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An Early Devonian clam shrimp community from Hunan Province, China

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Abstract.—The Devonian saw the emergence and subsequent diversification of the clam shrimp. To date, there are no credible records of any clam shrimp prior to the Devonian. Therefore, discoveries and taxonomic studies of early forms, especially the Early Devonian species, are essential to broaden our knowledge of the origin and early evolution of clam shrimp. An Early Devonian clam shrimp community that consists of four species, *Cornia cheni* n. sp., *Pseudestheria* cf. *P. diensti*, *Palaeolimnadiopsis zhangi* n. sp., and ?*Palaeolimnadia* sp. is described and discussed in detail in this study. These species are the oldest clam shrimp in China and among the oldest worldwide. This discovery indicates that clam shrimp communities with high diversity existed since the late Early Devonian and that their early forms may have had a profound effect on the origin and evolutionary trends of the following forms.

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Introduction

Clam shrimp, or "conchostracans," are a paraphyletic group of bivalved crustaceans known in fossil records from Devonian to recent times. They are sometimes considered as flagship groups in non-marine aquatic biotopes, with important stratigraphic, paleogeographic, and paleoenvironmental significance due to their rapid evolution, high environmental adaptability, and wide distribution. Carboniferous, Permian, and Mesozoic clam shrimp have been reported from all the present continents (e.g., Raymond, 1946; Kobayashi, 1954; Novojilov, 1957, 1970; Tasch, 1969, 1987; Zhang et al., 1976; Chen and Shen, 1985; Kozur and Weems, 2010; Ghosh, 2011; Gallego et al., 2020).

In the last century, researchers have described the "clam shrimp" of the Cambrian and Ordovician (Ulrich and Bassler, 1931; Soot-Ryen, 1960; Howell, 1963). However, all the records were proven to be of non-clam shrimp affinity (mollusks or stem-group crustaceans; see details in the discussion section). In other words, there are no credible records of any clam shrimp taxon prior to the Devonian. The Devonian saw the emergence and subsequent diversification of the early clam shrimp. Clam shrimp of the Devonian, including >20 genera, were mainly found in Europe (especially the Old Red Sandstone area), China, Central Asia (Kazakhstan), and North Asia (Siberia and adjacent areas in Russia). The earliest clam shrimp are several species from the Early Devonian: *Belgolimnadiopsis stockmansi* Maillieux, 1939 (see also in Defretin, 1950; Cuvelier et al., 2015); *Concherisma eifelense* Raymond, 1946; *Pseudestheria* (*Estheria*) *diensti* Gross, 1934; and *Pseudestheria* (*Tuvinopsis*) *arduennae* Novojilov, 1961. It is difficult to determine which one is the oldest because none of them is dated precisely (Hegna and Astrop, 2020). Moreover, their morphological descriptions and illustrations are relatively ambiguous and imprecise. Further studies on their stratigraphic placement and detailed taxonomic information are needed.

Most fossil clam shrimp are comprised of carapaces only. Important features of their crustacean body and appendages are often missing or poorly preserved in fossil records. As a result, the key characteristics of body and appendages that are crucial in the morphological taxonomy of modern clam shrimp could not be used for morphological comparison between fossil and modern species. It is not known if these Early Devonian forms represent the crown or stem-group of Spinicaudata (the main taxon of clam shrimp that includes the largest number of modern species), although their carapace character (presence of growth lines) indicates that they look like modern spinicaudatans. *Limnestheria arda* Wright, 1920, of the Moscovian (Westphalian, late Carboniferous) from Ireland was considered the oldest-known stem-group spinicaudatan because it possesses two pairs of claspers (Orr and Briggs, 1999), which is consistent with the characteristics of all modern spinicaudatan males (Hegna and Astrop, 2020).

Regardless, discoveries and taxonomic studies of early forms, especially the Early Devonian species, are still essential to broaden our knowledge of the origin and early evolution of clam shrimp. In this study, we discovered and described four species (including one sp. in open nomenclature) of four genera of clam shrimp from the Lower Devonian Yuankou Formation (Emsian) in Jiangyong, Hunan Province, China. They represent the oldest clam shrimp records in China. This discovery

