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Revision of *Cyprinus maomingensis* Liu 1957 and the first discovery of *Procypris*-like cyprinid (Teleostei, Pisces) from the late Eocene of South China

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Fossil cyprinids from the upper part of the upper Eocene Youganwo Formation of Maoming, Guangdong, China were first studied in 1957 by Liu, who referred the only specimen to the genus *Cyprinus* as a new species, *C. maomingensis*. And this was suggested as one of the earliest records for fossil cyprinids. Unfortunately, this specimen is poorly preserved and reveals no more morphological information than its serrated last unbranched dorsal and anal fin rays. Recently, some new specimens were unearthed from the same locality, where *C. maomingensis* was discovered. In addition to the serrated dorsal and anal fin rays, these new materials also show that the pattern and shape of their pharyngeal teeth obviously differ from that of *Cyprinus* but resemble that of *Procypris*. However, its number of the branched dorsal fin rays and number of vertebrae are much less than that in *Procypris*. Morphologically, these specimens are closer to *Procypris* than to *Cyprinus*. This is the first report of fossil *Procypris*-like fish, and it implies that *Procypris*-like fish is an early member of the Tribe Cyprinini *sensu stricto* (*sensu* Yang et al., 2010) and the origin of this group can be traced back at least to the late Eocene.

late Eocene, *Procypris*-like fish, South China

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The family Cyprinidae is the most diversified and species-rich freshwater fish group (Nelson, 2006) with a very interesting evolutionary and distributional history (Bănărescu, 1990, 1992; Cavender, 1991). However, the earliest fossil record of this group is poorly known thus far (Chang and Chen, 2008; Conway et al., 2010). Only six genera and species and a few unidentified isolate pharyngeal teeth were found from several Eocene localities in Asia (Figure 1). The six genera and species are †*Palaeogobio zhongyuanensis* and †*Rostrogobio maritima* (gobionins, Leuciscinae *sensu* Cavender and Coburn, 1992) from the lower middle Eocene Member IV of the Shahejie Formation, Zhongyuan Oil Field, China (Zhou, 1990) and the upper Eocene to lower Oligocene deposits in Primorye Province, East Siberia (Sytchevskaya, 1986) respectively; †*Tianshanicus liui* (Leuciscinae *sensu* Cavender and Coburn, 1992) from the upper Eocene of Junggar Basin, northern Xinjiang (Su, 2011); †*Planktophaga minuta* (xenocyprins, Leuciscinae *sensu* Cavender and Coburn, 1992) from the middle to upper Eocene of Na Duong Basin, North Vietnam (Böhme

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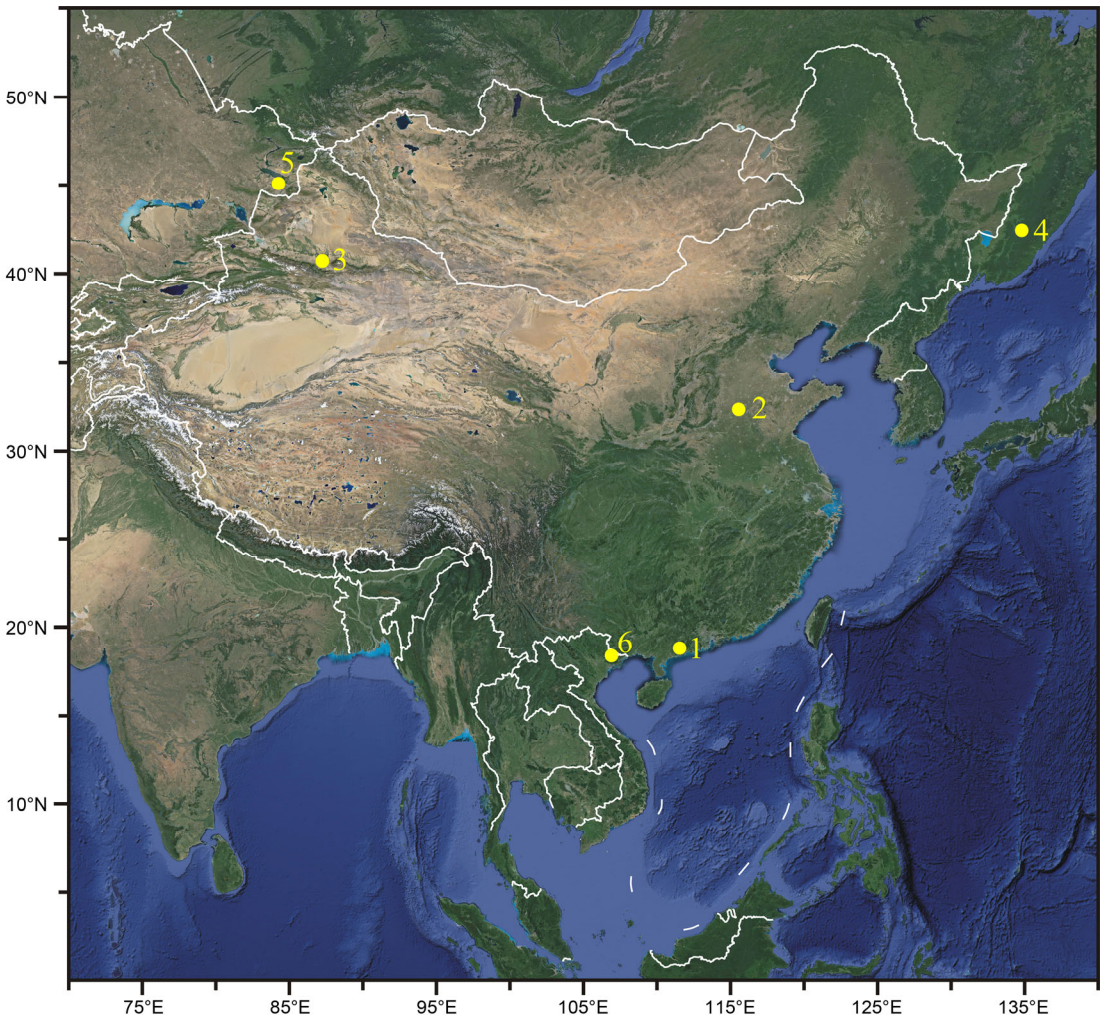

