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On some modern Ostracoda (Crustacea) from the Tibetan Plateau in SW China, with descriptions of three new species

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Abstract

Studies of Holocene ostracods of the Tibetan Plateau have mostly centred around valves and carapaces collected from lake sediments, some at or near the substrate surface and others from short cores. Reports from habitats other than lakes are scarce, and few living species found in this region have appendages described, hindering further taxonomic and phylogenetic work. For this study collections of living ostracods were made in mostly ponds, as well as two rivers and one lake. Six species, including three previously undescribed, were recovered: *Tonnacypris estonica* (Järvekülg, 1960), *Arctocypris edita* **n. sp.**, *Cypris pubera* O.F. Müller, 1776, *Potamocypris variegata* (Brady & Norman, 1889), *Ilyocypris tibeta* **n. sp.**, and *Fabaeformiscandona monticulus* **n. sp.** Specimens of *Tonnacypris estonica* include males, previously unknown for this species, and suggesting it is a geographical parthenogen. A revision of the fifth limb morphology of the genus *Arctocypris*, and a subsequent amended diagnosis of the genus are given. Based on carapace and appendage features, *Eucypris mareotica* (Fischer, 1855) is transferred to this genus: *Arctocypris mareotica* (Fischer, 1855) com. nov. There are now ca. 100 ostracod species reported from modern or subsurface sediments on the Tibetan Plateau, but only 19 of those can be confirmed as alive when collected (i.e. had appendages intact). The families Limnocytheridae and Ilyocyprididae are both relatively diverse on the plateau compared with the Palaearctic zoogeographical region generally. About one third of ostracod species reported from the Tibetan Plateau are only known from there, suggesting a potentially very high rate of endemism.

Key words: Qinghai Province, Tibet Province, Sichuan Province, taxonomy, high altitude, *Arctocypris*, *Ilyocypris*, *Fabaeformiscandona*

Introduction

The world's high-altitude regions above 4000 m are characterized by low oxygen, cold temperatures, strong winds and intense UV light. Due to harsh environments and sparse human habitation, the floras and faunas of such landscapes have remained comparatively endemic and relatively undisturbed by anthropogenic activities (Meyer *et al*. 2017). Among the world's great plateaus, the Tibetan Plateau (also known as the Qinghai—Tibet Plateau) receives special interests in the research of ecology (Geng *et al.* 2009), tectonics (Fang *et al*. 2007), and environmental changes (An *et al*. 2001) because of its height, vastness, as well as location under climates controlled by the Indian monsoon and westerly jet stream. Ostracods, important components of extant aquatic ecosystems as well as fossil assemblages, are potentially sensitive indicators of ecological and environmental changes across the Tibetan Plateau

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(Zhu *et al.* 2010). However, detailed taxonomic works on the living ostracods of the Tibetan Plateau (e.g. Jiang & Chen 1974) and the adjacent areas (e.g. Yin & Martens 1997) have been rare, hindering their applications in various fields.

Although a number of investigations on the ostracods in Tibetan habitats with elevations around or higher than 4000 m have been undertaken (e.g., Daday 1908; Yang *et al.* 1982; Huang *et al*. 1985; Mischke *et al*. 2007, 2010a; Song *et al*. 2014; Hou *et al*. 2000; Guo *et al*. 2016; Peng *et al*. 2013; Fürstenberg *et al*. 2015), these have mostly involved the collection of sediments at or near the surface to retrieve accumulated empty carapaces and valves. Many ostracods are seasonal, so that the appearance of adults of one species may not temporally coincide with those of other species. Thus the collection of accumulated valves and empty carapaces from sediments is advantageous in that one sample can give a more complete overview of the fauna. However, the lack of information of soft-part anatomy of some species has created uncertainties with respect to their taxonomic classification and phylogeny. It is also not clear which species are currently extant, obscuring the ecology and current distribution of these taxa, which impinges on (palaeo-) climatic studies. There is therefore an urgent need to re-investigate the taxonomy of ostracod faunas in this region by careful examination of the soft parts, in order to facilitate future research.

In this paper, we report living ostracods from various small water bodies in Tibet and one in Sichuan, with attention paid to both valve morphology and appendage chaetotaxy. This covers only a small part of the ostracod fauna of this vast plateau, but will hopefully be an important case study for future investigations.

Material, methods and terminology

The ostracods of 13 freshwater habitats are reported in this paper (Table 1). Twelve of these are small natural waterbodies with depths less than 1 m near the state roads from Linzhi to Lhasa, then to Shigatse and Ritu, in Tibet Province. The other site, OS09-1, is a small pond in Ganzi in the west-central part of Sichuan Province. In the field, surface sediments were collected from the littoral zone using a hand-held, fine fishing net and then transferred to a white sampling tray to observe living ostracods. Live ostracods were collected with a plastic pipette and placed in 1.5 ml centrifuge tubes, where they were stored with 99% ethanol after excess water was drained. One sample was taken at each site.

Ostracods were dissected with a pair of sharpened, fine needles attached to bamboo handles. Soft parts were sealed in Hydro-Matrix (Micro-Tech-Lab, Austria) and examined with a COIC (Chongqing Optical Instrument Co. Ltd) BK3300 microscope connected to a Canon EOS REBEL T2i camera. Photographs of appendages were traced in Microsoft PowerPoint 2010 to produce line drawings, with specimens examined simultaneously under the microscope to check fine details at different focus horizons. Valves were imaged with a Zeiss EVO 18 scanning electron microscope after coating with carbon. All specimens are housed in Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China.

Abbreviations. a—outer lobe (of *Ilyocypris* type hemipenis); A1—antennule; A2—antenna; b—inner lobe (of *Ilyocypris* type hemipenis); dl—dorsal lobe (of lateral shield of hemipenis); fg—flange; h—middle lobe (of *Ilyocypris* type hemipenis); Hp—hemipenis; il—inner list; im—inner margin of valve; LV—Left valve; L5—fifth limb; L6—sixth limb; L7—seventh limb; Md—mandible; ml—medial lobe (of lateral shield of hemipenis); mrp—marginal ripplet; ms—medial shield of hemipenis; Mx—maxillula; RO—Rome organ; RV—right valve; st—copulatory process/stylus (of *Ilyocypris* type hemipenis); str—striation on the marginal zone of left valve of *Ilyocypris*; sv—selvage; Ur—uropod; ZO—Zenker organ. Terminology of the appendage chaetotaxy follows Broodbakker & Danielopol (1982), Martens (1987) and Meisch (2000).

Results

A total of six species were found: *Tonnacypris estonica* (Järvekülg, 1960), *Arctocypris edita* **n. sp.**, *Cypris pubera* O.F. Müller, 1776, *Potamocypris variegata* (Brady & Norman, 1889), *Ilyocypris tibeta* **n. sp.**, and *Fabaeformiscandona monticulus* **n. sp.** These belong to the subfamilies Eucypridinae, Cypridinae, Cypridopsinae, Ilyocypridinae and Candoninae. Males of *Tonnacypris estonica* are reported for the first time, with soft-part anatomy described in detail.

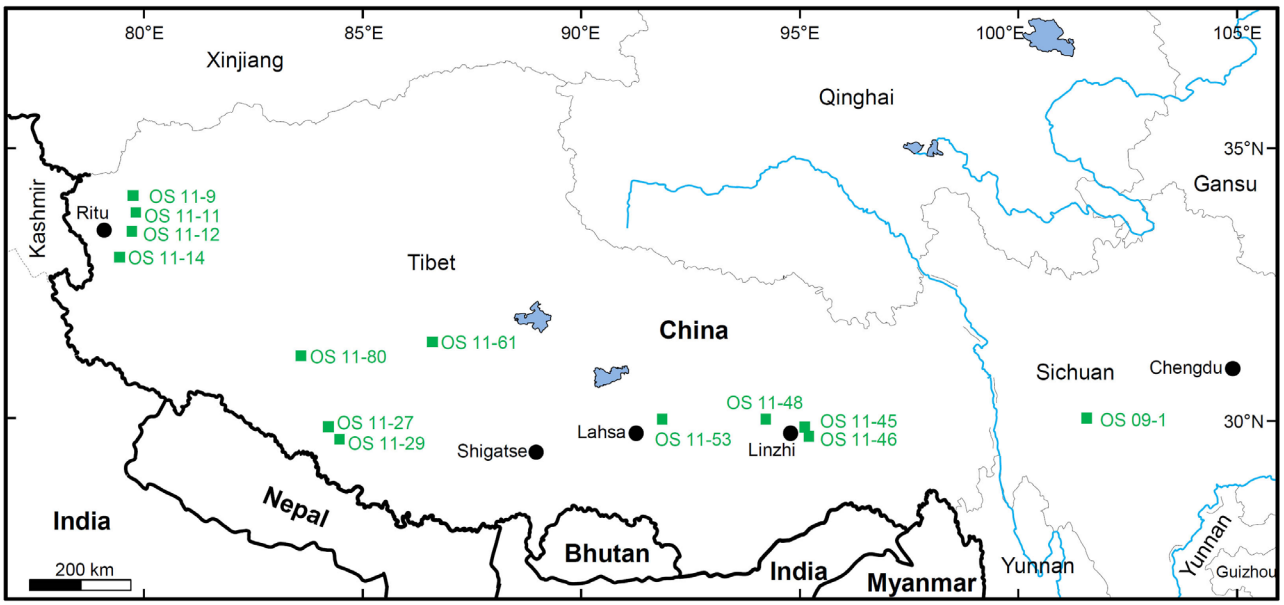

FIGURE 1. Map of the study area (redrawn from: https://map.baidu.com) showing the geographical distribution of the 13 sampling sites (green squares) in the provinces Tibet and Sichuan. Black dots show cities mentioned in the manuscript. Also see Table 1.

Order Podocopida Sars, 1866

Superfamily Cypridoidea Baird, 1845

Family Cyprididae Baird, 1845

Subfamily Eucypridinae Bronstein, 1947

Genus *Tonnacypris* Diebel & Pietrzeniuk, 1975

Tonnacypris estonica (Järvekülg, 1960)

(Figs 2–6)

For an abbreviated synonym list see Van der Meeren *et al*. (2009).

Material examined. Five dissected females (WOC13, WOC53, WOC55, WOC58, WOC59) and two dissected males (WOC54, WOC56) (Table 1).

Dimensions. Male (LV, n = 2) length 1.03–1.22 mm, H/L ratio 0.48–0.50. Female (LV) length 1.16–1.28 mm (n = 5), H/L ratio 0.47–0.49 (n = 4).

Description. Carapace (Fig. 2) sub-reniform in lateral view. Dorsal margin arched, with greatest height situated at about 38% to 42% of length from anterior margin (n = 8 valves). Anterior margin evenly and broadly rounded. Posterior margin narrowly rounded and more or less pointing downwards. Ventral margin slightly concave at middle part with wide and blunt inward projection. In dorsal view, greatest width situated at mid-length, equalling to about 1/3 of length. Both anterior and posterior margins pointed. Valves in interior view, calcified inner lamella wide, with selvage running very close to margin of outer lamella. With up to eight fine striae on anterior calcified inner lamella (Fig. 2I–K), less developed striae on posterior calcified inner lamella. Small antero-ventral peg of female LV (as described in Mongolian specimens; Fig. 1D, F, G of Van der Meeren *et al.* 2009) observed on both male (e.g., WOC56, Fig. 2D) and female (e.g., WOC53, Fig. 2J) Tibetan specimens, but absent in some specimens (e.g., WOC13, Fig. 2I, WOC54, unfigured).

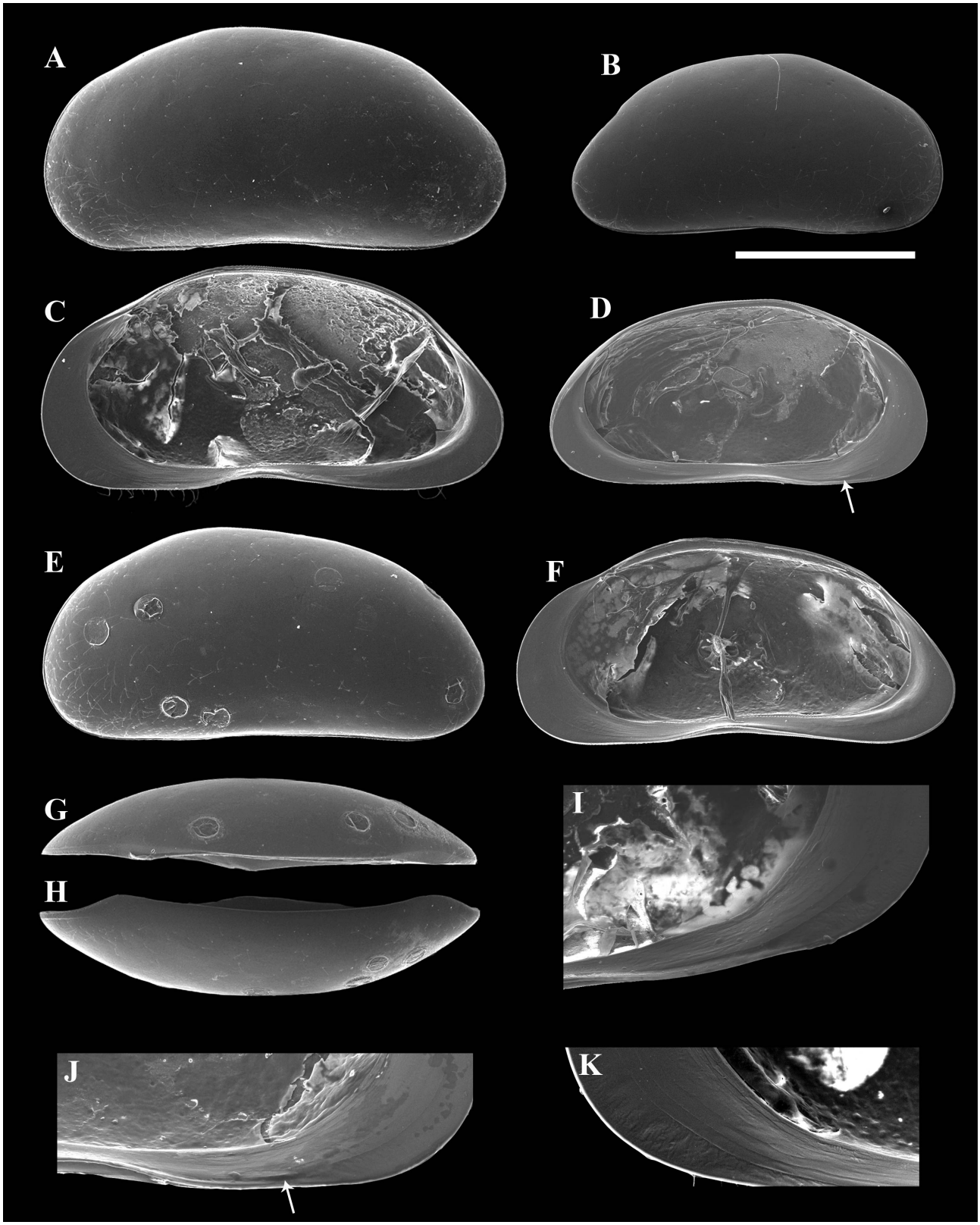

FIGURE 2. *Tonnacypris estonica* (Järvekülg, 1960). (A) Female LV, exterior view (WOC13); (B) male RV, exterior view (WOC56); (C) female RV, interior view (WOC13); (D) male LV, interior view (WOC56), with white arrow indicating antero-ventral peg; (E) male LV, exterior view (WOC54); (F) male RV, interior view (WOC54); (G, H) female (WOC53) RV (G) and LV (H), dorsal view; (I) antero-ventral part of female LV (WOC13), peg not observed; (J) antero-ventral view of female LV (WOC53), with white arrow indicating antero-ventral peg; (K) antero-ventral part of female RV (WOC13). Scale bar: A–H = 500 μm; I, J = 250 μm, K = 200 μm.

Soft parts of male. A1 (Fig. 3A) morphology similar to that of female (see Van der Meeren *et al*. 2009), with eight segments, first two of which fused into large base, supporting one short dorsal seta and two long, thick ventral setae. Third segment trapezoidal, with one fine dorso-apical seta extending to end of fourth segment and elongate RO, situated on ventro-apical part of segment. Fourth segment elongate, with one dorso-apical seta extending to mid-length of seventh segment, and one ventro-apical seta extending to end of fifth segment. Fifth segment sub-quadrate, with two long dorso-apical setae extending well beyond end of terminal segment and two ventro-apical setae. Sixth segment sub-rectangular, with two very long dorso-apical setae and two shorter ventro-apical setae. Seventh segment elongate, with four long setae on inner side, and one fine seta (α) on outer side extending beyond end of terminal segment with ca. 2/5 of its length. Eighth segment slender, apically with three setae, and comparatively long and fine aesthetasc y_a ca. twice as long as terminal segment. Ventral seta thick and slightly setulose.

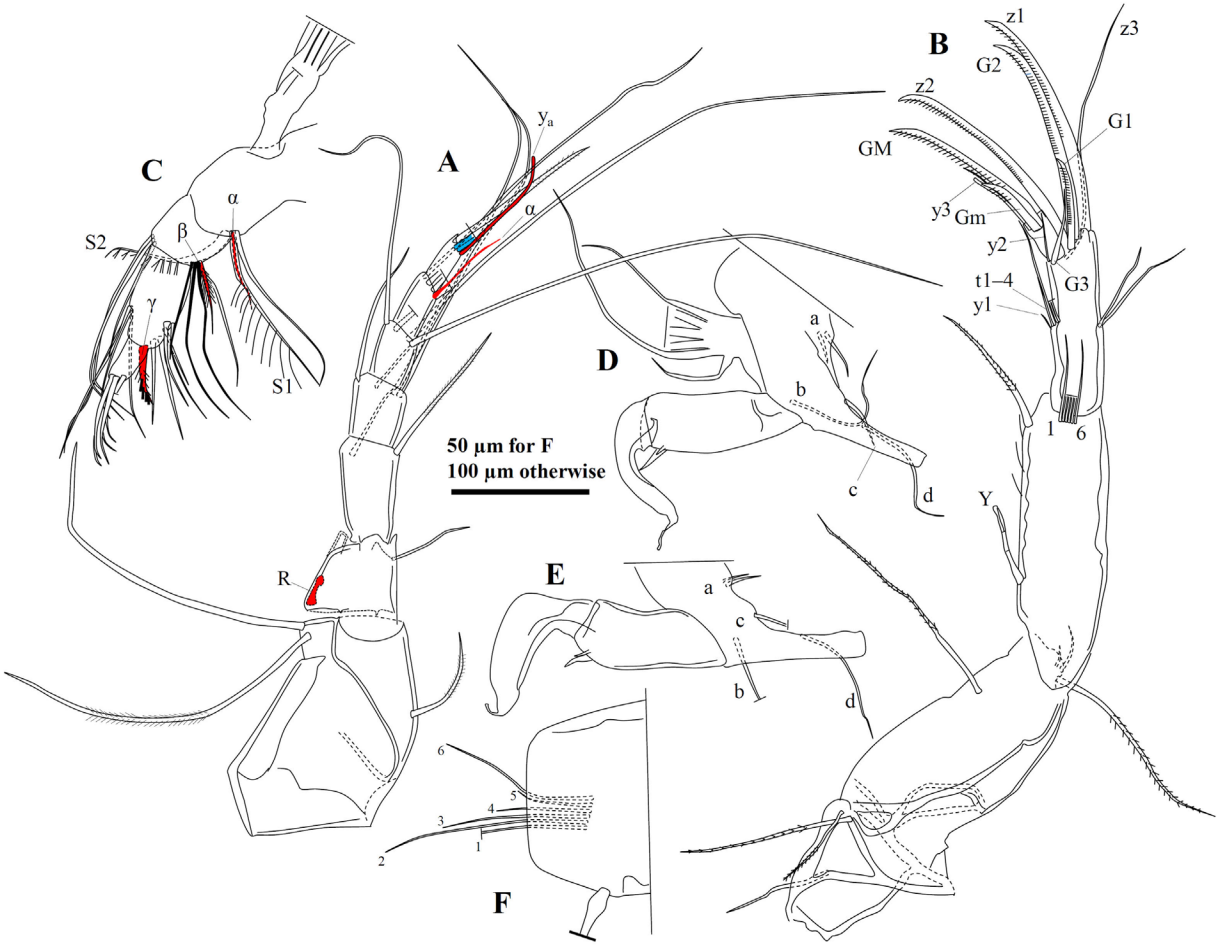

FIGURE 3. *Tonnacypris estonica* (Järvekülg, 1960), male (WOC54). (A) left A1, exterior view; (B) right A2, interior view; (C) left Md palp, posterior view; (D) left A5, interior view; (E) right A5, interior view (exopod not shown); (F) distal part of the first endopodal segment of left A2, showing lengths of the natatory setae.

A2 (Fig. 3B, F) first protopodal segment with one slender ventro-posterior seta and two slender, setulose, unequal ventro-apical setae. Second protopodal segment robust, with one plumose, ventro-subapical seta extending almost to end of first endopodal segment. Longest seta of exopodite slightly setulous along distal half, and extending about three-quarters of length of first endopodal segment. Other two exopodal setae much shorter. Aesthetasc Y situated well behind mid-length of first endopodal segment, reaching slightly beyond mid-length of this segment. Six setae on intero-apical part of first endopodal segment unequally long, with second one reaching mid-length of penultimate segment, second to fifth ones progressively shorter. Ventro-apical seta of first endopodal segment robust and setulose, reaching base of terminal segment or slightly beyond. Second endopodal segment not sub-divided, aesthetasc y1 minute, situated immediately behind t setae. t setae unequal in length, longest one reaching distal end of terminal segment. z1 and z2 transformed into robust, serrated claws, with z1 slightly longer. z3 not transformed, reaching slightly beyond z1. G1 reduced, ca. 1/3 of length of z1, serrated. G2 slightly shorter than z1, and serrated.

G3 very slender, seta-like, shorter than G1. Aesthetasc y2 fine, extending to about end of terminal segment. GM about 2.5 times length of Gm. GM and Gm serrated. Aesthetasc part of y3 slightly longer than Gm.

