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Revision of *Cypridea* (non-marine Ostracoda) from the Early Cretaceous Yixian Formation of the Beipiao–Yixian Basin in western Liaoning, northeast China

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ABSTRACT

The ostracod genus *Cypridea* Bosquet, which ranges in age from Kimmeridgian to Lower Eocene, frequently occurs abundantly in the Jianshangou and Jinggangshan beds of the Yixian Formation in western Liaoning, northeast China. However, the diversity of species has been considerably overestimated for many years, and this has led to a series of problems concerning taxonomic subdivision and stratigraphic correlation. Based on a large quantity of fossil material and more detailed descriptions of the morphological features, all of the published species of *Cypridea* from the Jianshangou and Jinggangshan beds are revised in this paper. As a result, 14 species erected previously are merged into three taxa: *Cypridea liaoningensis*, *C. jinggangshanensis* and *C. deplecta*.

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1. Introduction

Ostracods, crustacean arthropods having a bivalved carapace that can totally enclose the body and appendages, have an excellent fossil record extending back to the Early Ordovician by virtue of their small size and calcite shells (valves) (e.g., Horne, 2004; Williams et al., 2008). They occur in most aquatic environments from small, temporary ponds through to deep oceans.

Cypridea Bosquet, 1852 is a non-marine ostracod genus of the superfamily Cypridoidea, and the extinct family Cyprideidae, which has a stratigraphic range of Kimmeridgian–Early Eocene (Horne and Colin, 2005; Sames, 2011a). The modern diversity of the superfamily and the “Mesozoic explosion” of non-marine cypridoideans are mainly attributed to a global diversification of family Cyprideidae, namely the genus *Cypridea*, early Cretaceous representatives of which are the subject of this paper. The classification of the genus has been discussed in detail recently by Horne and Colin (2005) and Sames (2011a), both of whom listed the multitude of taxa known from literature and discussed their various attributions.

Representatives of *Cypridea* are common faunal elements of Cretaceous deposits worldwide apart from in Australia and Antarctica (Sames, 2011a). The specimens encountered in the Yixian Formation of the Beipiao–Yixian Basin are the earliest records of this genus in China (Cao, 1999; Guan et al., 2001). They have been studied

since the 1980s (Zhang, 1985; Zhang et al., 1985; Cao, 1999; Wang et al., 2004), but their diversity has been greatly exaggerated by previous authors, because the species and subspecies described have been based on an inadequate number of specimens. As a result, the taxonomic significance of certain carapace features was not apparent, and sexual dimorphism, ontogeny and ecophenotypic variation within populations were not taken into account. The present paper focuses on taxonomy and is based on a large number of fossils and descriptions of taxonomic features that are more precise than those presented previously. All of the published species of *Cypridea* from the Yixian Formation of the Beipiao–Yixian Basin are revised. The descriptions and application of morphologic terms follow Sames (2011a, b).

2. Geological setting

The Yixian Formation is the lowest formation of the Jehol Group (Sha, 2007). It consists of laminated to thin-bedded siliciclastic sediments, mainly sandstone, sandy limestone and shale, intercalated with extrusive basalts and tuffs and cross-cut by occasional dykes and sills (Sha, 2007; Jiang and Sha, 2007; Jiang et al., 2011). It rests unconformably on either the Tuchengzi Formation or the Lanqi Formation in the Beipiao–Yixian Basin and is conformably overlain by the Jiufotang Formation (Fig. 1). According to non-marine–marine correlation and radiometric dating, the Yixian Formation is middle–late Early Cretaceous in age (Hauterivian–Aptian, mainly Barremian) (Smith et al., 1995; Zhu et al., 2002, 2003, 2007; Sha et al., 2006, 2007; Sha, 2007; Yang et al., 2007; Chang et al., 2009).

