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A New Genus of Paleonisciformes from the Early Cretaceous Longjiang Formation in Heilongjiang Province, China

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Abstract: We report a new genus and species of Paleonisciformes–*Cretolepis dongbeiensis* gen. et sp. nov., from the Early Cretaceous Longjiang Formation in Qiqihar City, Heilongjiang Province. The new materials can be distinguished from other Paleonisciformes genera by possessing the following characteristics: a sclerotic ring composed of more than five small bones; three pieces of suborbitals; one dermohyomandibular; a jaw hanging apparently inclined anteriorly; long and tall horizontal branch of the preopercular, a short vertical branch, with the angle formed by the two branches slightly higher than 90°; a triangular dorsal fin in the middle point between the pelvic and anal fins. The discovery of Mesozoic Paleonisciformes in northeastern China adds to the biodiversity and geographic distribution of Paleonisciformes.

Key words: Paleonisciformes, Early Cretaceous, Longjiang Formation, northeastern China

1 Introduction

Paleonisciformes is an important clade of the Actinopterygii fishes that belong to Osteichthyes, which firstly appeared in the Silurian and flourished in the Devonian, spread throughout the world in the Carboniferous and Permian periods, and presently includes more than 200 species (Cloutier et al., 2004; Mickle et al., 2009; Zhu et al., 2009). However, the Holostei gradually took their place in the Triassic after the extinction event in the latest Permian and only several species survived in the Cretaceous (Hurley et al., 2006). In China, fossil remains of Cretaceous Paleonisciformes only have been uncovered from the Lower Cretaceous in Gansu and Xinjiang up to date. In 2017, the authors collected two specimens of Paleonisciformes during field-work in Heilongjiang Province. One of them was nearly complete, whereas, the other had incomplete skull and part of the anterior trunk. The new material represents a new genus and species based on the anatomical characteristics and comparisons with other Paleonisciformes.

2 Geological Setting

The fossil locality, Gannan County, is located in the east slope of the North Greater Khingan Range, wherein the Lower Cretaceous strata comprise the Longjiang Formation, the Jiufengshan Formation and the Ganhe Formation (in ascending order). The Longjiang Formation is derived from the Shanquan Section in Longjiang County and was studied by the first group of regional survey of Heilongjiang Province in 1972. The Longjiang Formation was originally defined as series of greyish-green and greyish-purple intermediate lavas, distributed in the lower 1–10 beds of this section, which also was called “middle Khingan volcanics”. In 1974, the Heilongjiang Bureau of Geology and Mineral Resources officially named the “middle Khingan volcanics” as the Longjiang Formation, referring to the greyish-purple and greyish-green andesites only and excluded volcanic clastic rocks, volcanic sedimentary rocks and acidic volcanic rocks that yielded conchostracans, ostracods, insects and some other fossils of the Jehol Group (Liu Zhaojun et al., 1992). In 1993, the upper part (mainly welded acidic tuffs) of the Longjiang Formation was separated and named the Guanghua Formation in the

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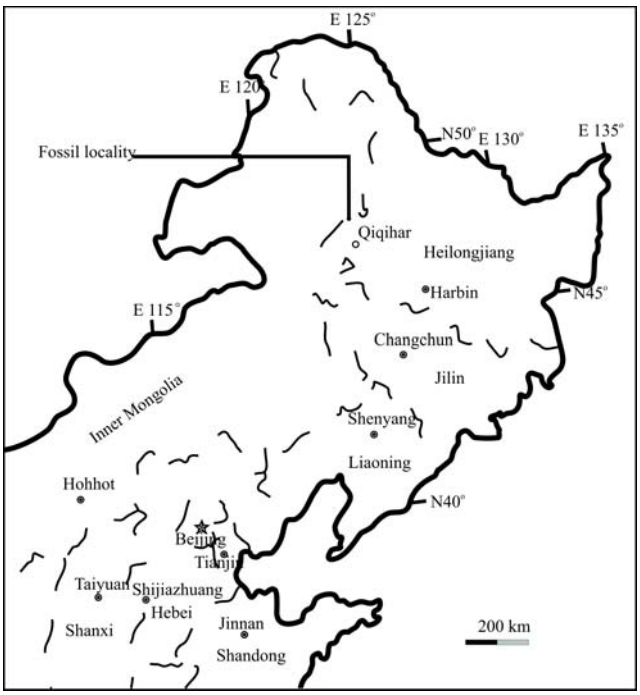

