Recent Ostracods of the Superfamilies Cytheroidea and Darwinuloidea (Crustacea) from Lake Biwa, a Japanese Ancient Lake

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Seven species of the ostracod superfamily Cytheroidea and four species of the superfamily Darwinuloidea were recovered from Lake Biwa in west-central Japan. Four of the cytheroidean species are newly described herein, all belonging to the genus *Limnocythere*: *L. kamiyai* sp. nov., *L. fude* sp. nov., *L. levigatus* sp. nov., and *L. cyphoma* sp. nov. Two others are new records for Lake Biwa, namely *Limnocythere stationis* Vávra, 1891 and *Metacypris digitiformis* Smith and Hiruta, 2004. The four newly described *Limnocythere* species may be an example of a small endemic species flock. Of the Darwinuloidea recovered, two species, *Darwinula stevensoni* (Brady and Robertson, 1870) and *Vestalenula* sp., have been previously recorded from the lake. *Vestalenula* sp. is herein identified as *V. cylindrica* (Straub, 1952), which was previously known only as a fossil from Europe and the Middle East: this is the first report of a living population. The two other darwinulid species, also belonging to the genus *Vestalenula*, are new records for Japan, namely *Vestalenula lundii* (Neale and Victor, 1978) and *V. molopoensis* (Martens and Rossetti, 1997). Their discovery in Lake Biwa dramatically extends the known distribution of all three *Vestalenula* species by thousands of kilometers and increases the number of darwinulids known in Japan from three to five.

Key Words: Crustacea, Ostracoda, Darwinuloidea, Cytheroidea, Lake Biwa, *Limnocythere*, *Vestalenula*, ancient lake.

Introduction

Lake Biwa is an ancient lake located in Shiga Prefecture, west-central Japan (Fig. 1), with a continuous history of lacustrine habitats stretching back one million years. Additionally, a series of four palaeo-lakes existed to the southeast of the present lake from about 4 million to 1.8 million years ago (Meyers *et al.* 1993; Nakajima and Nakai 1994). Like other ancient lakes of the world, it has a number of endemic species, representing approximately 9% of the reported fauna (Mori and Miura 1990; Nishino and Watanabe 2000). For detailed overviews of Lake Biwa, see Nakajima and Nakai (1994) and Rossiter (2000).

Recently, 18 species of ostracods of the family Candonidae (superfamily Cypri-

Fig. 1. Location of Lake Biwa and sampling localities.

doidea) have been reported from Lake Biwa, 11 of which were newly described (Smith and Janz 2008). Other groups of ostracods in Lake Biwa are poorly known, and the aim of this paper is to document the species of the superfamilies Cytheroidea and Darwinuloidea recovered from the lake between 1999 and 2007.

Cytheroidean ostracods are relatively diverse in freshwater habitats, but in Japan only a small number have been recorded: *Cytherissa lacustris* (Sars, 1863) and some unidentified *Limnocythere* species from Lake Biwa, an unidentified species of Cytheroidea from western Japan, and two species in Hokkaido, *Metacypris digitiformis* Smith and Hiruta, 2004 and *Uncinocythere occidentalis* (Kozloff and Whitman, 1954) (Smith and Kamiya 2001; Okubo 2004; Smith and Hiruta 2004).

The family Darwinulidae is the only extant family of the suborder Darwinulocopina, and although it was the first ostracod group to colonize freshwater habitats (in the Carboniferous, over 350 Ma), today it is of low diversity with only about 30 extant species known worldwide (Horne 2003). A small number of darwinulid species, in particular *Darwinula stevensoni* (Brady and Robertson, 1870), have a widespread or cosmopolitan distribution, but most species are known from much more restricted geographical ranges, or even just from their type localities (Artheau 2007). The group has been noted as being particularly rare in the world's few ancient lakes (Martens 1994). Previously, only two darwinulid species were known from Lake Biwa, *Darwinula stevensoni* and *Vestalenula* sp. (Okubo 2001; Smith and Kamiya 2008), and only one other darwinulid species, *Vestalenula cornelia* Smith, Kamiya and Horne, 2006, was known from the Japanese archipelago (Smith *et al.* 2006).

Samples from 63 localities (Fig. 1) in Lake Biwa taken between 1999 and 2007 yielded seven cytheroidean and four darwinulid species.

Material and Methods

Shore samples were taken by scooping up sediment and washing it through a 125 μ m sieve, before transferring the residue to a sample bottle. Offshore samples were taken from a boat with an Ekman sediment grab. The recovered sediment was washed through a 200 μ m Böttger net on a long pole submerged in the lake from the boat. The resulting residue was then transferred to a sample bottle. Samples were kept cool and live specimens were picked from them under a binocular microscope. For storage, picked specimens were transferred to small vials containing 70% ethanol.

Latitudes and longitudes were recorded using a hand-held Garmin GPS unit, using the Tokyo datum.

Appendages were dissected and mounted in glycerine on glass slides and drawn with the aid of a camera lucida. Carapaces are stored dry in micropalaeontological cavity slides. Carapaces used for SEM investigation were coated with gold before being photographed with a JEOL 5800 LV scanning electron microscope.

All type specimens of new species described herein are held at the Lake Biwa Museum (numbers: LBM 1430003497 to 1430003538). SMNS numbers refer to material held at the Staatliches Museum für Naturkunde Stuttgart, Germany.

