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Short communication

An Early Cretaceous branchiopod community in northeastern China: Discovery of daphniid (Cladocera: Anmopoda) ephippia in the early assemblage of the Jehol Biota

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ABSTRACT

Freshwater branchiopod communities exhibit morphological and ecological stasis with the remote past. Here, we describe a new freshwater branchiopod community from the Lower Cretaceous Dabeigou Formation near Weichang County, northern Hebei Province (China), representing an early assemblage of the famous Jehol Biota. This branchiopod community consists of notostracans, conchostracans and cladocerans. Our new discovery of cladoceran ephippia in this community is described and discussed. These *Ceriodaphnia*-like ephippia are saddle-shaped in outline, and each ephippium has one oval egg with its long axis parallel to dorsal margin. They represent the oldest known ephippia record from China. Our discovery broadens our knowledge about reconstruction of the early assemblage and palaeoecology of the Jehol Biota.

1. Introduction

Modern branchiopods comprise three orders: Notostraca, Anostraca and Diplostraca (Martin and Davis, 2001). Diplostracans are generally considered as two groups: the paraphyletic conchostracans (spinicaudatans and laevicaudatans) and the monophyletic cladocerans according to previous palaeontological studies. Although branchiopods of different ages have been found worldwide, diverse branchiopod communities that harbor more than two or three branchiopod groups are rarely reported. The Late Devonian branchiopod community that consists of anostracans, conchostracans and notostracans from Belgium indicated that ecological and morphological stasis of branchiopods had started at least 365 million years ago (Gueriau et al., 2016). Communities with conchostracans and notostracans were reported from the Permian and Triassic of France (Grand et al., 1997; Lopez et al., 2008). A community with cladocerans, conchostracans and anostracans was discovered from the Lower Cretaceous Koonwarra fossil bed in Australia (Talent, 1965; Jell and Duncan, 1986). Cladoceran ephippia from this community were re-studied and identified as *Ceriodaphnia* and *Simocephalus* (Hegna and Kotov, 2016). Another community from the Middle-Upper Jurassic Daohugou fossil bed of Inner Mongolia, China yielded well-preserved conchostracans and anostracans with soft bodies and eggs, and cladocerans with soft bodies (Huang et al., 2006; Shen and Huang, 2008; Huang, 2015, 2016).

2. Geological setting

The Dabeigou Formation is mainly exposed in the adjacent areas of Luanping and Weichang counties in northern Hebei Province, China. The Dabeigou Formation is a set of volcanic-sedimentary rocks. Tuffaceous shales at the lower part of the Dabeigou Formation have yielded abundant and diverse fossils, including birds, fishes, branchiopods, insects, bivalves, gastropods, ostracods and plants. The fossil assemblage could be typically assigned within the

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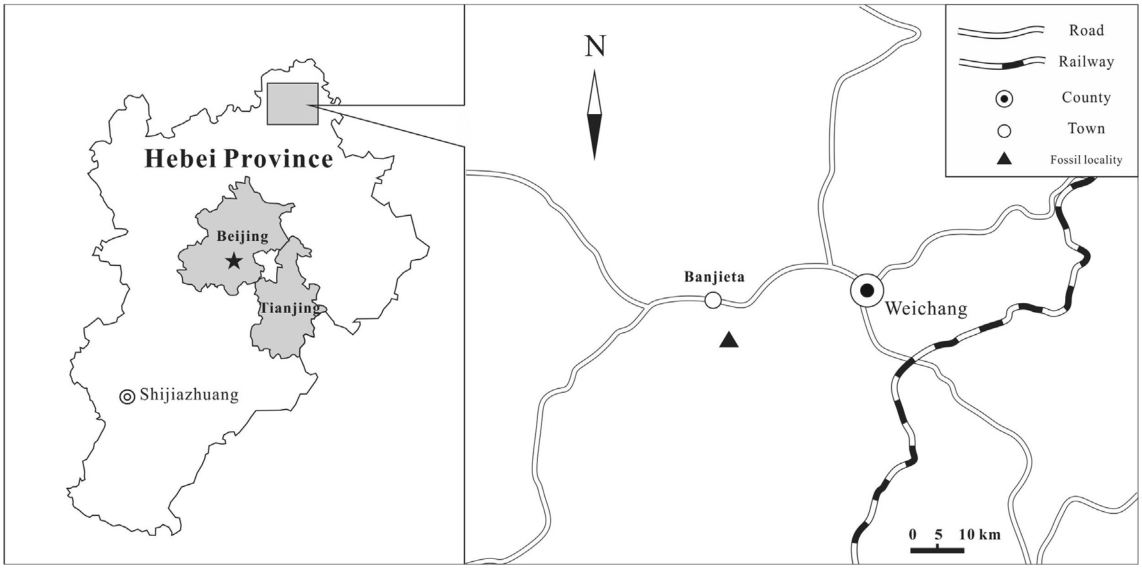

