

A new Eocene catostomid (Teleostei: Cypriniformes) from northeastern China and early divergence of Catostomidae

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A new Eocene catostomid genus and species, †*Plesiomyxocyprinus arratiae*, is described from Huadian, Jilin Province, northeastern China. The materials include a nearly complete skeleton, dozens of pharyngeal bones with teeth, and a number of disarticulated bones. The new articulated specimen is large-sized and deep-bodied, with an estimated standard length of ca. 300 mm and body depth of 156 mm or about half of its standard length. The assignment of the fish to the Catostomidae is based on its falciform pharyngeal bone with one row of numerous (more than 50) compressed teeth, and the bone is much smaller than in cyprinids, especially given the size of the fish. The new fish distinguishes itself from all known catostomids (both extinct and extant) in its long anal fin with four unbranched and 17–18 branched rays, and its extremely short caudal peduncle that is only about one fourth of its depth. †*Plesiomyxocyprinus arratiae* resembles the Eocene-Oligocene transpacific-distributed †*Amyzon* in many general skeletal characters. However, it shows a few characters uniquely shared with the Recent catostomid *Myxocyprinus asiaticus*. Those include a very long dorsal fin with about 50 branched fin rays, the end of dorsal fin rays being close to the caudal fin base, and anal rays stretching posteriorly beyond the base of caudal fin. It is the first fossil catostomid that shows a close relationship to the endemic *Myxocyprinus* now living in the Yangtze River and Minjiang River, China. The discovery of †*Plesiomyxocyprinus arratiae*, along with two previously described possible catostomid genera †*Jianghanichthys* and †*Vasnetzovia*, may indicate that the divergence of the Catostomidae started much earlier, in the middle Eocene or earlier, on the western side of the Pacific than on its eastern side.

a new catostomid genus, Eocene, northeastern China, early divergence

Extant catostomids include 13 genera and 72 species that live in temperate rivers and lakes^[1,2]. Except two Asiatic species, they are widely distributed in North America. Of the two Asiatic species, *Catostomus catostomus* lives in northeastern Siberia and *Myxocyprinus asiaticus* is endemic to the Yangtze and Minjiang rivers in southern China^[2,3]. This peculiar transpacific distribution has also been observed on fossil catostomids^[4,5]. Contrary to their limited modern distribution pattern, catostomids were found from many parts of Asia during the Eocene^[5–8].

The first fossil catostomid record of Asia, the Gobi “*Catostomus*”, consisted of a few disarticulated opercles and vertebrae from the middle Eocene of Inner Mongolia, China^[9]. Nelson^[10] examined the opercular series of the Catostomidae and pointed out that the opercles found from Gobi might be assigned to either *Carpiodes*

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group or the genus *Myxocyprinus*, and might not be catostomids. Thus, the Gobi specimens were probably misidentified as *Catostomus*, but the presence of catostomids in that area was later confirmed by Zhou Jia-jian and others' fieldwork.

Sytchevskaya^[4] described a new genus, †*Vasnetzovia* from Southern Premorie in eastern Siberia. She also erected several new species belonging to †*Amyzon* and Recent genera in the same paper, which were later invalidated^[1,8]. The first unambiguous report of catostomid from China was †*Amyzon hunanensis* (Cheng, 1962) that was initially referred to cyprinids^[5,11].

The first fossil catostomid genus and species †*Amyzon mentale* was erected by Cope in 1872 from the Eocene-Oligocene paper-coal of Osino, Nevada, USA^[12]. More fossil species were referred to this genus subsequently. Its record could be traced back to the Paleocene Paskapoo Formation of Alberta, Canada^[13]. Although Cavender^[14] claimed that the Paleogene catostomids may have belonged to several distinct genera, merely two genera (†*Amyzon* and †*Vasnetzovia*) have been accepted so far. Among the species of †*Amyzon*, Brunner^[15] suggested that only four of the seven described species were undoubtedly valid. Catostomids belonging to extant genera appeared by the middle or late Miocene on both sides of the Continental Divide^[14]. Several fossil catostomids were studied in detail^[16–20], and some were

assigned to Recent species^[21,22].

A number of systematic studies of catostomids were done in the past using morphological, biochemical, developmental, and molecular characters^[1,23–28]. Smith^[1] published the most comprehensive phylogenetic analysis on the Catostomidae involving 63 recent catostomid species and one fossil genus †*Amyzon* using a data matrix of 157 characters. He subdivided the Catostomidae into three subfamilies: Ictiobinae, composed of *Ictiobus* and *Carpiodes*; Cycleptinae, comprising *Cycleptus* and *Myxocyprinus*; and Catostominae, containing the remaining genera with more than 60 species. The fossil genus †*Amyzon* was assigned to Ictiobinae. However, Nelson^[24] proposed that *Myxocyprinus* may form a subfamily of its own based on the morphology of Weberian complex. This suggestion is supported by recent phylogenetic analyses based on molecular data, which claim that *Myxocyprinus* should be removed from Cycleptinae and form a subfamily of its own, Myxocyprininae^[28,29].

In this paper, we describe a new catostomid genus and species, based on a nearly complete skeleton, as well as a number of disarticulated bones and pharyngeal bones with teeth. The specimens were collected from the Huadian Formation in several Coal Mines of Gonglangtou, Dachengzi and Daboji Village, Huadian City, Jilin Province (Figure 1).

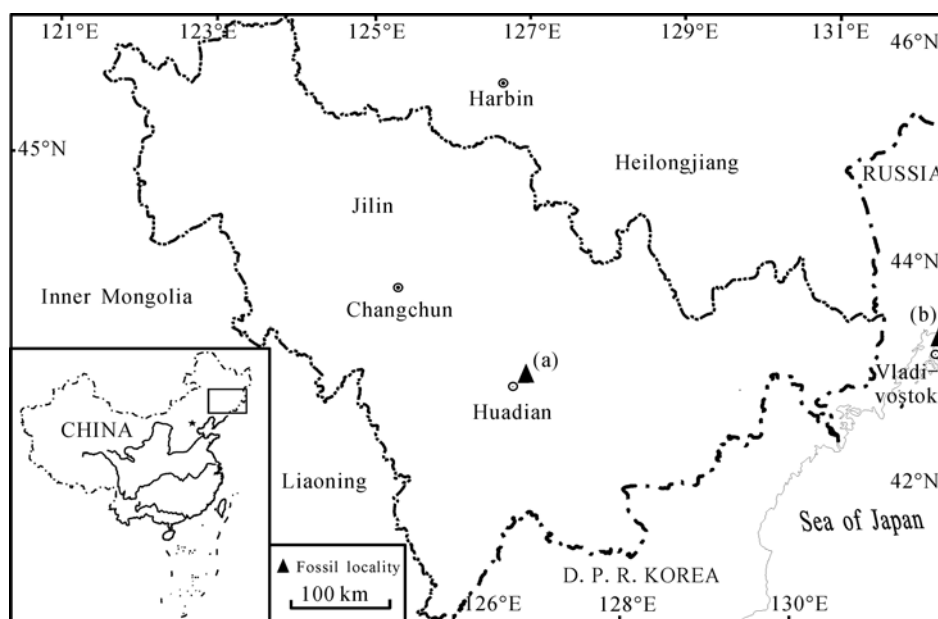


Figure 1 Localities of fossil catostomid †*Plesiomyxocyprinus arratae* gen. et sp. nov. Huadian, Jilin Province, China (a), and †*Vasnetzovia artemica* from Premorie, near Vladivostok, Russia (b).