Abbreviations used in the text are as follows: An1, antennule; An2, antenna;

cp, copulatory process; dl, distal lobe; Md, mandible; Mx, maxillula; L5, fifth limb; L6, sixth limb; L7, seventh limb; UR, uropodal ramus; CS, caudal seta; FRO, female reproductive organ; Hp, hemipenis. Terminology of the appendages follows that of Rossetti and Martens (1998), Meisch (2007), and Smith and Kamiya (2008).

Synonymy lists in the Systematics section below are abbreviated and only show the first recorded name of the species, subsequent nomenclature changes, and junior synonyms.

Systematics

Superfamily **Cytheroidea** Baird
 Family **Limnocytheridae** Klie
 Subfamily **Limnocytherinae** Klie
 Genus ***Limnocythere*** Brady
Limnocythere stationis Vávra, 1891
 (Figs 2A–C, 3)

Limnocythere stationis Vávra, 1891: 108, fig. 38.

Material examined. 1 male and 2 females (LBM 1430003497), 1 male (LBM 1430003498), 1 male (LBM 1430003499), and 1 female (LBM 1430003500), Lake Biwa, north basin, 35°28'40.6"N, 136°08'07.1"E, rocky shore with pebbles, coarse sand, and reeds, depth 0.2 m, 21 September 2006.

Description. Female carapace length 351–363 μm , height 211–221 μm (H/L=0.60), male carapace length 360–370 μm , height 188–195 μm (H/L=0.51–0.54). Female in lateral view with maximum height at anterior quarter (Fig. 2A). Dorsal margin straight, gently sloping down to evenly curved posterior margin. Anterior margin evenly rounded. Ventral margin slightly concave. Sulcus at mid-length. Each valve with tubercle on either side of sulcus near dorsal margin, a third tubercle at center point of carapace, and one posteroventral ala (Fig. 2C). Surface of carapace with numerous coarse pits. Male more elongate than female with longer hinge (Fig. 2B). Ornamentation features of male carapace in similar position to those of female, but slightly less developed, especially posteroventral ala.

Appendages of female closely matching those reported for European female specimens (e.g., Meisch 2000), including reduced L7. Male An1, Md, Mx, L5, and L7 (Fig. 3A, D, E, F, H) very similar to those of female. Male An2 with anterior distal-most claw bifurcated towards distal end (Fig. 3B, C) (not bifurcated in female). L6 of male (Fig. 3G) with proportionally shorter terminal claw than in female. Brush-

Fig. 2. *Limnocythere stationis* Vávra, 1891 (A–C), *L. kamiyai* sp. nov. (D–F), and *L. fude* sp. nov. (G–I). A, Right view of female carapace; B, right view of male carapace; C, dorsal view of female carapace, anterior to right; D, right view of female carapace; E, right view of male carapace; F, dorsal view of female carapace, anterior to right; G, right view of female carapace; H, right view of male carapace; I, dorsal view of female carapace, anterior to right. A–C, LBM 1430003497; D, F, LBM 1430003501, paratype; E, LBM 1430003502, paratype; G, I, LBM 1430003506, paratype; H, LBM 1430003505, paratype.

Fig. 3. *Limnocythere stationis* Vávra, 1891, males, LBM 1430003498 (A–D, F–H, J, K) and LBM 1430003499 (E, I). A, An1; B, An2; C, detail of distal-most claw of An2; D, Md; E, Mx (setae on endites not drawn); F, L5; G, L6; H, L7; I, brush-shaped organs; J, Hp; K, cp of Hp.

shaped organs well developed, with long, slender segment supporting numerous setae (Fig. 3I). Hp relatively large, with broadly rounded outer margin and with large, triangular dl (Fig. 3J). Below dl, inner margin with well-sclerotized, rounded lobe (marked with asterisk in Fig. 3J). Cp relatively short, thickened proximally, and narrow and sinuous distally (Fig. 3K).

Remarks. In lateral and dorsal views the Lake Biwa specimens closely match *Limnocythere stationis* reported from Europe except for missing the denticles on the posterior-dorsal margin of the right valve (cf. Meisch 2000, fig. 177A). Martens (1984) reported female specimens from Sudan also missing these denticles. The specimens from Sudan had longer claws on the antennae than both European (as figured by Meisch 2000, fig. 177D) and Japanese specimens.

This is the first confirmed record of this species in Japan, although Okubo (2004) noted that an unidentified species from Lake Biwa resembles *L. stationis*. Other localities include Western Europe (Meisch 2000), Sudan (Martens 1984), South Africa, Uzbekistan, the Far-East of Russia, Korea, and China (Schornikov and Trebukhova 2001; Schornikov 2004; Yu *et al.* 2005). Schornikov (2004) figured a male carapace from the region of Peter the Great Bay, Far-East of Russia, which closely matches the male carapaces found in Lake Biwa. The single valve figured by Martens (1984) of a possible male of this species from Sudan is considerably different in shape to males from both the Far-East of Russia and Lake Biwa. Herein is the first description of the sexually dimorphic appendages of the male of this species.

In Lake Biwa this species was found twice, at a depth of 0.2 m among pebbles and coarse sand, and at 16 m in sandy mud. Localities (Fig. 1): 2, 41.

