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Integrative Taxonomy of Cyclocyprididae Kaufmann, 1900 (Ostracoda: Podocopa) with Description of a New Genus and Species

Maria Bisquert-Ribes[1,*], Juan Rueda[1], Ferran Palero[1], Sukonthip Savatenalinton[2], and Francesc Mesquita-Joanes[1]

[1]*Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Catedràtic José Beltrán Martinez, 2, Paterna, 46980, Spain.*
**Correspondence: E-mail: maria.bisquert@uv.es (Bisquert-Ribes)*
E-mail: juan.rueda@uv.es (Rueda); ferran.palero@uv.es (Palero); francesc.mezquita@uv.es (Mesquita-Joanes)
[2]*Department of Biology, Faculty of Science, Mahasarakham University, Maha Sarakham 44150, Thailand.*
E-mail: sukonthip.s@msu.ac.th (Savatenalinton)

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The two widespread ostracod genera *Cypria* Zenker, 1854 and *Physocypria* Vávra, 1897 are traditionally distinguished based on the presence or absence of tubercles on the right valve margin. However, recent research based on soft body parts has uncovered new cryptic genera within *Cypria* and *Physocypria*. Following this line of research, a new Cyclocyprididae genus and species, *Vizcainocypria viator* gen. nov. sp. nov., is here described from individuals collected in rice fields and wetlands of the Iberian Peninsula. *Vizcainocypria* is compared with *Cypria*, *Physocypria*, *Dentocypria* Savatenalinton, 2017, *Keysercypria* Karanovic, 2011, *Brasilocypria* Almeida et al., 2023, and *Claudecypria* Almeida et al., 2023 based on morphological evidence. Besides the presence or absence of tubercles on the right valve, these genera can be distinguished according to their mandibular palp, second thoracopod, caudal ramus, and male hemipenis. Molecular analyses using mitochondrial (COX1), and nuclear (28S rDNA) genes provide further support for the differentiation of *Cypria*, *Dentocypria*, *Physocypria* and *Vizcainocypria* gen. nov. The present study highlights the importance of using an integrative taxonomy approach, combining shell and soft-body parts morphology and molecular data, to characterize the rich diversity of freshwater ostracods.

Key words: DNA barcoding, Identification key, *Physocypria*, *Vizcainocypria*, Wetland

BACKGROUND

The most widely accepted classification of Ostracoda is probably the one proposed by Hartmann and Puri (1974). They considered that the family Candonidae Kaufmann, 1900 comprised three subfamilies, namely Candoninae Kaufmann, 1900, Cyclocypridinae Kaufmann, 1900, and Paracypridinae Sars, 1923. This classification has been followed by most ostracodologists working on living taxa (*e.g.*, Martens 1992; Martens et al. 1998; Wouters 1999; Meisch 2000; Maddocks 2005), but paleontologists have followed alternative classifications. While Moore (1961) proposed ranking the three subfamilies as families despite lacking information on soft body parts, Liebau (2005) followed the classification proposed by Hartmann and Puri (1974) for both fossil and living taxa. Among researchers working on living ostracods in the Nearctic, one of the most influential works were those of Delorme (1970a b), which used the family rank for Candonidae and Cyclocyprididae, although he later used the subfamily rank for Cyclocypridinae, first including them in the family Cyprididae (Delorme 2001) and finally in the Candonidae (Smith and Delorme 2010). Karanovic (2011) and several other authors (Külköylüoğlu et al. 2017; Savatenalinton 2017; Külköylüoğlu 2018; Meisch

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et al. 2019; Pieri et al. 2020; Almeida et al. 2023) followed Hartmann and Puri (1974) and considered the Cyclocypridinae as a subfamily within the Candonidae. Nevertheless, Hiruta et al. (2016) showed Candonidae to be paraphyletic, using molecular data, and proposed raising the three candonid subfamilies (*i.e.*, Candoninae, Paracypridinae and Cyclocypridinae) to family rank within the Cypridoidea superfamily. Karanovic and Cho (2017) also provided support for this change in ostracod classification with new molecular evidence. Although the subfamily rank is still maintained for the three candonid taxa in the most recent list of freshwater ostracods of the world (Meisch et al. 2019), we will use the family rank for the Cyclocyprididae from now on in this manuscript.

In a comprehensive review of the family, Karanovic (2011) noted that most authors assigned almost every *Cypria*-like species with tubercles on the valve margin to the genus *Physocypria*, and she proposed a new classification using soft parts. She recognized six genera within the Cyclocyprididae (as Cyclocypridinae in her publication): *Allocypria* Rome, 1962, *Cyclocypris* Brady and Norman, 1889, *Cypria*, *Keysercypria*, *Kempfcyclocypris* Karanovic, 2011 and *Physocypria* (Karanovic 2011 2012). Savatenalinton (2017) established a new genus, *Dentocypria*, to include four new species from Thailand with tubercles on the right valve margin and a tooth on the internal antero-ventral part of the left valve, which differ from *Physocypria* in its soft parts (Savatenalinton 2017). Later on, Külköylüoğlu (2018) erected the monotypic genus *Namiotkocypria* Külköylüoğlu, 2018 to include a new species from North American groundwaters (*i.e.*, *Namiotkocypria haysensis* Külköylüoğlu, 2018). While Karanovic (2011) classification prioritized soft parts over valve characters, Meisch et al. (2019) supported a more traditional approximation on the basis that shell traits are observable in both living and fossil ostracods. Thus, according to Meisch et al. (2019) the family Cyclocyprididae (Cyclocypridinae in their list) comprised eight genera (*Allocypria*, *Cyclocypris*, *Cypria*, *Dentocypria*, *Kempfcyclocypris*, *Mecynocypria* Rome, 1962, *Namiotkocypria* and *Physocypria*), splitting *Keysercypria* species among *Physocypria* and *Cypria*, and rejecting the synonymy of *Mecynocypria* and *Physocypria* established by Karanovic (2011). Recently, two new genera, *Brasilocypria* and *Claudecypria*, have been raised for species with tubercles on the right valve margin (belonging to *Physocypria s.l.*) collected from Brazilian floodplains (Almeida et al. 2023). Furthermore, Almeida et al. (2023) reestablished the validity of *Keysercypria*, although in a more restricted form. Considering all these new contributions, the family Cyclocyprididae is now composed of eleven genera.

Recent surveys from rice fields and wetlands in the southern and eastern Iberian Peninsula revealed the presence of a new Cyclocyprididae species differing from all previously known taxa, and for which the genus *Vizcainocypria* gen. nov. is here erected. The classification of controversial genera (*e.g.*, *Cypria*, *Dentocypria*, *Keysercypria*, and *Physocypria*) is discussed and clarified with new diagnoses, and a genus-level identification key is provided, based both on the morphology of valves and soft parts, and validating the use of hemipenis morphology for genus-level classification within the Cyclocyprididae. In addition, a new diagnosis for the Cyclocyprididae and *Mecynocypria*, and brief comments on *Allocypria*, *Brasilocypria* and *Claudecypria* are provided. Preliminary phylogenetic analyses were also carried out based on mitochondrial (COX1) and nuclear (28S) sequences to check for support (or its lack thereof) of morphological classifications. Finally, taxonomic characters used for distinguishing between the close genera *Brasilocypria*, *Claudecypria*, *Cypria*, *Dentocypria*, *Keysercypria*, *Physocypria*, and *Vizcainocypria* gen. nov. are discussed.

MATERIALS AND METHODS

Specimen collection, dissection, and scientific drawings

Sampling was mostly carried out as part of multiple surveys in the Albufera Natural Park (eastern Iberian Peninsula) between 2013 and 2021. Ostracods were collected with a 250-µm hand net and immediately preserved in 96% ethanol. In the laboratory, individual specimens were isolated using Pasteur pipettes under a Leica M205 C stereoscope. Ostracod dissections followed Namiotko et al. (2011). Soft parts were placed in a glass slide with HydroMatrix® for permanent preparations, and valves were stored dry in micropaleontological slides. Digital drawings were completed using a graphic tablet and Adobe Illustrator 2020 (https://www.adobe.com/products/illustrator.html), in combination with photographs taken with a Nikon Eclipse E-800 microscope. Scanning electron microscopy (SEM) images were obtained with a Hitachi S-4800 microscope at the Central Service for Experimental Research (SCSIE) of the University of Valencia. Images of whole individuals were obtained with a Nikon D3400 attached to a Leica M205 C stereoscope. Limb chaetotaxy descriptions follow Broodbakker and Danielopol (1982) as revised by Martens (1987) and Meisch (2000).

The following abbreviations are used in the text and figure captions: A1, antennula; A2, antenna; AT, Afrotropical; AU, Australasian; CpD, carapace dorsal view; CpF, carapace frontal view; CpL, carapace lateral view; CR, caudal ramus; EA, East Asia; H, height; IP, Iberian Peninsula; L, length; LV, left valve; LVi, left valve interior view; Md, mandible; Mxl, maxillula; NA, Nearctic; NT, Neotropical; OL, Oriental; PA, Palearctic; RV, right valve; RVi, right valve interior view; SEA, South East Asia; T1, T2, T3, first, second and third thoracopods; US, United States; W, width.

DNA analyses

Ethanol-fixed ostracods were individually transferred to 1.5 mL eppendorfs using a thin brush. Single specimens were digested at 55°C overnight using 180 µL T1 Buffer and 20 µL proteinase K, and DNA was extracted with the Nucleospin DNA extraction kit (Macherey-Nagel™) following the manufacturer's instructions. The cytochrome oxidase subunit I mitochondrial gene (COX1) was amplified using ArF1: 5'-GCNCCWGAYATRGCNTTYCCNCG-3' (Gibson et al. 2014) and Fol-degen-rev: 5'-TANACYTCNGG RTGNCCRAARAAYCA-3' (Yu et al. 2012) primers, already tested with success on decapod crustaceans (Genis-Armero et al. 2022). The large ribosomal subunit (28S) nuclear gene region was amplified using a newly designed pair of primers: 5'-CCCGTCTTGAAACACG GACCAAGGAG-3' and 5'-GTTCGATTAGTCTTTCG CCCCTATAC-3'. Amplifications were carried out using ~10 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham), 1x buffer (Amersham), 0.2 mM of each primer and 0.12 mM dNTPs. The polymerase chain reaction (PCR) thermal profile included an initial denaturation step at 94°C for 4 min, followed by 30 cycles of 94°C for 30 s, 50°C for 30 s, 72°C for 30 s and a final extension at 72°C for 20 min. Sequences were obtained using the Big-Dye Ready-Reaction kit ver. 3.1 (Applied Biosystems) on an ABI Prism 3770 automated sequencer at the MACROGEN sequencing facilities. Chromatograms for each DNA sequence were checked with BioEdit v7.2.5 (Hall 1999) and sequence alignments were conducted with Muscle v3.6 (Edgar 2004). Model selection was carried out for each sequence alignment using the Bayesian Information Criterion (BIC) as implemented in ModelTest-NG v0.1.7 (Darriba et al. 2020). Maximum likelihood phylogenetic reconstruction was then completed with the corresponding DNA substitution model for each gene with ultrafast bootstrap (1000 replicates) as implemented in IQ-TREE v2.0 (Minh et al. 2020). Finally, to allow for comparison with previous COX1 genetic distance estimates obtained within and between ostracod species and genera by Nigro et al. (2016), Kimura 2-Parameter (K2P) genetic distances and their standard errors were estimated from our COX1 dataset using MEGA X (Kumar et al. 2018).

RESULTS

SYSTEMATICS

Class Ostracoda Latreille, 1802
Subclass Podocopa Sars, 1866
Order Podocopida Sars, 1866
Suborder Cypridocopina Baird, 1845
Superfamily Cypridoidea Baird, 1845
Family Cyclocyprididae Kaufmann, 1900

Diagnosis (after Cyclocypridinae *sensu* Meisch (2000) and Karanovic (2012)): Carapace short, less than 1 mm in length, relatively stout in lateral view (except *Allocypria*, with elongated valves), moderately compressed to ovate in dorsal view. Eyes fused with a single eye cup. A1 usually 7-segmented and Rome organ present. Male sexual bristles on A2 (transformed t2 and t3 setae) present or absent, swimming-setae usually well-developed, sometimes reduced and rarely absent. Endopod of female T1 developed, transformed into 2-segmented prehensile palps in males. T3 (cleaning leg) always 4-segmented, last segment bearing two short (h1 and h2) and one long (h3) setae. Zenker organ with seven spine whorls (five along the central tube, and one at each end of the organ) and proximal part (entrance) spherically enlarged (not funnel shaped). CR not reduced and sp-seta insertion around medial part of CR.

