The evolution of lamprey (Petromyzontida) life history and the origin of metamorphosis. *Reviews in Fish Biology and Fisheries* 28: 828-838. https://doi.org/10.1007/s11160-018-9536-z

GESS R. W., COATES M. I. & RUBIDGE B. S. 2006. — A lamprey from the Devonian period of Southern Africa. *Nature* 443: 981-984. https://doi.org/10.1038/nature05150

HARDISTY M. W. 1979. — *Biology of Cyclostomes*. Chapman and Hall, London.

HARDISTY M. W. 1981. — The skeleton, *in* HARDISTY M. W. & POTTER I. C. (eds), *The Biology of Lampreys*. Volume 3. Academic Press, Toronto: 333-376.

HUBBS C. L. & POTTER I. C. 1971. — Distribution, phylogeny and taxonomy, *in* HARDISTY M. W. & POTTER I. C. (eds), *The Biology of Lampreys*. Volume 1. Academic Press, London: 1-65.

HARDISTY M. W. & POTTER I. C. 1981. — The skeleton, in The biology of lampreys. in HARDISTY M. W. & POTTER I. C. (eds), *The Biology of Lampreys. Volume 3*. Academic Press, New York: 118-124.

JANVIER P. 1974. — The structure of the naso-hypophysial complex and the mouth in fossil and extant cyclostomes, with remarks on amphiaspiforms. *Zoologica Scripta, Stockholm* 3: 193-200. https://doi.org/10.1111/j.1463-6409.1974.tb00816.x

JANVIER P. 1993. — Patterns of diversity in the skull of jawless fishes, *in* HANKEN J. & HALL B. K. (eds), *The Skull*. University of Chicago Press, Chicago: 131-188.

JANVIER P. 1996. — *Early Vertebrates*. Clarendon Press, Oxford: 393 p.

JANVIER P. 2006. — Modern look for ancient lamprey. *Nature* 443: 921-924. https://doi.org/10.1038/443921a

JANVIER P. & ARENAULT M. 2007. — The anatomy of *Euphanerops longaevus* Woodward, 1900, an anaspid-like jawless vertebrate from the Upper Devonian of Miguasha, Quebec, Canada. *Geodiversitas* 29: 143-216.

JANVIER P. 2008. — Early jawless vertebrates and cyclostome origins. *Zoological Science* 25: 1045-1056. https://doi.org/10.2108/zsj.25.1045

JANVIER P. 2015. — Facts and fancies about early fossil chordates and vertebrates. *Nature* 520: 483-489. https://doi.org/10.1038/nature14437

JANVIER P. & LUND R. 1983. — *Hardistiella montanensis* n. gen. et sp. (Petromyzontida) from the Lower Carboniferous of Montana, with remarks on the affinities of the lampreys. *Journal of Vertebrate Paleontology* 2: 407-413. https://doi.org/10.1080/02724634.1983.1001194

JOHNELS A. G. 1948. — On the development and morphology of the skeleton of the head of Petromyzon. *Acta Zoologica* 29: 139-279. https://doi.org/10.1111/j.1463-6395.1948.tb00030.x

JIN F. 1995. — Late Mesozoic Acipenseriformes (Osteichthyes: Actinopterygii) in Central Asia and their biogeographic implications, *in* SUN A. & WANG Y. (eds), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press, Beijing: 15-21.

JOHNSON N. S., BUCHINGER T. J. & LI W. 2015. — Reproductive ecology of lampreys, *in* DOCKER M. F. (ed), *Lampreys: biology, conservation, and control*. Springer, New York: 265-303. https://doi.org/10.1007/978-94-017-9306-3_6

KHIDIR K. T. & RENAUD C. B. 2003. — Oral fimbriae and papillae in parasitic lampreys (Petromyzontiformes). *Environmental Biology of Fishes* 66: 271-278. https://doi.org/10.1023/A:1023961910547

LETHBRIDGE R. C. & POTTER I. C. 1981. — The skin, *in* HARDISTY M. W. & POTTER I. C. (eds), *The Biology of Lampreys*. Volume 3. Academic Press, Toronto: 377-448.