1 Geology

The Huadian Formation consists of brown, dark grey and black oil shale, and was deposited in northwestern Huadian Basin, eastern Jilin. The coalmines there have been studied since the 1930s. The Formation was named by Li Yongxiao in 1962 (unpublished report) and tentatively assigned to Paleocene-Oligocene epoch by the Bureau of Geology and Mineral Resources of Jilin Province^[30]. It is sandwiched between the Early Cretaceous Heiweizi Formation^[31,32] and the middle Miocene Tumenzi Formation^[33] unconformably. All of the fossils of Huadian Formation were uncovered from the oil shale that were dug out from the three closed coalmines in Gonglangtou, Dachengzi and Daboji villages, Huadian County. During the 1980s and the 1990s, Jiajian Zhou of IVPP (see institutional abbreviations) collected many fossil teleosts of various groups (e.g. Amiiiformes, Clupeiformes, Perciformes and Catostomidae of Cypriniformes). The first author of this paper and her coworkers from IVPP excavated in Gonglangtou and Dachengzi Mine area in 2007 and collected more catostomid pharyngeal bones with teeth and disarticulated bones, and fragments of bowfins and perciforms.

Based on similar fish assemblages, Zhou and Sun^[34] and Zhang et al.^[31] correlated the Huadian Formation with the Green River Formation in North America, and suggested a late early Eocene age for the Huadian Formation. In addition to fish, other fossil vertebrates, e.g., mammals, birds and reptiles, have also been found from Gonglangtou Oil Shale Mine^[31,32,34,35]. The mammalian fauna of rodents *Zelomys*, primates *Asiomomys*, and three insectivore genera indicates that the Huadian Formation is comparable to the Uintan of North American Land Mammal Ages^[32], now considered as middle Eocene^[36]. Thus, we preliminarily consider the age of the Huadian Formation within the range of early-middle Eocene.

2 Materials and methods

2.1 Materials

Referred materials. The holotype (IVPP V 12572.1) and IVPP V 12572.2–72 were collected by Zhou Jiajian, and IVPP V 15711.1–39 by the first author of this paper and her coworkers. All specimens were stored in the IVPP collections.

Materials for comparison. Materials used for comparison include one fossil species and dry skeletons and

articulated and disarticulated bones of 10 Recent species:

†*Amyzon hunanensis*, IVPP V 1102, a nearly complete fish lacking caudal fin, the holotype of the species described by Cheng^[11]; IVPP V 12571.1, a complete fish, the specimen mentioned by Chang et al.^[5].

Carpiodes carpio, IVPP OP 325, disarticulated skull bones and postcranial skeleton.

Catostomus columbianus, IVPP OP 326, disarticulated skull bones, vertebrate column and caudal skeleton.

Catostomus macrocheilus, IVPP OP 327, neurocranium, disarticulated skull and pectoral bones.

Catostomus platyrhynchus, IVPP OP 328, neurocranium and disarticulated skull bones.

Chasmistes liorus, IVPP OP 329, neurocranium and disarticulated skull and pectoral bones.

Deltistes luxatus, IVPP OP 333, disarticulated skull bones and postcranial skeleton.

Cycleptus elongatus, IVPP OP 330, neurocranium with vertebrate column and disarticulated skull, appendicular bones (SL 328 mm).

Ictiobus bubalus, IVPP OP 331, nearly complete skeleton removed right cheek bones.

Moxostoma macrolepidotum, IVPP OP 332, neurocranium vertebrate column and disarticulated bones.

Myxocyprinus asiaticus, IHB 79iv001 skull (HL 166 mm) and pectoral girdle; IHB79iv002, complete skull (HL 179 mm); IHB79iv003, postcranial skeleton without paired fins and girdles (PDL 216 mm); IVPP OP 320, complete alcoholized fish (SL 440 mm) from IHB, and dissected later; IVPP OP 321, complete fishes fixated in ethyl alcohol (SL 119 mm); IVPP OP 322, complete fishes fixated in ethyl alcohol (SL 110 mm); IVPP OP 323, small specimen (SL 45 mm), cleared and alizarin-stained in glycerol; IVPP OP 324, small specimen (SL 13 mm), cleared and alizarin-stained in glycerol.

All skeletal specimens of extant North American taxa were given to the IVPP by Frank Cross of KU (see the abbreviations) in 1985.

2.2 Methods

(1) Preparation methods. The fossils were prepared mechanically. The cleared and stained specimens of *Myxocyprinus asiaticus* were made using the method of Talyor and Van Dyke^[37].

(2) Nomenclature and measurements. The nomenclature and measurements of the pharyngeal bone and teeth follow Chu^[38] and Eastman^[39], those of the opercular

series are after Nelson^[10], and the other anatomical names follow Wilson^[40] and Grande et al.^[41]. Since the holotype (IVPP V 12572.1) is the only nearly complete skeleton available to us, the measurements and meristic data are taken from it. As the snout part of the specimen is missing, the standard length of the holotype is estimated by assuming that the head length is approximately 3 times the width of the opercle, as in *Myxocyprinus asiaticus*, *Ictiobus bubalus*, and †*Amyzon hunanensis*.

The subfamilies Ictiobinae, Cycleptinae and Catostominae used in this paper are according to Smith^[1] unless it is specified.

The dagger symbol “†” is used to denote extinct taxa.

(3) Anatomical abbreviations. A, anal fin; Af, anterior fontanelle; C, caudal fin; Cl, lateral surface of cleithrum; ClI, left cleithrum; clm, median flange of cleithrum; Clr, right cleithrum; Cp, coronoid process of dentary; D, dorsal fin; d, dorsal surface of pharyngeal bone; den, dentigerous surface of pharyngeal bone; ep, epural; Fpf, frontoparietal fontanelle; Gr, gnathic ramus of dentary; h, hypural; i, ischial process of pelvic bone; nc, neural complex; Op, Opercle; Opa, opercular arm; Opp, auricular process of opercle; P, pectoral fin; p, pitted surface of pharyngeal bone; paf, pterygiophore of anal fin; pal, anterior limb of pharyngeal bone; pb, pharyngeal bone with teeth; pdb, predorsal bone; pdf, pterygiophore of dorsal fin; ph, parhypural; ppl, posterior limb of pharyngeal bone; pv, pelvic bone; rna, rudimentary neural arch of pu1; V, pelvic fin; s, splint of pelvic bone; Sop, subopercle; us, urostyle.

