Suckers (Fish, Catostomidae) from the Eocene of China account for the family's current disjunct distributions

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Abstract Unequivocal Eocene suckers from China are for the first time reported here. This discovery demonstrates that catostomids of the Eocene Epoch (some 55—35 Ma ago) are scattered widely on mainland Asia as well as western North America. The present day disjunct distribution pattern of catostomids, with 68 extant species widespread in North America and the northern part of Middle America and only two in the restricted areas of Asia, is the result of their post-Eocene decline in Asia due to the competitive pressure from cyprinids, their Late Cenozoic radiation in North America, and the vicariant and dispersal events triggered by the changed biogeographic landscape. All of these prove to be a historical product of the geological, biological, and climatic changes throughout the Cenozoic.

Keywords: China, catostomids, Eocene, biogeography.

Suckers (Catostomidae) are now one type of the most widespread freshwater fishes in North America, with a southern extension into Mexico and Guatemala. Among the family's 69 extant species[1,2], only two occur elsewhere: one in northeastern corner of Siberia and the other in the Yangtse River and Minjiang River (Fujian Province), China[3,4]. This disjunct distribution (fig. 1(a)) has long puzzled ichthyologists and biogeographers alike. Although Darlington's[5] scenario of eastern Asian origin of catostomids and their subsequent dispersal routes gained acceptance[6—8], it is currently considered problematic because it lacked a robust phylogenetic analysis and an adequate fossil record. Surprisingly, with an almost blank record of fossil suckers in east Asia but quite a few from the then so-called "Oligocene" and "Miocene" in North America[9—11], Darlington[5] postulated that "catostomids originated in eastern Asia, moved primarily from Asia to North America, and (except for *Myxocyprinus*) have been replaced in Asia by cyprinids; that catostomids have radiated secondarily in North America; and that one *Catostomus* has returned to the near corner of Asia." At the time of his writing, the Tertiary fossil record of catostomids in North America comprised a genus †*Amyzon* with five species from what was then thought to be the Oligocene or Miocene, but now known as the Eocene, of Nevada, Colorado, and British Columbia. Since then, however, catostomids have been known from the Eocene and even Paleocene localities

throughout western North America[12,13] (fig. 1(b)). They were all referred to the genus †*Amyzon*[15–18] (fig. 2(b)), though the monophyly of the genus[17] and the validity of some included species[19] were questioned. Suckers belonging to modern genera did not appear until the middle or late Miocene (approximately 15 Ma ago); once they did, they occurred on both sides of the Continental Divide of North America[13,20,21] (fig. 1(b)).