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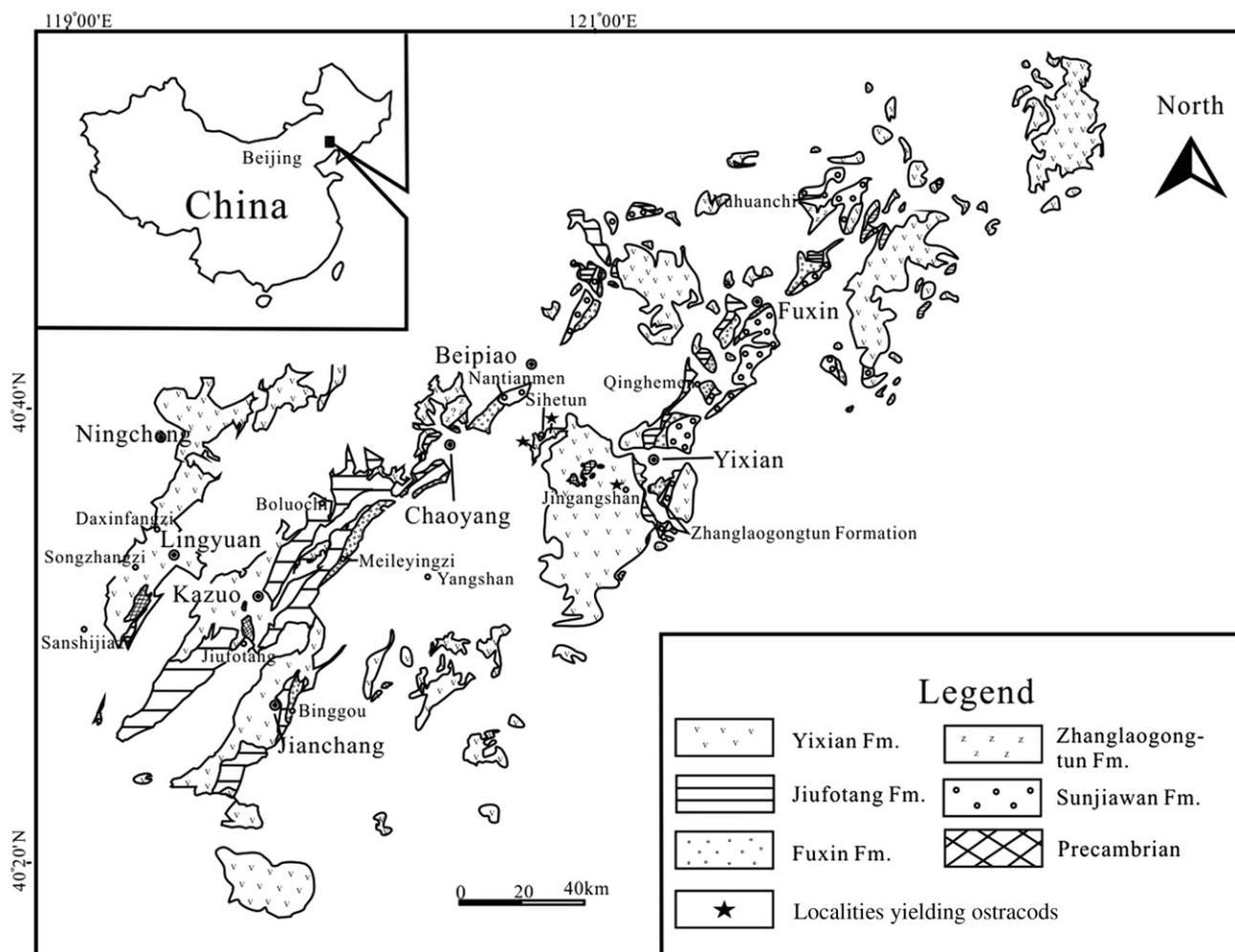


Fig. 1. Distribution of the Cretaceous formations and fossil localities in western Liaoning (after Jiang and Sha, 2007, fig. 1).

3. Material

The samples studied were collected from the Jianshangou Bed (the Lower Member of the Yixian Formation) and the Jingangshan Bed (the Upper Member of the Yixian Formation) during 2007–2009, in the sections near Sihetun (Libalanggou, Dabeigou), Beipiao County (GPS: N41°34'43.5", E120°36'44.5") and Jingangshan (Caocishan), Yixian County (GPS: N41°27'42.4", E121°09'12.8") (Fig. 1).

The specimens derive from mudstone and calcareous silt- and sandstones. The samples were immersed in warm water for 3–6 h, and washed through sieves (500, 250 and 125 μm). The material from the 500 μm fraction was inspected and well-preserved specimens were picked out for examination under a scanning electron microscope (SEM).

All the specimens described in this paper are topotypes and housed in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science (NIGPAS). Some species listed in the synonymies were not found in the Beipiao–Yixian Basin; we have, therefore, compared our material with the published descriptions and figures.

The size parameters used in this paper are as follows: very small, length 0.02–0.60 mm; small, length 0.60–1.00 mm; medium, length 1.00–1.50 mm; large, length 1.50–5.00 mm (Sames, 2011a). The following abbreviations are used: LV, left valve; RV, right valve; L, length; H, height; W, width.

4. Systematic paleontology

Class Ostracoda Latreille, 1802
 Order Podocopida Müller, 1894
 Suborder Cypridocopina Jones, 1901
 Superfamily Cypridoidea Baird, 1845
 Family Cypridae Martin, 1940
 Genus *Cypridea* Bosquet, 1852

Cypridea jingangshanensis Zhang, 1985, emend.
 Fig. 3A–J

- 1985 *Cypridea* (*Cypridea*) *jingangshanensis* Zhang, p. 24, pl. 3, figs. 4a–c, 5a–c.
- 1985 *Cypridea* (*Cypridea*) ex gr. *jingangshanensis* Zhang, p. 81, pl. 4, fig. 4.
- 1985 *Cypridea* (*Cypridea*) *zaocishanensis zaocishanensis* Zhang, pp. 24, 25, pl. 3, figs. 6a–c, 7, 8a, b.
- 1985 *Cypridea* (*Cypridea*) *zaocishanensis congenita* Zhang, p. 25, pl. 4, fig. 1a–c.
- 1985 *Cypridea* (*Cypridea*) *dorsobispina* Zhang, p. 30, pl. 7, figs. 1a–c, 2a–c.
- 1985 *Cypridea* (*Cypridea*) *placida* Zhang, pp. 25, 26, pl. 4, fig. 2a–c.
- 1985 *Cypridea* (*Cypridea*) *trispinosa* Zhang, pp. 30, 31, pl. 7, figs. 3a–d, 4a–c, 5.

2002 *Cypridea jingangshanensis* Zhang; Hou et al., pp. 424, 425, pl. 163, figs. 1–3.

