

Nonmarine ostracod fauna from the Lower Cretaceous Shinekhudag Formation (southwest Mongolia): taxonomy, biostratigraphy, and paleoecology

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Abstract.—This work provides the detailed investigation (taxonomy, biostratigraphy, and paleoecology) of a nonmarine ostracod fauna from the Shinekhudag Formation in Gobi–Altai area, southwest Mongolia. The samples from two sections (Tsagaan Tsuvarga and Oshih Hollow East) yielded various ostracods assigned to nine species belonging to six genera: *Cypridea verrucata* Neustrueva, 1974, *C. ihsienensis* Hou, 1958, *C. unicastata* Galeeva, 1955, *C. tumefacta* Neustrueva, 1974, *Yumenia* cf. *Y. oriformis* Hou, 1958, *Scabriculocypris subscalara* Zhang and Chen in Ye et al., 2003, *?Trapezoidella* sp., *Candona* sp., and *Vlakomia ulanense* Neustrueva, 1977. The biostratigraphic application of our taxonomic results suggests that the age of the Shinekhudag Formation is Barremian–Aptian. In addition, the ostracod fauna shows strong affinities to faunas from northeast China and potentially northwest China, providing evidence of faunal exchanges between these regions and southwest Mongolia. The new discovery of *Vlakomia ulanense* indicates that mid-Cretaceous (Albian) species in northeast China probably originated in Mongolia at the time of deposition of the Shinekhudag Formation. Two ostracod assemblages in the studied sections reflect that different paleoenvironment settings have existed during deposition; the Tsagaan Tsuvarga Section represents a shallow-littoral zone of athalassic (inland) saline lake under arid climate, and the dominance of cypridoideans of the Oshih Hollow East Section is indicative of ephemeral water bodies.

Introduction

Cretaceous lacustrine oil shales are widely distributed in rift basins near Mongolia's eastern and southeastern borders with China, forming a well-known petroleum system of eastern Asia (e.g., Yang et al., 1985; Graham et al., 2001; Johnson et al., 2003; Prost, 2004; Hasegawa et al., 2018). Due to the high organic carbon oil shale, many petroleum explorations have been conducted. In particular, Johnson et al. (2015) stated that this petroleum system extends west into the Gobi–Altai region of Mongolia according to seismic data, cores, and sedimentological outcrop studies. However, the age of oil-shale-bearing formations in the Gobi–Altai region is debated because of a lack of well-defined regional stratigraphic nomenclature and age determination (e.g., Khand et al., 2000; Johnson et al., 2015), which has hindered understanding of the formation of this big petroleum system in eastern Asia.

Ostracoda, a group of microcrustaceans with an excellent fossil record, are widely applied to biostratigraphy as well as paleoenvironmental and paleoclimate reconstruction (e.g., Horne, 2009; Sames, 2011a, b; Sames and Horne, 2012; Wang et al., 2015; Choi et al., 2021; Wang and Zhong, 2022). In particular, the well-known ostracod faunas from the so-called Purbeck–Wealden interval (latest Tithonian to earliest Aptian; see Sames and Horne, 2012 for details) deposits were notably

expedited by oil and gas exploration, including the marginal marine to nonmarine basins in Europe, Africa, and South America as well as the nonmarine rift basins of China (e.g., Erlian and Hailaer basins of China) (e.g., Gou et al., 1986; Ye et al., 2003; Liu et al., 2004). However, it should be noted that the taxonomic composition of Purbeck–Wealden type ostracod faunas from different basins in several continents can be quite different, as can the stratigraphic intervals represented. For example, the genus *Theriosynoecum* Branson, 1936 is widely reported from the Purbeck–Wealden type ostracod faunas of Europe, Africa, South America, and North America, but it is rarely found in the Purbeck–Wealden type ostracod faunas of China (e.g., Hou et al., 2002; Hou and Gou, 2007; Sames, 2011b).

In this study, we describe a moderately diverse Purbeck–Wealden type nonmarine ostracod fauna from the Shinekhudag Formation in the Gobi–Altai region of Mongolia. Our ostracod biostratigraphic data provide a new age constraint for the oil-shale-bearing Shinekhudag Formation in this area. In addition, our results provide insights into potential microfaunal interchange between distant nonmarine settings around eastern Asia. Moreover, paleoenvironmental interpretations based on ostracods provide new insights into the formation mechanism of source rocks in Gobi–Altai region.

Geological setting

The Gobi–Altai region of southern Mongolia comprises intramontane basins that contain a succession of Jurassic–Cretaceous

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Figure 1. Locality map of the studied sections of the Lower Cretaceous Shinekhudag Formation, Gobi–Altai area, southwestern Mongolia (a: Tsagaan Tsuvarga; b: Oshih Hollow East).

sediments and lavas unconformably overlain by lesser volumes of Neogene–Recent alluvial fan, fluvial, and lacustrine deposits (Cunningham et al., 2009) (Fig. 1). In this region, the Lower Cretaceous strata consist of the Tsagaantsav, Shinekhudag, Khukhteeg, and Zuunbayan formations in ascending order (Fig. 2) and their equivalents (Khand et al., 2000; Johnson et al., 2015).

The Shinekhudag Formation is also transcribed as “Shinhudag Formation” in several papers (see Graham et al., 2001; Johnson et al., 2015). It should be noted that Mongolian place and stratigraphic names have been spelled in many different ways. To minimize confusion, the translation standards suggested by Benton et al. (2000) are used in this study. The Shinekhudag Formation is well exposed in the type section of the Shine Khudag locality in the Shaazangiin Gobi area of the Darnogobi Province (Ando et al., 2011; Hasegawa et al., 2018). In the Gobi–Altai region, Johnson et al. (2015) assigned the rock unit locally mapped and identified as Manlai Formation previously to the Shinekhudag Formation (= Shinhudag Formation) because of the age equivalence of the formations. The Shinekhudag Formation (~ 50–1,600 m thick in different regions; see Khand et al., 2000; Johnson et al., 2015; Adiya et al., 2017) is composed mainly of sandstones, silty mudstones, silty claystones, and oil shales; it overlies the Tsagaantsav Formation (also spelled “Tsagantsav Formation” and equals locally mapped “Undur Formation”) and underlies the Khukhteeg Formation (also spelled “Huhteeg Formation”) in the Gobi–Altai region (Khand et al., 2000; Johnson et al., 2015; Hasegawa et al., 2018). To date, the age of the Shinekhudag Formation is still controversial. A Hauterivian–Barremian age for the Shinekhudag Formation had been proposed by several authors on the basis of ostracod fossils and $^{40}\text{Ar}/^{39}\text{Ar}$ ages (e.g., Khand

et al., 2000; Johnson et al., 2015). Hasegawa et al. (2018) assigned an Aptian age to this formation on the basis of biostratigraphic correlations and U–Pb dating of zircons in intercalated tuff samples.

Materials and methods

The studied ostracod specimens were recovered from the dark silt claystones and mudstones of the Shinekhudag Formation in Tsagaan Tsuvarga (45°11'21"N, 99°02'55"E) and Oshih Hollow East (44°96'16"N, 103°13'94"E) areas of the petroleum blocks IV and V (Fig. 1; for Mongolia petroleum blocks, also see online map: <https://www.petromatadgroup.com/mongolia/oil-in-mongolia/>). The rock samples from the outcrops were collected by an American–Mongolian petroleum investigation group during July 2011. However, because only the sample numbers and height were given by the field geologists, the detailed information (e.g., lithology and sedimentary structures) of the sections is not represented in this study. Since the ostracods are associated with bivalves that shall remain intact, we could not use the “standard method” of chemical rock disintegration. Thus, we use fine needles and brushes to clean the surrounded sediments of each ostracod carapaces/valves and expose specimens. Selected ostracod specimens were coated with gold and photographed using a scanning electronic microscope TESCAN Maia3 at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Nanjing, China).

Morphologic terminology of this study follows Sames (2011c). Ostracod size ranges are as follows: very small: <0.40 mm; small: 0.40–0.50 mm; medium: 0.51–0.70 mm; large: 0.71–1.00 mm; very large: 1.01–2.00 mm; gigantic: >2.00 mm (Ayress and Whatley, 2014). We use the following

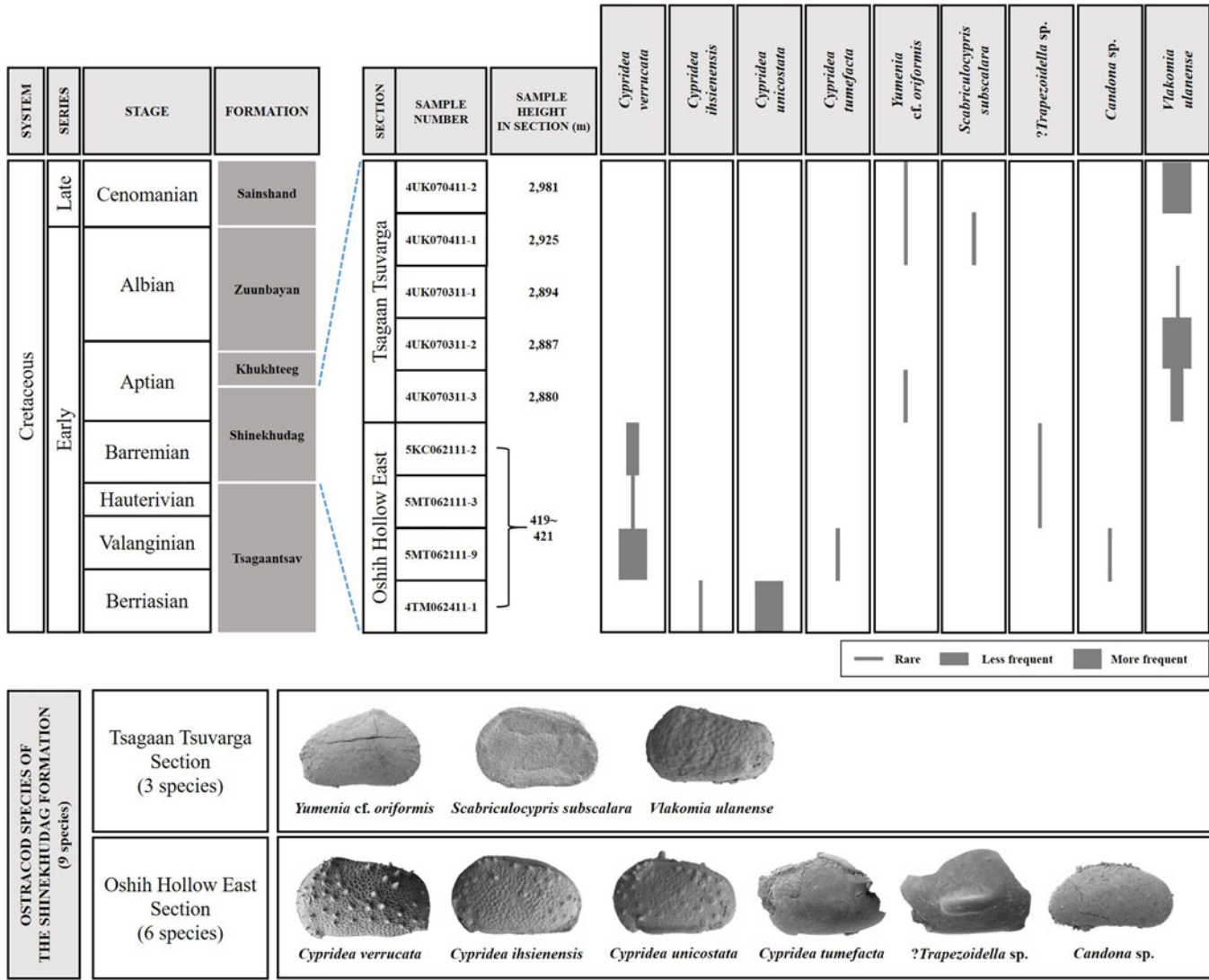


Figure 2. Stratigraphic distribution and occurrence of ostracod species in the Shinekhudag Formation, southwestern Mongolia (stratigraphic chart modified from Johnson et al., 2015).

abbreviations: L = length; H = height; W = width; LV = left valve; RV = right valve.