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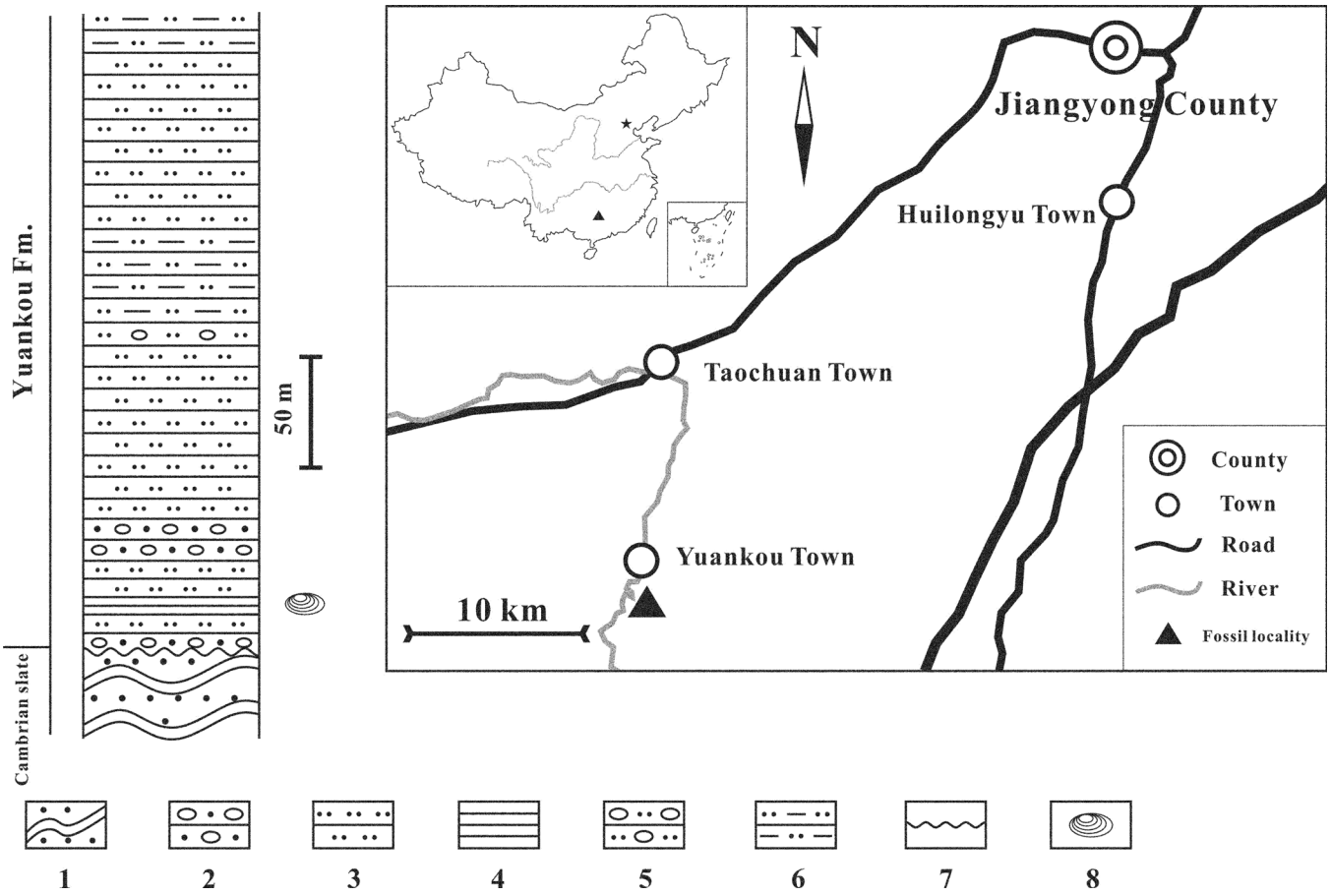

Figure 1. Stratigraphic column and locality of the Yuankou Formation at Yuankou Town, Hunan Province, China. 1. sandy slate; 2. quartz sandstone with gravels; 3. quartz sandstone; 4. shale; 5. Fine-grained quartz sandstones with gravels; 6. muddy quartz sandstones; 7. unconformity; 8. fossil clam shrimp.

indicates that highly diverse clam shrimp communities already appeared in suitable biotopes on Earth at that time and provides clues for the diversification that occurred after the Early Devonian.

Geological setting

The Yuankou Formation, mainly exposed in southwestern Hunan Province and northern Guangxi Province, China, is a set of continental-coastal clastic sediments. Before the 1970s, continental-coastal clastic sediments that were widely distributed in the region were collectively referred to as the "Tiaomajian Formation." The age of the Tiaomajian Formation was considered to be Eifelian (early Middle Devonian). In the early 1970s, the regional geological survey team of Hunan Province divided the sediments into three members from bottom to top according to lithology and sedimentary rhythm (Bureau of Geology and Mineral Resources of Hunan Province, 1988, 1997). The lowest member of the three is a set of purple-red and gray to white-grayish clastic sediments, which consist of quartz sandstones, quartz sandstones with gravels, and shales (Fig. 1). The fossil plant *Zosterophyllum* Penhallow, 1892, was found in the member and its age was considered to be the latest Early Devonian (Wang, 1979). Subsequently, Risheng Yu measured the section near the river in southwestern Yuankou Town, Jiangyong County (24.9933°N, 111.0757°E) and named the member "Yuankou Formation" in 1979 (Yu in Bureau of Geology and Mineral Resources of Hunan Province, 1988, 1997). The section in southwestern Yuankou Town unconformably overlies a set of Cambrian slates. Although the top of the section is covered by Quaternary sediments, making its contact with the Tiaomajian Formation invisible, outcrops in other regions indicate that the Yuankou Formation is conformably overlain by the Middle Devonian Tiaomajian Formation (Bureau of Geology and Mineral Resources of Hunan Province, 1988, 1997). Fossil clam shrimp, bivalves, and plants have been found in the lower part of the Tiaomajian Formation (Wang, 1979; Bureau of Geology and Mineral Resources of Hunan Province, 1988, 1997; Gao and Wang, 1990). Fossil plants consist of *Zosterophyllum* cf. *Z. yunnanicum* Hsü, 1966; *Emplectophycus yunnanensis* Li and Cai, 1978; *Hostimella*; *Aphyllopteris*; *Psilophylon*; and *Taeniocrada*; similar to the *Drepanophycus spinaeformis* Göppert, 1852-*Zosterophyllum yunnanicum* flora, which was widely distributed in the late Early Devonian continental strata in southwestern China (Wang, 1979; Gao and Wang, 1990). *Zosterophyllum yunnanicum* is generally considered an index species of the Emsian in southwestern China (Li and Cai, 1977; Wang, 1979). Gao and Wang (1990) studied spores of the Yuankou Formation and concluded that the formation was correlated to the Guijiatun Formation in Yunnan Province and the

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Nagaoling Formation in Guangxi Province. According to the latest stratigraphic age framework of the Devonian in China, the age of the Guijiatun Formation is latest Pragian to early Emsian, while the age of the Nagaoling Formation is Pragian (Qie et al., 2019). Therefore, with all the information above, we think that the age of the Yuankou Formation is most likely early Emsian. The formation consists of continental-coastal clastic sediments, which indicate a coastal wetland environment. Most of the fossils, including plants, clam shrimp, and brackish bivalves, were found in very close horizons in the lower part of the section. Wang (1979) mentioned the existence of fossil brachiopods in the section, but the exact horizon and taxonomic information of these brachiopods were not reported. We assume the Devonian clam shrimp inhabited a coastal wetland with seawater sources and influences.