Fig. 1. The geographic location of *Cretolepis dongbeiensis* gen.et sp. nov.

Regional Geological Chronicles of Heilongjiang Province (Heilongjiang Bureau of Geology and Mineral Resources, 1993). Recently, the Longjiang Formation was revised to comprise andesites, dacites, volcanic clastic rocks and sedimentary clastic rocks, with medium-term biological fossil assemblages of the Jehol Biota (Ding Qiuhong et al., 2014). These authors considered the Guanghua Formation as the upper part of the Longjiang Formation and obtained an absolute age of 125.4±1.8 Ma by whole-rock $^{40}Ar/^{39}Ar$ from a sample in the Shanquan Section, Longjiang County. The studied fossil fish materials in this paper were recovered from greyish-white tuffs in Xinjian Village, Xinglong Town, Gannan County, Qiqihar City (Fig. 1), together with typical assemblages of the Jehol Biota. Thus, we conclude that the materials belong to the Lower Cretaceous Longjiang Formation, which is equivallent to the Yixian Formation in western Liaoning (Wang et al., 2017; Yang et al., 2017). The Yixian Formation is famous for yielding fishes, pterosaurs, feathered non-avian dinosaurs, avians and mammals; however, no Paleonisciformes were previously reported (Jin Fan, 1996; Xu and Wang, 2004; Ji et al., 2009; Wang et al., 2013; Zhou, 2014; Lü et al., 2016; Wang et al., 2017; O'Connor et al., 2018). The discovery provides important information for the Jehol Biota in a different area.

3 Systematic Paleontology

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii Cope, 1887 (*sensu* Rosen et al., 1981)

Order Paleonisciformes Hay, 1902 (*sensu* Berg et al., 1940)

Family Incertae sedis

Cretolepis dongbeiensis gen.et sp. nov.

Diagnosis: Medium-sized Paleonisciformes, with body length greater than 25 cm: the body is slender and spindle-shaped, with body length to body height ratio of about 6. The skull height is about 1/5 of the body length. The orbit is medium-sized, possessing more than five slim sclerotic rings. There are three pieces of suborbitals. One dermohyomandibular is in between the preoperale and the opecle. The horizontal branch of the preopercular is long and tall, whereas the vertical branch is short, and the angle formed by the two branches is slightly greater than 90°. The jaw hanging is especially inclined anteriorly. Sharp conical teeth are present on the maxilla, the premaxilla and the dentary. The dorsal fin is located caudally in the middle point between the pelvic and anal fins and is triangular. The caudal fin is deeply forked and the dorsal lobe is much larger than the ventral lobe. The whole body is covered by rhombic-shaped, peg-and-socket articulated scales.

Holotype: GMC.V2418 (Fig. 2). The specimen is well preserved in nearly complete articulation and is housed in the Geological Museum of China.

Referred specimen: GMC.V2419 (Fig. 3). An incomplete skull with part of the anterior trunk.

Locality and horizon: Xinglong Town, Gannan County, Qiqihar City, Heilongjiang Province (48°04′32″N, 123°40′51″E). Lower Cretaceous Longjiang Formation (approximately 125 Ma) (Ding Qiuhong et al., 2014).

Etymology: The generic name is derived from the Latin word *Creta* (meaning Cretaceous) and refers to the fossil age; the specific name is derived from the Chinese pinyin *dongbei* (meaning Northeast China) and refers to the fossil locality.