LIU Y. Q., KUANG H. W., PENG N., XU H., ZHANG P., WANG N. S. & AN W. 2015. — Mesozoic basins and associated palaeogeographic evolution in North China. *Journal of Palaeogeography* 4: 189-202. https://doi.org/10.1016/j.gr.2014.10.014

LUND R. & JANVIER P. 1986. — A second lamprey from the Lower Carboniferous (Namurian) of Bear Gulch, Montana (U.S.A.). *Geobios* 19: 647-652. https://doi.org/10.1016/s0016-6995(86)80061-4

MARINELLI W. & STRENGER A. 1954. — *Vergleichende Anatomie und Morphologie der Wirbeltiere. I Lieferung. Petromyzon marinus* (L.). Deuticke, Wien.

MARINELLI W. & STRENGER A. 1956. — *Vergleichende Anatomie und Morphologie der Wirbeltiere. II Lieferung. Myxine glutinosa* (L.). Deuticke, Wien.

MIYASHITA T., COATES M. I., LARSON P. L. & MANNING P. L. 2019. — Hagfish from the Cretaceous Tethys Sea and a reconciliation of the morphological-molecular conflict in early vertebrate phylogeny. *Proceedings of the National Academy of Sciences* 116: 2146-2151. https://doi.org/10.1073/pnas.1814794116

MIYASHITA T. 2020. — A Paleozoic stem hagfish *Myxinikela siroka* revised anatomy and implications for evolution of the living jawless vertebrate lineages. *Canadian Journal of Zoology* 98: 850-865. https://doi.org/10.1139/cjz-2020-0046

MIYASHITA T., GESS R. W., TIETJEN K. & COATES M. I. 2021. — Non-ammocoete larvae of Palaeozoic stem lampreys. *Nature* 591: 408-412. https://doi.org/10.1038/s41586-021-03305-9

NEWMAN M. J. & TREWIN N. H. 2001. — A new jawless vertebrate from the Middle Devonian of Scotland. *Palaeontology* 44: 43-51. https://doi.org/10.1111/1475-4983.00168

OISI Y., OTA K. G., KURAKU S., FUJIMOTO S. & KURATANI S. 2013. — Craniofacial development of hagfishes and the evolution of vertebrates. *Nature* 493: 175-180. https://doi.org/10.1038/nature11794

POTTER I. C. 1980. — The Petromyzoniformes with particular reference to paired species. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 1595-1615. https://doi.org/10.1139/f80-207

POTTER I. C., HILLIARD R. W. & BIRD D. J. 1982. — Stages in Metamorphosis, *in* HARDISTY M. W. & POTTER I. C. (eds), *The Biology of Lampreys*. Volume 4. Academic Press, Toronto: 137-164.

POTTER I.C. & HILLIARD R. W. 1987. — A proposal for the functional and phylogenetic significance of differences in the dentition of lampreys (Agnatha: Petromyzontiformes). *Journal of Zoology* 212: 713-737. https://doi.org/10.1111/j.1469-7998.1987.tb05966.x

POTTER I. C., GILL H.S., RENAUD C.B. & HAOUCHER D. 2015. — The taxonomy, phylogeny, and distribution of lampreys *in* DOCKER M. F. (ed.), *Lampreys: Biology, Conservation and Control*, Fish & Fisheries Series. Springer Netherlands: 35-73. https://doi.org/10.1007/978-94-017-9306-3_2

RICHARDSON M. K. & WRIGHT G. M. 2003. — Developmental Transformations in a Normal Series of Embryos of the Sea Lamprey Petromyzon marinus (Linnaeus). *Journal of Morphology 257*: 348-363. https://doi.org/10.1002/jmor.10119

RENAUD C. B. 2011. — Lampreys of the World. An annotated and illustrated catalogue of lamprey species known to date. *FAO Species Catalogue for Fishery Purposes* no. 5. Food and Agriculture Organization of the United Nations, Rome: 109 p.