Md (Fig. 3C) palp four-segmented, first segment's vibratory plate with 5+1 wide rays. Setae S1 and S2 robust, plumose, accompanied by smooth seta of sub-equal length. Setae α fine and long, reaching to almost mid-length of S1. Second segment with three dorso-apical setae extending almost to tips of terminal claws. Antero-apical setal group on second segment with three setae extending to about end of terminal segment, accompanying seta slightly shorter. Seta β setulose, reaching mid-length of grouped setae. Third segment with 10 setae, including four long dorso-apical setae, seta γ (robust, plumose or serrated, situated on interior surface) and five unequal ventro-apical setae. Terminal segment with three robust, smooth claws and about four smaller setae.

Mx (not shown) nearly identical to female described by Van der Meeren *et al.* (2009). First segment of palp with eight setae. Second segment of palp with three larger and three smaller claws/setae. Tooth bristles on 3rd (distal) endite lobe smooth. Two setae on first (proximal) endite lobe with long setules (resembling those on S1 and S2 of Md palp).

L5 palps (Fig. 3D, E) asymmetrical. Each trunk (1st endopodal segment) with two unequally sized sensory organs on ventro-apical part. 2nd endopodal segment finger-shaped and curved, with small terminal sensory organ. Right 'finger' wider than left one. Setae a and c much shorter than b and d. Vibratory plate with 6–7 rays, 1–2 of which shorter than others.

L6 (Fig. 4A) with five segments. Setae d1 and d2 short. Seta e and f comparatively long. Seta g accompanied by much smaller seta. h1 similar length to g, conspicuously setulose. Claw h2 serrated along distal half. Seta h3 slightly shorter than h1. Setae d1, d2, e, f, g, and h3 faintly setulous.

L7 (Fig. 4B, E) with three articulated segments, less sclerotized compared with other limbs. Seta d1 reaching well beyond distal end of first segment. Seta d2 sub-equal in length to d1, reaching slightly beyond mid-length of second segment. Seta dp extending to about distal end of second segment. Seta e setulose, extending to about end of terminal segment. Seta f setulose, situated at mid-length of third segment, extending to about end of segment. Seta h2 stiff. Seta h3 comparatively long and bearing small curve at middle part. Second to fourth segments with areas of clustered pseudochaetae.

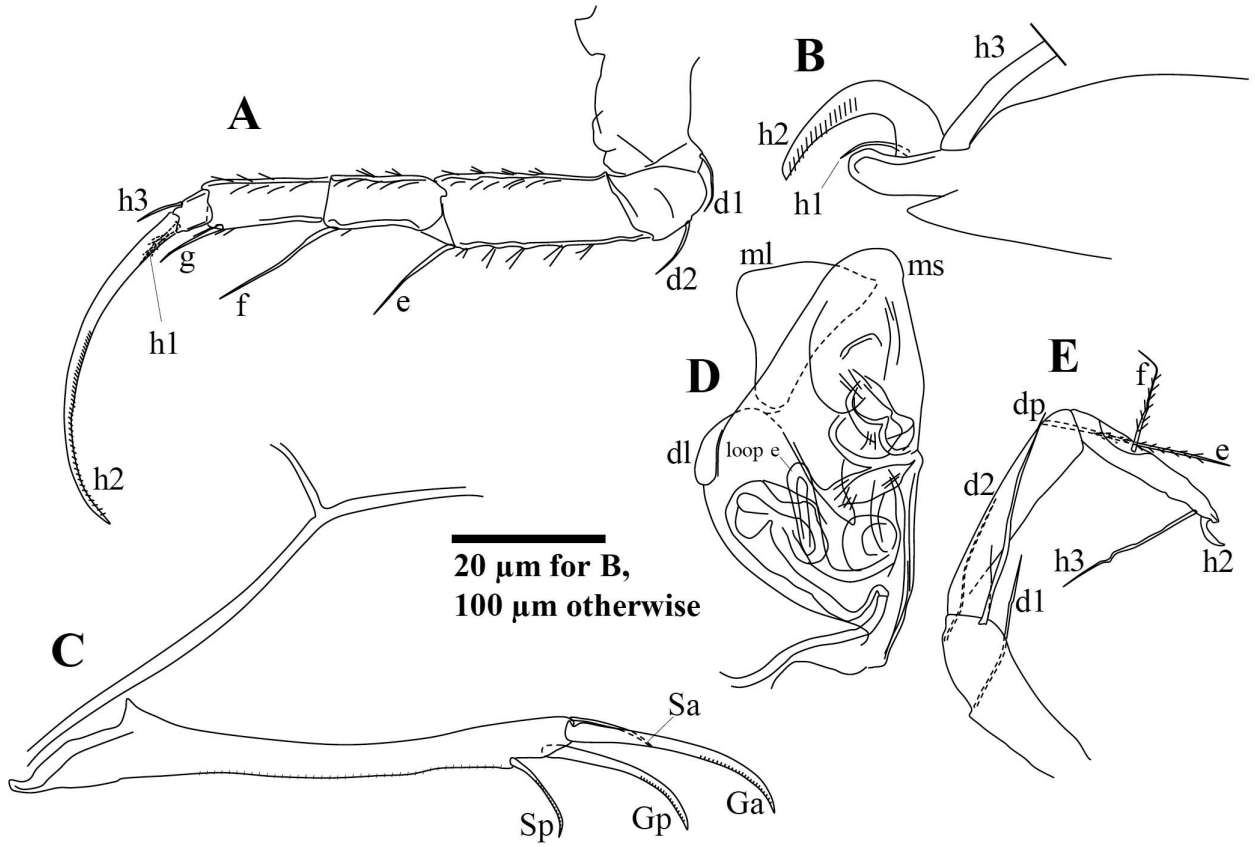

FIGURE 4. *Tonnacypris estonica* (Järvekülg, 1960), male (WOC54). (A) Left A6, interior view; (B) detail of apical structures of left L7, exterior view; (C) right Ur and attachment; (D) Hp; (E) right L7, exterior view.

Ur ramus (Fig. 4C) comparatively long, bearing fine, short pseudochaetae along ventral edge. Sp situated close to distal end of ramus, robust, claw-like, serrated. Gp shorter than Ga, both serrated. Sa about 1/3 length of Ga. Ur attachment simple, unequally bifurcated.

Hp (Figs 4D and 5) lateral shield with wide, sub-triangular medial lobe (ml) and small dorsal lobe (dl). Medial shield (ms) triangular, distally rounded and smooth. Loop 'e' distinctly recurving.

ZO (Fig. 6) with 20–21 internal rosettes of spines.

FIGURE 5. *Tonnacypris estonica* (Järvekülg, 1960), the two Hp of male (WOC54). See also Fig. 4D.

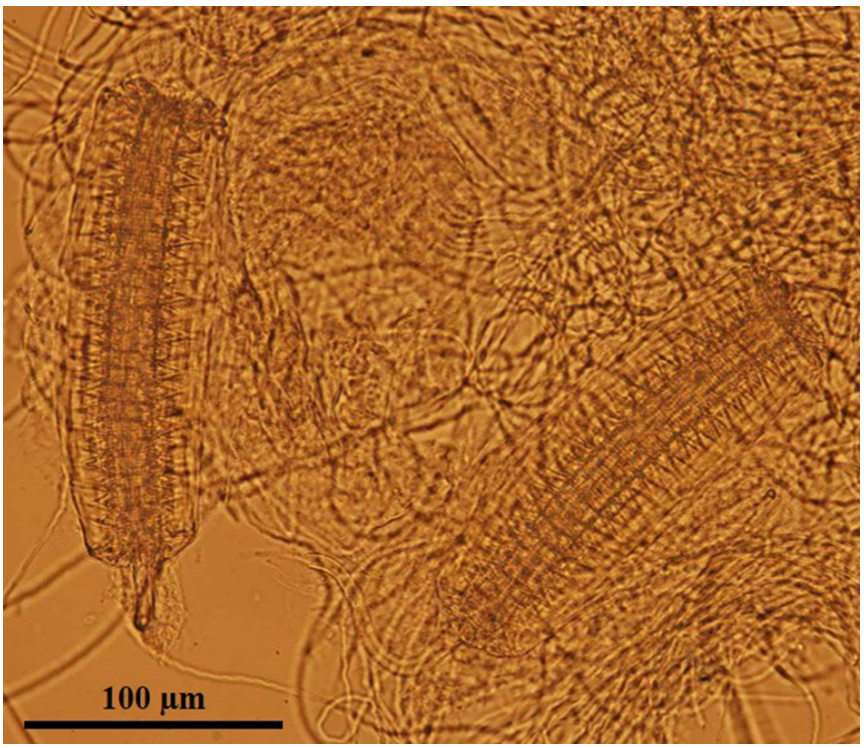

FIGURE 6. *Tonnacypris estonica* (Järvekülg, 1960), Zenker organs of male (WOC54).

Remarks. The present specimens match the type specimens from Estonia (Järvekülg 1960), and specimens from Mongolia (Van der Meeren *et al*. 2009), in both valve morphology and chaetotaxy structures, especially in some details that are apparently very specific. For the soft parts, the key morphologies include lengths of the A2 swimming setae and the L5 a–d setae, setae and claw lengths of the L6, the presence and arrangements of pseudochaetae on the L6 and Ur, as well as the claw-like appearance of seta Sp on the Ur. Other aspects of the chaetotaxy are also generally consistent. Although some of the present specimens lack the small peg on the antero-ventral part of the LV, we consider this as intra-specific variation.

With the presence of males, however, it is shown that several aspects of the morphology of this species differ from other members of this genus. Firstly, the medial lobe (outer lobe) of the Hp is very wide, triangular, and unlike the slender and tapering distal medial lobe in other *Tonnacypris* species described in Van der Meeren *et al*. (2009). Secondly, the apical part of the medial shield is smooth, not with a roughened surface as in other *Tonnacypris* species. Thirdly, the number of ZO internal rosettes (20–21) is significantly smaller (39 in *Tonnacypris edlundi* Van der Meeren *et al.*, 2009, about 43 in *Tonnacypris mazepovae* Van der Meeren *et al.*, 2009, and about 46 in *Tonnacypris lutaria* (Koch, 1838)).

The above differences imply that *T. estonica* may be phylogenetic distant from some of the other species in the genus for which males are known. The type species of the genus, *Tonnacypris loessica* Diebel & Pietrzeniuk, 1975, is only known from fossil specimens, so it is currently not possible to say which species are the most phylogenetic similar to it based on male characters. However, the large differences in the morphologies of the hemipenes and Zenker organs suggest there are possibly two lineages within the genus.

Eucypris gyirongensis Yang, 1982 (in Huang *et al*. 1982), later reported by Akita *et al.* (2016) (as *Tonnacypris gyirongensis*) from Tibet, is similar to *T. estonica* in valve morphology, except that the reticulated pattern on the medio-dorsal part of left valve has not been observed in *T. estonica* (Van der Meeren *et al*. 2009; this study). Mischke *et al.* (2010b) considered that *E. gyirongensis* is a junior synonym of *Eucypris afghanistanensis* Hartmann, 1964, but detailed study of the soft-part anatomy of *T. gyirongensis* is required to verify its taxonomic identity.

Tonnacypris estonica has a disjunct known distribution, first described from Estonia (Järvekülg 1960), and later from the Mongolian Valley of the Great Lakes and in the northeastern part of the Mongolian Altai mountains (Van der Meeren *et al.* 2009). It has been recorded in high densities in springs, but is also found in streams and lakes, predominantly occurring in oligotrophic habitats (Van der Meeren *et al.* 2009). On the Tibetan Plateau it was collected from small ponds and a slowly flowing river at altitudes of 3325–4548 m (Table 1). The discovery of males in this study suggests that *T. estonica* is a geographic parthenogen, similar to *T. lutaria* (and possibly *Tonnacypris glacialis* (Sars, 1890)) (Griffiths *et al*. 1998; Van der Meeren *et al.* 2009).

Genus *Arctocypris* Petkovski *et al.*, 2016

Diagnosis (amended from Petkovski *et al*. 2016). Carapace relatively small (0.8 to 1.2 mm in length), sub-triangular in lateral view, maximum height anterior of mid-length, greater than half of length. Anterior margin broadly rounded, posterior margin narrower, but rounded. Ventral margin concave with small expansion in mouth region. Dorsal view rounded to marginally lateral compressed, anterior end pointed and sometimes slightly compressed, posterior end more rounded. LV overlaps RV along entire free margin. LV with one or two lists on anterior calcified inner lamella, and one list on posterior calcified inner lamella. RV anterior and posterior calcified inner lamellae each with one list. Palp of Mx with cylindrical terminal segment, about twice as long as broad. Tooth bristles on third Mx endite serrated. L5 with d and b setae, no c-seta. Base of L6 with d1 seta; d2 absent.

Species included. *Arctocypris fuhrmanni* Petkovski *et al*., 2016 (type species), *Arctocypris arctica* (Olofsson, 1918), *Arctocypris foveata* (Delorme, 1968), *Arctocypris dulcifons* (Diebel & Pietrzeniuk, 1969), *Arctocypris mareotica* (Fischer, 1855) comb. nov. (see Discussion for further details), *Arctocypris edita* **n. sp.**

Arctocypris edita n. sp.

(Figs 7–12)

Type Locality. Small pond in Rutog, Ngari, Tibet, China, 29.58616ºN, 84.76981ºE, altitude 4626 m (site OS11-29; Table 1).

Type Material. Holotype: a dissected female (WOC47), with appendages mounted on a glass slide and valves stored in a micropalaeontological cavity slide, collected from the type locality (site OS11-29; Table 1).

Paratype: a dissected female (WOC28), with appendages mounted on a glass slide and valves stored in a micropalaeontological cavity slide, collected from site OS11-9 (Table 1).

Other specimens: Seven dissected females (WOC25, 33, 34, 60, 65–67), each with appendages mounted on a glass slide and valves stored in a micropalaeontological cavity slide, collected from sites OS11-9, OS11-11 and OS11-80 (Table 1).

Derivation of name. From the Latin *editus*, meaning high or lofty, and referring to the high altitudes where this species was collected.

Dimensions. Female (LV) length 1.00–1.29 mm (n = 9), H/L ratio 0.56–0.59 (n = 9).

Diagnosis. In lateral view posterior margin more tightly curved than anterior margin, dorsal margin curved, with slight hump at maximum height, immediately anterior of mid-length. In dorsal view anterior margin slightly laterally compressed. Surface of valves with numerous tiny pits. LV with two closely spaced inner lists on anterior calcified inner lamella, and one list very close to inner edge of posterior calcified inner lamella. RV with single list on anterior calcified inner lamella. Aesthetasc ya on A1 long, over twice as long as terminal segment. Swimming setae extending slightly beyond end of claws of A2. Mx terminal segment with five setae/claws. L5 with no c-seta (see Discussion), but with b and d setae.

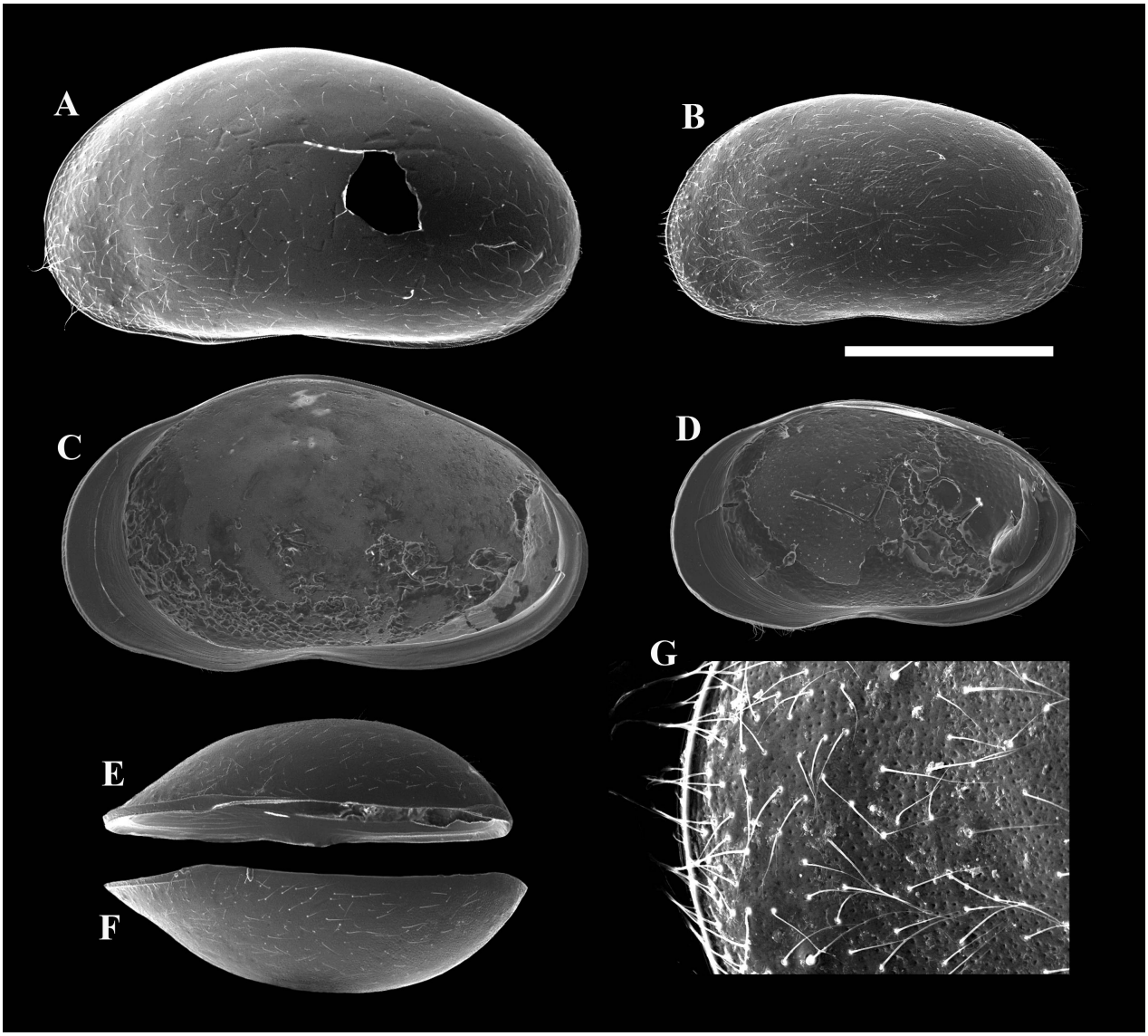

FIGURE 7. *Arctocypris edita* **n. sp.**, green-shell phenotype, female (A, C, WOC60; others, WOC47, holotype). (A) LV, exterior view; (B) LV, exterior view; (C) RV, interior view; (D) RV, interior view; (E) RV, dorsal view; (F) LV, dorsal view; (G) enlargement of anterior part of (B). Scale bar: A–F = 500 μm; G = 115 μm.

Description of female. Carapace (Figs 7 & 10) sub-ovate in lateral view. Dorsal margin moderately arched with highest point situated slightly anterior of mid-length. Ventral margin concave, with small lobe-like expansion at antero-ventral LV. Anterior margin broadly rounded, slightly compressed laterally. Posterior margin narrowly rounded. In interior view, anterior calcified inner lamella much wider than that of posterior. Selvage slightly displaced inwards along posterior and postero-ventral margins of RV. RV with one, LV with two inner lists running in medial area of anterior calcified inner lamella, accompanied by number of striae. Shell surface pitted, covered with fine setae. Colour, in white-shelled phenotype, whitish but stained with small brown patterns, probably due to micro-organism colonization; greenish in green-shelled phenotype.

A1 (Figs 8A & 11A) with eight segments, first two of which fused into large base, supporting one shorter dorsal seta and two longer ventro-apical setae. Third segment wide and short, bearing one dorso-apical seta extending to about mid-length of next segment. RO situated on extero-ventral side of this segment, small, with enlarged base and tapering distally. Fourth segment elongate, with one dorso-apical seta and one short ventro-apical seta. Fifth segment sub-quadrate, with two very long dorso-apical setae and two unequal ventro-apical setae. Sixth segment with two very long dorso-apical setae and two ventro-apical setae extending far beyond terminal segment. Seventh segment elongate, with four very long apical setae on interior side and short seta α on exterior side extending somewhat beyond terminal segment. Eighth segment slender, with three distal setae and aesthetasc y_a, latter of which slightly longer than total length of three distal-most segments. Ventral seta slightly shorter than y_a. Two intermediate setae longer.

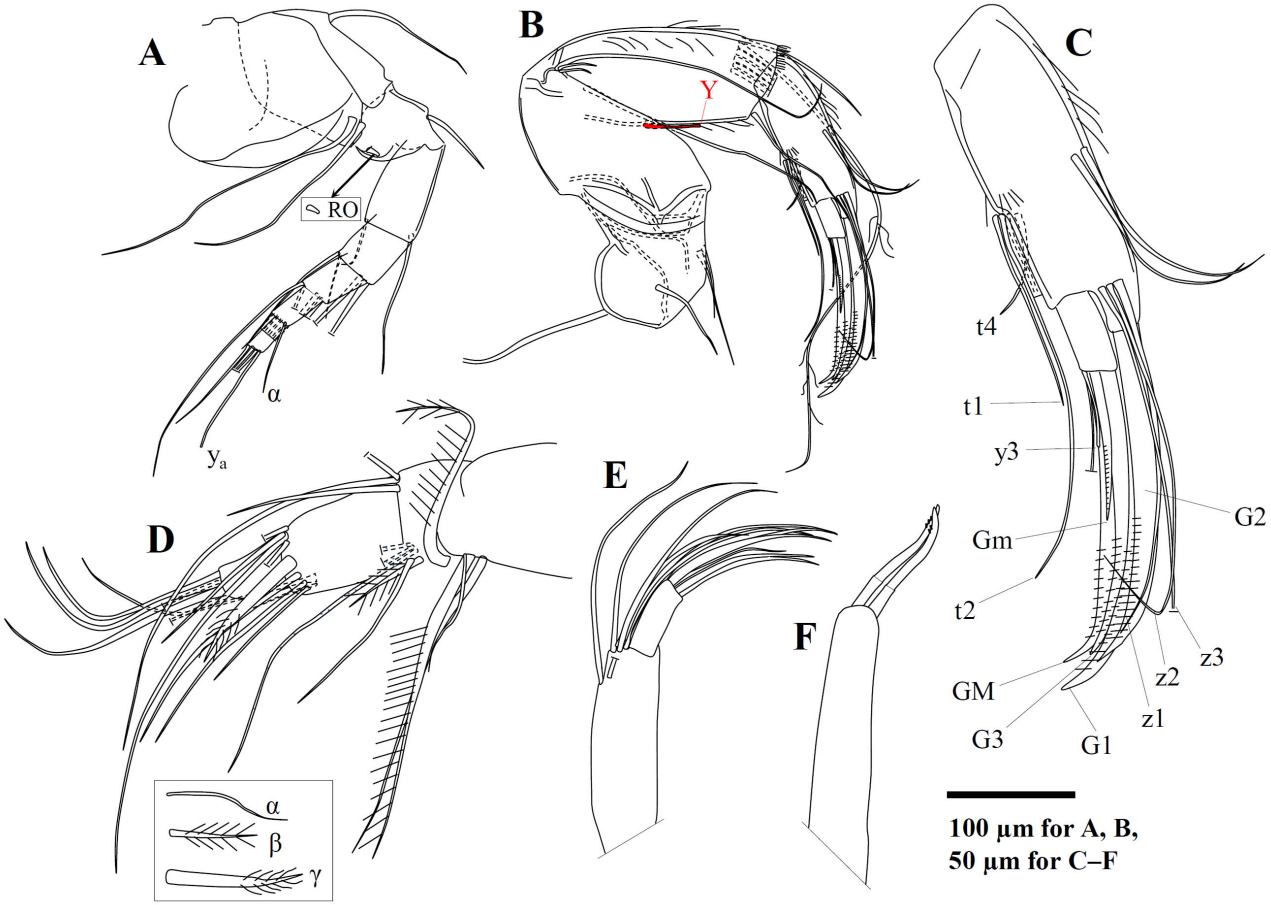

FIGURE 8. *Arctocypris edita* **n. sp.**, green-shell phenotype, female (WOC47, holotype). (A) Right A1, exterior view; (B) right A2, exterior view; (C) enlargement of distal part of (B); (D) right Md palp, interior view; (E) left Mx palp, interior view; (F) 3rd endite lobe of Mx.