Repository and institutional abbreviation.—The illustrated specimens in this study are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS) under the collection numbers NIGP 180012–180052.

Systematic paleontology

The classification above family level used herein follows Daniełopol et al. (2018) and Meisch et al. (2019). The taxonomy of lower ranks is based on Hou et al. (2002), Neustrueva et al. (2005), Sames (2011a, b), and Choi et al. (2020), although with revision that will be further discussed in this paper.

- Class Ostracoda Latreille, 1802
- Order Podocopida Sars, 1866
- Suborder Cypridocopina Baird, 1845

- Superfamily Cypridoidea Baird, 1845
- Family Cyprideidae Martin, 1940
- Genus *Cypridea* Bosquet, 1852

Type species.—*Cypris granulosa* Sowerby, 1836.

Cypridea verrucata Neustrueva, 1974 emended
Figure 3

- 1974 *Cypridea verrucata* n. sp., Neustrueva, p. 258, pl. 2, fig. 4a, b.
- 2005 *Cypridea verrucata* Neustrueva in Neustrueva et al., pl. 4, fig. 3.

Holotype.—Specimen no. 2945/20 (deposited in the Institute of Precambrian Geology and Geochronology, Russian Academy of Sciences [IGGD], St. Petersburg, Russia) from the Lower Cretaceous Khukhteeg Formation, Mongolia (Neustrueva, 1974, p. 258–259, pl. 2, fig. 4a, b).

Diagnosis (emended).—Very large *Cypridea*, valves somewhat asymmetrical in lateral view due to different shapes; subrectangular for LV and subovate for RV; LV larger than RV. Rostrum short but well defined. Alveolus (notch and furrow) short and indistinct. Selvage of larger LV overlapping RV along entire margin. Cyathus acute and distinct in LV. Surface covered by puncta and spine-like tubercles with four-forked ends.

Description.—Carapace very large, subrectangular in LV and subovate in RV (in lateral view). Maximum length at mid-height, maximum height at one-third of length (anterior cardinal angle), and maximum width near mid-length. LV larger than RV and overlapping RV along entire margin. Anterior margin broad and slightly infracurvate; anterior cardinal angle (~140°) somewhat angular and protruding in both valves, and a node-like swelling developed in LV. Rostrum short but well defined, its point overreaching the ventral margin. Alveolar notch very shortly incised. Alveolar furrow shallow and faint (reaching up to a maximum of one-eighth of the height) in both valves. Selvage of larger LV overlapping RV along entire margin (Fig. 3.8). Posterior margin nearly equicurvate to slightly infracurvate and narrower than anterior one; posterior cardinal angle somewhat rounded to angular. Dorsal margin of both valves straight and declined toward the posterior end. In dorsal view, a slightly incised hinge margin forms a shallow dorsal furrow. Ventral margin almost straight but weakly concave; posteroventral area protruding with acute triangular cyathus in LV, but angular shape in RV. Surface covered by distinct puncta, spines, and spine-like tubercles; tip of spines displaying three- or four-forked ends. Normal pore canals form in muri and center of spines and spine-like tubercles.

Internal characters.—Hinge lophodont, a straight/smooth hinge bar with anterior and posterior sockets (elongate for anterior one and short for posterior one) in RV, with corresponding groove and anterior and posterior teeth in LV. Calcified inner lamella moderately broad along the anterior area with maximum width at anteroventral area and narrow in posterior area with maximum width at cyathus area. Striae identified along the free inner lamella near anterior inner margin. Selvage distinct in both anterior and posterior margins, but more strongly developed in anterior one, and interrupted selvage not identified (continuous selvage developed in posterior side of rostrum). Attached area narrow, and its point not protruding.

Morphologic variation.—The development of tubercles varies. Strongly developed tubercles show elongate, spine-like shapes with distinct four-forked ends with a normal pore (Fig. 3.4), whereas the centers of small or blunt-shaped tubercles have a smooth end with a normal pore (Fig. 3.15). These characters are local ornamentation elements related to ecophenotypic variation and/or ontogenetic character (see Sames, 2011c). Sexual dimorphism is not observed in this study.

Ontogenetic variation.—Adults and A-1 instar are identified. Carapace length of an adult ranges from 0.9 to 1.11 mm, while the A-1 instar is about 0.71 mm (Fig. 3.15) long. Besides the development of tubercles (also possibly ecophenotypic variation) and size differences, no obvious morphologic differences have been observed between adult and A-1 instar stages.

Material.—Four carapaces and 11 valves from samples 5MT062111-9, 5MT062111-3, and 5KC062111-2 of the Oshih Hollow East Section.

Dimensions.—L: 0.71–1.11 mm; H: 0.58–0.68 mm; W: 0.41–0.62 mm.

Remarks.—In general, the selvage is discontinuous and interrupted along the rostrum's posterior side of the representatives of the genus *Cypridea* (see Horne and Colin, 2005, pl. 1, figs. 2, 4; Sames, 2011b, fig. 7f). Although the species *Cypridea verrucata* has a continuous selvage in the anteroventral region (see Fig. 3.8), it still perfectly matches the diagnostic characters of the genus *Cypridea*. Therefore, this species is assigned to the genus *Cypridea*.

Cypridea concina Hou, 1958 from the Lower Cretaceous Xiagou Formation of Gansu Province, China, is similar to *C. verrucata*, but the latter has a stronger valve asymmetry and a more distinct cyathus. In addition, *Cypridea yanjiensis* Gou, 1983 from the Lower Cretaceous Tongfosi Formation of the Yanji Basin is similar in carapace outline to *C. verrucata*, but the former has a very rounded posterior margin and cyathus area.

Cypridea ihsienensis Hou, 1958 emended
Figure 4.1, 4.2

1958 *Cypridea (Uwellia) ihsienensis* n. sp., Hou, p. 101, pl. 10, figs. 11–14.

1985 *Cypridea (Uwellia) ihsienensis*; Zhang, pl. 1, fig. 14.

1985 *Cypridea (Uwellia) ihsienensis*; Yang, p. 217, pl. 3, fig. 12.

1990 *Cypridea (Uwellia) ihsienensis*; Qi and Zhang, pl. 3, figs. 1, 2.

2002 *Cypridea ihsienensis*; Hou et al., p. 502, pl. 178, figs. 11–16.

Holotype.—Specimen no. 9252 (deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences [NIGPAS], Nanjing, China) from the Lower Cretaceous Fuxin Formation, Liaoning Province, China (Hou, 1958, p. 101–102, pl. 10, fig. 14).

Diagnosis (emended).—Very large *Cypridea*, subovate in lateral view; RV larger than LV, valve overlapping distinct in dorsal area of RV due to the dorsolateral extension. Rostrum short but broad in RV, and smaller with acute shape in LV. Alveolar notch short but well defined. Alveolar furrow elongated in RV, small and triangular in LV. Cyathus triangular in RV. Surface covered by puncta and conic tubercles.

Description.—Carapace very large, subovate in lateral view. Maximum length at mid-height and maximum height at nearly one-third of length (anterior cardinal angle). RV larger than LV and overlapping LV along entire margin, especially along the dorsal margin (due to the dorsolateral extension). Anterior margin rounded and slightly infracurvate; anterior cardinal angle (~140°) somewhat rounded but distinct, with a lateral node-like swelling developed in RV. Rostrum short but broadly developed in RV, small and very acute in LV; rostrum