SALLAN L., GILES S., SANSOM R. S., CLARKE J. T., JOHANSON Z., SANSOM I. J. & JANVIER P. 2017. — The 'Tully Monster' is not a vertebrate: Characters, convergence and taphonomy in Paleozoic problematic animals. *Palaeontology* 60: 149-157. https://doi.org/10.1111/pala.12282

SANSOM R. S., GABBOOTT S. A. & PURNELL M. A. 2010. — Decay of vertebrate characters in hagfish and lamprey (Cyclostomata) and the implications for the vertebrate fossil record. *Proceedings of the Royal Society B* 278: 1150-1157. https://doi.org/10.1098/rspb.2010.1641

SANSOM R. S., GABBOOTT S. A. & PURNELL M. A. 2013. — Atlas of vertebrate decay: a visual and taphonomic guide to fossil interpretation. *Palaeontology* 56: 457-474. https://doi.org/10.1111/pala.12037

VLADYKOV V. D. 1973. — A female sea lamprey (*Petromyzon marinus*) with a true anal fin, and the question of the presence of an anal fin in the Petromyzontidae. *Canadian Journal of Zoology* 51: 221-224. https://doi.org/10.1139/z73-032

ZHANG J. Y., JIN F. & ZHOU Z. H. 1994. — A review of Mesozoic osteoglossomorph fish *Lycoptera longicephalus*. *Vertebrata PalAsiatic* 32: 41-59. (in Chinese with English summary)

ZHOU Z. H. 2014. — The Jehol Biota, an Early Cretaceous terrestrial Lagerstätte: new discoveries and implications. *National Science Review* 1: 543-599. https://doi.org/10.1093/nsr/nwu055

ZHOU Z. H. & WANG Y. 2017. — Vertebrate assemblages of the Jurassic Yanliao Biota and the Early Cretaceous Jehol Biota: Comparisons and implications. *Paleoword* 26: 241-252. https://doi.org/10.1016/j.palwor.2017.01.002

APPENDICES

APPENDIX 1. — Prebranchial length/branchial length (measured as the interval of seven gill openings to permit comparison to living species): the species with a ratio falling in the range of *Mesomyzon* include *Entosphenus macrostomus* (1.5, parasitic), *E. minimus* (1.7, parasitic), *E. slimilis* (1.5, parasitic), *E. tridentatus* (1.3, parasitic), *Endontomyzon morii* (1.2, parasitic), *Geotria australis* (normal 1, spawning male nearly 1.5, parasitic), *Ichthyomyzon bdellium* (1.2, parasitic), *I. unicuspis* (1.2, parasitic), *Lampetra lanceolate* (1.2, parasitic), *Lethenteron alaskensis* (1.2, non-parasitic), *Mordacia lapicida* (normal 1.1, spawning male, 1.2, parasitic), *Tertrapleurodon spadiceus* (1.4, parasitic), the remaining species have a smaller ratio, mostly with the prebranchial region being shorter than the branchial region (data measured from Renaud 2011).

APPENDIX 2. — Species with prebranchial length/maximal head depth ratio of 2 or laerger: *Entosphenus minimus* (parasitic)*, E. macrostomus* (parasitic)*, E. similis* (parasitic)*, E. tridentatus* (parasitic)*, Eudontomyzon mariae* (non-parasitic)*, Eu. morii* (parasitic)*, Geotria australis* (parasitic)*, Ichthyomyzon castaneus* (parasitic)*, I. greeleyi* (non-parasitic)*, Lampetra aepypetra* (non-parasitic)*, L. fluviatilis* (parasitic)*, L. lanceolate* (non-parasitic)*, L. rechardsoni* (non-parasitic)*, L. alaskense* (non-parasitic)*, L. camtschaticum* (non-parasitic)*, L. kessleri* (non-parasitic)*, Mordacia lapicida* (parasitic)*, M. mordax*(parasitic)*, M. praecox* (non-parasitic)*, Petromyzon marinus* (parasitic)*, Tetrapleurodon spadiceus* (parasitic) (data measured from Renaud 2011).