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Taxonomy, ontogeny, and ecology of *Tonnacypris stewarti* (Daday 1908) comb. nov. (Ostracoda: Cyprididae) from Nam Co, Tibetan Plateau

MAURICIO BONILLA-FLORES[1,5,*], PAULA ECHEVERRÍA-GALINDO[1,6], PETER FRENZEL[2,7], LISETH PÉREZ[3,8], NICOLE BÖRNER[1,9], KATHARINA DULIAS[1,10], JUNBO WANG[4,11] & ANTJE SCHWALB[1,12]
[1]*Institute of Geosystems and Bioindication, Technische Universität Braunschweig, 38106 Braunschweig, Germany*
[2]*Institute of Geosciences, University of Jena, 07749 Jena, Germany*
[3]*Chair of Organic Biochemistry in Geo-systems, RWTH Aachen University, 52056 Aachen, Germany*
[4]*State Key Laboratory of Tibetan Plateau Earth System, Environment and Resources (TPESER), Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China*
[5] *m.bonilla-flores@tu-braunschweig.de; https://orcid.org/0000-0002-5593-6522*
[6] *p.echeverria-galindo@tu-braunschweig.de; https://orcid.org/0000-0003-0210-4607*
[7] *peter.frenzel@uni-jena.de; https://orcid.org/0000-0002-3821-4632*
[8] *liseth.perez@emr.rwth-aachen.de; https://orcid.org/0000-0002-5256-3070*
[9] *nicole.boerner@tu-braunschweig.de; https://orcid.org/0000-0001-8833-6665*
[10] *k.dulias@tu-braunschweig.de; https://orcid.org/0000-0002-3938-6663*
[11] *wangjb@itpcas.ac.cn; https://orcid.org/0000-0003-2335-519X*
[12] *antje.schwalb@tu-braunschweig.de; https://orcid.org/0000-0002-4628-1958*
**Corresponding author*

Abstract

Taxonomic clarification of *Tonnacypris stewarti* **comb. nov.** (= *Herpetocypris stewarti*), a non-marine ostracod first described by Daday in 1908, was required due to the existence of various synonyms without detailed morphological descriptions. Our study examined specimens from Mang-tsa, Nam Co (Tibetan Plateau) and Lake Band-e Amir (Afghanistan). We identified seven definitive synonyms (*Herpetocypris stewarti* Daday 1908, *Ilyodromus estonicus* Järvekülg 1960, *Eucypris afghanistanensis* Hartmann 1964, *E. gyirongensis* Yang 1982, *E. rischtanica* Schneider 1963 in Mandelstam & Schneider 1963, *Tonnacypris estonica* (Järvekülg 1960), and *T. gyirongensis* (Guo *et al*. 2016). After a detailed study of the morphology of valves and soft parts supplemented by a literature review, we propose combining the genus *Tonnacypris* with the specific epithet *stewarti*, resulting in the new name *Tonnacypris stewarti*. We documented the ontogenetic series of *T. stewarti* in surface sediment samples from Nam Co. Only female specimens were found, consistent with observations in Mongolia, where they were considered asexual populations. Sexual populations were reported from Afghanistan and the southern Tibetan Plateau, suggesting geographic parthenogenesis in the Palearctic region. Because of widely missing males, we explored the use of female genital lobes as a distinguishing feature for taxonomy. Considering current ecological knowledge, *T. stewarti* could serve as a (paleo)—bioindicator of cold, oligotrophic, and fresh to slightly brackish habitats, including rivers, lagoons, and lakes. This study emphasizes the importance of resolving taxonomic issues for future paleolimnological research. Moreover, our investigation highlights the potential use of sclerotized internal female genital lobes as distinctive characteristics for species differentiation, especially in asexual populations.

Key words: Eucypridinae, female genital lobes, ontogenetic stages, reproductive strategies, synonyms

Introduction

High-altitude lakes, which are highly vulnerable to climate change, exhibit extreme sensitivity to variations in temperature, precipitation, and solar radiation (Pastorino & Prearo 2020). These lakes are significant due to their distinct biodiversity and their role as habitats for endemic species (Jacobsen & Dangles 2017). The Tibetan Plateau, also referred to as the Qinghai-Tibet Plateau, harbors abundant lakes, rivers, and glaciers, earning it the moniker "Asia's water tower" (Qiu 2008; Mischke 2012). The Tibetan Plateau (TP) covers six regions: Tibet Autonomous Region (TAR), Qinghai, Gansu, Sichuan, Yunnan, and Xinjiang Uygur Autonomous Region. The primary sections of TAR and Qinghai constitute the main part of the TP, encompassing 60.6% of the plateau's total area (Zhang *et al*. 2021).

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Studies on ostracods from the Tibetan Plateau have mostly focused on assessing changes in salinity and lake levels (Zhang *et al*. 2008; Wrozyna *et al*. 2009a; Frenzel *et al*. 2010, Li *et al*. 2021). However, there remains limited understanding of their taxonomy, particularly their soft-part morphology and ecology (Yin & Martens 1997; Mischke *et al*. 2003; Li *et al*. 2010; Peng *et al*. 2013; Fürstenberg *et al*. 2015; Peng *et al*. 2021; Wang *et al*. 2021). To enhance our understanding of ostracods in this region, it is crucial to conduct meticulous taxonomic revisions by analyzing ostracod specimens from scientific collections, modern environments, and existing literature. These taxonomic studies are essential for interpreting paleolimnological and paleoecological data, providing valuable insights into the historical and ecological dynamics of the Tibetan Plateau and other regions in China (Mischke *et al*. 2003; Yu *et al*. 2009; Li *et al*. 2010; Peng e*t al*. 2021; Peng *et al*. 2013). Additionally, the ontogeny of ostracods is crucial for understanding their growth patterns and life history. The growth ratio serves as a valuable tool in taxonomic identification; analyzing variations in this ratio provides insights into species-specific growth patterns, aiding the differentiation of closely related species (Brooks 1886; Watabe & Kaesler 2004). Furthermore, analyzing the ontogenetic composition of ostracod taphocoenoses allows assessment of transport processes (Boomer *et al*. 2003).

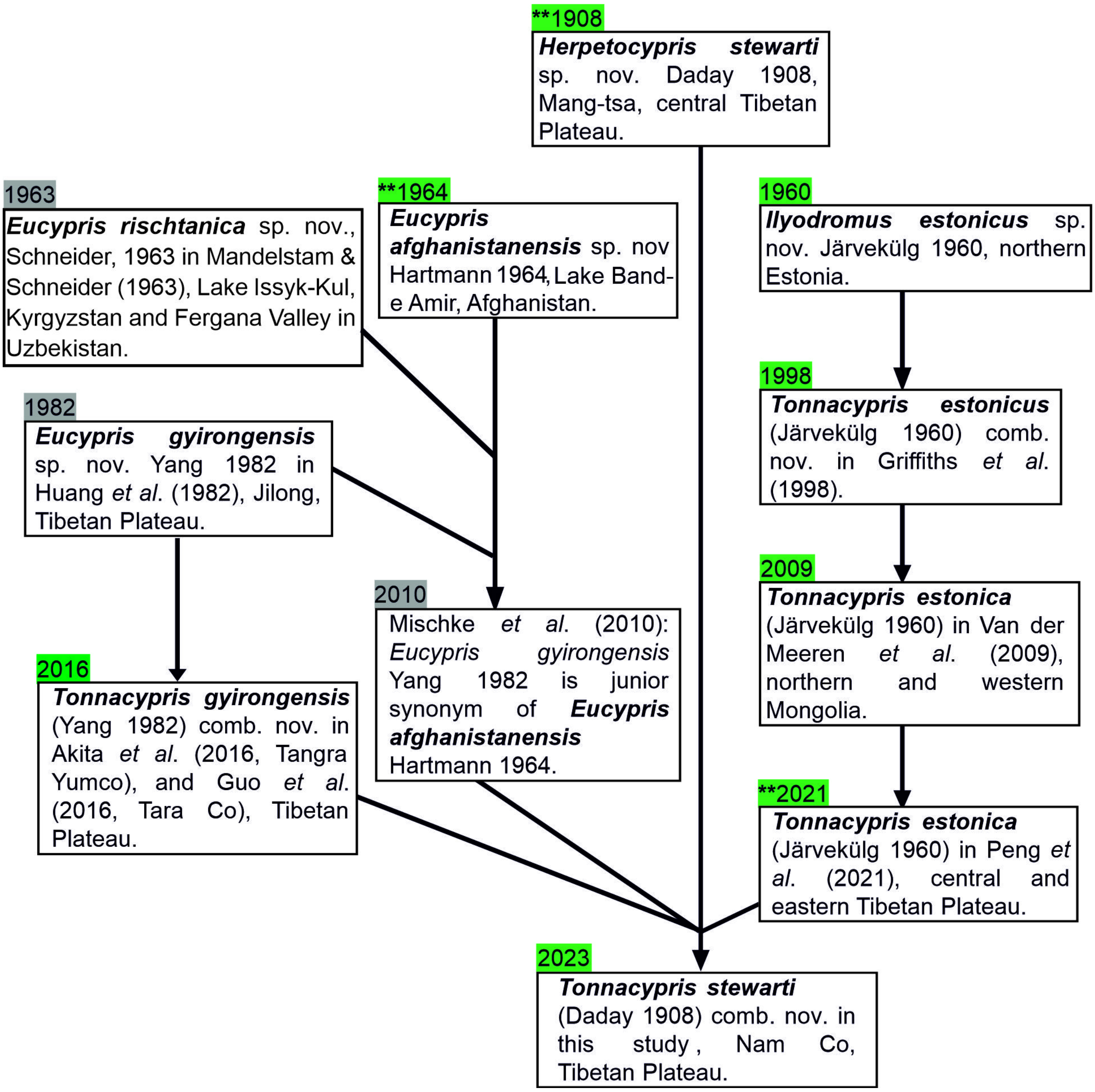

FIGURE 1. Chronological overview of descriptions and synonyms for *Tonnacypris stewarti* since 1908. The green rectangle designates living specimens with preserved soft anatomical structures. The incorporation of two asterisks (*) further signifies the inclusion of male specimens exhibiting soft anatomical structures. The gray rectangle denotes scrutinized fossil and subfossil specimens.

Nam Co, the second largest lake on the Tibetan Plateau, has been extensively studied in relation to its ostracod fauna, with research focusing on taxonomy, paleoecology, and molecular studies (Wrozyna *et al*. 2009b; Xie *et al*. 2009; Frenzel *et al*. 2010; Schütt *et al*. 2010; Wrozyna *et al*. 2010; Anslan *et al*. 2020; Echeverría-Galindo *et al*. 2021). Wrozyna *et al*. (2009b) identified eight species, including *Eucypris gyirongensis* Yang 1982 (Huang *et al*. 1982), in modern surface sediments and sediment cores from the Holocene. They noted its close resemblance to *E. afghanistanensis* Hartmann 1964, and suggested a potential junior synonym relationship. However, they emphasized the necessity of conducting a detailed analysis and description of recent individuals, especially focusing on their soft parts. Similar observations and suggestions have been made by other researchers (Huang *et al*. 1982; Mischke *et al*. 2010b; Guo *et al*. 2016; Akita *et al*. 2016; Echeverría-Galindo *et al*. 2021; Peng *et al*. 2021). Nevertheless, further investigation is still required to address this issue (Fig. 1).

It is important to note that in the global list of non-marine ostracod species (Meisch *et al*. 2019) and the list of ostracods from SW Tibet (Peng *et al*. 2021), *Eucypris gyirongensis* is recognized as a synonym of *E. afghanistanensis*. However, in both lists the authors noted that there was some uncertainty associated with including the species in the genus *Eucypris*, because it was highlighted that this species needed more detailed taxonomic analysis.

The genera *Tonnacypris* Diebel & Pietrzeniuk 1975 and *Eucypris* Vávra 1891 belong to the subfamily Eucypridinae Bronstein 1947 (Meisch *et al*. 2019). Guo *et al*. (2016) and Akita *et al*. (2016) were the first to transfer *Eucypris gyirongensis* to the genus *Tonnacypris*, but based their decision on valve characteristics only, without considering the soft parts.

Tonnacypris is characterized by its smooth carapace and the presence of an anteroventral tooth in the calcified portion of the left valve lamella. Additionally, its A2 swimming setae are reduced, and the d2 seta on the second thoracopod is twice as long as d1. In contrast, the genus *Eucypris* exhibits distinct traits such as an elliptical valve, typically warty anterior valve surface, a d1 seta three times longer than d2 on the second thoracopod, and a terminal segment of the Maxillula palp (Mx1) that is either distally cylindrical or curved (Meisch 2000; Karanovic 2012; Rasouli *et al*. 2016).

A taxonomic review of the genus *Tonnacypris* in Mongolia documented four species (Van der Meeren *et al*. 2009), providing valuable insights into the local taxonomy and differentiation between the two genera. The presence of *Tonnacypris estonica* (Järvekülg 1960) in Mongolia was indicated with *Ilyodromus estonicus* (Järvekülg 1960), identified as its first synonym, originally described in Estonia. However, subsequent studies from the Tibetan Plateau did not compare this species with *Tonnacypris gyirongensis* and *Eucypris gyirongensis* (Frenzel *et al*. 2010; Akita *et al*. 2016, Guo *et al*. 2016). Only Peng *et al*. (2021) recorded *T. estonica* at different sites in Tibet and the adjacent Sichuan province, but the synonym problem of the species *Eucypris gyirongensis* was not resolved.