***Limnocythere kamiyai* sp. nov.**
(Figs 2D–F, 4A, B)

Material examined. Holotype: male (LBM 1430003503), dissected, Lake Biwa, southern basin, east shore, 35°02'01.5"N, 135°54'36.5"E, coarse, poorly sorted angular sand with a little organic detritus, depth 0.1 m, 23 November 2005. Allotype: female (LBM 1430003504), dissected, same data as holotype. Paratypes: whole male (LBM 1430003502) and whole female (LBM 1430003501), same data as holotype.

Diagnosis. Carapace small, with male much more elongate than female. Dorsal margin of female gently curved, sloping down at approximately 8° from point of maximum height, this being situated at anterior quarter. Male with straight dorsal margin and with two denticles on postero-dorsal margin of right valve. Valves of both sexes with sulcus, three tubercles, and postero-ventral ala. Anterior end beak-like in dorsal view. L7 reduced, much smaller than both L5 and L6. Male Hp with trapezoidal dl and very elongate cp.

Description. Female carapace length 363–403 µm, height 221–240 µm (H/L=0.58–0.63), male length 325–344 µm, height 175–188 µm (H/L=0.54–0.55). Maximum height of female in lateral view at anterior quarter (Fig. 2D). Dorsal margin gently curved, sloping down at approximately 8° to relatively tightly curved posterior margin. Apex of curve of posterior margin below mid-height, less inflated than anterior margin. Ventral margin slightly concave. Sulcus at mid-length. Large tubercle on either side of sulcus near dorsal margin, third tubercle at center point of

carapace (Fig. 2F). Large, angular ala posterior of sulcus near ventral margin (elongate in dorsal view). Surface of carapace with numerous small pits, less abundant in central area. Left valve overlapping right along posterior margin. Male ($H/L=0.50$) more elongate than female ($H/L=0.60$) with longer and straighter hinge and two denticles on postero-dorsal margin of right valve (Fig. 2E). Sulcus and tubercles in similar position to those of female, but slightly less developed.

Appendages of both male and female very closely matching those of *L. stationis* with exception of Hp. Hp with rounded outer margin and dl tapering to trapezoidally truncated end (Fig. 4A). Inner margin concave, with small, rounded projection supporting approximately ten fine setae. Below projection inner margin well-sclerotized and slightly curved (marked with asterisks in Fig. 4A). Cp very elongate, proximally strongly curved and thickened, tapering to long, flexible distal part (Fig. 4B).

Remarks. The carapace of this species closely resembles that of *Limnocythere stationis*. Differences include a more tightly curved posterior margin, more steeply sloping dorsal margin, and shallower pits in *L. kamiyai*. Additionally, the Hp of this species is significantly different to that of *L. stationis*, with the dl and cp clearly distinguishing the two species (compare Fig. 3J, K with Fig. 4A, B). *Limnocythere xinanensis* Zhao, 1987 from Pleistocene to Recent sediments of Guizhou and Yunnan Provinces, China, is also similar to this new species, but the female carapace of the former is slightly more elongated, the dorsal margin straighter, the posterior margin more evenly rounded, and the dorsal view narrower compared with *L. kamiyai*. Males of *L. xinanensis* were reported, but not figured (Zhao 1987), and the appendages of this species remain unknown.

A third species that resembles *Limnocythere kamiyai* is *Limnocythere dorsosicula* De Deckker, 1981, reported from inland waters of Australia. The carapace of *L. dorsosicula* is most similar to that of *L. stationis* in that the posterior margin of the female is more inflated than in *L. kamiyai*. The Hp of *L. dorsosicula* is also most similar to that of *L. stationis*, especially the well-sclerotized, rounded lobe on the inner margin below dl. However, De Deckker (1981) reported that the L7 is the largest walking leg in *L. dorsosicula*, in contrast to any of the *Limnocythere* species from Lake Biwa, in which this limb is the smallest walking leg.

Limnocythere kamiyai was found twice, at a depth of 0.1 m in a substrate of coarse, angular, poorly sorted sand, and a depth of 5.5 m on sandy mud. Localities (Fig. 1): 45, 60.

Etymology. Named in honour of Professor Takahiro Kamiya (University of Kanazawa, Japan).

Limnocythere fude sp. nov.

(Figs 2G–I, 4E, F)

Material examined. Holotype: male (LBM 1430003507), dissected, Lake Biwa, north basin, off western shore, 35°17'09.3"N, 136°01'58.5"E, substrate of poorly sorted, angular sand and gravel, depth 9.7 m, 19 August 2006. Allotype: female (LBM 1430003508), dissected, same data as holotype. Paratypes: whole male (LBM 1430003505) and whole female (LBM 1430003506), same data as holotype.

Diagnosis. Carapace small, less than 400 μ m in length, with female much less

Limnocythere kamiyai sp. nov. *Limnocythere levigatus* sp. nov. *Limnocythere fude* sp. nov. *Limnocythere cyphoma* sp. nov.

Fig. 4. Holotypes of *Limnocythere kamiyai* sp. nov., LBM 1430003503 (A, B), *L. levigatus* sp. nov., LBM 1430003509 (C, D), *L. fude* sp. nov., LBM 1430003507 (E, F), and *L. cyphoma* sp. nov., LBM 1430003517 (G, H). A, C, E, G, Hp; B, D, F, H, cp of Hp.

elongate than male. Female with maximum height at anterior quarter, dorsal margin sloping down steeply to tightly curved posterior margin. Male dorsal margin with slight angle. Both sexes with sulcus. Female with well developed ala, this missing in male. L7 reduced, much smaller than L5 and L6. Male Hp very large, with finger-like projection on dl. Inner margin with large, hook-shaped structure and large brush of setae.