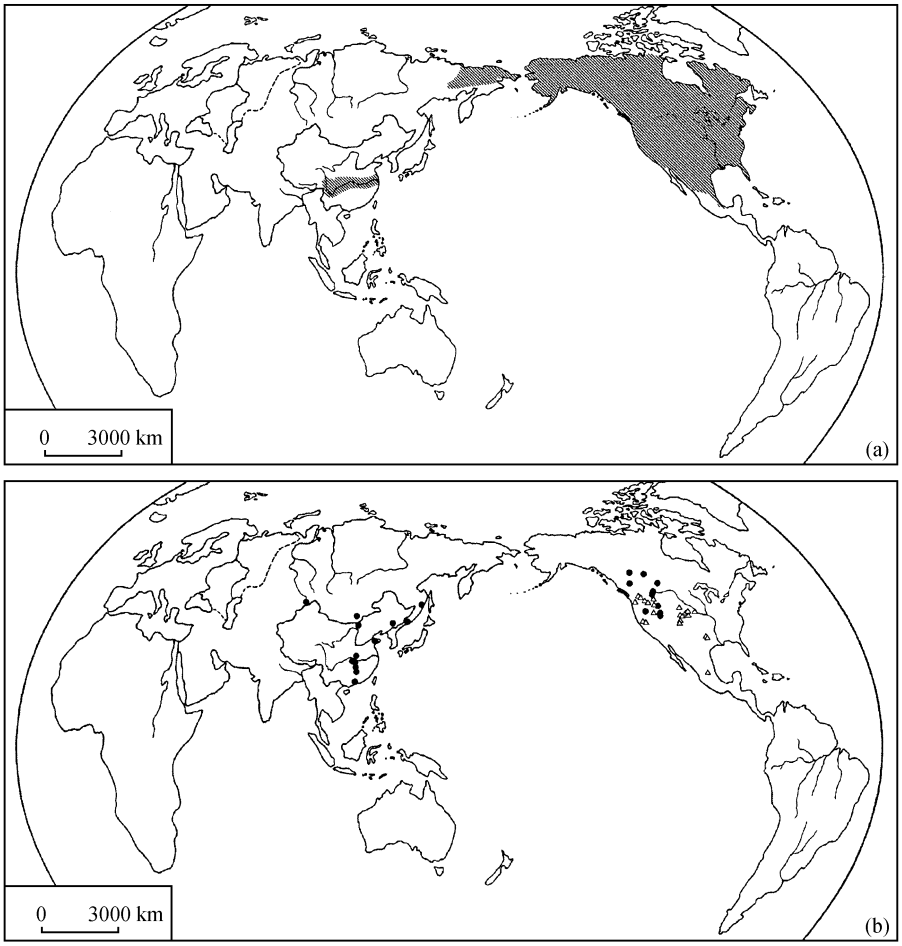

Fig. 1. Distribution of modern suckers ((a), hatched areas), modified from Nelson[14] and Tertiary suckers (b), showing the Eocene catostomids spreading across mainland Asia and western North America, and Late Tertiary catostomids restricted to North America. Black spots indicate early Tertiary localities, triangles indicate late Tertiary localities.

Prior to this report, fossil suckers were conspicuously absent from China except a few disarticulated operculars and vertebrae assigned as *Catostomus* sp. from the middle Eocene of Inner Mongolia, China[1,22]. In fact, the fossil record of suckers from Asia as a whole was sketchy. Sytchevskaya[7] described a late Eocene or early Oligocene sucker, †*Vasnetzovia*, from the Far East coastal area of Russia but did not mention its pharyngeal teeth. Other fossil suckers described by the same author from the early-middle Eocene and early Oligocene of Zaysan Basin, East Kazakhstan, were based on detached pharyngeal teeth alone. Among her findings, all but an ictiobine,

†*Vasnetzovia*, were dismissed by Smith[1]. Besides, their occurrences were restricted to northern Asia[7].

1 Systematics

Here we describe a newly recognized catostomid from Xiawanpu, Xiangxiang, Hunan Province, southern China based on abundant materials previously referred to *Osteochilus*, a Recent cyprinid[23,24].

Order Cypriniformes
Family Catostomidae
Genus †*Amyzon* Cope, 1872
Species †*Amyzon hunanensis* (Cheng), 1962 (fig. 2(a))

Emended diagnosis. Eocene †*Amyzon* with a combination of the following characters: terminal mouth; frontoparietal fontanelle present; dorsal fin elongate and emarginate with 19—20 principal rays; caudal fin shallowly emarginated with round-tip lobes and 16 branched rays; anal fin with 10 principal rays; total number of vertebrae including the Weberian apparatus 34—35, 14—15 being caudal; anterior dorsal profile comparatively rounded, body depth to standard length ratio 0.35—0.43; head length to standard length ratio 0.27—0.29; ratio of caudal peduncle depth to standard length 0.13—0.18.