When addressing these challenges, a comprehensive search for existing synonyms and the determination of the oldest species descriptions are crucial in taxonomic revisions. Access to collections and historical literature is essential, as they provide valuable information on the subject matter.

With this in mind, we document and clarify the taxonomic inconsistencies of *Tonnacypris stewarti* **comb. nov.** by describing (1) the morphology of hard and soft parts of material from the Tibetan Plateau and from ostracod collections (Hungarian Museum of Natural History and Zoological Museum of Hamburg); (2) the ontogeny of the valves found in surface sediment samples from Nam Co; and (3) the ecological conditions in which this species was found in lakes on the Tibetan Plateau. Finally, we provide an overview of its current geographic distribution and reproductive strategies.

Study area

Nam Co and its catchment area: Nam Co (latitude: 30.70°N to 30.86 °N; longitude: 90.28°E to 91.04°E) is a high-altitude lake (4,730 m a.s.l.) of 2,018 km^2, the second largest lake located on the southern Tibetan Plateau (Kai *et al*. 2020).

Nam Co is an endorheic and dimictic lake, strongly influenced by solar radiation and large-scale atmospheric systems such as the Indian summer monsoon and the Westerlies (Zhu *et al*. 2008; Wang *et al*. 2020). The lake is considered oligohaline (1.78 g/l) (Wang *et al*. 2009), and the dominant ions include $HCO_3^- < SO_4^{2-}$ and $Na^+ < Mg^{2+}$ (Wrozyna *et al*. 2009a). Winters in the Nam Co area are dry, and precipitation occurs during the summer months from May to September, with an annual average of 406 mm (Anslan *et al*. 2020). It is important to specify that on the southwestern side of the basin there is an extensive glacial area of approximately 700 km^2. Melting glaciers produce multiple rivers that are connected to the lake (Kang *et al*. 2021).

Material and methods

Sampling

Tonnacypris stewarti was collected in July 2018 and September 2019 from different environments of the Nam Co area by the Sino-German Research Training Group TransTiP. A total of 19 surface sediment samples from the lake, as well as from lagoons and rivers nearby, were analyzed (Fig. 2, Table 1). Littoral samples (0.5–1.0 m water depth) were extracted with a spatula and a hand net (125 µm mesh). Samples from deeper water were collected with an Ekman grab sampler, of which only the top three centimeters of sediments were taken. All sediment samples were preserved in 95% ethanol and transported to the Nam Co Observation and Research Station for Multisphere (NAMORS), Chinese Academy of Sciences. In addition, in-situ limnological variables were determined (water depth, electrical conductivity, temperature, pH, dissolved oxygen) at the different collection sites with an YSI-EXO2 multiparameter probe. The alkalinity was determined separately by titrimetric kit (VISO HE Nfp. Alkalinität AL 7) with a standard solution.

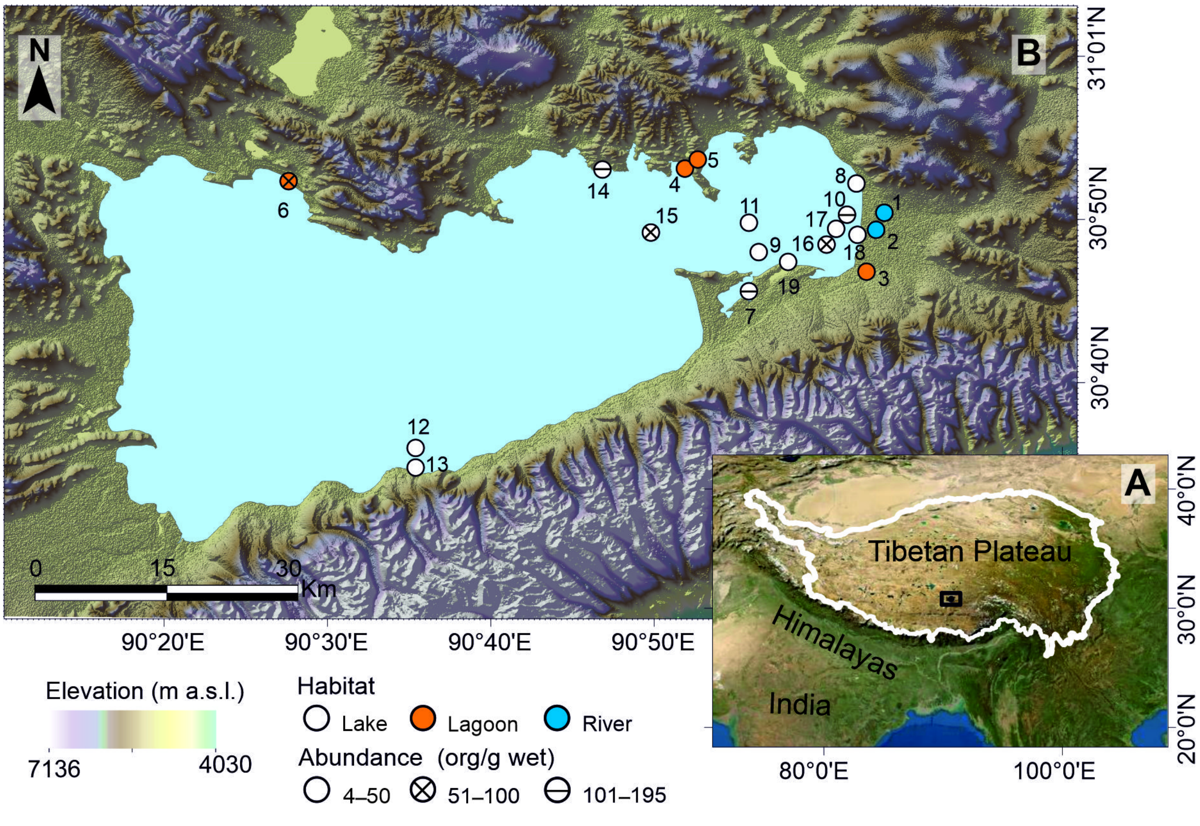

FIGURE 2. Study area. A) Location of Nam Co on the Tibetan Plateau, and B) sampling sites according to the habitat type and abundances (living and sub-fossil organism (2 valves = 1 organism) per gram wet weight, org/g wet) of *Tonnacypris stewarti* (Daday 1908) in Nam Co. Abundance distribution was categorized into three distinct patterns: a complete circle (indicating low abundance), a cross-circle (indicating medium abundance), and a circle with a central line (indicating higher abundance). Sample numbers correspond to Table 2. The elevation bar corresponds to map B. Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

TABLE 1. Total abundance of *T. stewarti* and environmental data from sampling sites at Nam Co (NC). In each sample, we counted the number of organisms per 1 gram of sediment. Abbreviations: NC = Nam Co, TA = Total abundance (organism/1 g wet sediment), Lat = Latitude, Lon = Longitude, Alt = Altitude, EC = Electrical Conductivity, WT = Water Temperature, DO = Dissolved Oxygen, Alk = Alkalinity, nd = no data.

Sample-ID	Date	Habitat	TA	Lat. (N)	Lon. (E)	Alt. (m a.s.l)	Depth (m)	EC (µS/cm)	WT (°C)	pH	DO (mg/l)	Alk. (mmol/l)
1-NC18-S-1	2018.07.02	River	41	30.83	91.06	4742	0.1	149	9.3	8.1	6.9	1.3
2-NC18-S-3	2018.07.02	River	5	30.83	91.06	4740	0.2	270	9.9	8.0	6.4	2.9
3-NC19-S-9	2019.09.02	Lagoon	50	30.78	91.05	4732	0.18	228	11.2	8.4	6.5	2.5
4-NC18-S-32	2018.07.05	Lagoon	36	30.89	90.87	4721	0.2	1888	19.8	9.0	7.1	16.6
5-NC18-S-33	2018.07.05	Lagoon	4	30.89	90.87	4727	0.3	1894	14.4	9.0	6.9	17.3
6-NC18-S-37	2018.07.06	Lagoon	100	30.87	90.46	4715	0.3	196	18.9	9.0	6.6	1.4
7-NC19-S-41	2018.07.06	Lake	174	30.76	90.93	4733	4.8	1543	13.1	9.0	5.6	15.9
8-NC18-S-6	2018.07.02	Lake	13	30.87	91.04	4733	0.3	1292	16.2	8.9	4.6	10.0
9-NC18-S-10	2018.07.03	Lake	10	30.80	90.94	4725	35.0	1305	9.5	10.0	nd	18.0
10-NC18-S-12	2018.07.02	Lake	195	30.83	91.03	4723	27.1	1305	9.5	10.0	nd	14.0
11-NC18-S-18	2018.07.04	Lake	6	30.83	90.93	4714	38.0	1313	9.8	11.2	nd	18.2
12-NC18-S-67	2018.07.10	Lake	38	30.60	90.59	4719	56.0	1872	3.6	9.1	7.9	18.0
13-NC18-S-69	2018.07.10	Lake	20	30.58	90.59	4713	17.7	1831	7.7	9.1	7.1	17.0
14-NC18-S-73	2018.07.12	Lake	186	30.87	90.78	4722	40.3	1861	6.8	9.0	7.2	17.8
15-NC18-S-75	2018.07.12	Lake	94	30.82	90.83	4725	60.7	1891	5.4	9.1	7.3	15.2
16-NC18-S-84	2018.07.13	Lake	91	30.81	91.01	4727	11.5	1779	11.1	9.0	6.4	16.6
17-NC18-S-85	2018.07.13	Lake	17	30.82	91.02	4724	8.0	1894	9.1	9.1	7.0	18.1
18-NC18-S-88	2018.07.13	Lake	9	30.82	91.04	4722	1.4	1406	13.3	9.0	6.6	12.6
19-NC19-St2	2019.09.13	Lake	27	30.79	90.97	4724	0.1	1543	13.1	9.0	5.6	15.9

Ostracod analysis

One gram of wet sediment from each sample was sieved using a sieve with a mesh size of 63 µm. All adults with well-preserved soft parts were stored in Eppendorf vials with 95% ethanol. Ostracod dissections, semi-permanent (glycerin) and permanent preparations (Hydro-Matrix, Micro-Tech-Lab, Austria), were made (Danielopol *et al*. 2002). The soft parts were examined under a LEICA DM500 microscope. All collected specimens will be deposited at the Paleontology Institute of the Chinese Academy of Sciences in Nanjing, China.

Empty valves and complete carapaces of juveniles and adults were extracted with a fine brush and stored in micropaleontological slides. In addition to the organisms from Nam Co, examination extended to the type materials of *Herpetocypris stewarti* studied by Daday (1908) from a spring-fed wetland at the village Mang-tsa, Tibet, and *Eucypris afghanistanensis* studied by Hartmann (1964) from Lake Band-e Amir, Afghanistan. The type material of *H. stewarti* and *E. afghanistanensis* is deposited in the Hungarian Museum of Natural History and in the Zoological Museum of Hamburg, respectively. Two paratypes, one male and one female *H. stewarti* (reference number HNHM-IV-369), and two specimens (one female and one male) of *E. afghanistanensis* (reference number ZMH-27716), were dissected and their valves were photographed using a Keyence microscope (VHX-E100; objective x100–x500) at the Faculty of Mechanical Engineering, TU Braunschweig. To document the female genital lobes, one female from each site (Nam Co, Taro Co on the Tibetan Plateau, and Lake Band-e Amir, Afghanistan) were selected and photographed using a Keyence microscope (VHX-E100) with objectives ranging from x100 to x500. Abbreviations used in text and figures are as follows: RV = right valve, LV = left valve, H = height of valves in lateral view, L = length of valves in lateral view, A1 = first antenna, A2 = second antenna, Md = Mandibular coxa, Md-Palp = Mandibular palp, Mx1 = Maxilulla, T1 = first thoracopod (maxilliped), T2 = second thoracopod, T3 = third thoracopod, CR = caudal ramus. Terminology and chaetotaxy of the limbs follow Danielopol & McKenzie (1977), Broodbakker & Danielopol (1982), Meisch (2000), and Karanovic (2012). In the case of A2, the terminology from Horne (2005) was employed. We consider the terminology employed for the hemipenis (dorsal lobe (dl), lateral shield (ls), and medial shield (ms)) by referencing the studies conducted by Baltanás *et al*. (1993), Savatenalinton & Martens (2009), and Savatenalinton & Suttaji (2016). The systematic position of the suprageneric taxa follows Meisch *et al*. (2019).

Statistical analysis

Measurements of the length and height of the right and left valves of each stage of development based on empty valves and living ostracods were made to obtain size variability and abundance data. Likewise, the measurements of the central tendency (average and standard deviation) were obtained, using the R Studio version 1.4.1106 (R Core Team 2022) and the ggplot2 package version 3.3.5 (Wickham 2016).

The growth ratio refers to the relationship between the average length and height of an instar compared to the preceding growth stage. Calculating the mean growth ratio involves determining the average of these ratios across all growth phases. A deviation from the value of 1.260 signifies a departure from Brooks' rule (Brooks 1886; Watabe & Kaueler 2004).