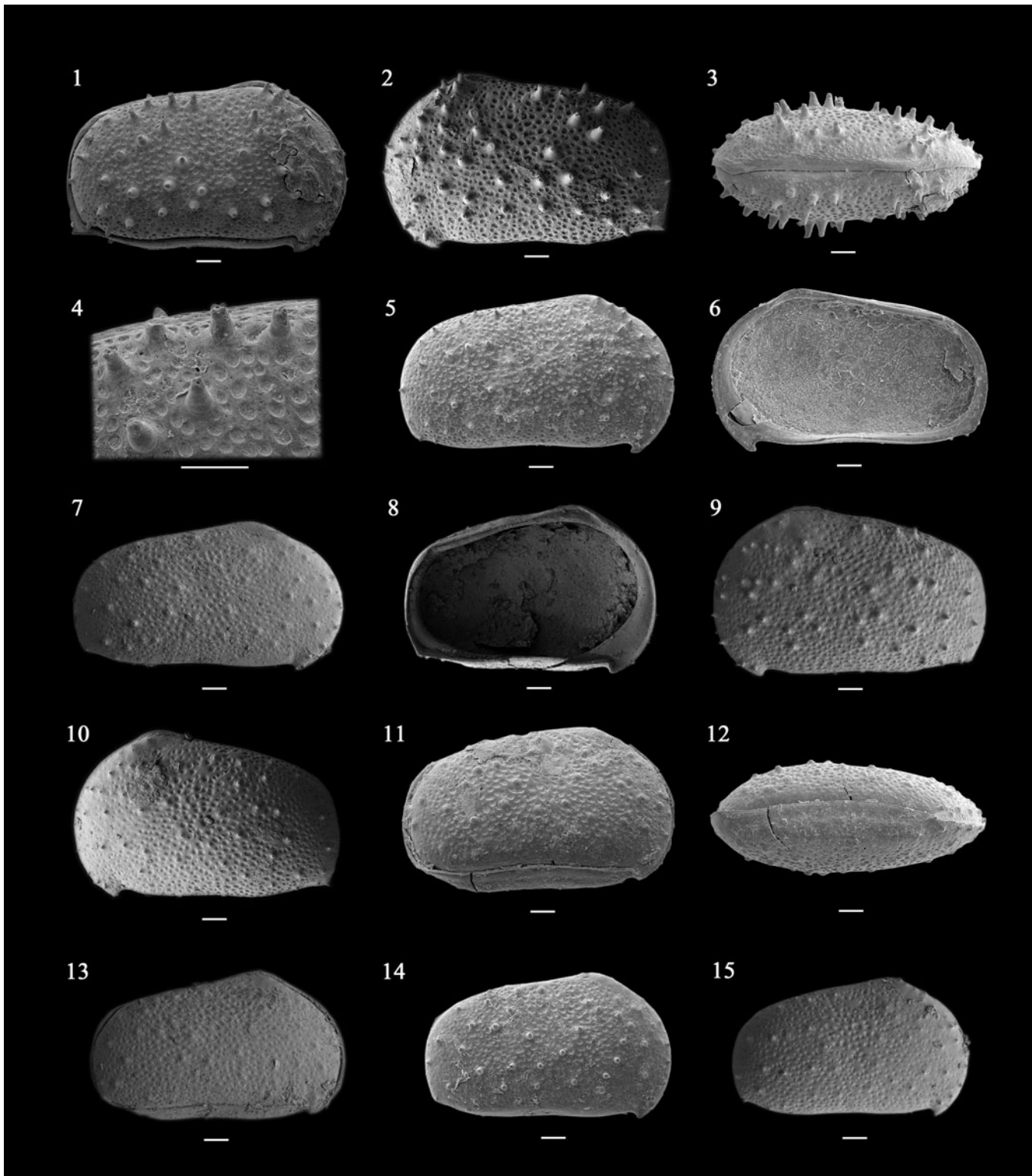


Figure 3. *Cypridea verrucata* (Neustrueva, 1974). (1–4) Adult carapace, NIGP 180012, sample 5KC062111-2: (1) right view; (2) left view; (3) dorsal view (anterior end to the right); (4) detail of carapace surface. (5, 6) Adult right valve, NIGP 180013, sample 5KC062111-2: (5) lateral view; (6) internal view. (7) Lateral view of adult right valve, NIGP 180014, sample 5MT062111-9. (8, 9) Adult left valve, NIGP 180015, sample 5KC062111-2: (8) internal view; (9) lateral view. (10) Lateral view of adult left valve, NIGP 180016, sample 5MT062111-3. (11, 12) Adult carapace, NIGP 180017, sample 5MT062111-9: (11) right view; (12) ventral view (anterior end to the right). (13) Right view of A-1 instar carapace, NIGP 180018, sample 5MT062111-9. (14) Lateral view of A-1 instar right valve, NIGP 180019, sample 5MT062111-9. (15) Lateral view of A-1 instar right valve, NIGP 180020, sample 5MT062111-3. Scale bars = 100 μ m.

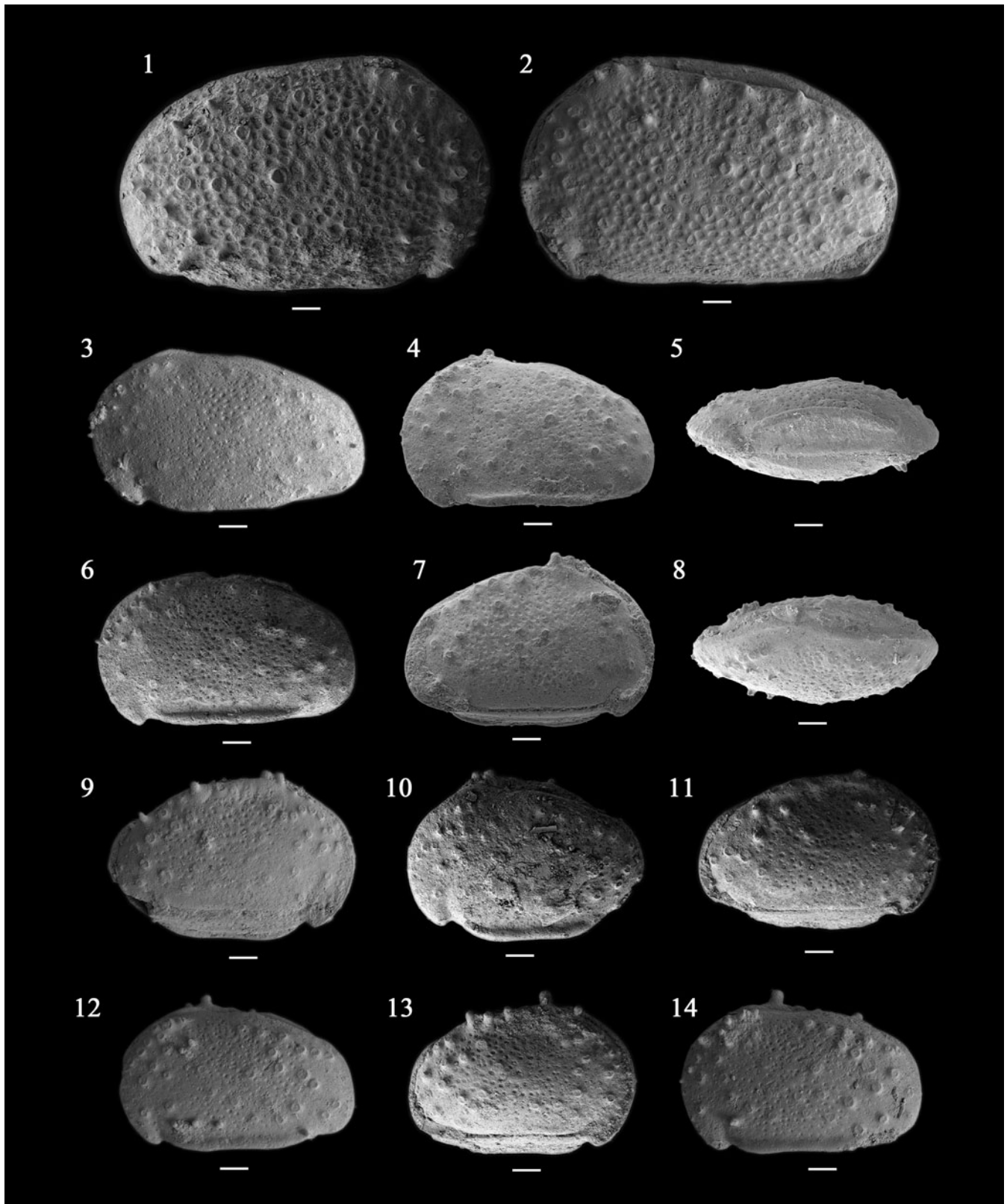


Figure 4. (1, 2) *Cypridea ihsienensis* (Hou, 1958): (1) right view of carapace, NIGP 180021, sample 4TM062411-1; (2) left view of carapace, NIGP 180022, sample 4TM062411-1. (3–14) *Cypridea unicostata* (Galeeva, 1955): (3) left view of carapace, NIGP 180023, sample 4TM062411-1; (4, 5) carapace, NIGP 180024, sample 4TM062411-1: (4) left view, (5) ventral view (anterior end to the left); (6) left view of carapace, NIGP 180025, sample 4TM062411-1; (7, 8) carapace, NIGP 180026, sample 4TM062411-1: (7) right view, (8) dorsal view (anterior end to the left); (9, 10) carapace, NIGP 180027, sample 4TM062411-1; (9) right view, (10) left view; (11) right view of carapace, NIGP 180028, sample 4TM062411-1; (12) left view of carapace, NIGP 180029, sample 4TM062411-1; (13, 14) carapace, NIGP 180030, sample 4TM062411-1: (13) right view, (14) left view. Scale bars = 100 μ m.

point bending backward and slightly overreaching the ventral margin. Alveolar notch short but well defined. Alveolar furrow elongated and narrow in RV (reaching up to a maximum of one-fifth of the height), but much smaller and triangular in LV. Posterior margin slightly infracurvate and narrower than anterior margin; posterior cardinal angle obtuse rounded in both valves. Dorsal margin of both valves slightly declined toward posterior end; dorsal outline slightly convex to straight in RV, nearly straight in the LV. Ventral margin straight in both valves, but ventral outline of RV slightly convex by weakly developed ventral ridge; posteroventral area of RV somewhat protruded by triangular cyathus, but indistinct and rounded in LV. Surface covered by puncta tending toward reticulation, with conic tubercles particularly in anterolateral, posterocentral, posterolateral, and dorsolateral areas of carapace.

Material.—Two carapaces from sample 4TM062411-1 of the Oshih Hollow East Section.

Dimensions.—L: 1.39 mm; H: 0.88–0.89 mm; W: 0.58–0.68 mm.

Remarks.—Sames (2011b, p. 381, and references therein) rejected the subgenus *Uwellia* Anderson, 1939, and this opinion is followed here. *Cypridea ihsienensis* is similar to *C. muriculata* Zhang, 1985 from the Lower Cretaceous Yixian Formation, but the latter has a much broader rostrum in LV. *Cypridea justa* Lülimova, 1956 from the Zuunbayan Formation of Mongolia and the Hailaer Basin of China is similar to *C. ihsienensis* in rostrum shape, subovate outline, and ornamentation pattern. However, *C. justa* has more distinct anterior cardinal angle and a rounded cyathus area. According to Wang et al. (2017a), the specimens of *C. justa* in Lülimova (1956) are probably juveniles of *C. beipiaoensis* Cao, 1999. *Cypridea beipiaoensis* from the Yixian Formation, northeast China, differs from *C. ihsienensis* by a strong overlap of the larger valve along the entire margin and angular cardinal angles. *Cypridea subrectangular obtusovata* Li and Cao, 2002 from the Chaoshui Basin, northwest China, resembles the outline of *C. ihsienensis* at first glance, but the former has a much-inflated ventral outline with a rounded cyathus area. *Cypridea copulenta* Lülimova, 1956 from the Barunbayan Formation, Mongolia, has much larger rostrum in the RV than *C. ihsienensis*, and its point is strongly overreaching the ventral margin.

Cypridea unicastata Galeeva, 1955 emended
Figure 4.3–4.14

- 1955 *Cypridea unicastata* n. sp., Galeeva, p. 34, pl. 4, fig. 2a–d.
1956 *Cypridea unicastata*; Lülimova, pl. 7, fig. 2a–c.
1974 *Cypridea unicastata*; Hao et al., p. 34, pl. 9, fig. 1a–g.
non 1976 *Cypridea unicastata*; DOFEAD, p. 33, pl. 3, figs. 2a–4b.
1985 *Cypridea (Cypridea) unicastata*; Zhang, pl. 1, fig. 6.
1985 *Cypridea unicastata*; Yang, p. 217, pl. 3, fig. 11.
non 1985 *Cypridea unicastata*; Shou, p. 59, pl. 2, fig. 9.

- 1988 *Cypridea unicastata*; Qi, p. 130, pl. 3, figs. 1–3.
1993 *Cypridea unicastata*; Sinita, p. 201, pl. 1, figs. 3, 4.
1999 *Cypridea unicastata*; Nikolaeva and Neustrueva, pl. 8, fig. 2.
non 2002 *Cypridea unicastata*; Ye et al., p. 148, pl. 2, fig. 3a–c.
2002 *Cypridea unicastata*; Hou et al., p. 452, pl. 166, figs. 20, 21.
2005 *Cypridea unicastata*; Neustrueva et al., pl. 4, figs. 4–6, pl. 5, figs. 1–4.