A2 (Figs 8B, C & 11B, E) basal segment (first protopodal segment) with one lateral seta and two unequal ventro-subapical setae. Second segment robust, carrying one seta with medial curve, extending slightly beyond distal end of third segment. Exopod small, bearing one long seta extending slightly beyond distal end of third segment (first endopodal segment) and two short setae. Third segment elongate, with three-segmented aesthetasc Y situated

at about mid-length of ventral margin, and ventro-apical seta reaching basal part of terminal segment. Swimming setae extending beyond terminal claws with 20–30% of length. Sixth seta extending to mid-length of fourth segment (second endopodal segment). Ventro-apical seta of third segment extending to about distal end of terminal segment. Fourth segment elongate and undivided, with two dorso-medial setae. Setae t1–4 unequally long, with t2 being longest, extending beyond middle of terminal claws. Setae t1 and t4 shortest, extending only slightly beyond distal end of penultimate segment. Aesthetasc y1 tiny. Aesthetasc y2 small, extending slightly beyond mid-length of terminal segment. z-setae untransformed, with z2 and z3 longer than z1, extending to or slightly beyond longest terminal claw. G1 somewhat longer than G3 and G2. GM extending to about distal end of G2. Gm extending to or slightly beyond mid-length of GM. All G-claws serrated. Aesthetasc part of y3 extending to mid-length of Gm.

Md palp (Figs 8D & 11C) with four segments. First segment (basis) bearing four ventro-apical setae. Setae S1 and S2 on first segment with long pseudochaetae. Accompanying seta smooth, sub-equally long to S1. Seta α slender and smooth. Second segment short, with three unequally long dorso-apical setae, and five ventro-apical setae: stout and setulose seta β, three smooth grouped setae and shorter accompanying seta. Third segment elongate, with total of ten setae, including seta γ, plumose along distal half. Terminal segment with three long and two shorter setae/claws. Vibratory plate with about five wide rays and two small setae.

Mx (Figs 8E, F & 11D) palp with two segments. First segment with eight setae. Second segment elongate and cylindrical, with five setae/claws. Tooth bristles on distal protopodal endite with variable serration, with both bristles (WOC66), proximal bristle (WOC28, 33, 34, 65, 67), or no bristle (WOC25, 60) serrated, or only faintly serrated (WOC47).

L5 (Figs 9A & 12A, B) protopod with two small setae a, longer setae b and d. Setae b and d setulose in some specimens. Palp with three distal setae, seta h2 very long. Vibratory plate with six rays.

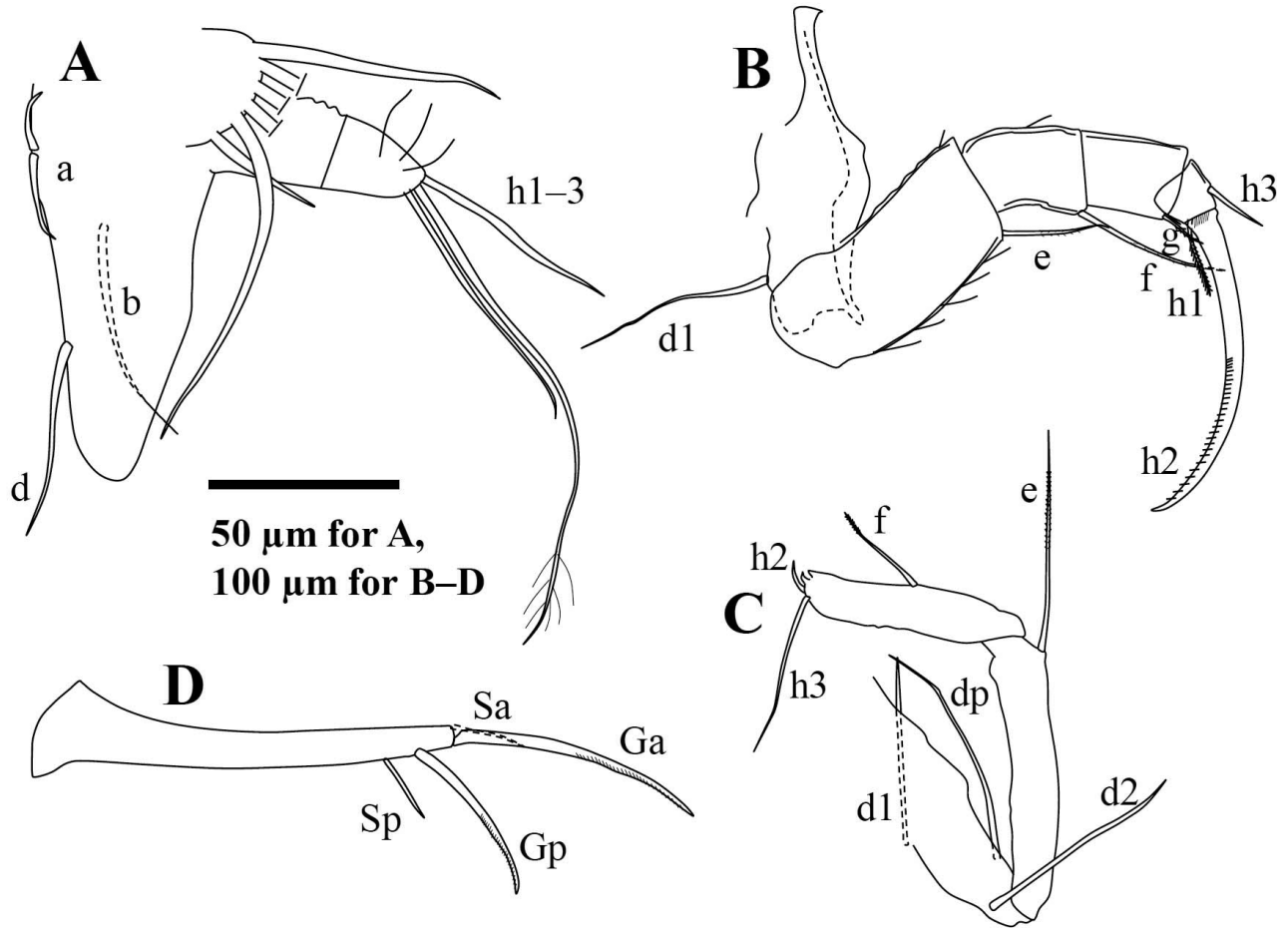

FIGURE 9. *Arctocypris edita* **n. sp.**, green-shell phenotype, female (WOC47, holotype). (A) Left L5, exterior view; (B) right L6, interior view; (C) left L7, exterior view; (D) right Ur, exterior view.

L6 (Figs 9B & 12C) robust, with five segments. First segment proximally with elongate anchor structure connecting limb to body, and bearing long seta d1. Seta d2 absent. Second segment carrying pseudochaetae along anterior margin, with seta e extending to about distal end of third segment. Third segment sub-rectangular, with seta f extending somewhat beyond distal end of fourth segment. Fourth segment slightly elongate, with short seta g. Fifth segment small and trapeziform, with robust and serrated claw h2 and short, sub-equally long setae h1 and h2. Seta h1 setulose.

L7 (Figs 9C & 12D) comparatively well sclerotized, consisting of three articulated segments. Basal segment with long Setae d1, d2 and dp. Setae e and f setulose distally. Pincer organ present, typical of subfamily. Seta h3 slightly longer than f, not S-shaped.

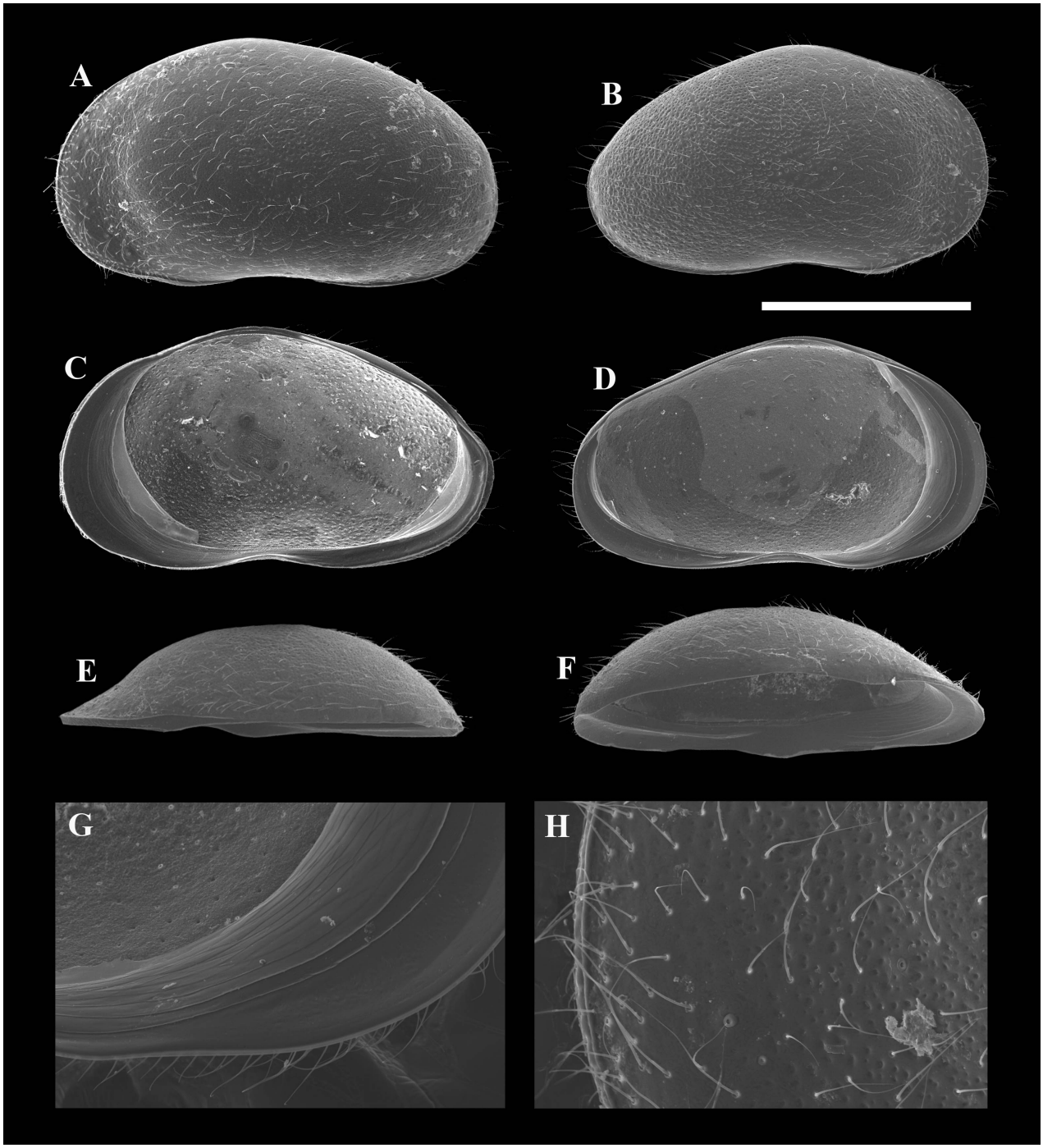

FIGURE 10. *Arctocypris edita* **n. sp.**, white-shell phenotype, female. (A) LV, exterior view (WOC25); (B) RV, exterior view (WOC28); (C) RV, interior view (WOC25); (D) LV, interior view (WOC28); (E) RV, dorsal view (WOC34); (F) LV, oblique-dorsal view (WOC34); (G) enlargement of antero-ventral part of (D); (H) enlargement of anterior part of (A). Scale bar: A–F = 500 μm; G = 145 μm; H = 105 μm.

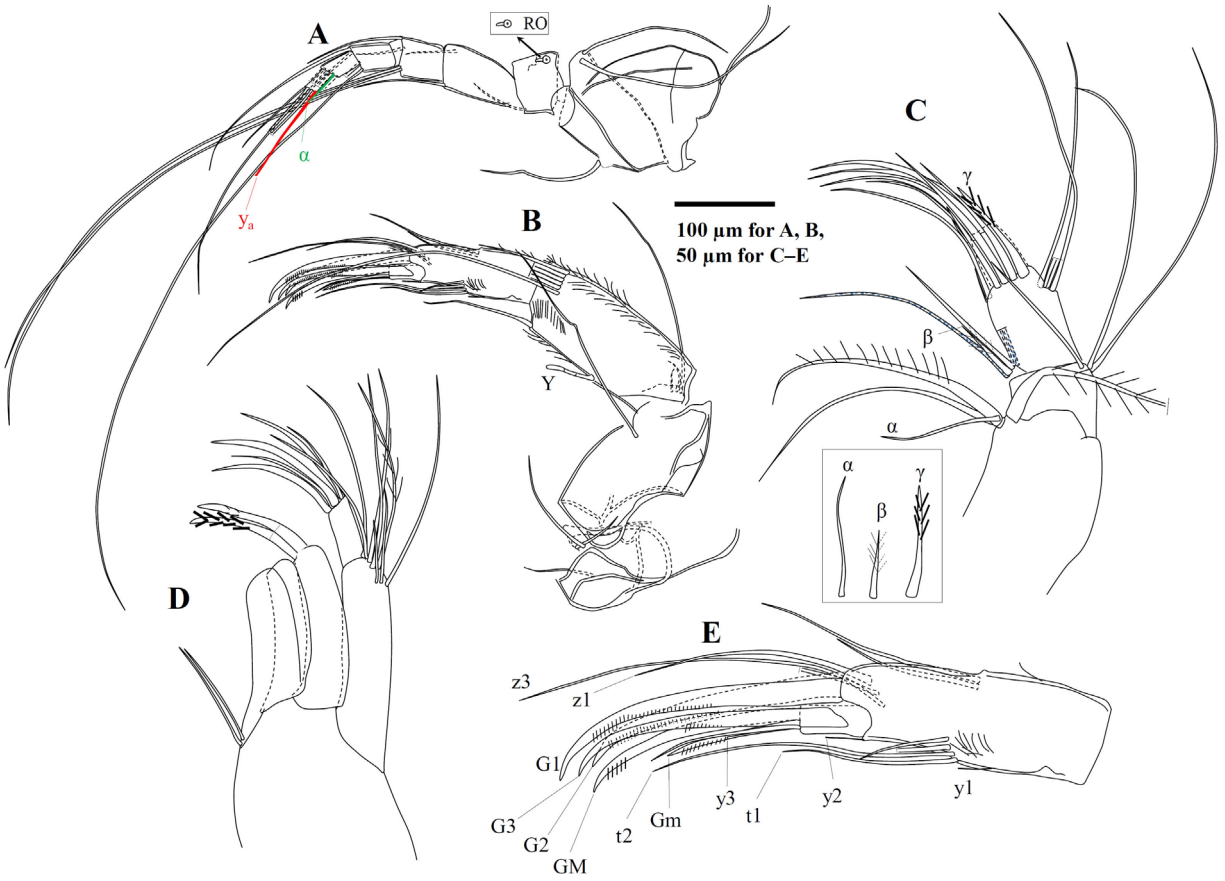

FIGURE 11. *Arctocypris edita* **n. sp.**, white-shell phenotype, female (WOC28). (A) Right A1, exterior view; (B) right A2, interior view; (C) right Md palp, interior view; (D) right Mx, interior view; (E) distal part of (B).

Ur (Figs 9D & 12E, F) ramus slightly curved. Sp situated at 1/6 length of ramus from distal end. Gp significantly shorter than Ga, both serrated.

Males unknown.

Remarks. Specimens of this species are represented by two colour types, green (from sites OS11-29, 80; Table 1) and white (sites OS11-9, 11). As there are no obvious morphological differences in carapace shape and chaetotaxy, or size between the two types, we conclude they are conspecific. Differences in the colour of specimens may be related to environmental factors, and similar colour variations have been recorded in other species (e.g. *Dolerocypris ikeyai* Smith & Kamiya, 2006; Smith 2011).

Of the five other species in the genus *Arctocypris*, three are extant and two are known from valves only. *Arctocypris fuhrmanni* and *A. arctica* are found living in Spitsbergen (Olofsson 1918; Petkovski *et al.* 2016), while *A. mareotica* comb. nov. is living in North Africa, parts of Europe, and Central Asia (see review of distribution in Rasouli *et al.* 2016). Valves of *A. mareotica* comb. nov. from modern sediments have also been recorded from the Tibetan Plateau (e.g. Li *et al.* 2010; Song & Wang 2014; Song *et al.* 2015a; 2015b; Zhang *et al.* 2013). *Arctocypris foveata* and *A. dulcifons* were originally reported from Pleistocene deposits in Canada and Germany respectively, with valves of *A. dulcifons* later found in Siberia and the Qinghai region of China (Mischke *et al.* 2003; Wetterich *et al*. 2005; Li *et al.* 2010).

Arctocypris edita **n. sp.** resembles the type species of the genus, *A. fuhrmanni,* with an overall similar lateral view of the carapace, similar number and positions of inner lists on the calcified inner lamellas of both valves and similar chaetotaxy of the appendages. Compared to *Arctocypris edita* **n. sp.**, the carapace of *A. fuhrmanni* is noticeably less elongate, the dorsal margin more angular and the surface ornamentation more pronounced. The appendages of both species are a close match, but they differ in the length of the A1 y_a aesthetasc: this is about twice as long as the terminal segment in *A. fuhrmanni* (remeasured from the type specimens, somewhat longer than that figured in the original description by Petkovski *et al.* (2016)—B. Scharf, Bremen, Germany, pers. comm.), but 3–4

times the length of the terminal segment in *Arctocypris edita* **n. sp.** The numbers of setae/claws on the terminal segment of the Mx are five in both species (four was reported for *A. fuhrmanni* by Petkovski *et al.* (2016), but there are actually five—B. Scharf, Bremen, Germany, pers. comm.). Both tooth bristles on the third endite of the Mx are serrated in *A. fuhrmanni*, but in *Arctocypris edita* **n. sp.** the tooth bristles are rather variable in the amount of serration expressed. *Arctocypris arctica* and *A. mareotica* comb. nov. are both smooth and have different lateral outlines of the valves compared to *Arctocypris edita* **n. sp.** The original description of *A. dulcifons* shows a species that is noticeably less elongate than *Arctocypris edita* **n. sp.** (Diebel & Pietrzeniuk, 1969), but later reports of this species figure slightly more elongate specimens (e.g. Wetterich *et al.* 2005; Fuhrmann 2012). This species can be distinguished from *Arctocypris edita* **n. sp.** by its more inflated postero-ventral margin, straighter postero-dorsal margin, stronger ornamentation, less laterally compressed anterior and less elongate lateral outline. *Arctocypris foveata* is the least elongate species in the genus, with a rather truncated posterior margin (Delorme 1968), producing a lateral outline quite different to that of *Arctocypris edita* **n. sp.**

Arctocypris edita **n. sp.** was found in shallow waters of ponds and the littoral zone of a lake on either a sandy or muddy substrate, once with submergent macrophytes, at altitudes of 4191–4626 m (Table 1).