Samples containing *Tonnacypris stewarti* were classified by Hierarchical Cluster Analysis based on their associated environmental factors and using PAST 4.12b (Hammer *et al*. 2001). Environmental factors measured are water depth, electrical conductivity, water temperature, and pH. Oxygen concentration was excluded from the analysis due to three missing values and the limited significance of a single measurement. We used log-transformation of water depth and electrical conductivity, and a z-transformation of the complete dataset in order to weight all factors equally. Alkalinity was excluded from the cluster analysis because of a very high correlation with electrical conductivity, thus electrical conductivity also represents alkalinity in our analysis. The algorithm WARD's method with Euclidian distance was used. Means and ranges of environmental factors and abundance of *T. stewarti* were calculated based on a group assignment of samples to identify ecological preferences of this species.

Results

The species *Tonnacypris stewarti* has been recorded in at least 39 studies (Table 2), starting with a description by Daday (1908) and continuing to the most recent report by Wang *et al*. (2022). Sixteen studies recorded the species in different lakes on the Tibetan Plateau (see systematic list). In total, seven synonyms were identified: *Herpetocypris stewarti* Daday 1908, *Ilyodromus estonicus* Järvekülg 1960, *Eucypris afghanistanensis* Hartmann 1964, *E. gyirongensis* Huang *et al*. 1982, *Eucypris rischtanica* Schneider 1963 in Li *et al*. (2010), *Tonnacypris estonica* (Järvekülg 1960) and *T. gyirongensis* (Huang *et al.* 1982) new comb. by Guo *et al*. (2016). Below, a synonym list is shown giving the sites in which the species was recorded.

TABLE 2. Historical records of *Tonnacypris stewarti* synonyms from 1908 to present, uncertain taxonomic attributions are marked with "?".

Year	Reference
1908	*Herpetocypris stewarti* **sp. nov.** Daday 1908, p. 334–336; fig. 6.a–k; Recent, Mang-tsa, Tibet.
1960	*Ilyodromus estonicus* **sp. nov.** Järvekülg 1960, p. 32; fig. 1–5; Recent, Estonia.
1963	*Eucypris rischtanica* **sp. nov.** Schneider, 1963 in Mandelstam & Schneider (1963) (p. 180–181, plate 35, fig. 5; Quaternary, Lake Issyk-Kul, Kyrgyzstan, also Quaternary, Fergana Valley in Uzbekistan.
1964	*Eucypris afghanistanensis* **sp. nov.** Hartmann 1964, fig. 17a–f, 18; Recent, shore of Lake Band-e Amir, Afghanistan.
?1974	*Parastenocypris delormei* **n. sp.** Singh (1974); p. 107–108; figs. 4C–E, 5 F–J, 7 F–K.; Recent and Pleistocene, Ladakh, India.
1977	*Ilyodromus estonicus* (Järvekülg 1960), in Danielopol & McKenzie (1977); p. 309; fig. 9C–F, 10F, 11E; Recent, northern Estonia.
1982	*Eucypris gyirongensis* **sp. nov.** Yang in Huang *et al*. 1982, p. 328–329; plate I, fig. 1–4; Quaternary, Jilong, Tibetan Plateau.

...Continued on the next page

TABLE 2. (Continued)

Year	Reference
?1982	*Eucypris subgyirongensis* **sp. nov.** Yang in Huang *et al*. 1982, p. 330; plate I, fig. 5–10; Quaternary, Jilong, Tibetan Plateau.
1988	*Eucypris gyirongensis* Yang 1982, in Yang (1988); Recent, northwestern Qinghai Plateau.
1997	*Eucypris gyirongensis* Yang 1982, in Peng (1997), plate 2, fig. 10–11; Late Pleistocene and early Holocene, Peiku Co, southern Tibetan Plateau.
1998	*Eucypris afghanistanensis* Hartmann 1964, in Kotlia *et al*. (1998); p. 183; plate 1 K–q; K; Quaternary, Lamayuru, Trans-Himalaya.
1998	*Tonnacypris estonicus* (Järvekülg 1960) **comb. nov.** in Griffiths *et al*. (1998), p. 523
?2002	*Eucypris afghanistanensis* Hartmann 1964, in Shukla *et al*. (2002), p. 418; fig. 6e–f, Quaternary of Ladakh, Himalayan region.
2002	*Eucypris rischtanica* Schneider 1963, in Hou *et al*. (2002), p. 141–142, plate 18, fig. 15–18; copies Huang *et al*. (1982).
?2002	*Eucypris subgyirongensis* Yang 1982, in Hou *et al*. (2002), p. 169, plate 19, fig. 1–4; copies Huang *et al*. (1982).
2006	*Eucypris gyirongensis* Huang 1982, in Mischke *et al*. (2006); p. 59, plate 1, fig. 14; Pleistocene of Qaidam Basin, Tibetan Plateau.
2009	*Tonnacypris estonica* (Järvekülg 1960), in Van der Meeren *et al*. (2009); p.5, fig. 1, 2A, 3, 4, 5D, 6, 21; Recent, northern Mongolia.
2009	*Eucypris afghanistanensis* Hartmann 1964, in Kramer & Holmes (2009); p. 33, plate 1, fig. 7–11; Pleistocene, Kashmir valley, northern India.
2009	*Eucypris gyirongensis* Yang 1982, in Yu *et al*. (2009), p. 36, Tibetan plateau, checklist.
?2009	*Eucypris gyirongensis* Yang 1982 and ?*Eucypris gyirongensis* Yang 1982, in Wrozyna *et al*. (2009b); plate 3, fig. 1,2; recent, northwest Nam Co, Tibetan Plateau.
2009	*Eucypris gyirongensis* Yang 1982, in Xie *et al*. (2009); p.393–394; Quaternary, northeastern Nam Co, Tibetan Plateau.
2010	*Eucypris gyirongensis* Yang 1982, in Frenzel *et al*. (2010), p. 159, Holocene, Nam Co, Tibetan Plateau.
2010	*Eucypris afghanistanensis* Hartmann 1964; *Eucypris gyirongensis* Huang *et al*. (1982), in Schütt *et al*. (2010); p. 109. fig. 7 C and D; Quaternary of Nam Co, Tibetan Plateau.
?2010	*Eucypris rischtanica* Schneider 1963, in Li *et al*. (2010); p. 884; plate 1, fig.4; plate 2, fig. 16; recent in lake Qinghai, Tibetan Plateau.
2010	*Eucypris afghanistanensis* Hartmann 1964, in Mischke *et al*. (2010a), p. 594–600; recent in lake Donggi Cona, Qinghai Province, China.
2010	*Eucypris afghanistanensis* Hartmann 1964, in Mischke *et al*. (2010b), p. 78, Quan Ji in the eastern central Qaidam Basin, China.
2010	*Eucypris gyirongensis* Huang *et al*. 1982, in Zhu *et al*. (2010); fig. 3, panel 11.; Quaternary of Nam Co, Tibetan Plateau. (Fig. 3.12 is a left valve of *Candona xizangensis*).
?2010	*Tonnacypris estonica* (Järvekülg 1960), in Sohar & Meidla (2010); Holocene of Pandivere, northern Estonia. (most probably *Tonnacypris glacialis*).
2012	*Eucypris afghanistanensis* Hartmann 1964, in Mischke (2012); fig. 15.3 No. 11; Recent and Quaternary of the Tibetan Plateau.
2013	*Eucypris afghanistanensis* Hartmann 1964, in Zhang *et al*. (2013); p. 45, figs. 7–8; Recent in Kunlun mountains, northern Tibetan Plateau.
2013	*Eucypris gyirongensis*, in Peng *et al*. (2013); p. 49; Quaternary of lake Pumoyum Co, Tibetan Plateau.
2015	*Tonnacypris gyirongensis* **comb. nov.** Guo *et al*. (2016); p. 4; fig. 2; Quaternary of Taro Co, southwestern Tibetan Plateau.
2016	*Tonnacypris gyirongensis* **comb. nov.** Akita *et al*. (2016); p. 29; fig. 5; recent in Tangra Yumco, Tibetan Plateau.
?2020	*Eucypris* cf. *afghanistanensis* Hartmann 1964, in Mischke *et al*. (2020); p. 5; Holocene in lake Balkhash, Kazakhstan.
2021	*Tonnacypris estonica* (Järvekülg 1960), in Peng *et al*. (2021); p. 503; fig. 2; Recent, near lake Dang Reyongcuo, Sichuan and Linzhi, Tibetan Plateau.

...Continued on the next page

TABLE 2. (Continued)

Year	Reference
2021	*Tonnacypris estonica* (Järvekülg 1960), in Li *et al*. (2021); p. 4,5; fig. 2 I, J; Recent, Lake Ngoring, northeastern Qinghai–Tibet Plateau.
2021	*Tonnacypris gyirongensis* **comb. nov.** Akita *et al*. (2016), in Echeverría-Galindo *et al*. (2021); p. 987, fig. 2; recent in Nam Co, Tibetan Plateau.
2022	*Tonnacypris estonica* (Järvekülg 1960), in Wang *et al*. (2022); p. 6, fig. 4; Recent, Yamdrok-tso basin, Tibetan Plateau.
2023	*Tonnacypris estonica* (Järvekülg 1960), in Mao *et al*.(2023); p. 5–6, fig. 5; sediments from Holocene, Dalongchi Lake, from southern slope of the central Tianshan Mountains, northwestern China.

Systematic list

Class Ostracoda Latreille 1802

Order Podocopida Sars 1866

Suborder Cypridocopina Baird 1845

Superfamily Cypridoidea Baird 1845

Family Cyprididae Baird 1845

Subfamily Eucypridinae Bronstein 1947

Genus *Tonnacypris* Diebel & Pietrzeniuk 1975

Tonnacypris stewarti (Daday 1908) **comb. nov.**

Material examined

Valves and individuals with soft parts from ten lakes on the Tibetan Plateau and Afghanistan were investigated, including measurements of right and left valves (Table 3). In general, both females and males had longer and higher left valves compared to right valves. Specifically, when using the left valve as a reference, we observed that the valves of females from Mang-tsa, Tangqung Co, and Nam Co on the Tibetan Plateau were, on average, longer and higher (L= 1231 µm; H= 571 µm) than those of females recorded from Afghanistan (L= 1200 µm; H= 554 µm). Regarding males from Mang-tsa, their left valves were also longer (1276 µm) and higher (573 µm) compared to males from Afghanistan (L= 1097 µm; H= 514 µm).

In total, we examined 88 females from Nam Co, Mang-tsa, a pond near Tangqung Co, a peatland at Taro Co, rivers at Tangra Yumco, Xuru Co (Tibetan Plateau), Heihai lake (material provided by Steffen Mischke, University of Iceland), Donggi Cona, Huanglong Ravine pond, and Yushu (Qinghai), and the shore of Lake Band-e Amir (Afghanistan), as well as 17 males from Mang-tsa (Tibetan Plateau) and Lake Band-e Amir (Afghanistan).

Morphological description of *Tonnacypris stewarti* from Nam Co, Tibetan Plateau: The morphological description includes the dissection of eight adult females, and the measurements (L= length and H= height) of 284 right valves and 277 left valves of different instars.

Carapace description: Carapace whitish (Nam Co) and sometimes yellowish (Afghanistan) (Fig. 3); smooth, elongated at the posterior end, and reniform in lateral view. Almost straight dorsal margin and slightly sinuous ventrally. Rounded anterior margin and triangular posterior end with an angle of approximately 45° on the right valve and 50° on the left. The left valve is longer and higher (L= 1171 µm, H= 591 µm) than the right valve (L= 1108, H= 545 µm) (Fig. 3). In interior view, both valves present a wide calcified inner lamella in the anterior and posterior parts, along with multiple surface pores with setae. Furthermore, both valves exhibit marginal pore canals

(Fig. 3 E1). In the left valve, generally, a small anteroventral peg is present, but sometimes the peg is inconspicuous (Fig. 4 A3). In this case, the left valves of females from Nam Co are very small, and in specimens from Tangra Yum Co and Afghanistan the anteroventral peg is very inconspicuous (Fig. 4 C1, C2).

TABLE 3. Females and males of *Tonnacypris stewarti* described from the Tibetan Plateau and Afghanistan, with data regarding sex and measurements of valve length and height. Symbosl: (*) TU Braunschweig, Germany; (**) Friedrich-Schiller Universität Jena, Germany; (***) Faculty of Earth Sciences, University of Iceland.

