

LETTERS

A lamprey from the Cretaceous Jehol biota of China

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Widespread nowadays in freshwater and coastal seas of the cold and temperal zones, lampreys are a jawless vertebrate group that has been in existence for more than 300 million years but left a meagre fossil record. Only two fossil lamprey species, namely *Mayomyzon pieckoensis*^{1,2} and *Hardistiella montanensis*^{3–5}, have been recognized with certainty from North American Carboniferous marine deposits⁶. Here we report a freshwater lamprey from the Early Cretaceous epoch (about 125 million years ago) of Inner Mongolia, China. The new taxon, *Mesomyzon mengae*, has a long snout, a well-developed sucking oral disk, a relatively long branchial apparatus showing branchial basket, seven gill pouches, gill arches and impressions of gill filaments, about 80 myomeres and several other characters that are previously unknown or ambiguous. Our finding not only indicates *Mesomyzon*'s closer relationship to extant lampreys but also reveals the group's invasion into a freshwater environment no later than the Early Cretaceous. The new material furthers our understanding of ancient lampreys, bridges the gap between the Carboniferous ones and their recent relatives, and adds to our knowledge of the evolutionary history of lampreys.

Class Agnatha

Order Petromyzontiformes (Hyperoartii)

Family Petromyzontidae

Mesomyzon mengae gen. et sp. nov.

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) collection number V14719, a nearly complete adult specimen, without preservation of the tail.

Referred material. IVPP V14718A, B (part and counterpart), a complete specimen with the anterior tip of the snout unpreserved.

Etymology. The generic name derives from meso (Greek): Mesozoic; myzon (Greek), sucker. The species name honours Meng Qingwen from the University of Fisheries, Shanghai, whose lifelong studies on Chinese fishes have inspired us.

Horizon and locality. Yixian Formation, Lower Cretaceous; Ningcheng, Inner Mongolia, China.

Diagnosis. A small lamprey, body elongated, eel-shaped, length 12 times its depth, 4 times its head length; preorbital region fairly long, nearly one-third of the head length, 5 times the eye diameter; oral opening surrounded by radiating rectangular depressed areas, presumably covered by tooth plates with teeth, forming sucking disk; branchial basket well developed, with seven gill pouches, branchial apparatus obviously longer than preorbital region; first gill pouch posteroventral to otic capsule; eight or nine preserved gonads of rounded shape, non-metameric; trunk muscle segments more than 80; paired fins and anal fin absent, dorsal fin above posterior portion of body, caudal fin diphyccercal.

The two specimens of the new lamprey *Mesomyzon* are nearly of the same size. The body is elongated and eel-shaped (Fig. 1a–c). The anterior portion of the body is rounded, whereas the tail is more compressed laterally and tapers posteriorly. The body length

measured in the holotype of *Mesomyzon* V14719 (with the tail missing) is about 83.5 mm, whereas in V14718B (without the tip of the snout) it is 85 mm. Thus, the specimens of *Mesomyzon* are longer than those of *Mayomyzon* (33–61 mm) from Illinois^{1,2}, but slightly shorter than the complete one of the three known *Hardistiella* specimens ("which does not exceed 10 cm in total length"^{3,5}) from Montana, and much shorter than most recent lampreys^{7,8}. Its ratio of body length to body depth is about 12 (on the basis of both V14718B and V14719). The corresponding ratio is 8 to 9 in *Mayomyzon*¹, 10 in *Hardistiella* (inferred from Fig. 1A of ref. 2) and 12–20 in the recent lampreys from China⁸ and elsewhere in the world⁷. *Mesomyzon* is thus obviously slenderer than the two Carboniferous lampreys and closer in body proportion to the living ones. In the holotype in which the head is well preserved, the ratio of body length to head length (measured from the tip of the snout to the posterior margin of the last gill pouch) is about 4, approaching that of the recent *Lampetra* from China (4.5–6.0)⁸. The snout (or preorbital region) is well developed. The head length is roughly 2.8 times the preorbital length in the holotype, falling in the range of the recent *Lampetra* from China (2.7–3.4)⁸. The length of the snout is five times of the eye diameter in the same specimen, and much longer in proportion than that in *Mayomyzon*, namely 3.5 (ref. 1).