4 Descriptions

Both materials are preserved in greyish-white hard tuffs. The type specimen (GMC.V2418) is preserved nearly complete in lateral view. The referred specimen (GMC.V2419) is represented by the skull in ventral view and part of the anterior trunk in lateral view. The descriptions are mainly based on the type specimen and some skull descriptions are based on the referred specimen.

The type specimen is about 256 mm long from the anterior rostral end to the distal end of the caudal fin. The highest part at the posterior skull is about 40 mm high. The skull is about 55 mm long, i. e., approximately 1/5 of the body length. The tail is nearly 40 mm long, with the

Fig. 2. Photo of the holotype of *Cretolepis dongbeiensis* gen.et sp. nov.

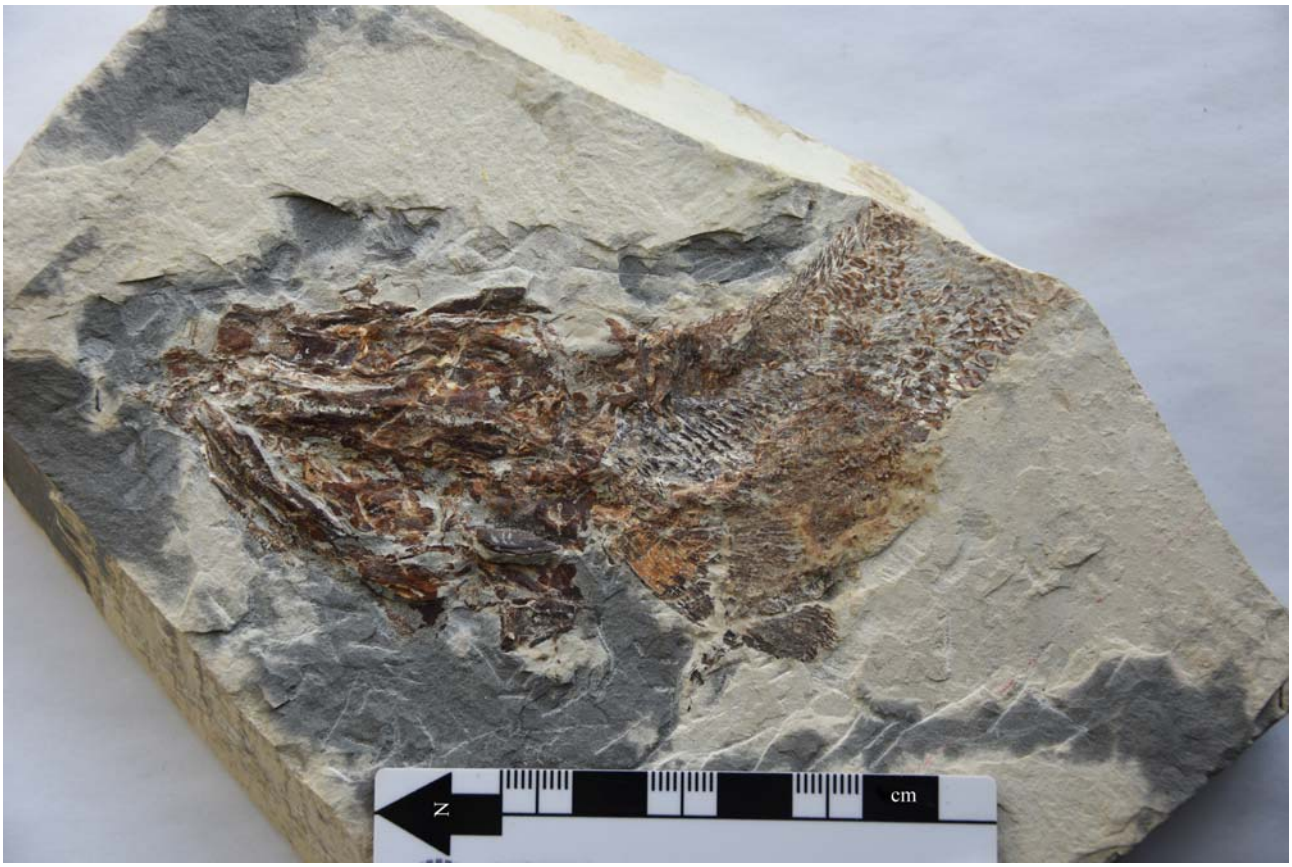

Fig. 3. Photo of the referred specimen of *Cretolepis dongbeiensis* gen.et sp. nov.

caudal peduncle 20 mm high.