Description. Female carapace length 344–357 μm , height 214–221 μm , H/L=0.61–0.64. Male carapace length 337–350 μm , height 169–178 μm , H/L=0.50–0.51. In lateral view maximum height at anterior third, marked by distinct dorsal hump (Fig. 2G). Straight hinge sloping down towards posterior margin at approximately 12° angle. Posterior margin tightly curved, anterior margin rounded. Sulcus at mid-length, and with four tubercles, one on either side of sulcus near dorsal margin, two below dorso-anterior tubercle, and with large postero-ventral ala swept backwards with rounded end. In dorsal view posterior margin rounded, anterior margin beak-shaped (Fig. 2I). Surface of carapace covered with fine pits, these coarser in female than in male. Male carapace with maximum height at mid-length, marked by subdued angular dorsal hump (Fig. 2H). Postero-dorsal margin with two denticles on right valve. Anterior margin evenly rounded. Ventral margin slightly concave. Sulcus at mid-length and with three tubercles: one on either side of sulcus near dorsal margin, and one at center point of carapace. Postero-ventral ala absent. Both male and female right valves with two tiny denticles on dorsal-posterior margin.

Appendages very similar to those of *Limnocythere stationis*, with exception of male Hp. Hp large and elongate. Inner edge with large, paintbrush-shaped group of fine setae pointing distally (marked with triangle on Fig. 4E) and large, robust, hook-like process. Dl large and sub-rectangular, with distinctive pointed process on distal-outer corner. Cp with stout wide base, tapering to long, flexible distal end (Fig. 4F).

Remarks. The male carapace of this species is similar to that of *Limnocythere stationis*, including the presence of two denticles on the posterior-dorsal margin of the right valve. The hinge, however, is slightly bent producing a weak dorsal hump, and the postero-ventral ala is absent. The hemipenes are very different in shape to those of the other species of *Limnocythere* from Lake Biwa, in particular the shape of the dl, the presence of the hook-like process, and the large, paintbrush-shaped group of fine setae on the inner edge, indicating that it is a separate species. The females are slightly less elongate than those of *L. stationis* and the dorsal margin slopes towards the posterior margin at a steeper angle. The postero-ventral alae of the female are also much larger than those of *L. stationis*.

This species was found at a depth of 9.7 m in a substrate of poorly sorted, angular sand and gravel. Locality (Fig. 1): 16.

Etymology. Named after the Japanese calligraphy brush, “fude” (noun in apposition), due to the shape of the group of fine setae on the inner edge of the male Hp.

***Limnocythere levigatus* sp. nov.**
(Figs 4C, D, 5A–C)

Material examined. Holotype: male (LBM 1430003509), dissected, east side of

northern basin of Lake Biwa, 35°13'54.1"N, 135°57'49.6"E, pebbles, coarse angular sand, and some algae in 2 m depth of water, 16 June 2006. Allotype: female (LBM 1430003512), dissected, same data as holotype. Paratypes: dissected male (LBM 1430003513), whole male (LBM 1430003511), and whole female (LBM 1430003510), same data as holotype.

Diagnosis. Carapace with sulcus and three weakly-developed tubercles, one on either side of sulcus near hinge, the third located antero-ventrally, and with weakly developed postero-ventral ala. In dorsal view anterior end beak-like. Surface of valves covered with very small and shallow pits. Right valve with two denticles just posterior of hinge. L7 reduced, much smaller than L5 and L6. Hemipenes large and hook-shaped, with well-developed, tongue-shaped dl lobe.

Description. Carapace, female length 396–422 μm , height 227–234 μm ($H/L=0.55\text{--}0.58$), male length 318–351 μm , height 156–179 μm ($H/L=0.49\text{--}0.52$). Female with slightly curved dorsal margin, with two denticles on postero-dorsal margin of right valve (Fig. 5A). Maximum height at anterior quarter of length, with gently curving dorsal margin sloping posteriorly from maximum height. Sulcus at mid-length with one weakly developed tubercle on either side of it near dorsal margin and one smaller tubercle below anterior one of these, and weakly developed ala near postero-ventral margin. Surface of carapace with very small pits towards posterior and anterior margins. In dorsal view anterior end beak-like, posterior end rounded (Fig. 5B). Male carapace considerably smaller and more elongate than that of female and lacking postero-ventral ala (Fig. 5C). Hinge straight, right valve with two small denticles on postero-dorsal margin.

Appendages similar to those of *L. stationis*, with exception of male Hp. Hp large, elongate, and broadly hook-shaped, wide distally (Fig. 4C). Outer margin well-rounded, dl tongue-like and rounded. Inner margin strongly indented, with strongly sclerotized margin supporting small number of setae towards proximal end (marked with asterisks in Fig. 4C). Cp with rounded, stout base, tapering to long, flexible distal end (Fig. 4D).

Remarks. This species is similar to *Limnocythere stationis*, but differs in the following: the carapace is much smoother with just fine pits towards the anterior and posterior margins; in dorsal view the tubercles are weakly expressed, especially the postero-ventral ala. The male hemipene is significantly different in shape, with the distal part much more developed than that of *L. stationis*.

This species was found three times at depths of 2 to 10 meters. Localities (Fig. 1): 5, 8, 29.