Holotype.—Specimen no. 200-16 (deposited in the All-Russia Petroleum Research Exploration Institute [VNIGRI], St. Petersburg, Russia) from the Lower Cretaceous Zuunbayan Formation, Mongolia (Galeeva, 1955, p. 34–35, pl. 4, fig. 2a–d.).

Diagnosis (emended).—Large *Cypridea*, subovate to subtriangular in lateral view; LV overlaps RV along all margins except the hinge margin; a well-developed ventrolateral ridge presents in the ventral margin area of LV. Rostrum short but broad and stout. Alveolus moderately to well developed; alveolar notch broad, alveolar furrow crescent shaped in LV and indistinct in RV. Cyathus rounded but distinctly developed in LV but indistinct in RV. Surface covered by fine puncta and cylindric tubercles.

Description.—Carapace large, subovate to subtriangular in lateral view. Maximum length at one-fifth of height near the cyathus area, maximum height at nearly one-third of length (anterior cardinal angle), and maximum width at mid-length. LV larger than RV and overlapping RV along entire margin. Anterior margin broad, weakly equicurvate to infracurvate; anterior cardinal angle (~150°) rounded but protruding in LV with an indistinct lateral node-like swelling, but nearly rounded in RV. Rostrum short but broad and stout, its point somewhat blunt and not reaching the ventral outline. Alveolar notch short but moderately broad. Alveolar furrow slightly crescent and moderately incised in LV, reaching up to one-fourth of height, but smaller in RV and more indistinct than the former (reaching up to a maximum of one-fifth of the height). Posterior margin strongly infracurvate and tapering in LV but equicurvate to slightly infracurvate with narrow margin in RV; posterior cardinal angle area somewhat angular in LV and rounded in RV. Dorsal margin convex and declined toward the posterior end; dorsal outline prominent and more distinctive in LV due to the dorsal ridge. In dorsal view, hinge margin incised between anterior and posterior cardinal angle areas, forming a dorsal furrow. Ventral margin and outline nearly straight in RV, inflated ventral outline in LV with very well-developed ventrolateral ridge; posteroventral area narrowly rounded by cyathus in LV, but moderately rounded in RV. Surface covered by fine puncta and cylindrical tubercles of variable size.

Morphologic variation.—Some specimens show very inflated ventral outline. However, this feature is identified only in LV. Thus, specific characters for male/female distinction in *Cypridea unicastata* are not observed.

Ontogenetic variation.—It is unclear due to the narrow range of sizes between specimens and because internal characters are not observed.

Material.—Eleven carapaces from sample 4TM062411-1 of the Oshih Hollow East Section.

Dimensions.—L: 0.86–0.96 mm; H: 0.52–0.58 mm; W: 0.37–0.43 mm.

Remarks.—The strong valve asymmetry combined with the remarkably inflated ventral outline and ventrolateral ridge of LV in *C. unicostata* are very distinguishable from the morphology of other *Cypridea* species. *Cypridea figurata* Neustrueva, 1974 from the Shinekhudag Formation (Neustrueva et al., 2005) is similar to *C. unicostata*, but the former has a narrower alveolus (notch and furrow), a distinct and well-developed dorsal ridge between anterior and posterior cardinal angles, as well as development of spine-like tubercles. *Cypridea bicostata* Wang (in Qi and Wang, 1981) from the Lower Cretaceous Xinmingpu Group resembles *C. unicostata* in outline and shape of the ventrolateral ridge, but the valve overlap of the former is more distinctive, and the cyathus area is smooth and more rounded than in *C. unicostata*. In addition, *Cypridea liaoningensis* Zhang, 1985 from the Yixian Formation has a similar carapace outline and some features of *C. unicostata*, but *C. liaoningensis* has ventrolateral ridges and anterior swellings in each valve, and the presumed functional significances of these features are upside-down swimming and eye tubercles, respectively (see Wang et al., 2013, p. 106).

Cypridea tumefacta Neustrueva, 1974
Figure 5.1

1974 *Cypridea tumefacta* n. sp., Neustrueva, p. 260, pl. 3, fig. 1a–c.

1989 *Langtonia tumefacta*; Neustrueva, pl. 1, figs. 1, 2.

1999 *Langtonia tumefacta*; Nikolaeva and Neustrueva, pl. 9, figs. 1, 2.

2005 *Langtonia tumefacta*; Neustrueva et al., pl. 13, figs. 1–3.

Holotype.—Specimen no. 2945/27 (deposited in the Institute of Precambrian Geology and Geochronology, Russian Academy of Sciences [IGGD], St. Petersburg, Russia) from the Lower Cretaceous Zuunbayan Formation, Mongolia (Neustrueva, 1974, p. 260–261, pl. 3, fig. 1a–c).

Material.—One partial left valve from sample 5MT062111-9 of the Oshih Hollow East Section.

Remarks.—Despite many missing and crushed parts (partial anterior, dorsal, and posterior areas), the low L/H ratio and rostrum/alveolus shapes of the studied specimen fit well into *Cypridea tumefacta* Neustrueva, 1974 (also known as *Langtonia tumefacta* in some literature, e.g., Nikolaeva and Neustrueva, 1999). However, this species shows typical features of the representatives of the *Cypridea laevigata/setina* group (see more details in Sames, 2011b, p. 396–397). Although their affinities are controversial and unsolved so far (Schudack and Schudack, 2009; Sames, 2011b; Trabelsi et al., 2011, 2015), the representatives of the *C. laevigata/setina* group have a completely smooth carapace surface. Rostrum/

alveolus size ranges and shapes are variable in this species group (e.g., well-developed rostrum/alveolus of *C. ex gr. laevigata* in Trabelsi et al., 2015); however, many Early Cretaceous species have a small rostrum and small/inconspicuous alveolus (see Anderson, 1985; Schudack and Schudack, 2009; Sames, 2011b). *Cypridea tumefacta* herein also has a totally smooth surface and small rostrum/alveolar notch; therefore, this species is considered a representative of the *C. laevigata/setina* group. Among this species group, some European species with a low L/H ratio (*C. laevigata* var. *camelodes* and *C. laevigata* var. *dotica* in Anderson, 1962) are similar to *C. tumefacta*. However, European variants of *C. laevigata* have a much smaller carapace size and rostrum (see also Anderson, 1985).

Family Alloicyprideidae Ayress and Whatley, 2014
Genus *Yumenia* Hou, 1958

Type species.—*Cypridea (Yumenia) oriformis* Hou, 1958.

Remarks.—Hou (1958) established the new subgenus *Cypridea (Yumenia)*. However, because it lacks a rostrum and alveolar notch, this subgenus has been excluded from the genus *Cypridea* as well as from the family Cyprideidae (e.g., Horne and Colin, 2005; Sames, 2011b). *Yumenia* has been placed into the Trapezoidellidae Sohn, 1979 (Nikolaeva and Neustrueva, 1999) or the Alloicyprideidae Ayress and Whatley, 2014 (Wang et al., 2017b). Many representatives of the family Trapezoidellidae are, however, very different from *Yumenia* in carapace shape and local and area-wide ornamentation elements. Here we follow the view of Wang et al. (2017b) that *Yumenia* is assigned to the family Alloicyprideidae.

The representatives of *Yumenia* are quite similar to those of the genus *Scabriculumcypris* Anderson, 1941 in general morphology, such as typical *Cypridea*-like carapace shapes (subrectangular to subtrapezoidal in lateral view) but lacking rostrum/alveolus and cyathus. The maximum heights of both genera are usually at the anterior cardinal angle. In addition, except for some taxa, the area-wide ornamentation elements in many representatives of both genera are very similar (reticulation or punctation). Therefore, *Yumenia* is potentially synonymous with *Scabriculumcypris*. However, some *Yumenia* species (including questionable species) in previous studies show more various morphology and ornamentation types (e.g., smooth surface of ?*Y. acutiuscula* (Zhang, 1985) in Wang et al., 2016 and large spines of ?*Y. ordinata* (Ye in Hao et al., 1974) in Wang et al., 2017b). The ornamentation trends in *Scabriculumcypris* species consist of reticulation/punctation and may or may not have local ornamentation elements. Many of these characters are insignificant to divide two genera; hence, the phylogenetic relationship between *Yumenia* and *Scabriculumcypris* needs further investigation.

Yumenia cf. *Y. oriformis* Hou, 1958
Figure 5.2, 5.3

1958 *Cypridea (Yumenia) oriformis* n. sp., Hou, p. 94, pl. 9, figs. 1–5.