Material and methods

Clam shrimp specimens in this study were collected by the second author on November 26, 1979, from the lower part of the Lower Devonian (Emsian) Yuankou Formation in southwestern Yuankou Town, Jiangyong County, Hunan Province, China (Fig. 1). Chen and Shen (1985) mentioned the presence of these clam shrimp in their published book "An Introduction to Fossil Conchostracans." However, no further research has been conducted. The outcrop of the Yuankou Formation still exists, but some parts of the section, including the fossil-bearing beds, are covered by thick vegetation. This makes it very difficult to excavate fossils by hand and general tools. As a result, we rely on a very limited number of fossil specimens that were collected tens of years ago. The specimens were preserved in dark-grayish muddy shales. Twenty-one individuals with only carapaces preserved on several rock pieces were collected. All the rock pieces were from the same horizon. Individuals NIGPA174183 (Fig. 2.1) and NIGPA174186 (Fig. 2.4) occur on the same rock piece. Moreover, individuals NIGPA174185 (Fig. 2.3) and NIGPA174189 (Fig. 3.3) occur on the same piece.

The fossils were observed and photographed under a Zeiss Discovery V16 microscope. Polarizing coatings were used for observation and photography to eliminate the redundant reflection of light on the surface of the specimens. Considering that the microstructures might be preserved on the surface, a LEO 1530 VP scanning electron microscope was also used for observation. However, no valuable microstructure was found on the surface owing to poor preservation. The invert function of the software Adobe Photoshop 7.0 was used to reverse images taken from the specimens to demonstrate their characteristics more clearly than previously. In the descriptions, we follow the recent classification of spinicaudatans by Martin and Davis (2001) and the fossil classification by Chen and Shen (1985), combining the proper terms and suggestions of Chen and Shen (1985) and Scholze and Schneider (2015).

Repository and institutional abbreviation.—Types, figured, and other specimens examined in this study are deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing, Jiangsu Province, China.

Systematic paleontology

Class Branchiopoda Latreille, 1817
Order Diplostraca Gerstaecker, 1866
Suborder Spinicaudata Linder, 1945
Family Vertexiidae Kobayashi, 1954
Genus *Cornia* Lutkevich, 1937

Type species.—*Cornia papillaira* Lutkevich, 1937 from the upper Permian (Lopingian) at Kuznetsk Basin, Siberia, Russia, by original designation.

Cornia cheni new species
Figure 2.1–2.3

Holotype.—NIGP174183, a whole carapace from the Lower Devonian (Emsian) Yuankou Formation at Yuankou Town, Hunan Province.

Diagnosis.—Carapace small in size, oval in outline; dorsal margin straight and long; larval valve small, bearing an oval node on its top; umbo in anterior and marginal position; anterior margin sharply curved; posterior margin very sharply curved.

Occurrence.—Lower part of the Yuankou Formation in southwestern Yuankou Town, Jiangyong County, Hunan Province, China (Fig. 1).

Description.—Carapace small in size, oval in outline, 3.2–4.1 mm in length (L), 2.0–2.9 mm in height (H); H/L ratio between 0.63–0.70; dorsal margin straight and long, ratio of dorsal-margin length/carapace length between 0.65–0.70; larval valve small; umbo in anterior and marginal position; an oval or round tubercle (or node) situated on top of the larval valve; anterior margin sharply curved; posterior margin very sharply curved; growth lines fine; 10–12 growth bands, relatively wide and sparsely distributed on the carapace.

Etymology.—In memory of Professor Peiji Chen (1936–2019), who contributed significantly to the study of fossil branchiopods of the world and co-authored the book "Fossil Conchostracans of China" in 1976.

Materials.—Holotype: NIGP174183 (Fig. 2.1); paratypes: NIGP174184 (Fig. 2.2), NIGP174185 (Fig. 2.3).

Remarks.—This species differs from the type species of the genus, *C. papillaira* from the Upper Permian in Russia (Lutkevich, 1937), in its outline, tubercle feature, and position; the latter is round in shape and its tubercle is more like a spine instead of a round node, which is situated at a much lower position in the umbo. The genus *Cornia* is widely distributed. Species of this genus have often been reported in the Permian–Carboniferous and Triassic continental or continental-marine strata in Europe, China, Africa, North America, South America, India, and Antarctica (see details in Lutkevich, 1937; Raymond, 1946; Cardoso, 1962; Zaspelova,