Fig. 1. Fossil locality of the Lower Cretaceous Dabeigou Formation near Fengjiadian Village, Banjieta Township, Weichang County, Hebei Province.

lower part of the Jehol Biota, as most researchers attributed the Jehol Biota into three formations from bottom to top: the Dabeigou Formation, the Yixian Formation, and the Jiufotang Formation (Wang, 1990; Chen, 1999; Zhou, 2006). Some fossil representatives from the Dabeigou Formation closely resemble those from the Yixian Formation, but they are represented by different species such as those belonging to *Ephemeropsis* and *Coptoclava* (Fig. 2b).

Tuffaceous sediments of the Dabeigou Formation lie on the rhyolite of the Zhangjiakou Formation and are underlain by the Xiguayuan-Huajiying Formation in northern Hebei. Some researchers have suggested that the Dabeigou sediments were the phase changes of the Zhangjiakou rhyolite (Yang et al., 2006). Isotopic dating research indicated that the age of the upper part of the Dabeigou Formation was approximately 130 Ma (Liu et al., 2003). The bottom of the Zhangjiakou Formation that lies on the Tuchengzi Formation with a distinct unconformity indicates the Phase B of the Yanshan Movement with an age of 135 Ma (Huang, 2015, 2016, 2019). Therefore, the early assemblage of the Jehol Biota is approximately 135 to 130 Ma in age and is yielded in the Zhangjiakou-Dabeigou Formation in northern Hebei. The Zhangjiakou-Dabeigou sediments are absent in western Liaoning.

Here, we describe abundant fossils collected from a well-known locality near Fengjiadian Village, Banjieta Town, Weichang County, Chengde City, Hebei Province (Fig. 1). This locality has yielded numerous fossil insects such as *Ephemeropsis* sp. and *Coptoclava* sp., and branchiopods, including notostracans and conchostracans. Abundant newly discovered cladoceran ephippia are also reported and described herein.

3. Material and methods

Fossils in this study were collected from the Lower Cretaceous Dabeigou Formation (upper Valanginian to Hauterivian) near the Fengjiadian Village, Weichang County, Hebei Province (Fig. 2a). They are preserved in gray-whitish tuffaceous shales that also yield notostracans and insects (Fig. 2b-f). More than 800 cladoceran ephippia preserved on 21 rock pieces were collected and studied. All these fossils are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Some were carefully prepared by using a sharp knife before detailed observation. They were observed and photographed under a Zeiss Discovery V16 microscope. Because the micro structures might be preserved on the surface, a LEO 1530 VP scanning electron microscope (SEM) was also used for observation. However, no valuable micro structures were found on the surface.

4. Results

The cladoceran ephippia are saddle-shaped (or D-shaped) in outline, 0.71–1.13 mm in length and 0.48–0.78 mm in height. Ratios of height/length range from 0.57 to 0.69. Their anterior and posterior sides are slightly asymmetrical rounded. Dorsal margins are slightly arched, and the apexes of dorsal margins locate between the midpoints and anterior ends (Fig. 3a–h). There are two spines at the anterior and posterior ends of each ephippium (Fig. 3a, 3b, 3h). We assume that the spine at the posterior end is probably a seta or connecting to a seta. Ventral margins of the ephippia are regularly curved. Both dorsal and ventral margins are smooth and lack spines. Each ephippium contains one oval egg with the long axis parallel to the dorsal margin. The eggs are 0.23–0.54 mm in diameters (long axes). There are no valuable micro-structures on the surface of the ephippia.