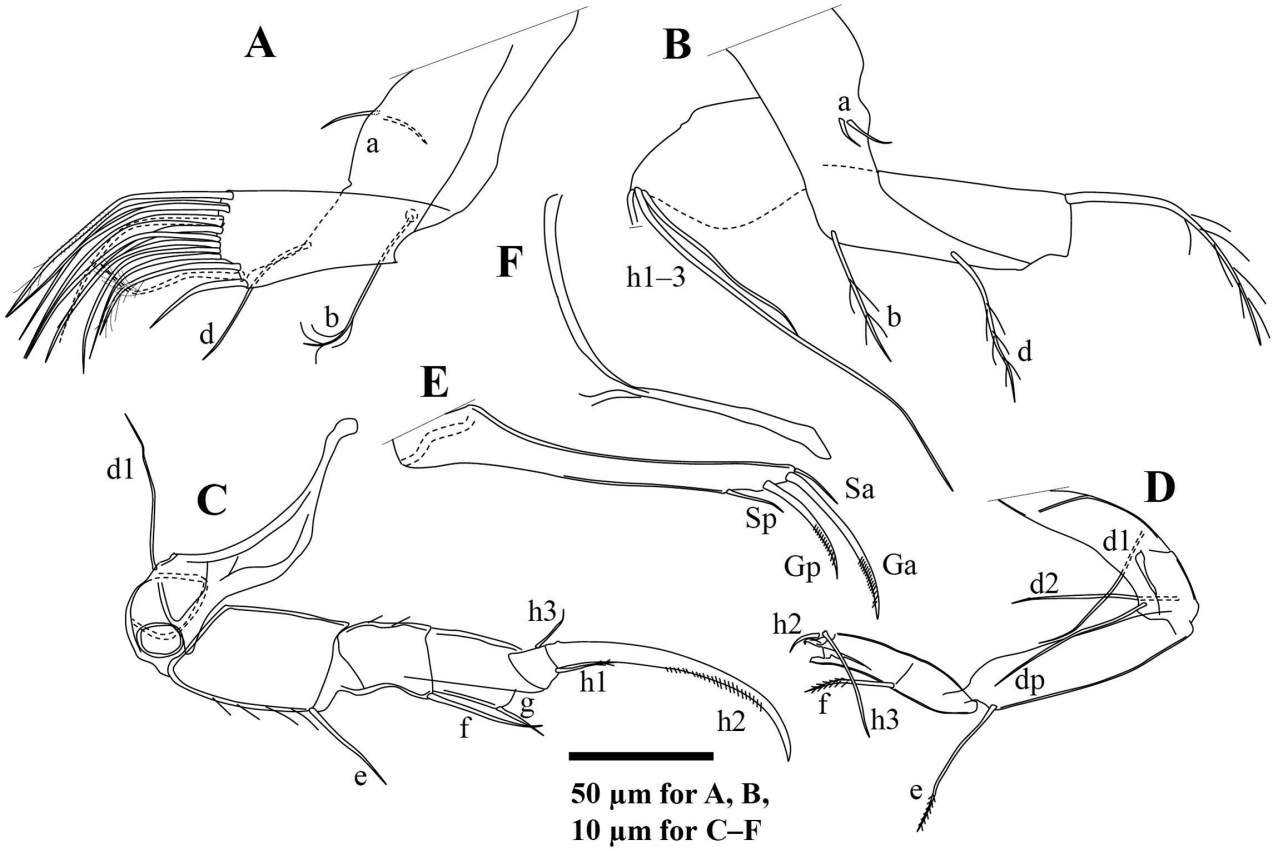

FIGURE 12. *Arctocypris edita* **n. sp.**, white-shell phenotype, female (A, WOC34; B–F, WOC65). (A) Left L5, exterior view; (B) left L5, interior view; (C) left L6, exterior view; (D) right L7, exterior view; (E) Ur; (F) Ur attachment.

Subfamily Cypridinae Baird, 1845

Genus *Cypris* O.F. Müller, 1776

***Cypris pubera* O.F. Müller, 1776**
(Figs 13–15)

For an abbreviated synonym list see Meisch *et al.* (2019), but also see below.

Material examined. Two dissected females (WOC9, WOC10) (Table 1).

Dimensions. Female (LV, n = 2) length 2.30–2.50 mm, H/L ratio 0.54–0.57.

Description of female. Shell (Fig. 13) sub-triangular in lateral view. Dorsal margin strongly arched, with greatest height slightly in front of mid-length. Postero-dorsal margin bluntly angular. Anterior margin broadly rounded. Posterior margin narrowly rounded. Ventral margin weakly sinuous with small expansion at mouth area. Small spines (or denticles) present near anterior and posterior margins. Longer spine situated at postero-ventral part of RV. Shell surface strongly pitted and densely covered with small setae, with small number of tiny bumps on both anterior and posterior areas. Structure of marginal zone asymmetric in interior view. In RV, selvage significantly displaced inward along anterior, postero-ventral, and most part of ventral margins, with valve margin defined by flange. Inner list present but only easily recognised at postero-ventral part of shell. In LV, selvage only slightly displaced inward at anterior and postero-dorsal margins and being peripheral along rest of free margin. Inner list well developed and running close to inner margin. Carapace inflated in dorsal view, with greatest width slightly behind mid-length.

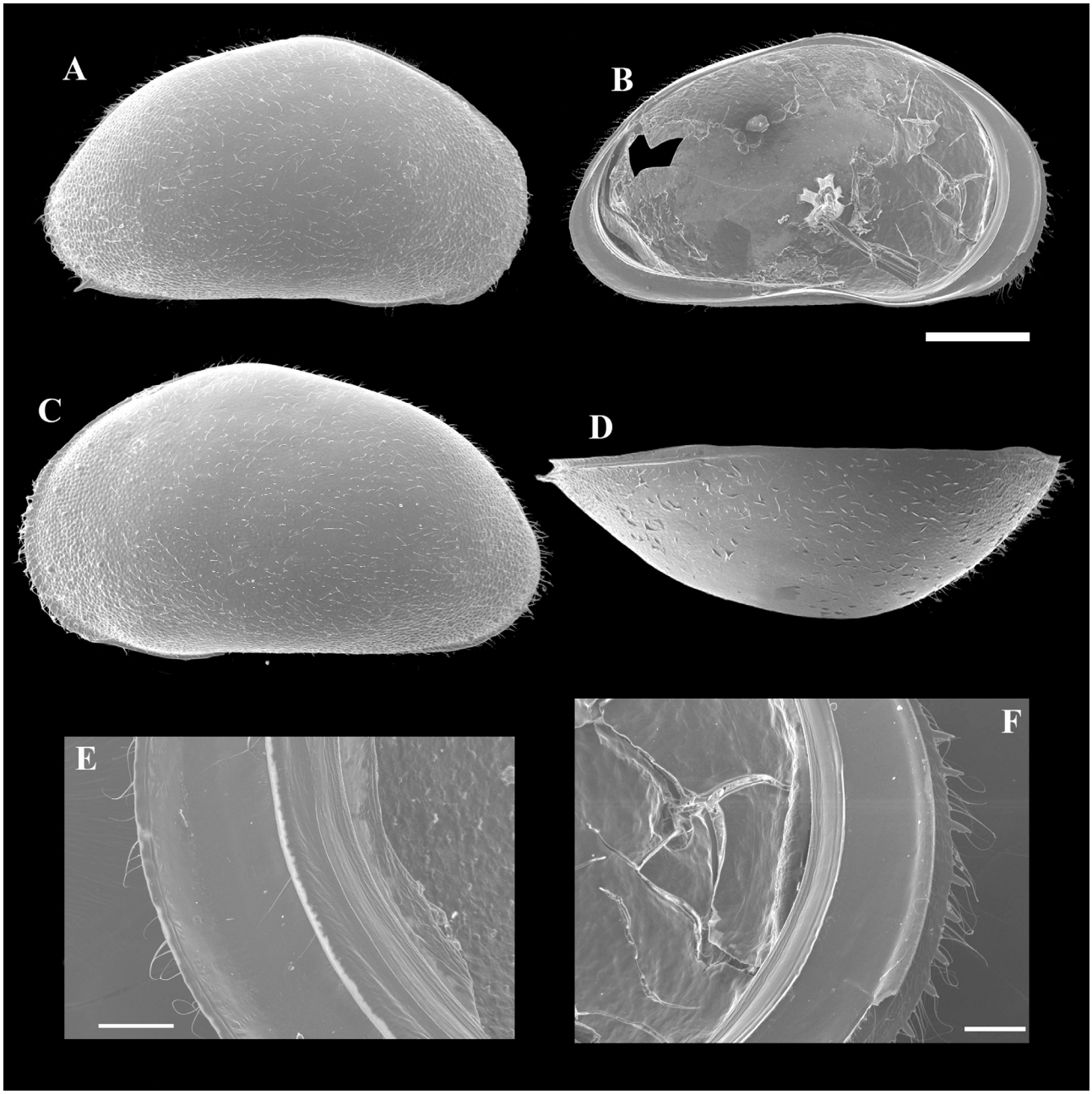

FIGURE 13. *Cypris pubera* O.F. Müller, 1776, female. (A) RV, exterior view (WOC9); (B) LV, interior view (WOC9); (C) LV, exterior view (WOC10); (D) LV, dorsal view with anterior end on the left (WOC10); (E) enlargement of antero-ventral margin of RV (WOC10); (F) enlargement of anterior margin of LV (WOC9). Scale bars: A–D = 500 μm; E, F = 100 μm.

A1 (Fig. 14A, B) with eight segments, first two of which fused forming large base, carrying one short dorsal seta and two intermediately long ventral setae. Third segment short, with one short dorso-apical seta. RO stemmed from lobe-like structure on extero-ventral surface of third segment, very small compared with segment, distally with slightly enlarged opening. Fourth segment elongate, with one dorso-apical seta extending beyond next segment, and one short, plumose seta extending to about end of next segment. Fifth segment sub-quadrate, with two very long, plumose setae extending far beyond terminal segment with up to 80% of total length, and two unequally long ventral setae, one of which plumose, extending to end of sixth segment, other one smooth, extending to end of terminal segment. Sixth segment slightly elongate, with three very long, plumose setae and one intermediately long, smooth seta. Seventh segment elongate, with four very long, plumose setae and very short, sinuous seta α. Eighth segment slender, with three apical setae and aesthetasc y_a, latter of which about twice as long as terminal segment. Ventral seta shorter than y_a, not claw-like. Two medial setae very long.

A2 (Fig. 14C, D) basal segment with one postero-lateral seta and two unequally long ventral setae. Second segment robust, with one ventro-apical seta extending to or beyond middle of penultimate segment. Longest exopodal seta extending beyond mid-length of third segment (first endopodal segment), plumose along distal half. Other two exopodal setae progressively shorter. Aesthetasc Y short, situated behind mid-length of third segment. Third segment with one plumose ventro-apical seta extending to basal part of terminal segment. Swimming setae with long pseudochaetae, and extending slightly beyond tip of claws. Sixth seta only extending to 1/3 length of penultimate segment from proximal part. Third segment also with well-developed pseudochaetae on both dorsal and ventral areas. Aesthetasc y1 very short, situated behind t-setae. All t-setae plumose, among which t2 and t3 being longest, extending to 1/3 or 1/4 of length of claws from tips. Dorso-medial setae of penultimate segment (second endopodal segment) extending beyond terminal segment. z-setae not transformed, not extending to tip of claws. Aesthetasc y2 short. G1 longest claw, G2 and G3 sub-equal in size. GM reaching tips of G2 and G3. Gm reaching about distal third of GM. All claws serrated. Aesthetasc part of y3 about 1/3 length of Gm.

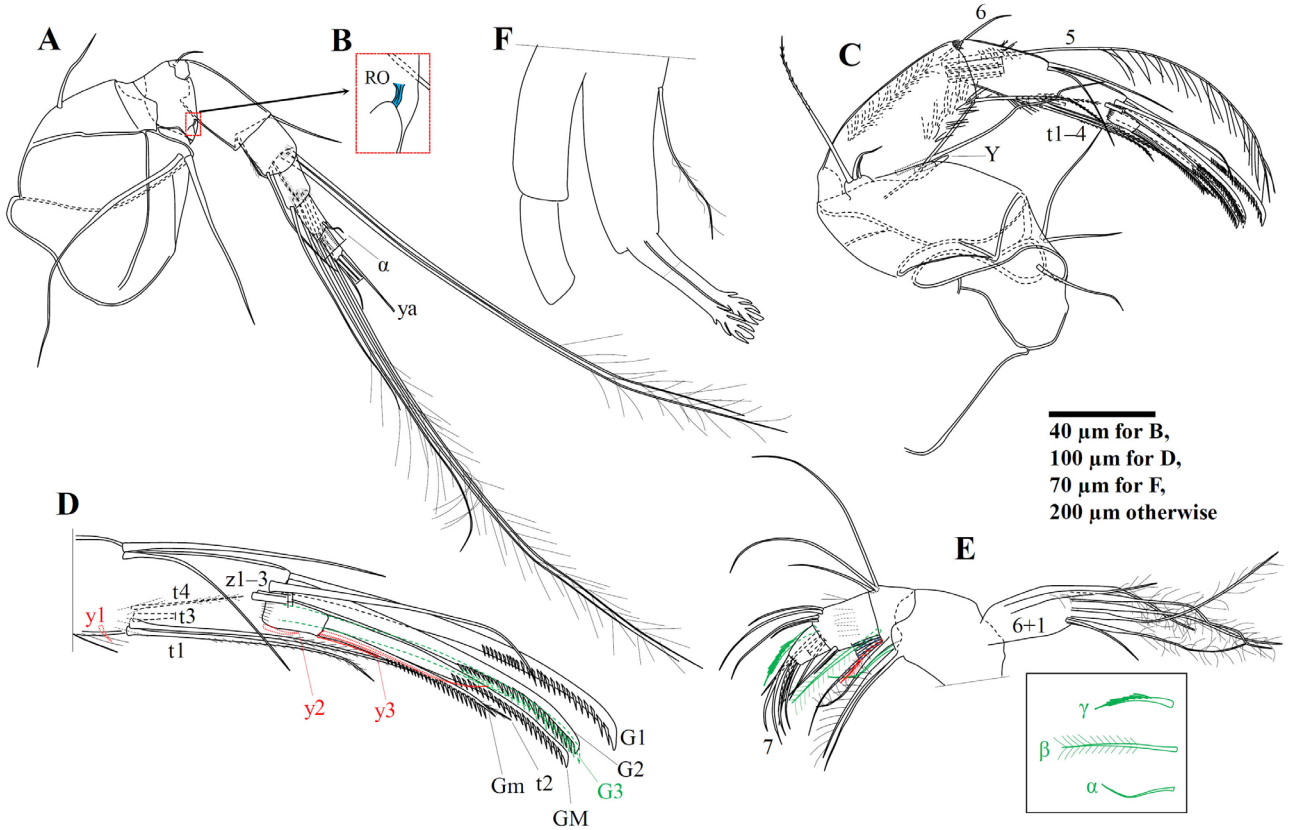

FIGURE 14. *Cypris pubera* O.F. Müller, 1776, female (WOC10). (A) Right A1, exterior view; (B) close-up view of RO; (C) right A2, exterior view; (D) distal part of (C); (E) left Md palp, exterior view; (F) left Mx palp and 1st endite, exterior view (not all structures drawn).

Md palp (Fig. 14E) with four segments. First segment (basis) with slender seta α accompanied by three unequal setae, two of which with setules. Second palp segment (first endopodal segment) with three dorso-apical setae of unequal length, and ventrally with four smooth, grouped setae, slightly shorter but plumose seta β, and shorter plumose accompanying seta. Third segment with ten apical setae, including strongly setulose seta γ. Third segment also with fine, long pseudochaetae on interior side. Fourth segment with seven distal setae/claws. Vibratory plate (exopod) with 6+1 plumose filaments.

Mx (Fig. 14F) with tooth bristles on third protopodal endite lobe strongly serrated distally. Third endite lobe also with plumose proximal seta.

L5 (Fig. 15A) protopod with two small setae a and plumose setae b and d. Palp (endopod) carrying three moderately long, plumose distal setae.

L6 (Fig. 15B) robust, consisting of four segments (penultimate segment undivided). First segment short, proximally with elongate, sclerotized anchoring structure, bearing long seta d1 and short, plumose seta d2. Second segment robust, bearing long pseudochaetae and antero-apical seta e, with setules distally. Third segment elongate, not sub-divided, bearing pseudochaetae, carrying medially plumose seta f and distally short seta g. Fourth segment short and sub-quadrate, bearing plumose seta h1, strongly serrated claw h2, and short seta h3.

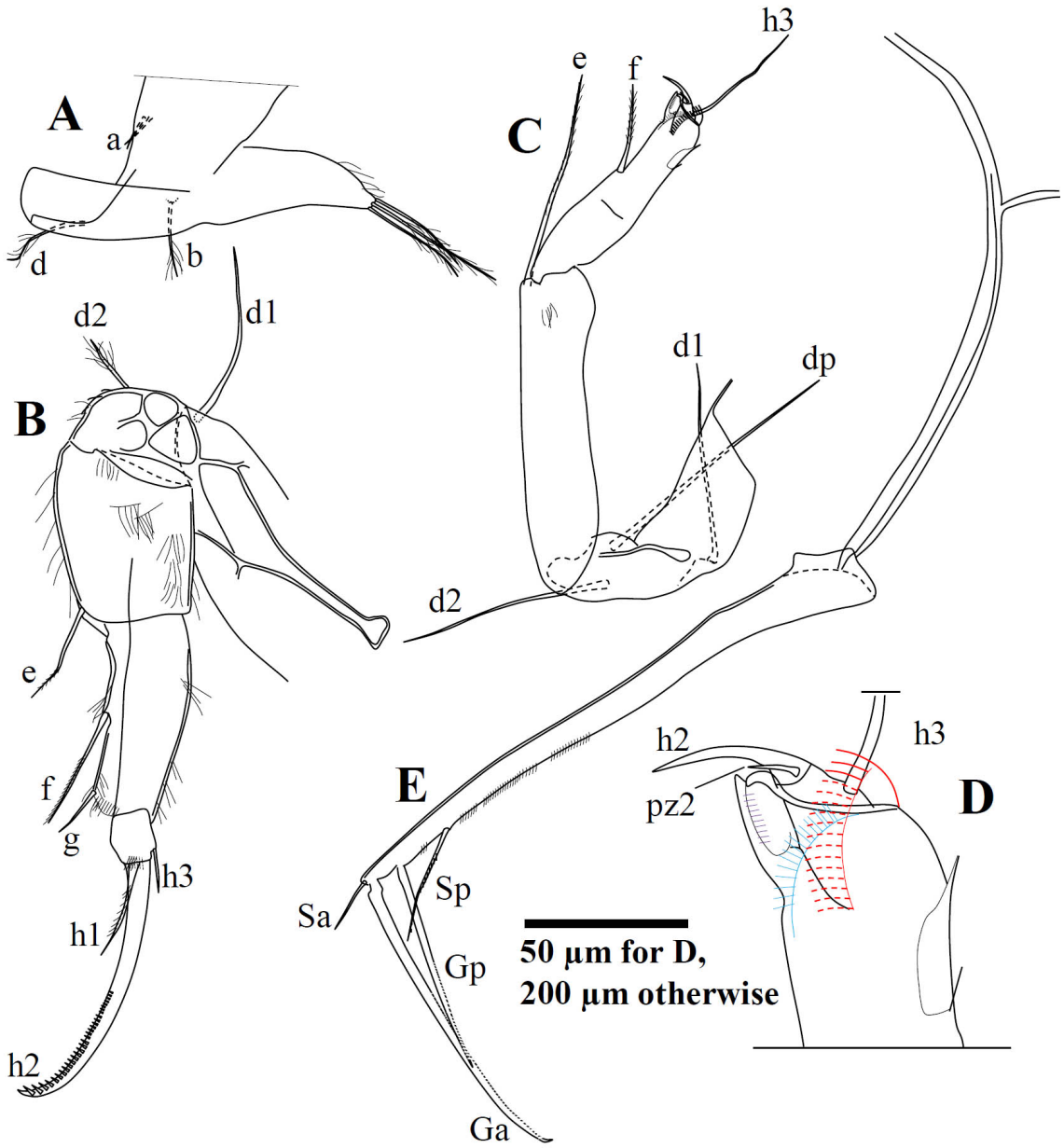

FIGURE 15. *Cypris pubera* O.F. Müller, 1776, female (WOC10). (A) Left L5, exterior view (exopod not drawn); (B) left L6, exterior view; (C) right L7, exterior view; (D) distal part of right L7; (E) Ur and attachment.

L7 (Fig. 15C, D) with three segments. Basal segment bearing sub-equally long setae d1, d2 and dp. Second segment longest, bearing plumose seta e extending to about distal end of terminal segment, and with few pseudochaetae at sub-apical part. Third segment bearing plumose seta f and distally well developed pincer organ.

Ur ramus (Fig. 15E) thin and elongate, with short pseudochaetae along distal half of posterior margin. Claw Ga slightly longer than half length of ramus, slightly serrated. Gp claw about 1/3 length of ramus, slightly serrated. Sp seta situated close to distal claws, plumose, about twice as long as Sa. Main branch of Ur attachment curved, with small dorsal branch about two-thirds of length from ramus.

Remarks. This species can be identified by the shape, large size of the carapace, presence of small denticles along the anterior and posterior margins of both valves, as well as by the development of a longer spine at the postero-ventral margin of the RV. *Cypris triaculeata* (Daday, 1892) is very similar to *C. pubera,* mostly differing in the position and numbers of spines on the postero-ventral part of the RV. These differences were considered as intraspecific variation by Meisch *et al.* (2019) leading to them listing *C. triaculeata* as a junior synonym of *C. pubera.* However, Mesquita-Joanes *et al.* (2020) considered the two species as separate based on morphology and a genetic analysis. They judged that some previous reports and figures of *C. pubera* actually refer to *C. triaculeata*, causing the confusion between the two species. With our specimens, the largest posterior spine on the RV is located near the ventral edge, corresponding to *C. pubera* (the largest spine is higher up on the posterior edge and near the point at maximum carapace length in *C. triaculeata*).

Cypris pubera is a widespread species mostly occurring in the Holarctic (e.g. Meisch 2000), but with additional records from South America and New Zealand (e.g. Coviaga *et al.* 2018; Eager 1994). However, as noted by Mesquita-Joanes *et al*. (2020), some of these records could be misidentifications of *C. triaculeata.* Previous Chinese records include those from Nyalam District, Tibet (Jiang & Chen 1974; Chen 1982). During this study, *C. pubera* was found once in a shallow pond with a sandy substrate and macrophytes at an altitude of 4167 m (Table 1).

Subfamily Cypridopsinae Kaufmann, 1900

Genus *Potamocypris* Brady, 1870

Potamocypris variegata (Brady & Norman, 1889)

(Figs 16, 17)

Cypridopsis variegata Brady & Norman, 1889

Material examined. One dissected female (WOC57) (Table 1).

Dimensions. Female (LV, n = 1) length 0.60 mm, height 0.35 mm, H/L ratio 0.58.

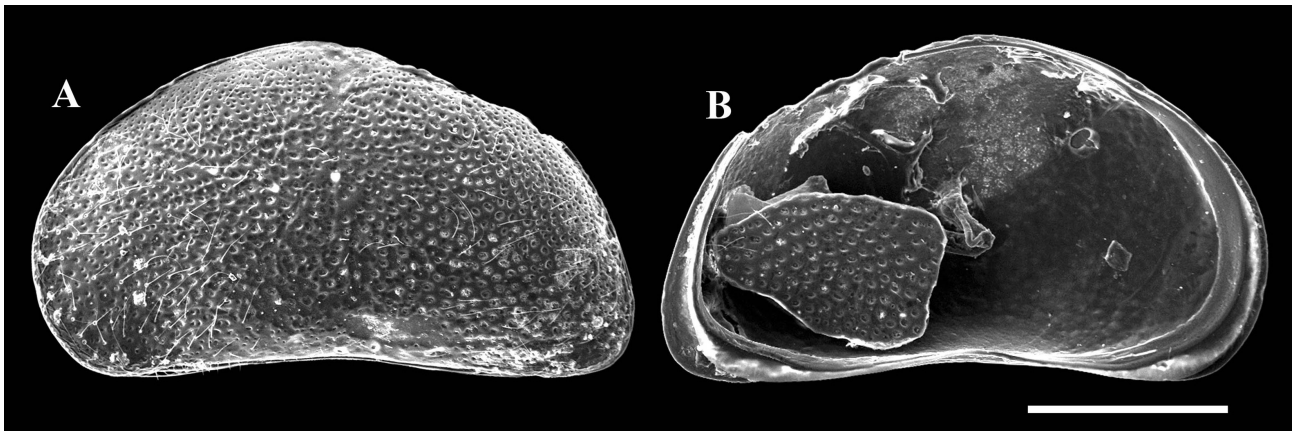

FIGURE 16. *Potamocypris variegata* (Brady & Norman, 1889), female (WOC57). (A) LV, exterior view; (B) LV, interior view (with a piece of RV fragment). Scale bar = 200 μm.