Lake/Location	Sample-ID	Number of individuals	Sex	Right valves (min–max)		Left valves (min–max)		Collector
				Length (µm)	Height (µm)	Length (µm)	Height (µm)	
Nam Co, Tibetan Plateau	*NC18-S-37	12	Female	1011–1251	473–581	1020–1256	481–585	P. Echeveria-Galindo
	*NC18-S-1a	7	Female	1053–1220	494–555	1213–1262	571–575	
	*NC18-S-12	10	Female	985–1185	471–546	990–1231	457–576	
	*NC18-S-67	6	Female	1113–1243	490–562	1190–1239	566–578	
	*NC18-S-73	13	Female	976–1230	458–563	986–1196	451–561	
Pond near Tangqung Co, Tibetan Plateau	TIP11-75B	4	Female	1142–1306	535–591	1142–1296	535–610	Akita *et al*. (2016).
Taro Co, Tibetan Plateau	TIP11-105, 106	2	Female	1092–1131	503–538	1016–1143	513–555	Akita *et al*. (2016).
Tangra Yumco, Tibetan Plateau	TIP11-15	6	Female	1020–1100	480–530	1054–1190	489–560	Akita *et al*. (2016).
	TIP11-29	5	Female			1090–1260	490–580	
Xuru Co, Tibetan Plateau	TIP11-1	12	Female	928–1062	453–504	978–1028	481–507	Akita *et a*l. (2016).
Yamtso Yumco, Tibetan Plateau	**TIP08-25,	1	Female	1372	628	1370	647	P. Frenzel
	**TIP08-26	1	Female	1314	608	1331	623	P. Frenzel
Heihai lake, Qinghai	***KX-28	10	Female	1065–1102	449–496	1033–1114	484–519	S. Mischke
Donggi Cona lake, Qinghai	***DCS-106	4	Female	1203	561	1256–1250	595–588	S. Mischke
Huanglong Ravine, Qinghai	***SET-33	7	Female	1256–1292	556–576	1166–1282	552–604	S. Mischke
Site CTP_34; Qinghai, Tibetan Plateau	***04-CTP-34	7	Female	1166–1205	574–614	1104–1183	561–592	S. Mischke
Mang-Tsa, Tibetan Plateau	HNHM-IV-369	8	Female	1195–1286	491–574	1200–1295	510–587	Daday (1908)
		4	Male	1245–1274	555–576	1260–1280	563–580	
Lake Band-e Amir, Afghanistan	ZMH-K27716; ZMH-K27574a; ZMH-K-27581; ZMH-K-27582-583	11	Female	1004–1388	456–610	1033–1392	466–638	Hartmann (1964)
		13	Male	974–1159	475–551	981–1165	453–521	

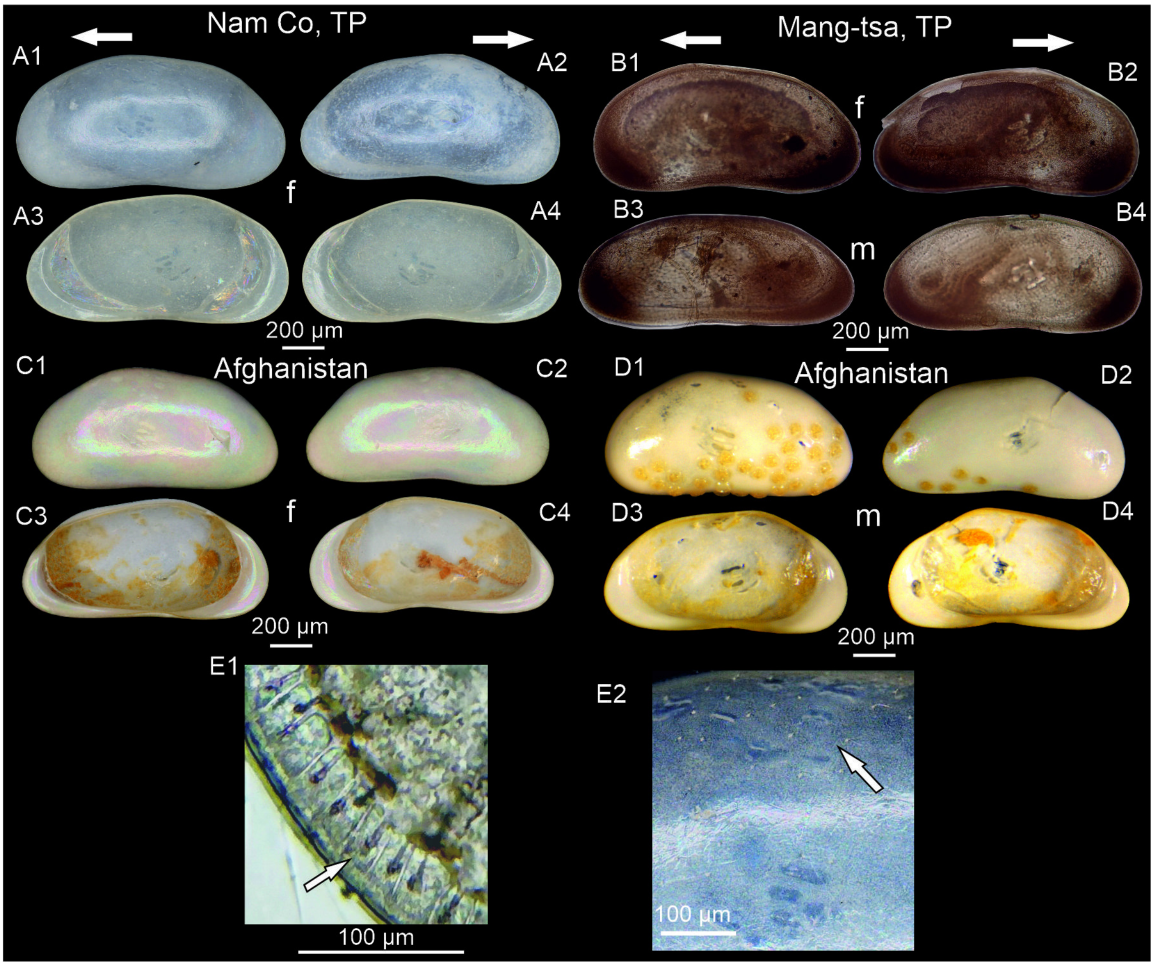

FIGURE 3. Valve images of *Tonnacypris stewarti* (f = female, m = male): (A1) exterior view of left valve (LV) and (A2) right valve (RV); interior view (A3–A4) of a female from Nam Co (reference-ID NC18-S-37). Exterior view of LV (B1) and RV (B2) of a female; interior view of RV (B3) and LV (B4) of male from Mang-tsa, Tibetan Plateau (TP) (Daday 1908; reference-ID HNHM-IV-369). Arrows above Figures A1–A2 and B1–B2 point to anterior end of the valve. Exterior view of LV (C1) and RV (C2); interior view (C3–C4) of a female; exterior view of LV (D1) and RV (D2); interior view (D3–D4) of a male from Lake Band-e Amir, Afghanistan (Hartmann 1964; reference-ID ZMH-K27716). (E1) shows the marginal pore canals in the anteroventral side in the right valve, and (E2) denotes the scars on the dorsal part of the left valve of *T. stewarti*.

Description of soft parts of a female from Nam Co: A1 (Fig. 5A). Divided into seven segments: segment I with two setae, which are twice as long as the long segment and present setules and one shorter seta on the dorsal side; segment II with a seta on the dorsal side; segment III with two setae, one ventral and one dorsal; segments IV and V each with two setae on the ventral side and two on the dorsal side; segment VI with four long seta and one α seta; terminal segment with two long setae, a short sturdy claw, and a much shorter ya aesthetasc.

A2 (Fig. 5B). Divided into five segments. Coxa with two setae with setules and one without setules; second segment or basis is robust with a seta on the ventral part. Exopodite with three setae, two short and the longest with setules. First endopodal segment with aesthetasc Y in the ventral part, on the apical side a large seta and a group of six short swimming setae, unequal in length (not reaching tips of terminal claws), the first on the apical side is the longest while the second to the fifth are progressively shorter. Second endopodal segment undivided, with two setae on the dorsal side, four t-setae (t1–t4) with the longest t2 and t3. Aesthetasc y1 on the ventral side and y2 on the distal part of the second endopodal segment, aesthetasc y3 is located on the interior-distal side of the third endopodal segment with a accompanying seta. In the apical part of the penultimate segment there are three claws (G1–G3) and three z setae, z1 slightly longer than the other two (z2 and z3). In addition, there is a GM (greater claw) and a Gm (minor claw) in the last endopodal segment.

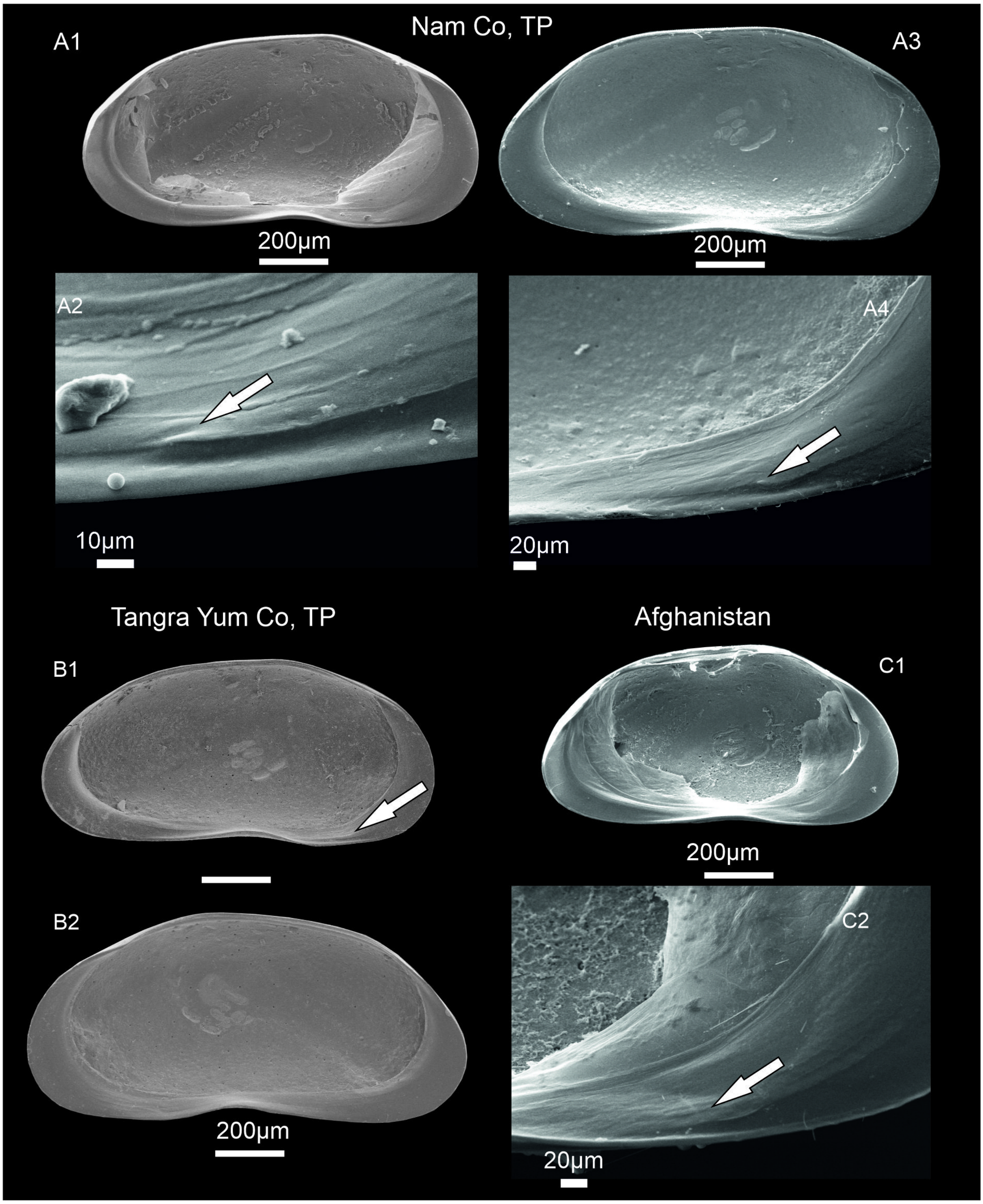

FIGURE 4. Left valves of two individuals from Nam Co (A1–A3) (reference-ID NC18-S-37). A2 and A4 indicate the inconspicuous anteroventral peg of each one. Left and right valves from Tangra Yum Co, TP (B1–B2) (reference-ID TIP11-29); left valve of a female from Lake Band-e Amir, Afghanistan (C1) (reference-ID ZMH-K27716), with a close-up of anteroventral part (C2).