2002 *Cypridea zaocishanensis* Zhang; Hou et al., p. 425, pl. 163, figs. 4–6.

2002 *Cypridea trispinosa* Zhang; Hou et al., p. 426, pl. 163, figs. 14–16.

2002 *Cypridea placida* Zhang; Hou et al., pp. 427, 428, pl. 164, figs. 6–8.

Material. About 30 carapaces, moderately to well-preserved: L, 1.15–1.45 mm; H, 0.73–0.91 mm; W, 0.50–0.66 mm.

Emended diagnosis. Carapace elongated trapezoid to subquadrate in lateral outline; rostrum weakly developed; alveolar furrow barely noticeable to absent; alveolar notch absent. Whole carapace surface covered with reticulum-like punctation, often bearing scattered minor tubercles, and with two spines on each valve at cardinal angles.

Description. Medium sized carapace, elongate-trapezoid to subquadrate in lateral view. Maximum length at mid-height, maximum height at anterior cardinal angle (one-quarter of length); maximum width at three-fifths of length. LV overlaps RV along all except the dorsal margin; anterior and posterior overlap strongly marked. Anterior margin broad and slightly obliquely rounded, more narrowly rounded towards venter with very delicate antero-ventral rostrum; anterior cardinal angle well-marked, 140–145°. Posterior margin wide and symmetrically rounded, posterior cardinal angle rounded, 140–150°. Dorsal margin straight and gently inclined towards the posterior end. Ventral margin straight to somewhat concave. Alveolar furrow barely noticeable to absent; alveolar notch absent. Carapace punctate to finely reticulate, bearing scattered minor tubercles and usually with one pair of alternate lateral spines at each cardinal angle.

Discussion. *Cypridea* (*C.*) *placida*, *C.* (*C.*) *jingangshanensis*, *C.* (*C.*) *dorsobispina*, *C.* (*C.*) *zaocishanensis*, and *C.* (*C.*) *trispinosa* were all described by Zhang (1985). *Cypridea* (*C.*) *placida*, *C.* (*C.*) *jingangshanensis* and *C.* (*C.*) *zaocishanensis* are from the upper part of the Yixian Formation, whereas *C.* (*C.*) *dorsobispina* and *C.* (*C.*) *trispinosa* are from the lower part of the Jiufotang Formation. All five species have similar lateral outlines (see Fig. 2D–I), a weakly developed rostrum, a barely noticeable alveolar furrow, and a carapace covered with puncta. Hardly any differences in form of the tubercles, node-like tubercles and spines were observed among these species.

Cypridea (*C.*) *placida* Zhang was established on the basis of only one broken specimen with the dorsal part missing. Zhang (1985) regarded the absence of the four spines to be a taxonomically significant feature at species level. Sames (2011a, b) however, considered the presence or absence of spines in *Cypridea* to be generally of limited taxonomic significance. Hence, *C.* (*C.*) *placida* is considered to be a synonym of *C. jingangshanensis* herein.

The descriptions and figures of specimens of *C.* (*C.*) *dorsobispina* and *C.* (*C.*) *zaocishanensis* (Zhang, 1985) fit the diagnosis very well, except for the degree of development of scattered tubercles. Apart from its more strongly developed spines and tubercles, *C.* (*C.*) *trispinosa* Zhang is otherwise very similar to *C. jingangshanensis*. According to Sames (2011a, b), the presence or absence of local ornament in *Cypridea* such as tubercles, node-like tubercles or spines, is generally of little taxonomic significance and might be merely ecophenotypic or ontogenetic features. Furthermore, all of the specimens of these three species are from approximately the same strata in a single basin. Thus, *C.* (*C.*) *dorsobispina* and *C.* (*C.*)

zaocishanensis (Zhang, 1985) are merged with *C. jingangshanensis*, and *C.* (*C.*) *trispinosa* is considered to be a strongly ornamented ecophenotype of this species. All of the taxa discussed above are, therefore, considered to represent intraspecific variants of *C. jingangshanensis*.

Cypridea depecta Zhang, 1985, emend.

Figs. 3K–R, 4A

1985 *Cypridea* (*Cypridea*) *depecta* Zhang, p. 26, pl. 4, fig. 3a–c.

1985 *Cypridea* (*Cypridea*) *veridica arguata* Zhang, pp. 27, 28, pl. 4, figs. 8a–c, 9a–c.

1985 *Cypridea* (*Cypridea*) *veridica veridica* Zhang, p. 28, pl. 5, figs. 1a–c, 2a–c, 3–6.

1985 *Cypridea* (*Cypridea*) *veridica arrecta* Zhang, pp. 28, 29, pl. 5, fig. 7a–c.

1985 *Cypridea* (*Cypridea*) *yumenensis* Zhang, pl. 7, figs. 6a–c, 7a–c.

?1985 *Cypridea* (*Cypridea*) *xiaogushanensis* Zhang, pl. 9, fig. 7a–c.

2002 *Cypridea arguata* Zhang; Hou et al., pp. 448, 449, pl. 165, figs. 15–17.

2002 *Cypridea arrecta* Zhang; Hou et al., p. 448, pl. 165, figs. 12–14.

2002 *Cypridea veridica* Zhang; Hou et al., p. 448, pl. 165, figs. 18–20.