The preserved skull includes the nasal, the frontal, the parietal, the dermosphenotic, the dermopterotic and the posttemporal (Fig. 4). However, some of these bones' boundary lines are not well observed because the specimen is depressed in the head.

At the front of the skull, two stick-shaped bones are preserved; they are probably the nasal (na) and one of them connects with the frontal.

The frontal (fr) contacts the dermosphenotic anteriolaterally, which is longer than the height and narrows anteriorly. A weak impression of the sensory canal can be observed on the frontal surface.

Only one square-like parietal (pa) can be seen, shorter but wider than the frontal, which may contacts with dermopterotic laterally and with the extrascapular (exc) caudally,

The dermosphenotic (dsp) is rectangular-like in shape, about half the length of the parietal.

The dermopterotic (dpt) is strip-shaped, longer than the

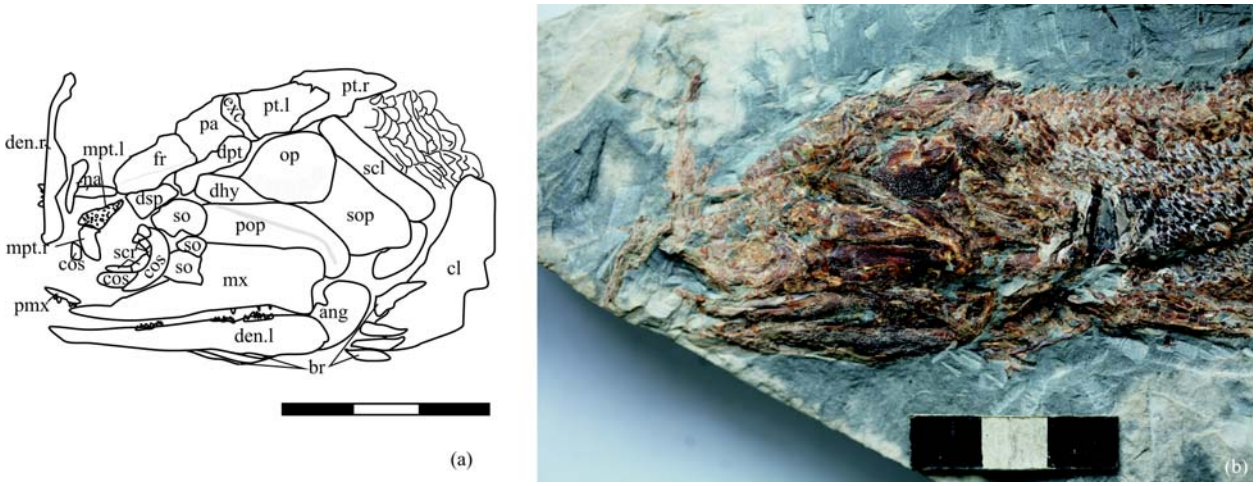

Fig. 4. Line-drawing (a) and photo (b) of the skull of the holotype of *Cretolepis dongbeiensis* gen.et sp. nov. (scale bar = 3 cm)