Figure 1 Map of localities of Eocene cyprinids. 1. Maogming, Guangdong, China; 2. Fanxian, Henan, China; 3. Junggar, Xinjiang, China; 4. Primorye, Siberia; 5. Zaisan, Kazakhstan; 6. Na Duong, Vietnam.

et al., 2013); †*Cyprinus maomingensis* (cyprinins, Cyprininae *sensu* Cavender and Coburn, 1992) from the upper Eocene Youganwo Formation of Maoming, Guangdong Province, China (Liu, 1957); and †*Parabarbus* (barbins, Cprininae *sensu* Cavender and Coburn, 1992) from the lower-middle Eocene of Zaissan Basin, East Kazakhstan (Sytchevskaya, 1986). Among these earliest fossils, however, †*Parabarbus* and †*Planktophaga minuta* are presented solely by isolate pharyngeal teeth, and the taxonomic position of the fossil from the Maoming Basin and the age of the fossil from the Zaissan Basin are in some doubts (Chang and Chen, 2008), so it is necessary to further study the earliest cyprinid.

Fossil cyprinids from the upper part of the upper Eocene Youganwo Formation of Maoming, Guangdong Province, southern China were first studied by Liu in 1957 (Liu, 1957). He referred the specimen (IVPP V.855, Figure 2), unearthed from a drilling core 48 m below the ground surface, to the genus *Cyprinus* as a new species, †*C. maomingensis*. Although an age of the Miocene was assigned to †*Cyprinus maomingensis* by Liu (1957), its associated testudinid †*Anosteira maomingensis* (Chow and Liu, 1955; Chow, 1956) and Eomoropid †*Lunania* cf. *L. youngi* Chow (Wang et al., 2007) suggested that the age should be late Eocene. And the magnetostratigraphic study proposed that the Youganwo Formation belongs to the Reversed Chron 18 in the Geomagnetic Polarity Time Scale, which indicated that the strata were formed in the late Eocene (Wang et al., 1994). The specimen of †*Cyprinus maomingensis* is poorly preserved and reveals no more morphological information than its serrated last unbranched dorsal and anal fin rays. In fact, we are unable to observe any character from the specimen that seems to warrant its assignment to *Cyprinus*. Recently, some new specimens were collected from the outcrop of the same locality by a field team from the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. The morphological characters of the newly collected materials indicate that the specimens can be assigned at least to two types of fishes. One type of them shows the following characters: The number of the

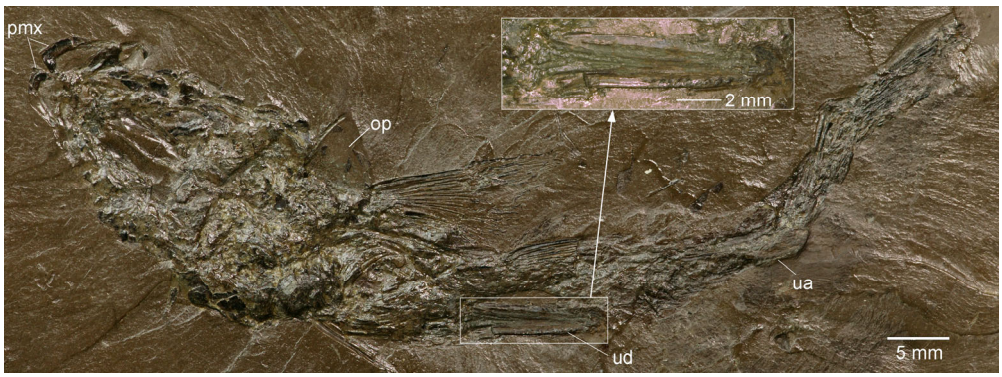

Figure 2 Photograph of the holotype. op, opercle; pmx, premaxilla; ua, last unbranched anal fin ray; ud, last unbranched dorsal fin ray.

branched anal fin ray is five, the last unbranched dorsal and anal fin rays are serrated, and the grinding surface of all the pharyngeal teeth except A1 is spoon-shaped. In the other type, though the number of the branched anal fin ray is also five, and the last unbranched dorsal fin ray serrated, the last unbranched anal fin ray is smooth; and at least one of the pharyngeal teeth is molar-like. From the morphological point of view, the first category is closer to *Procypris* than to *Cyprinus*, and the second one is probably a barbel.