The holotype lies, for the most part, on its flank but with its head and anterior portion of the body rotated (along its axis) slightly towards its left so that the right side of the head is turned somewhat upwards. As a result of the rotation, the right eye, as a round dark stain (i.e., Fig. 1d, e), is situated near the top line of the head, whereas the left eye, as a faint circle with rough interior (r.e., Fig. 1d, e), is situated under, and partly overlapped by, the right eye. A small circle in the middle of the bigger circle of the right eye may indicate the presence of the lens. The left and right otic capsules (l.ot. and r.ot., Fig. 1d, e) are just behind the eyes and displayed in the same way as the eyes. The nasohypophysial opening was not seen in either of the specimens because of the state of preservation.

No parts or imprints of the endoskeleton of the cranium could be observed because it was neither calcified nor ossified. However, it is extremely fortunate that, on the holotype, a subterminal sucking oral disk (or.d., Fig. 1d, e) is clearly shown in the form of depressed rectangular areas divided by ridges, arranged in radiating rows around the oral opening. This is somewhat similar to the mouth structure of the enigmatic lamprey-like *Pipiscius* (see Figs 3–5 in ref. 9) from the Carboniferous period of Illinois^{10,11}. We could count four or five such areas on the nearly half of the oral disk preserved on the holotype. These depressed areas presumably carried tooth plates with teeth when the animal was alive¹², although no horny teeth were found on the specimens. If this were so, the oral tooth plates in *Mesomyzon* must be much bigger, and fewer in number, than in *Pipiscius*⁹ and recent lampreys^{7,8,12}.

The usually cartilaginous visceral skeleton in the form of the branchial basket (br.b., Fig. 1d, e) shows its distinct general outline and structure in light-grey stain on the holotype. The branchial

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basket of lamprey has not previously been observed in fossils, although elongated branchial baskets with many branchial units have been seen in the Late Devonian anaspid-like form *Euphanerops longaevis* from Miguasha, Québec, Canada^{5,10}. Not only are the outlines of the seven gill pouches (g.p., Fig. 1d, e) clearly visible but the impressions of the gill filaments (g.f., Fig. 1d, e) can also be traced in many places posterior to the vertical bars (gill arches, g.a., Fig. 1d, e) of the branchial basket. The length of the branchial apparatus obviously exceeds that of the preorbital region, whereas the gill pouches in *Mayomyzon* and *Hardistiella* are closely set and the branchial apparatus is hardly longer than the preorbital region^{4,10}. The first gill pouch is situated posteroventral to the otic capsule, as in recent lampreys but in sharp contrast to *Mayomyzon*^{1,2} and *Hardistiella*³, in which it is situated close behind the eyes. Unfortunately, no distinct gill openings could be detected on the specimens, although we believe there should be seven separate ones because in other respects *Mesomyzon* is too similar to the extant lamprey. Posterior to the last gill pouch, faintly visible are the upper and lower parts of the anterior portion of the pericardial cartilage (p.c.c., Fig. 1d, e). Two thin lines, stretching forwards from the anterior part of the branchial apparatus, seem to enclose a rod-like structure. Conceivably, it could be interpreted as the piston cartilage (p.c.?, Fig. 1d, e) that supports the rasping tongue. Behind the anterior part

of the pericardial cartilage, the outline of the liver (l., Fig. 1d, e) can also be traced. As judged from the situation in recent lampreys, the liver might be longer than that in our illustration. The digestive tract (d.t.?, Fig. 1d, e) is probably represented by a thin dark band that extends backwards from the end of the branchial basket, along the upper border of the liver, to an area below the dorsal fin, where it bends down to the probable anus (a., Fig. 1c). However, the interpretation of the thin dark band as the dorsal aorta is not ruled out.