Abbreviations: ang, angular; br, branchiostegal ray; cl, cleithrum; cos, circumorbital series; den.l, left dentary; den.r, right dentary; dhy, dermohyomandibular; dpt, dermopterotic; dsp, dermosphenotic; exc, extrascapular; fr, frontal; mpt.l, left mesopterygoid; mpt.r, right mesopterygoid; mx, maxilla; na, nasal; op, opercular; pa, parietal; pmx, premaxilla; pop, preopercular; pt.l, left posttemporal; pt.r, right posttemporal; scl, supracleithrum; scr, sclerotic ring; so, suborbital; sop, subopercular.

parietal, becomes concave medially, and probably contact the dermosphenotic anteriorly, the frontal and caudo-lateral of the parietal lateromedially and the dermohyomandibular and opercular laterally. This condition is similar to that of *Palaeoniscum* .

Two fragments similar in size above the orbit can be interpreted as the mesopterygoids (mpt) based on the fine denticulate structures and strip outline.

Around the eye area, three series of bones are preserved, i.e. the sclerotic ring (scr), the circumorbital series (cos) and the suborbital (sob).

The sclerotic ring (scr) is located at the posterior of the orbit and comprises small pieces of bones. At least five pieces are observed in the holotype, which is apparently different from other Paleonisciformes (normally four pieces) but similar to *Paratarrasius* (Lund et al., 1982).

The circumorbital series (cos) are not completely preserved but several bones are observed around the outer parts of the sclerotic ring. Among them, the postorbital is relatively large and semi-circular. The infraorbital is relatively short and strip-shaped. The antorbital is broken, with only a square-like fragment left.

The suborbital (sob) is located at the posterior of the postorbital and the anterior of the preopercular and the maxilla. Three suborbitals can be observed in the holotype. The uppermost suborbital is the largest (10 mm long) and is located at the ventral of the dermosphenotic and the anterior of the preopercular. The middle suborbital is the smallest (less than 5 mm long) and its posterior covers the anterior boundary of the preopercular and the maxilla. The lowermost suborbital is about 7 mm and overlaps with the postorbital anteriorly.

The jaw hanging inclines anteriorly and approximately horizontal, similar to that of the Devonian *Cheirolepis* (Cloutier et al., 2004).

The opercular (op) is preserved incompletely and is round, with many punctuate ornaments on the surface. The subopercular (sop) is quadrilateral-shaped judging by the impressions and is probably larger than the opercular. Six to seven branchiostegal rays (br) are visible and strip-shaped.

The preopercular (pop) is subdivided into two parts: the upper (horizontal branch) is rectangular, extremely inclined anteriorly and almost parallel to the maxilla; the lower (vertical branch) is fan-shaped, with a narrow lower end. The horizontal and vertical branches contact the maxilla anteriorly. The angle formed by the two branches is slightly greater than 90°.

A wedge-shaped dermohyomandibular (dhy) is located between the opercular and the preopercular and its maximum width is half of the preopercular.

The maxilla (mx) is large, with slim anterior and rectangular posterior. The former is relatively shorter than the latter. This condition is similar to most Paleonisciformes. An incomplete premaxilla (pmx) is preserved in the holotype. Conical teeth are visible in the premaxilla of the holotype and in the maxilla of the referred specimen.

A strip-shaped lower jaw is preserved in both the holotype and the referred specimen. The anterior tip is sharp. The boundary of the dentary (den) and the angular (ang) is ambiguous.

The posttemporal (pt) is large and wide, with tuberculate ornaments on the surface but no sensory canal

visible.

The supracleithrum (scl) is stick-shaped judging by the impressions and it is at the back of the opercular system and connects the posttemporal with the cleithrum.

The cleithrum (cl) is robust and crescent-shaped, with a wide middle portion, whereas the horizontal branch narrows anteriorly and the vertical branch narrows upwards. The two branches are similar in size.