Diverse views exist on the division of the family Cyprinidae and there is no consistency in the allocation of taxa to suprageneric groupings (Berg, 1940; Nikolsky, 1954; Ramaswami, 1955; Wu et al., 1964, 1977; Gosline, 1978; Chen et al., 1984, 1998). In traditional systematic works based on morphology, *Procypris* has been grouped commonly with *Cyprinus*, *Carassius*, and *Carassioides* and uncommonly with *Puntioplites* and a few other genera (Fang, 1936; Zhang, 1959; Wu et al., 1977; Taki and Katsuyama, 1979; Wang, 1979; Rainboth, 1981, 1991; Chen et al., 1984; Meng, 1985; Zhou, 1989; Yue et al., 2000; Kottalat, 2001). This group has been treated as a subfamily of the Cyprinidae by many ichthyologists working on Asian cyprinids (Tchang, 1930; Chu, 1935; Chen and Huang, 1977; Chen et al., 1984; Luo and Yue, 2000). Chen et al. (1984), Howes (1991), and Cavender et al. (1992) suggested the division of the Cyprinidae into two major lineages. Howes (1991) and Cavender et al. (1992) used the subfamily names Cyprininae and the Leuciscinae to designate these lineages. Each subfamily includes a few lineages or tribes. Their Cyprininae includes tribes labeonins, barbins, cyprinins, and a few other subgroups. The genera *Cyprinus* and *Carassius* are included in the cyprinins (Cavender and Coburn, 1992) or barbins (Howes, 1991). Some recent works on molecular phylogeny have included *Procypris*, *Cyprinus*, *Carassioides*, and *Carassius* in the same group (Zhang et al., 2009; Wu et al., 2010; Yang et al., 2010, 2012; Pasco-Viel et al., 2014). In addition, *Sinocyclocheilus*, traditionally included in the Barbini (Wu et al., 1977; Wang et al., 1999; Shan et al., 2000; Xiao et al., 2005), has been shifted to this group. However, Yang et al. (2010) were not sure about the validity of their "Cyprinini-*Sinocyclocheilus*" clade and "call for a thorough morphological systematic study on this clade". Furthermore, they considered that the relationship between *Sinocyclocheilus* and the four genera mentioned above was "weakly supported by MLBS (BP<50%) and BA (BPP= 84%)" in their own work and was "not robustly supported by bootstrap analyses" in Wu et al. (2010). Thus, Yang et al. (2010) finally returned to the stand of accepting the monophyly of the group of the Cyprinini *sensu stricto* as excluding *Sinocyclocheilus*, on the basis of the two synapomorphies suggested by Rainbith (1981) in his PhD thesis: Possession of serrated anal spine and the dorsal fin with no fewer than 10 branched fin rays. By this definition, the group contains four genera, *Cyprinus*, *Carassius*, *Carassioides*, and *Procypris*, as Rainboth (1981) suggested. Yang et al. also used the morphological data from Zhou (1989) to supplement their molecular data in supporting their result, though the intrarelationships within the group proposed by Zhou (1989) are different. In this paper we use Yang et al.'s recent suggestion of reconfirming Rainboth's (1981) definition and scope of the Tribe Cyprinini *sensu stricto*.

The earliest cyprinid materials are rare, and no *Procypris*-like cyprinid fossil has been reported thus far. In the remainder of this paper, we describe the new fossil materials in order to further understand the morphology and differentiation of the early cyprinid fishes.

1 Materials and methods

The fossil materials include the specimen IVPP V.855 studied by Liu in 1957, and the newly collected specimens (listed in "Additional materials" in "2 Systematic paleontology") from the same locality. The comparative materials include pharyngeal bone with teeth of *Puntioplites waandersi* (IOH 78IV0003) and *Cyprinus carpio* (IVPP OP335), cleared and stained specimens of *Procypris rabaudi* (IOH IV0002) and *Cyprinus fuxianensis* (IOH 637153).

The terminology of the skeletons follows Conway et al. (2008), whereas that of the pharyngeal bone and teeth

follows Chu (1935). Tooth positions in the adult dentition are numbered according to Nakajima (1984). Thus, the most medial row is named as the main row (or row A), and lateral rows as outer and most-outer row (or rows B and C). Tooth position is numbered from anterior to posterior in each row. So, A1, A2, and A3 represent the first, second, and third tooth of the main row (row A), whereas B1 and C1 represent the first tooth of row B and row C respectively.

The drawings were based on observations under a Wild M7A microscope and the photographs.

The dagger symbol "†" is used to denote extinct taxa.

Institutional Abbreviations. IOH, Institute of Hydrobiology, Chinese Academy of Sciences; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of China.

2 Systematic paleontology

Superorder Ostariophysi Sagemehl, 1885
Order Cypriniformes Bleeker, 1859/60
Family Cyprinidae Bonaparte, 1840
Subfamily Cyprininae *sensu* Cavender and Coburn, 1992
Tribe Cyprinini *sensu* Yang et al. 2010
†*Eoprocypris* gen. nov.

Etymology: eo-, Greek, means early, primitive; *-procypris*, name for a genus of the Cyprinidae.

Type species: †*Eoprocypris maomingensis* (Liu), 1957.

Diagnosis: Small-sized cyprinin that differs from all other genera in the Tribe Cyprinini with the combination of following characters: body relatively deep, standard length about three times of head length, origin of dorsal fin anterior to insertion of pelvic fin, dorsal fin base relatively short, at least two rows of pharyngeal teeth, number of pharyngeal teeth in main row four, all teeth except A1 with a spoon-shaped grinding surface.

†*Eoprocypris maomingensis* (Liu), 1957

Synonym: †*Cyprinus maomingensis* Liu, 1957.

Holotype: IVPP V.855, a nearly complete fish skeleton, slightly distorted showing its ventral side.

Paratype: IVPP V18953.8, two rows of pharyngeal teeth and many other disarticulated bones.