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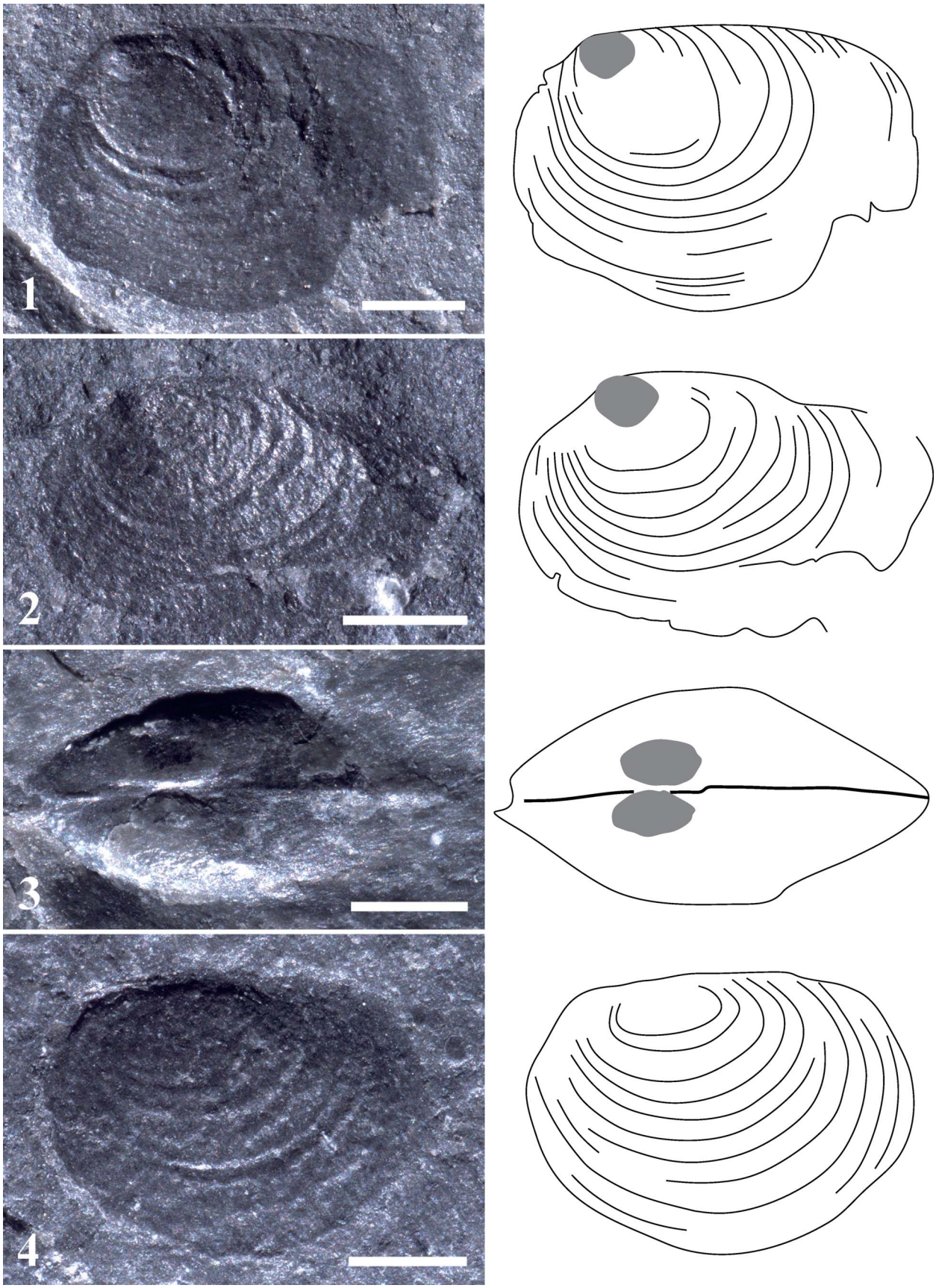

Figure 2. Photographs and sketches of *Cornia cheni* n. sp. (**1–3**) and *Pseudestheria* cf. *P. diensti* (**4**). (**1**) *Cornia cheni* n. sp., holotype, NIGP174183, left valve, the gray part on the larval valve shows the tubercle; (**2**) *Cornia cheni* n. sp., paratype, NIGP174184, left valve, the gray part on the larval valve shows the tubercle; (**3**) vertical view of the two valves of an individual of *Cornia cheni* n. sp., paratype, NIGP174185, the gray parts on the larval valve show a pair of tubercles; (**4**) *Pseudestheria* cf. *P. diensti*, NIGP174186, left valve. All scale bars = 1 mm.