Material. More than 100 carapaces, moderately to well-preserved: L, 1.05–1.25 mm; H, 0.65–0.75 mm; W, 0.53–0.62 mm.

Emended diagnosis. Carapace elongated subtriangular in lateral view; antero-ventral rostrum well-marked; alveolar furrow shallow but distinct and reaching up to one-fifth of height; alveolar notch very weak to almost absent; cyathus absent; surface finely punctate.

Description. Medium sized carapace elongated subtriangular in lateral view; maximum length at mid-height, maximum height at anterior cardinal angle (one-third of length), maximum width at one-half of length. LV overlaps RV along entire margin. Anterior margin broadly rounded; anterior cardinal angle rounded-obtuse, 135–145°. Posterior margin narrower than anterior margin; posterior cardinal angle strongly rounded, 145–155°. Dorsal margin convex and inclined towards the posterior end; hinge margin area strongly incised, forming a well-developed dorsal furrow. Ventral margin slightly convex in the LV but straight in the RV. Antero-ventral rostrum well-marked; alveolar furrow shallow but distinct and reaching up to one-fifth of height, somewhat less expressed in the RV; alveolar notch very weak to almost absent, cyathus absent. Carapace surface covered with puncta.

Discussion. The species *C.* (*C.*) *depecta* and *C.* (*C.*) *veridica* and the three subspecies of the latter, *C.* (*C.*) *veridica arguata*, *C.* (*C.*) *veridica veridica*, and *C.* (*C.*) *veridica arrecta* were all erected by Zhang (1985) from the upper part of the Yixian Formation in the Zaocishan area. The subspecies were subsequently elevated by Hou et al. (2002) to species level: *C. veridica*, *C. arguata* and *C. arrecta*.

C. arguata and *C. veridica* share exactly the same outline (see Fig. 2J, K), well-defined rostrum and alveolar furrow, and a punctate carapace; they differ only in size. However, size ranges of 1.21–1.45 mm can be easily accepted in populations of cypridoidean species (e.g., Baltanás et al., 2002; Nye et al., 2008). Nye et al. (2008) suggested that size differences of specimens of *Cypridea clavata* Anderson, 1939 may be an ontogenetic character. Baltanás et al. (2002) pointed out that size could be a fairly sound basis upon which to discriminate between genders. We think that