Differential diagnosis: The family Cyclocyprididae can be distinguished from other Cypridoidea families through its Zenker organ (not funnel-shaped proximally and with seven spine whorls) and other characters of the soft parts and valves. In the case of the Zenker organ of Cyprididae Baird, 1845, it has at least 8 spine whorls and their T3 has a pincer organ in most species (absent in Cyclocyprididae). The Zenker organ of Ilyocyprididae Kaufmann, 1900 has 15–20 spine whorls, and members of this family have a subrectangular carapace (ovate or subovate in Cyclocyprididae). Members of the Notodromadidae Kaufmann, 1900 present a unique Zenker organ, funnel-shaped in both extremes and with spines not arranged in separate whorls. Moreover, members of this family also present a divided eye (not divided in Cyclocyprididae) and external eye tubercles (not present in Cyclocyprididae). Candonidae *s.str.* (previously subfamily Candoninae) lack the Rome organ of A1 and the swimming-setae of A2, which are

usually present and well-developed in Cyclocyprididae. Moreover, these two families can be differentiated by the prehensile palps of T1 in males; 2-segmented in Cyclocyprididae and 1-segmented in Candonidae. Paracyprididae differs from Cyclocyprididae by the presence of d1 and d2 setae on T2 (d2, and sometimes also d1, absent in Cyclocyprididae) and the marine ecological affinities of most of its representatives (freshwater in the Cyclocyprididae). However, more studies on Paracyprididae are needed to be able to give a more reliable differential diagnosis at the family level.

Cypria Zenker, 1854

Cypris (*Cypria*) Zenker, 1854: 77.
Cypria s.l. Brady and Norman, 1889: 68.
Cypria s.str. Vávra, 1891: 62.
Candocypria Furtos, 1933: 458, Pl. 8, Figs. 13–17; Pl. 14, Figs. 22–23.
Bentocypria Kovalenko, 1987: 99.
Keysercypria (partim) Karanovic, 2011: 23, Fig. 17.
Type species: *Cypria exsculpta* (Fischer, 1855) Brady and Norman, 1889.

Diagnosis: Carapace in lateral view short, ovate or subovate; in dorsal view, laterally compressed. RV margin without tubercles, LV overlapping RV, sometimes with an internal antero-ventral tooth. A1 7-segmented, natatory setae of A2 well-developed. Penultimate segment of male A2 divided, t2 and t3 seta transformed into sexual bristles. Terminal segment of Md palp three or four times longer than wide. Terminal segment of Mxl palp squared. Third endite of the Mxl with bristles. Prehensile palps asymmetrical. Basal d1-seta of T2 absent. Terminal segment of T3 subquadrate, g-seta very short. CR well-developed, with a short sp-seta (no longer than half the length of Gp), claws well-developed. Hemipenis with two lobes, a-lobe (outer) usually longer than b-lobe (inner), Zenker organ with seven spine whorls.

Other species: The list of *Cypria* species and their synonyms can be found in Meisch et al. (2019).

Distribution: PA, NA, NT, AT, AU and OL.

Remarks: Karanovic (2011) provided the last diagnosis for *Cypria*. She opted to prioritize the soft part morphology over the valve characters to differentiate between the two classical genera, *Cypria* and *Physocypria*. She allocated some *Physocypria* species with tubercles on the RV margin to the genus *Cypria*. Meisch et al. (2019) followed a more conservative approach and returned to the classical differentiation between *Physocypria* (with tubercles) and *Cypria* (without tubercles). In the present work, *Cypria* and *Physocypria* are rearranged using both soft parts morphology and valve information (see below for details).

Karanovic (2011) placed *C. pellucida* and *C. obtusa* in *Keysercypria* based on the hemipenis morphology and the chaetotaxy of T2 and T3. However, none of these two species have tubercles on the RV, while all other species in *Keysercypria* do (see below), for that reason we have maintained these two species in *Cypria*.

Savatenalinton (2017) already noted that some species of *Cypria s.l.* (*i.e.*, *C. bicolor* and *C. javana*) could belong to a different genus due to their variability in some appendages (*e.g.*, long sp-seta on CR) and the morphology of the male copulatory organ. However, many *Cypria* species descriptions are incomplete, so we decided to maintain these dubious species in *Cypria* and strongly recommend a revision of the genus. In fact, the hemipenis morphology is very variable within *Cypria*, probably due to the number of species accumulated over the years. Surprisingly, the hemipenis of the type species, *Cypria exsculpta*, is very different to its congeners. While the hemipenis lobes of *C. exsculpta* are both broad, with an a-lobe longer, with pointed tip, and a b-lobe with rounded tip, most *Cypria* species have elongated lobes with both tips either pointed or rounded. The morphology of the hemipenis of *Cypria exsculpta* is reminiscent of the hemipenis of *Cyclocypris*, the type genus of the family, which may indicate that *C. exsculpta* hemipenis represents the ancestral state within the genus.

Dentocypria Savatenalinton, 2017

Type species: *Dentocypria mesquitai* Savatenalinton, 2017.

Diagnosis: As in Savatenalinton (2017).

Other species: Species described by Savatenalinton (2017), *D. crenulata* (Sars, 1903) comb. nov., *D. dumonti* Martens, 1982 comb. nov.

Distribution: AT, NT, PA and OL.

Remarks: New combinations are established here for *D. crenulata* comb. nov. and *D. dumonti* comb. nov., reallocating these species from *Physocypria* to *Dentocypria*, because both taxa have tubercles on the RV margin, a very elongated terminal segment of the Md palp, absence of d1-seta on T2 basal segment, and a long sp-seta on the CR. All those traits do not fit with the description of *Physocypria bullata* Vávra, 1897 (see Karanovic 2011), the type species of the genus. In addition, *D. dumonti* comb. nov. has a subtriangular protrusion on the right prehensile palp of the male, a character unique to *Dentocypria*. Moreover, the morphology of the hemipenis lobes is closer to *Dentocypria* than to *Physocyria* (see below). The transfer of these two species from *Physocypria*

s.l. to the genus *Dentocypria* has zoogeographical implications. The genus *Dentocypria* was considered endemic to Thailand (Savatenalinton 2017), but with the new combinations this genus is now present in other parts of Asia and in Africa; *Dentocypria crenulata* was originally described from Sumatra (Indonesia), and *D. dumonti* was described from Somalia (Africa).

Other species assigned to *Physocypria* may also belong to *Dentocypria*, but descriptions are often incomplete and generic position cannot be ascertained. The length of the Md palp terminal segment is unknown in *P. furfuracea* (Brady, 1886), *P. larensis* Hartmann, 1964 and *P. minuta* Victor and Michael, 1975, but they do not have d1-seta on T2 (a distinguishing character for *Physocypria*), and the sp-seta of the CR is long. Their distribution (OL and PA) is also congruent with *Dentocypria* distribution; however, more information is needed to confirm their generic position. Museum material of these species should be checked paying special attention to hemipenis and prehensile palp morphology.

Keysercypria Karanovic, 2011

Physocypria (partim) Meisch et al., 2019: 87.
Type species: *Keysercypria affinis* (Klie, 1933) Karanovic 2011.

Diagnosis (modified after Karanovic (2011)): Carapace in lateral view usually ovate. RV margin tuberculated anteriorly and posteriorly, LV overlapping RV anteriorly. Surface of carapace smooth, sometimes with long-setae. A1 7-segmented, five long natatory setae of A2 reaching beyond tip of terminal claw, outermost seta completely reduced. Penultimate segment of male A2 divided, t2 and t3 setae transformed into sexual bristles. Terminal segment of Md palp extremely elongated (> 5x longer than wide). Terminal segment of Mxl palp squared. Third endite of the Mxl with bristles. Male T1 with asymmetrical prehensile palps, first segment of right prehensile palp usually with a robust finger-like protrusion. Basal d1-seta of T2 absent. Terminal segment of T3 subquadrate, g-seta very short, d2-seta on T3 absent. CR well-developed, with long sp-seta (longer than half of Gp length). Hemipenis with b-lobe short, pointed distally and shorter than a-lobe; a-lobe elongated, finger-like, thin in its middle length, with a rounded distal end usually wider than the middle part. Zenker organ with seven spine whorls.

Other species: *K. deformis* (Klie, 1940), *K. longiseta* (Klie, 1930), *K. schubarti* (Farkas, 1958), *K. xanabanica* (Furtos, 1936).

Distribution: NT.

Remarks: Karanovic (2011) included in *Keysercypria* nine species previously assigned to *Physocypria* and *Cypria*. Meisch et al. (2019) returned these species to their original genera, but Almeida et al. (2023) reestablished the genus with a more restricted diagnosis based mainly on the chaetotaxy of T2 and T3 (see discussion). They kept in the genus *Keysercypria* some species of the *Physocypria s.l.* group: the type species *K. affinis*, plus *K. deformis* and *K. schubarti*. However, we consider that also two more *Physocypria* species assigned by Karanovic (2011) to *Keysercypria* do merit this genus-level distinction (*K. longiseta* and *K. xanabanica*), mostly because of their hemipenis morphology. Three former *Physocypria* species (*P. circinata* Würdig and Pinto, 1993, *P. sanctaeannae* Margalef, 1961 and *P. ivanae* (Díaz and Lopretto, 2011)) assigned to *Keysercypria* by Karanovic (2011) or by Díaz and Lopretto (2011) are excluded because their hemipenis morphology is not congruent with the others or cannot be confirmed due to lack of males. We decide to maintain *C. obtusa* and *C. pellucida* in the genus *Cypria* because their hemipenes are clearly distinct from *Keysercypria affinis* (type species) and because of the absence of RV marginal tubercles, as pointed out by Almeida et al. (2023).

Mecynocypria Rome, 1962

Physocypria (partim) Karanovic, 2011: 42.
Type species: *Mecynocypria obtusa* (Sars, 1910); Rome 1962.

Diagnosis (after Rome (1962)): Elongated carapace, height equal or less than half the length. RV margin without tubercles, LV overlap RV. A1 7-segmented, A2 with long natatory setae reaching beyond tip of terminal claws. Penultimate segment of male A2 divided, t2 and t3 setae transformed into sexual bristles. Terminal segment of Md palp elongated (> 2x longer than wide). Terminal segment of Mxl palp squared. Third endite of the Mxl with bristles. Male T1 with asymmetrical prehensile palps. T2 with basal d1-seta. Terminal segment of T3 subquadrate, g-seta short or absent. CR well-developed, with sp-seta long or short, claws well-developed. Hemipenis with lobes a and b well-developed; a-lobe elongated, usually longer than b-lobe, and bent towards b-lobe. Zenker organ with seven spine whorls.

Other species: The list of *Mecynocypria* species and their synonyms can be found in Meisch et al. (2019).

Distribution: AT.

Remarks: Karanovic (2011) synonymized the genus *Mecynocypria* with *Physocypria* because of the position of the ovaries and the presence of the d1-seta on T2. However, following Meisch et al. (2019), *Mecynocypria* differs from *Physocypria* because of the absence of marginal tubercles on the valves. We have

provided here a new diagnosis for the genus based on Rome's first description of the genus *Mecynocypria* but updating appendage nomenclature.

Physocypria Vávra, 1897

Physocypria Vávra, 1897: 7.
Keysercypria (partim) Karanovic, 2011: 23, fig. 11–16.
Type species: *Physocypria bullata* (Vávra, 1897) G. W. Müller, 1912.

Diagnosis: Carapace ovoid in lateral view. RV margin tuberculated anteriorly and posteriorly, sometimes LV tuberculated. LV overlaps RV ventrally, anteriorly, and posteriorly, sometimes RV overlapping LV. Surface of carapace smooth, sometimes with some setae. A1 7-segmented, long natatory setae of A2 reaching beyond tip of terminal claws. Penultimate segment of male A2 divided, t2 and t3 setae transformed into sexual bristles. Terminal segment of Md palp elongated (not more than two times longer than wide). Terminal segment of Mxl palp squared. Third endite of the Mxl with bristles. Male T1 with asymmetrical prehensile palps. T2 with basal d1-seta. Terminal segment of T3 subquadrate, g-seta very short. CR well-developed, with sp-seta usually long, claws well-developed. Hemipenis lobes well-developed and long, a-lobe usually longer and curved towards b-lobe. The latter usually curved at the base towards a-lobe, but distally pointed and curved towards the opposite direction (*i.e.*, sinuous shape). Zenker organ with seven spine whorls.