Additional material: IVPP V18953.1, an incomplete skeleton with the anterior part of the head and the posterior part of caudle portion missing, part and counterpart; IVPP V18953.2, an incomplete skeleton with an incomplete pharyngeal bone with one tooth; IVPP V18953.3, the caudal part of skeletons with anal and caudal fins, part and counterpart; IVPP V18953.4, an incomplete anterior body with two pharyngeal teeth; IVPP V18953.5, a left pharyngeal bone with two teeth and other detached bones and pharyngeal teeth; IVPP V18953.6, an incomplete pharyngeal bone with four teeth; IVPP V18953.7, 9–10, detached pharyngeal teeth; and V18953.11, the caudal part of skeleton with anal and caudal fins, part and counterpart. Among these specimens, V18953.1 is similar to the holotype in bearing serrated last unbranched dorsal and anal fin rays. The pattern and shape of pharyngeal teeth preserved in V18953.8 are similar to those in *Procypris* with no molar-like teeth, and obviously differ from the materials in the second category as mentioned above. Although the anal fin rays of V18953.2 are poorly preserved, its last unbranched dorsal fin ray is clearly serrated as in the holotype; in addition, its pharyngeal tooth *in situ* bears spoon-like grinding surface as in V18953.8, so we tentatively refer V18953.2 and V18953.8 to the same species as the holotype. V18953.3 and V18953.11 are similar to the holotype in bearing serrated last unbranched anal fin ray. The shape of the pharyngeal teeth in V18953.4-7 and V18953.9-10 is similar to that in V18953.2 and V18953.8. Consequently, we tentatively assign all these specimens to the same species.

Locality and horizon: Jintang, Maoming County, Guangdong Province, South China, Youganwo Formation, upper Eocene.

Diagnosis: see genus diagnosis. P, 15; D, iii-9; A, iii-5.

Description

(1) General appearance. Small-sized cyprinin. The holotype is somewhat distorted, showing its ventral view. The total length of the holotype (IVPP V.855) is about 87 mm, the head length and the standard length is about 26 mm and 71 mm respectively, so the head length is longer than one-third of the standard length. In IVPP V18953.2, the standard length is about 85 mm, with its head length slightly shorter than one-third of the standard length. The specimen IVPP V18953.1 shows that the body is relatively deep, possibly equal to the head length. The origin of the dorsal fin is anterior to the insertion of the pelvic fin, and the origin of the anal fin is posterior to the end of the dorsal fin base, both last unbranched dorsal and anal fin rays are robust with serrations on their posterior edges (Figures 2, 3).

(2) Skull bones. The skull bones are not well-preserved,

Figure 3 †*Eoprocypris maomingensis* (Liu), 1957. IVPP V18953.1. An incomplete fish in lateral view, showing its serrated last unbranched dorsal and anal fin rays. Anterior is facing left.

so the outline of most bones in the head almost cannot be distinguished. The specimen V.855 shows that the premaxilla has no teeth on it and has an ascending process at its anterodorsal end. IVPP V 18953.8 shows the detached supraorbital bone and infraorbital 3. They are arc-like thin bones. The infraorbital 3 has more or less the same depth through the entire length, as the case in most cyprinin fishes but *Carassius*. There is a sensory canal running through the orbital edge of the infraorbital 3 (Figure 4(a), (b)). A detached preopercle and an incomplete opercle are preserved in V 18953.8. The dorsal and the ventral limbs of the preopercle are about equal in length and width. The preopercular sensory canal runs along the midline of the bone (Figure 4(c), (d)). In the anterodorsal part of the opercle there is a