Description of female. Carapace (Fig. 16) sub-triangle in lateral view. Dorsal margin strongly arched with highest point near mid-length. Anterior margin broadly rounded with maximum curvature at antero-ventral area.

Postero-dorsal angle prominent with central posterior margin slightly curved and running down to tightly curved postero-ventral margin. Ventral margin concave. Valve surface densely pitted and covered with fine setae; pits slightly smaller towards periphery of valves compared with central area. In interior view, selvage displaced inwards. Anterior inner list running along medial part of calcified inner lamella. Posterior inner list situated very close to inner margin of calcified inner lamella.

A1 (Fig. 17A) with eight segments. First two segments fused into elongate base, supporting one short dorsal seta and two long ventral setae. Third segment sub-trapezoidal, with one short dorsal seta. Fourth segment slightly elongate, with one dorso-apical seta extending well beyond end of fifth segment, and one tiny ventro-apical seta not reaching to end of fifth segment. Fifth segment stout, with two unequal dorso-apical setae, and two very short, unequal ventro-apical setae. Sixth segment slightly elongate, with two very long, dorso-apical setae of sub-equal length, and two ventro-apical setae of different lengths, one of which claw-like. Seventh segment with four apical setae reaching tips of longest apical seta of sixth segment. Seta α not observed. Eighth segment slender, with slender aesthetasc y_a, about twice as long as eighth segment, ventro-apical seta, slightly longer than y_a, and two medial, much longer setae.

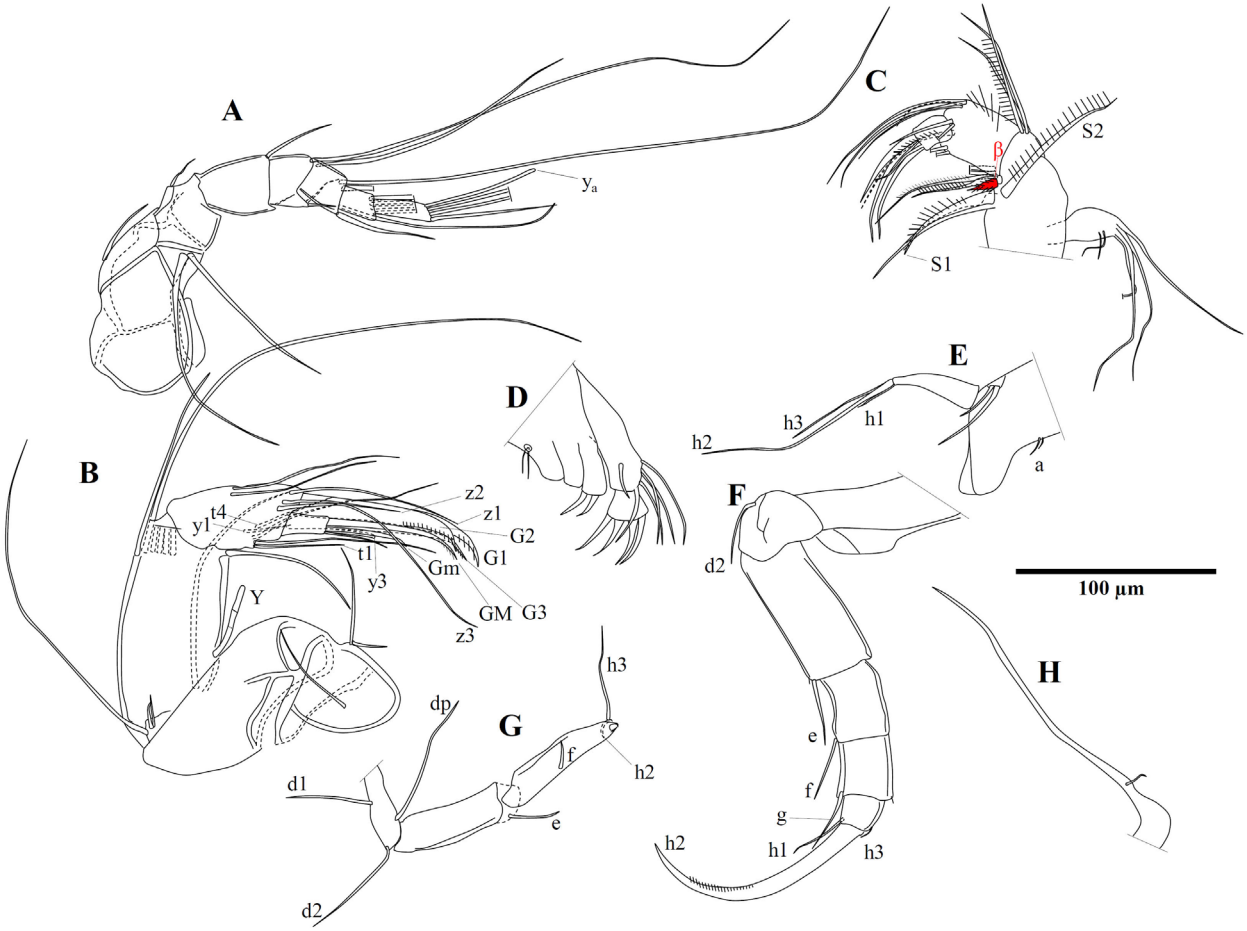

FIGURE 17. *Potamocypris variegata* (Brady & Norman, 1889), female (WOC57). (A) right A1, exterior view; (B) right A2, exterior view; (C) right Md palp, interior view; (D) left Mx, interior view (exopod not shown); (E) right L5, exterior view; (F) right L6, interior view; (G) right L7, interior view; (H) Ur. Note that the vibratory plate of L5 (panel E) has been deformed so that it is difficult to discern, and that the two setae changed their direction after dissection.

A2 (Fig. 17B) basal segment with one slender latero-posterior seta and two unequal ventro-apical setae. Second segment with one long ventro-apical seta. Longest exopodal seta with very fine distal part, reaching mid-length of penultimate segment or beyond. Aesthetasc Y situated proximal to mid-point of first endopodal segment, slender, 2- or 3-segmented, reaching beyond mid-length of segment. Natatory setae extending beyond terminal claws with ca. half of length. Sixth seta reaching to about end of terminal segment. Ventro-apical seta of this segment reaching to about tip of aesthetasc y3. Penultimate segment with two medio-dorsal setae of slightly unequal length. t-setae

unequal in length, with t2 and t3 longest, extending beyond terminal segment with more than half length. Aesthetasc y1 situated proximally of t setae, extending slightly beyond penultimate segment. z-setae unequal, with z3 longest and z2 shortest. G claws serrated. G1 longest claw, G2 most robust and most serrated. GM slender and finely serrated at distal part, only slightly longer than G2. Gm 3/5 length of GM. Aesthetasc part of y3 extending slightly beyond mid-length of Gm.

Md palp (Fig. 17C) 4-segmented. S1 and S2 robust, covered with long pseudochaetae. Accompanying seta slender and smooth. Seta α not observed. Setal group of second segment with three sub-equally long, slightly plumose setae extending to about mid-length of terminal claws. Accompanying seta shorter, plumose. Seta β short, stout, plumose. Second segment with three slender antero-apical setae one of which plumose. Third segment with about nine apical setae: Four antero-apical, slender, smooth, unequally long setae, one latero-exterior, plumose seta extending beyond mid-length of terminal claws, two slender, smooth latero-interior setae, and about two slender, smooth postero-apical setae. Fine pseudochaetae present at antero-medial part of penultimate segment. Terminal segment with two long, robust claws, one shorter, robust claw, and one short, slender seta. Vibratory plate with two tiny setae and four long rays.

First segment of Mx palp (Fig. 17D) with one short latero-interior seta and five anterior setae. Second segment of Mx palp spatulate, with four claws. Two largest tooth bristles of third endite lobe slightly unequal in length and smooth.

Setae a of L5 (Fig. 17E) protopod tiny. Setae b, c, and d absent. Palp poorly sclerotized, with very long h2 and unequally long h1 and h3. Vibratory plate with two unequal setae.

L6 (Fig. 17F) with four endopodal segments. Seta d1 absent. Seta d2 well developed. Setae e, f, g, and h1 subequally long. Claw h2 robust, serrated. Seta h3 tiny.

L7 (Fig. 17G) with three segments. Seta d1 slightly shorter than d2. Seta dp comparatively short, only slightly longer than d2. Seta e short, not extending to mid-length of terminal segment. Seta f very short. Pincer organ small. Seta h3 slightly S-shaped.

Ur (Fig. 17H) with slightly swollen base, carrying long flagelliform structure and short sub-apical seta.

Remarks. The one specimen of this species recovered during this study is tentatively assigned to the species *Potamocypris variegata* based on the following characters: pitted carapace, long swimming setae, four setae on the terminal segment of the maxillula palp, and two rays on the maxillula branchial plate (Fig. 17). The LV is noticeably more elongate (height / length = 0.56) compared to some other figured specimens of *P. variegata* (height / length = 0.64, Meisch 1985; 0.60, Fuhrmann 2012), and is similar to *Potamocypris smaragdina* (Vávra, 1891). However, *P. smaragdina* has only one ray on the maxillula branchial plate (Meisch 1985). *Potamocypris variegata* has been previously reported from North America and western parts of Eurasia, including western Russia and Iran (see review in Meisch 1985; 2000). The records of this species from Tibet in this study and those from Beijing (Zhai *et al.* 2017, specimens not illustrated) are therefore much further east than previous records. The solitary specimen herein was collected from a small, turbid pond at an altitude of 3075 m.

Family Ilyocyprididae Kaufmann, 1900

Subfamily Ilyocypridinae Kaufmann, 1900

Genus *Ilyocypris* Brady & Norman, 1889

Ilyocypris tibeta n. sp.
(Figs 18–22)

? 2009a *Ilyocypris* cf. *mongolica* Martens, 1991—Wrozyna *et al.*: 8, 12, 14–17, plate 1: 1–8, figs 6–8.
? 2009b *Ilyocypris* cf. *mongolica* Martens, 1991—Wrozyna *et al.*: 672, 673, plate 3: 7–11.
? 2013 *Ilyocypris* cf. *bradyi* Sars, 1890—Zhang *et al.*: 40–43, 45, figs 2, 4, 6 (6–10).
? 2015a *Ilyocypris bradyi*—Song *et al.*: 587, 589–592, figs 1 (1&2), 3, 4 table 1.
? 2016 *Ilyocypris* sp.—Akita *et al.*: 27–30, 35, 37, 38, Figs 3 (16–18), 7, 9, 10, 12, tables 4, 5, 6.

Type locality. A shallow pond in Rutog, Ngari, Tibet, China (32.93723ºN, 79.80317ºE, altitude 4390 m) (OS11-14, Table 1).

Type material. Holotype: a dissected male (WOC39) from type locality (Table 1). Allotype: a dissected female (WOC38) from type locality. Paratypes: two dissected females (WOC40, WOC45) and two dissected males (WOC36, WOC37) (Table 1). Carapace of WOC40 damaged during dissection.

Other material examined. One dissected, probably male specimen (WOC35) with soft parts deteriorated (only Md coxa remained).

Derivation of name. From name of the province where the specimens were collected.

Dimensions. Male (LV, n = 3, WOC35 not included) length 0.77–0.89 mm, H/L ratio 0.52–0.54. Female (LV, n = 3) length 0.83–0.98 mm, H/L ratio 0.51–0.52.

Diagnosis. Medium-sized *Ilyocypris*. Shell surface covered with small, rounded pits. In interior view, LV with numerous sparsely distributed marginal ripplets in distal area of posterior inner calcified lamella. A2 natatory setae extending to tips of terminal claws. Male L5 palps sub-equal, with sub-apical part of fingers slightly inflated. L6 penultimate segment divided. L7 penultimate segment with two setae (f and g) and apically bearing ca. four unequal length, hook-like structures. Inner lobe (b) of Hp elongate and slender, distally curved towards middle lobe. Middle lobe (h) with relatively narrow neck distally widening to sub-triangular distal part, distal inner corner sharply angled, outer edge angled to rounded. Outer lobe (a) short, distally evenly rounded and partly overlapping middle lobe. Copulatory process (st) slender, with pointed end. ZO with 16–17 internal rosettes of spines.

Description. Carapace (Figs 18 & 19) sub-rectangular in lateral view. Dorsal margin nearly straight, only slightly concave at immediately posterior of mid-length. Highest point situated at 1/4 of valve length from anterior end. Anterior margin broadly rounded. Posterior margin slightly less arched than anterior margin. Ventral margin concave. Anterior sulcus situated at ca. 1/3 of valve length from anterior. Posterior sulcus situated at mid-length. Carapace sub-elliptical in dorsal view. Anterior end bluntly pointed, posterior end more rounded. Greatest width situated immediately behind posterior sulcus. Shell surface densely covered with small, shallow, rounded pits and two tubercles, one in postero-ventral area, and one in anterior dorsal margin, immediately anterior of sulcus. LV with more than 25 short marginal ripplets and number of striations in distal area of calcified inner lamella of postero-ventral margin, and more than 15 short, weakly developed marginal ripplets and number of striations along calcified inner lamella of antero-ventral margin.

A1 (Fig. 20A) with eight segments, first two of which fused, carrying one slightly setulous dorsal seta and two unequally long, smooth ventral setae. Third segment short and stout with one dorso-apical seta extending beyond fourth segment. Fourth segment sub-squarish with one fine dorso-apical seta extending to mid-length of seventh segment and one fine ventro-apical seta reaching mid-length of sixth segment. Fifth segment quadrate with two long dorso-apical setae extending beyond terminal segment with about half of length and two shorter, unequal ventro-apical setae, one of which reaching beyond terminal segment, other one to terminal end of seventh segment. Sixth segment quadrate with two dorso-apical setae extending well beyond terminal segment and two ventro-apical setae, one of which extending beyond terminal segment with 1/5–1/4 of length, other one shorter and claw-like. Seventh segment sub-quadrate with five apical setae, shortest one (seta α) situated at exterior side of segment and extending almost to tip of aesthetasc y_a. Eighth segment slightly elongate with three apical setae and aesthetasc y_a situated at dorsal corner, shorter than claw-like seta at ventral corner. Two medial setae unequal in length.

A2 (Fig. 20B, C) penultimate segment undivided in both sexes. First segment with one ventro-basal seta and two ventro-apical setae, shorter one of which sparsely plumose. Second segment with one ventro-apical seta extending to or slightly beyond mid-length of penultimate segment. Longest exopodal seta reaching distal end of third segment (first endopodal segment). Aesthetasc Y situated at mid-length of third segment, nearly reaching terminal end of third segment (first endopodal segment). Five long swimming setae on third segment reaching terminal claws or only slightly beyond, while sixth one only beyond middle of penultimate segment. Seta t1 extending somewhat beyond terminal segment. Setae t2 to t4 shorter, sub-equal in length, not reaching to end of segment. Seta z1 of male short, slightly claw-like. Setae z2 and z3 not transformed, extending to tips of claws. Female z-setae untransformed. G2 longest and most robust claw. G1 slightly shorter than G2. Male G3 very thin. Female G3 claw-like. Aesthetasc y2 very fine, reaching end of terminal segment. Male terminal segment with GM claw reaching tip of G2. Gm slightly shorter than GM. Aesthetasc part of y3 ca. 1/3 length of GM.

Md and Mx (not shown) typical of genus, with few specific features. Vibratory plate of Mx with four robust reflexed setae.

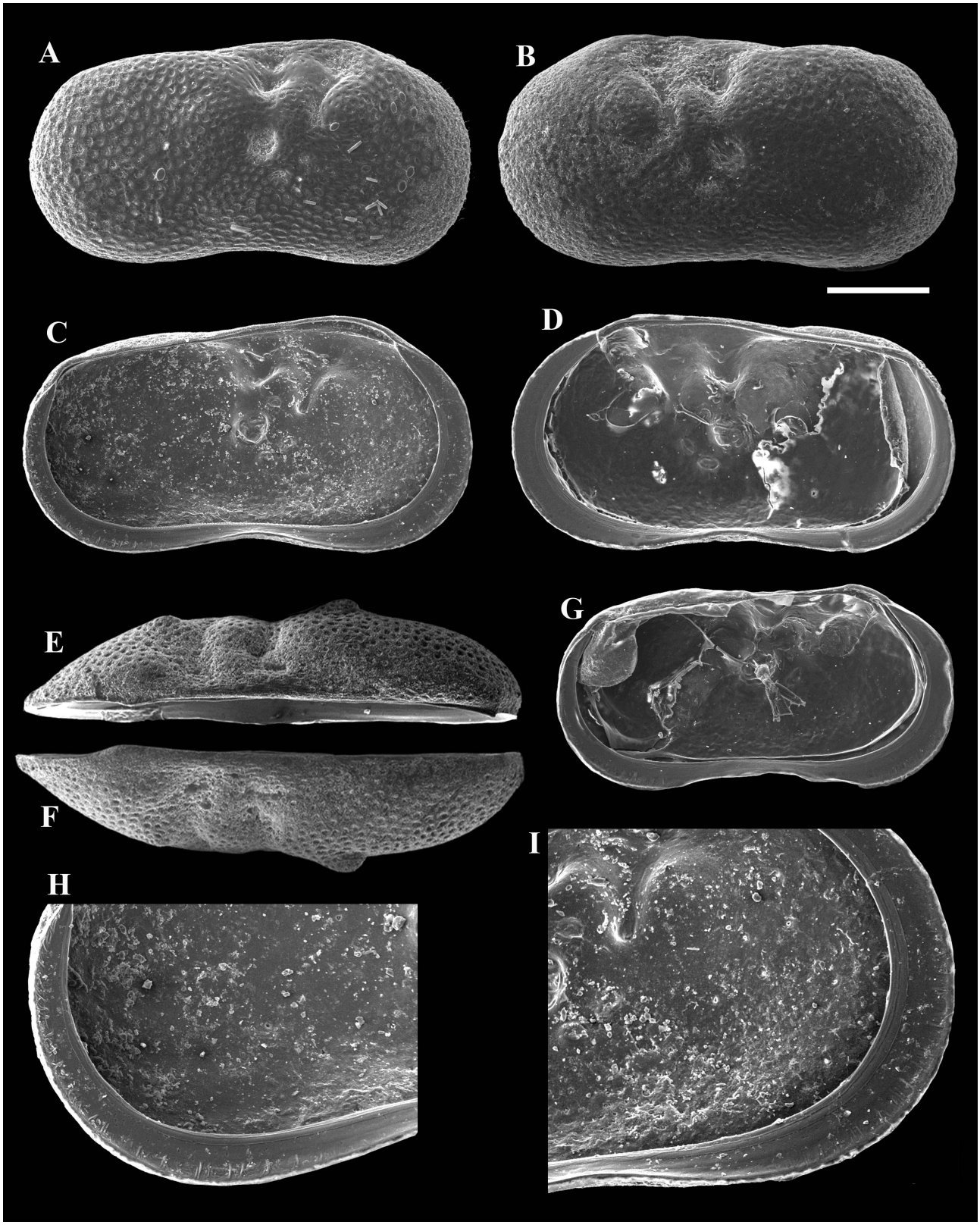

FIGURE 18. *Ilyocypris tibeta* **n. sp.**, male and female. (A) Male RV, exterior view (WOC37); (B) female LV, exterior view (WOC45); (C) male LV, interior view (WOC37); (D) female RV, interior view (WOC45); (E) male RV, dorsal view (WOC35); (F) male LV, dorsal view (WOC35); (G) male LV, interior view (WOC39); (H) enlargement of postero-ventral part of male LV (WOC37), showing marginal ripplets; (I) enlargement of antero-ventral part of male LV (WOC37), showing marginal ripplets. Scale bar: A–G = 200 μm; H = 110 μm; I = 105 μm.

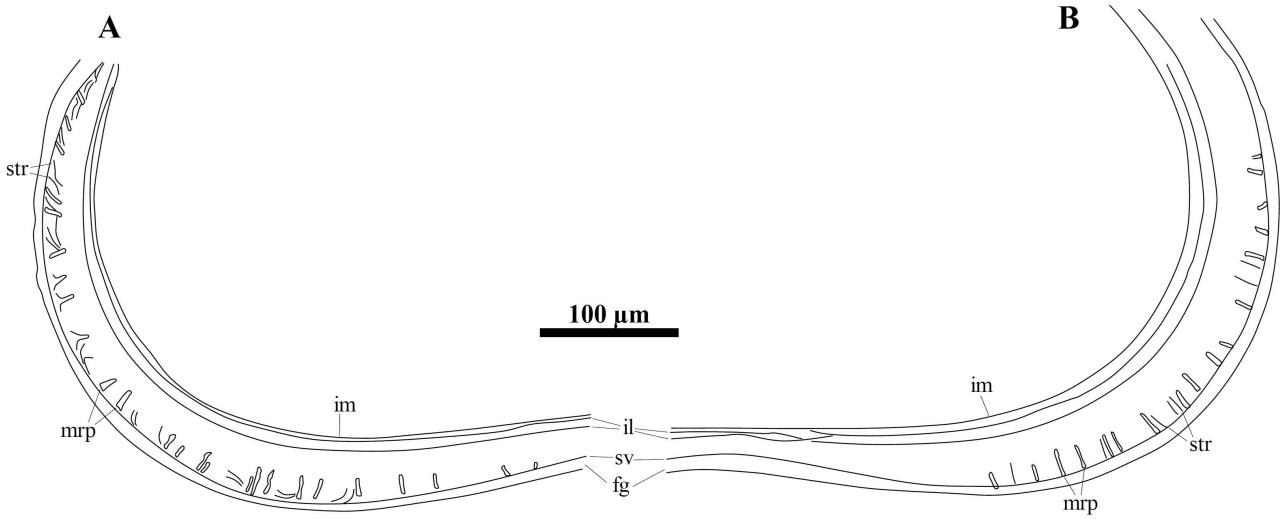

FIGURE 19. *Ilyocypris tibeta* **n. sp.**, male (WOC37). Line drawings showing marginal ripplets on posterior (A) and anterior (B) margins of LV. Also see Fig. 18H, I.