Other species: The list of *Physocypria* species and their synonyms can be found in Meisch et al. (2019), with some exceptions: *P. affinis*, *P. deformis*, *P. longiseta*, *P. schubarti* and *P. xanabanica* have been transferred to *Keysercypria* either by Almeida et al. (2023) or by this work (see above); *P. crenulata* and *P. dumonti* have been transferred by us to *Dentocypria* (see above); and *P. granadae* has been reallocated to the new genus *Vizcainocypria* gen. nov. (see below).

Distribution: AT, PA, NA, NT and OL.

Remarks: *Physocypria nipponica* and *P. biwaensis* are closely related taxa (Smith and Janz 2008; Karanovic 2015). The former lacks d1-seta on T2, so it should not be considered a *Physocypria* species. Nevertheless, we decided to keep *P. biwaensis* and *P. nipponica* in *Physocypria* since their hemipenis morphology is very similar to other *Physocypria* species (see below).

Physocypria pustulosa, *P. inflata* and *P. kerkyrensis* present RV marginal tubercles, but lack d1-seta on T2 and have short sp-seta (d1-seta present and sp-seta long in *Physocypria*). However, incomplete original descriptions or hemipenis morphology (see below) suggests these species to be kept in *Physocypria*. As indicated in the remarks section for other genera, some species might be allocated to other genera rather than *Physocypria*, but the information available in the bibliography is often incomplete. We strongly recommend a careful revision of the genus.

Other genera

The genera *Allocypria*, *Brasilocypria*, *Claudecypria*, *Cyclocypris*, *Kempfcyclocypris* and *Namiotkocypria* are not presented here with full diagnoses (also for *Dentocypria*, see above) because we consider that the original descriptions or their redescription by Karanovic (2011) are sufficient to verify their taxonomic affinities. Nevertheless, we present here a short differential diagnosis for these genera.

Allocypria was described by Rome (1962) from Lake Tanganyika. Karanovic (2011) provided an updated diagnosis, and the list of species and their synonyms can be found in Meisch et al. (2019). This genus differs from *Dentocypria*, *Keysercypria*, *Brasilocypria*, *Claudecypria* and *Vizcainocypria* gen. nov. by the absence of RV marginal tubercles; from *Cypria* by the reniform carapace shape and the presence of d1-seta on T2 (absent in *Cypria* but present in *Physocypria* too). *Allocypria* can be differentiated from *Mecynocypria* by the usually squared terminal segment of the Md palp (elongated, 2x times longer than wide, in *Mecynocypria*); by bearing bristles on the second and third endites of the Mxl (only in the third endite in *Mecynocypria*), and by presenting ovaries curved upwards (curved downwards in *Mecynocypria*). However, the last two traits (Mxl bristles and ovaries curvature) must be taken with caution (see discussion).

The two recently raised genera from Brazilian floodplains (Almeida et al. 2023), *Brasilocypria* and *Claudecypria*, share with *Keysercypria* (another Neotropical genus) the absence of the short seta accompanying the five natatory setae on A2, and the absence of the d2-seta on T3; setae which are present in *Cypria*, *Dentocypria*, *Physocypria*, and *Vizcainocypria* gen. nov. Furthermore, *Cypria* lacks RV marginal tubercles (present in *Brasilocypria* and *Claudecypria*); *Physocypria* presents d1-seta on T2 (absent in both new Neotropical genera); and *Vizcainocypria* gen. nov. presents a short sp-seta on CR, which is long in *Brasilocypria* and *Claudecypria*. The Md palp terminal segment is very elongated (3x longer than wide) in *Brasilocypria*, and elongated (2x longer than wide) in *Claudecypria*; while it is extremely elongated in *Keysercypria* (5x longer than wide). *Brasilocypria* can also be differentiated from *Claudecypria* by

the presence of dp-seta on T3 in males, which is absent in *Claudecypria*. The hemipenis can be used for differential diagnoses of these genera too (see discussion). *Allocypria* and *Mecynocypria* differ from the recently raised Neotropical genera by their reniform carapace shape and by the presence of d1-seta on T2.

Cyclocypris, the type genus of family Cyclocyprididae, and *Kempfcyclocypris*, described from Australian groundwaters, are two related genera that share the absence of sexual bristles on male A2 (t2 and t3 not transformed), what makes them different from other Cyclocyprididae genera. Moreover, *Cyclocypris* has a very elongated T3 terminal segment, and *Kempfcyclocypris* has a 6-segmentend A1 (7-segmented for other genera) and it lacks natatory setae on A2. Both genera also lack RV marginal tubercles, present a wider carapace in dorsal view, have an elongated (2x longer than wide) terminal segment of the Md palp, and bear d1-seta on T2.

Namiotkocypria is a North American groundwater genera that lacks the d1-seta on T2 and RV marginal tubercles. The natatory setae on A2 are reduced and the Md palp terminal segment is elongated (2x longer than wide), which makes this genus different from the Cyclocyprididae genera mentioned above.

Vizcainocypria gen. nov. Bisquert-Ribes et al.

urn:lsid:zoobank.org:act:B9CBEF1C-0880-4C29-822A-BA20245FE678

Type species: *Vizcainocypria viator* gen. nov. sp. nov.

Etymology: Named after Mr. Antonio Vizcaino in recognition of his significant contributions to the management and protection of the Albufera Natural Park (Valencia, Spain), type locality of this new genus.

Diagnosis: Carapace ovate or subovate in lateral view; elliptical, subelliptical or subovate and laterally compressed in dorsal view. RV margin tuberculated anteriorly and posteriorly, LV overlapping RV anteriorly, ventrally, and posteriorly, usually with an internal tooth on antero-ventral part. A1 7-segmented, long natatory setae of A2 reaching beyond tip of terminal claws. Penultimate segment of male A2 divided, t2 and t3 setae transformed into sexual bristles. Terminal segment of Md palp very elongated (> 2x longer than wide). Terminal segment of Mxl palp quadrate. Third endite of Mxl with bristles. Male T1 with asymmetrical prehensile palps, first segment of right prehensile palp usually with a spine-like or finger-like protrusion. Basal d1-seta of T2 absent. Terminal segment of T3 subquadrate, g-seta short. CR well-developed, with short sp-seta. Hemipenis with well-developed lobes, subequal or b-lobe slightly longer; a-lobe subtriangular, b-lobe distally thin, elongated and with a rounded tip. Zenker organ with seven spine whorls.

Differential diagnosis: *Vizcainocypria* gen. nov. can be clearly distinguished from other Cyclocyprididae genera. The hemipenis presents a subtriangular a-lobe, shorter than b-lobe, whereas *Allocypria* and *Mecynocypria* have elongated, digitiform a-lobes, usually longer than b-lobe. *Vizcainocypria* gen. nov. also lacks the elongate carapace shape of both genera, d1-seta on T2 and elongated (twice longer than wide) terminal segment of Md palp of *Mecycnocypria*, and bristles in the second Mxl endite present in *Allocypria*. *Cyclocypris* differs from *Vizcainocypria* gen. nov. by its more globose carapace in dorsal view and by holding not transformed sexual bristles of t2 and t3 on male A2, while *Kempfcyclocypris* is unique by its 6-segmented A1. The smooth RV margin and reduced A2 natatory setae of *Namiotkocypria* are not observed in the new genus. *Vizcainocypria* gen. nov. is closest to *Cypria*, *Dentocypria*, *Physocypria*, *Keysercypria*, *Brasilocypria* and *Claudecypria*. It differs from *Cypria* by the RV margin (smooth in *Cypria* and tuberculated in *Vizcainocypria* gen. nov.), from *Physocypria* by the d1-seta on T2 (absent in *Vizcainocypria* gen. nov. and present in *Physocypria*), from *Dentocypria* by the short sp-seta on CR (long in *Dentocypria*), and from *Keysercypria*, *Brasilocypria* and *Claudecypria* by the presence of a short accompanying natatory seta on A2 (absent in the three Neotropical genera). Moreover, the length of the terminal segment of the Md palp is very elongated in *Vizcainocypria* gen. nov. (and *Brasilocypria*), extremely elongated in *Keysercypria* and elongated in *Claudecypria*. The new genus can be differentiated from *Brasilocypria* by the sp-seta on CR (very long in *Brasilocypria* and short in *Vizcainocypria* gen. nov.). Furthermore, in most species of these genera (including their type species), the a-lobe of the hemipenis is elongated and longer than b-lobe, while it is the opposite in the new genus (b-lobe elongated and longer than a-lobe, which is subtriangular).

Other species: *V. granadae* (Hartmann, 1959) comb. nov.

Distribution: PA, NA and NT.

Remarks: We have allocated *V. granadae* comb. nov. to this new genus because of its sexual and non-sexual characters. This species presents marginal tubercles on the RV, does not have d1-seta on T2, the terminal segment of the Md palp is very elongated and the sp-seta on the CR is short. These are the non-sexual characters that differentiate *Vizcainocypria* gen. nov. from other genera of the family. Moreover, the hemipenis morphology of *V. granadae* comb. nov. is very similar to the type species of the genus. The a-lobe is subtriangular and slightly shorter than the

b-lobe, which is elongated and thin, and with a rounded tip. Finally, the right prehensile palp of the male has a spine-like protrusion, similar to the type species. Nevertheless, new specimens of this species need to be collected and studied to corroborate its position in the new genus due to the lack of information of many traits in its first description by Hartmann (1959).

Physocypria inflata and *P. pustulosa* are two species that could belong to *Vizcainocypria* gen. nov. because some of the non-sexual and sexual characters are similar to those of the genus. Both species lack the d1-seta on the basal segment of T2, and the sp-seta of the CR is short. The right prehensile palp of the two species seems to present a spine-like protrusion; however, it looks bigger than in the other *Vizcainocypria* gen. nov. species. We take in these cases a conservative approach not allocating these two species to *Vizcainocypria* gen. nov. because the morphology of the hemipenis is not as similar as that of *V. granadae* comb. nov., and some non-sexual characters cannot be confirmed with the original descriptions, such as the length of the Md palp.

Other species also present a spine-like protrusion on the right prehensile palp, including *C. lacrima*, *C. subsalsa* or *P. gibbera*, among others. In some of these cases, the non-sexual characters are not congruent with the genus *Vizcainocypria* gen. nov., like the absence of the tubercles on the RV margin. However, especially relevant is the hemipenis morphology for determining the genera position of the species. For example, *C. lacrima* has an a-lobe shorter than b-lobe, as in *Vizcainocypria* gen. nov., however, the general morphology of the hemipenis is different from *Vizcainocypria* gen. nov. (see below).

Vizcainocypria viator gen. nov. sp. nov. Bisquert-Ribes et al.

(Figs. 1–4)

urn:lsid:zoobank.org:act:40734E2C-60B9-40B8-9FC3-C88E7D13F341

Physocypria sp.: Bou et al., 2019: 41.
Dentocypria sp.: Giménez et al., 2020: Fig. 29.

Type materials: *Holotype*: Soft parts of a dissected ♂ preserved in HydroMatrix® on a slide, and valves stored dry in a micropalaeontological slide (MUVHNZY0011). *Allotype.* ♀ stored like the holotype (MUVHNZY0012). *Paratypes.* Two dissected ♂ (MUVHNZY0013 and MUVHNZY0014) and three dissected ♀ (MUVHNZY0015, MUVHNZY0016 and MUVHNZY0017) stored like the holotype.

Repository: The holotype, allotype and paratypes are deposited in the Museum of Natural History of the University of Valencia (MUVHN), Burjassot, Spain.

Type locality: Albufera lake, Albufera Natural Park, Valencia, Comunitat Valenciana, Spain. Material collected in 2014, coordinates: 39°19'10"N, 0°19'27"W. Accompanying ostracod fauna: *Cypridopsis vidua* (Müller, 1776).

Other localities: 1) Rice field, Albufera Natural Park, Valencia, Comunitat Valenciana, Spain. Material collected on 14 December 2020, coordinates 39°16'32"N, 0°18'54"W. 2) Rice field, Marjal Pego-Oliva Natural Park, Pego, Comunitat Valenciana, Spain. Material collected on 30 May 2018, coordinates 38°53'8"N, 0°3'59"W. 3) Rice field, Girona, Catalunya, Spain. Material collected on 17 July 2018, coordinates 41°58'14"N, 3°8'48"E., Leg: J. Sala.

Etymology: The new species is named in relation to the putative geographical dispersal of the species to large distances (see discussion below). The specific epithet means “traveler” in Latin.