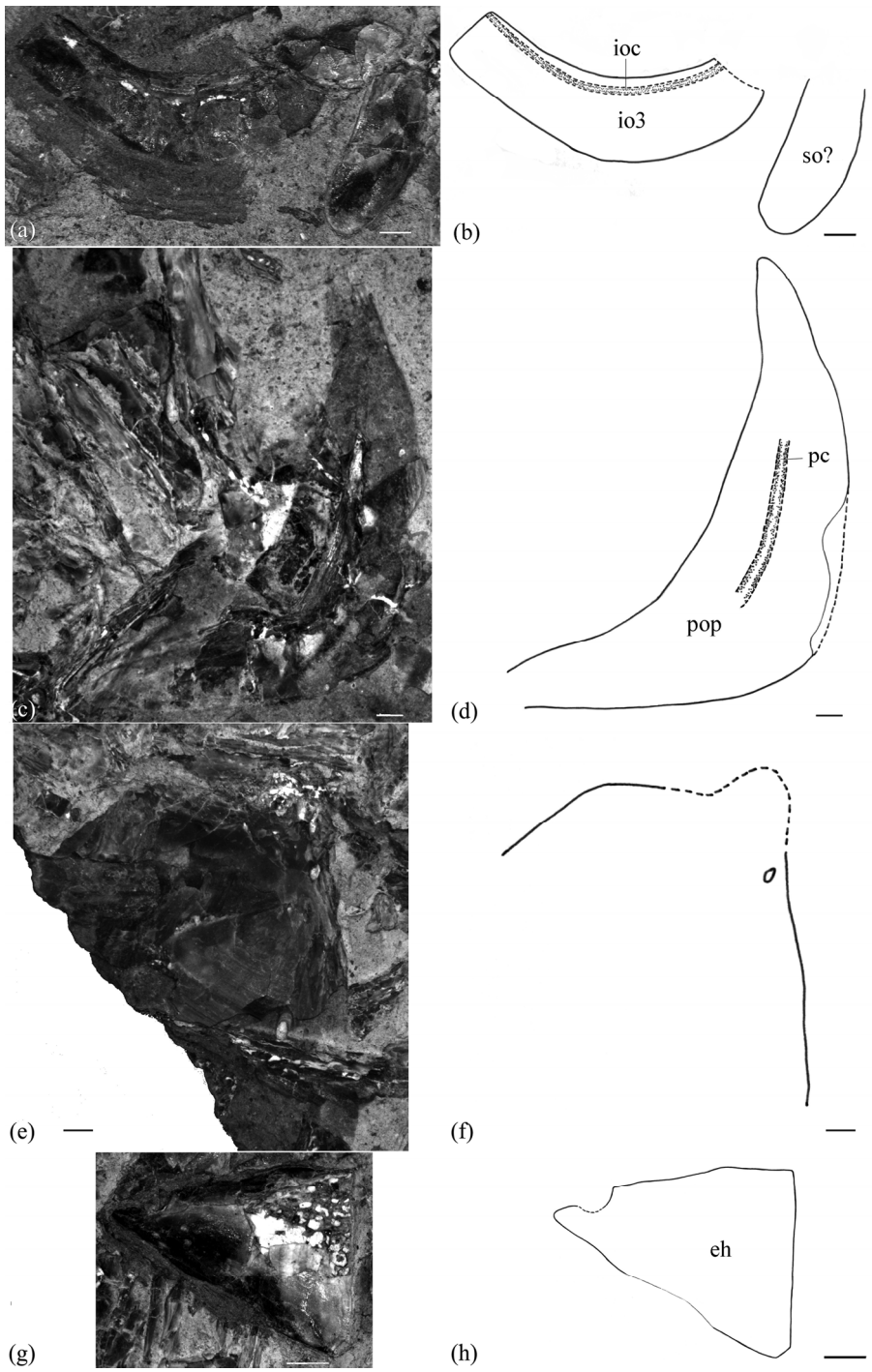

Figure 4 †*Eoprocypris maomingensis* (Liu), 1957. Detached infraorbital 3 ((a), (b)), preopercle ((c), (d)), opercle ((e), (f)), and epihyal ((g), (h)) in IVPP V18953.8. Scale bar equals 1 mm. Abbreviations: eh, epihyal; io, infraorbital; ioc, sensory canal of infraorbital; oc, opercular canal; pc, sensory canal of preopercle; pop, preopercle; so, supraorbital.

small opening (Figure 4(e), (f)), from which we infer that an opercular canal is present. A detached epihyal is also preserved in V 18953.8. It is a triangular, comparatively thick bone plate with an articular facet in its posterolateral part to articulate with the interhyal (Figure 4(g), (h)).

(3) Pharyngeal bone and teeth. The pharyngeal bone can be observed in specimens IVPP V18953.2, V18953.5, and V18953.6. The bone in V18953.5 is well-preserved. The posterior part of the posterior limb in V18953.2 and the anterior part of the anterior limb in V 18953.6 are lost. The pharyngeal bone is arc-shaped, broad, and bending in the middle of the bone. Its length/width ratio is about 3. The anterior limb is slightly shorter than the posterior one. The posterior limb is laterally compressed, with the tip bluntly pointed. The anterior limb is broad at the base, but pointed at its anterior tip. The anterior angle is rounded, probably opposite to the posterior margin of A2 judging from V18953.6. The posterior angle is obsolescent. There are several pits on the pitted surface which were the pass-way of vessel and nerves. The morphological comparison with *Procypris rabaudi* and *Puntioplites waandersi* is shown in Figure 5.

There are at least two rows of pharyngeal teeth judged from IVPP V18953.5 (Figure 5(a)), V18953.8 (Figure 6(a)), and V18953.6. IVPP V18953.8 (Figure 6(a), (b)) and V18953.6 show that there are four teeth in the main row. In V18953.8-2 two rows of pharyngeal teeth are preserved, one with two teeth and the other with three teeth. This indicates that the number of the pharyngeal teeth in B row is at least two. Among the pharyngeal teeth, A1 is the largest, with a conical shape. The tip of A1 is pointed but not recurved, unlike all other teeth that have a pointed and more