The vertebrae are not completely ossified, although covered by scales. A series of small rectangular bone pieces above the vertebrae may be the dorsal spines.

The two pectoral fins are incompletely preserved and are roughly located at the posteroventral of the skull, with ten fin rays preserved.

The pelvic fins are better preserved than the pectoral fins. The distal end of the pelvic fin base is opposite to the proximal end of the dorsal fin. Each pelvic fin comprises 4 + 20 fin rays.

The dorsal fin, comprising 3+20 fin rays, is triangular and is located at the posterior trunk.

The anal fin, comprising 14 fin rays, is smaller than the dorsal fin but similar in shape. The proximal end of the anal fin base is opposite to the distal end of the dorsal fin base.

The heterocercal caudal fin is deeply forked with the dorsal lobe much larger than the ventral lobe. The ventral lobe comprises 70 fin rays.

The basal and fringing fulcra are present at the anterior of the dorsal and ventral fins and at both the dorsal and ventral lobes of the caudal fin. At least four basal scales can be recognized at the anterior-ventral portion of the ventral lobe of the caudal fin.

The scales on the trunk are small rhombic ganoin scales, comprising 20 longitudinal and more than 100 transverse columns. Peg-and-socket articulations are observed on the longitudinal scales. Some scales possess serrations posteriorly.

5 Discussion

The new materials have some typical characteristics of Paleonisciformes: (1) the body is long and spindle-shaped; (2) the vertebrae are not completely ossified; (3) the whole body is covered by rhombic-shaped scales; (4) The anterior portion of the maxilla is slim and the posterior portion is wide and rectangular; (5) the preopercular closely contacts the maxilla; (6) the jaw hanging is apparently inclined anteriorly and sharp conical teeth are present and (7) the caudal fin is deeply forked and the dorsal lobe is much larger than the ventral lobe.

Most genera and species of Paleonisciformes are classified based on character assemblages because it is difficult to recognize unique characteristics; thus, we also define the new materials based on their character assemblages.

According to the arrangement of the skull bones and the type or the position of the fins, the new materials can be distinguished from other genera in Paleonisciformes by (1) the sclerotic ring with more than five small bones; (2) three pieces of suborbitals and only one dermohyomandibulart; (3) the anterior inclination of the jaw hanging; (4) the long and tall horizontal branch of the preopercular and the short vertical branch, with the angle formed by the two branches slightly greater than 90° and (5) the caudally located triangular dorsal fin in the middle point between the pelvic and anal fins.

Nearly 20 genera of Paleonisciformes have been described in China. Most of them are from the Triassic or much older strata (Su Dezao, 1999; Lu Liwu, 2002; Liu Guanbang and Shen Changming, 2006; Tan kai et al., 2015; Tan kai, 2017). Among them only two genera were uncovered from the Cretaceous: *Coccolepis yummenensis* (Liu Tungsheng, 1957; Ma Fengzhen, 1993) and *Uighuroniscus sinkiangensis* (Su Dezao, 1980; Su Dezao, 1985) (Fig. 5).

Coccolepis yummenensis was uncovered from the Lower Cretaceous Chijinpu Group in Yumen, Gansu Province and was originally identified as *Sunolepis yumenensis* (Liu Tungsheng, 1957). Ma Fengzhen (1993) revised it as a new species of *Coccolepis* based on more materials from the same locality. *Coccolepis yummenensis* and the new materials have similar shape and arrangement of skull bones and locations of the dorsal and ventral fins but different preopercular and scales. The horizontal branch of the preopercular is triangular. The vertical branch is as long as the horizontal branch and the angle between the two branches is greater than 90°. Finally, the trunk scales are circular in *Coccolepis yummenensis* (Ma Fengzhen, 1993; Hilton et al., 2004). In contrast, the horizontal branch of the preopercular is rectangular and the vertical branch is short and narrow. The scales have peg-and-socket articulation and are rhombic in the new materials.