Etymology. From the Latin adjective *levigatus*, meaning smooth or polished and referring to the smooth appearance of the carapace.

***Limnocythere cyphoma* sp. nov.**
(Figs 4G, H, 5D–F)

Material examined. Holotype: male (LBM 1430003517), dissected, east side of the north basin of Lake Biwa, 35°09'52.0"N, 136°03'44.2"E, beach at base of rocky shore, cobbles and boulders, with coarse angular sand, depth 0.2 m, 24 August 2006. Allotype: female (LBM 1430003518), dissected, same data as holotype. Paratypes: dissected male (LBM 1430003519), whole male (LBM 1430003515), and 2 whole fe-

males (LBM 1430003514, LBM 1430003516), same data as holotype; 1 whole female (LBM 1430003520), west side of the north basin of Lake Biwa, 35°14'22.2"N, 135°58'13.7"E, very poorly sorted mud, sand, angular gravel, and organic detritus, depth 25 m, 10 June 2005; 1 male (LBM 1430003521), dissected, west side of the north basin of Lake Biwa, 35°13'54.3"N, 135°57'48.4"E, gravel and sand, depth 9 m, 16 June 2006.

Diagnosis. Very small carapace, less than 500 μm in length, with sulcus and small indentation near anterior end of hinge. Male with bent dorsal margin. In dorsal view anterior beak-shaped and posterior pointed. Valve surface covered with very fine pits and weak reticulation. L7 reduced and significantly smaller than both L5 and L6. Male hemipenis large and L-shaped.

Description. Carapace length 331–337 μm , height 181–195 μm in females (H/L=0.55–0.58), length 344–351 μm , height 181–188 μm (H/L=0.53–0.54) in males. Male (Fig. 5F) elongate with anterior margin more inflated than posterior margin, ventral margin slightly concave, dorsal margin bent producing dorsal hump just posterior of mid-length. Carapace with sulcus at mid-length and small indentation near anterior end of hinge. Anterior end of carapace beak-like in dorsal view. Surface of valves covered with fine pits and weak reticulation. Female carapace (Fig. 5D, E) slightly smaller and less elongate than that of male, with straight hinge, sloping down to relatively tightly curved posterior margin.

Appendages very similar to those of *L. stationis*, with exception of Hp. Hp (Fig. 4G) large and wide and approximately L-shaped. D1 rounded-rectangle with small, finger-like lobe projecting backwards on inner edge. Inner margin with well-sclerotized and slightly rounded edge supporting small number of short setae towards proximal end. Cp relatively long, robust and stout (Fig. 4H).

Remarks. This species is similar to *Limnocythere stationis* but differs in the following: the female carapace is smaller and not so elongate; the postero-ventral tubercle is absent and the other tubercles are very weakly expressed; the surface of the valves is covered in very fine pores and weak reticulation; in dorsal view the posterior end of the carapace is more pointed; the male carapace is missing the two denticles on the right valve; the male carapace has a distinctive dorsal hump at mid-length; the male hemipenis is considerably different in form, being large and L-shaped.

Nineteen males and 16 females of this species were recovered from a boulder strewn coarse-sandy beach on the eastern side of the north basin (locality 44). One additional male (LBM 1430003521, length 422 μm , height 234 μm) was recovered at

Fig. 5. *Limnocythere levigatus* sp. nov. (A–C), *L. cyphoma* sp. nov. (D–F), *Cytherissa lacustris* (Sars, 1863) (G, H), and *Metacypris digitiformis* Smith and Hiruta, 2004 (I, J). A, Right view of female carapace; B, dorsal view of female carapace, anterior to right; C, right view of male carapace; D, right view of female carapace; E, dorsal view of female carapace, anterior to right; F, right view of male carapace; G, female left valve, external view; H, dorsal view of female carapace, anterior to right; I, female left valve, external view; J, dorsal view of female carapace, anterior to right. A, B, LBM 1430003510, paratype; C, LBM 1430003511, paratype; D, LBM 1430003516, paratype; E, LBM 1430003514, paratype; F, LBM 1430003515, paratype; G, LBM 1430003525; H, LBM 1430003526; I, LBM 1430003522; J, LBM 1430003523. Scale bar=195 μm for A–F, 287 μm for G and H, and 481 μm for I and J.

locality 29, and one additional female (LBM 1430003520, length 447 μm , height 244 μm) from locality 22, both on the western side of the north basin. Compared to specimens recovered on the eastern side, these additional male and female are similar in morphology (including the male hemipenes), but the carapace is approximately 30% larger.

Etymology. After the Greek *kyphoma* (noun in apposition) meaning hump, referring to the humped dorsal margin of the carapace and strongly hunched outer margin of the Hp.

Subfamily **Timiriaseviinae** Mandelstam
Genus ***Metacypris*** Brady and Robertson
Metacypris digitiformis Smith and Hiruta, 2004
(Fig. 5I, J)

Metacypris digitiformis Smith and Hiruta, 2004: 38, figs 2, 3, 4A, B, 5.

Material examined. 1 female (LBM 1430003522, Fig. 5I), dissected, north part of north basin of Lake Biwa, 35°25'15.4"N, 136°08'55.4"E, depth 0.8 m, 13 August 2001; 1 whole female (LBM 1430003523, Fig. 5J), same data; 1 male (LBM 1430003524), dissected, same data.