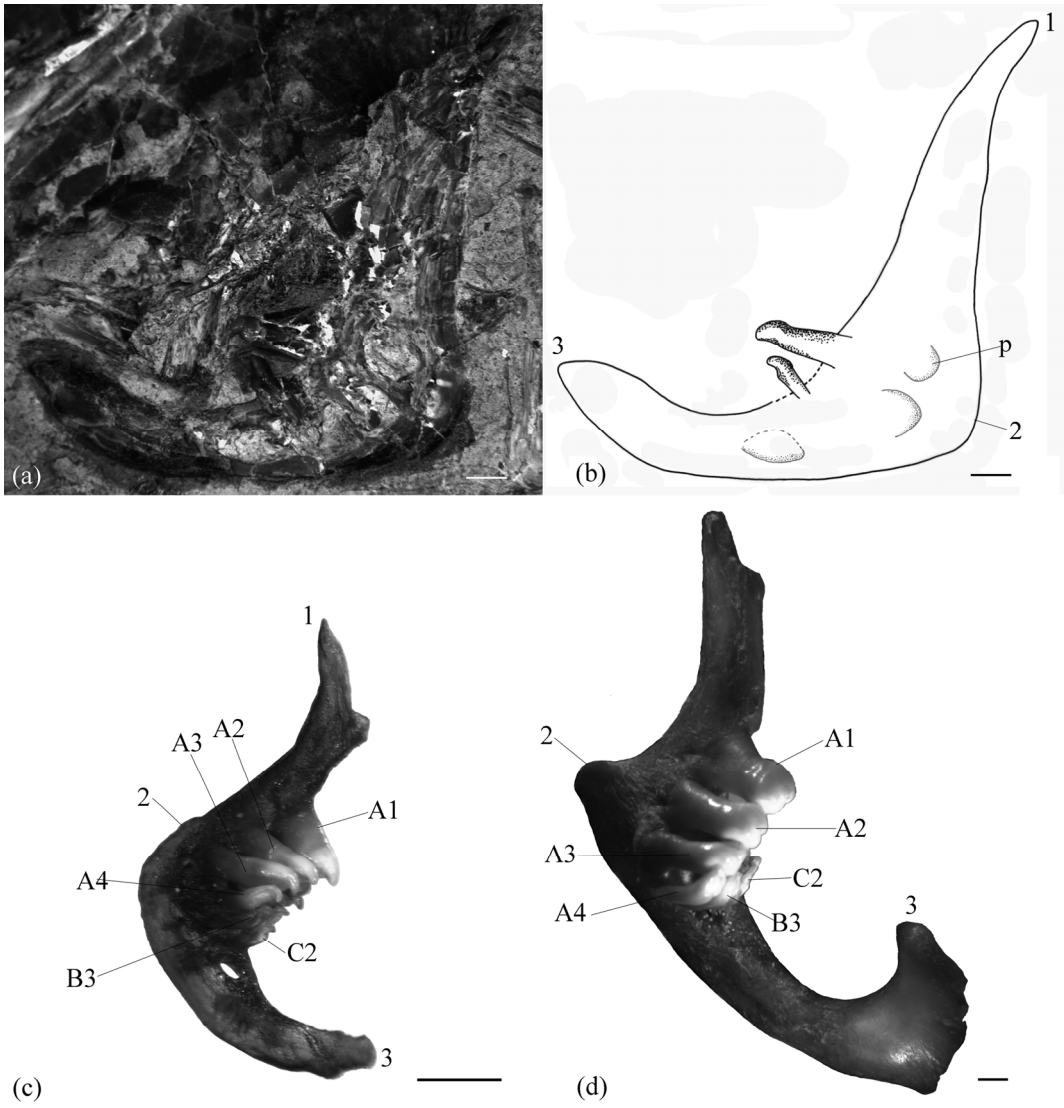

Figure 5 Pharyngeal bone of †*Eoprocypris maomingensis* (Liu), 1957, IVPP V18953.5 ((a), (b)), *Procypris rabaudi*, IOH IV0002 (c), *Puntioplites waandersi*, IOH 78IV0003 (d). Scale bar equals 1mm. 1, tip of anterior limb; 2, anterior angle; 3, tip of posterior limb; A, tooth in the main row; B, tooth in the outer row; C, tooth in the most outer row; p, pit.

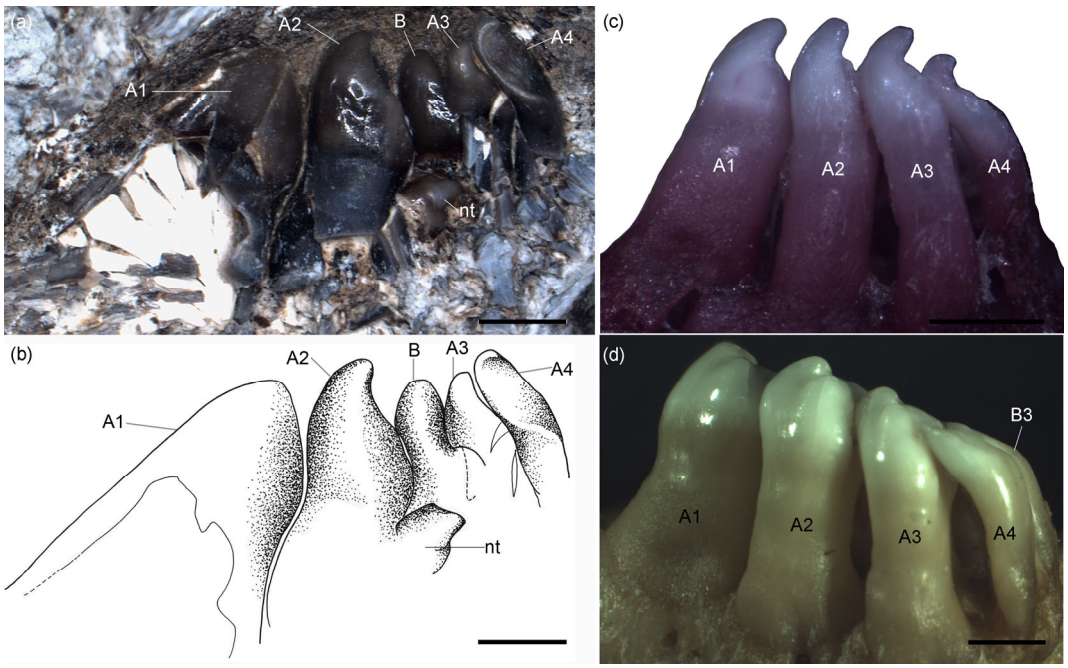

Figure 6 Pharyngeal teeth of the paratype of †*Eoprocypris maomingensis* (Liu), 1957, IVPP V18953.8 ((a), (b)), *Procypris rabaudi*, IOH IV0002 (c), *Puntioplites waandersi*, IOH 78IV0003 (d). Scale bar is 1mm for (a), (b) and (d), and 0.5 mm for (c). A, tooth in the main row; B, tooth in the outer row; nt, newly formed replacement tooth.