Diagnosis: Carapace in lateral view ovate, valve surface smooth with some setae, RV antero-dorsal margin with a slight depression. RV margin tuberculated anteriorly and posteriorly. LV with an internal tooth on antero-ventral part. Rome organ on A1 large and mushroom-like, penultimate segment of A1 with a dorso-apical claw, terminal segment of Md palp very elongated (c.3 times longer than wide), T2 with g-seta and accompanying-seta subequal, and long e-seta. CR with short sp-seta. Right prehensile palp of male T1 with a spine-like protrusion, left prehensile palp with two subapical spines, one long and one short. Hemipenis with b-lobe slightly longer than a-lobe and a-lobe subtriangular (shark fin shaped), distinctly wider than b-lobe.

Differential diagnosis: *Vizcainocypria viator* gen. nov. sp. nov. is characterized by a spine-like protrusion in the right prehensile palp, subtriangular a-lobe of hemipenis and dorso-apical claw in the penultimate segment of A1. In addition, the length of the e-seta on T2 is different from other species. *V. granadae* comb. nov. can be distinguished by its more subrectangular carapace (more ovate in *V. viator* gen. nov. sp. nov.), more elongated male clasping organs and a narrower a-lobe of the hemipenis. The a-lobe of *V. granadae* comb. nov. also has more parallel margins (wider and more divergent in *V. viator* gen. nov. sp. nov.), and the margin of a-lobe closer to b-lobe bearing a bump (straight in *V. viator* gen. nov. sp. nov.). However, a revision of the type material of *V. granadae* comb. nov. and of new specimens of this species are needed to update the original description of Hartmann (1959).

Description of female (Fig. 1): Measurements (mean, in μm): LV (n = 6), L = 578.7, H = 374.4; RV (n = 6), L = 541.9, H = 354.8; Carapace (n = 6), L =

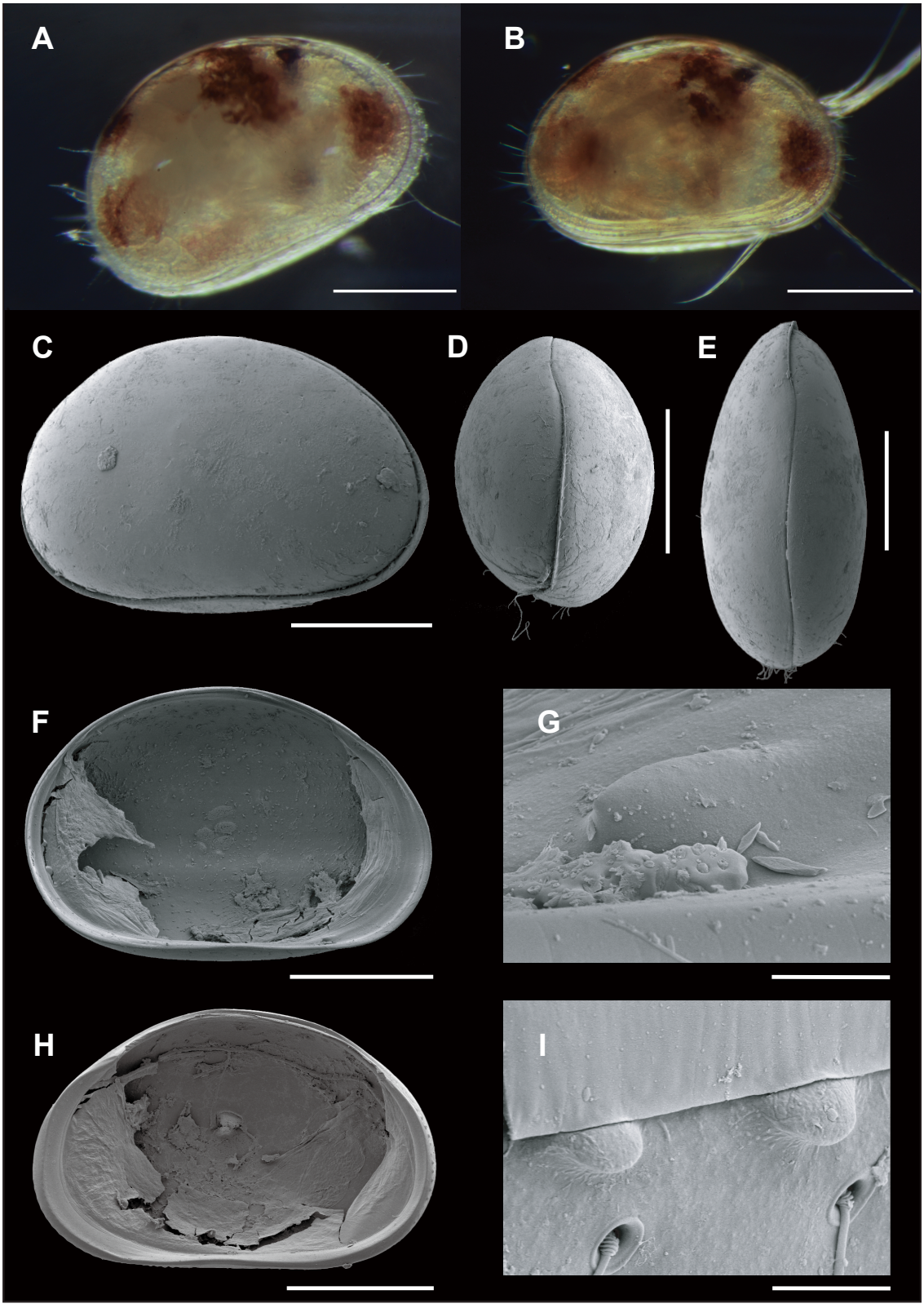

Fig. 1. *Vizcainocypria viator* gen. nov. sp. nov., female (A, C–G, I), male (B, H). A: Mature female specimen. B: Mature male specimen. C: CpL from right side (MUVHNZY0020). D: CpF (MUVHNZY0019). E: CpD (MUVHNZY0018). F: LVi (MUVHNZY0016). G: Detail of the internal tooth (MUVHNZY0016). H: RVi (MUVHNZY0011). I: Detail of the tubercles on RV margin (MUVHNZY0017). Scale bars: A–F, H = 200 μm; G = 10 μm; I = 5 μm.

579.2, H = 374.5, W = 277.2. Valves not homogeneously pigmented (Fig. 1A, B); one large dorsal dark patch between mid-length and the eye spot, and between dorsal margin and mid height of valve (muscle scars); another distinctive patch in the marginal anterior and central part of the valve; one smaller posterodorsal dark patch and another posterior marginal patch, less intense, at mid height. Carapace in lateral view (Fig. 1C) ovate, anterior and posterior margins rounded, LV overlapping RV anteriorly, ventrally and posteriorly, valve surface smooth with some short setules, with small tubercles on the right valve margin anteriorly and posteriorly.

CpF (Fig. 1D) ovate, widest at mid-height.

CpD (Fig. 1E) elliptical, laterally compressed, widest at or slightly behind mid-length.

LVi (Fig. 1F) selvage anteriorly wider than posteriorly, internal tooth (Fig. 1G) on antero-ventral part, calcified inner lamella anteriorly wider than posteriorly, small pits complementary of right valve tubercles anteriorly and posteriorly.

RVi (Fig. 1H) selvage anteriorly wider than posteriorly, complementary pit of internal tooth on antero-ventral part, slight depression of the valve margin on antero-dorsal part, valve margin tuberculated (Fig. 1I) anteriorly and posteriorly, posterior tubercles more prominent than anterior ones, calcified inner lamella anteriorly wider than posteriorly.

A1 (Fig. 2A) 7-segmented, first segment with small proximal Wouters organ, one long dorso-subapical seta (reaching beyond tip of next segment), and two long ventro-apical setae, reaching terminal segment. Second segment more than twice as wide as long, with one dorso-apical seta (reaching tip of next segment) and large mushroom-like Rome organ. Third segment bearing two setae: one long dorso-apical seta (reaching tip of fifth segment) and one shorter ventro-apical seta (reaching beyond tip of next segment). Fourth segment with two very long dorsal setae (reaching far beyond tip of terminal segment, but one more than twice as long as the other) and two ventral setae (shortest one not reaching half of sixth segment, longer one reaching half of sixth segment). Fifth segment with two very long-setae (longer than entire limb) dorsally, and with two setae ventrally (short one reaching tip of terminal segment and long one reaching beyond the terminal segment and about one third longer than the short seta). Penultimate segment with four (two dorsal and two ventral) very long apical setae and one dorsal claw (about three times the length of the terminal segment). Terminal segment with two very long apical setae, one apical claw-like seta and one aesthetasc ya, length of the latter c. 1/2 of the claw-like seta.

A2 (Fig. 2B) exopod with three (one long, two short) setae, long one reaching beyond tip of first endopodal segment. First endopodal segment with five very long (reaching far beyond tip of terminal claws) natatory setae and one short accompanying-seta, length of the shortest seta less than half of penultimate segment, aesthetasc Y long (almost reaching tip of corresponding segment), ventro-apical seta long, reaching tip of terminal claws. Penultimate segment undivided, distally with three serrated claws (G1, G2, G3), G2 shorter (length of G2 c. 1/2 that of G1), aesthetasc y2 reaching beyond tip of terminal segment, three subapical setae: seta z1 claw-like, short (length of z1 c. 1/2 of that of z2) and wide; z2–z3 setae long, z3 longer than z2; medially with two long dorsal setae, four ventral setae of unequal length (t1–t4) and aesthetasc y1, the latter long (reaching tip of corresponding segment). Terminal segment distally with two serrated claws (GM and Gm), length of Gm c. 4/5 of that of GM; medially with ventral aesthetasc y3, length of aesthetasc y3 c. 2/3 that of accompanying-seta.

Md palp (Fig. 2C–E) first segment with two large hirsute setae, one long and slender seta, and a very short, smooth α-seta. Second segment dorsally with two unequal long apical setae (long one reaching beyond half of penultimate segment, length of the short one c. 2/3 of the long one); ventrally with group of two long hirsute setae, one long smooth seta and a small, plumose, dome-shaped β-seta. Penultimate segment consisting of two groups of four setae each and one isolated seta. Dorsally with a group of four similar, long, subapical setae; laterally with apical γ-seta and three unequal apical setae: the longest one slightly beyond tip of γ-seta, the most dorsally one with length 2/3 of γ-seta and the most ventral one with length 1/2 of γ-seta; in the middle part with one isolated, long subapical seta (length similar to terminal segment). Terminal segment very elongated (c. 3 times as long as wide, length similar to penultimate segment) bearing three claws and one long-seta.

Mx1 (Fig. 2F) with 2-segmented palp, three endites and large branchial plate; basal segment of palp dorsally with two groups of setae, one group with two apical setae (one plumose and another smooth) and another group of four long subapical setae (reaching beyond tip of terminal segment); in the middle part of the palp with one plumose subapical seta. Terminal segment subquadrate, apically with three claws and three setae (two long claws and one slightly longer than the setae). Two unequally long bristles on third endite, length of short one c. 3/4 times that of long one. This endite with four short apical setae, one ventro-apical short seta and one long ventral seta. Second endite with four long and one short apical setae, and one short ventro-apical seta. First endite with two long and seven shorter apical setae, shorter ones about 2/3 the