Remarks. This species has only previously been reported from marshlands in Hokkaido, northern Japan (Smith and Hiruta 2004). In Lake Biwa, specimens were collected from a gravelly substrate along a short stretch of the northern-most shore. Only ten adult female specimens and one badly preserved adult male were recovered, although juveniles were very abundant. Localities (Fig. 1): 6, 7.

Family **Cytherideidae** Sars
Genus ***Cytherissa*** Sars
Cytherissa lacustris (Sars, 1863)
(Fig. 5G, H)

Cythere lacustris Sars, 1863: 222.

Cytherissa lacustris: Sars 1925: 153, pl. 70.

Material examined. 2 females (LBM 1430003525, Fig. 5G; LBM 1430003526, Fig. 5H), whole, north basin of Lake Biwa, 35°11'50.9"N, 135°59'13.6"E, mud, depth 70 m, 10 June 2005; 1 female (LBM 1430003527), dissected, north basin of Lake Biwa, 35°14'22.2"N, 135°58'13.7"E, very poorly sorted mud, sand, angular gravel, and organic detritus, depth 25 m, 10 June 2005.

Remarks. This species was found at depths ranging from 25 to 87 m, on a variety of substrates. It was most abundant on sediments rich in organic detritus. This species has a Holarctic distribution and is commonly found in the deeper, cooler parts of lakes (Meisch 2000). Localities (Fig. 1): 10–14, 17–19, 21–27, 29, 31–40, 42, 43.

Superfamily **Darwinuloidea** Brady and Norman
 Family **Darwinulidae** Brady and Norman
 Genus ***Darwinula*** Brady and Robertson
Darwinula stevensoni (Brady and Robertson, 1870)

Polycheles stevensoni Brady and Robertson, 1870: 25, pls 7 (1–7), 10 (4–14).

Darwinula stevensoni: Brady and Robertson 1885: 346.

Darwinula improvisa: Turner 1895: 336, pl. 81 (1–3) (*partim*).

Darwinula protracta Roma, 1953: 39, pl. 2. [Synonymized by Rossetti and Martens 1996: 76]

Darwinula variabilis Tagliasacchi-Masala, 1968: 624, pls 3, 4. [Synonymized by Rossetti and Martens 1996: 76]

Darwinula sphenoides Rome in Rome and De Decker, 1977: 253, pl. 5. [Synonymized by Rossetti and Martens 1998: 59]

Material examined. 1 female (LBM 1430003250), dissected, south basin of Lake Biwa, 35°04'21.0"N, 135°56'08.3"E, willow tree root mat, depth 0.1 m, 17 April 2005; 1 female (LBM 1430003251), dissected, south basin of Lake Biwa, 35°04'21.0"N, 135°56'08.3"E, willow tree (*Salix* sp.) root mat, depth 0.1 m, 7 June 2005.

Remarks. *Darwinula stevensoni* is a cosmopolitan species, which in Lake Biwa was mostly found down to a depth of 5.6 m, although one specimen was recovered from a depth of 26.6 m. This species has been previously reported from Lake Biwa by Okubo (2001) and Smith and Kamiya (2008). Localities (Fig. 1): 1–5, 9, 15, 20, 46–63.

Genus ***Vestalenula*** Rossetti and Martens
Vestalenula danielopoli-group
Vestalenula cylindrica (Straub, 1952)
 (Figs 6A–H, 7, 8)

Darwinula cylindrica Straub, 1952: 497, figs 19–20.

Vestalenula cylindrica: Janz *et al.* 2001: 185, pl. 3 (22–26).

Vestalenula sp.: Smith and Kamiya 2008: 275–302, figs 15–17.

Material examined. 2 females (LBM 1430003528, LBM 1430003529), whole, south basin of Lake Biwa, 35°04'19.9"N, 135°56'16.4"E, sand and organic detritus, depth 0.05 m, 28 February 2005; 1 female (LBM 1430003530), dissected, south basin of Lake Biwa, 35°04'21.0"N, 135°56'08.3"E, root mat of willow tree, depth 0.1 m, 22 April 2005; 1 female (LBM 1430003531), dissected, south basin of Lake Biwa, 35°04'21.0"N, 135°56'08.3"E, root mat of willow tree, depth 0.1 m, 5 July 2005; 1 female (LBM 1430003532), dissected, south basin of Lake Biwa, 35°04'21.0"N, 135°56'08.3"E, root mat of willow tree, depth 0.1 m, 5 July 2005.

Description. Carapace length 461–481 μ m, height 208–221 μ m, H/L=0.45–0.46. Lateral view elongate with straight hinge, anterior dorsal margin sloping to tightly curved anterior margin (Fig. 6A). Posterior margin evenly curved. Right valve (Fig. 6D) with elongate keel on ventro-posterior margin (Fig. 6C). Left valve internally with elongate tooth at ventro-anterior margin. Maximum width in dor-

sal view at posterior third (Fig. 6B). Adductor muscle scars ranging from eight to ten in number, in typical darwinulid pattern (Fig. 7F).

Eye present. An1 (Fig. 7A) six-segmented, all segments short and robust. First segment with one dorsal seta. Second segment with one long and one short seta on apico-ventral corner. Third segment with robust but short apico-dorsal seta (s1). Fourth segment with short apico-dorsal seta (s2). Fifth segment with four apical setae, dorsal-most one longest. Final segment with two apical setae and short aesthetasc. An2 (Fig. 7B) with small hook h on first segment. Second segment with four small aesthetascs (Ac). Fourth segment with short z1 claw, approximately 50% as long as G2 and G3 claws. Claw G3 very short, z2 tiny. Final segment with very small GM claw, less than half as long as Gm.