(4) Measuring abbreviations. HL, head length; PDL, postdorsal distance, from origin of dorsal fin to base of caudal fin; SL, standard length.

(5) Institutional abbreviations. IHB, Institute of Hydrobiology, Chinese Academy of Sciences; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, both are affiliated to the Chinese Academy of Sciences (CAS). KU, University of Kansas, USA.

3 Systematic paleontology

Superorder Ostariophysi Sagemehl, 1885

Order Cypriniformes Bleeker, 1859/60

Catostomidae Bonaparte, 1840

†*Plesiomyxocyprinus* gen. nov.

Etymology: Plesio-, derived from the Greek *plesio*, meaning close, near; -myxocyprinus, genus name, *Myxocyprinus*, of the only Recent catostomid dwelling

in China.

Type species: †*Plesiomyxocyprinus arratiae* gen. et sp. nov.

Diagnosis: Comparatively large-sized catostomid with the following combination of characters: body deep, depth almost half of standard length; skull roof with small anterior cranial fontanelle and long frontoparietal fontanelle; dorsal and anal fins fairly long, with around 50 and 17–18 rays respectively, origin of anal fin in front of end of dorsal fin, end of both dorsal and anal fins close to caudal fin base, posterior anal rays extending caudally beyond base of caudal fin; caudal peduncle very short, about one fourth its depth; pharyngeal bone falciform, with more than 50 compressed teeth with slightly curved tip, tightly set in comb-like pattern; total number of vertebrae 42, including Weberian complex and 20 caudal.

†*Plesiomyxocyprinus arratiae* gen. et sp. nov

Synonym: Catostomidae indet. Chang et al., 2001, pp. 580–581, fig. 3.

Etymology: The species name is dedicated to Dr. Gloria Arratia for her great contributions to the study of early fossil teleosts.

Holotype: IVPP V 12572.1, a nearly complete skeleton lacking anterior part of head and most of caudal fin (Figure 2).

Paratypes: IVPP V 12572.2, a well-preserved right pharyngeal bone with teeth, described in Chang et al.^[5]; IVPP V 15711.29 (Figures 3(a) and (b)), a nearly complete right frontal; IVPP V 15711.30 (Figures 3(c) and (d)), a complete right dentary; IVPP V 15711.14 (Figures 4(a) and (b)), a right opercle in medial view; IVPP V 15711.17 (Figures 4(c) and (d)), a left opercle in lateral view; IVPP V 15711.21 (Figures 4(e) and (f)), a left preopercle; IVPP V 15711.3 (Figure 5), a right pharyngeal bone with teeth; IVPP V 15711.31 (Figures 6(e), (f), (g) and (h)), a nearly complete cleithrum; IVPP V 15711.36 (Figures 6(j) and (k)), a nearly complete post-cleithrum; IVPP V 12572.71 (Figure 6(a)), a nearly complete right pelvic bone; IVPP V 12572.67 (Figure 6(i)), a nearly complete caudal skeleton.

Referred specimens: IVPP V 12572.3–25, opercles; IVPP V 12572.26–31, preopercles; IVPP V 12572.32–35, subopercles; IVPP V 12572.36–39 interopercles; IVPP V 12572.40–56, pharyngeal bones with teeth; IVPP V 12572.57, premaxillae; IVPP V 12572.58–60 dentaries; IVPP V 12572.61–64, quadrates; IVPP V 12572.65 endopterygoid; IVPP V 12572.66, part of su-

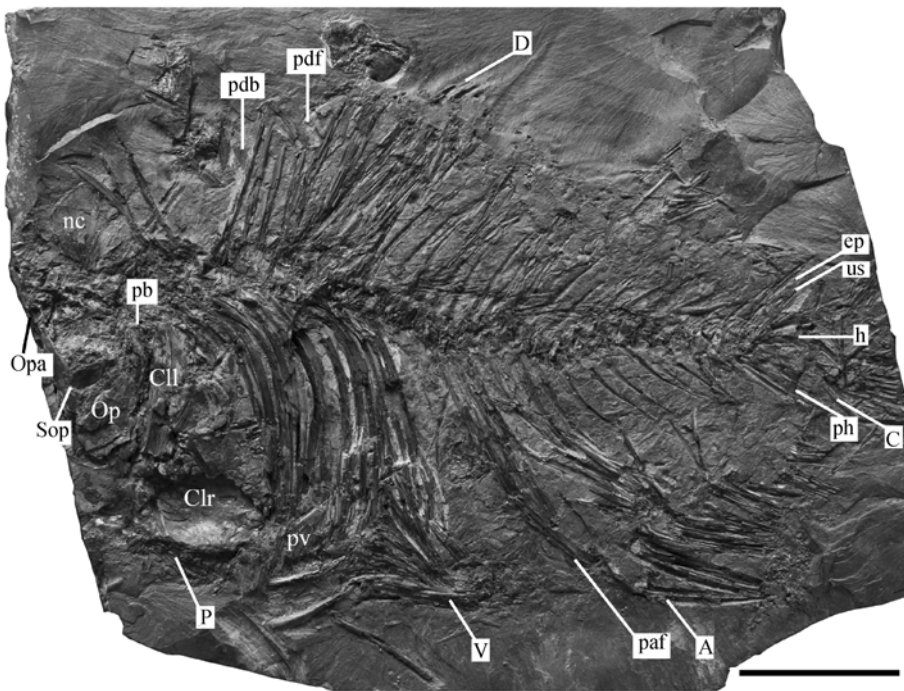


Figure 2 †*Plesiomyxocyprinus arratae*, gen. et sp. nov. The holotype (IVPP V 12572.1). Scale bar equals 5 cm.

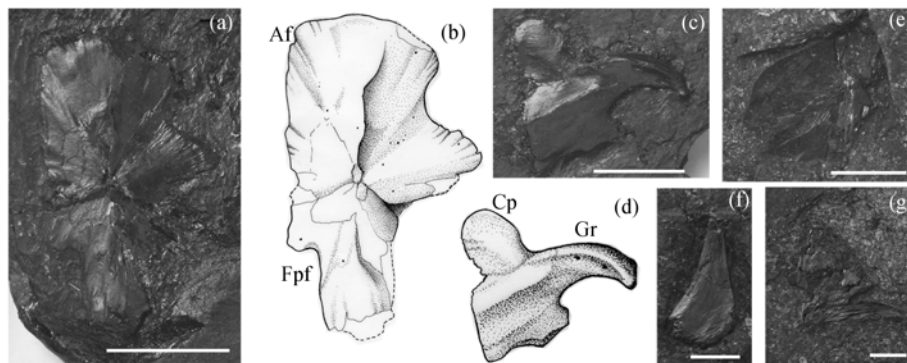


Figure 3 †*Plesiomyxocyprinus arratae* gen. et sp. nov. Roofing bones, jaw bones and palatine. Photograph (a) and drawing (b) of right frontal in dorsal view, IVPP V 15711.29. Photograph (c) and drawing (d) of right dentary in lateral view, IVPP V 15711.30. (e) Right endopterygoid in lateral view, IVPP V 12572.65; (f) Part of left premaxillar in medial view, IVPP V 12572.57; (g) Left quadrate in lateral view, IVPP V 12572.62. Anterior of (a) and (b) facing above, of (c)–(f) facing right, and of (g) facing left. Scale bar is 1 cm for (a)–(c), and 0.5 cm for (f) and (g).