Uighuroniscus sinkiangensis was uncovered from the Lower Cretaceous Shengjinkou Formation in Xinjiang, which was not well preserved, but still was considered to belong to the independent family of Uighuroniscidae (Su Dezao, 1980). *Uighuroniscus* has similar characteristics with the new materials, such as the long and spindle-shaped body and many suborbitals and strong pectoral bones. However, despite the similarities that suggest similar evolution for the two genera, there are many differences. The opercular is larger than the preopercular. There are two dermohyomandibulars. The sclerotic ring

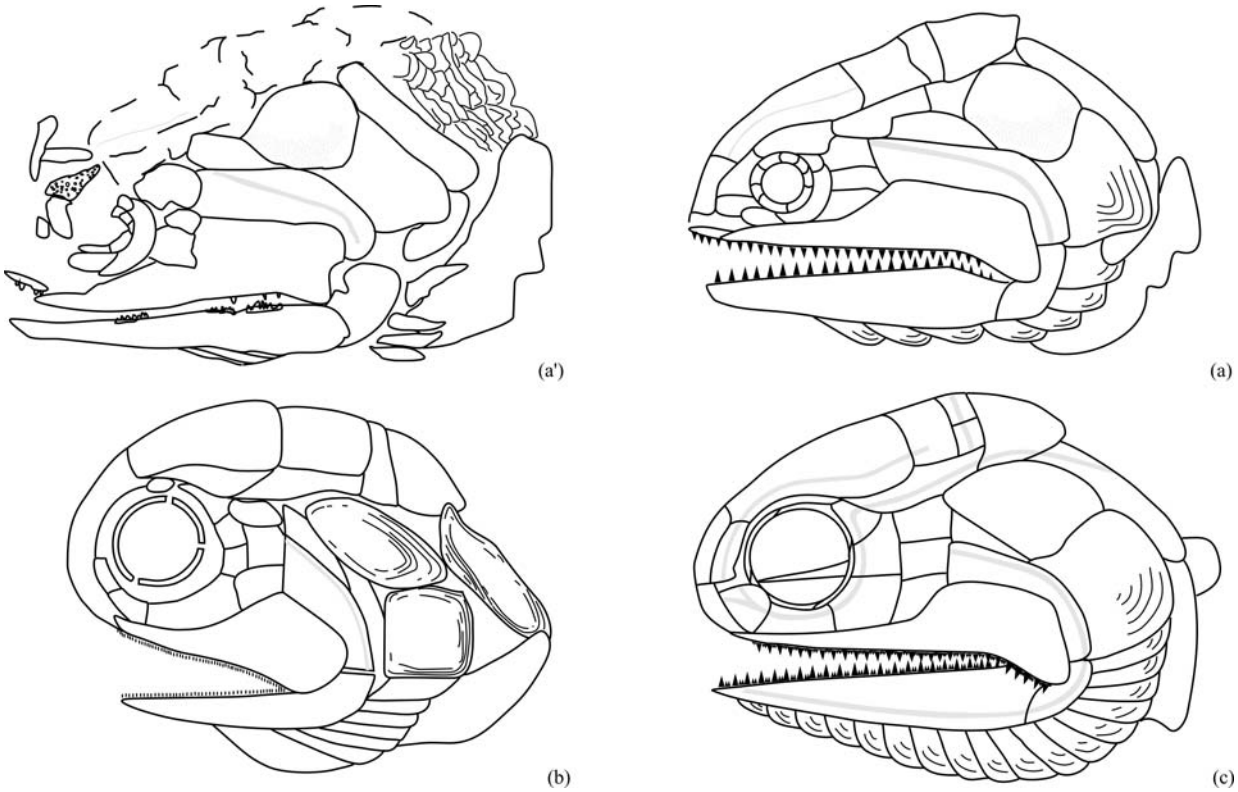

Fig. 5. Skull comparisons of several Cretaceous paleoniscoid fishes from China
(a'), *Cretolepis dongbeiensis* gen.et sp. nov. (a). restored picture of *Cretolepis dongbeiensis* gen.et sp. nov.; (b), *Uighuroniscus sinkiangensis* ; (c), *Coccolepis yumenensis*.(Fig. b and Fig. c are modified from Su Dezao, 1985 and Ma Fengzhen, 1993 respectively)