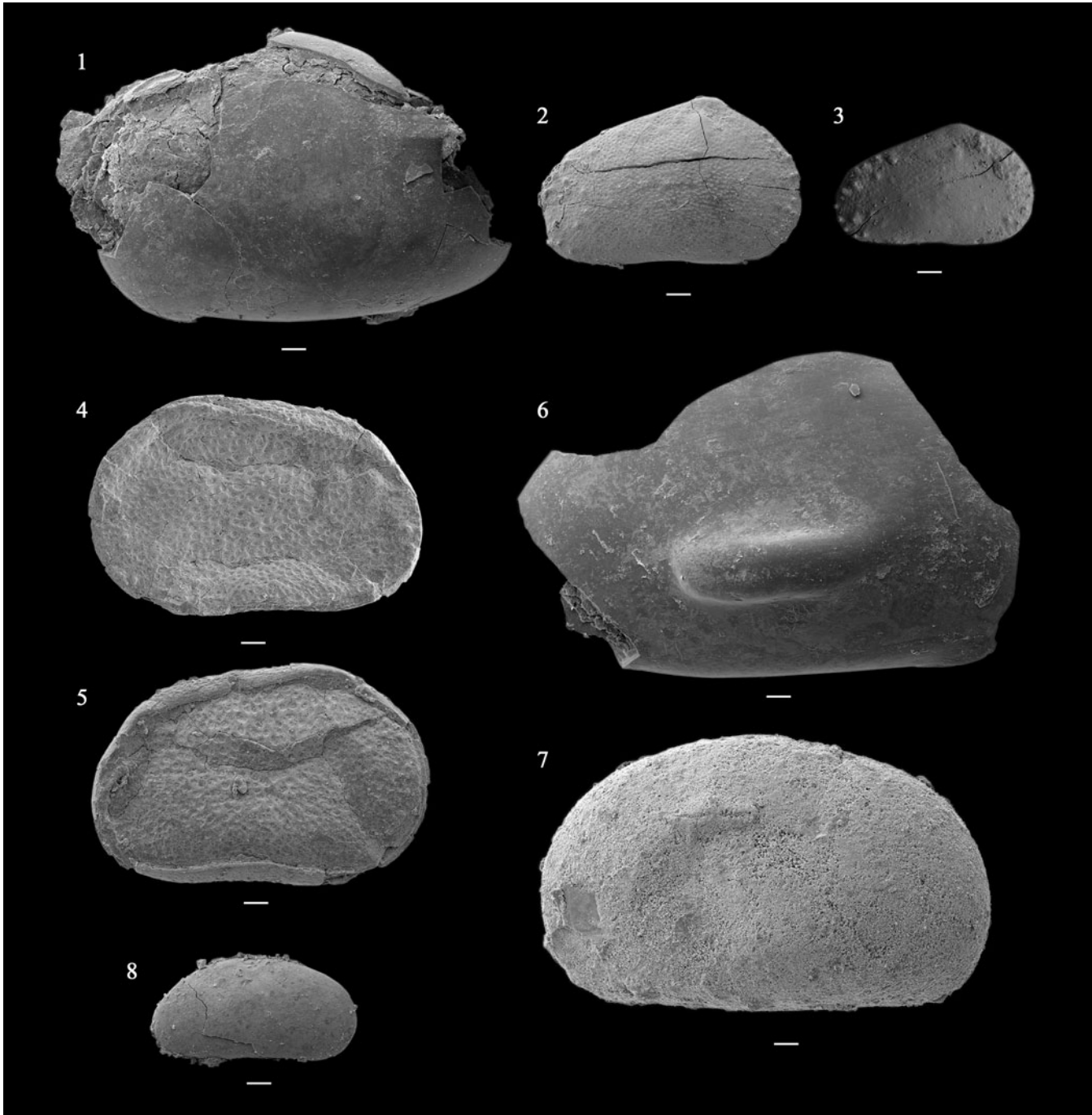


Figure 5. (1) *Cypridea tunefacta* (Neustrueva, 1974), left view of valve, NIGP 180031, sample 5MT062111-9. (2, 3) *Yumenia* cf. *Y. oriformis* (Hou, 1958): (2) right view of adult valve, NIGP 180032, sample 4UK070411-2; (3) right view of ?A-2 instar valve, NIGP 180033, sample 4UK070411-1. (4, 5) *Scabriculocypris subscalara* (Zhang and Chen in Ye et al., 2003), adult carapace, NIGP 180034, sample 4UK070411-1: (4) left view; (5) right view. (6, 7) ?*Trapezoidella* sp.: (6) left view of valve, NIGP 180035, sample 5MT062111-3; (7) left view of internal mold, NIGP 180036, sample 5KC062111-2. (8) *Candona* sp., lateral view of right valve, NIGP 180037, sample 5MT062111-9. Scale bars = 100 μ m.

1958 *Cypridea* (*Yumenia*) *suboriformis* n. sp., Hou, p. 95, pl. 9, figs. 6–9, 11.

1958 *Cypridea* (*Yumenia*) *pentanoda* n. sp., Hou, p. 95, pl. 9, figs. 10, 12–14.

2002 *Yumenia oriformis*; Hou et al., p. 611, pl. 254, figs. 1, 2.

Holotype.—Specimen no. 9224 (deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of

Sciences [NIGPAS], Nanjing, China) from the Lower Huihuipu Series, China (Hou, 1958, p. 94–95, pl. 9, fig. 1).

Description.—Valve large, subtriangular in lateral view. Maximum length at one-third of height and maximum height at near one-third of length (anterior cardinal angle). Valve overlapping unknown (in Hou, 1958, LV larger than RV). Anterior margin broadly rounded and weakly infracurvate to

equicurvate; anterior cardinal angle (~140°) angular and distinct. Posterior margin much narrower than anterior one and infracurvate; posterior cardinal angle nearly rounded and inconspicuous. Dorsal margin straight and deeply declined toward the posterior end. Ventral margin almost straight but weakly concave in near mid-length. Surface covered by fine puncta, with small tubercles particularly in anterolateral and posterolateral areas or totally absent.

Ontogenetic variation.—Presumed A-2 instar (0.80 mm long) is smaller than the adult (1.02 mm long). The morphologic characters in a presumed A-2 instar are the same as in the adult.

Material.—Three valves from samples 4UK070311-3, 4UK070411-1, and 4UK070411-2 of the Tsagaan Tsuvarga Section.

Dimensions.—L: 0.80–1.02 mm; H: 0.52–0.71 mm; W: unknown.

Remarks.—The classification of this species is based only on several valves. Thus, the species assignment is questionable. However, on the basis of general shape and local/area-wide ornamentation pattern, we presume that the studied specimens are related to or same taxon of *Yumenia oriformis* Hou, 1958.

Some representatives of the genus *Yumenia* in Hou (1958) are likely synonymous with *Y. oriformis* as follows: *Yumenia suboriformis* Hou, 1958 has concave ventral margin, and *Y. pentanoda* Hou, 1958 has a more slender carapace than *Y. oriformis*, but other features fit the features of the latter. Thus, these species are considered synonyms in this study.

Yumenia remota (Lübmimova, 1956) in Nikolaeva and Neustrueva (1999) shows strong similarities to *Y. oriformis* in carapace shape and ornamentation. The original illustrations and photos of *Y. remota* in Lübmimova (1956) and Neustrueva et al. (2005), however, show a more trapezoidal shape with convex ventral margin in both valves. *Janinella tsaganensis* Neustrueva, 1977 from the Shinekhudag Formation is similar to *Yumenia* cf. *Y. oriformis* in carapace shape and ornamentation, but the former exhibits a small rostrum-like structure and slightly incised alveolar notch in both valves.

Genus *Scabriculocypris* Anderson, 1941

Type species.—*Scabriculocypris trapezoides* Anderson, 1941.

Scabriculocypris subscalara Zhang and Chen in Ye et al., 2003
Figure 5.4, 5.5

2003 *Limnocypridea subscalara* n. sp., Zhang and Chen in Ye et al., p. 95, pl. 18, fig. 5a–c; pl. 20, figs. 1, 2, 4.

2003 *Limnocypridea huangqimiaoensis* n. sp., Huang in Ye et al., p. 95, pl. 20, fig. 3a, b; pl. 21, fig. 1a–c.

2004 *Limnocypridea subscalara*; Liu et al., pl. 2, fig. 3a, b.

Holotype.—Specimen no. DQH191 (deposited in the Institute of Petroleum Exploration and Exploitation, Division Company of Corporation Ltd., Daqing, China) from the Nantun Formation of the Hailaer Basin, China (Ye et al., 2003, p. 95).

Description.—Carapace very large, subtrapezoidal in lateral view. Maximum length at mid-height and maximum height at one-third of length (anterior cardinal angle). LV larger than RV and overlapping RV entire margin, especially along the dorsal margin by the dorsal ridge. Anterior margin equicurvate; anterior cardinal angle (~140°) rounded and indistinct in both valves. Posterior margin rounded and infracurvate; posterior cardinal angle somewhat more angular than anterior one. Dorsal margin straight and slightly declined toward the posterior end. Ventral margin straight in LV but concave in mid-length of RV. Surface covered by puncta tending toward reticulation. Local ornamentation elements absent.

Material.—One carapace from sample 4UK070411-1 from the Tsagaan Tsuvarga Section.

Dimensions.—L: 1.33 mm; H: 0.86 mm; W: Unknown (due to the compressed carapace).

Remarks.—This species was formerly assigned to the genus *Limnocypridea*. However, it differs from trapezoidellids by strongly inclined dorsal margin, a somewhat weaker dorsal overlap, and a reticulation-like punctation. Therefore, we transfer this species to the genus *Scabriculocypris*. *L. huangqimiaoensis* Huang (in Ye et al., 2003) differs from *S. subscalara* by only the elongated carapace shape, but other features fit the diagnostic characters of the latter. Furthermore, these two species have been reported from the same strata and basin. Thus, *L. huangqimiaoensis* is considered a junior synonym of *S. subscalara*.

Genus *Trapezoidella* Sohn, 1979

Type species.—*Bythocypris (Bairdiocypris) trapezoidalis* Roth, 1933.

?*Trapezoidella* sp.
Figure 5.6, 5.7

Material.—One partial valve and one internal mold from samples 5MT062111-3 and 5KC062111-2 of the Oshih Hollow East Section.

Dimensions.—L: 1.90 mm; H: 1.20 mm; W: unknown.

Remarks.—This species is distinguished from other species by (presumed) gigantic size and thick/elongate lateral ridge, but the details of the species are very limited due to the fragmentary material. However, a distinct lateral ridge and smooth carapace are relatively common in the genus *Trapezoidella* (see Sohn, 1979). Therefore, here we tentatively assign this taxon to the species of *Trapezoidella*. Some species are partially similar to ?*Trapezoidella* sp. in this study but differ in the size and other characters; *Trapezoidella hornei* Khand, Sames, and Schudack, 2007 has also been recorded from the Shinekhudag Formation, but this species shows a thin lateral ridge, punctate area-wide ornamentation elements, and a much smaller carapace size (maximum

1.13 mm long). Thus the specimens of *T. hornei* in Khand et al. (2007) could be juvenile forms of *?Trapezoidella* sp. in this study. However, this view needs further investigation (due to sparse data). *Trapezoidella rothi* Sohn, 1979 from the Lower Cretaceous Lakota Formation, USA, shows a smooth carapace, but the lateral ridges are more displaced toward the ventral margin than in *?Trapezoidella* sp. The elongate and thick lateral ridge is also confirmed in several trapezoidellid species, such as *Falklandicypris petrasaltata* Ayress and Whatley, 2014 from the North Falkland Basin, South Atlantic, and *Limnocypridea bitumulosa* Lülimova, 1956 from Mongolia. However, except for the existence of a lateral ridge, they are totally different in shape.

Family Candonidae Kaufmann, 1900
Genus *Candona* Baird, 1845

Type species.—*Cypris candida* Müller, 1776.

Candona sp.
Figure 5.8

Description.—Valve large, elongated and ovate in lateral view. Maximum length at slightly below mid-height and maximum height near three-fifths of length (posterior cardinal angle). Anterior margin rounded and nearly equicurved; anterior cardinal angle rounded and very inconspicuous. Posterior margin much narrower than anterior one and equicurved to slightly supracurved. Dorsal margin somewhat convex and rounded. Ventral margin almost straight. Surface smooth.

Material.—One valve from sample 5MT062111-9 of the Oshih Hollow East Section.

Dimensions.—L: 0.71 mm; H: 0.40 mm; W: unknown.

Remarks.—The studied material includes only a single valve; therefore, more specimens are required for more detailed investigation and comparison. However, the small valve and elongate/ovate shape with convex dorsal margin of this specimen are typical of the representatives of the genus *Candona* in much of the literature. The general outline of this species is somewhat to that of *Candona* sp. 1 from the Tongfosi Formation of the Yanji Basin (Choi et al., 2020). However, the latter has a broad posterior area (beyond the posterior cardinal angle) and a concave ventral margin.

Superfamily Cytheroidea Baird, 1850
Family Limnocytheridae Sars, 1928
Subfamily Limnocytherinae Sars, 1928
Genus *Vlakomia* Gramm, 1966 emended

1966 *Vlakomia*, Gramm, p. 83.

1993 *Tsetsenia*, Sinitsa, p. 223.

Type species.—*Vlakomia ustinovskii* Gramm, 1966.

Included species.—*Vlakomia ustinovskii* Gramm, 1966; *Vlakomia jilinensis* Gou, 1983; *Vlakomia ulanense*

Neustrueva, 1977 (= *Theriosynoecum ulanense* Neustrueva, 1977) (wrongly described as *Tsetsenia ulanensis* by Neustrueva et al., 2005); *Vlakomia mira* Sinitsa, 1993 (= *Tsetsenia mira* Sinitsa, 1993); *?Vlakomia temperata* Sinitsa, 1993 (= *Tsetsenia temperata* Sinitsa, 1993).