pracleithrum; IVPP V 12572.68–70, caudal skeletons; IVPP V 12572.72 pelvic bones; IVPP V 15711.2 and 4–10, pharyngeal bones with teeth; IVPP V 15711.1 and 11, two specimens of single pharyngeal tooth; IVPP V 15711.12–13, 15–16 and 18–20, opercles; IVPP V 15711.22–25, preopercles; IVPP V 15711.26, a right interopercle; IVPP V 15711.27–28, left frontals; IVPP V 15711.32–34 cleithra; IVPP V 15711.35 and 37–39, postcleithra.

Locality and horizon: Huadian Basin, Jilin Province, northeastern China; Huadian Formation, early to middle

Eocene.

Diagnosis: See the generic diagnosis.

Description

(1) General appearance. The holotype (Figure 2) shows that the new species is a laterally compressed, comparatively large and relatively deep-bodied fish. The length of the preserved portion of the fish, approximately from the anterior border of opercle to the end of the caudal peduncle, is 240.4 mm, and the estimated standard length is about 300 mm. The maximum body depth is at the origin of the dorsal fin and measures 156 mm. Thus, the body depth is approximately half of the

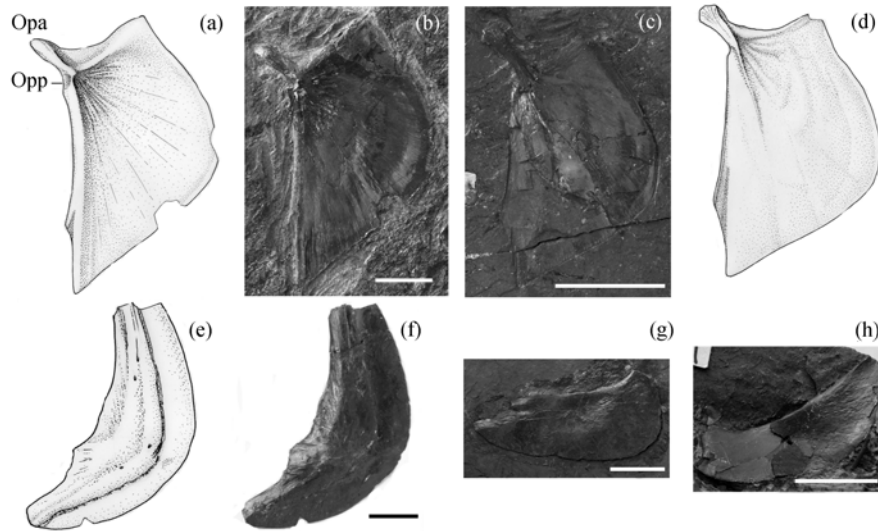


Figure 4 †*Plesiomyxocyprinus arratae* gen. et sp. nov. Opercular series. Drawing (a) and photograph (b) of right opercle in medial view, IVPP V 15711.14. Photograph (c) and drawing (d) of left opercle in lateral view, IVPP V 15711.17. Drawing (e) and photograph (f) of left preopercle in lateral view, IVPP V 15711.21. (g) Right interopercle in medial view, IVPP V 12572.36; (h) right subopercle in medial view, IVPP V 12572.32. Anterior facing left. Scale bars equal 1cm.

standard length, much more than that in †*Amyzon* (0.21–0.44)^[5,40,41] and †*Vasnetzovia* (0.33)^[41]. Judged from the preserved part of the cleithrum in the holotype, the depth of the head must be much smaller than that of the body. The dorsal fin is especially long, with its origin slightly anterior to that of the pelvic fin, and, probably, closer to the tip of the snout than to the caudal base. The origin of the anal fin is in front of the end of the dorsal fin. Both the dorsal and anal fins end close to the caudal fin base. Consequently, the caudal peduncle is very short; its length (11 mm) is only about one fourth of its depth (47 mm). The anal fin has a large number of rays. Among them the posterior ones extend caudally beyond the caudal fin base.

(2) Skull roof. Of the skull roofing bones only a few disarticulated frontals are preserved. The frontal is rectangular (Figures 3(a) and (b)) with a much broader anterior part (having a prominent posterolateral process) than its posterior part. The anterior border is slightly convex. The frontal is smooth, having a longitudinal ridge on its dorsal surface. As in other catostomids (both extinct and extant), the lateral-line system is not associated with the dorsal roofing bones^[41]. Although a few tiny pits can be seen scattered on the surface of the frontal, they are apparently not related to the lateral-line system. Two distinct notches are present at the medial border of the frontal: a small one at the anteromedial border forming the posterolateral margin of the anterior

cranial fontanelle, and a broader and longer one along the medial border of the posterior narrow part of the bone forming the anterolateral border of the frontoparietal fontanelle. An anterior cranial fontanelle is observed in †*Amyzon*^[41] and *Ictiobus bubalus*, *Carpiodes carpio* (belonging to the Ictiobinae), *Cycleptus elongatus*, *Myxocyprinus asiaticus* (referred to the Cycleptinae), whereas it is lacking in the rest of species. Our own observations and the information from the literature suggest the absence of an anterior cranial fontanelle in all catostomines^[1,16,19,42,43], whereas the frontoparietal fontanelle is present in all known catostomids except *Cycleptus*. The fontanelle is present in most species of †*Amyzon*, but its presence or absence in *Vasnetzovia* is not clear. In †*Plesiomyxocyprinus arratae*, the length of the notch in the frontal, forming the frontoparietal fontanelle is about one third of the total length of the bone, as in *Myxocyprinus* and *Carpiodes*.

(3) Jaws and palatine bones. The dentary (Figures 3(c) and (d)) is comparatively short, with a well-developed, rounded coronoid process, extending posterodorsally. The gnathic ramus of the dentary is also short and edentulous. The posterior portion of the dentary expands ventrally and ends shortly behind the coronoid process. Its posterior margin has a small notch where the anguloarticular inserts. A pronounced ridge runs posteriorly from the tip of the gnathic ramus to the base of the coronoid process, apparently for the lip to attach. Two other longitudinal ridges on the outer surface of the

dentary are less prominent. Two pores are present on the ventral surface of the gnathic ramus under the pronounced ridge.

The premaxilla (Figure 3(f)) is triangular, with a deep anterior ascending process. A small posterior portion of its horizontal process is missing.

The quadrate (Figure 3(g)) consists of a plate-like dorsal part and rod-like ventral part. The posterior deep notch between the two parts is for the symplectic to insert, whereas the anteroventrally-situated condyle is for the articulation with the anguloarticular.