According to the present classification system of Cladocera, extant cladocerans comprise four infraorders: Ctenopoda, Anomopoda, Onychopoda and Haplopoda (Fryer, 1995; Martin and Davis, 2001; Xue and Du, 2008). In addition, two extinct (Jurassic) infraorders Cryptopoda and Proanomopoda have been established (Kotov, 2007, 2013). Among those four extant infraorders, only anomopods possess ephippia (Fryer, 1991, 1995; Dumont and Negrea, 2002; Kotov, 2009b). In these anomopods, daphniids (including the genus *Monia*) possess well-elaborated ephippia, and other clades such as chydorids,

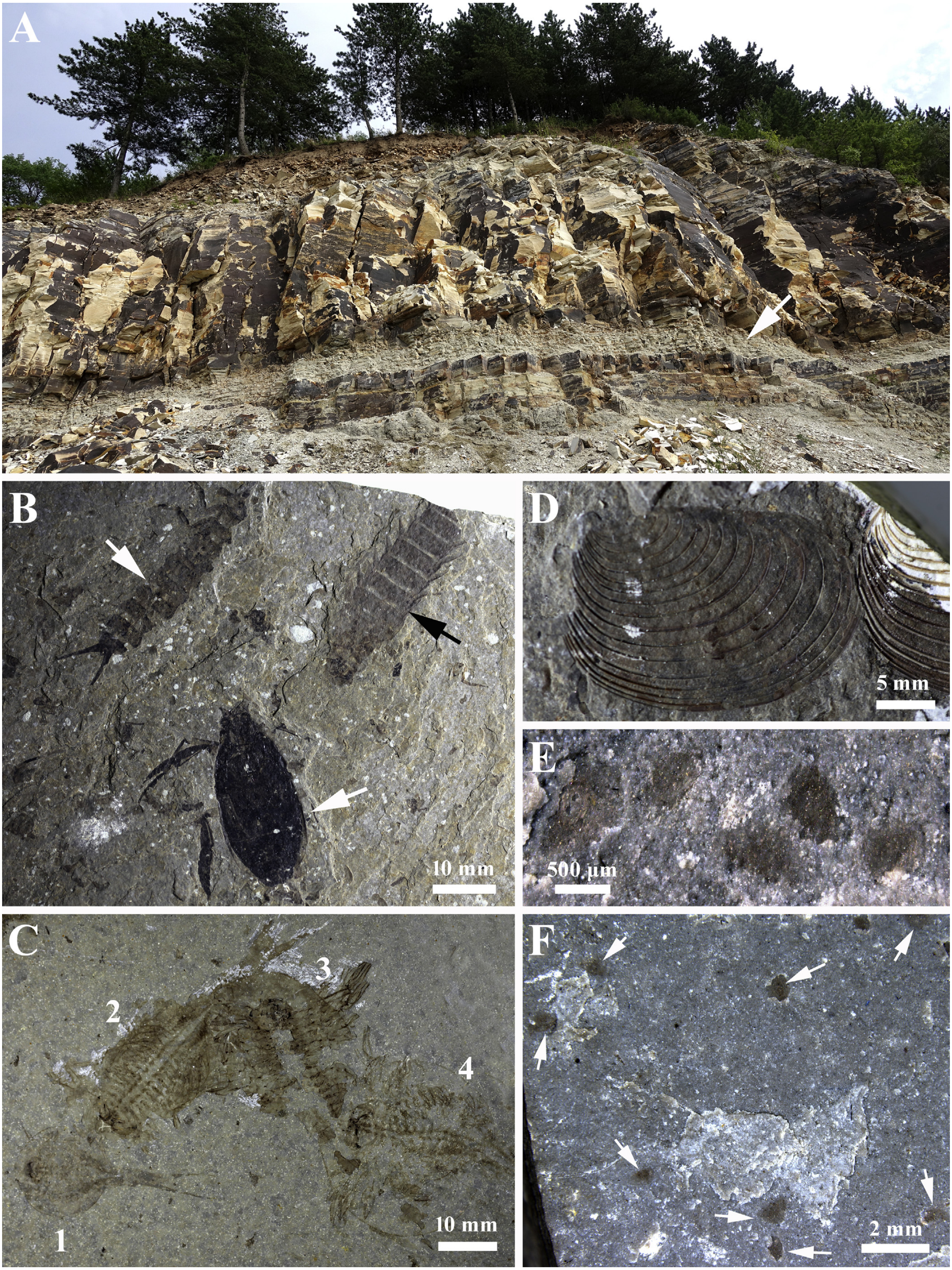

Fig. 2. Outcrop and key fossil representatives of the Lower Cretaceous Dabeigou Formation near Fengjiadian Village, Banjieta Town, Weichang County, Heibei Province. a. the outcrop of the Dabeigou Formation, with arrow pointing to where the cladoceran ephippia were recovered; b. representative insects (NIGP171006), *Coptoclava* sp (two white arrows point to a larva (upper) and an adult (lower) respectively) and larva of *Ephemeropsis* sp (black arrow); c. four individuals of *Weichangiops rotundus* (Notostraca) (NIGP171007); d. conchostracan carapace (show left valve) of *Nestoria* sp (NIGP171008); e. five cladoceran ephippia (NIGP171009); f. several cladoceran ephippia (pointed by white arrows) (NIGP171010).