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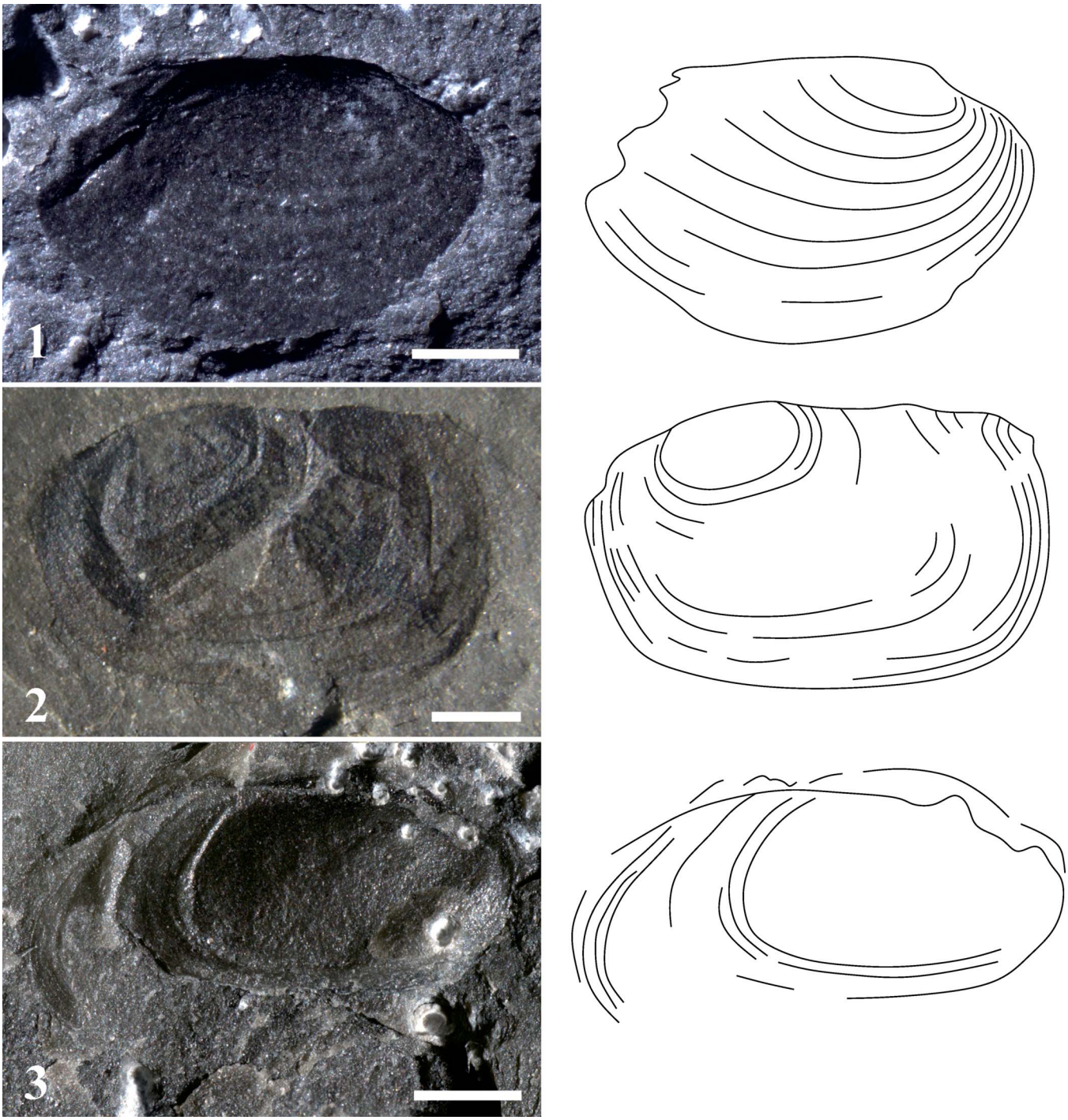

Figure 3. Photographs and sketches of *Pseudestheria* cf. *P. diensti* (**1**), *Palaeolimnadiopsis zhangi* n. sp. (**2**), and ?*Palaeolimnadia* sp. (**3**) (**1**) *Pseudestheria* cf. *P. diensti*, NIGP174187, right valve; (**2**) *Palaeolimnadiopsis zhangi* n. sp., holotype, NIGP174188, left valve; (**3**) ?*Palaeolimnadia* sp., NIGP174189, right valve. All scale bars = 1 mm.

1965; Molin, 1968; Novojilov, 1970; Zhang et al., 1976; Kozur, 1983; Tasch, 1987; Kozur and Mock, 1993; Kozur and Weems, 2010).

Characteristics, such as carapace outline, size, and tubercle feature, among different species are diverse and distinctively different. Some species share similarities in outline and tubercle features with the new species, although the differences are still easy to observe. For example, *C. angolata* Tasch, 1987, from the Upper Triassic in Angola possesses a very similar outline and tubercle to the new species, but is smaller and possesses fewer growth bands compared to the new species. *Cornia laminata* Raymond, 1946, from the Permian in the USA also shares similarities in outline and tubercle features with the new species, while its growth bands are also much fewer in number. Based on the diagnosis of the genus, growth bands of corniids were ornamented with punctae or hachures (lirae) (Tasch, 1987). In

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addition, a specimen identified as "*C. papillaira*" (Lutkevich, 1937) from the Maltsevo Formation in the Babiy Kamen section of Siberia displayed a transition of reticulations and lirae on its carapace (Sabirova et al., 2019). Unfortunately, no useful ornamentation was found in our specimens due to poor preservation. Moreover, the limited number of our specimens makes it impossible to fully understand both the preservation variability and the intraspecific variability. Regardless, considering that it may be the oldest known *Cornia* with very significant implications for the origin and early evolution of the genus and correlation of Early Devonian continental strata in southern China, we established this new species. It is noteworthy that differentiating *Cornia* from *Lioestheria* Depéret and Mazeran, 1912, may be not easy when the fossils are not well preserved. *Lioestheria* shows a morphologically variable (conical to pillar-shaped or, especially, oval to elongate-shaped) tubercle on its larval valve. Well-preserved *Cornia* usually shows a spine-like tubercle on its larval valve. However, the spines on the larval valves of some corniids also could appear to be oval to round when the carapaces are heavily compacted. But it should be noted that the larval valves of lioestheriids are usually larger than one-third of the valves' length (Holub and Kozur, 1981; Kozur and Sittig, 1981; Scholze et al., 2019). Larval valves of this new species are obviously not that large, hence we assign it to *Cornia* instead of *Lioestheria*.

Family Euestheriidae Defretin, 1965
Genus *Pseudestheria* Raymond, 1946

Type species.—*Pseudestheria brevis* Raymond, 1946, from the lower Permian (Cisuralian) Wellington Formation at Noble County, Oklahoma, USA, by original designation.