The endopterygoid (Figure 3(e)) is a palmate lamina. The anterodorsal border is rather heavy, composing the ball and socket process with the palatine. The posterodorsal edge is completely smooth, showing a free edge of the endopterygoid. The inferior articulate surface between the endopterygoid and mesopterygoid is sharply jagged, and the anteroventral articulate surface is relatively smooth, indicating a loose connection with the ectopterygoid.

(4) Opercular series. All opercles have a straight anterior border, long opercular arm (Figures 4(a)–(d)), and broad, slightly concave superior border. The angle between the anterior and ventral margins is 50° – 80° . The height of opercle is about one and a half to two times of its width. The articular process for the hyomandibular is at the base of opercular arm. The surface of the opercle is, on the whole, smooth, with fine striations radiating from the base of opercular arm towards periphery.

It is difficult, however, to decide to which group, according to Nelson's (1949) classification, these opercles should be referred. It is not clear whether the variations shown in the opercles of catostomids have any generic bearing.

The preopercle (Figures 4(e) and (f)) is triangular and is broad in its middle portion, with its vertical arm slightly longer than the horizontal. Both arms meet at an obtuse angle ranging from 105° to 122° . The preopercular sensory canal is partially enclosed in the bone, and runs along the middle line of it. Thus, the anterior part of the bone is thicker than the posterior. In *Ictiobus*, *Carpionodes*, *Cycleptus* and *Myxocyprinus*, partly embedded preopercular sensory canal is also observed.

The subopercle (Figure 4(h)) is a long, blade-like bone. It has a slightly concave dorsal and rounded, convex ventral border. The two borders are nearly parallel in most extent of the bone except for its posterior part,

which narrows towards the rear. A small rod-like process is extending upwards from its anterodorsal corner. The length/depth ratio of the bone is from 2.9 to 3.4.

The interopercle (Figure 4(g)) is a laminar bone, with its posterior portion deeper than the anterior. Its posterodorsal corner protrudes upwards into an angle, making the posterior part of the dorsal margin of the bone concave. The ventral and posterior margin of the bone is rounded. As in other catostomids, a notch at the anterior end and a groove on the anterolateral surface of the bone are apparently for the mandibular ligament to attach.

(5) Pharyngeal bones and teeth. A few tooth crowns and a worn fragment of pharyngeal bone are found scattered in the gill region of the holotype (IVPP V 12572.1). The teeth are laterally compressed, with a flat, hooked tip. In comparison to the body size, the pharyngeal bones and teeth are much smaller than those in cyprinids. The presence of the pharyngeal bone and teeth *in situ* and their relative size to the body are solid evidence for the unequivocal identification of the specimen as a catostomid.

All 27 pharyngeal bones are comparatively slender (Figure 5). The teeth in the well-preserved right pharyngeal bone IVPP V 12572.2 (see Chang et al.^[5], Figure 3) are arranged in a single row. On the specimen, 40 teeth were counted on its ventral half, and spaces for more than 10 missing teeth could be estimated on its dorsal half. A total number of more than 50 teeth can be estimated, which is similar to that in †*Amyzon*, *Myxocyprinus*, *Cycleptus* and catostomines^[41]. The teeth on the ventral half of the pharyngeal bone are relatively large, whereas on the dorsal half of the bone their size decreases posterodorsally. Most of the preserved teeth are closely set, arranged in a comb-like pattern. The first few teeth have obliquely truncated tops. Teeth in the middle part of the bone are dorsoventrally compressed, with a flat, hooked tip, just as the detached ones observed in the holotype. The remaining teeth on the dorsal half of the bone are very delicate; some are notched at the top. Measurements taken from the paratype IVPP V 12572.2 are: length of the pharyngeal bone being 28.0 mm, width of the bone being 3.3 mm, and length of its anterior edentulous branch being 12.0 mm.

Another pharyngeal bone specimen IVPP V 15711.3, almost freed from the matrix, shows its falciform shape (Figures 5(a) and (b)), and one row of teeth arranged in a comb-like pattern on its dentigerous surface. Only 14

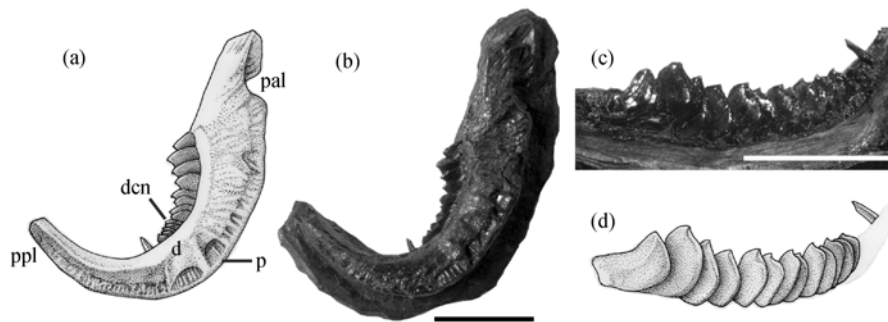


Figure 5 †*Plesiomyxocyprinus arratae* gen. et sp. nov. Pharyngeal bone and teeth. Drawing (a) and photograph (b) of right pharyngeal bone in dorsal view, IVPP V 15711.3. Photograph (c) and drawing (d) of ventral view of the same specimen showing the teeth. Anterior facing above. Scale bars equal 1cm.

teeth (Figures 5(c) and (d)) are found on the ventral half of the bone, whereas the rest of the teeth are missing. This specimen also shows the pitted surface, which is similar to that in Recent catostomids, narrow and cancellous. The bone is broad in its anterior part and narrows posterodorsally.

The pharyngeal bones and teeth obviously fall into Eastman's^[39] "type 2". Compared to the figure of †*Amyzon gosiutensis*, the tooth shape is comparatively similar to that of †*Amyzon* in having a flat conical corona and dorsal hooked tip (see Grande et al.^[41], Figure 6(a)).

(6) Vertebral column and caudal skeleton. There are 42 vertebrae (including Weberian apparatus), 20 of which are caudal. The number is slightly higher than in †*Amyzon* (33–41)^[5,40,41], but less than in †*Vasnetzovia* (44)^[4].

The neural complex and the 4th neural spine are visible on the holotype, preserved partly as bone and partly as impression. Both are shifted anteriorly to the upper part of the skull due to post-mortem displacement. The neural complex is slanting slightly anteriorly, and the 4th neural spine, posteriorly. The neural complex is triangular. Its anterodorsal margin is rounded, with a prominent angular posterodorsal corner, whereas the posterior and short anterior margins are almost straight. The shape of neural complex is somewhat like the one in ictiobines^[24].

There are 18 pairs of ribs preserved (exclusive of the Weberian related), two of which are impressions. About six predorsal bones are located above the 4th to 10th neural spine; five of them are partly preserved. Thin intermuscular bones are preserved dorsal and ventral to the vertebral column. Ventrally they are restricted to the caudal region behind the ribs. The bones are comparatively short and do not go beyond the distal end of the

neural and haemal spines.