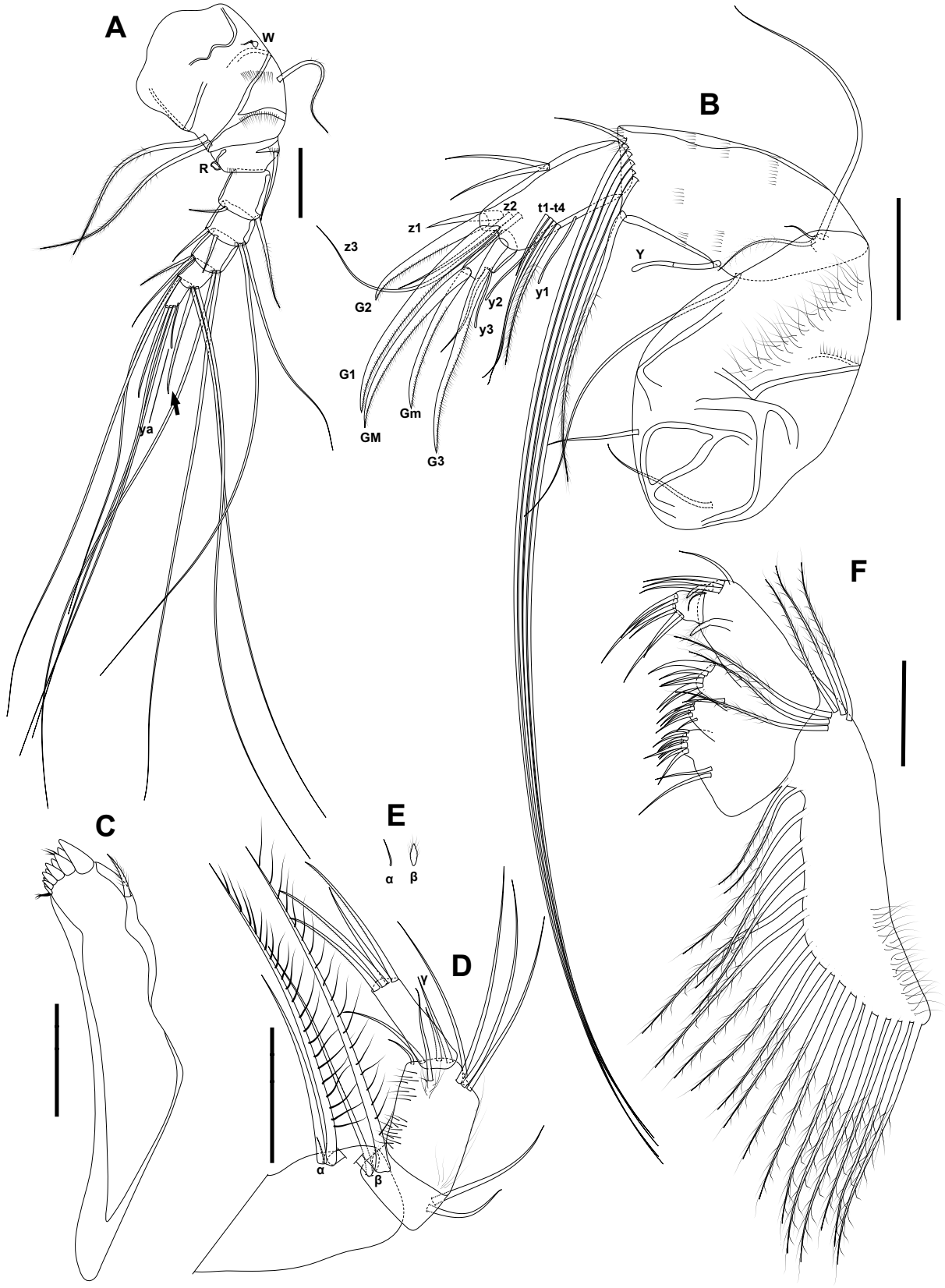

Fig. 2. *Vizcainocypria viator* gen. nov. sp. nov., female (MUVHNZY0012). A: A1 (arrow pointing to apical claw on penultimate segment). B: A2. C: Md coxa. D: Md palp. E: Detail of α and β setae. F: Mxl. Scale bars: A–F = 50 µm.

length of the longer ones. Ventrally with two long-setae. Branchial plate with c. 19 ventral rays, the two most basal of which being half the length of the longer ones, and six reflexed dorsal rays.

T1 (Fig. 3A) protopodite with two subequal short a-setae, long b-seta and long d-seta and additional long and hirsute seta, and distally with c. 13 hirsute apical setae of unequal length. Endopod weakly built palp with three short and unequal apical setae. Branchial plate with five rays.

T2 (Fig. 3B) without d1 and d2 basal setae. Second segment with long e-seta (reaching tip of penultimate segment). Penultimate segment divided, proximal segment bearing normally developed f-seta (length 3/4 of length of distal segment), distal segment with apical g and accompanying-setae (both subequal in length). Terminal segment with two (one dorsally, one ventrally) apical h1 and subapical h3 setae and apical serrated claw (h2), as long as the penultimate and antepenultimate segments together.

T3 (Fig. 3C) first segment with long d1, d2 and dp setae, d1 and d2-setae subequal in length. Second segment with subapical e-seta (length c. 1/2 of penultimate segment). Third segment with sub-medially f-seta (reaching tip of corresponding segment), g-seta short. Terminal segment subquadrate, with three setae, two short h1 and h2 setae (subequal in length with h2 slightly longer), and one reflexed subapical h3 seta, length of the latter equal to that of three last segments.

CR (Fig. 3D) well-developed, robust, ventrally with three parallel rows of setules, Ga and Gp large, serrated, length of Ga c. half that of ramus, length of Gp c. 2/3 that of Ga. Sa short (less than half of Ga), sp-seta short (length c. 1/3 of Gp).

CR attachment (Fig. 3E) with two distal branches.

Description of male: Measurements (mean, in μm): LV (n = 6), L = 527.5, H = 336.1; RV (n = 6), L = 527.7, H = 314.3; Carapace (n = 6), L = 528.4, H = 338.2, W = 275.3. Carapace (Fig. 1B) and valves as in female, but somewhat smaller. All limbs as in the female (not illustrated), except for last two segments of A2 and T1 (illustrated).

A2 (Fig. 4A) with penultimate segment divided and t2 and t3 setae transformed into sexual bristles, long (reaching slightly beyond tip of terminal segment) and subequal. Setae z1 and z2 transformed into claws, length of z1 half of z2; claw G1 reduced, appearing smaller and shorter than that of female; claw G3 reduced to seta (length about twice the length of terminal segment).

T1 with asymmetrical prehensile palps (endopods). Right prehensile palp (Fig. 4B) with first segment bearing one short apical spine, distal margin with large spine-like protrusion, distal part wider than basal part; second segment large, subtriangular. Left prehensile palp (Fig. 4C) with elongated first segment bearing two subapical spines, one long and the other shorter; second segment narrow, hook-like and pointed tip.

Hemipenis (Fig. 4D) b-lobe elongated and thinner than a-lobe, slightly bent towards a-lobe, and with a rounded tip; a-lobe wide, subtriangular, with a shark fin shape and slightly shorter than b-lobe.

Zenker organ (Fig. 4E) sub-elongated, length c. 2 times width, set with seven chitinous spiny whorls, five along the central tube, two at the extremes.

Key to the genera of the family Cyclocyprididae

1a. RV margin smooth 2
1b. RV margin tuberculated 7
2a. d1-seta on T2 present 3
2b. d1-seta on T2 absent 6
3a. A1 7-segmented; A2 natatory setae well-developed 4
3b. A1 6-segmented; A2 natatory setae reduced; t2 and t3 on male A2 not transformed into sexual bristles ..... ***Kempfcyclocypris***
4a. Carapace subovate in lateral view; terminal segment of T3 very elongated (3x–4x longer than wide); g-seta on T3 well-developed; t2 and t3 on A2 male not transformed into sexual bristles ..... ***Cyclocypris***
4b. Carapace elongated in lateral view; terminal segment of T3 subquadrate (< 3x longer than wide); g-seta on T3 short or absent; t2 and t3 on A2 male transformed into sexual bristles ... 5
5a. Imprints of ovaries curved upwards; bristles on 2nd and 3rd endites of Mxl present; terminal segment of Md palp usually squared ..... ***Allocypria***
5b. Imprints of ovaries curved downwards; bristles present only on 3rd endite of Mxl; terminal segment of Md palp elongated (2x longer than wide) ..... ***Mecynocypria***
6a. T3 terminal segment elongated; A2 natatory setae reduced; terminal segment of Md palp elongated (2x longer than wide) .... ***Namiotkocypria***
6b. T3 terminal segment subquadrate; A2 natatory setae well-developed; terminal segment of Md palp very elongated (> 2x longer than wide) ..... ***Cypria***
7a. A2 short accompanying natatory seta absent 8
7b. A2 short accompanying natatory seta present 10
8a. Terminal segment of Md palp elongated (2x longer than wide) or very elongated (3x–4x longer than wide) 9
8b. Terminal segment of Md palp extremely elongated (5x longer than wide); lobe-a of the hemipenis with a boxing glove-like distal end ..... ***Keysercypria***
9a. Terminal segment of Md palp very elongated (3x longer than wide); presence of dp-seta on T3 ..... ***Brasilocypria***
9b. Terminal segment of Md palp elongated (2x longer than wide); absence of dp-seta on T3 ..... ***Claudecypria***
10a. Terminal segment of Md palp elongated (2x longer than wide); d1-seta on T2 usually present ..... ***Physocypria***
10b. Terminal segment of Md palp very or extremely elongated (3–5x longer than wide); d1-seta on T2 absent 11
11a. sp-seta on CR long; 1st segment of right prehensile palp with apical subtriangular protrusion and without finger-like protrusion; a-lobe of hemipenis slender and longer than b-lobe .... ***Dentocypria***
11b. sp-seta on CR short; 1st segment of right prehensile palp with apical spine or finger-like protrusion; a-lobe of hemipenis wide and shorter than b-lobe ..... ***Vizcainocypria***

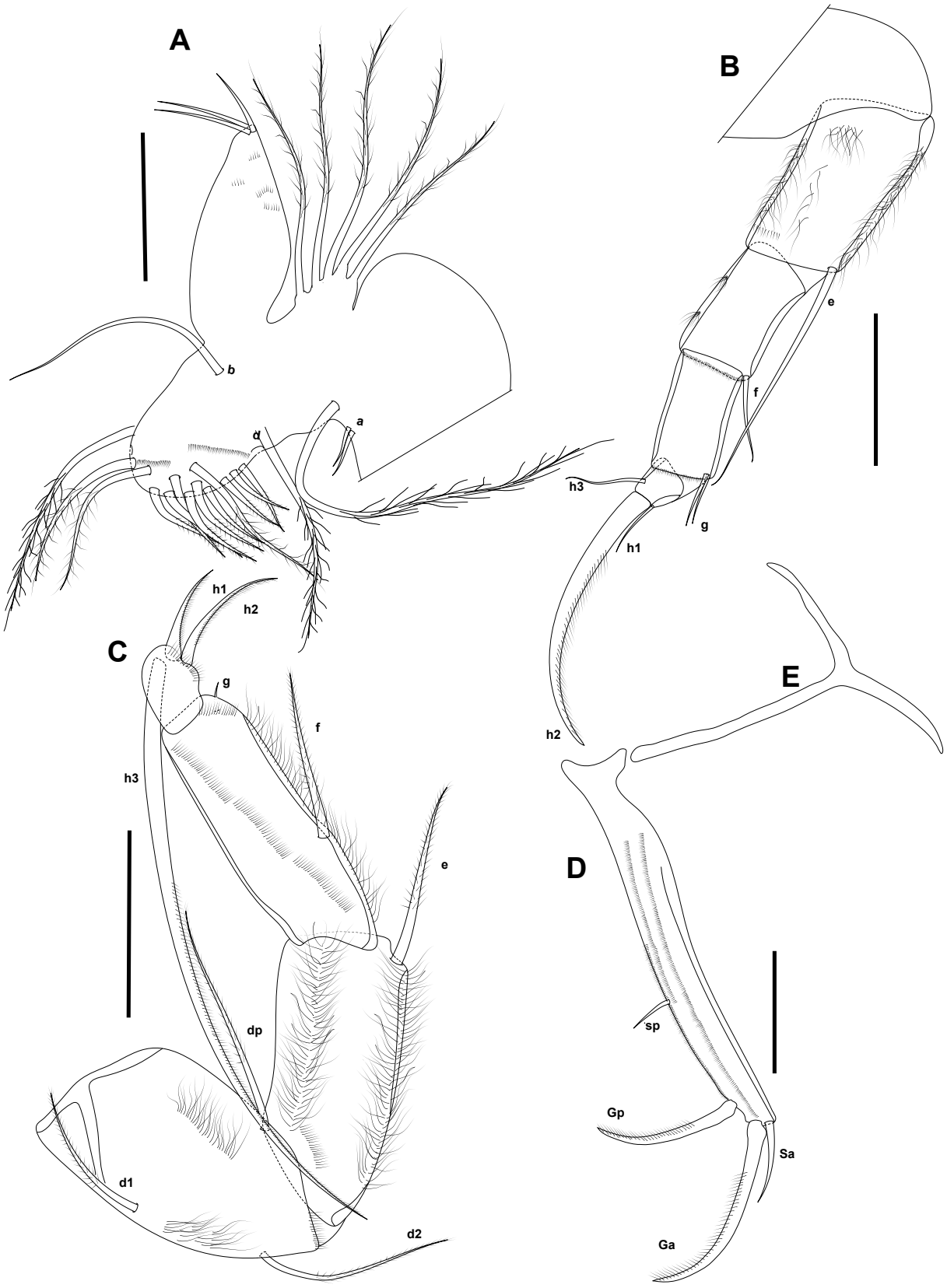

Fig. 3. *Vizcainocypria viator* gen. nov. sp. nov., female (MUVHNZY0012). A: T1. B: T2. C: T3. D: CR. E: Caudal attachment. Scale bars: A–E = 50 μm.