Remarks.—The genus *Pseudestheria* Raymond, 1946, is one of the most common late Paleozoic genera and has high biostratigraphic value (e.g., Martens, 1983; Schneider and Scholze, 2018; Scholze et al., 2019). Its type species, *P. brevis*, is oval in outline and possesses a small larval valve with an umbo near the anterior end (Raymond, 1946). The genus diagnosis was amended by Holub and Kozur (1981) and Martens (1983). Raymond mentioned that *Pseudestheria* and *Euestheria* Depéret and Mazeran, 1912, were much alike and that their difference was mainly in the ornamentation: polygonal reticulations could be observed on the growth bands of the latter under high-power microscopes (Raymond, 1946). He realized that it was impossible in many cases to make definite identifications of the genus, and that the genus inevitably would become a sort of dumping ground for many fossils that were not well preserved (Raymond, 1946). As expected, many poorly preserved fossils were assigned to *Pseudestheria* in the following decades. In terms of shape and size, *Pseudestheria* strongly resembles *Euestheria*, *Lioestheria*, and *Polygrapta* Novojilov, 1946. This has resulted in many taxonomic and biostratigraphic issues and puzzles for researchers, especially in poorly preserved specimens with limited and ambiguous morphological characteristics. Fortunately, some constructive suggestions and distinguishing criteria have been proposed to differentiate *Pseudestheria* from other similar forms (e.g., Houlb and Kozur, 1981; Kozur and Sittig, 1981; Kozur and Seidel, 1983; Scholze et al., 2019; for detailed discussions see Scholze et al., 2019). However, it should be emphasized that differentiating the genus from other similar forms is still a difficult task when the specimens are poorly preserved. Recently, some studies have shown that different species of *Pseudestheria* possess different ornamentations on their carapaces. For example, *P. novacastrensis* Mitchell, 1927, from the Babiy Kamen section in Siberia, and *P. chatangensis* Novojilov, 1946, from the Obnora Formation in Russia, are ornamented with pits (punctae), whereas *P. exigua* Eichwald, 1860, from the Monastery Ravine section and *Pseudestheria* cf. *P. itiliana* Novojilov, 1950, from the Cheremushka Ravine section in Russia, are ornamented with reticulations (Zharinova et al., 2018; Sabirova et al., 2019).

Pseudestheria cf. *P. diensti* Gross, 1934
Figures 2.4, 3.1

Occurrence.—The same as above.

Description.—Carapace small in size, oval in outline, 3.3–4.3 mm in length (L), 2.2–2.7 mm in height (H); H/L ratio between 0.63–0.73; dorsal margin straight or slightly arched, long to very long; ratio of dorsal-margin length/carapace length between 0.60–0.81; larval valve very small; umbo in anterior and marginal position; anterior margin sharply curved; posterior margin very sharply curved; 9–12 growth lines; fine growth bands relatively wide and sparsely distributed on the carapace.

Materials.—NIGP174186 (Fig. 2.4), NIGP174187 (Fig. 3.1).

Remarks.—The specimens of *Pseudestheria* cf. *P. diensti* were poorly preserved, with limited visible characteristics: each of them possesses an oval or sub-oval carapace (single valve) with a small umbo, which is situated at the anterior position of the dorsal margin. There are two important characteristics that distinguish this species from *Cornia cheni* n. sp.: (1) it has no tubercle (or spine) on the larval valve, which is present in *Cornia cheni* n. sp.; and (2) its larval valve is obviously smaller than that of *Cornia cheni* n. sp.: ratio h/H (height of the larval valve/total height of the valve) of this species is ~0.2, while ratio h/H of *Cornia cheni* n. sp. is ≥0.4.

Our specimens share similarities in outline and umbo position with some individuals of *P. diensti* Gross, 1934, from the Lower Devonian of Germany. However, Gross' specimens possess more growth lines (15–18) than our specimens. In addition, as in Gross (1934), our specimens also show differences in outline among different individuals; some are oval and some are sub-oval to round. We consider that they all belong to one species and that their different shapes may be caused by compression deformation or sexual heteromorphism. Unfortunately, these speculations could not be confirmed due to a limited number of specimens and poor preservation. Further research is needed when better-preserved specimens are collected in the future.

Family Palaeolimnadiopseidae Defretin, 1965
Genus *Palaeolimnadiopsis* Raymond, 1946

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Type species.—*Palaeolimnadiopsis carpenteri* Raymond, 1946, from the lower Permian (Cisuralian) Wellington Formation at Noble County, Oklahoma, USA, by original designation.

Palaeolimnadiopsis zhangi new species
Figure 3.2

Holotype.—NIGP174188, a whole carapace from the Lower Devonian (Emsian) Yuankou Formation at Yuankou Town, Hunan Province.

Diagnosis.—Carapace small in size, oval in outline; dorsal margin straight to slightly arched and long; larval valve small; umbo in sub-medial and inframarginal position; anterior margin very sharply curved; posterior margin sharply curved; 3–5 growth lines slightly recurved at postero-dorsal area.

Occurrence.—The same as above.

Description.—Carapace small in size, oval in outline, 4.8 mm in length (L), 3.1 mm in height (H); H/L ratio 0.64; dorsal margin straight to slightly curved and long, ratio of dorsal-margin length/carapace length 0.71; larval valve small; umbo in sub-medial and inframarginal position; 11 fine growth lines; 3–5 growth lines slightly recurved at postero-dorsal area; growth bands wide and sparsely distributed on the carapace.

Etymology.—In memory of Professor Wentang Zhang (1924–2013), who contributed significantly to the study of fossil branchiopods of the world and lead-authored the book "Fossil Conchostracans of China" in 1976.

Materials.—Holotype: NIGP174188 (Fig. 3.2).

Remarks.—This species differs from all the other individuals from the same locality by the presence of ~3–5 growth lines, which slightly recurved at the postero-dorsal area of the carapace, forming a small cape at the postero-dorsal end. Although only one poorly preserved specimen was found, the slight recurvature of growth lines provided a crucial basis for assigning the specimen to the genus *Palaeolimnadiopsis*. The genus is known from Devonian–Cretaceous (e.g., Webb, 1978; Shen, 1985; Tasch, 1987; Gallego, 2005; Carbonaro et al., 2013).