The caudal skeleton is preserved in the holotype (IVPP V 12572.1), IVPP V 12572.67 (Figure 6(i)) and a few other specimens. It resembles that of other catostomids in having a compound centrum (pu1+u1+u2), carrying the rudimentary neural arch of pu1^[44], fused with the urostyle posterodorsally and hypural 2 posteroventrally. The parhypural and hypural 1 are articulated with the compound centrum under the hypural 2, whereas h2–3 are fused to the centrum (observed in IVPP V 12572.68) and h4–5 are attached under the urostyle. The fusion of the third hypural to the compound centrum is also seen in *Ictiobus bubalus*, *Carpionodes carpio*, *Myxocyprinus asiaticus* and *Cycleptus elongates*. While the junction is found in *Moxostoma macrolepidotum* and *Catostomus columbianus* (observed in specimens at our disposal), Eastman^[44] asserted that the junction of hypural 3 with the compound centrum is usually indicated by a suture. However, the unfused condition occurs in catostomines but not in the other two subfamilies based on our observations. The hypurals decrease in size dorsally. An accessory neural spine is present on pu2 of the holotype, which is frequently seen in catostomids^[44]. It seems that a thin epural is adhered to the anterodorsal side of the urostyle.

(7) Dorsal and anal fin. Although the dorsal fin is not very well preserved in the holotype, we can still see from the remaining rays and pterygiophores that it is quite long. By counting the rays and pterygiophores, we are almost certain that the fin consists of around 50 rays. This number is even much greater than that of †*Amyzon* (12–33), which until now had the highest number, also deemed the main character of the genus, among all known catostomids^[15]. †*Vasnetzovia* had 20 dorsal rays (5 unbranched and 15 branched)^[4]. Among the extant

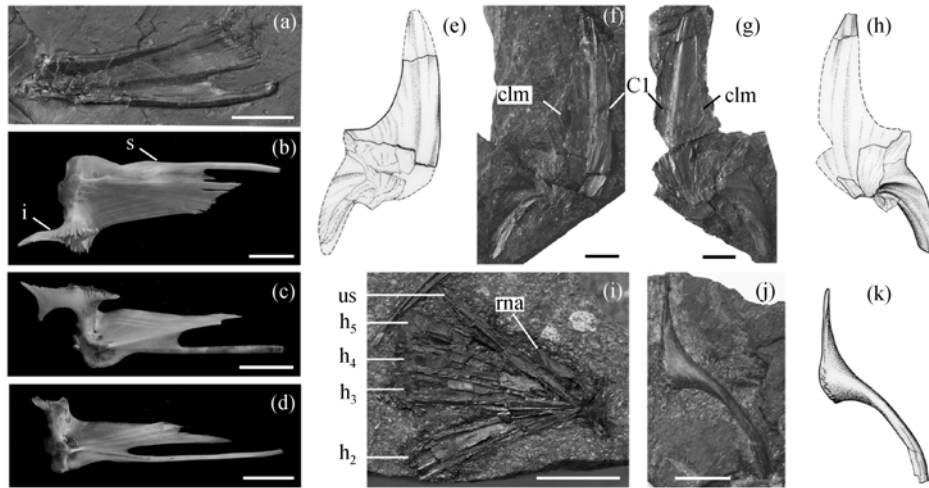


Figure 6 †*Plesiomyxocyprinus arratiae* gen. et sp. nov. and extant catostomids. Appendicular and caudal skeleton. The specimens belonging to †*Plesiomyxocyprinus arratiae* without indication: (a) Splint of right pelvic bone, the others on its counterpart, IVPP V 12572.71b; (b) left pelvic bone of *Myxocyprinus asiaticus*, IVPP OP 320; (c) right pelvic bone of *Cycleptus elongatus*, IVPP OP 330; (d) right pelvic bone of *Moxostoma macrolepidotum*, IVPP OP 332. Drawing ((e), (h)) and photograph ((f), (g)) of the part and counterpart of right cleithrum, IVPP V 15711.31. (i) Caudal skeleton, IVPP V 12572.67. Photograph (j) and drawing (k) of postcleithrum, IVPP V 15711.36. Anterior of (a)–(f) and (i) facing right, of (g), (h), (j) and (k) are left, and of (j) and (k) are not clear. Scale bars equal 1cm.

catostomids, only *Myxocyprinus asiaticus* has a comparable number of dorsal rays (VI, 49–56, pers. obs.). In other catostomids the numbers are variable but less than 37^[2]. The dorsal fin originates approximately at one third of the trunk length, and slightly anterior to the origin of pelvic fin. The first dorsal pterygiophore bears a thin anterodorsal flange, and inserts between the 6th and 8th neural spine. The posterior fin rays extend posteriorly and end above the caudal fin base.

The anal fin is the longest among all catostomids known to date, with the length of its base being 65.4 mm, approximately 1/5 of the estimated standard length. It consists of IV, 17–18 rays, whereas the fin in †*Amyzon* contains 6–10 branched rays^[5, 40, 41], and †*Vasnetzovia*, 10^[4]. In the extant catostomids, *Myxocyprinus asiaticus* has 11–13 branched rays^[45], ictiobines, 7–11, and cycleptines and catostomines, 7 anal rays^[2]. The fin originates well in advance of the vertical through the end of the dorsal fin, and is supported by 11 pterygiophores.

Both dorsal and anal fins extend close to the caudal fin base, and the posterior anal rays actually exceed the base of caudal fin. These are synapomorphic characteristics shared by †*Plesiomyxocyprinus arratiae* and *Myxocyprinus asiaticus*.

(8) Pectoral bones. The part (IVPP V 15711.31a) and counterpart (IVPP V 15711.31b) of a cleithrum (Figures 6(e), (f), (g) and (h)) show that the bone is composed of two sections. The lateral section is elongated, and con-

sists of a vertical ramus and an anteroventral limb. The medial section is a thin, curved plate, expanding medially from the lateral section, and is very broad, typical for catostomids^[20].

In the holotype, the vertical limb of the left cleithrum is preserved behind the gill region (Figure 2). That resulted in the subopercle glided upward under the opercle (Figure 2). A nearly complete impression of the broad ventromedial flange of the right cleithrum was observed behind the left cleithrum.

The postcleithrum (Figures 6(j) and (k)) is a thick rod-like long bone. Similar to that in other catostomids, it consists of a dorsal ramus with a sharply-pointed tip and a vertical anterior edge where it articulates with the cleithrum, and a curved ventral ramus, extending posteroventrally. The length of the dorsal ramus almost equals the preserved part of the ventral ramus. In other species we examined, the length of the ventral ramus is more than double of the dorsal ramus.