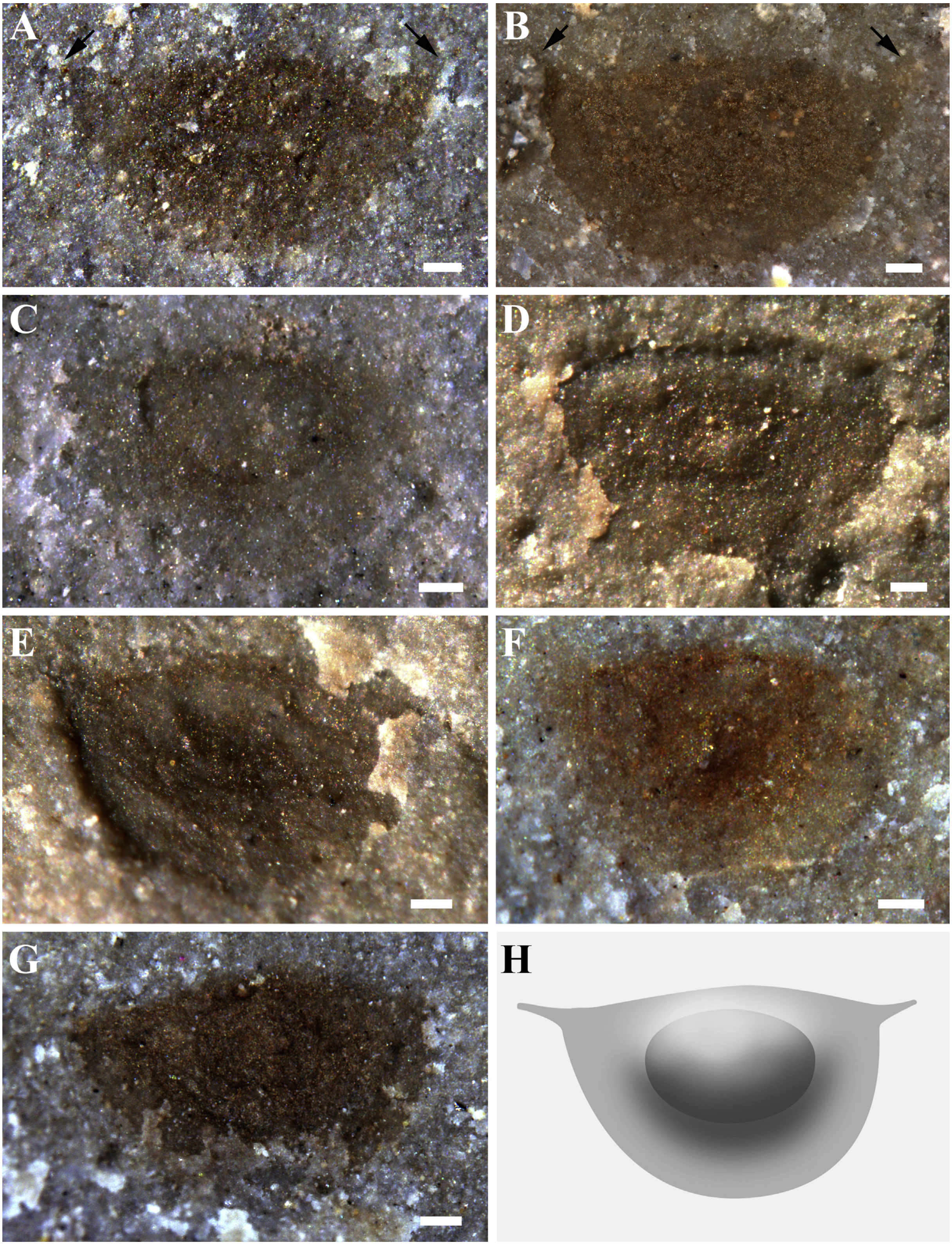

Fig. 3. Cladoceran ephippia from the Lower Cretaceous Dabeigou Formation near Fengjiadian Village, Banjieta Town, Weichang County, Heibei Province. a. an ephippium with saddle-shaped outline (two black arrows point to the anterior and posterior sides, respectively) (NIGP171011); b. an ephippium with saddle-shaped outline (two black arrows point to the anterior and posterior sides, respectively) (NIGP171012); c. an ephippium with saddle-shaped outline and an oval egg (NIGP171013); d. an ephippium with saddle-shaped outline and an oval egg (NIGP17104); e. an ephippium with saddle-shaped outline and an oval egg (NIGP171015); f. an ephippium with saddle-shaped outline and an oval egg (NIGP171016); g. an ephippium with saddle-shaped outline and an oval egg (NIGP171017); h. reconstruction of the ephippium. Scale bars = 100 μm.

bosminids and most macrothricids possess 'proto-ephippia', which are simply organized and slightly sclerotized (Scourfield, 1902; Smirnov, 1971, 1976; Xue and Du, 2008; Kotov, 2009b, 2013). Although some macrothricids and ilyocryptids also possess well-elaborated ephippia (Smirnov, 1976), they are distinctly different in shape from those mentioned above.

Two most important features of the ephippia in this study include a saddle-shaped outline and one single oval egg with the long axis parallel to the dorsal margin. Both features correlate to the characteristics of *Ceriodaphnia* ephippia. Other daphniids have either differently shaped ephippia, each ephippium with two eggs, or both (see the details in Kotov, 2009b, 2013). For