Male L5 palps (Fig. 20D, E) sub-equal, 2-segmented. Basal segment (i.e., trunk) elongate with two ventro-apical setae. Terminal segment (i.e., finger) narrower at middle, with one robust apical seta and one short dorso-subapical seta.

L6 (Fig. 20F) five-segmented. Seta d1 short, d2 absent, e, f and g sub-equal in length. Seta h1 longer than h3. Claw h2 faintly serrated along distal part.

L7 (Fig. 21A, B) with four segments. Seta d1 robust, somewhat claw-like. Setae e and f sub-equally long, shorter than g. Penultimate segment apically with group of small, hook-like structures, two large, one intermediate, and one small sized. Seta h1 shorter but more robust than h2. Seta h2 shorter than h3.

Ur (Fig. 21C) ramus comparatively robust for genus. Sp situated at ca. 2/3 length of ramus, extending to base of claws. Distal half of ramus with fine, long pseudochaetae. Ga and Gp slightly longer than half of ramus length.

Hp (Figs 21D & 22A) inner lobe (b) elongate and slender, distally curved towards middle lobe. Middle with relatively narrow neck distally widening to sub-triangular distal part, distal inner corner sharply angled, outer edge angled to rounded. Outer lobe (a) short, distally evenly rounded and partly overlapping middle lobe. Copulatory process (st) slender, with pointed end.

ZO (Fig. 22D) with ca. 16–17 internal rosettes of spines, both ends inflated but proximal end much larger.

Female reproductive organ (Fig. 21E) with one elongate, ovate lobe.

Remarks. The five-segmented L6, inflated proximal end of the ZO, and 'blade-type' copulatory process of the Hp indicates that *Ilyocypris tibeta* **n. sp.** belongs to the *Ilyocypris japonica* Okubo, 1990 group of Asian species as defined by Smith *et al.* (2019). The new species is particularly similar to *Ilyocypris japonica*, *Ilyocypris mongolica* Martens, 1991 and *Ilyocypris innermongolica* Zhai & Xiao, 2013 in terms of carapace, L7 (with apical hook-like structures on the third segment) and Hp morphologies (Okubo 1990; Martens 1991; Zhai & Xiao 2013; Smith *et al.* 2019). Differences include the following: The A2 natatory setae of *Ilyocypris tibeta* **n. sp.** reach to about the tips of the terminal claws, while these are much longer in the other three species extending significantly beyond the terminal claws by almost 1/2 of their lengths. The setae on the three distal-most segments of the A1 of *Ilyocypris tibeta* **n. sp.** are also much shorter than those of *I. japonica*, *I. mongolica* and *I. innermongolica* (Smith *et al.* 2019; D. Zhai, unpublished data; Zhai & Xiao 2013). The copulatory process (st) of the Hp of *Ilyocypris tibeta* **n. sp.** is distally more slender than those of both *I. mongolica* and *I. japonica*, and most similar to *I. innermongolica.* The outer lobe (a) is small, narrow and evenly rounded in *Ilyocypris tibeta* **n. sp.**, while more angular in *I. innermongolica* and wider in both *I. japonica* and *I. mongolica.* The Hp middle lobe (h) of *Ilyocypris tibeta* **n. sp.** is similar to those of *I. japonica* and *I. mongolica*, although this lobe is slightly more rounded on the outer distal edge and less inflated in *Ilyocypris tibeta* **n. sp.** The Hp middle lobe of *I. innermongolica* is significantly different to *Ilyocypris tibeta* **n. sp.** and the other two species, being distally much less inflated. The ZO of all the male *I. mongolica* specimens (Zhai & Zhao 2014) have 13–14 rows of spines; while the number is larger in *Ilyocypris tibeta* **n. sp.** (16–17),

similar to *I. japonica* (15–17) and *I. innermongolica* (17–21). The hook-like structures of the L7 are well-developed in *Ilyocypris tibeta* **n. sp.**, similar to those of *I. mongolica,* and more pronounced than those of *I. japonica* and *I. innermongolica*.

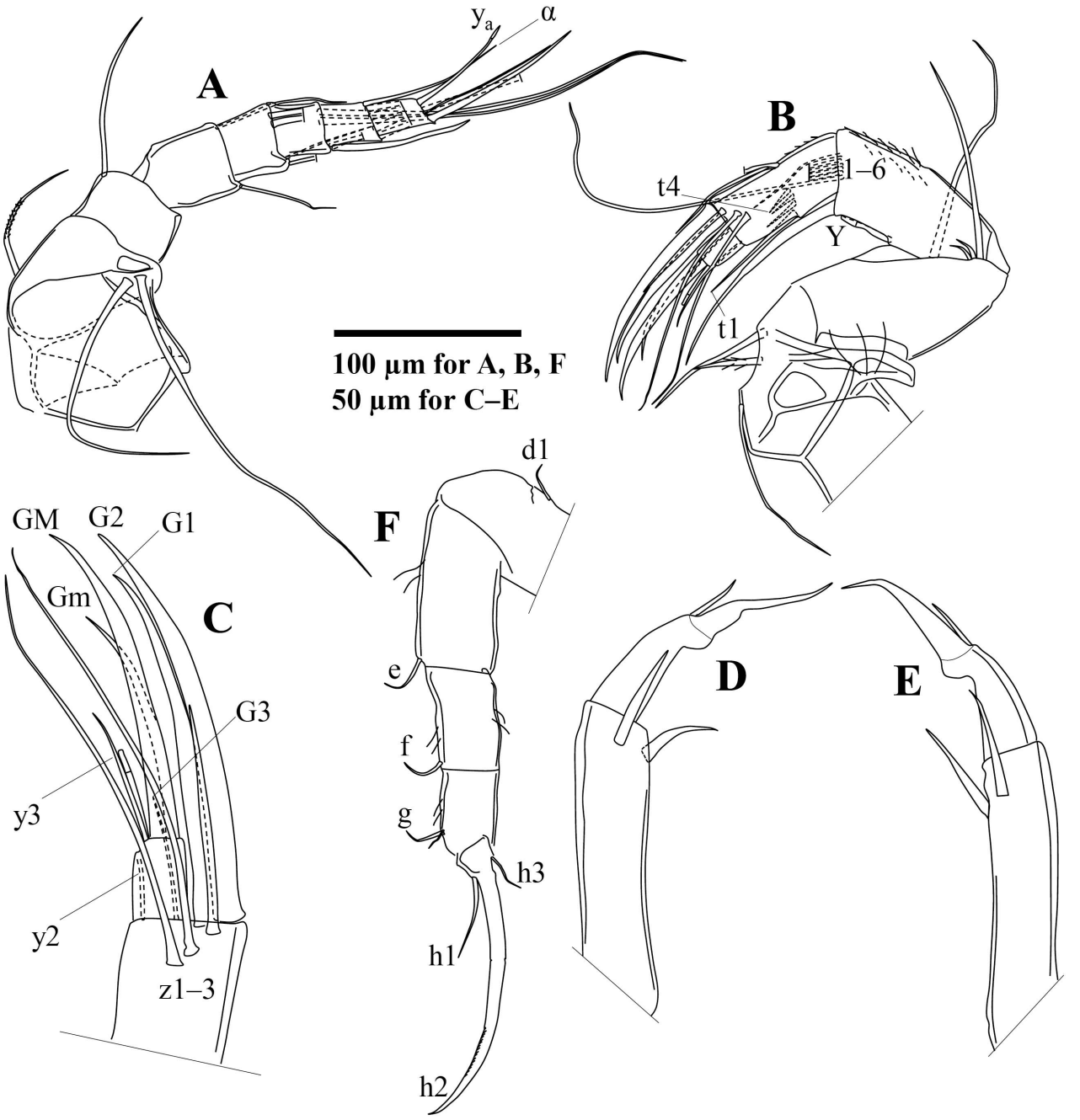

FIGURE 20. *Ilyocypris tibeta* **n. sp.**, male (WOC39). (A) Right A1, exterior view; (B) left A2, exterior view; (C) distal part of (B); (D) left L5 palp; (E) right L5 palp; (F) left L6, exterior view.

The type locality of *Ilyocypris tibeta* **n. sp.** is a small, shallow pond with a soft, yellowish substrate, a few macrophytes and animal footprints around the edges. It was also found in two other places, a pond with a soft mud substrate, and in the riffle zone of a slowly flowing river (Table 1). Altitudes of these sites ranges from 4325 to 4593 m.

Several reports of *Ilyocypris* species from the Tibetan Plateau figure valves that are very similar to *Ilyocypris tibeta* **n. sp.** (e.g. Wrozyna *et al*. 2009a; 2009b; Zhang *et al*. 2013; Song *et al*. 2015a; Akita *et al*. 2016; see synonymy list above). The carapaces of *Ilyocypris* species generally show a strong resemblance to each other, but can also show high amounts of intraspecific variation (e.g. tubercle development, and lateral view of the carapace), complicating identification on valves alone (e.g. Mazzini *et al.* 2014; Smith *et al.* 2019). The most reliable characters for

identification are found on the appendages and male sexual organs. Thus it is not possible to determine if valves previously figured are definitely conspecific with *Ilyocypris tibeta* **n. sp.**, and highlights the importance of soft part examination when possible.

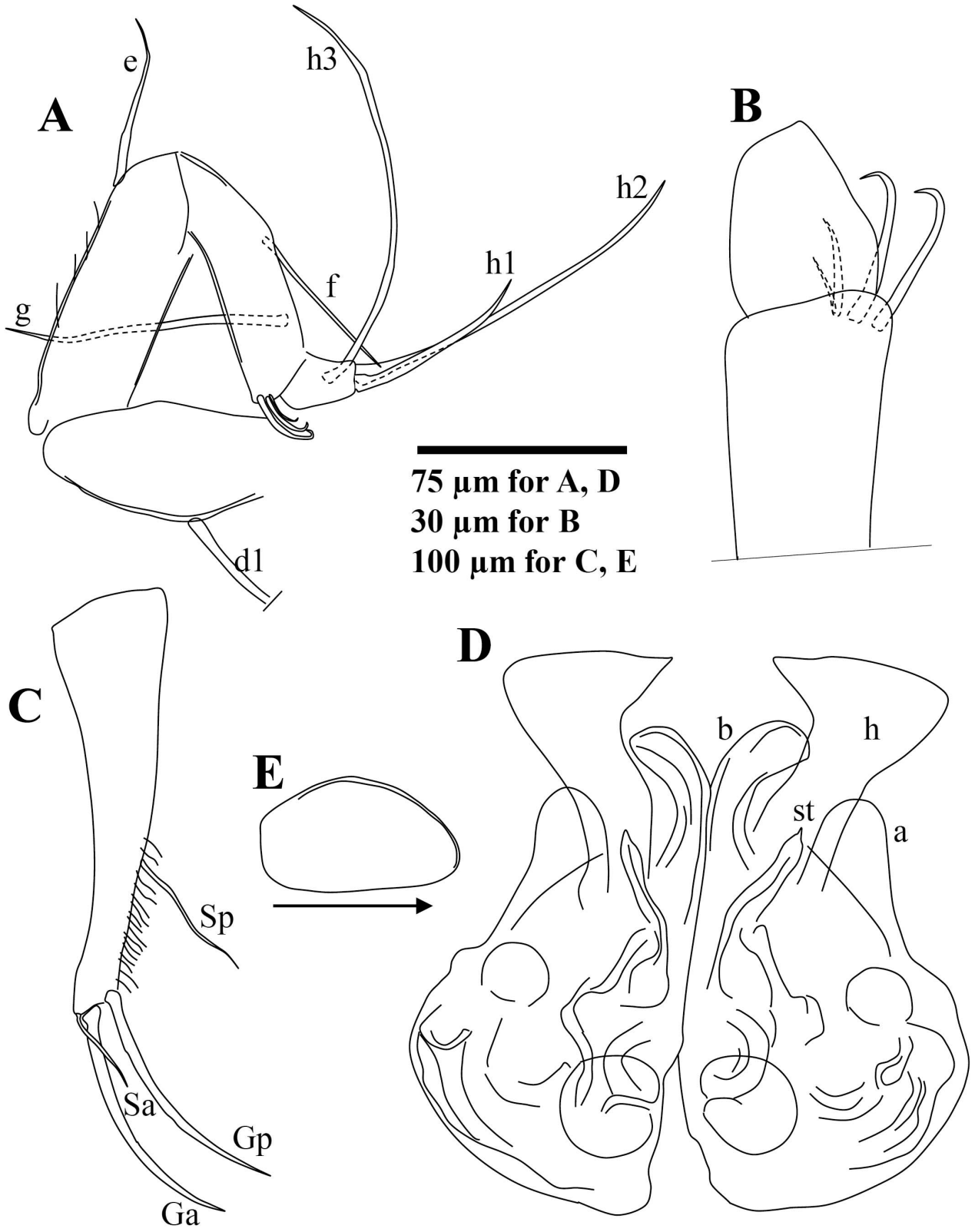

FIGURE 21. *Ilyocypris tibeta* **n. sp.**, male (A, B, D, WOC39) and female (C, WOC45; E, WOC40). (A) Right L7, exterior view; (B) distal part of left L7, interior view, showing the hook-like setules; (C) Ur; (D) Hp; (E) outline of female reproductive organ, arrow indicates anterior.

The scattered known localities of living (and possible conspecific sub-fossil) material of this species suggests that it could be widespread at least in the southern and western parts of Tibet, and it probably favours shallow, muddy habitats.

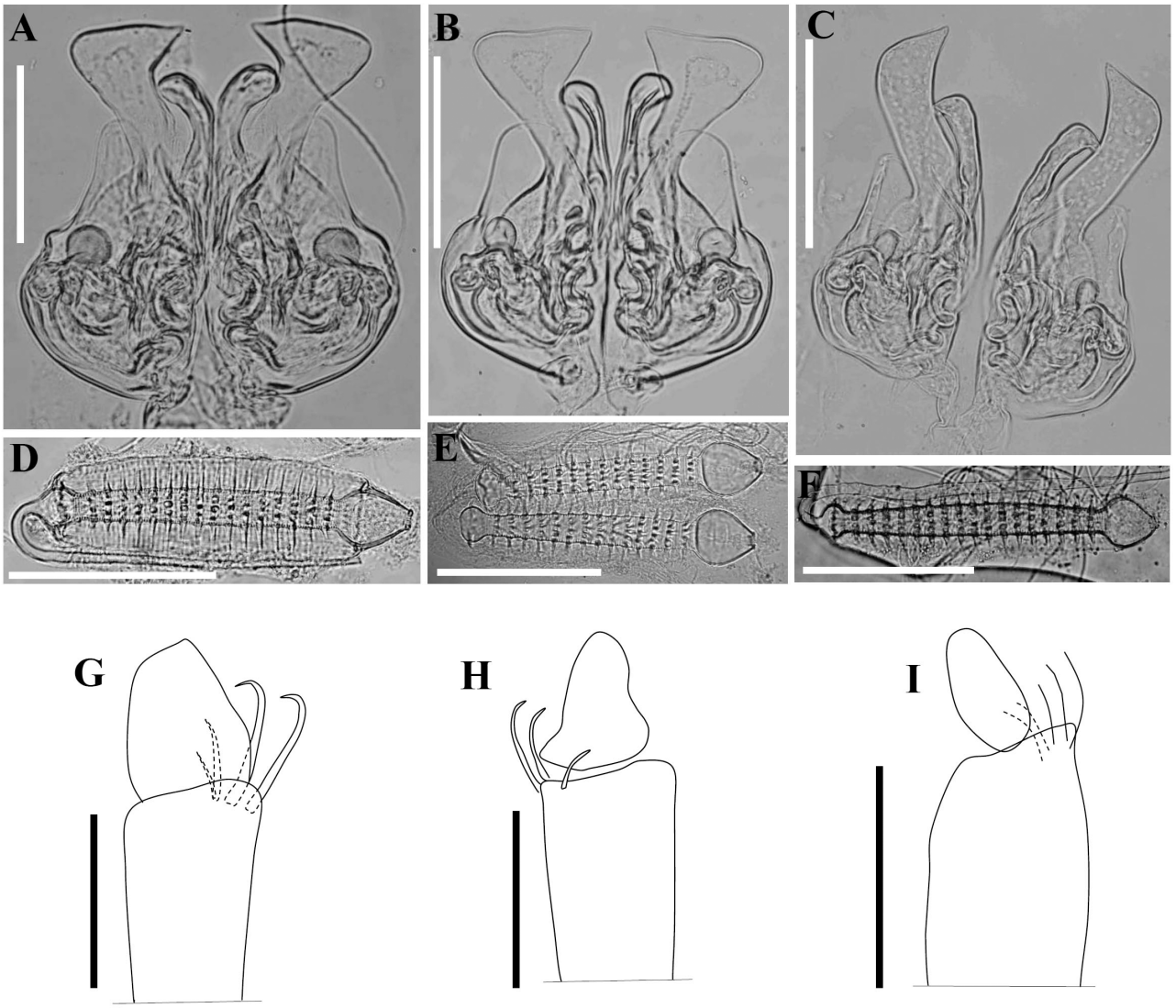

FIGURE 22. Comparisons between male morphologies of *Ilyocypris tibeta* **n. sp.**, *Ilyocypris mongolica* Martens, 1991 and *Ilyocypris innermongolica* Zhai & Xiao, 2013. (A) Hp of *I. tibeta* **n. sp.**, WOC39; (B) Hp of *I. mongolica*, dyzoc321; (C) Hp of *I. innermongolica*, dyzoc100 (paratype); (D) ZO of *I. tibeta*, WOC39; (E) ZOs of *I. mongolica*, dyzoc320 (cf. Zhai & Zhao, 2014); (F) ZO of *I. innermongolica*, dyzoc5 (paratype); (G) distal setules on penultimate L7 podomere of *I. tibeta* **n. sp.**, WOC39; (H) L7 setules of *I. mongolica*, dyzoc320 (revised from Zhai & Zhao, 2014); (I) L7 setules of *I. innermongolica*, dyzoc8 (holotype). Scale bars: A–F = 100 μm; G–I = 30 μm.

Family Candonidae Kaufmann, 1900

Subfamily Candoninae Kaufmann, 1900

Genus *Fabaeformiscandona* Krstić, 1972

***Fabaeformiscandona monticulus* n. sp.**
(Figs 23–26)

Type locality. A pond in Kangding, Garze, Sichuan, China (30.07745ºN, 101.79605ºE, altitude 4207 m) (OS09-1, Table 1).

Type material. Holotype: one dissected male (WOC14) from type locality (Table 1). Allotype: one dissected female (WOC15) from type locality. Paratype: one dissected male (WOC17) from type locality (Table 1).

Derivation of name. From the Latin *monticulus*, the diminutive form of mountain, and referring to the large and triangular a lobe of the Hp, which is reminiscent of a mountain peak. The name is a noun in apposition.

Dimensions. Male (LV, n = 2) length 0.82–0.84 mm, H/L ratio 0.55. Female (LV, n = 1) length 0.79 mm, H/L ratio 0.54.

Description of male. Carapace (Fig. 23) sub-reniform in lateral view. Dorsal margin nearly evenly arched, with highest point at about 1/3 of length from posterior end. Both anterior and posterior ends broadly rounded, maximum curvature of anterior margin in antero-ventral area. Ventral margin significantly concave. Valve surface sparsely covered with fine setae. In dorsal view, carapace moderately compressed, with anterior end more pointed than posterior end. In interior view, antero-ventral area of calcified inner lamella unusually wide in LV of both sexes, with inner margin straight or even slightly curved inwards.

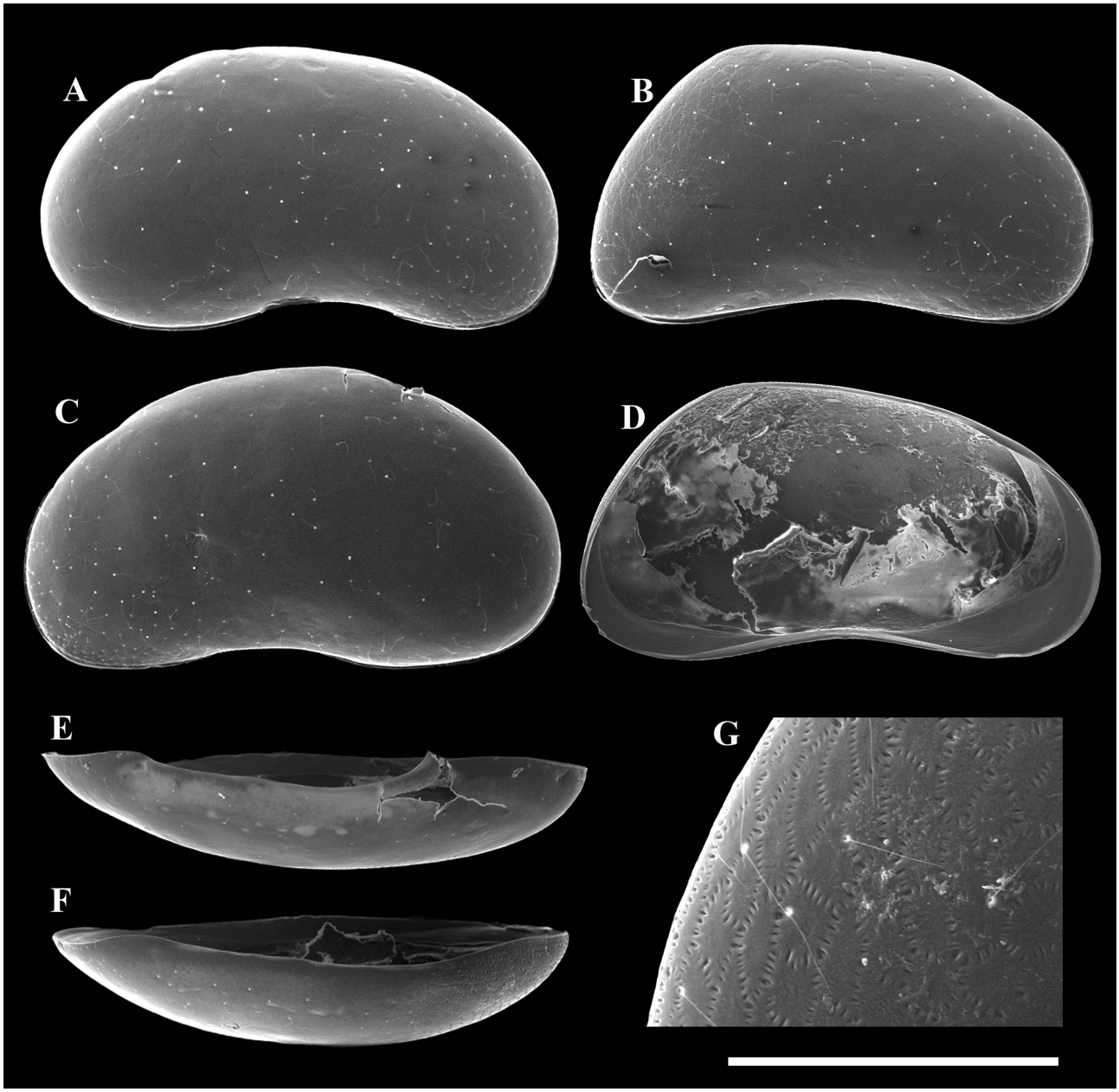

FIGURE 23. *Fabaeformiscandona tibeta* **n. sp.**, male and female. (A) Male RV, exterior view (WOC17); (B) female RV, exterior view (WOC15); (C) male LV, exterior view (WOC14); (D) female LV, interior view (WOC15); (E) male LV, dorsal view (WOC14); (F) female LV, dorsal view (WOC15); (G) enlargement of postero-dorsal part of (B). Scale bar: G = 100 μm; others = 500 μm.