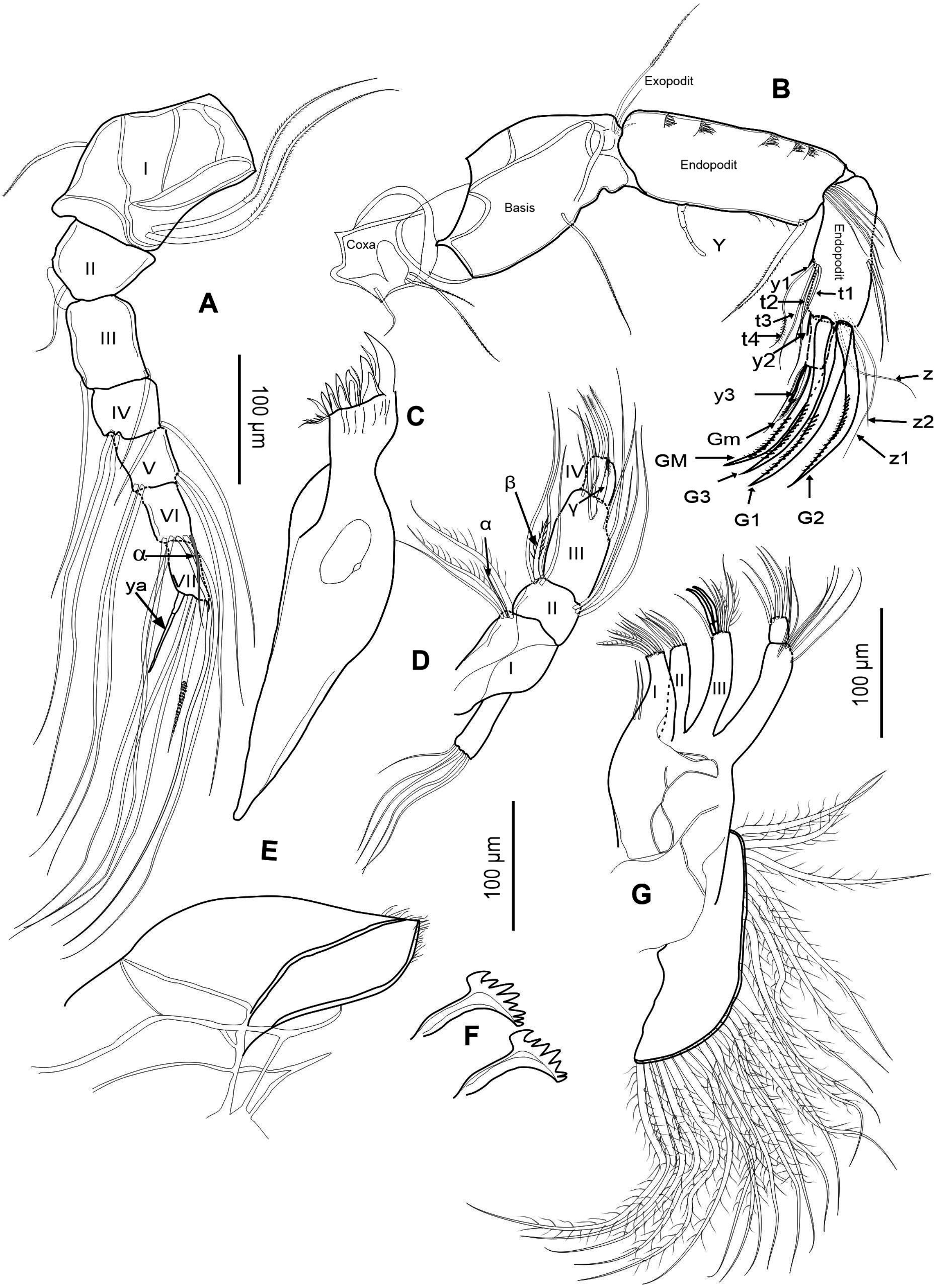

FIGURE 5. *Tonnacypris stewarti*, female from Nam Co (reference-ID NC18-S-37). A) left A1, exterior view; B) left A2, interior view; C) left Md coxa, exterior view; D) left Md-palp, interior view; E) upper lip; F) rake-like organ; G) right Mx1 with vibratory branchial plate, interior view. (See Broodbakker & Danielopol (1982) for chaetotaxy.)

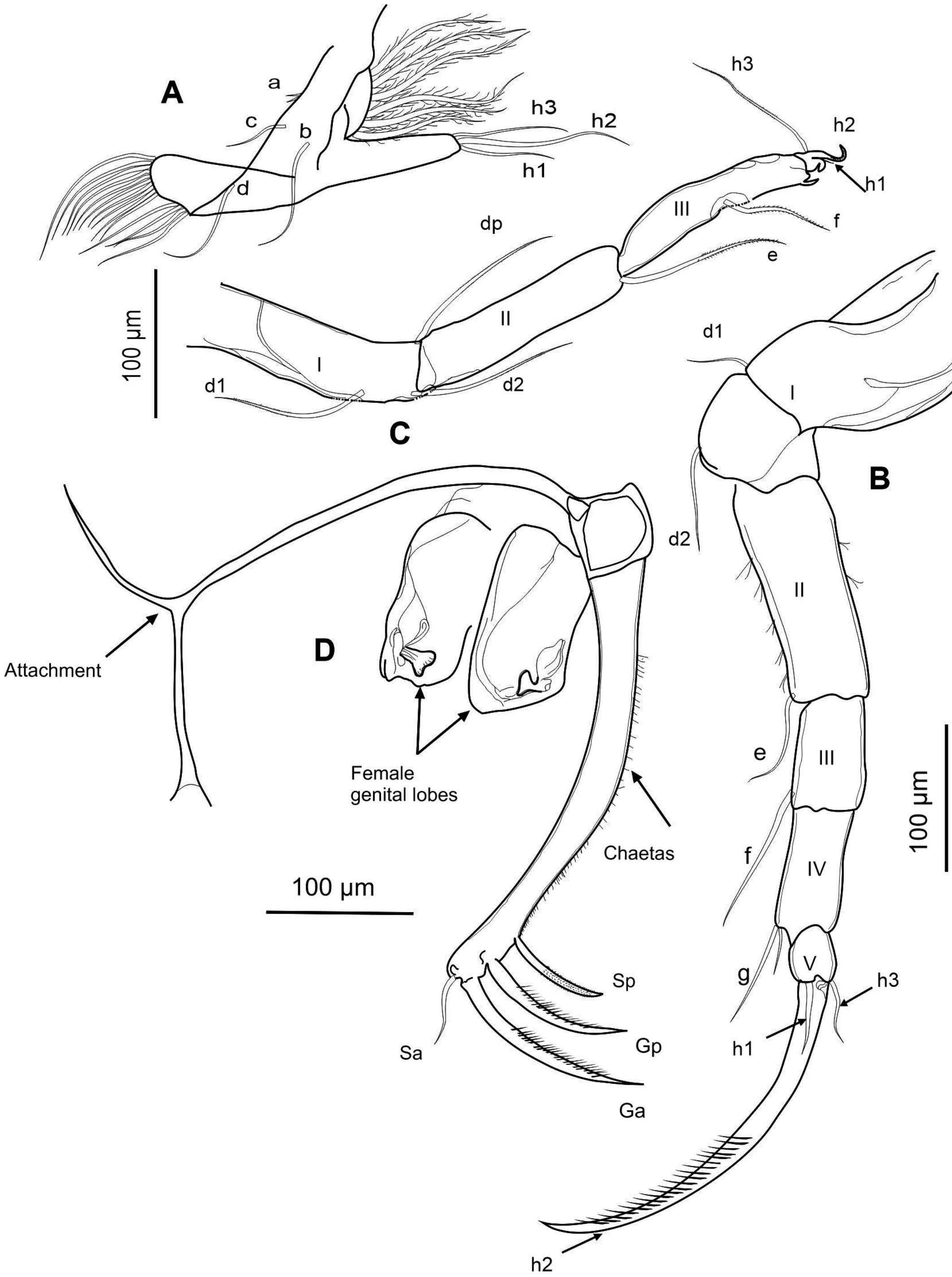

FIGURE 6. *Tonnacypris stewarti*, female from Nam Co (reference-ID NC18-S-37). A) left T1, exterior view; B) left T2, exterior view; C) left T3, exterior view; D) right CR with attachment and the female genital lobes. (See Broodbakker & Danielopol (1982) for chaetotaxy.)

Md coxa sclerotized (Fig. 5C) and 4-segmented palp of mandible (Fig. 5D). Md coxa has seven teeth with a plumed seta in the lateral region. First palp-segment with a respiratory plate with five setae, similar in length, except for a shorter one on the subapical part. It presents a group of four apical setae on the inner side including the α seta, two long plumed setae (S1 and S2), and one long smooth seta. Second segment with a group of three smooth setae. The β seta is next to the three distal smooth setae on the interior side. The third segment has ten smooth setae, four on dorsal side, and five situated more ventrally to a γ seta. The fourth segment has seven distal setae, three of them with setules, while four are smaller and smooth (setae incompletely illustrated).

Upper lip and rake-like organ (Fig. 5E, F). Rake-like organ with seven teeth on the right and eight on the left.

Mxl (Fig. 5G). Composed of maxillular palp, three endites, and a branchial plate. The palp is two-segmented: the first rectangular with eight setae, the second trapezoidal with five smooth setae. The first endite has four smooth setae plus two setae with setules; second endite with six setae; the third endite has four smooth setae and two with setules, in addition, there are two smooth Zahnborsten. The branchial plate consists of 23 plumed setae.

T1 (maxilliped) of female (Fig. 6A). The endopodite has one long smooth seta (h2) and two shorter setae (h1 and h3). The gnatobasic endite has 14 smooth setae (incompletely illustrated). Respiratory plate with six plumed setae. In the protopodite, there are two short a-setae, a single c-seta, b-seta and d-seta; b and d are smooth and longer than c.

T2 (Fig. 6B). Protopodite with a 33 µm long d1 seta and d2 seta approximately twice as long, 63 µm. First and second endopodal segments each with a smooth seta (e and f) in the distal part. Third endopodal segment with one g-seta and one short seta. Terminal segment with two short setae (h1 and h3) and curved serrated claw (h2).

T3 (Fig. 6C) with four segments. The first with a long and tiny plumed seta (d1), and with two tiny plumed d2 setae and a dp seta located at the base. In the distal part of the second segment, it presents an e-seta with setules similar to the f-seta on the third undivided segment. The fourth segment, a pincer organ, has a small h1 seta, distally serrated h2 seta and the smooth h3 seta.

CR (Fig. 6D) is an elongated structure of approximately 340 µm length. It has a line of chaetae on the ventral edge. The distal part has two claws, Gp smaller than Ga. In addition, there are two setae, Sa and Sp, the latter is thicker and stronger ornamented with setules. CR attachment simple, without loop. Next to the CR there are two well-differentiated genital lobes.

Female genital lobes of *T. stewarti* (Fig. 6D). Each female presents two lobes with crescent-shaped sclerotized tissue, without projections. The anterior part is triangular and in the internal part, there is an intersection where a tube joins.

Description of soft parts of a male from Lake Band-e Amir, Afghanistan: A1 (Fig. 7A). Regarding the morphology, the male is similar to the female, and composed of seven segments. Segment I has a short seta on the dorsal side and two long setae on the ventral region. Segment II has a trapezoidal shape, with a short seta on the dorsal zone. Segment III possesses a ventro-apical seta that extends to the end of segment four, and a dorsal-apical seta that reaches segment VII. Segment IV is slightly square-shaped, featuring two long dorsal-apical setae and one ventro-apical seta. Segment V has two long ventro-apical setae that reach the segment VII. Segment VI is elongated and bears four long apical setae and one short α seta. Finally, segment VII is somewhat slender, with three (two long and one short) apical setae and a sensory aesthetasc (ya).

A2 (Fig. 7B) is divided into four segments. The coxa exhibits three short setae, one smooth ventro-posterior seta, and two setae with setules on the ventro-apical region. The basis is a robust segment with a long seta on the ventro-apical region, extending to the endopodal segment. The exopodite consists of two short setae and one long seta with setules. The first endopodal segment contains a sensory aesthetasc Y located ventrally at the midpoint of the segment, a robust seta with setules on the ventro-apical region, and six natatory setae of unequal length in the apical region. Moving to the second endopodal segment, there is a tiny sensory aesthetasc y1 on the ventral side, along with four short t-setae. Additionally, there are two short setae in the mid-dorsal region, with two claws (z1 and z2), and a z3 seta. The z3 seta is long and extends to the z1 claw. G1 is short and robust with denticles, measuring 1/3 the length of G2. G3 is short and thin, located close to the sensory aesthetasc y2 and accompanied by a short seta. Claw z2 is slightly shorter than z1. Gm is half the length of GM, together with the slender aesthetasc y3.

Md (Fig. 7C) is composed of a sclerotized coxa and a Md-palp with four segments (Fig. 7D). Md coxa bears seven teeth, with one seta with setules on the ventral region and another smooth seta on the dorsal region. The first segment of Md-palp features a branchial plate consisting of five setae, with the subapical seta being shorter. On the interior side, there is a group of four apical setae, including the α seta, two long plumed setae (S1 and S2), and one long smooth seta. The second segment possesses three smooth setae. Seta β is situated alongside the three distal smooth setae on the interior side. The third segment has ten smooth setae (incompletely illustrated), with four on the dorsal side and five located more ventrally towards a γ seta. The fourth segment has seven distal setae (incompletely illustrated), three of them with setules, while the remaining four are smaller and smooth.

Upper lip and rake-like organ (Fig. 7E) with seven teeth on the right and eight on the left.