Description and comparison. †*Amyzon hunanensis* is a comparatively small fish with maximum body length of 200 mm, whereas the body length of †*A. gosiutensis* (regarded by Bruner[19] as junior synonym of †*A. aggregatum*) from Green River, Wyoming[18] may exceed 300 mm. The anterior dorsal profile seems more rounded than in †*A. aggregatum*. It has an edentulous, terminal mouth, as in all other †*Amyzon* (M. V. H. Wilson, pers. comm.). The upper jaw margin is bordered by both the premaxilla and maxilla, as in other catostomids. The smooth and somewhat concave medial margin of the frontal indicates presence of an open frontoparietal fontanelle. The dorsal fin is elongate and slightly emarginate behind the first, longest fin ray, with 19—20 principal rays, less than that in †*A. aggregatum* (21—27) from Horsefly, British Columbia[16] and †*A. gosiutensis* (22—24) from Green River, Wyoming[18]. The caudal fin is shallowly emarginate. Its upper and lower lobes have rounded tips. There are 16 branched caudal rays. The caudal skeleton is of the cyprinid and catostomid type. The compound ural centrum (possibly a fusion of the first preural and the two ural centra) has an urostyle and a short neural spine, with 3—5 upper hypurals and one epural. The anal fin has 10 principal rays and thus, in most cases, has more rays than that in †*A. aggregatum* (8—10) and †*A. gosiutensis* (7—8). The total number of vertebrae including the Weberian apparatus is 34—36, of which 14—15 are caudal. The number is comparable to or less than that in †*A. aggregatum* (36—41) but comparable with that in †*A. gosiutensis* (34—35). The maximum depth of the body is at the origin of the dorsal fin or just in front of it.

The depth to standard length ratio is 0.35—0.43, close to that in †*A. aggregatum* (around 0.41) and †*A. gosiutensis* (0.36—0.44). The head length to standard length ratio is 0.27—0.29 and is slightly smaller than that in both †*A. aggregatum* (0.30) and †*A. gosiutensis* (0.29—0.33). The depth of peduncle to standard length ratio is 0.13—0.18, and thus falls within the range of †*A. aggregatum* (0.094—0.189) and similar to that of †*A. gosiutensis* (0.14—0.17). Among the aforementioned characters the component of the upper jaw margin and the number of the principal branched caudal fin rays are two more easily recognized differences between catostomids and cyprinids in addition to the pharyngeal teeth. In cyprinids, the upper jaw margin is bordered by the premaxilla alone and there are 17 principal branched caudal fin rays.

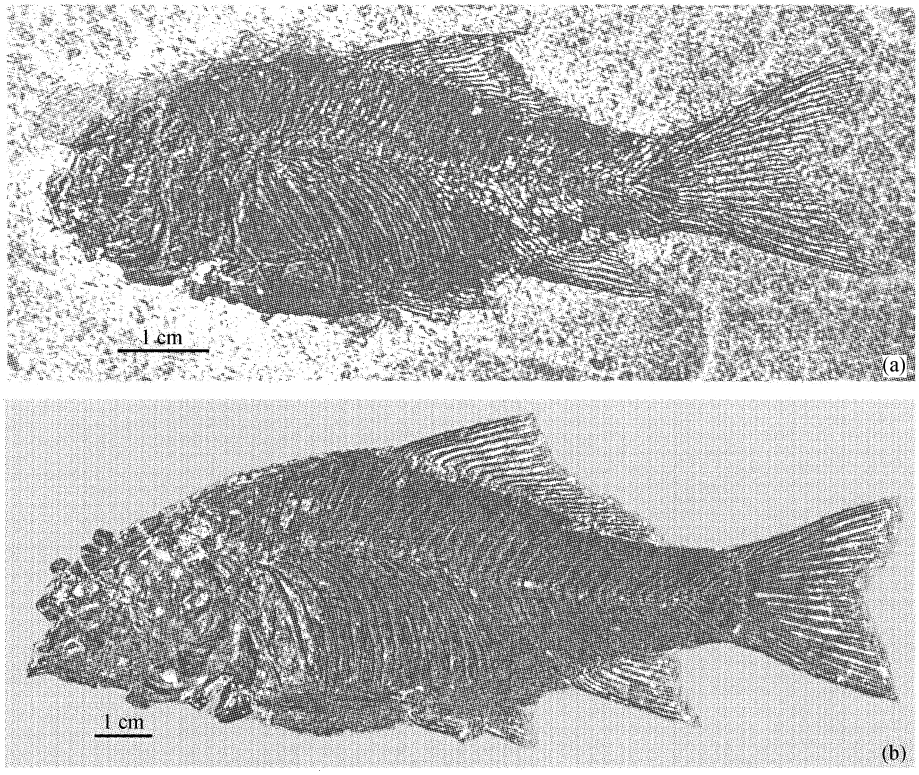

Fig. 2. Two species of †*Amyzon*: †*A. aggregatum* Wilson (a) from Horsefly Mine L88, BC, Canada (Royal Ontario Museum 11051[16]), a complete fish; and †*A. hunanensis* (Cheng) (b) from Xiawanpu, Xiangxiang, Hunan, China (V12571.1), a nearly complete fish with tip of snout lacking.