example, *Simocephalus* ephippia are quite unique in possessing rapidly narrowed posterior sides among extant daphniids (Lai and Li, 1987a; Fryer, 1991; Smirnov, 1992; Orlova-Bienkowskaja, 1998; Kotov, 2009b; Kotov and Taylor, 2011). *Daphnia* (*Ctenodaphnia*) ephippia share a similar saddle-shaped outline, whereas the majority of them with two eggs (Vandekerkhove et al., 2004; Kotov and Taylor, 2011). It is noteworthy, however, that some extant *Daphnia* (*C.*) also have one-egged ephippia (Kotov and Taylor, 2011).

In addition to the outline and the number of eggs, the new ephippia display some unique characteristics: 1) they possess slightly arched dorsal margins, unlike other fossil *Ceriodaphnia* ephippia with straight dorsal margin that were reported in previous studies (e.g. Jell and Duncan, 1986; Lai, 1990; Hegna and Kotov, 2016); and 2), they have two spines at the anterior and posterior ends, which are rarely observed in other fossils. Unfortunately, there are no micro-structures observed from their surface, thus it is challenging to make the classification any further.

The ephippia substantially vary in size: the lengths range from 0.71 mm to 1.13 mm, and the heights range from 0.48 mm to 0.78 mm. The same variance is quite normally observed in some extant cladocerans. For example, in the description of Vandekerkhove et al. (2004), the size of *D.* (*C.*) *magna* ephippia ranges from 1.03 mm to 1.59 mm. A similar range 1.14 mm–1.53 mm has been also revealed by Boersma et al. (2000), who concluded that the ephippium size is highly determined by the size of the mother.