Filled with coarse sediments, lined in a row and situated in the posterior half of the abdomen are eight or nine circular spaces, here interpreted as gonads (g., Fig. 1c), although they might alternatively be interpreted as gut. They are not arranged metamericly. Lamprey females have a single horseshoe-shaped ovary, whereas the testis of males consists of leaf-like lobes^{7,13,14}. The appearance of the gonads in the new form seems similar to that in the latter. Numerous myosepta (ms., Fig. 1c) are distinctly visible in the holotype. About 80 or more trunk myomeres can be counted. Under the dorsal margin of the body and parallel to the margin is the notochord (nc., Fig. 1c), a dark-stained thick band that stretches from the head region back to the end of the body. The traceability of the notochord in the fossils of many soft-bodied animals is certainly due to the more decay-resistant characteristic of its sheath¹⁵. The myoseptum that crosses

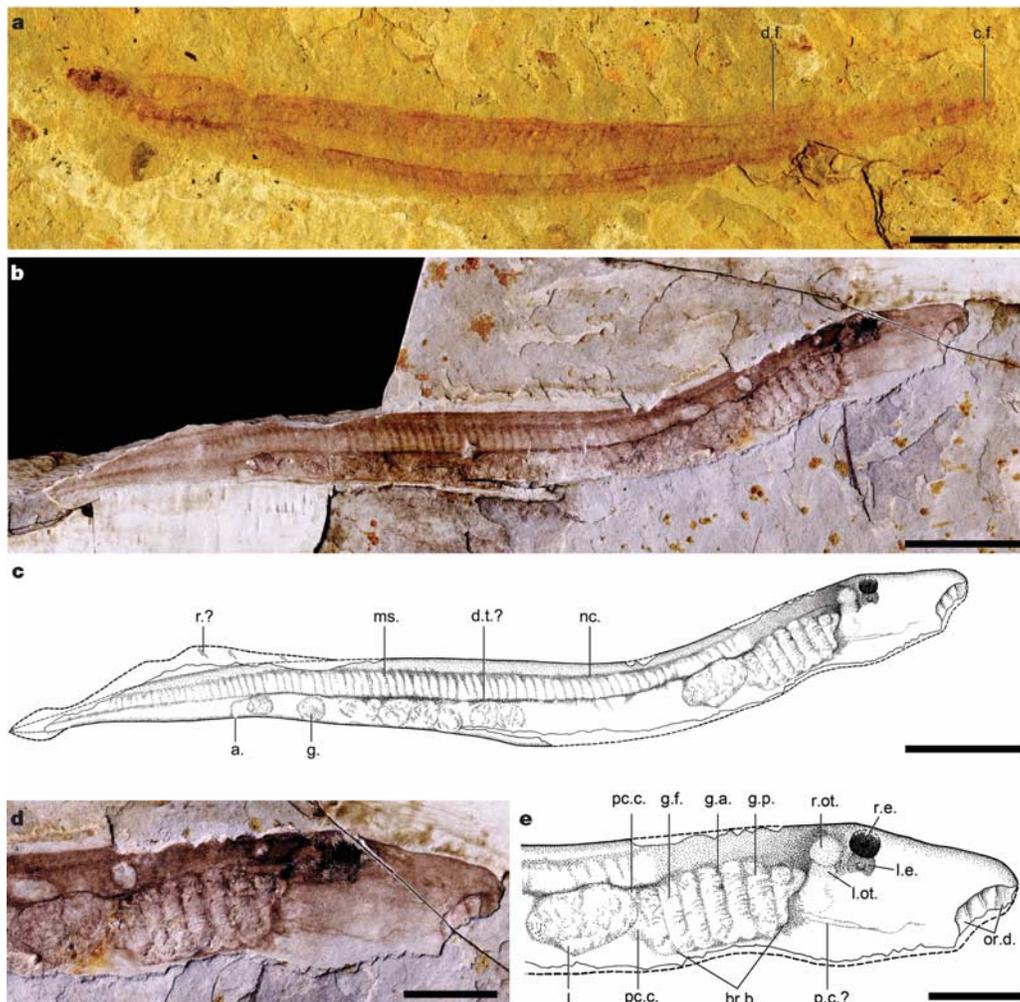


Figure 1 | *Mesomyzon mengae* gen. et sp. nov. **a**, A complete fish (IVPP V14718A) in left view. **b**, Holotype (IVPP V14719) in right view. **c**, Drawing of the holotype, with the dorsal fin and caudal region reconstructed on the basis of IVPP V14718A. **d**, Photograph of head and anterior part of body of the holotype. **e**, Drawing of the same part as in **d**. Scale bars, 10 mm (**a–c**)