or less recurved tip. A2 is larger than A3, A4, and the tooth on B row. The tooth crown of all pharyngeal teeth except A1 is convex at the anterior margin but concave at the posterior margin. Consequently, their grinding surfaces have a spoon-like shape. The grinding surface is somewhat broad and concave, with ridges on its two lateral edges. On the whole, the shape of these pharyngeal teeth is rather like that in *Procypris* (Figure 6 (c)) and some barbin species, for example, *Cyclocheichthys armatus* (Pasco-Viel et al., 2014, Figure 2), but differs from that in *Puntioplites* (Figure 5(d), Pasco-Viel et al., 2014, Figure 2) . In some specimens, for example, V 18953.9, there is a low ridge running along the middle of the grinding surface of the tooth. In V18953.8, there is a small tooth with unworn crown but without tooth-neck between the tooth-neck of A2 and A3, and we think it is a newly formed replacement tooth.

(4) Post-cranial skeleton and fins. Bones of pectoral girdle are not well-preserved. The pectoral fin is long, reaching the insertion of the pelvic fin (V. 855, Figure 2). The number of the pectoral fin rays is 15 (IVPP V18953.1, Figure 3). The insertion of pelvic fin lies at about the middle point of the distance between the pectoral and anal fin, posterior to the origin of dorsal fin. The dorsal fin base is relatively short compared with most other cyprinin species, but resembles that of primitive *Cyprinus* species (e.g., *C. fuxianensis*) (Chen and Huang, 1977; Luo and Yue, 2000; Chen and Yang, 2002) and the Oligocene cyprinin species †*Huashancyprinus robustispinus* Chen et al. (2011) from the Ningming Basin, Guangxi Province. The last unbranched dorsal fin ray is robust with serrations on its posterior edge. In specimen IVPP V18953.2, the preserved part of the last unbranched dorsal fin ray is about 19 mm long, with the thickness of the most robust part about 1.5 mm. The serrations in the upper part of the ray are slightly robust than those in the middle part. The number of the branched dorsal fin rays is 9 in V18953.1, similar to that in the primitive *Cyprinus* species (e.g. *C. fuxianensis*) and the Oligocene cyprinin species †*Huashancyprinus robustispinus*. Two anterior dorsal pterygiophores are preserved on V18953.1. They are long, wedge-shaped bones. The anal fin rays were well-preserved on IVPP V18953.3 (Figure 7). The number of the branched fin rays is five. The anterior unbranched anal fin rays are missing. The last unbranched anal fin ray is very robust, with a thickness of the most robust part about 2 mm. There are serrations on the posterior edge of the ray. In IVPP V18953.1, two unbranched and five branched anal fin rays and five anal pterygiophores are preserved. The last unbranched anal fin ray is about 16 mm long, with its most robust part about 1.7 mm thick. The serrations on both dorsal and anal unbranched long rays stand with the tips pointing proximally. The vertebral column is not well-preserved. Judged from the length of the vertebrae remained in IVPP V18953.2, the number of vertebrae is probably slightly more than 30. And there are 10-11 caudal vertebrae in V18953.11.

3 Discussions

3.1 Taxonomic question of the new form

With five branched anal fin rays and serrated last unbranched

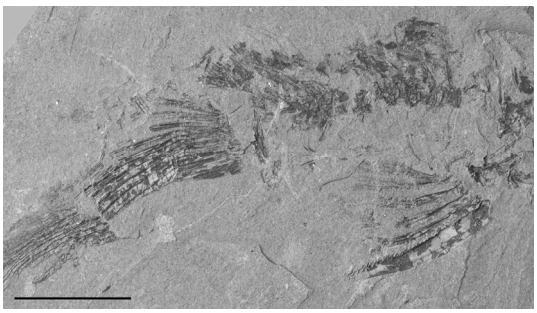

Figure 7 Caudal part of †*Eoprocypris maomingensis* (Liu), 1957, IVPP V18953.3, showing anal fin rays. Anterior is facing right. Scale bar equals 10 m.