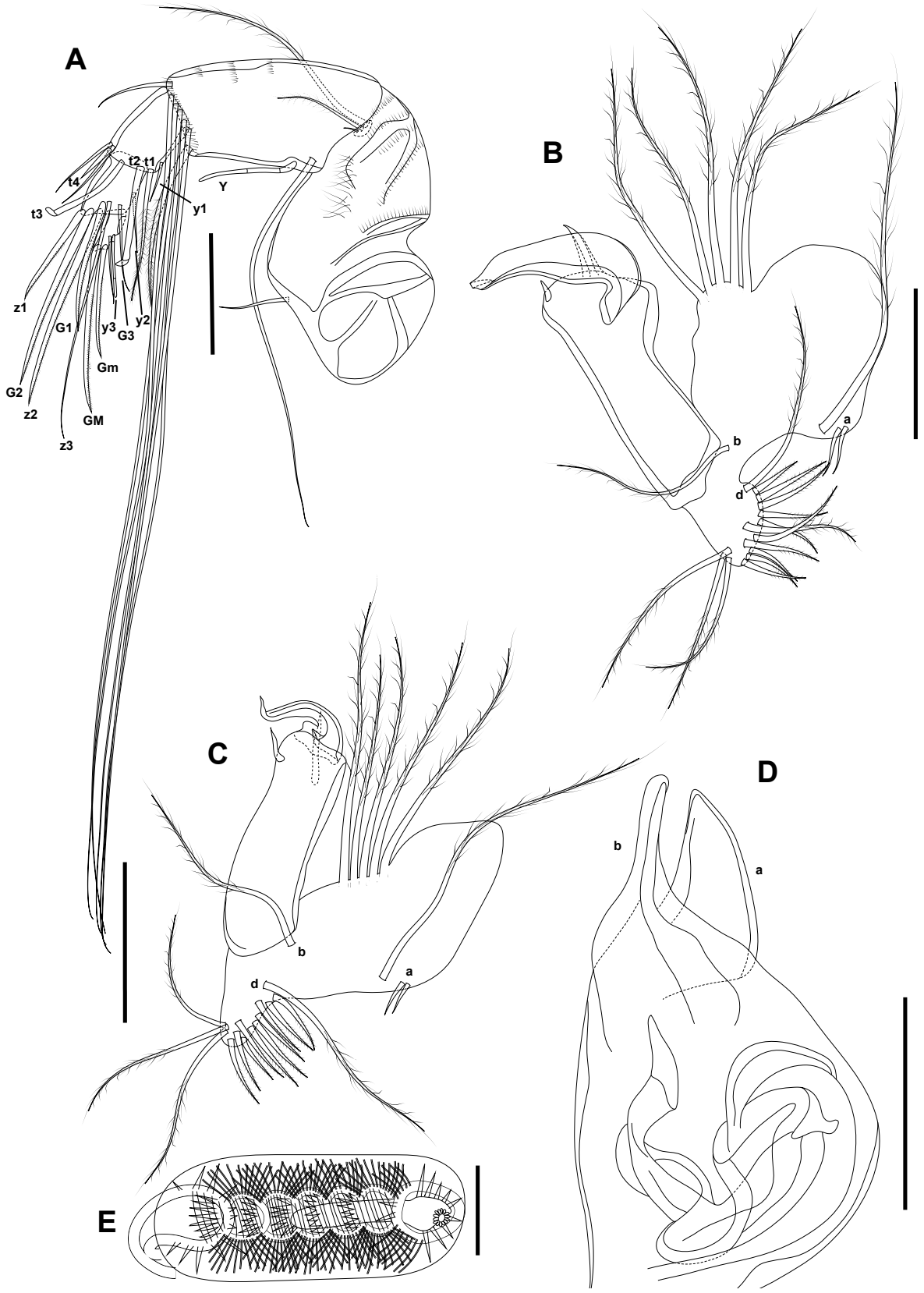

Fig. 4. *Vizcainocypria viator* gen. nov. sp. nov., male (MUVHNZY0011). A: A2. B: Right prehensile palp. C: Left prehensile palp. D: Hemipenis. E: Zenker organ. Scale bars: A–E = 50 µm.

Molecular analyses

New COX1 gene sequences have been obtained for *D. smithi* (GenBank accession number: OP208069) and *V. viator* gen. nov. sp. nov. (OP208070) and new 28S rDNA sequences for *D. smithi* (OP216521), *V. viator* gen. nov. sp. nov. (OP216522) and *C. ophtalmica* (OP216523). After trimming the alignments, the final COX1 and 28S rDNA datasets had 438 bp and 234 bp, respectively. The best DNA substitution models selected were TPM1uf+I+G4 (lnL: -3413.67) for COX1 and TPM3uf+G4 (lnL: -670.17) for 28S rDNA. Phylogenetic trees for the mitochondrial (lnL: -3418.29) and nuclear markers (lnL: -666.44) were both congruent, showing representatives of Cyclocyprididae *s.str.* (*i.e.*, *Physocypria*, *Cypria*, *Dentocypria* and *Vizcainocypria*) to form a monophyletic clade despite no significant (> 70) bootstrap support. The new *C. ophtalmica* 28S rDNA sequence and *C. exsculpta* from GenBank clustered with putative *Cypridopsis* sp. and *P. nipponica* sequences (Fig. 5A; see Discussion). Despite internal nodes not showing significant bootstrap values, most likely because ribosomal genes are highly conserved, *V. viator* gen. nov. sp. nov. appeared as an early-splitting lineage within Cyclocyprididae (Fig. 5). Groups of taxa appear to be better defined for the COX1 gene tree, with *Physocypria* sequences clustering together. Phylogenetic affinities between Cyclocyprididae genera could not be resolved, but genetic differentiation among the four main genera was high for the COX1 gene

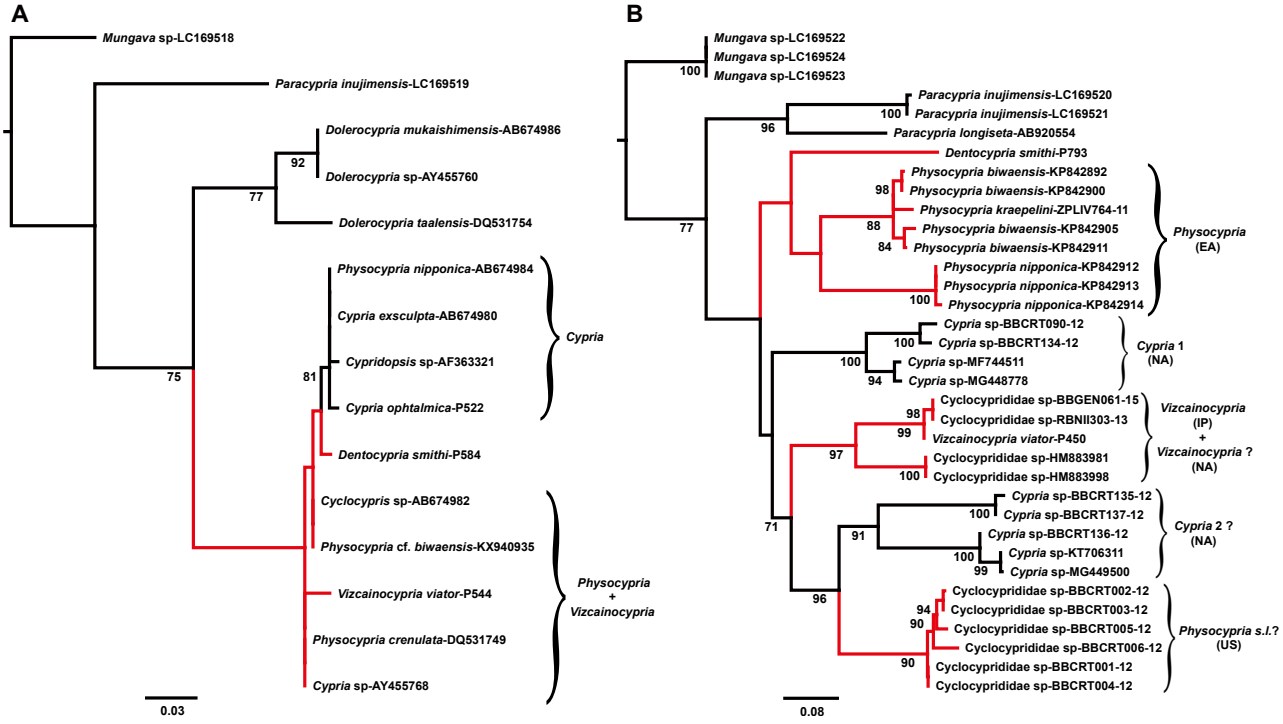

Fig. 5. Maximum likelihood tree for 28S (A) and COX1 (B) genes. Red branches indicate the presence of tubercles on the RV margin.

Table 1. Estimates of evolutionary divergence (Kimura 2-parameter) between genera. The number of base substitutions per site from averaging over all sequence pairs between groups and the standard error estimates are shown

	Physocypria	*Dentocypria*	Cyclocyprididae	*Vizcainocypria*	*Cypria* 2	*Mungava*	*Cypria* 1
Dentocypria	0.202 ± 0.024						
Cyclocyprididae	0.233 ± 0.023	0.188 ± 0.025					
Vizcainocypria	0.216 ± 0.022	0.227 ± 0.027	0.222 ± 0.023				
Cypria 2	0.241 ± 0.022	0.266 ± 0.029	0.211 ± 0.022	0.235 ± 0.023			
Mungava	0.233 ± 0.024	0.256 ± 0.031	0.258 ± 0.029	0.253 ± 0.026	0.270 ± 0.026		
Cypria 1	0.227 ± 0.023	0.236 ± 0.028	0.222 ± 0.023	0.229 ± 0.023	0.255 ± 0.024	0.224 ± 0.024	
Paracypria	0.254 ± 0.023	0.277 ± 0.030	0.252 ± 0.024	0.250 ± 0.023	0.261 ± 0.023	0.257 ± 0.026	0.258 ± 0.024

(Fig. 5B; Table 1). *Vizcainocypria viator* gen. nov. sp. nov. clustered significantly (97% bootstrap) with four putative "Candonidae" sequences from the BOLD database (which seem to be in fact Cyclocyprididae specimens collected in US and Canada, see Discussion). Our *D. smithi* sequence clustered with *Physocypria* sequences from Eurasia. It should be pointed out that GenBank sequences assigned to *Cypria* formed two clusters (Fig. 5B).

COX1 genetic distances between genera are shown in table 1, and between species in table S1. K2P distances between the four main clusters of Cyclocyprididae were very similar, and mean distance between genera was 0.240 ± 0.025. The lowest K2P distances were observed among Cyclocyprididae gen. and *Dentocypria* (0.188 ± 0.025), between *Physocypria* and *Dentocypria* (0.202 ± 0.024) and then between *Physocypria* and *Vizcainocypria* (0.216 ± 0.022). Distances between the *Cypria* 2 clade and *Vizcainocypria* (0.235 ± 0.023) were lower than distances between *Cypria* 2 and *Physocypria* (0.241 ± 0.022) or between *Cypria* 2 and *Dentocypria* (0.266 ± 0.029). Finally, K2P distances between sequences assigned to *Vizcainocypria* are similar or even lower than distances between *Physocypria* species (Table S1).

DISCUSSION

The historical accumulation of species within two Cyclocyprididae genera (*Cypria* and *Physocypria*) has resulted in a wastebasket of taxa with highly diverse soft parts, including sexual and non-sexual characters. Nevertheless, the recent allocation of some *Physocypria* species into new genera (Karanovic 2011) and the description of new genera (Savatenalinton 2017; Külköylüoğlu 2018; Almeida et al. 2023) have improved our understanding of this family. In the present study, a new genus and species (*Vizcainocypria viator* gen. nov. sp. nov.) is erected to host specimens showing affinities with the most controversial group of cyclocyprid genera (*Brasilocypria*, *Claudecypria*, *Cypria*, *Dentocypria*, *Keysercypria* and *Physocypria*). Sexual and non-sexual characters are proposed to characterize them, describing their hemipenis morphology and comparing them with the type genus of the family, *Cyclocypris*. Our taxonomical results are expected to be particularly useful for discriminating cyclocyprids in future studies. Furthermore, we provide new molecular information, contributing to a preliminary phylogeny for the most controversial Cyclocyprididae genera, which unfortunately still remains to be fully resolved.