(9) Pelvic bones. As in other catostomids, the pelvic bone consists of two parts, an anterior splint and a posteromedial ischial process with articulation facet at its medial side to join its counterpart from the opposite side. The anterior splint is well shown in specimen IVPP V 12572.71b (Figure 6(a)). It is shallowly forked anteriorly. The fork divides the short anterior part of the bone (less than 1/4 of the length of the splint) into a lateral rod-like strut and a medial relatively broad plate. The plate has

an oblique anterior margin and shows about 20 narrow grooves or plicae close to the margin. The posterior ischial process with the articulation facet can be seen in the counterpart of the specimen (IVPP V 12572.71a) and IVPP V 12572.72, but is not very well preserved. The depth of the fork is variable in Recent catostomids: shallow in *Myxocyprinus* (Figure 6(b)), *Ictiobus* and *Carpiodes*, intermediate in *Cycleptus* (about a half of the strut, Figure 6(c)), and very deep in *Moxostoma* (Figure 6(d)). As far as the shallow fork, the comparatively broad medial plate and the numerous plicae on the anterior portion of the plate are concerned, the pelvic bone is more similar to that of *Myxocyprinus asiaticus* than any other catostomid.

(10) Scales. Fragments and impressions of scales seen on the holotype show that the scales were comparatively large, with densely arranged circuli and observable radii.

4 Discussion

4.1 Comparison

The materials described in this paper were all collected from the oil shale of the Huadian Formation in Huadian Basin. A fragment of a delicate pharyngeal bone and a few pharyngeal teeth of catostomid type found in the gill region of the holotype IVPP V 12572.1 make the assignment of the specimen to the Catostomidae unequivocal. The long dorsal fin, the anal fin close to caudal fin, and comparatively short intermuscular bones shown in this specimen are also common to catostomids. The large number of disarticulated pharyngeal bones with teeth and bones from the skull roof, cheek, jaws, palate, paired fin girdles and caudal skeleton associated with the holotype added significant information to our understanding of the new fish †*Plesiomyxocyprinus arratiae*. The delicate falciform pharyngeal bone carrying a single comb-like row of more than 50 flat teeth resembles that of catostomids. In proportion to the body size, the pharyngeal bone is much smaller as compared to that in cyprinids. Also typical for catostomids are the characters such as the shape of the frontal, the two notches at its medial margin indicating the presence of the anterior cranial and frontoparietal fontanelles, and the separation of the sensory canal system from the bone. The other catostomid characteristics of this new taxon include the short dentary with short mouth gape, the L-shaped premaxilla, the long opercular arm, the broad preopercle, the interopercle with a groove on its lateral surface for

the mandibular ligament, the cleithrum with broad ventromedial flange and the forked pelvic bone consisting of a lateral strut and broad medial lamina.

†*Plesiomyxocyprinus arratiae* is, however, distinguished from all other catostomids in its large number of anal fin rays and extremely short caudal peduncle. Among Recent catostomids, *Myxocyprinus asiaticus* has the highest number of anal fin rays, 11–13 branched rays, preceded by 2–4 unbranched rays as reported by Fang^[45] and 12–14 rays, by Meng et al.^[3] and Nelson^[2]. Our own counts from six specimens of *Myxocyprinus asiaticus* are IV, 10–11. In other extant catostomids, the branched anal fin rays are no more than 10. In fossil catostomids, †*Amyzon aggregatum* has 6–10 and †*A. brevipinne* has 8–10 branched rays with a few unbranched anal rays respectively^[40], †*A. gosiutensis* has 7–8 branched rays and 3–4 unbranched accessory rays^[41], whereas †*Vasnetzovia artemica* and †*A. hunanensis* have 10 branched anal rays^[4, 5]. In †*Plesiomyxocyprinus arratiae* the number of anal fin rays is IV, 17–18, much greater than the highest count of known catostomids. Since the termination of the anal fin is very close to the caudal fin base, the length of caudal peduncle is extremely short, only about one fourth of its depth. Thus, the high number of anal rays and the very short caudal peduncle should be apomorphic to †*Plesiomyxocyprinus arratiae* and define it as a new genus and species.

Among known catostomids, both extant and extinct, †*Plesiomyxocyprinus arratiae* shares more characters with *Myxocyprinus asiaticus* than with other forms (Table 1). Its high number of dorsal fin rays (~50) is closest to that in *Myxocyprinus asiaticus* (III–V, 50–57)^[45], much higher than that of all other fossil and Recent catostomids. The number of branched rays is 20–26 in †*A. aggregatum*, 11–19 in †*A. brevipinne*^[40] and 19–20 in †*A. hunanensis*^[5], 21–23 in †*A. gosiutensis*^[41], 28–37 in *Cycleptus*, 22–32 in ictiobines, and 10–18 in catostomines^[2]. The number of anal fin rays in *Myxocyprinus asiaticus* is also the highest among the known catostomids, yet is lower than that of †*Plesiomyxocyprinus arratiae* (see above). The shape of pharyngeal bone and shape and number of its teeth (Figure 5), the presence of two fontanelles on top of the skull (Figures 3(a) and (b)), and the shallow fork of the pelvic bone with its broad medial lamina (Figure 6(a)), are all resembling those of *Myxocyprinus asiaticus*. In addition,

Table 1 Morphological characteristics of †*Plesiomxyxoprinus arratae*, gen. et sp. nov. and related forms^{a)}

Character	† <i>Plesiomxyxoprinus arratae</i>	† <i>Amyzon aggregatum</i>	† <i>A. gosiutensis</i>	† <i>A. hunanensis</i>	<i>Myxocyprinus asiaticus</i>
Maximum standard length (mm)	~300	242	240	200	1210
Ratio of body depth to standard length	~0.52	~0.41	0.36–0.44	0.35–0.43	0.26–0.59
Ratio of caudal depth to standard length	~0.16	~0.15	0.14–0.17	0.13–0.18	0.07–0.10*
Ratio of caudal length to standard length	~0.04	?	0.16–0.22	0.15*	0.08–0.11*
Ratio of dorsal fin base to standard length	~0.41	~0.35	0.32–0.37	0.25*	0.48–0.59*
Ratio of anal fin base to standard length	~0.22	~0.09	0.08–0.09	0.09*	0.06–0.08*
Number of dorsal fin rays	~50	?, 20–26	V–VI, 21–23	IV, 19–20*	III–V, 50–57
Number of anal fin rays	IV, 17–18	?, 6–10	IV–V, 6–7	IV, 10*	II–IV, 11–13
Number of pharyngeal teeth	>50	?	50–60	?	54–89**
Number of vertebrae (including Weberian apparatus)	42	36–41	34–35	34–35	44*
Origin of dorsal fin anterior to pelvic fin	yes	yes	yes	yes	yes*
Origin of anal fin anterior to the end of dorsal fin	yes	yes	yes	yes*	yes*
Posterior dorsal fin rays extending to caudal fin base	yes	no***	no***	no*	yes*
Posterior anal fin rays extending past caudal fin base	yes	no***	no***	no*	yes*
Anterior cranial fontanelle present	yes	?	yes	?	yes*
Preopercular sensory canal partially enclosed	yes	?	?	yes*	yes*
Hypural 3 fused to compound centrum	yes	no	?	no*	yes*

a) Otherwise indicated, data for †*Amyzon aggregatum* come from ref. [40], †*A. gosiutensis* from ref. [5], and †*A. hunanensis* from ref. [41], †*A. hunanensis* from ref. [5], and *Myxocyprinus asiaticus* from ref. [45]. * personal observation, ** from ref. [3]; *** observed from published figures of the respective studies.