comprises three pieces of bones in *Uighuroniscus sinkiangensis.* In contrast, the opercular is smaller than the preopercular; only one dermohyomandibular is present and the sclerotic ring comprises more than five pieces of bones in the new materials. Though the shape of preopercular seems similar, the preopercular of the new materials is inclined more anteriorly and its top is wider like a rectangle. Furthermore, the biggest specimen of *Uighuroniscus* is only 10 cm, whereas the two new materials are longer than 25 cm.

Nelson (1984) subdivided the Paleonisciformes into the Paleoniscoidei and Platysomoidei. Moreover he listed the diagnosis characteristics of Paleoniscoidei as follows: (1) the cheek bones are close and form a solid whole; (2) the jaw hanging apparently inclines anteriorly and (3) the caudal fin strongly deviates. However, subsequently, Nelson (2006) removed the Redfieldioidei and Dorypteroidei from Paleoniscoidei because of their special characteristics. Redfieldioidei had one or two plate bones evolved from branchiostegal rays and single external naris surrounded by distinctive “premaxilla” rostral, nasal and adnasal bones. Dorypteroidei has a very narrow caudal peduncle and few scales and its pelvic fin is in front of the pectoral fins. Typically, Palaeoniscoidei includes many primitive chondrosteans, such as Acrolepidae and *Acrolepis* and possibly *Boreosomus* and *Pteronisculus*, Birgeriidae (e.g., *Birgeria*) and Stegotrachelidae (e.g., the Devonian *Stegotrachelus* and *Tegeolepis*).

In Nelson’s subdivision scheme, *Cretolepis* gen. nov. could be assigned to the suborder of Paleoniscoidei according to the abovementioned descriptions. However, the phylogenetic relations of Paleonisciformes were analysed using cladistics and it was argued that Paleonisciformes, as a stem group, could not be a monophyletic group (Gardiner, 1984; Gardiner et al., 1989; Cloutier et al., 2004; Hilton et al., 2004, 2009; Xu et al., 2011, 2014). Therefore, the relations among the subgroups of Paleonisciformes remain moot.

The subdivision of the Paleonisciformes is beyond the scope of this study; furthermore, it is difficult to discuss the phylogenetic position of the new genus based on the current fossil materials. Therefore, we temporarily place *Cretolepis* gen. nov. under the order of Paleonisciformes that has an uncertain family status and are waiting for more and better preserved fossil materials.

6 Conclusions

(1) The new materials represent a new genus and species of Paleonisciformes, *Cretolepis dongbeiensi*s gen. et sp. nov.. It was uncovered from the Early Cretaceous Longjiang Formation, which is equivalent to the Yixian

Formation in western Liaoning, that has yielded abundant fossils of the Jehol Biota, but no Paleonisciformes to date. The new discovery adds to the biodiversity of the Jehol Biota, sheds light on the distribution and diversity of the Jehol Biota and provides important information on the Jehol Biota in different areas.

(2) *Cretolepis* gen. nov. is the first discovery of Mesozoic Paleonisciformes in northeastern China and expands the geographic distribution of this clade.

(3) To date, three genera of Paleonisciformes fishes, i.e. *Coccolepis*, *Uighuroniscus* and *Cretolepis* gen. nov. have been reported from the Early Cretaceous in three Mesozoic freshwater basins of Northwest-Northeast China. This suggests that the Palaeonisciformes were present in the Cretaceous in North China, even though the group declined in the Permian and finally became extinct at the end of the Cretaceous.

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