A1 (Fig. 24A, B) with eight segments, first two fused forming large base, carrying two dorsal setae and two unequally long ventro-apical setae. Third segment short and rectangular, with one dorso-apical seta. Fourth segment short, with one dorso-apical seta. Fifth segment sub-quadrate, with one dorso-apical seta extending beyond terminal segment with about half of length, and one short ventro-apical seta. Sixth segment sub-quadrate, with two long dorso-apical setae and one short ventro-apical seta. Seventh segment elongate, with two long dorso-apical setae and two short ventro-apical setae. Eighth segment slender, with three unequally long setae and dorso-apically situated aesthetasc y_a.

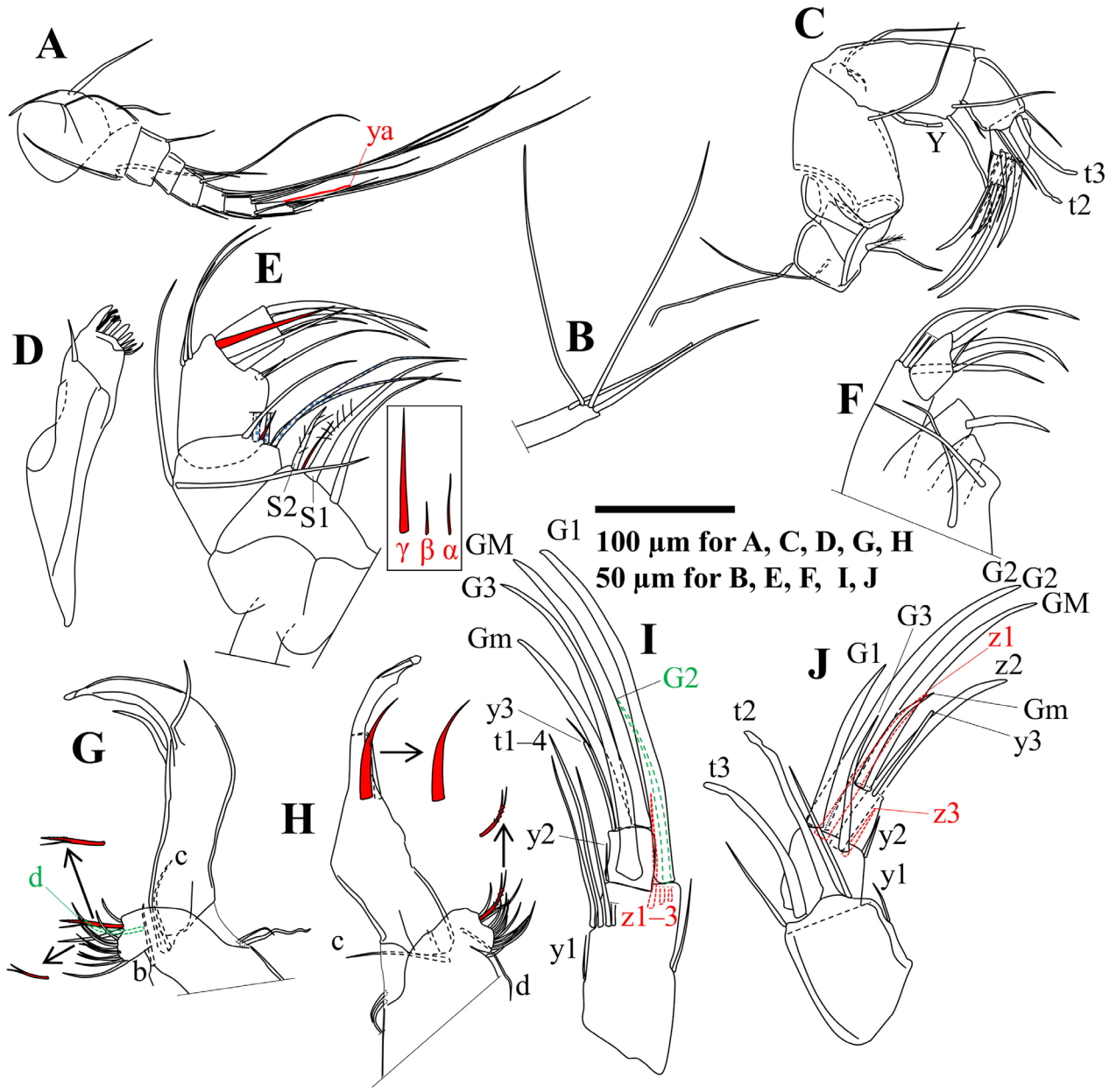

FIGURE 24. *Fabaeformiscandona tibeta* **n. sp.**, male (WOC14) and female (WOC15). (A) female left A1, interior view; (B) Distal part of male left A1, interior view; (C) Male left A2, interior view; (D) male Md coxa, interior view; (E) male Md palp, interior view; (F) male left Mx, interior view (exopod not shown); (G) male right L5, exterior view; (H) male left L5, exterior view; (I) distal part of female right A2, interior view; (J) distal part of male left A2, interior view (see also C).

A2 (Fig. 24C, I, J) first segment (coxa) with one long posterior seta and two unequal ventral setae, shorter one of which robust and plumose. Second segment (basis) robust, with one slender ventro-apical seta extending beyond terminal of next segment. Exopod plate small, carrying three progressively long setae, longest of which extending to about end of first endopodal segment. Endopod with penultimate segment sub-divided. Third segment (first endopodal segment) robust, with slender aesthetasc Y situated behind mid-length, extending to about ventro-apical

end of this segment, and with two sub-equal ventro-apical setae extending slightly beyond terminal segment. Fourth segment sub-rectangular, ventrally carrying small aesthetasc y1, distally carrying three t-setae, two of which transformed into male bristles, and one dorso-apical seta. Fifth segment quadrate, ventro-apically with small aesthetasc y2. z1 and z2 transformed into robust claws, with z2 longer and thicker than z1. z3 small, claw-like. G2 longest claw, two times length of G1. G3 slender. Terminal segment small. Gm extending to about tip of G2. Gm less than half length of GM. Aesthetasc part of y3 slender.

Md (Fig. 24D, E) coxa elongate, interiorly bearing ca. eight slender teeth. One stout seta present on antero-sub-apical part of coxa. Palp four-segmented. First segment robust, with four ventral setae, including smooth unnamed seta, plumose seta S1, short plumose seta S2, and thin, smooth seta α. Second segment short, with two dorso-apical setae and ventro-apically, group of four smooth setae, shorter accompanying seta and tiny seta β. Third segment with three slender dorso-subapical setae, two stiff intero-apical setae (including seta γ) and one long and one tiny ventro-apical setae. Fourth segment slightly elongate, with two more robust setae/claws and two slender setae.

First segment of Mx palp (Fig. 24F) with four dorso-apical setae. Second segment elongate, with two more robust claws/setae and two smaller setae. Tooth bristles on distal gnathobasic endite smooth. Two robust setae present on proximal side of proximal endite.

L5 (Fig. 24G, H) gnathobasic endite with ca. 14 apical setae, two of which bifurcate distally (one observed in left L5 of holotype). Right L5 palp progressively slenderer distally, bearing two sub-apical setae. Right L5 palp with blunt dorsal bump on median part of trunk, finger slender and elongate, one of two sub-apical setae claw-like.

L6 (Fig. 25A) with five segments. First segment elongate and less sclerotized, carrying intermediately long seta d1. Second segment long, with seta e reaching distal part of third segment. Third segment and fourth segment sub-equally long, each with one distal seta. Fifth segment elongate and trapezoidal, with seta h1 longer than h3. Claw h2 much longer than total length of three terminal segments, slightly serrated at sub-apical part.

L7 (Fig. 25B) generally well sclerotized, with four segments, penultimate segment undivided. First segment with setae d1 and dp. Second segment without seta. Third segment distally with curved seta g. Fourth segment elongate and rectangular, with setae h1, h2 and h3 progressively longer. Seta h3 only faintly curved at sub-apical part.

Ur (Fig. 25C, D) ramus stout and robust, basal part swollen. Sa slim. Ga sub-equally long to Gp but slightly more robust, both serrated. Sp situated at ca. 1/4 length of ramus from distal end, longer than Sa. Ur attachment medially with two branches and proximally with tri-ramous branch.

Hp (Fig. 25E) with large, triangular outer lobe a, small, triangular median lobe h, and interiorly, pointed, seta-like structure. M-process only slightly enlarged distally.

ZO (Fig. 26) with 5+2 rosettes each bearing numerous spines.

Additional description of female. Carapace (Fig. 23B & G) dorsal margin nearly straight and sloping anteriorly. Posterior end narrowly rounded (not broadly rounded as in male), with maximum curvature at postero-ventral area, postero-dorsal margin gently curving up to hinge. Anterior margin similar to that of male. Calcified inner lamella wide, especially in antero-ventral area; here inner edge of calcified inner lamella almost straight. Posterior part of both valves with polygonal pattern (Fig. 23G).

Distal morphology of A2 (Fig. 24I). t-setae subequally long but with t2 slightly longer, extending beyond terminal segment with half of length. z-setae extending slightly beyond terminal segment. G1 and G3 longest claws. G2 about half length of G1, slender. GM extending to or slightly beyond G1. Gm about 3/4 length of GM.

GL (Fig. 25C) very small and narrowly rounded.

Remarks. The smooth γ seta on the Md and the relatively laterally compressed carapace indicates that this species belongs to the genus *Fabaeformiscandona.* Of the 55 species in this genus, most have carapaces noticeably different in shape to those of *Fabaeformiscandona monticulus* **n. sp.**, but three do show a resemblance in the lateral view of the female: *Fabaeformiscandona balatonica* (Daday, 1894), *Fabaeformiscandona levanderi* (Hirschmann, 1912) and *Fabaeformiscandona danielopoli* Yin & Martens, 1997. The wide calcified inner lamella in the antero-ventral area of the female valves of *Fabaeformiscandona monticulus* **n. sp.** is a feature not seen to such an extent in the other species; it is also wide here in *F. levanderi* but not as wide as in *Fabaeformiscandona monticulus* **n. sp.** and it does not have an almost straight edge in *F. levanderi*. Males of all three species are sufficiently different in carapace and Hp morphologies to clearly distinguish them from *Fabaeformiscandona monticulus* **n. sp.** In particular the lobe a of the Hp of *Fabaeformiscandona monticulus* **n. sp.** is very large and triangular, much larger than the a lobes of the other species, and the posterior margin of the male more evenly rounded.

The arrangement of 4+1+β setae on the inner edge of the second Md palp segment indicates that *Fabaeformis-*

candona monticulus **n. sp.** belongs to the *acuminata*-group of *Fabaeformiscandona,* the same as *F. levanderi* and *F. danielopoli,* but different to *F. balatonica* (*balatonica*-group).

The polygonal pattern on the posterior part of the female carapace is a feature shared by some other Candonidae, such as *Fabaeformiscandona myllaina* Smith & Kamiya, 2007, *Neglecandona angulata* (G.W. Müller, 1900), *Candona muelleri jakutica* Pietrzeniuk, 1977, and *Candona xizangensis* Huang, 1982 (in Huang *et al.* 1982).

Although in a different genus, *Candona xizangensis*, also reported from the Tibetan Plateau, shows some similarity to *Fabaeformiscandona monticulus* **n. sp.** in overall carapace shape and the presence of a polygonal pattern in the female carapace (see figs in Akita *et al*. 2016). The female of *C. xizangensis* is more tightly curved posteriorly and the postero-dorsal margin longer than those in *Fabaeformiscandona monticulus* **n. sp.** The male carapaces of both species are similar, but the male of *C. xizangensis* is slightly more rounded posteriorly, and has a small convex expansion in the mouth region (absent in *Fabaeformiscandona monticulus* **n. sp.**). The appendages of *C. xizangensis* remain unknown, hindering further comparisons and confirmation of its generic status.

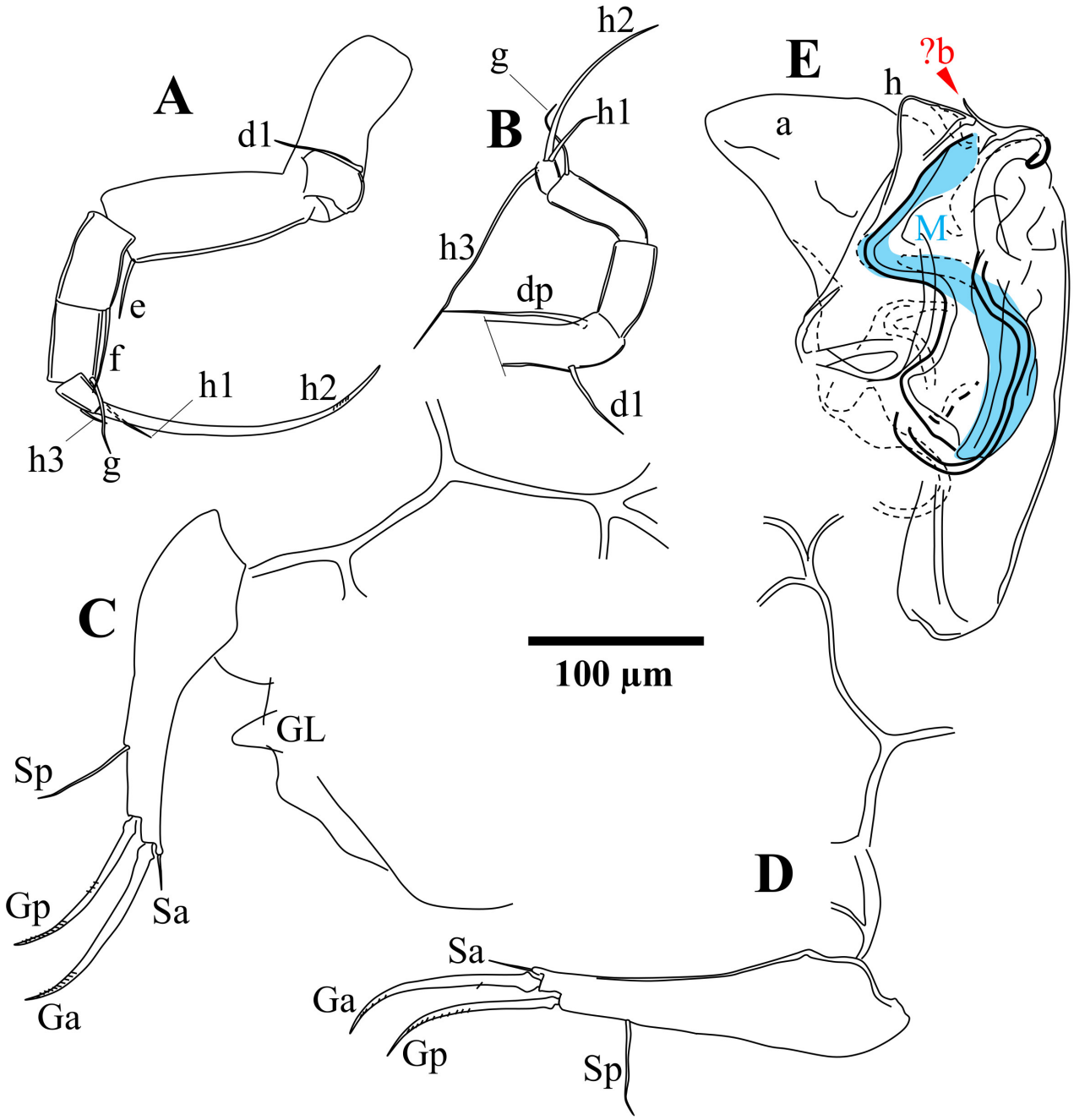

FIGURE 25. *Fabaeformiscandona tibeta* **n. sp.**, male (WOC14) and female (WOC15). (A) Male right L6, interior view; (B) male right L7, exterior view; (C) female Ur and GL; (D) male Ur; (E) Hp.

Fabaeformiscandona monticulus **n. sp.** was collected once during this study, from a pond with sparse aquatic plants near the shore at an altitude of 4207 m (Table 1).

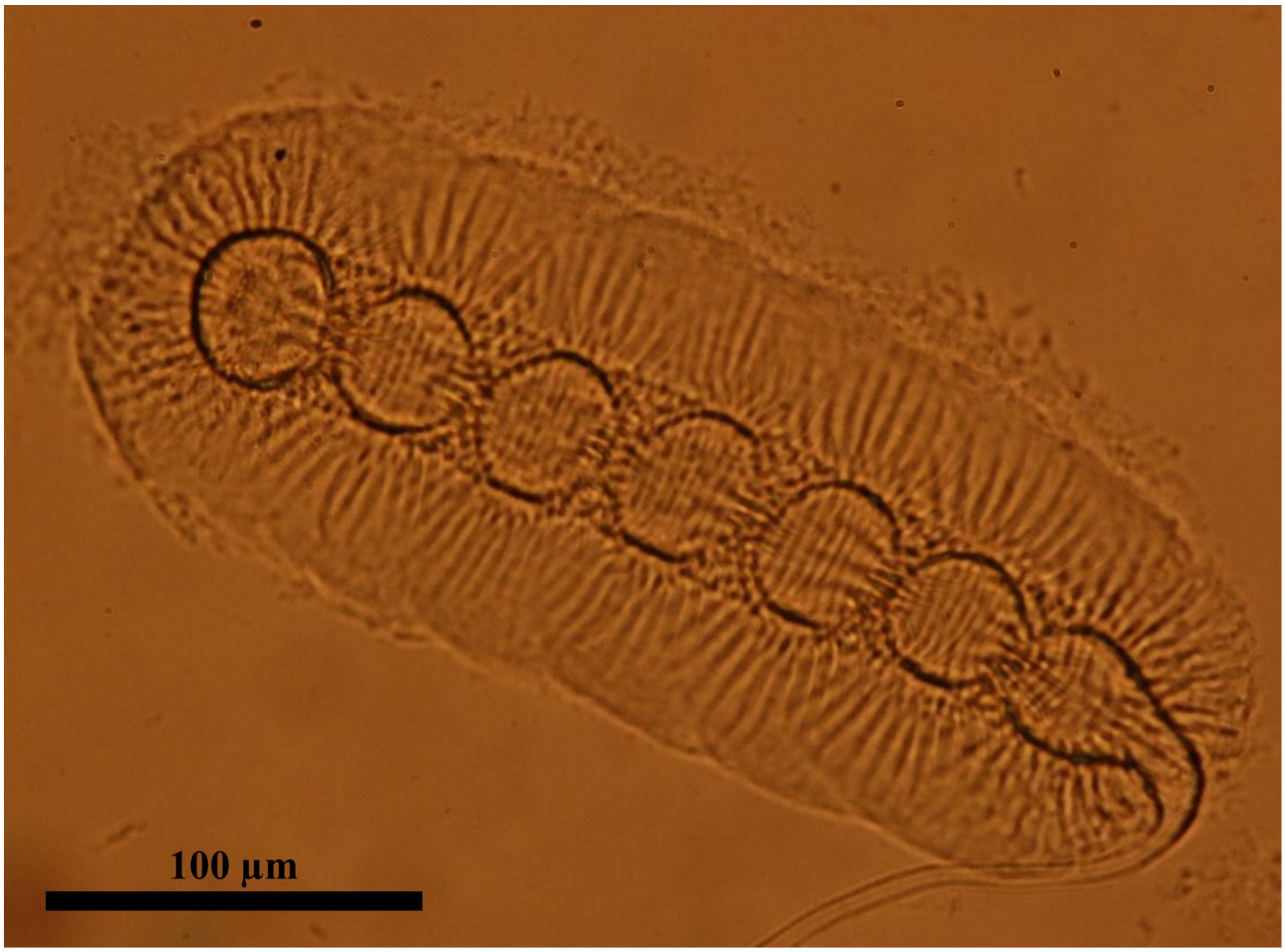

FIGURE 26. *Fabaeformiscandona tibeta* **n. sp.**, ZOs (WOC14).

Discussion

Ostracods at high altitudes

With the three new species and two new records reported herein, there are now over one hundred ostracod species that have been collected from modern or recently deposited sediments on the Tibetan Plateau. Of these, 64 species are recorded from Qinghai, 63 from Tibet, and two from Sichuan (Table 2). Twenty six species are recorded in both Tibet and Qinghai provinces of the Tibetan Plateau; whether this low number is due to problems of taxonomic harmonization or real differences between the faunas of these regions is currently unknown. Due to field work methods, many of these reports were based on carapaces and valves collected from dried surface or subsurface sediments, with only about 19 species represented by undoubtedly living specimens. It is therefore unclear which ostracod species are currently extant on the Tibetan Plateau or their living distributions. The taxonomy of Tibetan ostracods has relied mostly on carapace features alone, so there is an urgent need to study appendages to enhance and refine the taxonomy to provide a better understanding of these high altitude faunas. An inventory of extant species on the plateau is also crucial for (palaeo-) climatic and ecological studies in this area. The highest records of living ostracods are eight species from Pumayum Co, a lake situated at 5,030 m in the south west of Tibet (Peng *et al.* 2013; Fürstenberg *et al*. 2015). Many other records are from lakes over 4,000 m in altitude, but only a few records from habitats other than lakes, such as ponds, rivers, streams and puddles. Stygobitic ostracods are represented by only one species in this region (*Typhlocypris eremita* (Vejdovský, 1882)), but probably more exist. Thus research of the Tibetan Plateau ostracod fauna is still in its early stages, but has the potential to significantly contribute to wider studies on this region and surrounding areas.