Remarks. We recently discovered material from Huadian, Jilin Province, northeastern China with an unusually well preserved pharyngeal bone carrying one row of numerous and closely set teeth (fig. 3). This diagnostic feature unmistakably reveals its identity as a sucker and thus shows, unambiguously for the first time, the Asiatic occurrence of Eocene suckers. We also found a few tiny, compressed pharyngeal teeth on one specimen among hundreds from Songzi, Hubei Province, after nearly 20 years of searching and exquisite preparation. The fish, at the same

time, has many other characters similar to †*Amyzon*. Having compared these with the previously described Chinese fossils that were lumped under a living cyprinid genus *Osteochilus*[22—25], we came to realize that all of them in fact belong to Catostomidae[26,27]. Particularly, †*Osteochilus hunanensis* Cheng, 1962, from the middle Eocene of Hunan is strikingly similar to †*Amyzon aggregatum* (with †*A. gosiutensis* as its junior synonym) (compare fig. 2(a) with fig. 2(b)). The few differences between them include a more rounded anterior dorsal profile and a few minor meristic ones as discussed above. However, the specimen from Huadian differs from other Chinese catostomids in its unusually long anal fin. Therefore, while we tentatively refer †*Osteochilus hunanensis* to †*Amyzon* here, we prefer to describe the Huadian specimen in a more detailed study.

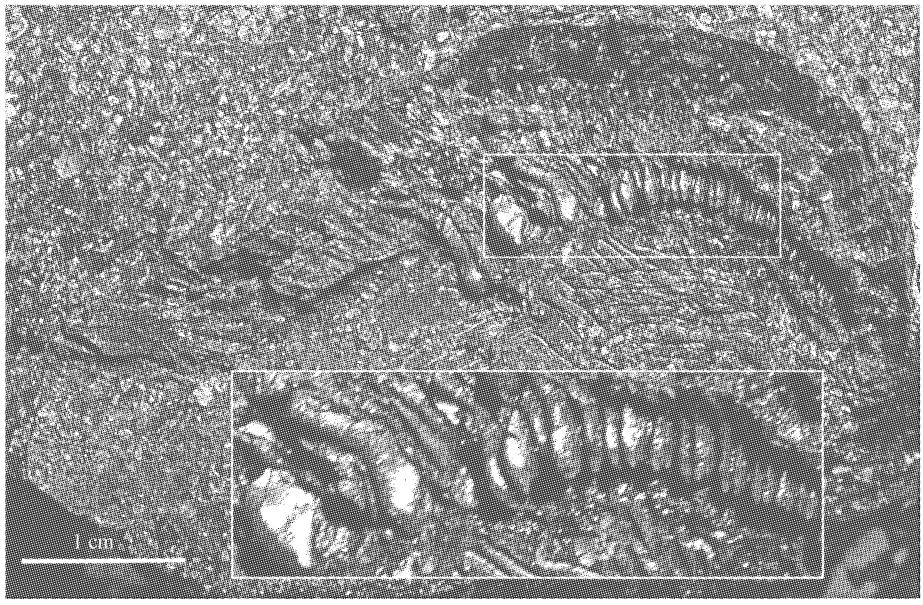

Fig. 3. Catostomidae indet. from Huanan, northeast China, pharyngeal bone with teeth (V12572.2).