Diagnosis (emended).—Small to large carapace (typically smaller than 0.80 mm), oblong and rhomboidal to subrhomboidal in lateral view. Anterior margin broad with a remarkable anterior cardinal angle. LV larger than RV and weakly overlapping RV along entire margin. Two sulci developed in anterodorsal area, one of them barely to weakly developed in some species. Lateral pore canals with simple and type C sieve pores. Hinge lophodont with strong anterior and posterior teeth/sockets, posterior tooth roundish, anterior tooth roundish or divided into three tiny and shallow teeth, hinge line straight. Surface reticulation. Common presence of large hollow tubercles with constant position and smaller tubercles with no fixed location. Sexual dimorphism visible; precocious sexual dimorphism also seen. Male elliptical in dorsal view and oblong in lateral view. Female rhomboidal in dorsal view with more rounded and broader posterior margin. Male always larger than female. Female with stronger ornamentation.

Occurrence.—‘Bon-Tsagaan Series’ deposits and Shinekhudag Formation of Central and Gobi–Altai regions of Mongolia, Barremian–Aptian; Tongfosi Formation of the Yanji Basin in Northeast China, Albian (Sinitsa, 1993; Choi et al., 2020; Zhong et al., 2021, and this study).

Paleoecology.—Nonmarine, fresh to (hyper-)saline water environment (Choi et al., 2020).

Remarks.—The genus *Tsetsenia* Sinitsa, 1993 is considered a junior synonym of *Vlakomia* because the type species of the former genus fits the diagnostic features of *Vlakomia* (general shape, two dorsolateral sulci, and reticulation) very well. Although Sinitsa (1993) tentatively assigned her genus *Tsetsenia* to the family Limnocytheridae, Nikolaeva and Neustrueva (1999) and Neustrueva et al. (2005) clearly stated that the genus *Tsetsenia* belongs to the family Limnocytheridae.

The family Limnocytheridae comprises two subfamilies, the subfamily Limnocytherinae and the subfamily Timiriaseviinae (Sames, 2011a; Danielopol et al., 2018). The taxonomy above species level of this family has been comprehensively discussed in several papers (e.g., Colin and Danielopol, 1978; Sames, 2011a; Danielopol et al., 2018 and references therein). Table 1 lists important carapace features to compare and differentiate several Late Mesozoic members of the family Limnocytheridae, including *Vlakomia* Gramm, 1966, *Theriosynoecum* Branson, 1936, *Timiriasevia* Mandelstam, 1947, and *Metacypris* Brady and Robertson, 1870. Among them, *Vlakomia* belongs to the subfamily Limnocytherinae while the other three genera are considered members of the subfamily Timiriaseviinae (Danielopol et al., 2018; Choi et al., 2020). In fossil representatives of the Timiriaseviinae, the female brood pouches are always present and mostly strongly developed (showing visible sexual dimorphism) (Sames, 2011a). The members of Limnocytherinae do not

Table 1. Comparison of taxonomically significant carapace features (taxonomic key) of selected genera from the family Limnocytheridae and their stratigraphic distribution (modified from Sames, 2011a, table 1).

Attribute	<i>Theriosynoecum</i> Branson, 1936	<i>Metacypris</i> Brady and Robertson, 1870	<i>Timiriasevia</i> Mandelstam, 1947	<i>Vlakomia</i> Gramm, 1966
Dorsal view of female	(elongated) Piriform, sometimes elongated cordiform	Cordiform	Oval-elongate to piriform, weak anterolateral constriction	Rhombus
Lateral view	Subrhomboidal to rounded oblong	Rounded oblong, ventrally convex	Rounded oblong, ventrally convex	Oblong to subrhomboidal
Hinge	Lophodont, rarely inverse, elements smooth, strong posterior tooth/socket	Lophodont, elements smooth, cardinal teeth narrow	Lophodont, elements smooth, cardinal teeth narrow	Lophodont, strong anterior and posterior teeth/sockets
Anterior dorsolateral sulci	Bisulcate, usually strongly developed	Monosulcate, sulcus weak	Nonsulcate	Bisulcate, usually strongly developed
Local ornamentation elements	Tubercles common, males almost always tuberculate, nodding common	No nodes or tubercles	No nodes or tubercles	Nodes common, rare tubercles
Area-wide ornamentation elements	Punctuation, in part with reticulation-like pattern	Punctuation	Concentrically striate, sometimes combined with punctuation	Reticulation
Lateral pore canals	Simple pores, sieve pore type B	Simple pores	Simple pores	Simple pores, sieve pore type C
Average maximum size	0.90–1.20 mm	0.50–0.60 mm	0.50–0.80 mm	0.50–0.80 mm
Stratigraphic range	Middle Jurassic to Early Cretaceous (up to Cenomanian?)	Early Cretaceous (Aptian) to Recent	Late Triassic to late Paleocene	Early Cretaceous

develop female brood pouches, and the male carapace is often larger than the female one (Meisch, 2000). In summary, the genus *Vlakomia* can be well determined on the basis of carapace characters and can be clearly distinguished from the genera *Theriosynoecum*, *Timiriasevia*, and *Metacypris* as well (see Table 1 for details).

V. pristina Zhang, 1982 is invalid since this species was established on the basis of one broken specimen without a shell (Choi et al., 2020). *?Vlakomia temperata* (Sinita, 1993) is questionable here because the figured type specimen of this species seems to be deformed by compression (see Sinita, 1993, pl. 16, fig. 5).

Vlakomia ulanense Neustrueva, 1977

Figure 6

1977 *Theriosynoecum ulanense*, Neustrueva, p. 140, pl. 2, figs. 14, 15.

2005 *Tsetsenia ulanensis*, Neustrueva et al., p. 55, pl. 26, figs. 7, 8.

Holotype.—Specimen no. 3589/12 (deposited in the Paleontological Institute, Russian Academy of Sciences [PIN], Moscow, Russia) from the Andaikhudag Formation (= Shinekhudag Formation; see Khand et al., 2000), Mongolia (Neustrueva, 1977, p. 140–141, pl. 2, figs. 14, 15).

Description.—Carapace medium to large, suboblong to subrhomboidal in lateral view. Maximum length near mid-height, and maximum height at one-fourth of length near anterior cardinal angle. LV larger than RV and slightly overlapping RV along all free margins. Anterior margin broadly rounded and infracurvate to slightly equicurvate; anterior cardinal angle remarkable (145° to 150° in male; 130° to 150° in female). Posterior margin in male broadly rounded but somewhat narrower than anterior one, equicurvate to slightly supracurvate; supracurvate in female. Hinge margin straight and slightly or deeply declined toward the posterior

end. Dorsolateral sulcus weakly incised behind anterior cardinal angle area. Ventral margin straight to slightly convex in females and moderately to strongly concave near mid-length in males. Surface covered by reticulation-like punctuation, except on the surface of nodes and in the central area of both valves where coincident with the muscle-scar field area in internal view. The pattern of puncta consists of round (globular to elongate) to polygonal shape. Two nodes: a round node in the ventrolateral area near the posteroventral region and more visible in the female; a ridge-like node in the dorsolateral area near the posterior cardinal angle, with broadly inflated (male) to somewhat convex (female) shape.

Internal characters.—Adductor muscle scars (AMS) consisting of a vertical row of four closely placed elongate scars, two scars (frontal and mandibular scars) situated just in front of AMS (Fig. 6.5). Hinge lophodont. Calcified inner lamella moderately broad; selvage and fused zone well visible along the anterolateral margin.

Sexual dimorphism.—Sexual dimorphism presents in A-1 instars and adults. Males have larger and more elongated carapaces/valves. The ridge-like node is more visible in males and somewhat overreaches the dorsal outline. Female is smaller than male, with broader anterior margin and the more visible ventrolateral node, the ridge-like node not or slightly overreaching the dorsal outline.

Ontogenetic variation.—The adult specimens are more than 0.60 mm long, but males are much larger (0.68 to 0.71 mm long) than females (0.60 to 0.62 mm long). A-1 instar (about 0.58 mm long) shares similar carapace features with the adult. The carapace shape of A-2 and A-3 instars (0.40 to 0.52 mm long) is nearly subrhomboidal to subtriangular due to narrow posterior margin and deeply declined hinge margin. Ridge-like nodes are less developed or absent in A-2 and A-3 instars. The separation of instars is based on size and general shape (Choi et al., 2020).

Material.—Nineteen valves and one broken carapace from samples 4UK070311-3, 4UK070311-2, 4UK070311-1, and 4UK070411-2 of the Tsagaan Tsuurga Section.