Md (Fig. 7C) with long z seta and medium-long w and x setae on second segment of palp. Final segment of palp with short c seta and five claws. Mx (Fig. 7D) palp two-segmented with two straight and one hooked setae on outer corner of first segment. Final segment small and quadrate, apically with two long and one short setae. Branchial plate with 24 normal and four reflexed rays.

L5 (Fig. 7E) with well-developed endite and three-segmented walking leg. Branchial plate (=exopodite) with 11 rays. L6 (Fig. 8A) five-segmented with short d1 seta and two d2 setae on first segment. Second segment with two e setae and long pd seta, latter extending past third segment. Third segment with robust f seta. Fourth segment with small g seta. Final segment with robust h1 seta and h2 claw, and short, slender h3 seta. L7 (Fig. 8B) five-segmented with two d2 setae on first segment. Second segment with medium length e seta. Third segment with long f seta, latter extending past fifth segment. Fourth segment with well developed g seta. Final segment supporting very elongate claw h2 (approximately twice as long as L6 claw) and very long h1 seta, latter approximately 40% as long as claw. UR (Fig. 8C) with small, elongate base supporting slender claw. Lengths of base and claw fairly variable between specimens. Post-abdomen elongate.

Remarks. This species was first recorded from Lake Biwa by Smith and Kamiya (2008) as *Vestalenula* sp. Comparison with Miocene specimens of *Vestalenula cylindrica* from Germany (Fig. 6E–H) and other specimens in the published literature has determined that the Lake Biwa specimens are conspecific. *Vestalenula cylindrica* is known from Miocene deposits in Germany, Austria, Turkey, Slovakia, and Iran, Pliocene deposits of Turkey, and Pleistocene deposits of Portugal (Straub 1952; Lutz 1965; Freels 1980; Janz 1997; Witt 1998, 2000; Janz *et al.* 2001; Gross 2004; Pipík *et al.* 2004; Cabral *et al.* 2005; Minati *et al.* 2008). Herein is the first

Fig. 6. *Vestalenula cylindrica* (Straub, 1952), Recent, Lake Biwa (A–D) and Miocene, Germany, reproduced from Janz (1997) (E–H), *V. lundi* (Neale and Victor, 1978) (I–L), and *V. cornelia* Smith *et al.*, 2006 (M). A, Right view of carapace (LBM 1430003529); B, dorsal view of carapace, anterior to right (LBM 1430003529); C, ventral view of right valve, anterior to left (LBM 1430003528); D, internal view of right valve (LBM 1430003528); E, external view of right valve (SMNS 62890/3); F, dorsal view of carapace, anterior to right (SMNS 62890/5); G, ventral view of right valve, anterior to left (SMNS 62890/4); H, internal view of right valve (SMNS 62890/2); I, right view of carapace (LBM 1430003533); J, dorsal view of carapace, anterior to right (LBM 1430003534); K, internal view of right valve (LBM 1430003535); L, ventral view of right valve, anterior to left (LBM 1430003536); M, ventral view of right valve, anterior to left (LBM 1430000883).

Vestalenula cylindrica

Fig. 7. *Vestalenula cylindrica* (Straub, 1952), LBM 1430003528 (A–C) and LBM 1430003530 (D, E). A, An1; B, An2; C, Md; D, Mx (setae on endites not drawn); E, L5; F, adductor muscle scars of left valve, internal view.

Fig. 8. *Vestalenula cylindrica* (Straub, 1952). A, L6 (LBM 1430003528); B, L7 (LBM 1430003528); C, UR (LBM 1430003531).

report of a living population and hence the first description of the appendages of this species. It differs from *Vestalenula cornelia*, the only other *Vestalenula* species previously known in Japan (Smith *et al.* 2006), in that its keel is longer (Fig. 6M), claw Gm is only half as long as GM (75% in *V. cornelia*), claw G2 is proportionally shorter, and the carapace is slightly more elongate ($H/L=0.43-0.45$ compared with $0.47-0.49$ for *V. cornelia*). *Vestalenula carveli* Artheau, 2007 is also very similar to *V. cylindrica* in carapace shape, but it is slightly more elongate than that of *V. cylindrica*, and *V. carveli* lacks an eye (Artheau 2007) (an eye is present in *V. cylindrica*).

This species was mainly recovered from shallow depths along the shore. Abundance was generally low, with the exception of the Karasuma Peninsula (site 55), where abundant specimens were recovered from the spongy, peaty root mats of willow trees lining the edge of the lake. Localities (Fig. 1): 29, 44, 46, 53, 55, 56.

***Vestalenula lundi* (Neale and Victor, 1978)**
(Fig. 6I-L)

Darwinula lundi Neale and Victor, 1978: 1084, figs 7-12.

Vestalenula lundi: Rossetti and Martens 1998: 71, figs 9A-D, 25N-P.

Material examined. 2 whole females (LBM 1430003533 Fig. 6I; LBM 1430003534, Fig. 6J), shore of north basin of Lake Biwa, 35°13'57.5"N, 136°10'06.4"E, interstitial in poorly sorted sand pebbles and a little mud, depth 0.25 m, 24 August 2006; 2 females (LBM 1430003535, Fig. 6K; LBM 1430003536, Fig. 6L), dissected, same data.