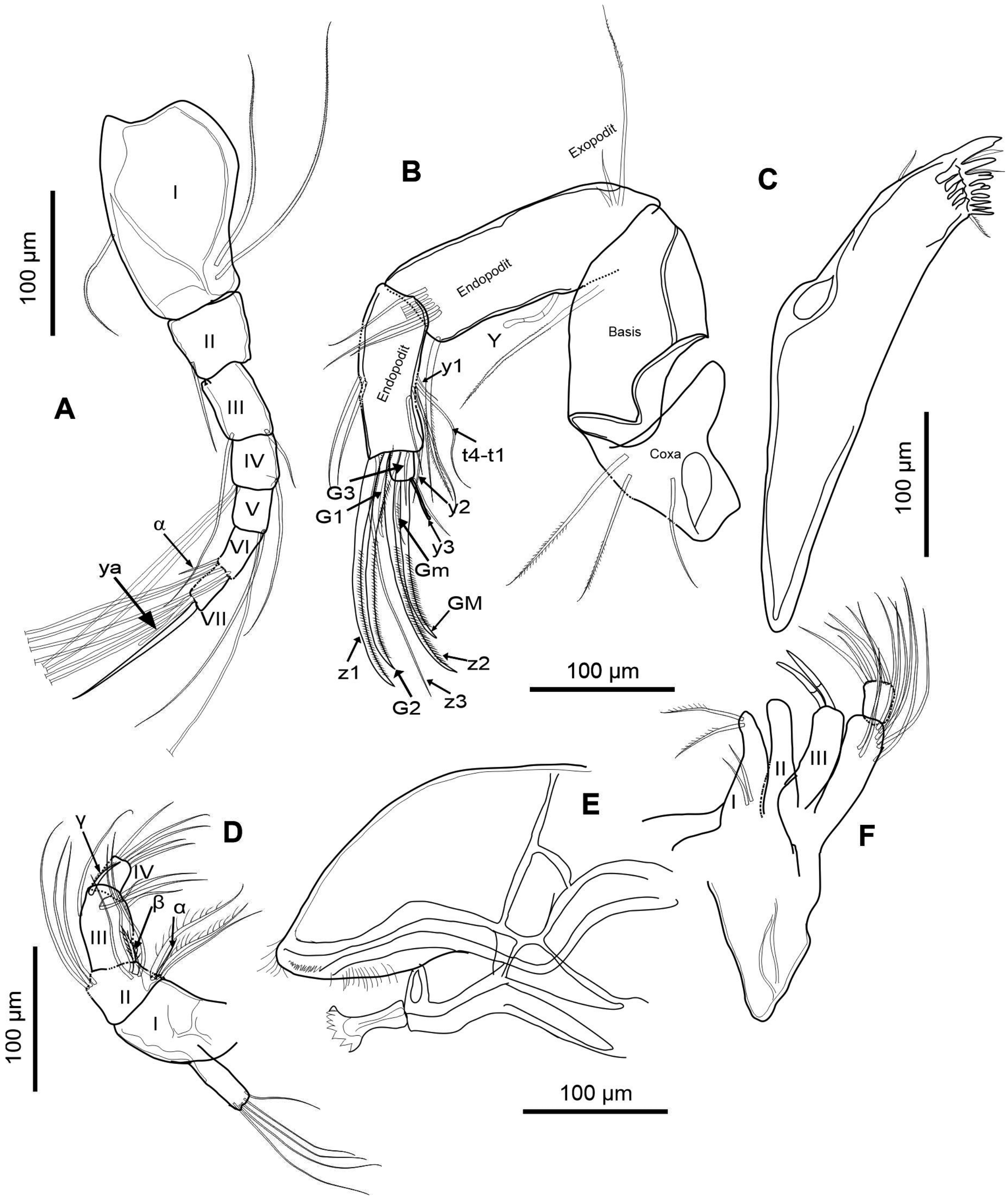

FIGURE 7. *Tonnacypris stewarti* (= *E. afghanistanensis*), male from Lake Band-e Amir, Afghanistan (reference-ID ZMH-K27716). A) left A1, exterior view; B) right A2, interior view; C) right Md-coxa, exterior view; D) right Md-palp, interior view; E) upper lip and rake-like organ, F) right Mx1, interior view. (See Broodbakker & Danielopol (1982) for chaetotaxy.)

Mx1 (Fig. 7F). In the male, the Mxl structure comprises a maxillular palp, three endites (with chaetotaxy incompletely illustrated), and a branchial plate (not illustrated). The palp is divided into two segments. The first segment is rectangular in shape and bears eight setae. The second segment is trapezoidal and features five smooth setae. The first endite has four smooth setae along with two setae adorned with setules. The second endite has six setae, while the third endite has four smooth setae, two setae with setules, and two smooth setae shaped like horns. The branchial plate is equipped with ~23 plumed setae.

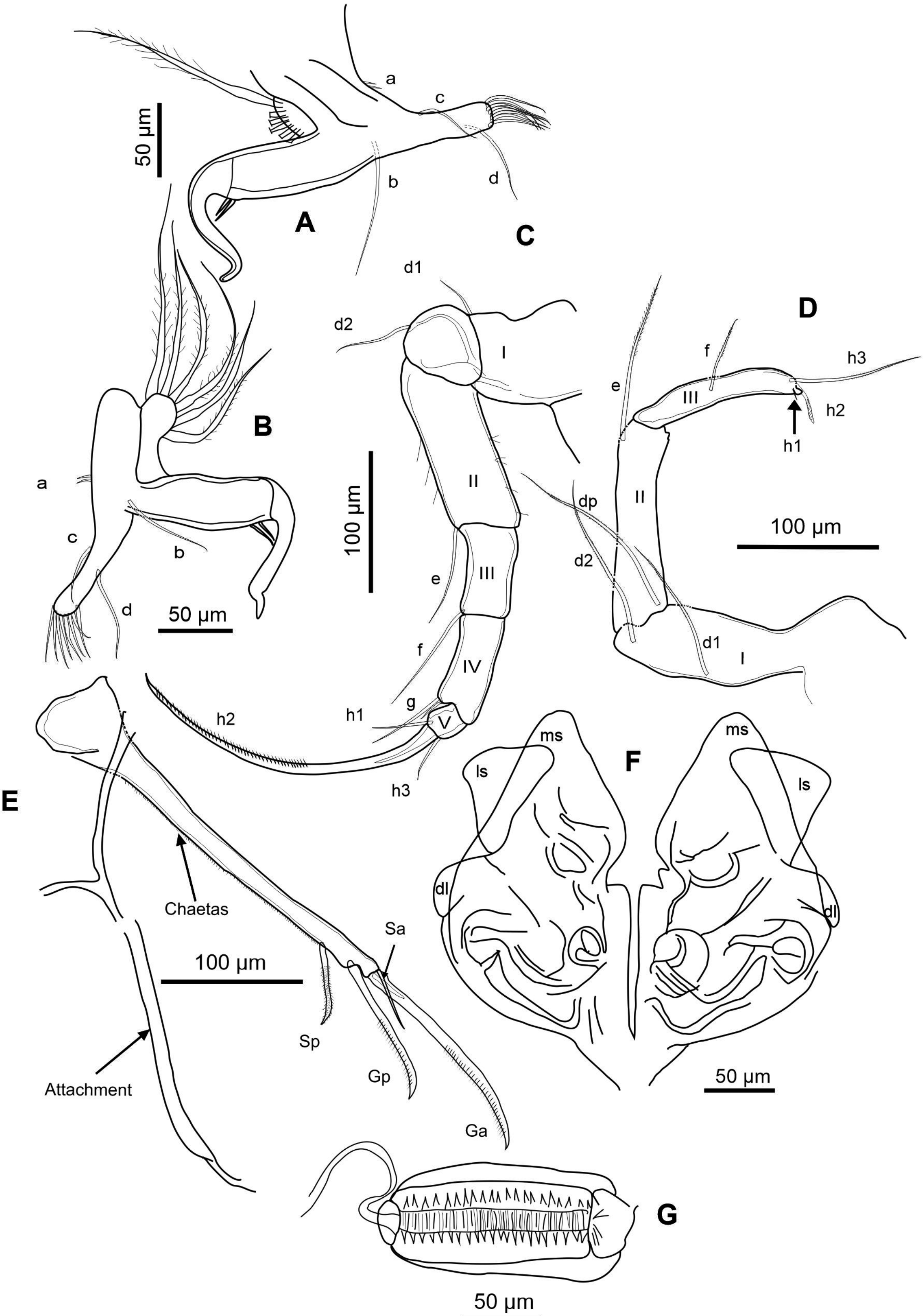

FIGURE 8. *Tonnacypris stewarti* (= *E. afghanistanensis*), male from Lake Band-e Amir, Afghanistan (reference-ID ZMH-K27716). A) right T1, interior view; B) left T1, exterior view; C) left T2, exterior view; D) right T3, interior view; E) CR with attachment; F) hemipenis; and G) Zenker organ. (See Broodbakker & Danielopol (1982) for chaetotaxy.)

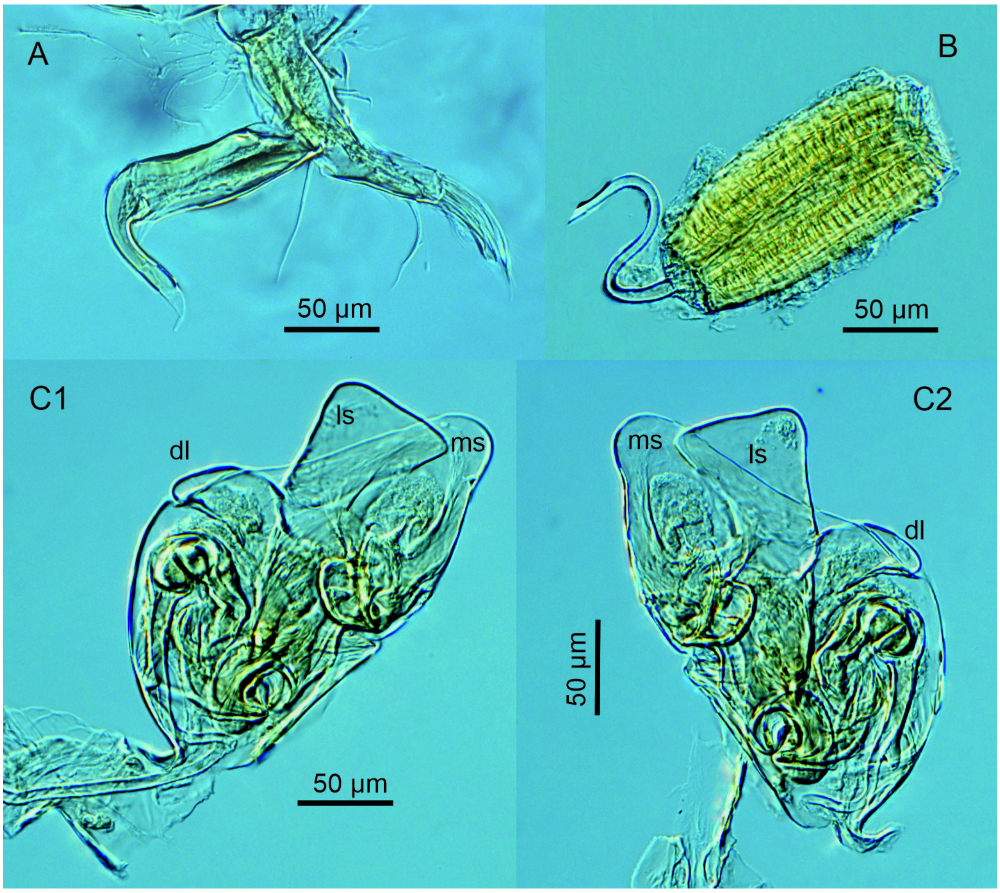

FIGURE 9. *Tonnacypris stewarti* (= *E. afghanistanensis*); male from Lake Band-e Amir, Afghanistan (reference-ID ZMH-K27716; Hartmann 1964), A) T1, B) Zenker organ, and C1–C2) hemipenis of male. Abbreviations: dorsal lobe (dl), lateral shield (ls), and medial shield (ms).

T1 (maxilliped) (Fig. 8A–B, 9A). Sexually dimorphic with prehensile palps, with a finger-shaped curvature, two small setae are located near the curvature of the endopodite on its ventral side. The gnatobasic endite is equipped with 13–14 smooth setae (incompletely illustrated). Additionally, the respiratory plate bears six plumed setae. Within the protopodite, there are two short a-setae, along with a single c-seta, b-seta, and d-seta. Both b and d setae are smooth and longer than c-seta.

T2 (Fig. 8B) shows a protopodite with a long d1 seta and a d2 seta, which is approximately twice as long. The first and second endopodal segments each have a smooth seta (e and f) at their distal parts. The third endopodal segment is equipped with one g-setae and one short seta. The terminal segment possesses two short setae (h1 and h3) and a curved serrated claw (h2).

T3 (Fig. 8C) consists of four segments. The first segment has a long and tiny plumed seta (d1) and two tiny plumed setae (d2 and dp) located at the base. In the distal part of the second segment, an e-seta with setules is present, similar to the f-seta found on the third undivided segment. The fourth segment, known as the pincer organ, contains a small h1 seta, a distally serrated h2 seta, and a smooth h3 seta.

CR (Fig. 8D) is an elongated structure. Along the ventral edge, there is a line of chaetae. The distal part of each ramus features two claws, with Gp being smaller than Ga. Additionally, there are two setae, Sa and Sp, with the latter being thicker stronger set with setules. CR attachment simple.