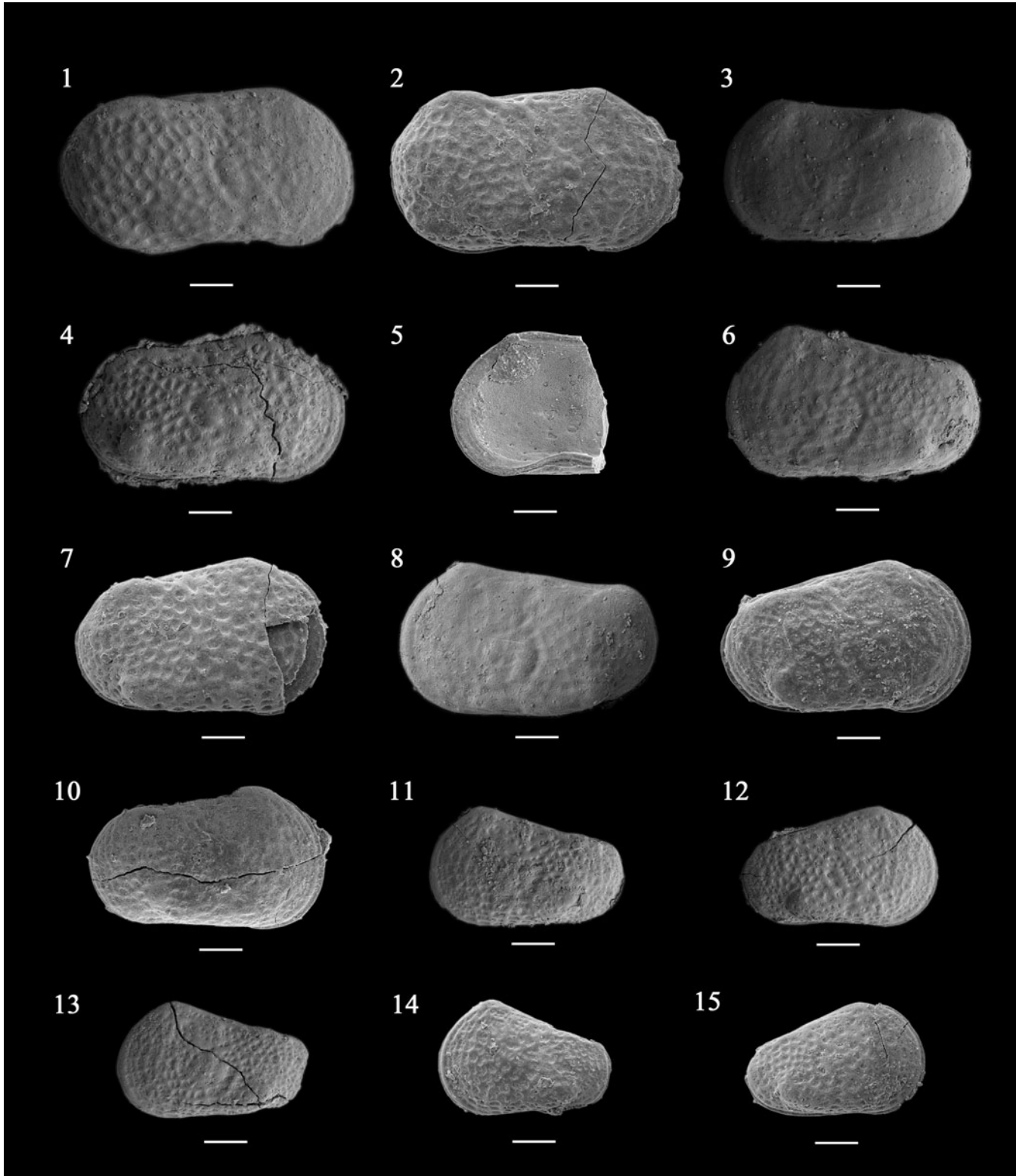


Figure 6. *Vlakomia ulanense* (Neustrueva, 1977). (1) Lateral view of adult male right valve, NIGP 180038, sample 4UK070311-1. (2) Lateral view of adult male right valve, NIGP 180039, sample 4UK070311-2. (3) Lateral view of A-1 instar male left valve, NIGP 180040, sample 4UK070311-1. (4) Lateral view of adult female right valve, NIGP 180041, sample 4UK070311-3. (5) Internal view of female adult right valve (part), NIGP 180042, sample 4UK070311-2. (6) Lateral view of adult female left valve, NIGP 180043, sample 4UK070411-2. (7) Lateral view of adult female right valve with anterolateral part missing, NIGP 180044, sample 4UK070311-2. (8) Lateral view of adult female left valve, NIGP 180045, sample 4UK070411-2. (9) Lateral view of adult female right valve, NIGP 180046, sample 4UK070411-2. (10) Lateral view of A-1 instar female left valve, NIGP 180047, sample 4UK070411-2. (11) Lateral view of A-2 instar left valve, NIGP 180048, sample 4UK070311-2. (12) Lateral view of A-2 instar right valve, NIGP 180049, sample 4UK070311-2. (13) Lateral view of A-2 instar left valve, NIGP 180050 (broken), sample 4UK070311-2. (14) Lateral view of A-3 instar left valve, NIGP 180051, sample 4UK070311-2. (15) Lateral view of A-3 instar right valve, NIGP 180052, sample 4UK070411-2. Scale bars = 100 μ m.

Dimensions.—Adult L: 0.60–0.71 mm; H: 0.37–0.41 mm; W: 0.31 mm. Juvenile L: 0.40–0.58 mm; H: 0.23–0.34 mm; W: Unknown.

Remarks.—Although Neustrueva et al. (2005) transferred the species *Theriosynoecum ulanense* of Neustrueva (1977) to the genus *Tsetsenia* without any explanation, they (Neustrueva et al., 2005) reillustrated type material of this species with much better-quality SEM photographs (wrongly described as *Tsetsenia “ulanensis”* therein). Our specimens fit all diagnostic features of “*Tsetsenia ulanensis*” (= *Theriosynoecum ulanense*). Meanwhile, *Tsetsenia* is considered a junior synonym of *Vlakomia* in this study (see the preceding discussion). Thus, we identify our specimens as *Vlakomia ulanense*.

Vlakomia ulanense is similar to *V. jilinensis* from the Tongfosi Formation of the Yanji Basin of northeast China (Gou, 1983; Choi et al., 2020), but the former has a different node distribution pattern and lesser degree of ornamentation development. The general pattern of nodes, spines, and punctation is a useful characteristic in specific levels, although some ontogenetic, sexual, and ecophenotypic variability can be found. Despite some details in the shape, *V. jilinensis* is relatively similar to *V. ulanense*, by trend younger than the latter, and thus considered to be closely related and possibly deriving from the Mongolian lineage designated as *V. ulanense*. *Vlakomia ustinovskii* differs from *V. ulanense* and *V. jilinensis* in having developed large “horn-like” anterocentral nodes and having a visible anterior cardinal angle in both sexes. *V. jilinensis* and *V. ustinovskii* both derive from the Albian Tongfosi Formation; however, the horizon from which *V. jilinensis* came is lower than that from which *V. ustinovskii* came. Thus, we propose a possible phylogenetic lineage: *V. ulanense*–*V. jilinensis*–*V. ustinovskii*. This lineage is endemic to East Asia to date.

Discussion

Ostracod biostratigraphy and paleobiogeography.—The “Purbeck–Wealden type” ostracod faunas from Mongolia had been reviewed by Nikolaeva and Neustrueva (1999), Khand et al. (2000), and Neustrueva et al. (2005). Khand et al. (2000) proposed a “*Cypridea fasciculata* Zone” for the Shinekhudag Formation in the Eastern Gobi and Choir–Nyalga basins, which includes ostracod species of the genera *Cypridea*, *Lycocypris*, *Rhinocypris*, and *Darwinula*. In addition, Neustrueva et al. (2005) established two assemblages for the lower and upper parts of the Shinekhudag Formation in southeast Mongolia: the *Cypridea unicostata*–*Cypridea figurata* assemblage and the *Janinella tsaganensis*–*Cypridea selenginensis*–*Langtonia tumefacta* (= *Cypridea tumefacta* in this study) assemblage, respectively. On the basis of biostratigraphic correlation, Khand et al. (2000) and Neustrueva et al. (2005) concluded that the age of the Shinekhudag Formation in southeastern and eastern Mongolia is Hauterivian to Barremian. However, in contrast to the well-established ostracod biostratigraphic framework in southeastern, eastern, and central Mongolia, there is limited research on the ostracod taxonomy in the Gobi–Altai area thus far, limiting its potential for biostratigraphic application.

Here we identify nine species of six genera from two sections of the Shinekhudag Formation in the Gobi–Altai region. The ostracod fauna from the Tsagaan Tsuvarga Section consists of three species of three genera. Among them, *Yumenia oriformis* was reported from the Lower Huihuipu Series (Hou, 1958), which is equal to the Xiagou Formation of China and known as early Aptian in age (Xi et al., 2019; Li et al., 2020). *Scabriculocypris subscalara* was found in the Barremian Nantun Formation of the Hailaer Basin, China (Ye et al., 2003; Xi et al., 2019). *Vlakomia ulanense* was found in the Andaikhudag Formation in the Altai region (Neustrueva et al., 2005) (which stratigraphically equals the Shinekhudag Formation; see Khand et al., 2000). In the Oshih Hollow East Section, six species of three genera are identified. Among them, *Cypridea ihsienensis* was reported from the Aptian–Albian Fuxin Formation (Hou, 1958; Wang et al., 2015). *Cypridea unicostata* is widely distributed in Hauterivian to Albian strata in China and Mongolia (Sinita, 1993; Neustrueva et al., 2005; Wang et al., 2015). *Cypridea verrucata* is distributed in the Barremian to Aptian strata of Mongolia (Neustrueva, 1974; Neustrueva et al., 2005; this study). Species of *Candona* and *Trapezoidella* are commonly reported from the Lower Cretaceous Strata of East Asia (Hou et al., 2002; Neustrueva et al., 2005; Wang et al., 2015, 2016; Choi et al., 2017, 2020, 2021). Consequently, we assign a Barremian–Aptian age for the Shinekhudag Formation in Gobi–Altai area (Fig. 7).

The high ratio of nonendemic ostracod species from the Shinekhudag Formation provides the evidence of the microfau- nal exchanges and paleobiogeographic relationships between the Cretaceous basins of East Asian regions. Three species (*Cypridea ihsienensis*, *C. unicostata*, and *Scabriculocypris subscalara*) have been reported from the Lower Cretaceous deposits in northeast China, such as the Liaoning area and the Hailaer Basin (Hou, 1958; Ye et al., 2003). *Yumenia oriformis* has been recorded from northwest China (Hou, 1958). *Cypridea tumefacta* is a member of the *C. laevigata/setina* group, and the representatives of this species group have been reported from the pre-Aptian strata (mostly Berriasian to Valanginian in Europe) of Eurasia (see species list in Schudack and Schudack, 2009). The post-Aptian members were reported from Europe (Portugal) and North Africa (Tunisia) (Cabral, 1998; Trabelsi et al., 2011). Thus, the members of this species group in Asia probably derived from immigrated representatives of the pre-Aptian European lineage, but many scenarios are possible. Therefore, it should be considered that origin and evolutionary trends in Asian species include *C. tumefacta*. Therefore, the ostracod fauna of the Shinekhudag Formation records relatively frequent faunal exchanges between southwest Mongolia and northeast China during the Early Cretaceous. However, it seems that there are only a few, single faunal relationships with other regions (i.e., northwest China).

Paleoecology.—In Mongolia, the paleoecology of Early Cretaceous ostracod faunas including species of the Shinekhudag Formation has not been studied thus far. Therefore, we here present first insights into paleoenvironmental interpretations of the Early Cretaceous nonmarine ostracod fauna in Mongolia. The taphonomic analyses are very limited or impossible since all specimens in this study had to be picked