and 5 mm (**d, e**). Abbreviations: a., anus; br.b., branchial basket; c.f., caudal fin; d.f., dorsal fin; d.t.?, possible digestive tract; g., gonads; g.a., gill arches; g.f., gill filaments; l., liver; l.e., left eye; l.ot., left otic capsule; ms., myosepta; nc., notochord; or.d., oral disk; p.c.?, possible piston cartilage; p.c.c., pericardial cartilage; r.e., right eye; r.ot., right otic capsule.

the notochord in each segment made it difficult to observe the shape of arcualia, if any is preserved there. Paired fins and anal fin are absent. The dorsal fin (d.f., Fig. 1a) is seen in V14718B above the posterior portion of the body. It most probably merges with the caudal fin (c.f., Fig. 1a). Very faint impressions of rays are occasionally seen in the dorsal fin in V14718B (r.?, Fig. 1c). The tail seems diphycercal rather than hypocercal on the same specimen.

Lacking mineralized tissues such as bone or calcified cartilage, lampreys are seldom preserved as fossils; their early evolutionary history is therefore still poorly known. *Mesomyzon* is the third fossil genus of the group ever discovered and in some respects is the best preserved. It lived more than 100 Myr ago, about 200 Myr more recent than their known precursors from the Carboniferous. The lamprey larvae—ammocoetes—are different from the adults. They are blind, with a short snout bending down, and without a sucking disk^{7,8,10}. Equipped with well-defined eyes, a long snout and a well-developed sucking oral disk, *Mesomyzon* is undoubtedly either an adult or a late transformer, instead of a larval form.

Mesomyzon possesses a slenderer body than its Carboniferous relatives, with the length-to-depth proportion close to that of the recent lampreys. Its snout is long and its oral sucker well developed. The structure of its branchial basket and pericardial cartilage is almost the same as in the recent lampreys. There are seven gill pouches. The ratios of the length of the branchial apparatus to that of the preorbital region are also intermediate between the Carboniferous precursors and the extant lampreys. Its first gill pouch is situated posteroventral to the otic capsule instead of close behind the eyes as in *Mayomyzon*^{1,2} and *Hardistiella*³. The distinctly shown trunk muscle segments are numerous (more than 80). Many of these characters have not previously been demonstrated in fossils. They suggest that *Mesomyzon* is unquestionably more closely related to the recent lampreys than to its Carboniferous kin. Consequently, the lamprey has already approximated to its current appearance by the Early Cretaceous. It therefore provides another interesting example from the fossil record in the discussion of rates of evolution. For about 100 Myr, lampreys underwent few morphological changes and therefore showed unusual morphological conservatism, or evolutionary stasis.

In living sea lampreys the teeth are numerous and are arranged in radiating rows, whereas in most river and brook lampreys they are not in radiating rows but in a more complicated pattern^{7,8,12}. The oral disk of *Mesomyzon* with radiating depressed areas (apparently covered by tooth plates) is more similar to the pattern of a sea lamprey. The development of an oral sucking disk brought about the possibility of a specific suctorial, parasitic mode of life. The material of *Mesomyzon* was collected from the freshwater shale deposits of the Yixian Formation. The new locality is not far from the famous Jehol Biota¹⁶ localities in Liaoning with its present latitude of about 41° N, which is within the range of the palaeolatitude of the Jehol Biota (40–45° N (ref. 17)) during the Early Cretaceous. Associated with the new lamprey are abundant fossils commonly found in the Jehol Biota, including insects, a teleost *Lycoptera davidi* (Osteoglossomorpha), a salamander, a lizard and an unidentified fossil bird. All of these animals are terrestrial or freshwater dwellers. There is also no indication whatsoever that the area has had any connection with

the sea since the Triassic period¹⁸. *Mesomyzon* was no doubt also a freshwater dweller. It probably evolved from an anadromous fore-runner because it still kept the basic pattern of an oral sucker characteristic of a sea lamprey. It seems likely that living lampreys originated from anadromous ancestors before some of them became landlocked in the freshwater environment.

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