TABLE 1. Habitat information of the sampling sites. GPS coordinates are based on the WGS84 system.

Site	Habitat description, coordinates and altitude	Date	EC (μs cm^{-1})	WT (ºC)	Species and specimens
OS09-1	small pond with a few macrophyta, 30.07745ºN, 101.79605ºE, 4207 m	2009, date na	106	13.2	*Tes* (woc13) *Fmt* (woc**14**, 15, **17**)
OS11-9	small weedy pond with sandy substrate, 33.57449ºN, 79.87441ºE, 4191 m	2011.8.14	368	14.6	*Aed*-w (woc25, 28)
OS11-11	shallow pond with muddy substrate, 33.49601ºN, 79.90305ºE, 4267 m	2011.8.20	436	25.6	*Aed*-w (woc33, 34, 65–67)
OS11-12	riffle zone of a slowly flowing river, 33.24971ºN, 79.75198ºE, 4325 m	2011.8.20	228	15.6	*Iti* (woc**35**, **36**, **37**)
OS11-14	shallow pond with muddy substrate, 32.93723ºN, 79.80317ºE, 4390 m	2011.8.20	288	12.9	*Iti* (woc38, **39**, 40)
OS11-27	pond with soft-mud bottom, 29.65356ºN, 84.19963ºE, 4593 m	2011.8.22	550	17.6	*Iti* (woc45)
OS11-29	shallow pond with sandy substrate, 29.58616ºN, 84.76981ºE, 4626 m	2011.8.22	248	15.5	*Aed*-g (woc47)
OS11-45	small weedy pond, 29.76433ºN, 94.74324ºE, 3325 m	2011.9.4	31	11.7	*Tes* (woc53, **54**)
OS11-46	small spring-feeding, weedy pool, 29.76423ºN, 94.74347ºE, 3326 m	2011.9.4	81	9.0	*Tes* (woc55, **56**)
OS11-48	small turbid pond, 29.73431ºN, 94.09846ºE, 3075 m	2011.9.4	67	23.9	*Pva* (woc57)
OS11-53	shallow weedy pond with sandy substrate, 29.70717ºN, 92.00119ºE, 4167 m	2011.9.4	58	22.1	*Cpu* (woc9, 10)
OS11-61	slowly flowing river with sandy substrate, 31.26686ºN, 86.63638ºE, 4548 m	2011.9.14	160	17.1	*Tes* (woc58, 59)
OS11-80	littoral zone of a lake with sandy substrate, 31.13905ºN, 84.31698ºE, 4576 m	2011.9.15	221	20.7	*Aed*-g (woc60)

Abbreviations for species: *Aed*-w, *Arctocypris edita* **n. sp.**, white-shell phenotype; *Aed*-g, *Arctocypris edita* **n. sp.**, green-shell phenotype; *Cpu*, *Cypris pubera*; *Fmt*, *Fabaeformiscandona monticulus* **n. sp.**; *Iti*, *Ilyocypris tibeta* **n. sp.**; *Pva*, *Potamocypris variegata*; *Tes*, *Tonnacypris estonica*.

Abbreviations for other information: EC, electronical conductivity; WT, water temperature; na, not available. Please note that water temperature should have varied among different seasons and throughout the day in natural waters.

Bold signifies a male specimen.

TABLE 2. A checklist of ostracods reported from modern and sub-modern sediments of the Tibetan Plateau (including the Qaidam Basin), province of occurrence, specimens collected alive (i.e. with appendages), and species potentially endemic to the plateau (End.?). Other synonyms also reported from the plateau are included. Specimens not identified down to the species level, varieties, and fossils are not listed. Data from Akita *et al*. 2016; Daday 1908; Fürstenberg *et al*. 2015; Jiang & Chen 1974; Li *et al*. 2010; Mischke *et al*. 2003, 2010; Peng *et al.* 2013; Song & Wang 2014; Song *et al.* 2014, 2015a, 2015b; Wrozyna *et al.* 2009a, 2009b; Yang *et al.* 1982; Yin & Martens 1997; Yu *et al.* 2009 (and refs. therein); Zhang *et al.* 2013; Zhu *et al.* 2010; this study. *Candona lactea* Baird, 1850 is a species considered dubious by G. W. Müller (1912) and Meisch *et al*. (2019). New names proposed by Yang *et al*. (1982; 2006) were not accompanied by descriptions (or figures) and thus are nomen nudum, but some are listed here as they were used by subsequent authors.

Taxonomy	Qinghai	Tibet	Sichuan	Alive	End.?
Order Podocopida Sars, 1866					
Suborder Cypridocopina Baird, 1845					
Superfamily Cypridoidea Baird, 1845					
Family Candonidae Kaufmann, 1900					
Subfamily Candoninae Kaufmann, 1900					
Candona candida (O.F. Müller, 1776)	O	O		O	
Candona houae Huang 1964	O	O			O
Candona lactea Baird, 1850 Also as: *Candoniella lactea* (Baird, 1850)	O	O			
Candona lijiangensis Huang, 1982		O			
Candona weltneri Hartwig, 1899	O				
Candona xizangensis Huang, 1982 (in Huang *et al.* 1982)		O			O
Candona yaguodongcuoensis Huang, 1985 (in Huang *et al.* 1985)		O			O
Candoniella mirabilis Schneider, 1963 Also as: *Candona mirabilis* (Schneider, 1963)		O			
Candoniella suzini Schneider, 1956	O				
Fabaeformiscandona caudata (Kaufmann, 1900)	O				
Fabaeformiscandona fabaeformis (Fischer, 1851)	O				
Fabaeformiscandona gyirongensis (Huang, 1982) Also as: *Fabaeformiscandona danielopoli* Yin & Martens, 1997	O	O		O	O
Fabaeformiscandona hyalina (Brady & Robertson, 1870)	O				
Fabaeformiscandona monticulus n. sp.			O	O	O
Fabaeformiscandona obtusa (Bronstein, 1947) Also as: *Candona nyensis* Gutentag & Benson, 1962 *Candona rawsoni* Tressler, 1957	O	O			
Fabaeformiscandona yaguodongcuoensis (Huang, 1985) Also as: *Candona yaguodongcuoensis* Huang, 1985		O			O
Neglecandona neglecta (Sars, 1887) Also as: *Candona neglecta* Sars, 1887	O	O			
Paracandona euplectella (Robertson, 1889)	O				
Pseudocandona albicans (Brady, 1864) Also as: *Candoniella albicans* (Brady, 1864)	O	O			
Pseudocandona compressa (Koch, 1838) Also as: *Candona compressa* Koch, 1838	O				
Pseudocandona renoensis (Gutentag & Benson, 1962) Also as: *Candona renoensis* Gutentag & Benson, 1962	O				
Typhlocypris eremita (Vejdovský, 1882)	O				

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TABLE 2. (Continued)

Taxonomy	Qinghai	Tibet	Sichuan	Alive	End.?
Subfamily Cyclocypridinae Kaufmann, 1900					
Cyclocypris globosa (Sars, 1863)	O				
Cyclocypris ovum (Jurine, 1820)	O				
Cyclocypris serena (Koch, 1838)	O				
Family Cyprididae Baird, 1845					
Subfamily Cypricercinae McKenzie, 1971					
Cypricercus moguntiensis Yang *et al.*, 2006 nomen nudum	O	O			O
Paracypricercus angulatus Yang, 1985		O			O
Paracypricercus angust Yang, 1982 (in Yang *et al.* 1982) nomen nudum		O			
Subfamily Cypridinae Baird, 1845					
Cypris granulata Daday, 1898 Also as: *Eurycypris subglobosa* (Sowerby, 1840)	O	O			
Cypris pubera O.F. Müller, 1776	O	O		O	
Subfamily Cypridopsinae Kaufmann, 1900					
Cypridopsis vidua (O.F. Müller, 1776) Also as: *Cypridopsis helvetica* Kaufmann, 1900 *Cypridopsis obesa* Brady & Robertson, 1869	O				
Potamocypris fulva (Brady, 1868)	O				
Potamocypris smaragdina (Vávra, 1891)	O				
Potamocypris stewarti Daday, 1908		O		O	O
Potamocypris variegata (Brady & Norman, 1889)		O		O	
Potamocypris villosa (Jurine, 1820)	O				
Sarscypridopsis aculeata (Costa, 1847)	O				
Zonocypris madagascarensis G. W. Müller, 1898	O				
Subfamily Cyprinotinae Bronstein, 1947					
Heterocypris incongruens (Ramdohr, 1808)	O			O	
Heterocypris salina (Brady, 1868) Also as: *Cyprinotus salinus* Brady, 1868 *Heterocypris salinus* (Brady, 1868)	O			O	
Heterocypris vandouwei (Brehm, 1923)	O				
Subfamily Dolerocypridinae Triebel, 1961					
Dolerocypris fasciata (O.F. Müller, 1776)	O				
Subfamily Eucypridinae Bronstein, 1947					
Arctocypris dulcifons (Diebel & Pietrzeniuk, 1969) Also as: *Eucypris dulcifons* Diebel & Pietrzeniuk, 1969	O				
Arctocypris edita n. sp.		O		O	O
Arctocypris mareotica (Fischer, 1855) comb. nov. Also as: *Eucypris mareotica* (Fischer, 1855) *Eucypris inflata* (Sars, 1903)	O	O			
Eucypris afghanistanensis Hartmann, 1964 Also as: *Eucypris gyirongensis* Yang, 1982 *Tonnacypris gyirongensis* (Yang, 1982)	O	O		O	
Eucypris lenghuensis Yang, 1988	O				O
Eucypris minuta Daday, 1908		O		O	O

.....continued on the next page

TABLE 2. (Continued)

Taxonomy	Qinghai	Tibet	Sichuan	Alive	End.?
Eucypris rischtanica Schneider, 1963	O	O			O
Eucypris salina Hartmann, 1964	O				
Eucypris tibetana Daday, 1908		O		O	O
Eucypris virens (Jurine, 1820)	O	O			
Eucypris zandaensis Yang, 1982		O			
Prionocypris gansenensis Huang, 1964	O	O			O
Tonnacypris estonica (Järvekülg, 1960)		O	O	O	
Tonnacypris tonnensis (Diebel & Pietrzeniuk, 1975)	O				
Subfamily Herpetocypridinae Kaufmann, 1900					
Herpetocypris reptans (Baird, 1835)	O				
Herpetocypris smaragdea Daday, 1908		O		O	O
Herpetocypris stewarti Daday, 1908		O		O	O
Stenocypria fischeri (Lilljeborg, 1883)	O				
Subfamily Scottiinae Bronstein, 1947					
Scottia pseudobrowniana Kempf, 1971	O				
Family Ilyocyprididae Kaufmann, 1900					
Subfamily Ilyocypridinae Kaufmann, 1900					
Ilyocypris bradyi Sars, 1890	O	O			
Ilyocypris cornae Mandelstam, 1961		O			
Ilyocypris dunschanensis Mandelstam, 1959		O			
Ilyocypris echinata Huang, 1979	O	O			O
Ilyocypris evidens Mandelstam, 1961: Province not specified.					
Ilyocypris gibba (Ramdohr, 1808) Also as: *Ilyocypris biplicata* (Koch, 1838)	O	O			
Ilyocypris lacustris Kaufmann, 1900	O				
Ilyocypris monstrifica (Norman, 1862) Also as: *Ilyocypris tuberculata* Brady, 1868		O			
Ilyocypris neoaspera Huang *et al.*, 1983		O			
Ilyocypris sebeiensis Yang and Sun, 2004	O	O			
Ilyocypris subdunshanensis Yang, 1982		O			
Ilyocypris tibeta n. sp. Also as: *Ilyocypris* cf. *mongolica* Martens, 1991?		O		O	O
Ilyocypris xizangensis Yang, 1982		O			
Family Notodromadidae Kaufmann, 1900					
Subfamily Cyproidinae Hartmann, 1963					
Cyprois marginata (Straus, 1821)	O				
Family unknown					
Megazonocypris fragilis Huang, 1979	O				
Superfamily Cytheroidea Baird, 1850					
Family Cytherideidae Sars, 1925					
Subfamily Cytherideinae Sars, 1925					
Cytherissa hutouliangensis Huang, 1985	O				O
Cytherissa lacustris (Sars, 1863)	O	O			
Cytherissa posterotuberosa Yang & Huang, 1991	O				O

.....continued on the next page

TABLE 2. (Continued)

Taxonomy	Qinghai	Tibet	Sichuan	Alive	End.?
Cytherissa sinensis Huang & Yang, 1991	O				O
Cyprideis torosa (Jones, 1850)	O	O			
Also as: *Cyprideis littoralis* (Brady, 1870)					
Family Limnocytheridae Sars, 1925					
Subfamily Limnocytherinae Sars, 1925					
Leucocythere bulla Huang, 1982 (in Yang *et al.* 1982) nomen nudum		O			O
Leucocythere dilatata Pang, 1985		O			
Leucocythere dorsotuberosa Huang, 1984	O	O		O	O
Also as: *Leucocythere postericosta* Huang, 1988					
Leucocythere exilitropis Huang, 1982		O			
Leucocythere mirabilis Kaufmann, 1892	O	O			O
Leucocythere parasculpta Huang, 1985		O			O
Leucocythere pseudosculpta Yang, 1985		O			O
Leucocythere subsculpta Huang-Li *et al*., 1991		O			
Leucocythere tropis Huang, 1984	O	O			O
Leucocytherella binoda Huang, 1982 (in Yang *et al.* 1982) nomen nudum		O			O
Leucocytherella enquinquechinata Huang, 1982 (in Yang *et al.* 1982) nomen nudum		O			O
Leucocytherella mononoda Yang, 1982 (in Yang *et al.* 1982) nomen nudum		O			O
Leucocytherella sexechinata Yang, 1982 (in Yang *et al.* 1982) nomen nudum		O			O
Leucocytherella sinensis Huang, 1982		O		O	O
Also as: *Leucocytherella biechinata* Huang, 1985					
Leucocytherella quadriechinata Yang, 1985					
Leucocytherella quinquechinata Huang, 1985					
Leucocytherella subtriechinata Huang, 1985					
Leucocytherella triechinata Huang, 1985					
Leucocytherella trinoda Huang, 1982					
Limnocytherellina bispinosa Pang, 1985					
Limnocytherellina kunlunensis Pang, 1985					
Limnocytherellina trispinosa Pang, 1985					
Leucocytherella subquinquechinata Yang, 1982 (in Yang *et al.* 1982) nomen nudum		O			O
Limnocythere binoda Huang, 1964		O			O
Limnocythere dubiosa Daday, 1903	O	O			
Limnocythere inopinata (Baird, 1843)	O	O		O	
Limnocythere sanctipatricii Brady & Robertson, 1869		O			
Also as: *Limnocytherina sanctipatricii* (Brady & Robertson, 1869)					
Limnocythere neocomensis Zschokke, 1894					
Paralimnocythere compressa (Brady & Norman, 1889)	O				
Paralimnocythere psammophila (Flössner, 1965)	O				
Superfamily Darwinuloidea Brady & Robertson, 1885					
Family Darwinulidae Brady & Robertson, 1885					
Darwinula stevensoni (Brady and Robertson 1870)	O				

Compared with Palaearctic non-marine habitats, the family Candonidae is under-represented on the Tibetan Plateau (25% of species compared with 46% in the Palaearctic generally (Meisch *et al.* 2019)), while the Ilyocyprididae (13% compared with 4% in the Palaearctic) and Limnocytheridae (21% compared with 6% in the Palaearctic) are relatively diverse at these higher altitudes. Other families form more or less similar proportions of the fauna on the Tibetan Plateau as in the Palaearctic generally.

In South America, there are about 46 species recorded from the Altiplano (average height about 3,750 m), but many of these have yet to be described and named (Delachaux 1928; Lerner-Seggev 1973; Laprida *et al*. 2010; Mourguiart & Montenegro 2002). The highest records are seven species from Huaroncocha, a lake in Peru at 4587 m (Delachaux 1928). Similar to the Tibetan Plateau, the Limnocytheridae shows higher species diversity on the Altiplano than surrounding areas; the family forms 14% of the Neotropical fauna generally (including unnamed species on the Altiplano), but 40% of the Altiplano's ostracod fauna. Many Limnocytheridae records from the Altiplano are from Lake Titicaca, an ancient lake (altitude 3812 m). The Limnocytheridae tends to produce species flocks in ancient lakes (e.g. Frogley *et al.* 2002), and this probably contributes to the high diversity of the family on the Altiplano. However, the relatively high diversity of Limnocytheridae on the Tibetan Plateau as well as the Altiplano could indicate that this family is more inclined to colonize large, high altitude plateaus than other families in these regions.

Outside of the Tibetan Plateau and Altiplano, few records of ostracods inhabiting areas over 3000 m exist: Löffler (1968) recorded 13 species from high altitudes in East Africa, including from Simba-Tarn at 4590 m, Mount Kenya, and two species were reported from Lake Peunde in New Guinea at an altitude of 3750 m (McKenzie 1971). Many species found at high altitude are widespread at lower altitudes, for example, *Candona candida* (O.F. Müller, 1776), *Cypris pubera*, *Heterocypris incongruens* (Ramdohr, 1808)*, Heterocypris salina* (Brady, 1868)*, Cypridopsis vidua* (O.F. Müller, 1776)*, Cyprideis torosa* (Jones, 1850), *Cytherissa lacustris* (Sars, 1863), *Limnocythere inopinata* (Baird, 1843), and *Darwinula stevensoni* (Brady & Robertson, 1870) (Table 2). Others are only known from high altitudes and are probably endemic to those areas. About one third of species reported from the Tibetan Plateau are so far only known from there, and are potentially endemic to these high altitudes (Table 2). These are mostly in the genera *Leucocytherella*, *Leucocythere*, *Eucypris* and *Cytherissa*, but in total 14 genera are represented by potential endemic species on the plateau. It is noted that some congeneric species listed in Table 2, such as *Leucocytherella mononoda* Yang, 1982, *L. binoda* Huang, 1982, *L. quadriechinata* Yang, 1985 (in Huang et al. 1985), and *L. quinquechinata* Huang, 1985 (in Huang et al. 1985), were distinguished from each other by the distribution of nodes and spines on the carapace. Recent studies, however, have shown that some species of the subfamily Limnocytherinae, for example, *Leucocytherella sinensis* Huang, 1982 (Fürstenberg *et al.* 2015) and *Limnocythere inopinata* (Baird, 1843) (Yin *et al.* 1999), include phenotypes with different distribution patterns of nodes and spines on the carapace, whose soft-part anatomies nonetheless indicate that they should be assigned as the same species. Therefore, the status of these species, which had been erected based on shell morphologies alone, needs to be confirmed with further work on their taxonomy and by collections in surrounding regions.

Endemism could also be potentially high for the Altiplano, but remains unclear due to the dearth of taxonomic studies on the fauna.

The taxonomic position of *Arctocypris* Petkovski *et al*., 2016

The genus *Arctocypris* was established to accommodate four species of the family Cyprididae, with *Arctocypris fuhrmanni* Petkovski *et al*., 2016 as the type species. The genus was placed in the subfamily Eucypridinae Bronstein, 1947 on account that the fifth limb has a c-seta on the protopodite. Petkovski *et al.* (2016) noted that the only unique diagnostic character of the subfamily is the presence of this seta, although it should be noted that some other subfamilies also contain species with a seta on the fifth limb that is perhaps homologous (e.g. Nagler *et al*. 2014). However, the c- and d-setae labelled in the diagrams of Petkovski *et al.* (2016) are not consistent with the position of these setae in other genera. In all Cyprididae genera, there are a number of setae that protrude from the endite of the limb towards the mouth cavity, often arranged in two subgroups: a larger group of about 8–10 in an apical position, and a smaller, slightly subapical group on the inner side (typically consisting of 3–4 setae). Up to five (very rarely six) other setae are present on the protopodite of this limb: the two a-setae near the base, b-seta towards the endopodite, and c- and d-setae towards the inner edge of the endite, but isolated from each other and the apical setae. In the diagrams of Petkovski *et al.* (2016), the seta labelled as the d-seta is not separated from the endite's subapical setae. The seta labelled as the c-seta is isolated, but in a homologous position to the d-seta in other groups. We consider

that *A. fuhrmanni* does not have a c-seta and that the seta labelled as c in Petkovski *et al.* (2016) is the true d-seta. The seta labelled by them as d-seta is an unnamed seta of the smaller, subapical endite group. This lack of a c-seta indicates that the genus does not fit the diagnosis of the subfamily Eucypridinae, and its position is thus problematic. The general lateral outline of the valves is similar to some *Eucypris* species (e.g. *Eucypris heinrichi* Diebel & Pietrzeniuk, 1978), but the appendages suggest affinities to the Cyprinotinae (no c-seta on the L5, no d2 on the L6). We retain the genus in the Eucypridinae for the present time, but note that it probably does not belong there.

In a detailed redescription of *Eucypris mareotica* (Fischer, 1855), Rasouli *et al*. (2016) noted that it also has no c-seta on the Mx or d2-seta on the L6, and thus it does not belong to the genus *Eucypris*. The lack of both of these setae corresponds to the diagnosis of *Arctocypris*. The carapace of *E. mareotica* generally also agrees with the diagnosis of *Arctocypris*, but it has only one inner list on the anterior calcified inner lamella of the left valve (there are two lists here in *A. fuhrmanni, Arctocypris edita* **n. sp.** and *A. dulcifons*; for *A. arctica* and *A. foveata* the features of the inner calcified lamellae have not been described). While *E. mareotica* does not have the same pitted surface ornamentation as the type species *A. fuhrmanni*, it is similar to the smooth carapace described for *A. arctica*. Overall, *E. mareotica* is more similar to the genus *Arctocypris* than *Eucypris* and we hereby refer to it as *Arctocypris mareotica* (Fischer, 1855) comb. nov.

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