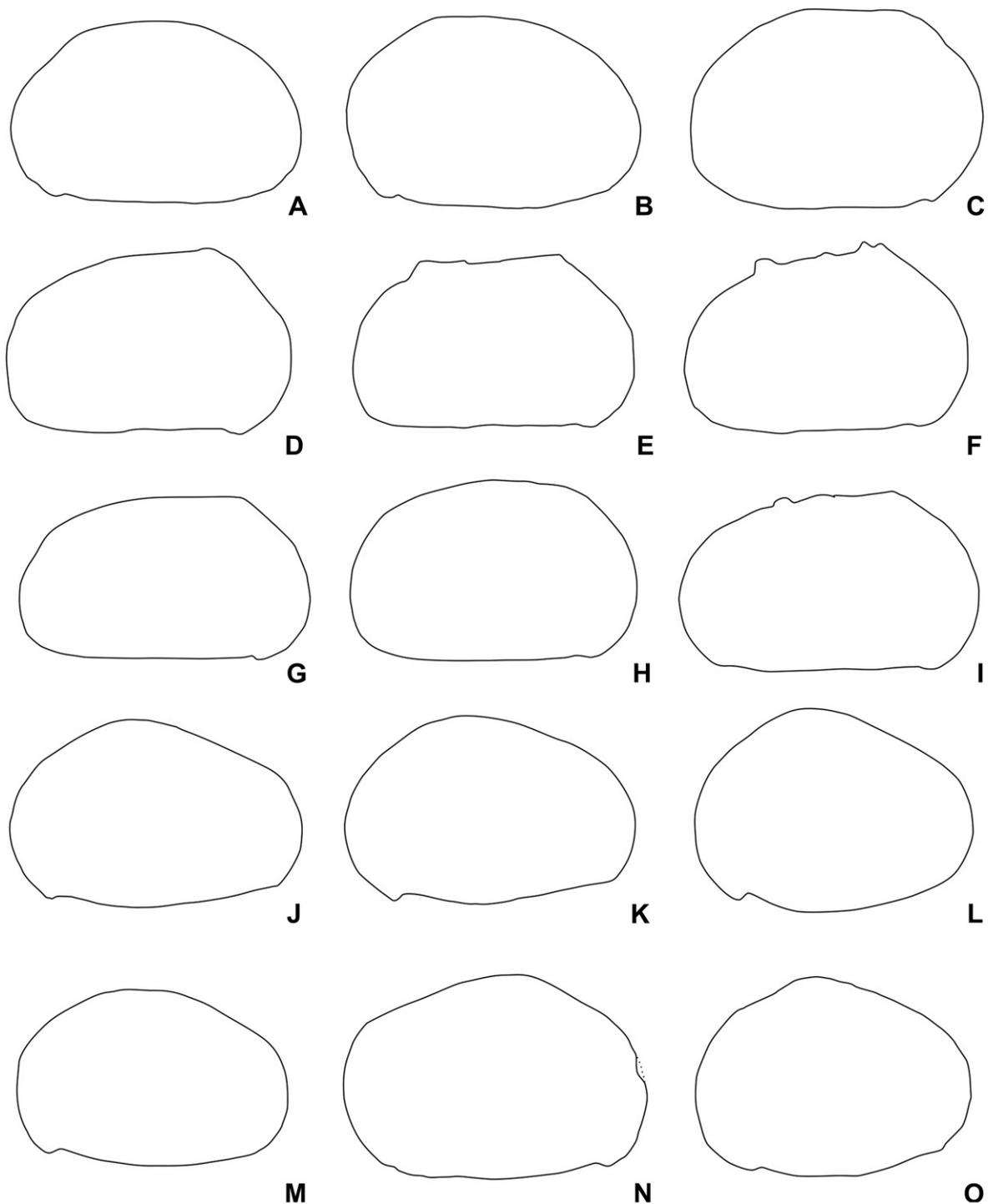


Fig. 2. Line drawings of the valve outlines of the various *Cypridea* taxa discussed. A, *C. liaoningensis* (Fig. 4D). B, *C. (C.) sisetunensis* (Cao, 1999, pl. 1, fig. 5). C, *C. (C.) miniflexcostata* (Gou et al., 1986, pl. 22, fig. 7). D, *C. (C.) jingangshanensis* (Zhang, 1985, pl. 3, fig. 4a). E, *C. (C.) caocishanensis caocishanensis* (Zhang, 1985, pl. 3, fig. 6a). F, *C. (C.) trispinosa* (Zhang, 1985, pl. 7, fig. 4a). G, *C. (C.) caocishanensis congenita* (Zhang, 1985, pl. 4, fig. 1a). H, *C. (C.) placida* (Zhang, 1985, pl. 4, fig. 2a). I, *C. (C.) dorsobispina* (Zhang, 1985, pl. 7, fig. 1a). J, *C. (C.) veridica veridica* (Zhang, 1985, pl. 5, fig. 1c). K, *C. (C.) veridica arquata* (Zhang, 1985, pl. 4, fig. 8c). L, *C. (C.) veridica arrecta* (Zhang, 1985, pl. 5, fig. 7c). M, *C. (C.) yunmenensis* (Zhang 1985, pl. 7, fig. 7c). N, *C. (C.) deplecta* (Zhang, 1985, pl. 4, fig. 3a). O, *C. (C.) xiaogushanensis* (Zhang, 1985, pl. 9, fig. 7c).

the differences in size between specimens of *C. arquata* and *C. veridica* are more likely to be related to sexual dimorphism, intraspecific variation, or an ontogenetic phenomenon rather than indicate different species. The specimens of *C. arquata* could well be juveniles or females of *C. deplecta*, because their dorsal margin is less inclined and their posterior margin more constricted than in

C. veridica. In this context, the specimens of *C. veridica* are either adult or male *C. deplecta*.

Cypridea veridica arrecta was described by Zhang (1985) on the basis of one specimen and is notable for the strongly convex ventral margin of the LV, which distinguishes it from the other subspecies. Our specimens sometimes show similar convexities at

the ventral margin of the LV (e.g., Fig. 3P), which can be easily explained as deformation resulting from compression. Thus, there is no reason to differentiate this subspecies from the others. All the subspecies of *C. (C.) veridica* share the same taxonomic features as *C. deplecta*, including their general outline (see Fig. 2J–L, N), overlap, development of rostrum and alveolus, and ornamentation.

Cypridea (C.) yumenensis from the lower part of the Jiufotang Formation in Yixian County was figured by Zhang (1985) but not described. Its outline (see Fig. 2M), obvious rostrum and dorsal furrow, and punctate carapace are quite similar to those of *C. deplecta*. It is, therefore considered to be a synonym of *C. deplecta*.

Zhang (1985) also illustrated but did not describe *C. (C.) xiaogushanensis* from the lower part of the Jiufotang Formation in Kazuo County. Although the figured specimens (Zhang, 1985, pl. 9, fig. 7a–c) are clearly similar to *C. deplecta* it is difficult to determine the ornamentation of carapace surface, because the preservation of the specimens is poor. This species is, therefore, only questionably placed in synonymy with *C. deplecta*.

Cypridea liaoningensis Zhang, 1985, emend.
Fig. 4B–I

- 1985 *Cypridea (Cypridea) liaoningensis* Zhang, p. 19, pl. 1, figs. 1–5.
1985 *Cypridea (Cypridea) liaoningensis liaoningensis* Zhang, pp. 19, 20, pl. 1, figs. 1a–d, 2a–c, 3.
1985 *Cypridea (Cypridea) liaoningensis biventricostata* Zhang, pp. 20, 21, pl. 1, figs. 4a–c, 5.
1986 *Cypridea (Cypridea) miniflexicostata* Wang et Gou, pp. 63, 64, pl. 22, figs. 3–8; pl. 24, figs. 11–14.
1999 *Cypridea (Cypridea) liaoningensis liaoningensis* Zhang; Cao, p. 134, pl. 2, figs. 8–13.
?1999 *Cypridea (Cypridea) sihetunensis* Cao, p. 134, pl. 1, figs. 1–10.
1999 *Cypridea (Cypridea)* sp. 1; Cao, p. 135, pl. 1, fig. 11.
1999 *Cypridea (Cypridea)* sp. 2; Cao, p. 135, pl. 1, figs. 12, 13.
2002 *Cypridea (Cypridea) liaoningensis* Zhang; Hou et al., pp. 426, 427, pl. 163, figs. 17–19.