Unlike the small size of this new form, other species of the genus are usually very large. Some can be extremely large in carapace size (e.g., *P. bassi* Webb, 1978, from the Middle Jurassic Hawkesbury Sandstone in Sydney, Australia is 17.5 mm in length). Moreover, *P.* sp. from the Upper Triassic Santa Maria Formation in Rio Grande do Sul State, Brazil, and *P. carpenteri* from the late Early Permian Wellington Formation in Oklahoma, USA both possess astonishingly large carapaces that reach 42.0 mm in length (Tasch, 1987). *Palaeolimnadiopsis vileness* Varentsov, 1955, from the Permian/Triassic Moscow Syneclise in Russia, is similar in shape and size to our new species. However, it possesses many more growth bands (up to 20, see details in Scholze et al., 2015, 2019). It is noteworthy that Chu et al. (2018) argued that "two-line typed" growth lines were present on the carapace of *P. vilujensis*. However, after consulting a large number of taxonomic descriptions and fossil photographs, we found little evidence of this distinctive characteristic in any other specimens of *Palaeolimnadiopsis*. Based on our observations of the photographs of *P. vilujensis* in Chu et al. (2018), we believe the "two-line typed" growth lines were caused by superposition of two valves when the carapace was preserved as compacted cast. Considering the especially small size and potential of significance of this individual for correlation of continental strata in southern China, we chose to establish this new species, although only one individual was found.

Family Palaleolimnadiidae Tasch, 1956
Genus *Palaeolimnadia* Raymond, 1946

Type species.—*Estheria wianamattensis* Mitchell, 1927, from the Triassic Wianamatta Group near Glenlee Homestead on the Great Southern Railway, New South Wales, Australia, by original designation.

?*Palaeolimnadia* sp.
Figure 3.3

Occurrence.—The same as above.

Description.—Carapace small in size, oval in outline, ~4.7 mm in length; dorsal margin straight to slightly curved and long, ratio of dorsal-margin length/carapace length ~0.70; larval valve large to very large, no tubercle or rib visible; umbo in sub-medial and inframarginal position; growth lines fine, unknown in number.

Materials.—NIGP174189 (Fig. 3.3).

Remarks.—The carapace was incomplete (i.e., the ventral and anterior areas of the carapace were missing), making it impossible to count the number of growth lines or measure the height of the carapace. However, its large larval valve without a tubercle or node structure differentiates it from other species of the same locality. There are many forms of clam shrimp that possess large or very large larval valves, including *Curvacornutus* Tasch, 1961, and *Tripemphigus* Novojilov in Molin and Novojilov, 1965, which possess large larval valves with morphologically variable tubercles (or nodes) (see details in Tasch, 1961; Novojilov, 1970; Chen and Shen, 1985), while *Mesolimnadia* Chen, 1975, *Yunmenglimnadia* Chen, 1975, and *Eolimnadia* Chen, 1975, possess large larval valves with visible imprints of shell glands (see details in Zhang et al., 1976; Chen and Shen, 1985). Larval valves of some species of *Palaeolimnadiopsis*, *Palaeolimnadia*, and *Asmussia* Pacht, 1849, are also relatively large (see details in Lutkevitch, 1937; Raymond, 1946; Varentsov, 1955; Novojilov, 1970; Zhang et al., 1976; Chen and Shen, 1985; Schneider and Scholze, 2018; Scholze et al., 2019). The species is obviously different from *Asmussia membranacea* Pacht, 1849, the type species of *Asmussia*, which was found in the Givetian (Middle Devonian) of Latvia. The ratio h/H of *A. membranacea* is ~0.4, while we estimate the ratio h/H of this species to be >0.6. In addition, unlike the typical oval outline of this species, *A. membranacea* is round in outline and possesses a

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relatively straight dorsal margin, which makes its antero-dorsal and postero-dorsal angles very prominent (observation of characteristics of *A. membranacea* is based on photographs and sketch from Chen and Shen, 1985). Therefore, the species is unlikely to belong to the genus *Asmussia*. We could not precisely determine the taxonomic placement of the species given its very limited morphological characteristics. Based on all its visible characteristics, it resembles some paleolimnadids. Thus, we questionably assigned it to the genus ?*Palaeolimnadia* at this stage, considering its incomplete carapace and poor preservation.

Discussion

To date, there are no credible records of any clam shrimp taxon prior to the Devonian. The small bivalved Cambrian "conchostracan" described by Ulrich and Bassler (1931) and discussed by Howell (1963) was subsequently shown to be a stem-group crustacean (Bradoriida + Eucrustacea sister to Marellomorpha [Hou et al., 2010]). *Eoasmussia* Soot-Ryen, 1960, described as a 'conchostracan,' has been referred to as a pelecypod mollusk (Pojeta, 1971). The late Silurian taxon *Asmussia*? *buchoti* Péneau, 1936 (see also in Bate et al., 1967), was apparently made without consulting Novojilov (1961), who had previously reclassified Péneau's (1936) taxonomy as *Glyptoasmussia buchoti* and found it to be Middle Devonian.