5. Discussion

Cladocerans, commonly called "water fleas", are a group of small, widespread, planktonic crustaceans. Ponds, seasonal puddles, paddy fields, swamps, reservoirs, lakes, rivers and even the surface of the ocean from all over the world are their habitats. Their widespread distribution is mainly due to their particular life cycle, which equips them with high dispersal potentials: most of them can reproduce via cyclical parthenogenesis in harsh conditions and some of them can produce resting eggs loaded in ephippia. These ephippia can be dispersed by wind or adhering to migrating animals (especially birds) after their habitats dry up (Carvalho, 1994). The ephippia are highly resistant to desiccation, freezing and passage through the digestive tracks of animals. It has been reported that some ephippia had remained viable for up to 150 years (Brendonck and De Meester, 2003). Tasch (1969) considered that body parts of cladocerans should be well-preserved in sediments after conducting drying experiments in pond mud. However, despite the widespread distribution of extant species, fossils with body parts are relatively sparse (e.g. Tasch, 1969; Smirnov, 1971, 1992; Jell and Duncan, 1986; Kotov and Korochinsky, 2006; Kotov, 2007, 2009a, 2013) due to the small and fragile bodies, which are easy to overlook. Tasch (1969) predicted that cladocerans probably arose during the Mesozoic after thoroughly seeking for fossils from Paleozoic strata with no success. Subsequently, more and more researchers tend to consider that Cladocera has a Palaeozoic origin (e.g. Fryer, 1995; Dumont and Negrea, 2002; Sacherová and Hebert, 2003; Forró et al., 2008). However, all known Paleozoic fossils are controversial: the Permian form reported by Smirnov (1970) from eastern Kazakhstan turned out to be of non-cladoceran origin (Kotov, 2007); the cladoceran-like crustacean from the Lower Devonian Rhynie chert reported by Anderson et al. (2004) lacks diagnostic appendages, not allowing researchers to take the classification any further; *Ebullitiocaris elatus* from the Carboniferous in North Yorkshire, UK, reported by Womack et al. (2012) is highly dubious as the position of the "second antennae" relative to the carapace conflicts with the body plan of all other known cladocerans (Hegna and Kotov, 2016). Compared with the body parts, ephippia are relatively easy to be preserved and identified. They have been found from the Late Jurassic to the Cenozoic sediments in Mongolia, China, Australia, North America and Germany (Frey, 1962, 1964; Jell and Duncan, 1986; Tang, 1987; Lai and Li, 1987a, 1987b; Lai, 1990; Lutz, 1991; Smirnov, 1992; Kotov and Korchinshy, 2006; Kotov, 2007, 2009b; Kotov and Taylor, 2011; Hegna and Kotov, 2016).

Ephippia are usually of simple characters and low morphological differences among species of the same genus, making it difficult to be identified to a species level. Moreover, their size and shape may vary substantially within species as mentioned above (Boersma et al., 2000; Jeppesen et al., 2002; Vandekerkhove et al., 2004). However, morphological analyses on ephippia are still very significant for broadening our understanding about the palaeodiversity and evolutionary history of cladocerans.

Herein, new *Ceriodaphnia*-like ephippia from the Lower Cretaceous Dabeigou Formation in northern Hebei Province, China are reported and described. They represent the oldest ephippia recorded from China to date. Tuffaceous sediments with micro horizontal bedding of the locality indicate a lacustrine environment under a relatively weak hydrodynamic condition, which was suitable for ancient branchiopods' living. Abundant conchostracans and notostracans have been found from the same locality, exhibiting the presence of a highly diverse Early Cretaceous branchiopod community that encompasses cladocerans, conchostracans and notostracans in the early assemblage of the Jehol Biota. Notostracans and cladoceran ephippia are usually found in very close but different micro layers from the section, likely indicating an unstable environment of the habitat: notostracans and cladocerans flourished and declined frequently with changes of the environment under frequent volcanic activities.

6. Conclusions

We report a highly diverse Early Cretaceous freshwater branchiopod community that existed in the early assemblage of the Jehol Biota in northern Hebei, China. The branchiopod community recovered from the Lower Cretaceous Dabeigou Formation near Weichang County, contains cladocerans, notostracans and conchostracans. The new *Ceriodaphnia*-like ephippia are the oldest records of ephippia reported from China.

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