Material. More than 40 carapaces and a few valves, moderately to well-preserved: L, 1.10–1.35 mm; H, 0.67–0.95 mm; W, 0.52–0.74 mm.

Emended diagnosis. LV larger than RV; lateral outline of carapace as presented by the LV rounded-subrectangular in lateral view, rostrum small, alveolus with a short alveolar furrow and a weak alveolar notch; surface covered with puncta and conical or node-like tubercles; distinct ventral ridges on both the LV and RV; distinct pair of lateral swellings/nodes below the anterior cardinal angle, more strongly developed in the LV.

Description. Medium sized carapace rounded-subrectangular in lateral view, elongate-ovoid in dorsal view. Maximum height close to anterior cardinal angle (one-quarter of length), maximum length at mid-height, maximum width at two-thirds of length.

Anterior margin broad, with a pair of lateral swellings/nodes immediately below the anterior cardinal angle, better developed in the larger LV; anterior cardinal angle well-marked, about 130°. Posterior margin wide and symmetrically rounded, posterior cardinal angle rounded, 140–145°. Dorsal margin straight to gently convex, hinge margin area strongly incised, forming a well-developed dorsal furrow with its broader and gentler left flank. Ventral margin straight with ventrolateral ridges on both valves. Rostrum short, with a slightly pointed tip and covered with small tubercles; alveolar furrow shallow and short; alveolar notch weak to almost absent. Carapace surface covered with small puncta. Conical or node-like tubercles mainly in antero- and posterolateral areas and margins.

Discussion. Zhang (1985) subdivided his new species *C. (C.) liaoningensis* into two subspecies: *C. (C.) liaoningensis liaoningensis* and *C. (C.) liaoningensis biventricostata*. *Cypridea (C.) miniflexicostata* Wang et Gou (in Gou et al., 1986) has almost the same outline as *C. (C.) liaoningensis* Zhang (see Fig. 2A, C); it also has distinct ventral ridges on both valves and a well-defined pair of lateral swellings immediately below the anterior cardinal angle. It is, therefore, considered to be as a synonym of *C. liaoningensis* (see Cao, 1999).

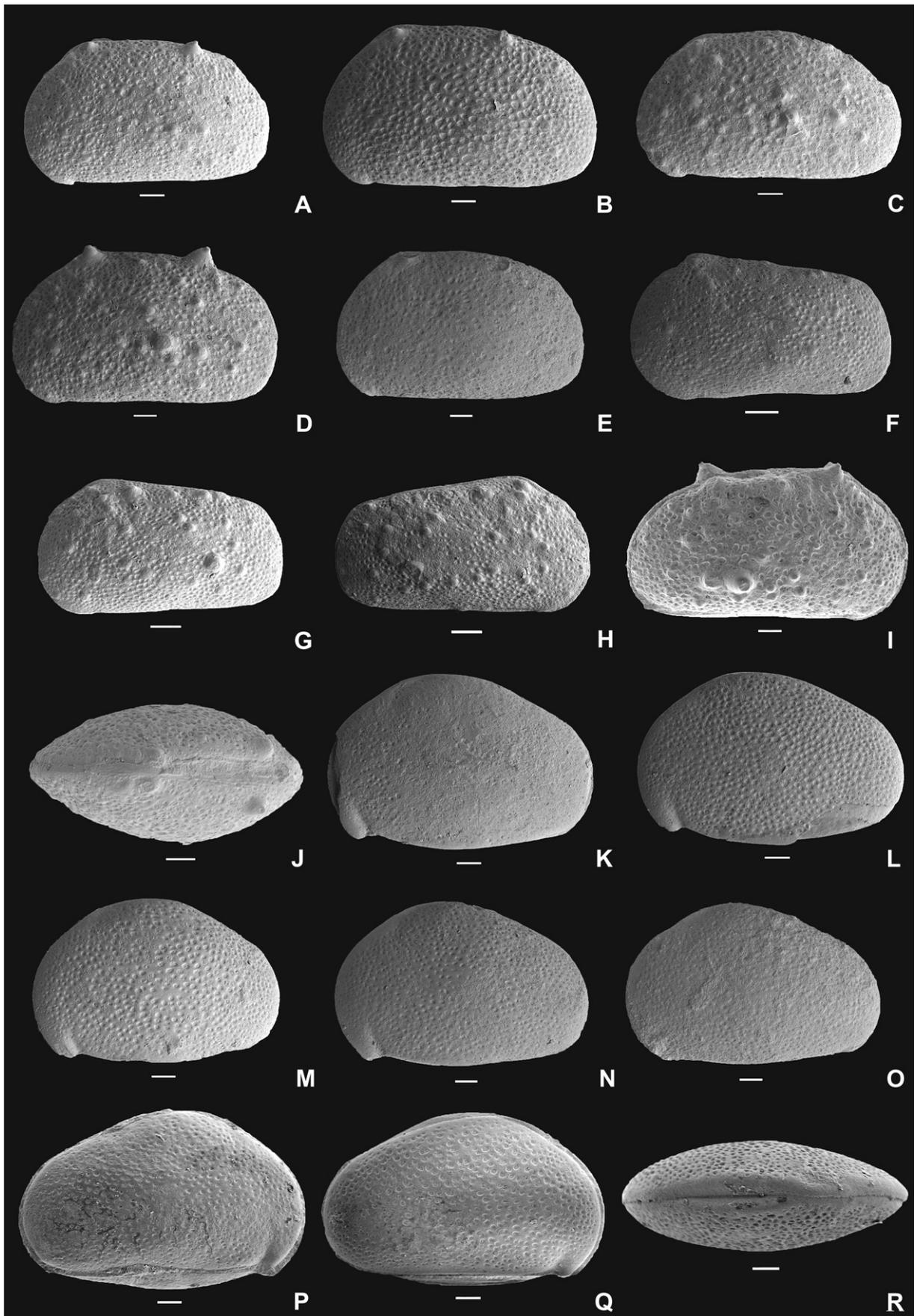
Cypridea (C.) sihetunensis Cao is very similar to *C. liaoningensis* in many respects, especially in its outline (see Fig. 2A, B) and weak alveolus, but it is smaller and has larger node-like tubercles and weaker ventral ridges. Taking into account the work of Sames (2011a, b) on the ornamentation of *Cypridea* and the finding of Horne and Smith (2004) that Recent *Potamocypris humilis* Sars 1924 shows strong tuberculation in juvenile stages but no ornamentation in the adult stage, we consider the specimens of *C. (C.) sihetunensis* described by Cao (1999) to be probable juvenile individuals of *C. (C.) liaoningensis*, because they are smaller than the latter, but have larger and more distinct node-like tubercles.