Although discerning the oldest clam shrimp is difficult, forms from the Early Devonian provide very important information on the origin and early evolution of clam shrimp. *Belgolimnadiopsis* Novojilov, 1958, and *Palaeolimnadiopsis* both belong to the family Palaeolimnadiopseidae Defretin, 1965, which is the most representative posterior-recurved-type clam shrimp. Their presence in the Early Devonian evinces that clam shrimp with posterior recurvation of growth lines were already diverse and widely distributed at the time. The recurvation of growth lines occurs mainly in species among five families: Palaeolimnadiopseidae; Sinoestheriidae Chen and Shen, 1982; Ipsiloniidae Novojilov, 1958; Vertexiidae Kobayashi, 1954; and Pemphilimadiopseidae Tasch, 1961. Tasch (1961) thought that the posterior recurvation of growth lines occurred at the genus level, independent of similar development in paleolimnadiopseids. Liao et al. (2019) agreed with Tasch's judgment and considered that the recurvation of growth lines occurred in many clam shrimp clades with diverse characteristics at different ages, indicating the consequence of convergent evolution. Therefore, we cannot say that the ancestral types of palaeolimnadiopseids—*Belgolimnadiopsis* and *Palaeolimnadiopsis*—have any inevitable connection with all the forms that possess recurved growth lines. Growth line recurvation has been observed in numerous species from Devonian to recent times (Daday, 1925; Shen, 1985). The cause of its formation and physiological significance are worth further exploration.

Concherisma eifelense (Raymond, 1946) from the Lower Devonian in Germany was first described and treated as an individual of "*Estheria diensti*" by Gross (1934). Raymond (1946) discussed that the posterior end of this specimen (in Gross, 1934, fig. 2) was not fully shown in the figure, the shape and recurved direction of some of the growth lines might be due to crushing, but still reassigned it into the genus *Palaeolimnadiopsis*. Novojilov (1961) reclassified this species as "*C. eifelense*" and displayed a sketch in his publication. According to Novojilov's (1961) sketches of five species of *Concherisma* Novojilov and Varentsov, 1956, they all possess narrow and long (elongate oval) carapaces and very sharply curved posterior margins, but none show apparent recurved growth lines. Therefore, it should be evident that *C. eifelense* is not a posterior-recurved-type form.

The genus *Pseudestheria*, as mentioned above, with the "dumping ground" issue, was once considered to have no stratigraphic significance (Raymond, 1946). Fortunately, however, some constructive suggestions and characteristics have been proposed to differentiate *Pseudestheria* from other similar forms, such as *Polygrapta*, *Euestheria*, and *Lioestheria* (e.g., Houlb and Kozur, 1981; Kozur and Sittig, 1981; Kozur and Seidel, 1983; Scholze et al., 2019; for detailed discussion see Scholze et al., 2019). Its biostratigraphic value has begun to be considered. *Pseudestheria* is one of the most common late Paleozoic genera and has a high biostratigraphic value, particularly in the Permian (e.g., Martens, 1983; Schneider and Scholze, 2018; Scholze et al., 2019). Moreover, based on the presently known records, it is also the most common genus in the Early Devonian. We think it is possibly related to the origin of *Polygrapta* and *Euestheria*. Holub and Kozur (1981) suggested that *Pseudestheria* was possibly derived from *Lioestheria*. However, based on the presently known fossil record, *Pseudestheria* appeared earlier than *Lioestheria*. *Lioestheria* shows a morphologically variable (conical to pillar-shaped or especially oval to elongate-shaped) tubercle located on the external surface of the umbo or the larval valve, which distinguishes it from *Pseudestheria*. In poorly preserved specimens with broken or strongly compressed umbonal areas, it is practical to separate the two genera by the following convention: forms with a larval valve smaller than one-third of the total valve length belong to *Pseudestheria*, and forms with a larval valve larger than one-third of the valve length belong to *Lioestheria* (Holub and Kozur, 1981; Kozur and Sittig, 1981; Scholze et al., 2019). We believe that *Lioestheria* may originate from or is closely related to *Cornia*, which also possesses a tubercle on the larval valve.

Based on the total fossil record, it can be seen that clam shrimp were diverse and widely distributed on Earth during the Early Devonian. In addition, different forms began to form communities with high diversity in suitable biotopes at the time. These earliest species include diverse types—forms with recurved growth lines (*Palaeolimnadiopsis* and *Belgolimnadiopsis*), forms with an oval tubercle on its larval valve (*Cornia*), forms with a very large larval valve (?*Palaeolimnadia* sp. in this study), and "normal" forms without distinctly special features, such as a tubercle, recurved growth lines, or very large larval valves (*Pseudestheria* and *Concherisma eifelense*). We assume that they had a profound effect on the origin and evolutionary trends of clam shrimp that later appeared on Earth. In the Middle and Middle/Late Devonian, global diversity of clam shrimp increased significantly. Some display morphological inheritance from forms of the Early Devonian. *Ipsilonia* Novojilov, 1953, of Givetian age possesses recurved growth lines (Novojilov, 1953). *Concherisma* and very similar forms, such as *Ovjurium* Novojilov and Varentsov, 1956, *Ubsanuria* Novojilov and Varentsov,

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1956, and *Dolichostheria* Novojilov and Varentsov, 1956, also were found in the Givetian strata (Novojilov and Varentsov, 1956; Novojilov and Kapel'ka, 1960). Some other forms of the Middle and Middle/Late Devonian from Russia, Europe, and China share distinct differences from those of the Early Devonian, possibly indicating the origin of new forms or emergence of new evolutionary trends.

Conclusions

A clam shrimp community that consists of four species, *Cornia cheni* n. sp., *Palaeolimnadiopsis zhangi* n. sp., *Pseudestheria* cf. *P. diensti*, and ?*Palaeolimnadia* sp., was found and described from the Early Devonian Yuankou Formation in Jiangyong County, Hunan Province, China. These species are the oldest-known fossil clam shrimp in China and are among the oldest in the world. The Devonian saw the emergence and subsequent diversification of the clam shrimp. This discovery indicates that highly diverse clam shrimp communities already had appeared in suitable biotopes on Earth by the Early Devonian. In addition, based on global records, Early Devonian forms may have had a profound effect on the origin and evolutionary trends of younger forms.

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