After the establishment of the new genus, the family Cyclocyprididae is composed of the following 12 recent genera: *Allocypria*, *Brasilocypria*, *Claudecypria*, *Cyclocypris*, *Cypria*, *Dentocypria*, *Kempfcyclocypris*, *Keysercypria*, *Mecynocypria*, *Namiotkocypria*, *Physocypria*, and *Vizcainocypria* gen. nov. The redescription of the type species of *Physocypria* by Karanovic (2011) allowed us to confirm the taxonomic position of some species, but the genus assignment of many others could not be verified due to incomplete descriptions. For those genera, a careful revision of museum material or new specimens from type localities is needed to strengthen our current understanding of the group.

On the validity of *Keysercypria*

Karanovic (2011) erected *Keysercypria* by uniting species of *Cypria* and *Physocypria* from the Neotropical region, prioritizing soft parts over valve characters (RV marginal tubercles). However, Meisch et al. (2019) argued that shell traits can be easily checked in both living and fossil specimens and defended a more conservative approach, reassigning *Keysercypria* species to *Cypria* or *Physocypria*.

Recently, Almeida et al. (2023) re-established *Keysercypria* with a more restricted diagnosis than Karanovic (2011). The authors agreed with Karanovic (2011) that three Neotropical *Physocypria s.l.* species that she had classified as *Keysercypria* were different from *Physocypria s.str*. However, Almeida et al. (2023) based their diagnoses of the genus mainly on the chaetotaxy of T2 (male), A2 and T3.

We agree with Karanovic (2011) and Almeida et al. (2023) on the validity of *Keysercypria*. However, we included two more species (see above) of *Physocypria s.l.* originally allocated by Karanovic (2011) to the genus *Keysercypria*, but which Almeida et al. (2023) did not include in their revision. The main criterion we followed for including the species in *Keysercypria* was their hemipenis morphology (see below), which is very similar in all the species that we assigned to *Keysercypria*, and distinct enough from other cyclocyprids to support the monophyly of *Keysercypria.* New specimens of *Keysercypria* species, where valves and soft parts can be accurately described, should be collected before a final consensus is achieved.

Non-sexual characters

Some non-sexual characters, such as the length of the Md palp terminal segment or the length of the sp-seta on CR, can be very useful for disentangling cryptic genera. Here, we discuss the validity of these morphological characters and their diagnostic utility to differentiate between the problematic genera

(*Brasilocypria*, *Claudecypria*, *Cypria*, *Dentocypria*, *Keysercypria*, *Physocypria* and *Vizcainocypria* gen. nov.).

RV marginal tubercles

Savatenalinton (2017) already noted the utility of RV marginal tubercles as a diagnostic character. In fact, marginal tubercles are also used to discriminate among Cyprinotinae Bronstein, 1947 genera: while *Hemicypris* Sars, 1903 has marginal tubercles on LV, *Heterocypris* Claus, 1892 and *Cyprinotus* Brady, 1886 present tubercles on the RV instead. This trait seems to participate in the enclosure of the valves, and it is related to the valve overlap because tubercles usually appear on the smallest valve. In the Cyclocyprididae, marginal tubercles are present in members of some genera (*Dentocypria*, *Keysercypria*, *Physocypria* and *Vizcainocypria* gen. nov.), but not others (*Allocypria*, *Cypria*, *Cyclocypris*, *Kempfcyclocypris*, *Mecynocypria* and *Namiotkocypria*). For those genera with tubercles, the tubercles always appear on the RV margin, except in *P. bullata* (the type species of the genus) and *P. ivanae*, both of which have tubercles on the two valves, and *P. dentifera*, which has tubercles on the LV. Following Meisch et al. (2019), we recommend using the presence/absence of RV marginal tubercles as one of the key characters. Our preliminary molecular results do not allow us to conclude that this character defines a single monophyletic clade. The largely unresolved 28S tree suggests a basal ancestor with tubercles and their disappearance in the *Cypria* clade, but the COX1 tree rather suggests that tubercles may have appeared repeatedly in different clades (assuming an ancestor with no tubercles) or their independent disappearance in different lineages.

Karanovic (2011) and Meisch et al. (2019) agree on the utility of another carapace trait, the curvature of the ovaries. However, this trait cannot be observed in fossil specimens, and it can be difficult to see in living animals, so we recommend only using the curvature of the ovaries as a key character in the diagnoses of the genera if it is absolutely necessary.

Morphology of T2

Karanovic (2011 2012) and Savatenalinton (2017) supported the utility of the presence or absence of the d1-seta on T2 for generic characterization. The partial redescription of *P. bullata* by Karanovic (2011) clarified the presence of the d1-seta on T2 in this genus. Whenever possible, we have allocated some species to *Dentocypria* or *Vizcainocypria* gen. nov. (both without d1-seta on T2) that had been previously assigned to *Physocypria* only because of their RV marginal tubercles. Species assigned to *Cypria*, *Dentocypria*, *Keysercypria* and *Vizcainocypria* gen. nov., as well as the recently raised genera *Brasilocypria* and *Claudecypria*, consistently lack the d1-seta on T2.

Another character of the T2 that has been considered as a generic character for Cyclocyprididae is the appearance of the e-seta. Meisch (2000) already mentioned this character this character as an important diagnostic trait to distinguish *Cypria* and *Physocypria*, as did Savatenalinton (2017), since all *Dentocypria* species present exceedingly long e-setae. Nevertheless, Almeida et al. (2023) suggested that the length of the e-seta on T2 could be relevant at the species rather than genus level, which is consistent with our rearrangement of species for *Dentocypria*, *Keysercypria*, *Physocypria*, and *Vizcainocypria* gen. nov.

Morphology of the Md palp

Savatenalinton (2017) discussed the length of the Md palp terminal segment and its use as a diagnostic character at the genus level, and Almeida et al. (2023) noted that closely related cyclocypridid genera (*Brasilocypria*, *Claudecypria* and *Keysercypria*) present differences in this trait. The Md-palp terminal segment is very elongated in *Vizcainocypria* gen. nov. (3x–4x longer than wide), distinguishing it from *Physocypria* (2x longer than wide) and *Keysercypria* (5x longer than wide). However, obtaining information on this character from original descriptions is often impossible because the Md palp had been widely overlooked. We would like to emphasize here the potential of some commonly overlooked characters, such as the Md palp, as useful guides for the classification of Cyclocyprididae ostracods, taking into account that some features of this palp, such as the number and morphology of a variety of setae, are important for distinguishing between Candonidae genera (Meisch 2000).

Morphology of CR

The morphology of the caudal ramus is usually described or illustrated in most original descriptions, so we could evaluate this appendix in most taxa. The sp-seta length is used here to differentiate genera with short sp-seta (*Cypria* and *Vizcainocypria* gen. nov.) from those with long sp-seta (*Claudecypria*, *Brasilocypria*, *Dentocypria*, *Keysercypria* and *Physocypria*). However, this trait alone cannot be used to characterize genera because some genera present different morphologies. Most *Cyclocypris* species have a short sp-seta, but others, such as *C. scrobiculata* Klie, 1936, present a long sp-seta. Similarly, some *Cypria s.l.* species, such as

C. bicolor or *C. javana*, also present a long sp-seta.

Problematic cyclocypridid genera can be disentangled and identified using a combination of non-sexual characters. Nevertheless, more research is needed on *Physocypria* and *Cypria* because they have accumulated many species over the years, partly becoming wastebasket genera for any slender Cyclocyprididae with or without marginal tubercles, respectively. The new information provided here allows us to better define the generic position of many species, not just based on RV marginal tubercles, but with the combination of characters discussed. Different traits can be used for classifying cyclocypridid genera. For example, the spined bristles present on the second and third endite of the Mxl palp are outstanding characters for *Allocypria*, as the remaining genera of the family only have bristles on the third endite of the Mxl palp. However, we should point out that the number of setae, claws and bristles of the Mxl could be difficult to interpret, and are therefore obviated in many descriptions. In addition, as most species of this family have bisexual populations, the particular morphology of the male copulatory organ should also be taken into account, as discussed below.

Male copulatory organ morphology

Non-sexual characters are useful for distinguishing between genera, especially when ostracod populations are parthenogenetic. However, when males are present, hemipenis morphology has been considered an important character in ostracod systematics, used to highlight differences among Cypridoidea genera (Danielopol 1969), differentiate taxa within the Cytheroidea (Martens 2000; Dung and Tsukagoshi 2014) or even within Candonidae *s.s.*, the closest group to Cyclocyprididae (Danielopol 1969; Smith and Kamiya 2006; Iepure et al. 2007). In this framework, copulatory organs can be very useful for clarifying and distinguishing seven cyclocypridid genera with similar morphologies (*i.e.*, *Brasilocypria*, *Claudecypria*, *Cypria*, *Dentocypria*, *Keysercypria*, *Physocypria* and *Vizcainocypria* gen. nov.). However, the internal parts of the hemipenis have not always been drawn, especially in the early descriptions. Our revision of the external morphology of the hemipenis in this group, focusing on the appearance of the a- and b-lobes and their relative size and position, allowed us to distinguish eight general morphotypes corresponding to *Cyclocypris*, the type genus of the family, plus the seven aforementioned genera (Fig. 6).

Cyclocypris type (Fig. 6A): The hemipenis of the type species *C. globosa* (Sars, 1863) has three lobes, the inner (b), the outer (a) and the medial (h), but sometimes only lobes a and b are observed or remarked in taxonomic works for other species of the genus. In any case, these lobes are usually wide (not elongated) and broadly rounded or with a distal flat plateau, as in the a-lobe of *C. ovum* (Jurine, 1820). The *Cyclocypris* type hemipenis, in terms of the morphology of its lobes, is closest to candonids than to other Cyclocyprididae genera (except *Kempfcyclocypris*), suggesting *Cyclocypris* could be an ancient representative of the group.

Cypria type (Fig. 6B): The lobes are subequal in length and always distinctly elongated in comparison with those of *Cyclocypris*. The a-lobe is usually broad with rounded distal end, sometimes pointed, whereas the b-lobe can be thinner or as broad as the a-lobe, but almost always pointed. The b-lobe is usually curved towards the a-lobe, which is also slightly curved towards the b-lobe. Both lobes are of similar length, but the a-lobe is usually slightly longer than the b-lobe. *Cypria exsculpta*, the type species of *Cypria*, presents a unique hemipenis morphology among the members of the genus, and it is also different from most other genera. This species has two lobes that are broader, shorter and with more rounded tips than other taxa, particularly regarding the b-lobe which is wide and similar to those of the genus *Cyclocypris*. In fact, hemipenis morphology is very variable among *Cypria* species, with some taxa such as *C. javana* showing hemipenis lobes closer to *Physocypria* or *Dentocypria* types. It must be pointed out that Savatenalinton (2017) has noted the possible existence of at least two genera within *Cypria* and hemipenis morphology could help to distinguish them.

Physocypria type (Fig. 6C): Both lobes are elongated, a-lobe longer or as long as b-lobe, with distal end curved towards the inner part of the hemipenis. The b-lobe is subelongated, broader at the base and with thin distal end, usually sinuous or S-shaped. The a-lobe is elongated, its tip usually wider than that of the b-lobe and rounded (more pointed in the b-lobe). Some *Physocypria* species, such as *P. nipponica* and *P. biwaensis*, do not seem to have d1-seta on T2, a distinctive character of *Physocypria*, but are here considered *Physocypria* because they present the characteristic male copulatory organ of the genus. Nevertheless, other species within *Physocypria s.l.* may not belong to the genus because they lack d1-seta on T2, but also present a hemipenis morphology different from the *Physocypria* type described here. In those cases, we decided to maintain the species in the genus because we take a conservative approach, but further information should be gathered to confirm their genus-level position.