Hemipenis (Fig. 8E and 9C1–C2) with small dorsal lobe (dl). The lateral shield (ls) and medial shield (ms) are sub-triangular, both are rounded and smooth. The ms is slightly longer than ls. (See also the descriptions by Daday 1908 and Peng *et al*. 2021.)

Zenker organ (Figs. 8F and 9B). The specimen from Lake Band-e Amir, Afghanistan with ~21 spines.

Comparing carapace and soft parts of specimens from Afghanistan, Nam Co, and Mang-tsa with specific observations: Specimens from Afghanistan exhibit numerous scars on the dorsal part of the right and left valves, a feature also observed in Nam Co individuals (Fig. 3 E2). Notably, females from Afghanistan display greater length (1392 µm) and height (638 µm) than those from Nam Co (1256 µm; 585 µm).

The structures and number of setae on the first antennae, second antennae, mandibles, maxilla, second thoracopod, third thoracopod, and caudal ramus remain consistent when compared with *T. stewarti* individuals from Nam Co (Figs. 5–8). Similarly, the T1 of males from Afghanistan present the same finger-shaped curvature as individuals from Mang-tsa (Fig. 8A).

In contrast, the hemipenis of the individual from Afghanistan displays more reduced medial and dorsal lobes than those of the Tibetan individuals that are slightly wider (Fig. 10A–C).

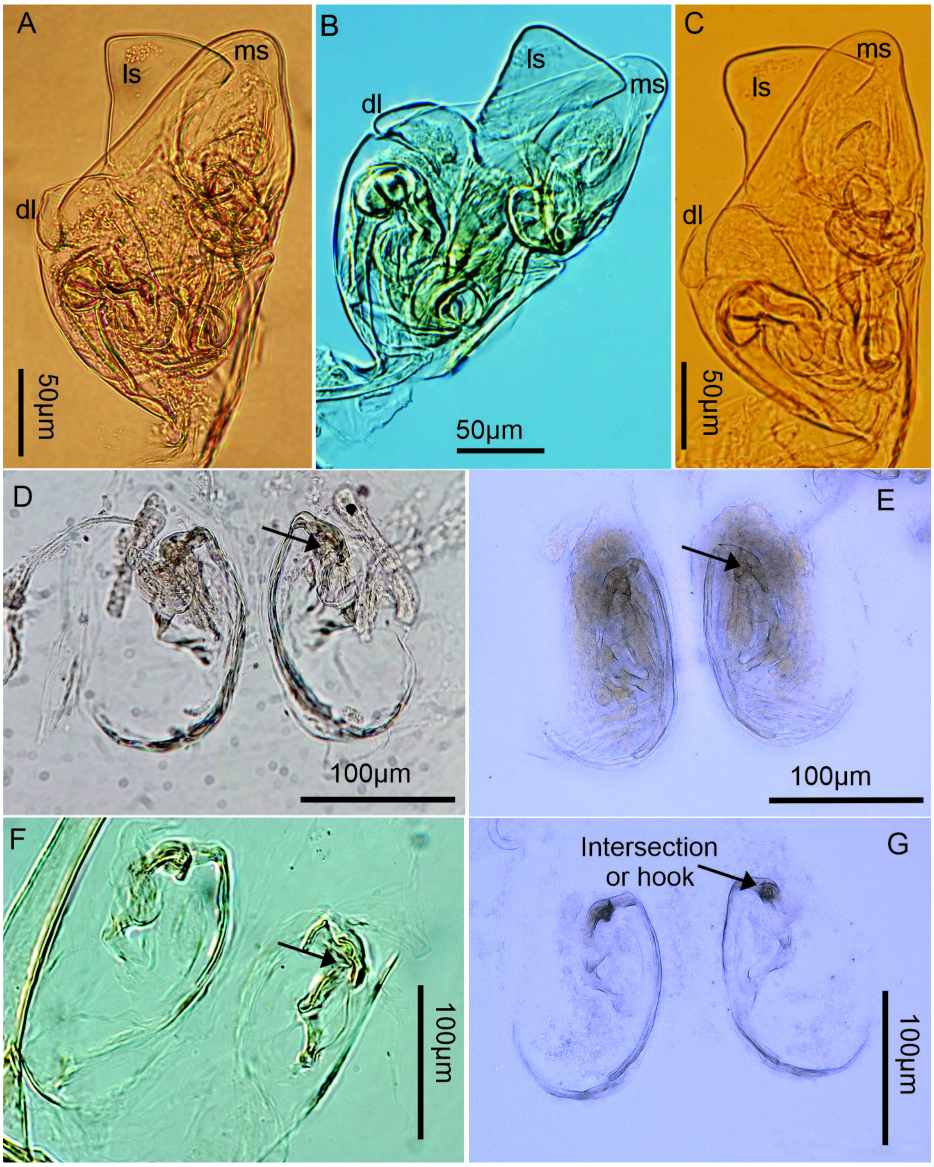

FIGURE 10. Hemipenis and female genital lobes of *T. stewarti* from: A) Mang-tsa, Tibetan Plateau (TP) (reference-ID HNHM-IV-369, Daday 1908); B) Lake Band-e Amir, Afghanistan (reference-ID ZMH-27716, Hartmann 1964); and C) near Linzhi, TP (modified from Peng *et al*. 2021). Dorsal lobe (dl), lateral shield (ls), and medial shield (ms). Female genital lobes from: D) Mang-tsa, TP (reference-ID HNHM-IV-369); E) Lake Band-e Amir, Afghanistan (reference-ID ZMH-27716); F) Nam Co, TP (reference-ID NC-18-S-37); G) Peat near Taro Co, TP (reference-ID TIP11-105). The arrows indicates the intersection or a hook.

We observed variations in the shape of the female genital lobes among species. Interestingly, female specimens of *Tonnacypris stewarti* consistently displayed lobes with a similar shape structure. Notably, the examined females of *T. stewarti* did not show variations, despite being collected at different sites on the Tibetan Plateau and in Afghanistan (Fig. 10D–G).

Carapace ontogeny: Eight development stages were recognized from juveniles A-7 to adults, with measurements of the valves in length and height (Fig. 11). In adult individuals, the average length of right valves was found to be 1108 µm, while the left valves measured 1171 µm. Additionally, adult right valves had an average height of 545 µm, while left valves had an average height of 591 µm (Table 4). Among A-7 juveniles, the average length of the right valve was recorded as 270 µm, and the left valve averaged at 276 µm. As for the height measurements, the right valve had an average of 163 µm, and the left valve measured 178 µm.

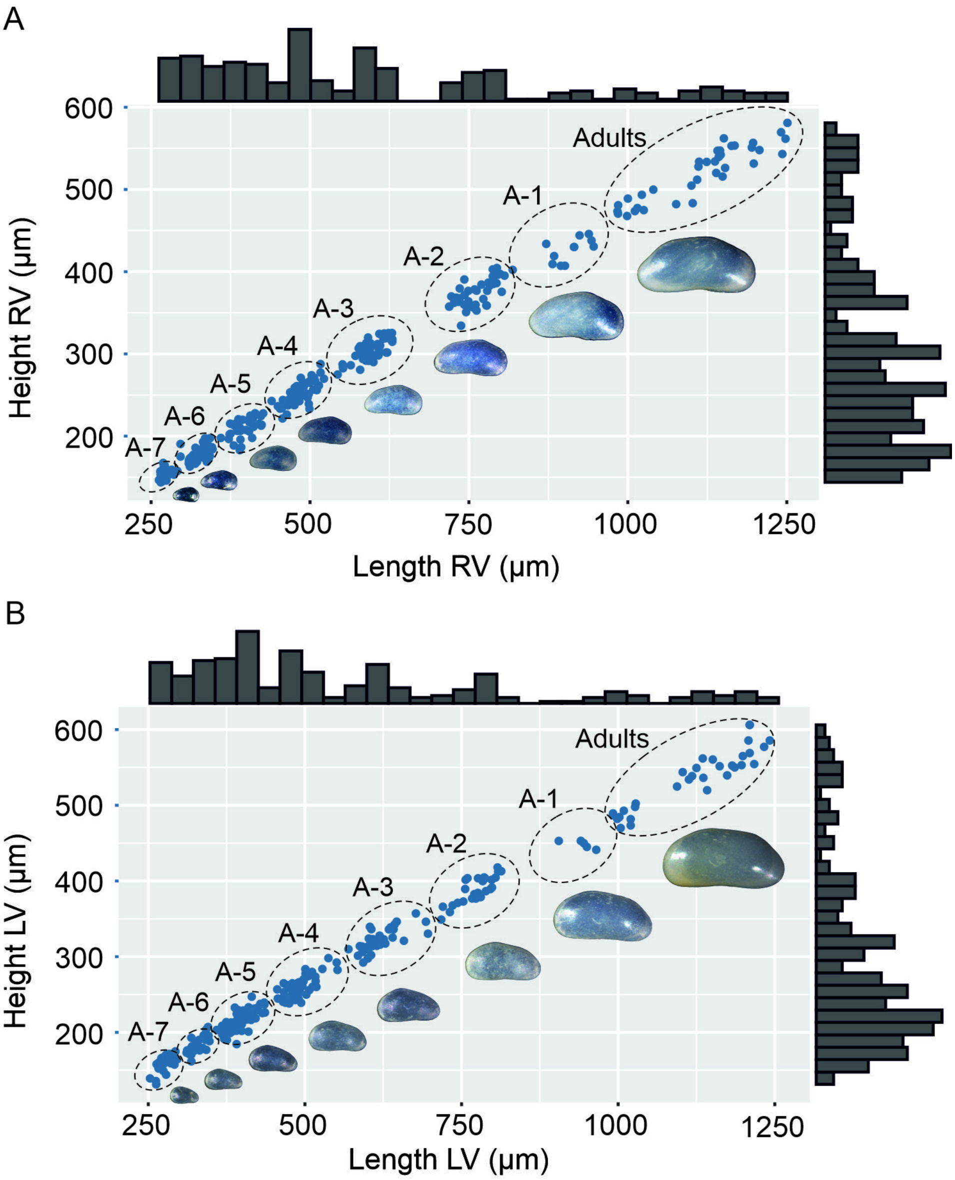

FIGURE 11. Carapace ontogeny of *Tonnacypris stewarti* (Daday 1908) from Nam Co (reference-ID NC18-S-37), measures in length and height of (A) right valves (RV) n = 284 and (B) left valves (LV) n = 277 clearly show the different developmental stages. The histograms show the abundances of the different stages with the scatter plot (juveniles A-7 to adults).

In order to identify a growth pattern of *T. stewarti* and to contribute to understandings of its ontogeny, we analyzed the average length and height measurements of the valves. Our findings revealed that the right valves exhibited a range from 1.188 to 1.282, with a mean of 1.224, while the left valves exhibited measurements between 1.187 and 1.283, with a mean of 1.230 (see Table 4). The valves' growth ratio of length and height follows Brooks' rule. Regularly, for the adults, the right and left valves have a distinct trapezoidal shape and are straight at the dorsal margin (Fig. 12). Both have well-recognized antero-dorsal and postero-dorsal angles, and the dorsal margin is almost straight. On the other hand, in the early juvenile stages the valves display a distinct triangular morphology in the posterior segment. This characteristic is attributed to the yet-to-develop posterior appendages in this body region, as opposed to the anterior segment where the initial appendages are more developed and specialized for swimming. The anterior part presents a rounded shape at the margin (Fig. 13).