Morphologically, *Cypridea* spp. 1 and 2 figured by Cao (1999) strongly resemble *C. (C.) liaoningensis* Zhang. They are, therefore, also placed in synonymy with *C. (C.) liaoningensis* herein.

Zhang (1985) and Cao (1999) considered *C. liaoningensis* to be closely related to *C. granulosa* Anderson, 1985, which was described from the Purbeck beds (Purbeck Limestone Formation) of southern England. Cao (1999) regarded the Yixian Formation as corresponding to *C. granulosa* Subzone of the Purbeck succession. However, the illustrations of *C. granulosa* (Anderson, 1985, pl. 3, figs. 8, 12; Horne, 2009, pl. 3, fig. 4) show an obvious rostrum and cyathus, a deep and elongate alveolar furrow, and a declined dorsal margin: these characters indicate that it is clearly different from *C. liaoningensis*.

The swellings at each anterior cardinal angle of *Cypridea liaoningensis* may be eye tubercles. The function of lateral ventral ridges may possibly have allowed the animal to hold itself upside down at the water–air interface by surface tension, in common with the extant ostracod *Notodromas*. Sames (2011b) has also suggested that the ventral ridge of *Cypridea* (only in the large valve) may have been a stabilization structure or served to enable the animal to adhere to, and “ice-skate” upside down on, the lower water surface.

Fig. 3. A–J, *Cypridea jingangshanensis*. A–E, left views of carapaces, adults; NIGP 154999, 155000, 155001, 155002, 155008 respectively. F, G, left views of carapaces, juveniles; NIGP 155003, 154998. H, right view of carapace, juvenile; NIGP 154998. I, right view of carapace, adult; NIGP 155002. J, dorsal view of carapace, adult, anterior end to the left; NIGP 154999. K–R, *Cypridea deplecta*. K–O, left views of carapaces; NIGP 155004, 155006, 155007, 155005, 155014 respectively. P, Q, right views of carapace, anterior end to the right; NIGP 155005, 155007. R, dorsal view of carapace; NIGP 155006. Scale bars represent 100 μ m.