the body in smaller individuals of *Myxocyprinus asiaticus* (with SL less than 560 mm) is unusually deep, though it becomes more elongated in larger individuals (with SL 756–1210 mm)^[45]. In fossil catostomids the body is usually deep, ranging from 36%–44% of standard length in †*A. gosiutensis*^[41], around 41% in †*A. aggregatum*^[40], and 35%–43% in *A. hunanensis*^[5]. The body depth of †*Plesiomyxocyprinus arratae* is around half of its standard length, closest to that in smaller individuals of *Myxocyprinus asiaticus*. The long dorsal and anal fins in †*Plesiomyxocyprinus arratae* seem to be uniquely shared with the only living catostomid endemic to Asia. The shape of pharyngeal bone and number of teeth, the presence of the anterior cranial fontanelle, the structure of the pelvic bone, and the high body depth are shared by †*Plesiomyxocyprinus arratae*, *Myxocyprinus asiaticus* as well as certain other catostomids. All these support a sister-group relationship between †*Plesiomyxocyprinus arratae* and *Myxocyprinus asiaticus*.

Another fossil catostomid from Asia, †*Vasnetzovia artemica*, was described based on two nearly complete skeletons from the late Eocene-early Oligocene Wuglovaya Formation of Artem lignite mine, north of Vladivostok, Primorje Province, East Siberia (Figure 1). It was claimed that †*Vasnetzovia* showed most similarities to representatives of the subfamily Ictiobinae, and is distinguished from †*Amyzon* in the position of anal fin behind end of dorsal^[4], longer rudimentary neural process on *pu1*, and higher number of vertebrae (44, including Weberian apparatus). Yet the posterior part of dorsal fin was damaged in the two specimens^[4], and the termination of dorsal fin cannot be observed. Comparison of Figure 1 in Grande et al.^[41] with Figure 206 in Sychevskaya^[4] reveals no obvious difference in the length of the neural process on *pu1* between the two forms. The characters distinguishing †*Vasnetzovia* and †*Amyzon* mentioned by Sychevskaya are the higher number of vertebrae and the position of anal fin posterior to the dorsal fin in †*Vasnetzovia*. According to her description, nearly all meristic and morphometric characters in †*Vasnetzovia* fall in the range of †*Amyzon*^[40,41], but are different from *Myxocyprinus asiaticus* and †*Plesiomyxocyprinus arratae*, except for the slightly higher number of vertebrae. Nevertheless, the anal fin stretching posteriorly beyond the caudal fin base is similar to †*Plesiomyxocyprinus arratae* and *Myxo-*

cyprinus asiaticus, but different from †*Amyzon*.

Another fossil fish from the middle Eocene Yangxi Formation of Dangyang, Songzi and Yidu city, Hubei Province, China, was originally described as †*Osteochilus hubeiensis*^[46] and was later given a new generic name †*Jianghanichthys* by the same author^[47]. Lei noticed in this fish several characters similar to catostomids, e.g., the premaxilla is triangular, not excluding the maxilla from the lateral margin of the mouth, the dentary is high and short, etc., but left it in family incertae sedis (see Chang and Chen^[8]). Since a few tiny, flat pharyngeal teeth of catostomid type were found in a specimen from Songzi, Hubei, one of the two localities where hundreds of specimens of †*Jianghanichthys hubeiensis* were collected^[5], we are inclined to think that †*Jianghanichthys* is a catostomid, pending more detailed study.

4.2 Early divergence of catostomids

The early divergence of catostomids was barely known. The adequately-studied fossil catostomids so far are mostly of the *Amyzon* type from the Paleogene, i.e., from the Paleocene^[13] through the early Oligocene. During the Eocene, they had a wide trans-Pacific distribution over Asia and North America (west of the Continental Divide). They have disappeared from Asia since the early Oligocene, except one endemic surviving species, *Myxocyprinus asiaticus*, and another, *Catostomus catostomus*, that possibly re-entered from North America. Except those based merely on detached pharyngeal teeth from Middle Asia, fossil catostomids belonging to extant North American genera started to occur in North America only since the middle or late Miocene^[4, 5, 8, 41]. They began to occupy areas on both sides of the Continental Divide and display a great diversity (72 species belonging to 13 genera) at present in North and Middle America.

The discovery of the early-middle Eocene catostomid †*Plesiomyxocyprinus arratae* provides significant information on the early divergence of the group. It adds a new, Paleogene non-*Amyzon*-type catostomid in Asia. If †*Vasnetzovia artemica* and †*Jianghanichthys hubeiensis* happen to be verified as valid genera other than †*Amyzon*, the early (Paleogene) diversity of catostomids on the Asian side of the Pacific increases a good deal and becomes much higher than that of their contemporaries in North America.

Smith^[1] subdivided the Catostomidae into the sub-

families Ictiobinae, Cycleptinae (including *Myxocyprinus* and *Cycleptus*) and Catostominae, based on morphological, biochemical, developmental and genetic data. Recent works on molecular systematics of the Catostomidae^[28, 29] are, on the whole, consistent with that of Smith^[1], showing differences mainly in the composition and position of the Cycleptinae. In Harris and Mayden's^[28] analysis based on the mitochondrial rDNA sequences, the Cycleptinae (*sensu* Smith^[1]) resulted not as a monophyletic group, with *Myxocyprinus* as the basal-most taxon of the Catostomidae, and *Cycleptus* as sister to the Catostominae. They suggested setting up a new subfamily Myxocyprininae to include only *Myxocyprinus asiaticus* from China and confine the Cycleptinae to the two species of *Cycleptus* from North America. Sun et al.^[29], based on the analysis of mitochondrial cytochrome b and nuclear 18S-ITS1-5.8S DNA sequences, suggested that catostomids began to diverge in the early or mid-Miocene, which agrees with the fossil evidence known from North America. With the discovery of

†*Plesiomyxocyprinus arratiae* the divergence time of the Catostomidae goes further back, at least, to the middle of the Eocene or even earlier. It is interesting to note that the non-*Amyzon*-type †*Plesiomyxocyprinus arratiae* shows morphological characters, uniquely shared with *Myxocyprinus asiaticus*, the endemic relic of the group in Asia (see above), and is most closely related to the latter. This provides fossil evidence indicating that the divergence between the *Amyzon*-type and *Myxocyprinus*-type catostomids goes back to a time earlier than the middle Eocene on the Asian side of the Pacific.

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