Dentocypria type (Fig. 6D): The hemipenis has both lobes elongated. The b-lobe is subtriangular, with

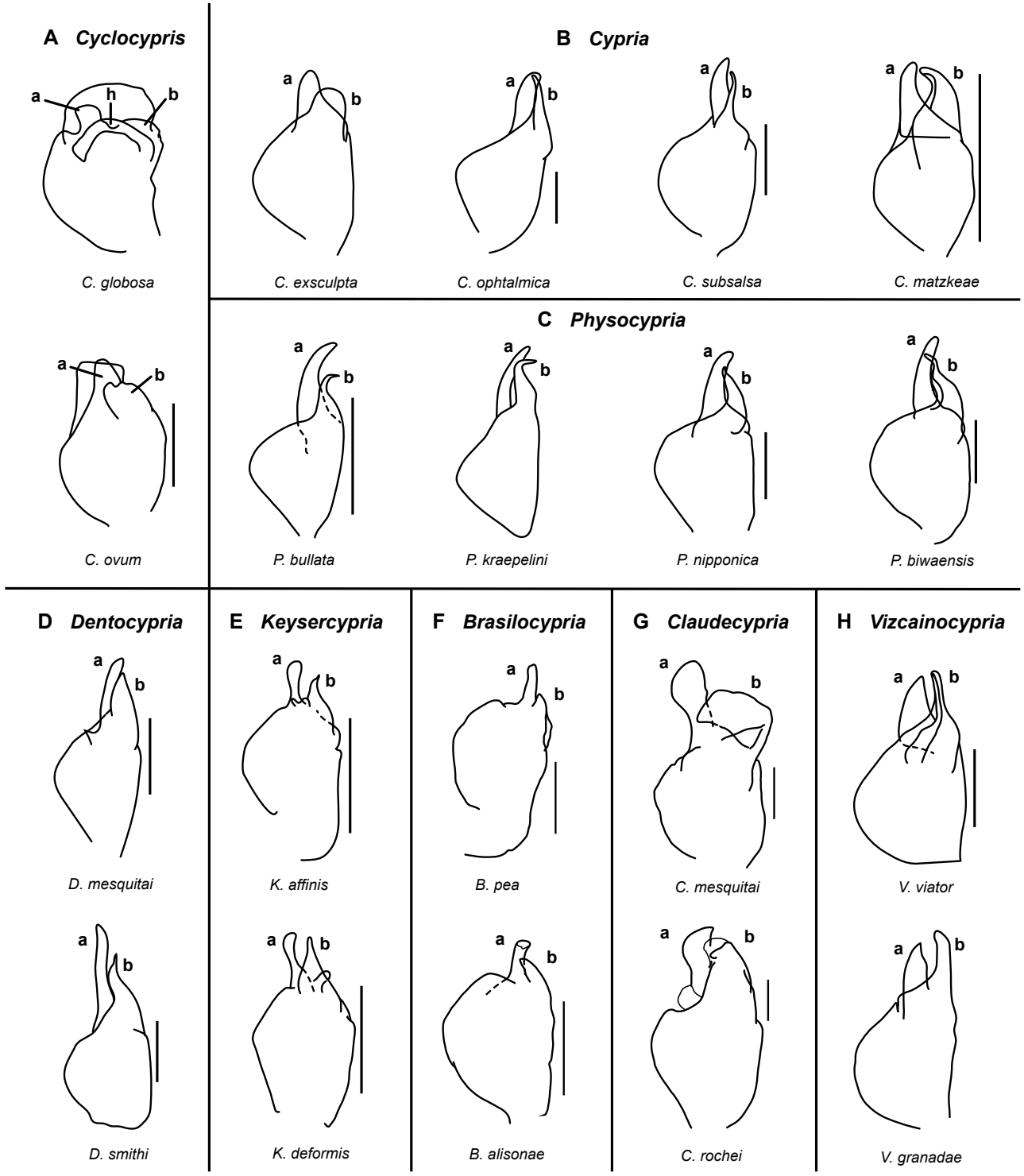

Fig. 6. Male copulatory organs (hemipenes) of different species of Cyclocyprididae. A: *Cyclocypris*, B: *Cypria*, C: *Physocypria*, D: *Dentocypria*, E: *Keysercypria*, F: *Brasilocypria*, G: *Claudecypria*, H: *Vizcainocypria*. Redrawn from Almeida et al. (2023): F, G; Karanovic (2011): C (*P. bullata*), E; Hartmann (1959): H (*V. granadae*); Meisch (2000): A, B (*C. exsculpta*, *C. ophtalmica*), C (*P. kraepelini*); Savatenalinton (2017): D; Smith and Janz (2008): B (*C. matzkeae*), C (*P. nipponica*, *P. biwaensis*); Wouters (1984): B (*C. subsalsa*). Scale bars are shown when available: *D. smithi* = 46 µm; *C. ovum*, *C. ophtalmica*, *C. subsalsa*, *P. nipponica*, *P. biwaensis*, *D. mesquitai*, *B. pea*, *B. alisonae*, *C. mesquitai*, *C. rochei*, *V. viator* = 50 µm; *C. matzkeae*, *P. bullata*, *K. affinis*, *K. deformis* = 100 µm.

a broad base and a thinner distal end, but it can also be similar to that of *Physocypria*, *i.e.*, with a double curve, sinuous and with a pointed tip. The a-lobe is elongated and with a more or less constant width, and its tip is rounded. The a-lobe is longer than the b-lobe, and straight, or slightly curved towards b-lobe.

Keysercypria type (Fig. 6E): The lobes are elongated, but shorter than in the other genera. The lobes are positioned with some separation from each other. The a-lobe presents a rounded, boxing glove-like distal end, usually wider than the central trunk of the lobe. The b-lobe is subtriangular, with a thin and pointed distal end. The a-lobe is slightly longer than the b-lobe.

Brasilocypria type (Fig. 6F): Species of this genus have a quite variable hemipenis morphology. However, they share an elongated a-lobe, broader at the base and with a thinner distal end. The b-lobe is usually shorter than the a-lobe and subtriangular in shape. The distal end of the b-lobe could be rounded or pointed.

Claudecypria type (Fig. 6G): The two lobes are elongated and subequal in length, with the a-lobe being slightly longer than the b-lobe. Both lobes are distinctly broad throughout their length, but with the distal part broader than the base. The a-lobe presents a big rounded distal end, similar to *Keysercypria* distal end, but markedly larger. The b-lobe presents a flattered distal end in comparison to the a-lobe.

Vizcainocypria type (Fig. 6H): The lobes are elongated and subequal in length or with b-lobe longer than the a-lobe; the latter being subtriangular and presenting a pointed distal end the b-lobe is elongated and thinner than the a-lobe. The distal end of the b-lobe is rounded and slightly curved towards the a-lobe. Both lobes are longer than in *Keysercypria* or *Brasilocypria* types.

Our results show clear differences between hemipenis morphotypes, which are also congruent with the other morphological traits and with molecular data. For example, the most similar hemipenis morphology between *Physocypria* and *Dentocypria* is congruent with the shortest K2P distances in the molecular analysis.

Hemipenis morphology could also be helpful when non-sexual characters are incongruent or incomplete. This is the case of some *Physocypria* species, like *P. biwaensis* or *P. nipponica*, that have a *Physocypria*-type hemipenis, while some non-sexual characters differ from the type specie of the genus. In those cases, hemipenis morphology should be favored as the main diagnostic character, following previous studies that proved its relevance for ostracod classification and evolutionary pathways related to sexual selection (Danielopol 1969; Martens 2000).

Molecular analyses

Many Cyclocyprididae sequences stored in public databases like NCBI or BOLD seem to be misidentified or left in open nomenclature at the genus, family or even order level, most likely because there is a shortage of ostracod taxonomists working on the genetics of living taxa. Therefore, we had to cross-check some unreliable sequences with those identified by renowned ostracodologists, taking also into account the region in which the specimens were collected, and reviewing specimen photographs when available. For the 28S gene, the *Cyclocypris* sp. (AB674982) specimen from Hiruta et al. (2016) may belong to *Physocypria* because it grouped with *P.* cf. *biwaensis* (KX940935) from Yoo et al. (2017), a publication coauthored by the ostracod specialist Dr. Ivana Karanovic (Karanovic 2011). A similar problem may apply to *P. nipponica* (AB674984) from Hiruta et al. (2016), which clusters with other *Cypria* species, rather than with *Physocypria*. The putative *Cypridopsis* sp. (AF363321) from Oakley and Cunningham (2002) was obtained from a commercial company and its true specific identity was not fully checked by a non-marine ostracod taxonomist (Todd Oakley, personal communication), and so most likely belongs to a Cyclocyprididae species. In fact, both sequences clustered with our *C. ophtalmica* (P522) specimens, which were carefully checked using soft parts, including hemipenis, following Meisch (2000) monograph, and came from a locality where the species had been recorded before (Rueda et al. 2013). Nevertheless, we should also take into account the short sequence available for comparison in this gene, and its potentially highly conserved sequence, which may make an otherwise sound comparison of these molecular data unreliable and consequently, our phylogenetic tree for this gene should be taken with caution, notwithstanding the high bootstrap value in our *Cypria* clade.

The locality for some COX1 sequences of *Cypria* (MG449500, KT706311, MG448778 and MF744511) corresponded to areas surrounding lakes Ontario or Erie in Canada, while others (BBCRT134-12 to BBCRT137-12 and BBCRT090-12) came from the southern U.S. (Texas and Florida). We decided to keep the original identification as *Cypria* because the most abundant genera of the family Cyclocyprididae in southern Canada is *Cypria*, with *C. ophtalmica* being the most abundant representative of the family in the area (Delorme 1970b). However, some of these specimens might have been incorrectly identified, as the picture provided in BOLD in some cases (*e.g.*, BBCRT134-12) seems to allow for an unclear, faint observation of pustules on the right valve, suggesting the specimen may belong to *Physocypria s.l.*, rather than

Cypria. In this context, we would like to remark on the importance of properly identifying the material that is used and uploaded to public databases. In addition, the COX1 sequences from BOLD belonging to specimen codes from BBCRT001-12 to BBCRT006-12 were included in our analyses as *Physocypria s.l.?* because we could observe tubercles on the RV margin when checking their photographs, even though they were identified in the repository just as candonids. Other specimens, sampled from North America, clustered with what we called "*Cypria* 2?", and their pictures showed valves pigmented with a pattern very similar to other *Physocypria s.l.*, which could be another indicator that the unknown *Cypria* sequences actually belong to *Physocypria* or even to *Vizcainocypria* or other similar genera, in case they were misidentified.

Although cyclocypridid genera with tubercles on the RV margin (*Dentocypria*, *Physocypria* and *Vizcainocypria* gen. nov.) appear separated from those (supposedly) without tubercles (*i.e.*, identified as *Cypria* in the repositories), our phylogenetic analyses should be considered just as preliminary results. The COX1 gene tree shows a polytomy, indicating that affinities between different cyclocypridid genera could not be fully resolved. In other words, molecular data cannot confirm whether *Vizcainocypria* gen. nov. is more closely related to *Physocypria* than to *Cypria*. Nevertheless, our molecular analyses do support genus-level differentiation between *Cypria*, *Dentocypria*, *Physocypria* and *Vizcainocypria* gen. nov. because average K2P distances between those cyclocypridid taxa (0.240 ± 0.025), agree with average K2P distances observed by Nigro et al. (2016) between different marine ostracod genera (0.260 ± 0.080).

Several COX1 sequences from public databases (BBGEN061-15, HM883981, HM883998 and RBNII303-13) were very close to *V. viator* gen. nov. sp. nov. and show K2P distances similar or even lower than those calculated between different species of *Physocypria*. This suggests that those unidentified specimens, collected from Ontario (Canada) (BBGEN061-15 and RBNII303-13) or Oklahoma (U.S.) (HM883981, HM883998) could belong to *Vizcainocypria* gen. nov. The new species described from Iberian waters might therefore belong to an ostracod lineage originated in the Nearctic that later colonized the Palearctic. This is in agreement with the high number of exotic ostracods in the sampled area (Valls et al. 2014) and the absence of micropaleontological remains of any morphologically similar ostracod during the Holocene in the Eastern Iberian Peninsula (Marco-Barba et al. 2013a b 2019) or elsewhere in Europe (Griffiths 1995; Fuhrmann 2012). Another piece of evidence supporting the Nearctic or Neotropical origin of the genus is the geographic distribution in Central America of the only other known species that can be included in the genus, *V. granadae* comb. nov. Two other species present in the Nearctic, *P. inflata* and *P. pustulosa*, could be allocated to *Vizcainocypria* gen. nov. as well, considering their shell and soft part anatomy, but type material or new specimens from type localities should be reviewed to confirm their allocation. Finally, considering the wide distribution of similar genera and the high number of worldwide human-induced invasions in aquatic organisms (Gherardi 2007), and ostracods in particular (Mckenzie and Moroni 1986), alternative origins such as eastern Asia or Southern Africa cannot be completely discarded.

CONCLUSIONS

This work stressed the importance of integrative taxonomy in Ostracoda, especially when congeners have very similar morphological traits and molecular data are limited. While classical taxonomy helps identifying diagnostic characters at a generic level, molecular information supports the genus-level distinction and allows for detection of misidentifications in public databases. Further integrative studies are needed, not only for Cyclocyprididae, but for any group of Ostracoda where taxa are difficult to disentangle based on morphology alone. On the other hand, an increasing number of molecular sequences in public databases may become senseless without proper morphological assessment.

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Supplementary Materials

Table S1. Estimates of evolutionary divergence (Kimura 2-parameter) between sequences. The number of base substitutions per site between sequences are shown. Standard error estimates are shown above the diagonal. (download)