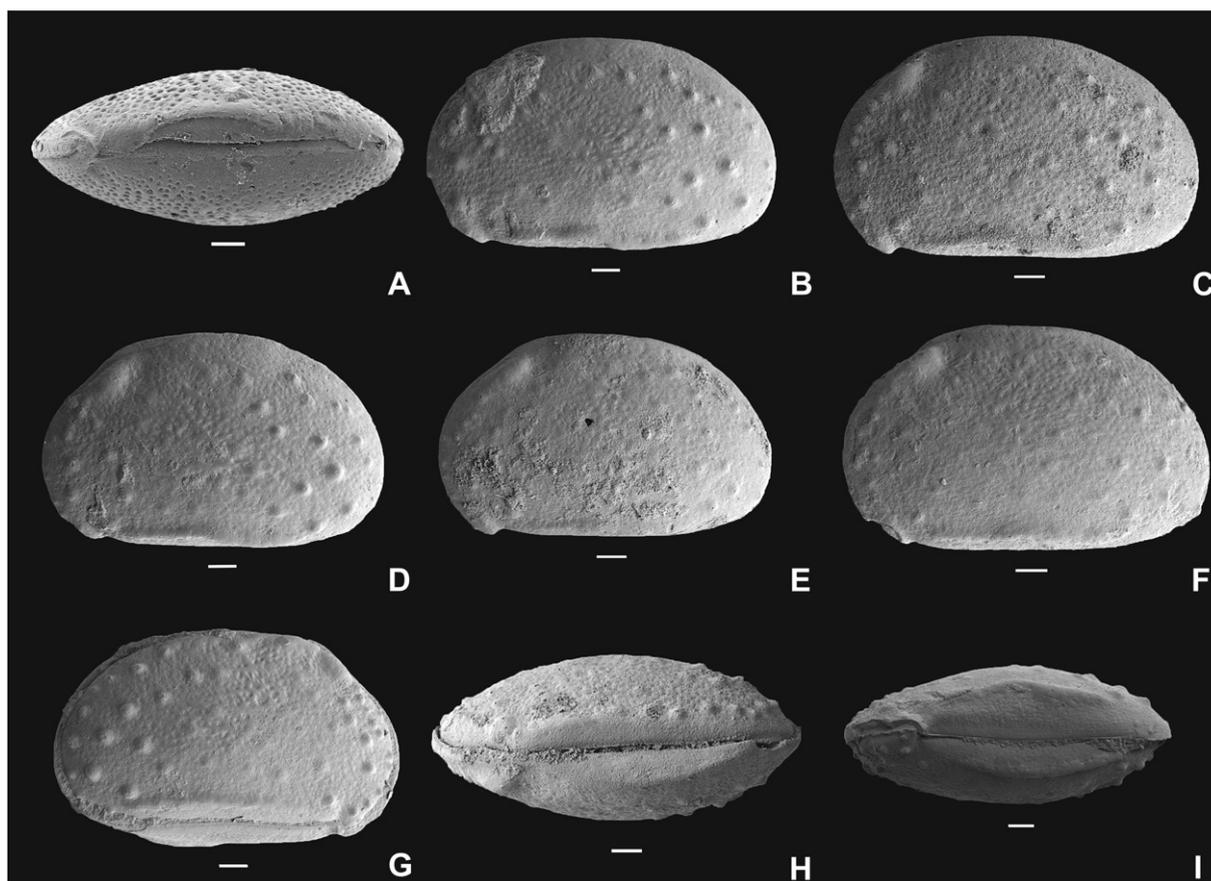


Fig. 4. A, *Cypridea depecta*, ventral view of carapace, anterior end to the left; NIGP 155007. B–I, *Cypridea liaoningensis*. B–F, left views of carapaces; NIGP 155009–155013 respectively. G, right view of carapace; NIGP 155011. H, dorsal view of carapace, anterior end to the left; NIGP 155010. I, ventral view of carapace, anterior end to the left; NIGP 155009. Scale bars represent 100 μm .

5. Discussion and conclusion

Cypridea has a worldwide distribution and is a good Late Jurassic–Cretaceous indicator (e.g., Horne, 2009; Sames, 2011a; Wang et al., 2012). However, the number of non-marine species seems to have been overestimated in the past, because in many cases, only minor morphological differences, possibly representing the normal variability of a species, were used to distinguish species or subspecies, resulting in further splitting without adequate differentiation. The *Cypridea* faunas in China, and Asia generally, certainly seem to be in need of detailed and thorough revision, and their distributions need to be considered in a supra-regional to global context (e.g., Sames and Horne, 2012). A considerable reduction in their apparent diversity (e.g., in China) would have significant implications for not only local and regional biostratigraphic analyses (e.g., in the Beipiao–Yixian and Kazuo–Jianchang basins) but also supra-regional and global correlations (e.g., Sames, 2010; Sames et al., 2010).

Cypridea has been widely used in stratigraphic correlation in China (e.g., Wang et al., 2012). However, the *Cypridea*-bearing Yixian Formation used to be regarded as Late Jurassic or Late Jurassic–earliest Cretaceous in age (e.g., Zhang, 1985; Cao, 1999; Wang et al., 2004), and has even been correlated with Purbeck Limestone Group of southern England, as noted above (Zhang, 1985; Cao, 1999). These determinations can no longer be sustained following recent non-marine and marine correlations in China (e.g., Sha, 2007; Sha et al., 2007) and a series of radiometric

and palaeomagnetic datings within the range 133.6–125.7 Ma (Smith et al., 1995; Zhu et al., 2002, 2003, 2007; Yang et al., 2007; Chang et al., 2009), all of which constrain the age of the Yixian Formation mainly to the Barremian, enabling it to be widely correlated in eastern Asia (Sha et al., 2012, fig. 2). Having reduced the number of species of *Cypridea* in the Yixian Formation from fourteen to three, and finding that there is no typical “Purbeck” form in the formation, it is clear that the formation cannot be correlated with the Purbeck succession. The composition of the assemblages is consistent with a Barremian determination.

Cypridea is known to have inhabited non-marine fresh to possibly brackish waters (e.g., Horne, 1995, 2002; Sames, 2011a) and is thought to have produced desiccation-resistant eggs (e.g., Horne and Martens, 1998; Horne, 2002), an adaptation that would have allowed it to colonize temporary (ephemeral) as well as permanent water bodies. The two levels in the Yixian Formation in which species of *Cypridea* occur, namely the Jianshangou and Jingangshan beds, represent different depositional conditions. The Jianshangou Bed accumulated in a permanent lake because, in addition to *Cypridea*, it also contains *Darwinula leguminella* and *Metacypris jianshangouensis*. Both of these species have brood pouches to care for eggs and juveniles, which would have confined them to permanent water bodies. On the other hand, the dominance of two *Cypridea* species in the Jingangshan Bed and the lack of darwinuloidean and cytheroidean forms (Wang, 2009) indicate deposition in an ephemeral environment.

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