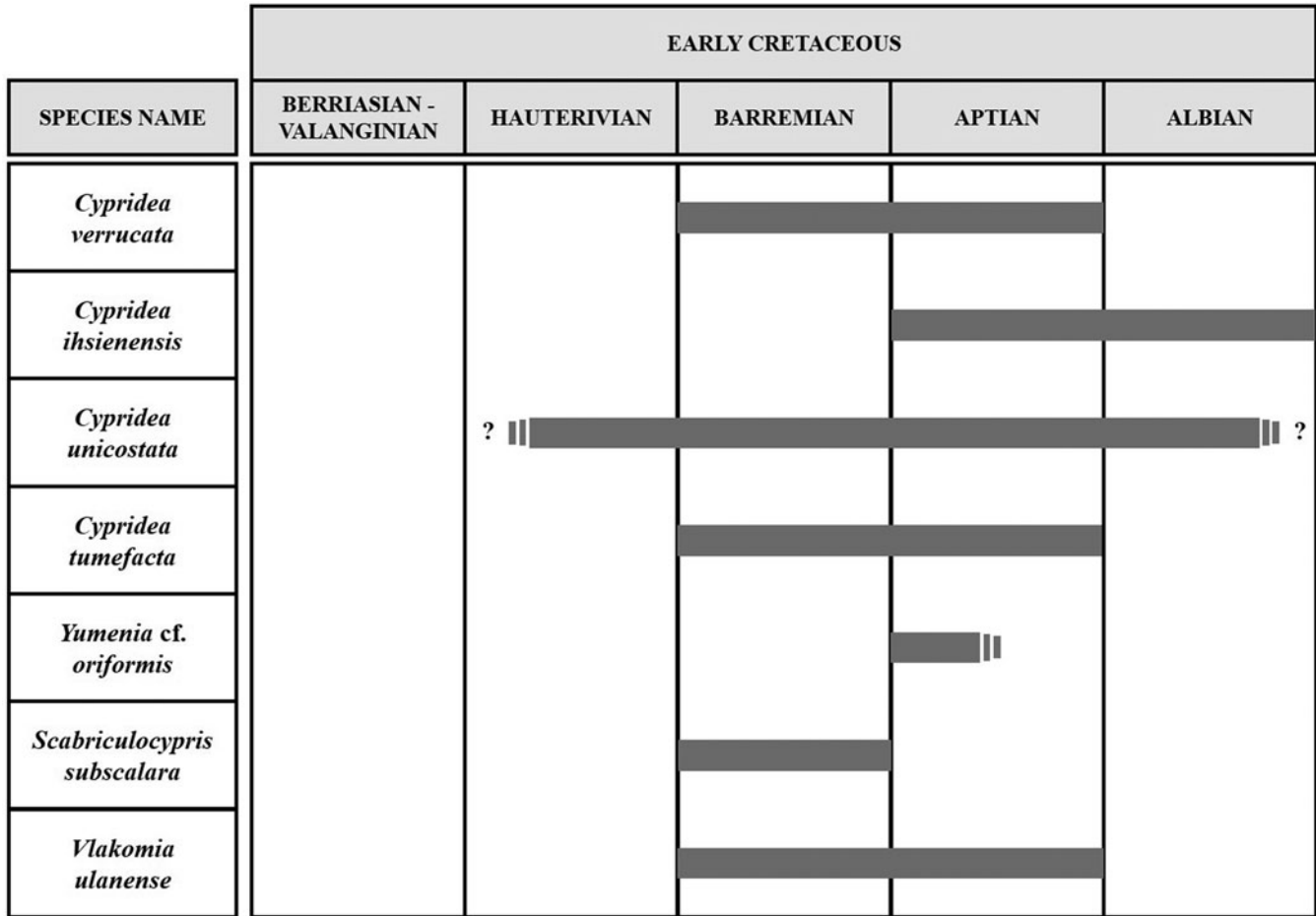


Figure 7. Stratigraphic ranges of the ostracod species in this study from the Shinekhudag Formation.

from the surfaces of the sedimentary rock samples (see “Materials and methods”). Because the studied sections (Tsagaan Tsuvarga and Oshih Hollow East) of the Shinekhudag Formation in this study are separated, the ostracod fauna can be divided into two assemblages, which show very different species composition and diversity. The first paleoenvironmental interpretations of each section are as follows.

Samples of the Tsagaan Tsuvarga Section are characterized by low diversity (three species) and the dominance of *Vlakomia ulanense*. Despite the small quantity of ostracod specimens available, the assemblage with various ontogenetic stages (A-3 to adult) of *Vlakomia ulanense* in the samples (4UK070311-3, 4UK070311-2, 4UK070311-1, and 4UK070411-2) is considered an in situ assemblage. The lack of *V. ulanense* in the sample 4UK070411-1 may indicate that the paleoenvironment of that time interval was unfavorable for this taxon, but the specific reason is uncertain and needs to be investigated (or *Vlakomia* specimens are just not discovered).

The genus *Vlakomia* is considered to have a wide range of paleoecological tolerance (Choi et al., 2020, p. 21) because their extant and fossil relatives of the subfamily Limnocytherinae of the family Limnocytheridae occur in both ephemeral and permanent water bodies, including fresh to saline water environments, and they are able to lay desiccation-resistant eggs (Horne and Martens, 1998; Meisch, 2000; Karanovic, 2012;

Santos Filho et al., 2021). In recent studies (Wang and Choi, 2019; Choi et al., 2020), representatives of the genus *Vlakomia* are interpreted to have tolerated high salinities in nonmarine water bodies (e.g., saline lakes) and in nonmarine to transitional environments with the influence of seawater. The two species of *Yumenia* and *Scabriculumypris* in the Tsagaan Tsuvarga Section are assigned to the superfamily Cypridoidea (family Alloicypridoidea). Almost all cypridoidean taxa (both living and fossil representatives) also certainly possess(-ed) desiccation-resistant eggs, which enable them to dwell in ephemeral water bodies and survive desiccation during dry periods (Horne and Martens, 1998; Horne, 2002; Sames, 2011b; Sames and Horne, 2012). Thus, the absence of permanent water-body indicators, such as the representatives of the subfamily Timiriaseviinae (family Limnocytheridae, superfamily Cytheroidea) and the superfamily Darwinuloidea (Horne and Martens, 1998; Horne, 2002; Sames, 2011a, b), could be explained by an increased aridity in the study area (Horne, 2002). In addition, the low diversity and high salinity tolerance of *Vlakomia* species may indicate an increased salinity. This kind of setting is comparable to the nonmarine saline to transitional settings with seawater influence of the Albian Tongfosi Formation of northeast China, where species of *Vlakomia* and *Scabriculumypris* dominate the ostracod assemblages (Wang and Choi, 2019; Choi et al., 2020). The saline conditions in the Tsagaan Tsuvarga area of the

Shinekhudag Formation are supported by the presence of carbonates, gypsum, and microbial–caddisfly bioherms in a shallow-littoral setting and have been interpreted as relatively alkaline, saline to hypersaline, and rich in Ca/Mg and bicarbonate ions in a paleolake (Adiya et al., 2017). Because the areas of Central Asia, including southwest Mongolia, were far from the sea during the Cretaceous, nonmarine ostracod taxa and other proxies in the Tsagaan Tsuvarga Section are indicative of the existence of an athalassic (salinity of inland waters not deriving from seawater) saline lake setting (see Horne, 2002). Therefore, we confirm that the saline lake conditions (possibly hypersaline, see Adiya et al., 2017, p. 27) under arid climate have persisted during the deposition periods of the sampling layers in the Tsagaan Tsuvarga Section.

The samples (4TM062411-1, 5MT062111-9, 5MT062111-3, and 5KC062111-2) of the Oshih Hollow East Section (Fig. 2) yielded a cypridoidean ostracod fauna of relatively high diversity (six species), including the genera *Cypridea*, *Candona*, and *Trapezoidella*. A common feature of these samples is lack of younger juveniles (under A-1 instar), which may suggest that smaller juveniles have been removed from the assemblage by postmortem current and deposited in much deeper areas of water bodies (Whatley, 1983, 1988; Boomer et al., 2003; Nye et al., 2008). However, due to the small number of ostracod specimens in the samples, the younger juveniles may have been overlooked. Thus, it is very difficult to interpret the taphonomic processes of the Oshih Hollow East Section.

The species composition of this section is characterized by only representatives of superfamily Cypridoidea. Especially, four species in this study belong to the genus *Cypridea* (extinct family Cypridoidea). The representatives of the genus *Cypridea* are the most common Late Mesozoic ostracod faunal elements of nonmarine settings worldwide (except Antarctica and Australia; Horne and Martens, 1998; Sames, 2011b). As many other cypridoideans, the genus *Cypridea* is adapted to both temporary and permanent water bodies due to their desiccation-resistant eggs and reproductive strategies (sexual or mixed reproduction; see Horne and Martens, 1998; Sames, 2011b), and therefore, the dominance of *Cypridea* species in deposits with a lack of Timiriaseviinae and darwinuloidean ostracods has been considered indicative of ephemeral water bodies or unstable lake environments (see Horne, 2002; Wang et al., 2013; Trabelsi et al., 2015; Choi et al., 2020, 2021; Santos Filho et al., 2021, and references therein). In addition, some of them possibly inhabited saline lakes, but mainly lived in freshwater environments (Horne, 2002; Sames, 2011b). Extant representatives of *Candona* are living in various aquatic environments, such as lakes/ponds and springs (Löffler and Danielopol, 1978; Carbonel et al., 1988; Meisch, 2000; Karanovic, 2012). *Trapezoidella* also belongs to superfamily Cypridoidea, and the representatives of the genus have been discovered from the typical Cretaceous nonmarine deposits in East Asia (e.g., Lübmova, 1956; Khand et al., 2007). Consequently, the dominance of cypridoideans and the lack of cytheroidean/darwinuloidean ostracods of the Oshih Hollow East Section are indicative of unstable and ephemeral water bodies (e.g., ephemeral lakes, ponds, and seasonal pools).

In summary, two studied sections of the Shinekhudag Formation show very different ostracod diversity and

paleoecological information; we interpret that the ostracod-bearing samples of the Tsagaan Tsuvarga Section have been deposited in a shallow-littoral zone of an athalassic saline lake and its ephemeral marginal areas, which might be influenced by chemical effects and fluctuation of paleolake under arid climate. The paleoenvironment of the Oshih Hollow East Section is interpreted to represent ephemeral water bodies.

Conclusions

A total of nine species belonging to six genera of an ostracod fauna were recovered from the Lower Cretaceous lacustrine sediments from two sections (Tsagaan Tsuvarga and Oshih Hollow East) of the Shinekhudag Formation, southwest Mongolia (Gobi–Altai area): *Cypridea verrucata*, *C. ihsienensis*, *C. unicostata*, *C. tumefacta*, *Yumenia* cf. *Y. oriformis*, *Scabriculocypris subscalara*, *Trapezoidella* sp., *Candona* sp., and *Vlakomia ulanense*.

This ostracod fauna suggests that the age of the Shinekhudag Formation is Barremian–Aptian, and there is evidence of active faunal exchange and migration between northeast China and the Gobi–Altai area of Mongolia, and potentially several other areas (e.g., northwest China). Among the taxa, *Vlakomia ulanense* is considered an ancestor group of the Far East group, such as species in the Tongfosi Formation (Albian), China.

Two different faunal compositions in the sections provide new information about paleoenvironment and paleoecology of ostracod fauna of the Shinekhudag Formation. In particular, the low diversity and paleoecological tolerance of *Vlakomia* in the Tsagaan Tsuvarga Section are interpreted to indicate a shallow-littoral zone in the athalassic saline lake (possibly hypersaline conditions) under arid climate. By contrast, the dominance of cypridoideans (especially the genus *Cypridea*) in the Oshih Hollow East Section indicates ephemeral water bodies. The absence of the subfamily Timiriaseviinae (family Limnocytheridae, superfamily Cytheroidea) and superfamily Darwinuloidea is also indicative of an arid climate in the Tsagaan Tsuvarga and Oshih Hollow East areas of the Shinekhudag Formation.

Our results suggest that the application of ostracod fauna in the Shinekhudag Formation can be a very useful tool for an interpretation of the Lower Cretaceous deposits of southwest Mongolia. Therefore, this investigation provides a new insight and better understanding for the biostratigraphy, paleobiogeography, paleoenvironment, and resource exploration in the Gobi–Altai area of Mongolia.

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Declaration of competing interests

The authors declare that they have no conflicts of interest.

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