2 Discussion

In retrospect, at least two factors could be allotted to the previous misidentifications of the Chinese fossil suckers as cyprinids. First, not only are catostomids morphologically similar to cyprinids but also the former share a part of the latter's ecological niches. In fact, the first extant sucker species was initially also described as a cyprinid, *Cyprinus catostomus*[28]. Cyprinids are characterized by fewer but larger pharyngeal teeth arranged in one to three rows on the pharyngeal bones[29], in contrast with catostomids' one row of numerous, laterally compressed, and comparatively small pharyngeal teeth[30]. On imperfect fossil specimens and in the absence of pharyngeal bones and teeth, it is not always easy to distinguish them. Second, cyprinids are one of the most dominant groups of extant freshwater fishes in Asia and have a reasonably good Asiatic fossil record from the middle Eocene onward. Catostomids, on the other hand, were then known to be a minor element in the Asian ichthyofaunas, both extant and extinct. Again in the absence of pha-

ryngeal bone and teeth and the specimens with well-preserved skeleton, it was only natural for the earlier authors[23,24] to refer their specimens to cyprinids instead of catostomids.

With recent discoveries and amended identifications of the previously described taxa, the Eocene and early Oligocene catostomids are now known to be widely spread across mainland Asia, from Mongolia in the north to Guangdong Province of China in the south and from eastern Kazakhstan in the west to the Far East region of Russia and Wutu, Shandong Province, China in the east (fig. 1(b)). Suckers are often found the most abundant fishes at the localities where they occur, on both sides of the Pacific. Therefore, it is clear that during the Eocene and early Oligocene, catostomids had a wide, transpacific distribution over Asia and western North America.

Except two surviving species, *Myxocyprinus asiaticus* and *Catostomus catostomus*, suckers have disappeared from Asia since early Oligocene. After the withdrawal of the Mid-Continental Seaway in the Paleocene, North America integrated into an extensive land but did not immediately allow suckers to exploit the various habitats on the eastern side of the Continental Divide, owing to the structural disturbances created by the Cretaceous-Eocene Laramide Orogeny and its ripple effects during the mid-Tertiary[31,32]. And due to the high eustatic sea levels much of the Atlantic and Gulf Coastal Plains were inundated during most of the Eocene[33]. Thus, it was not until the Oligocene did suckers spread to eastern North America. From the Miocene on, suckers of living species of *Cycleptus, Ictiobus, Carpiodes*, and many genera from the subfamily Catostominae started to conquer freshwater systems of the entire territory of North America. Catostominae, with a total of 59 species, comprises more than 80% of the species number of the whole family. Catostominae is restricted to North America and the northern part of Middle America except for one species, *Catostomus catostomus*, which also occurs in a very restricted part of east Siberia, presumably representing a postglacial dispersal of the species[1,13,15,31].

A biotic reorganization took place approximately at the Eocene/Oligocene boundary due to the global climatic change from warm and humid to cool and arid[34]. Conceivably, with this general reorganization ended the predominance of catostomids in the freshwater fish fauna of Asia, as did many other groups in the biota. Then why do suckers still continue to exist, expand, and even in some way, flourish in North America while most of their kin have vanished from Asia? The main factor contributing to the catostomids' decline in Asia is most probably the competitive pressure from cyprinids[5]. Both of them are of the few primary freshwater fish groups and are occupying similar ecological niches. When cyprinids first appeared in Asia in the middle Eocene[7,25,35], catostomids still dominated the scene. The Oligocene record of fossil fishes and other terrestrial animals are comparatively rare in China as well as in other parts of the world. The fish remains of this epoch from the known localities mainly consist of detached pharyngeal teeth of cyprinids, usually found in large quantity and along with the remains of small mammals. The fossil-bearing deposits are relatively coarse. No remains of suckers have ever been found from any Oligocene or later deposits of Asia. By the early Miocene cyprinids began to constitute the major-

ity of the freshwater fossil fish record from this area. Many Miocene and Pliocene fossil fishes are from lacustrine deposits and thus well preserved[35—39]. Cyprinids are dominant in the Recent freshwater ichthyofauna of Asia. Most of them are known to have a temperature preference for spawning, possibly adapted for the Monsoon climate. The uplift of the Himalayas and the Qinghai-Tibet Plateau beginning at the Eocene/Oligocene boundary created such a climate in southeastern Asia and caused the large eastward flowing rivers to develop; this climate and topographical changes may have favored cyprinids, probably at the expense of catostomids.