Remarks. In their taxonomic revision of the Recent and Holocene representatives of the family Darwinulidae, Rossetti and Martens (1998) stated in the diagnosis of *Vestalenula lundi* that it lacks a keel on the right valve. However, they went on to state that they were unable to definitively assess the presence or absence of a keel due to the decalcification of the type material. It is our opinion that this feature should therefore be excluded from the species diagnosis until its presence/absence can be confirmed in new material from the type locality. The specimens from Lake Biwa are otherwise identical with the redescription of this species by Rossetti and Martens (1998). As all other species of the genus *Vestalenula* have keels (so presumably the type specimens of *V. lundi* originally had keels before they became decalcified), we tentatively assign our specimens to *V. lundi*. Rossetti and Martens (1998) placed *V. lundi* in the *V. boteai* group, which is characterized by a short keel, although as no keel was observable in the type specimens the reasons for this placement are unclear. The keel on the right valve and the internal tooth in the left valve of the Japanese specimens are both elongate and demonstrate that this species belongs to the *danielopoli* group of *Vestalenula*. *Vestalenula lundi* was described based on specimens collected from a sandy riverbank with coarse gravel in Sri Lanka (Neale and Victor 1978). The specimens from Lake Biwa were abundantly recovered from interstitial samples from coarse sandy beaches. This is the first record of this species in Japan. Localities (Fig. 1): 28, 44.

***Vestalenula boteai*-group**

Vestalenula molopoensis (Martens and Rossetti, 1997)
(Fig. 9A–D)

Darwinula molopoensis Martens and Rossetti, 1997: 59–60, figs 1, 3H–N.

Vestalenula molopoensis: Rossetti and Martens 1998: 76, figs 11A–D, 27N–Q.

Material examined. 1 whole female (LBM 1430003537, Fig. 9A, B), 35°13'54.1"N, 135°57'49.6"E, shore of north basin of Lake Biwa, coarse, pebbly beach, depth 0.01 m, 9 October 2007; 1 female (LBM 1430003538, Fig. 9C, D), dissected, same data.

Remarks. Only a few specimens of this species were collected together with many specimens of *V. lundi*, from a coarse sandy beach. Previously this species has been reported from South Africa and Thailand (Martens and Rossetti 1997; Savatnalinton *et al.* 2008). This is the first record of this species from Japan. Locality (Fig. 1): 44.

Fig. 9. *Vestalenula molopoensis* (Martens and Rossetti, 1997), LBM 1430003537 (A, B) and LBM 1430003538 (C, D). A, Right view of carapace; B, dorsal view of carapace, anterior to right; C, internal view of right valve; D, ventral view of right valve, anterior to left.

Discussion

The genus *Limnocythere* in Lake Biwa

Five species of *Limnocythere* were recognized in the lake, including *L. stationis*, which is widely dispersed throughout Eurasia, parts of Africa, Uzbekistan, the Far-East of Russia, China, and Korea (Martens 1984; Meisch 2000; Schornikov and Trebukhova 2001; Schornikov 2004; Yu *et al.* 2005). The other four *Limnocythere* species so far only known from Lake Biwa may be an example of a small species flock that has evolved from the much more widely distributed *L. stationis*. These four species all have a subtly different carapace shape compared with *L. stationis*, but they show a strong resemblance to it; with the exception of the hemipenes, the appendages of all five species are indistinguishable between species, including the reduced seventh limb. The hemipenes, however, are very different in each of the five species, clearly indicating that, although the carapace and appendage morphologies are very similar, they are five distinct species. In light of the similar carapaces and similar habitats in which the five species were found, the significant differences in morphology among their relatively very large hemipenes suggest a strong influence of sexual selection in this lineage. All five species were only found a very small number of times, and hence it is possible that further sampling of Lake Biwa may reveal more species in this lineage.

The genus *Vestalenula* in Lake Biwa

The discovery of two more *Vestalenula* species in Lake Biwa brings the total for Japan to four (and the number of darwinulids in Japan to five). Three species,

Table 1. Comparison of the four species of *Vestalenula* so far reported from Japan.

Species	Length of carapace (μm)	Height/length of left valve	Length of keel (% of right valve length)
<i>V. lundi</i>	429–442	0.39–0.42	31
<i>V. cylindrica</i>	461–481	0.45–0.46	26
<i>V. cornelia</i>	427–449*	0.47–0.49	20
<i>V. molopoensis</i>	448–474	0.50–0.51	7

Data are for Japanese specimens only.

* From Smith *et al.* (2006).

namely *V. cylindrica*, *V. lundi*, and *V. cornelia*, have long keels (Fig. 6, Table 1) and hence belong to the *V. danielopoli*-group of Rossetti and Martens (1998). *Vestalenula molopoensis* has a much shorter keel and belongs to the *V. danielopoli*-group of Rossetti and Martens (1998), representing the first report of this group in N. E. Asia. Previously the genus *Vestalenula* has been considered to contain many endemic species (e.g., Rossetti and Martens 1999; Martens and Rossetti 2002; Artheau 2007), but the presence of *V. cylindrica*, *V. lundi*, and *V. molopoensis* in Japan, many thousands of kilometers away from previous records, suggests that this apparent high rate of endemism may partly be an artifact of a lack of sufficient sampling in many regions of the world.

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