dorsal and anal fin rays, the new form, †*Eoprocypris maomingensis*, undoubtedly belongs to the subfamily Cyprininae according to Howes (1991) and Cavender et al. (1992). Among the species-rich subfamily Cyprininae, there are only four extant genera (i.e., *Procypris*, *Cyprinus*, *Carassioides*, and *Carassius*) and two species of genus *Puntioplites* (i.e., *P. proctozystron* and *P. falcifer*) bearing serrated last unbranched dorsal and anal fin rays (Taki and Katsuyama, 1979; Chen and Huang, 1977; Luo and Yue, 2000; Yang et al., 2010). As mentioned above, the first four genera were included in a group named Tribe Cyprinini *sensu stricto* (Yang et al., 2010, 2012; Pasco-Viel et al., 2014), whereas *Puntioplites* was excluded from the group consisting of these four genera, based on some morphological studies (Taki and Katsuyama, 1979; Rainboth, 1981, 1991) and molecular analysis (Wu et al., 2010; Yang et al., 2010, 2012; Pasco-Viel et al., 2014). Compared with the five genera mentioned above, our new form is obviously different from *Cyprinus*, *Carassioides*, and *Carassius* in both the shape of the pharyngeal teeth (spoon-like vs. molar-like and shovel-like) and the number of the branched dorsal fin rays, but somewhat resembles *Procypris* and *Puntioplites* in their pharyngeal teeth bearing spoon-like gringding surface, and is also similar to *Procypris* in nearly equal length of anterior and posterior limbs of their pharyngeal bone (Figure 5(a) and (c)). However, there are obvious differences between the new form and *Procypris* and *Puntioplites*. The differences between the new form and *Procypris* include: (1) The former bears a relatively short dorsal fin with only 9 branched rays, resembling that of the primitive species in the genus *Cyprinus* (e.g., *C. fuxianensis*) (Chen and Yang, 2002) and the Oligocene cyprinin species †*Huashancyprinus robustispinus* Chen and Chang (2011), whereas the latter has a relatively long dorsal fin with 15–22 branched rays, like most species in the Cyprinini *sensu stricto*; (2) the former has fewer vertebrae (slightly more than 30), as in most other genera in the Cyprinini *sensu stricto*, and the latter has much more vertebrae (39–43); (3) the teeth of the former seem more robust and lower and the grinding surface wider than in the latter (Figure 6(a)–(c)). The new form differs from *Puntioplites* in that: the latter has (1) a very deep body; (2) a very long last unbranched dorsal fin ray; (3) a long posterior limb of the pharyngeal bone with enlarged and recurved end; (4) a produced prominent anterior angle of the pharyngeal bone; (5) the grinding surfaces of the teeth are less concave, and the two lateral ridges of the grinding surface modified to form small cuspids on their upper end; (6) its pleural rib of the 4th vertebra turns backward in the midpoint, forming a "<" shape (Zhou, 1989), which is an apomorphic character of the genus. Morphologically, the new form differs from all known cyprinids, but closest to *Procypris*. Consequently, from the morphological viewpoint, we consider that the new form is a member of the Cyprinini *sensu stricto*, and suggest a new genus name †*Eoprocypris* for it.

3.2 Distribution of the Cyprinini *sensu stricto*, Recent and fossil

Recent cyprinins include four genera living in Eurasia. Among them, *Cyprinus* is the most species-rich genus. One species (*C. carpio*) has a disjunct distribution in Eurasia, whereas all other species are restricted to East Asia and most of them occur only in several lakes in Yunnan and Xijiang River, South China (Bănărescu, 1990; Chen and Huang, 1977; Luo and Yue, 2000). *Carassius* has a continuous distribution over Asia and Europe. Two species of it demonstrate remarkable vicariant ranges, with *C. carassius* distributed throughout most Europe and Siberia, whereas *C. auratus* is a native of East Asia (Bănărescu, 1990). *Carassioides* is a southeastern Asian genus, dwelling in the Pearl River, Drainage in Hainan Island, and the Red River (Kottalat, 2001; Chen and Huang, 1977; Luo and Yue, 2000; Liu, 2013). *Procypris* is also a southeastern Asian genus. It includes only two species: *P. rabaudi* (rock carp) and *P. mera* (Chinese ink carp), both of which are listed as endangered species in the "China Red Data Book of Endangered Animal" according to Tuo (2009) and Zhang et al. (2006). The rock carp lives in the middle-upper reaches of the Yangtze River, whereas the Chinese ink carp inhabits the Xijiang River system (Chen and Huang, 1977; Luo and Yue, 2000) and North Vietnam (Kottalat, 2001). Consequently, southeastern Asia is a region with the richest Cyprinini genera and species. †*Eoprocypris maomingensis* falls in the distributional range of the Chinese ink carp. Here, we would like to mention that Kottelat (2001) pointed out that the correct name of Chinese ink carp is *Procypris mera* rather than *P. merus*, because *Procypris* is a feminine noun and *merus* is an adjective which has to agree in gender with the generic name.

To date, many fossil cyprinin fishes have been found. But they are mainly members of *Cyprinus* (Chang and Chen, 2008; Chen and Chang, 2011; Gaudant and García-Alix, 2014) and *Carassius*-like (Obrhelová, 1970; Sytchevskaya, 1986; Zhou, 1990; Gaudant, 1997; Gaudant et al., 2002; Sach et al., 2003; Rückert-Ülkümen and Yiğibaş, 2007;

Chang and Chen, 2008; Böhme, 2010) from the Neogene of Eurasia. Yet the Paleogene cyprinin fishes include only two genera and species thus far. One is †*Eoprocypris maomingensis* described here, and the other is †*Huashancyprinus robustispinus*, a *Cyprinus*-like fish, from the Oligocene, both are from South China.

4 Conclusions

As discussed above, it can be concluded that: (1) The *Procypris*-like fish described here is the earliest and a primitive member of the Cyprinini *sensu stricto*; (2) the Cyprinini *sensu stricto* is an early branch of Family Cyprinidae, the tribe has dwelled in southeastern Asia at least since the late Eocene, and at least by the time of early Miocene the tribe has been distributed to Europe; and (3) South China or southeastern Asia is probably the center of origin and diversification of the group. It is worth noting that the number of branched dorsal fin rays in fossil Cyprinini from the Paleogene and late early Miocene (e.g.,†*Lucyprinus*) (Zhou, 1990) is relatively few (9 and 10–11 respecvtively), obviously different from most members of Recent Cyprinini but similar to *Cyprinus fuxianensis* and *C. micristius*, the primitive members of the genus *Cyprinus* (Chen and Yang, 2002). It seems to indicate that low number of dorsal fin rays is a plesiomorphy of the Tribe Cyprinini, whereas more number of branched dorsal fin rays is a derived character in the tribe.

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