In North America, cyprinids appeared in the middle to late Oligocene, later than they did in Asia. They seem to have reached North America from Asia across Beringia. Only by the late Miocene were they widely distributed in western North America[40]. Of the 2010 living cyprinid species (belonging to 210 genera) of the world, some 1270 are known from Eurasia and only 270 from North America[41]. Nearly seventy percent of North American living cyprinid species dwell in the eastern region, a result of their recent explosive radiation[6]. It appears that the cyprinids' later arrival and blossoming in North America may account for catostomids' continued success there.

Suckers are only one of several fish groups which had a transpacific distribution during the Early Tertiary[7,35,42]. The transpacific distribution pattern started in the Late Cretaceous when a series of continental collisions in Beringia provided a broad passage for the dispersal of terrestrial and freshwater biota[32]. After the faunal reorganization at the Eocene/Oligocene boundary, many groups became extinct in Asia, e.g. Amiidae, Hiodontidae, and most of Catostomidae, but continued to exist in North America. Some forms belonging to these groups survive there even up to the present day.

In addition, this distribution pattern of freshwater fishes also mimics that of other vertebrate groups, especially mammals. Beard[43] even went so far as to call it "East of Eden" model and deem North America functioned primarily as a biogeographical cul-de-sac of Asia since at least Late Cretaceous. All in all, fossil record and historical geology now appear to favor Darlington's[5] dispersal hypothesis on historical biogeography of catostomids. However, in terms of the dispersal model, one could equally argue that catostomids might have originated in North America and their two crossings of Beringia were in the same direction: both from North America to Asia. Just as the available fossil evidence seems to corroborate Darlington's scenario, so the same evidence seems to be congruous with this alternative one.

Alternatively, this contradiction could be reconciled by adopting a vicariance model in light of Smith's[1] cladistic analysis of catostomids. Smith's[1] cladistic analysis largely resolved the intrarelationships of the family Catostomidae. In his phylogenetic scheme (fig. 4), the Early Tertiary †*Amyzon* is grouped with Recent ictiobines, i.e., *Ictiobus* + *Carpiodes*, to form the most primitive of the three subfamilies of the Catostomidae——Ictiobinae. The Chinese rouge fish *Myxocyprinus* is the sister group of the North American *Cycleptus*, and they together form the second subfamily Cycleptinae. The rest and the majority of species of suckers fall into the most advanced

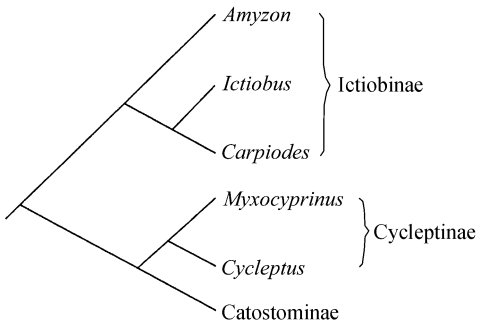

Fig. 4. Phylogeny of the Catostomidae, simplified from Smith[1].

subfamily Catostominae. As we stated earlier, the Eocene primitive ictiobine suckers of †*Amyzon* type had a wide distribution across Asia and western North America through the Bering Land Bridge. This wide longitudinal distribution may be due to global warming and a declining pole-to-equator temperature gradient during the Eocene[34]. In the subfamily Cycleptinae, *Cycleptus* may be represented by the Oligocene fossils from Montana, but the purported Asian *Cycleptus* based on isolated teeth was considered misidentified[1]. No fossil *Myxocyprinus* has ever been reported anywhere. The only two living species of the subfamily have a disjunct distribution, with *Myxocyprinus asiaticus* in the Yangtse and Minjiang rivers and *Cycleptus elongatus* mainly in the Mississippi valley. Consequently, the split between them might have been caused by the inundation of the Bering Land Bridge, thus the separation of Asia from North America. This, therefore, would represent a vicariant event. However, *Catostomus*'s occurrence in Siberia after the desiccation of the Bering Strait during Pleistocene and catostomids' spread to the eastern North America after its reunion with the western counterpart appear to be dispersal events. With this combination of vicariance and dispersal as influenced by the geological events and climatic changes it is possible to explain the current disjunct distributions of catostomids without invoking any scenario based on their presumed "center of origin."

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