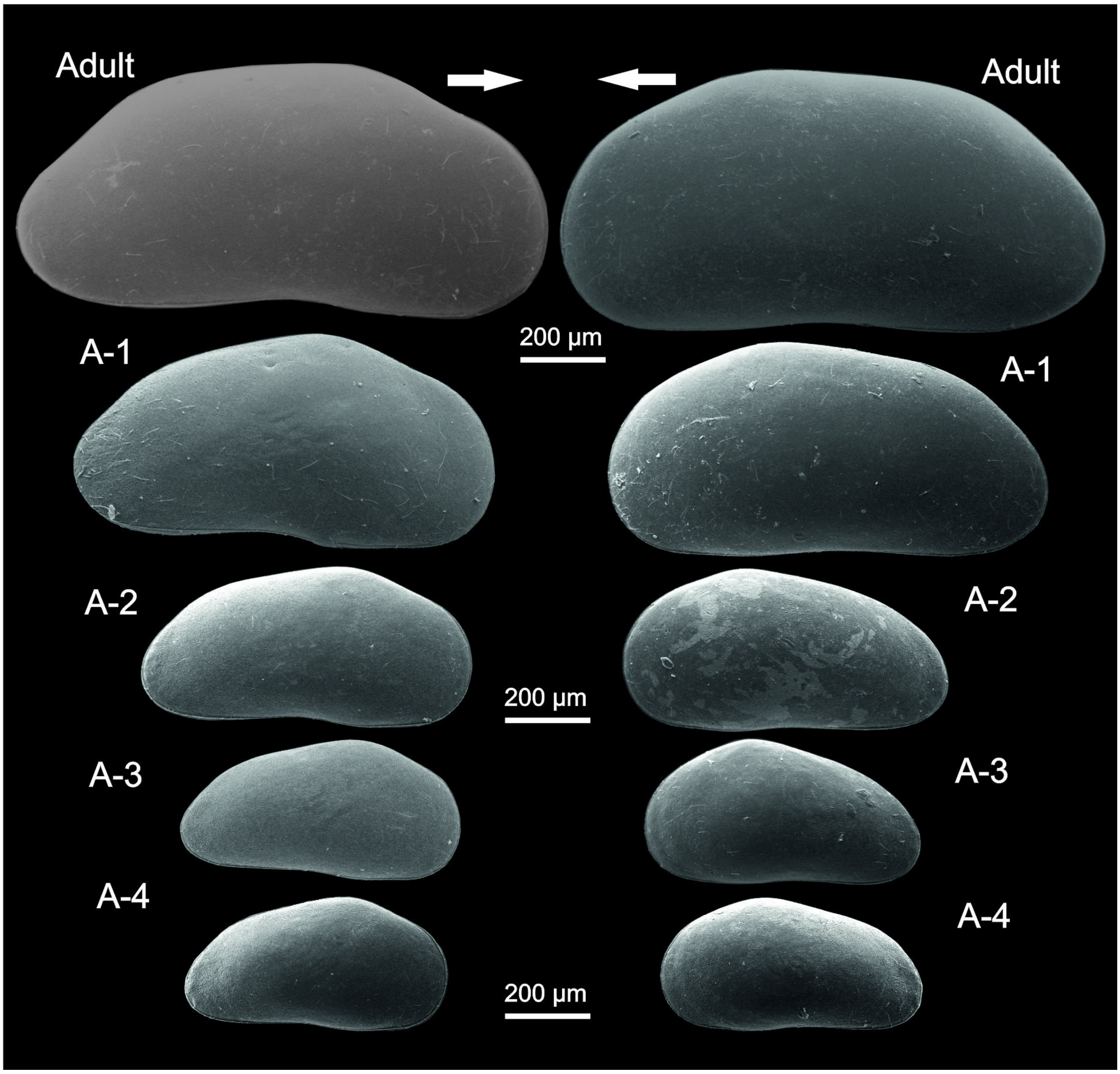

FIGURE 12. Valves of an adult and juveniles (A-1 to A-4) of *Tonnacypris stewarti* from Nam Co (reference-ID NC18-S-37). Arrow points to anterior.

TABLE 4. Average and standard deviation of right (RV) and left valves (LV) in length and height for each developmental instar of *T. stewarti* collected in Nam Co. n = number of measured valves, with a total of 284 for RV and 277 for LV. Growth ratio of length and height valves according to Brooks' rule for each growth instar.

Instar and phase of growth	Size and Growth ratio					
	Right valve		n	Left valve		n
	Length (µm)	Height (µm)		Length (µm)	Height (µm)	
Adult	1108±88	545±15	36	1171±46	591±11	32
A-1 to Adult	1.221	1.162		1.187	1.080	
A-1	907±24	469±39	12	986±36	547±15	5
A-2 to A-1	1.188	1.221		1.283	1.127	

...Continued on the next page

TABLE 4. (Continued)

Instar and phase of growth	Size and Growth ratio					
	Right valve		n	Left valve		n
A-2	763±26	384±15	38	768±31	485±9	29
A-3 to A-2	1.282	1.084		1.259	1.082	
A-3	595±20	358±4	47	610±27	448±4	40
A-4 to A-5	1.229	1.177		1.247	1.151	
A-4	484±18	304±12	54	489±18	389±16	48
A-5- to A-6	1.219	1.206		1.225	1.211	
A-5	397±16	252±13	38	399±19	321±16	66
A-6 to A-7	1.225	1.166		1.212	1.142	
A-6	324±14	216±7	40	329±11	226±35	31
A-7 to A-8	1.200	1.248		1.192	1.335	
A-7	270±6	173±16	19	276±11	168±15	26
Mean Growth Ratio	1.224	1.251		1.230	1.202	

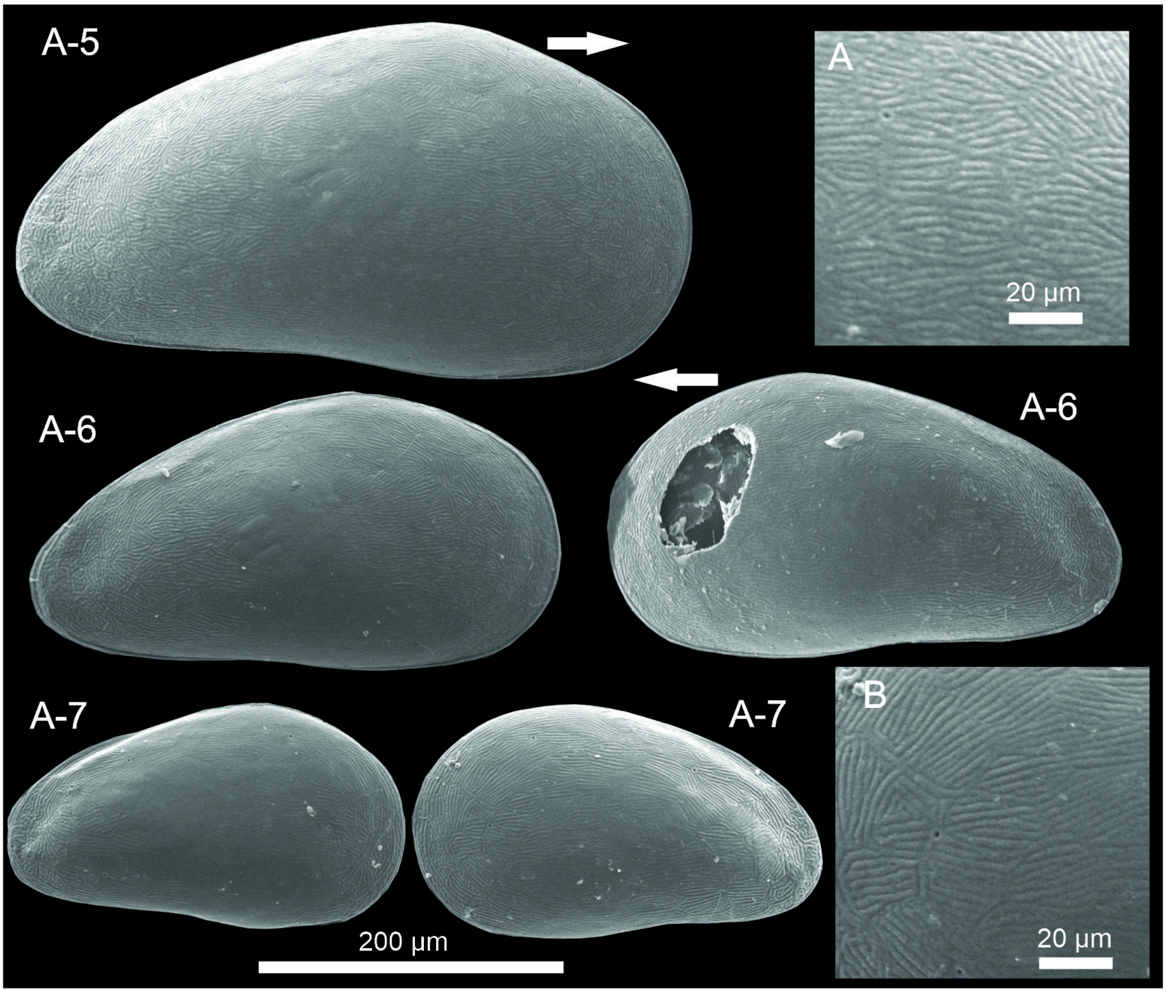

FIGURE 13. Valves of the first stages of development of *T. stewarti* from Nam Co (reference-ID NC18-S-37). They show a striated pattern on the surface of the valves. Right valve of juvenile A-5 and a close-up of center-dorsal of the valve (A). Right and left valves of juvenile A-6. Right and left valves of juvenile stage A-7, with a detail of the surface of the left valve (B). Arrow points to anterior.

Additionally, a detailed observation of the morphology of *T. stewarti* juveniles revealed a distinct striated pattern of lines, gradually fading in the A-1 stages and adulthood (Figs. 12 and 13).

Considering the total abundances of juveniles and adults, encompassing living and sub-fossil records (Fig. 14), high numbers were recorded mainly in samples from within the lake (samples 7, 10, 14, 15, and 16), with dominating juveniles. In the samples from rivers and lagoons, the individuals in samples 1, 5, and 6 were mainly adults. However, it was not possible to observe a clear pattern of abundances of juveniles or adults defined by the type of habitat, since the sampling was only undertaken during one season of the year.

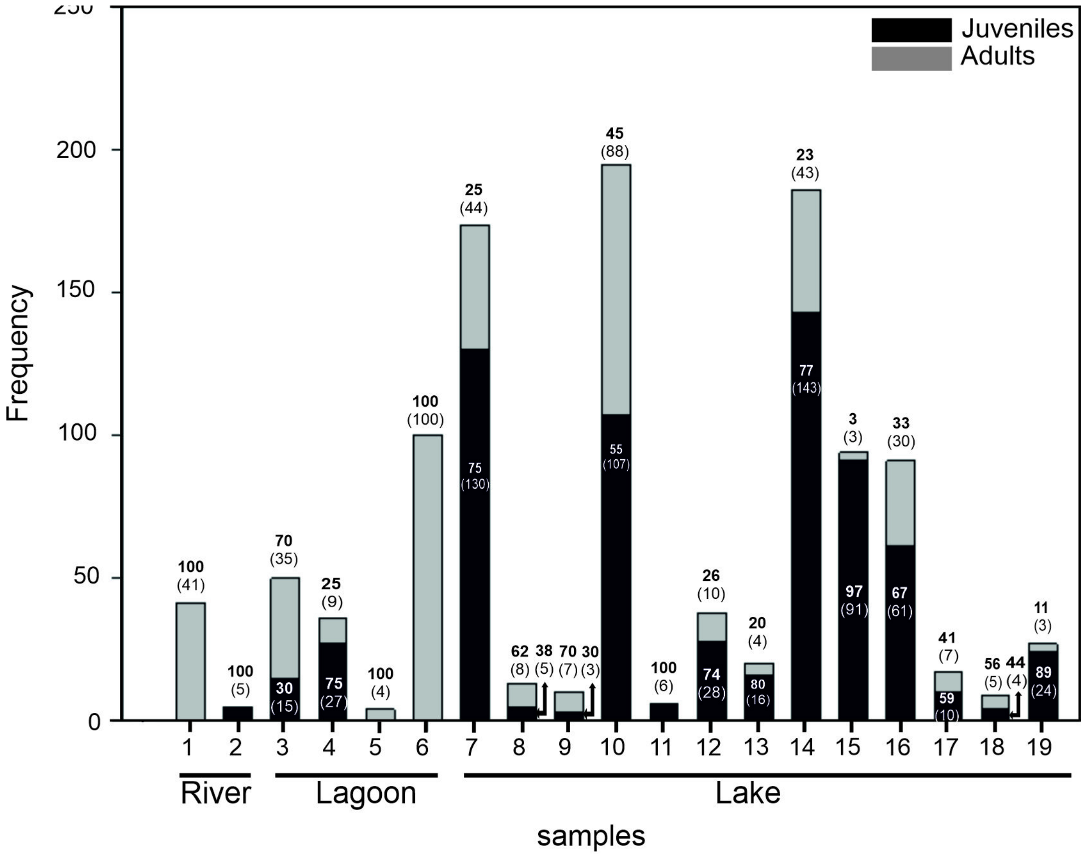

FIGURE 14. Total abundance of *T. stewarti* from Nam Co, including both living and subfossil specimens. Bold values indicate percentages, while absolute abundance is presented within parentheses. Valve categorization includes juveniles (A-7 to A-1) and adults. Sample differentiation is based on habitat type: river, lagoon, and lake. Adult specimens are represented by the gray bar, and juvenile specimens by the black bar. (Sample codes correspond to those listed in Table 1.)

Distribution and ecology of *T. stewarti* in Nam Co, Tibetan Plateau: The species was found at high elevations, reaching up to 4742 m a.s.l. Our results indicate that *T. stewarti* is widely distributed in Nam Co. The highest abundances were observed at three sites with varying water depths: sites 7 (174 individuals, 4 m depth), 10 (195 individuals, 27 m depth), 14 (186 individuals, 40 m depth). Additionally, *T. stewarti* can also be found in small numbers in lagoons and rivers; however, a notably higher abundance of living individuals occurs within littoral zones of Nam Co. The ecological preferences of *T. stewarti* are correlated with specific hydrological parameters. Notably, this species exhibits affinity to water conductivities spanning from 149 to 1894 µS/cm, water temperatures ranging from 3.6 to 18.9 °C, an average pH of 9.1, and a dissolved oxygen concentration of 6.8 mg/l. The prevailing alkalinities in the water body range from 1.3 to 18.2 mmol/l.

The cluster analysis reveals three groups of samples: Group A comprises samples from deeper lake water below 8 m depth, group B those from mostly shallow parts of the lake and open lagoons, and group C those from rivers and confined lagoons (Fig. 15A). Mean abundance of *Tonnacypris stewarti* is similar in all three groups but shows different ranges. Whereas minima range between 4 and 6 specimens/g for all three groups, samples of group A (deeper lake) show the highest maxima (Fig. 15B). These samples are characterized by highest conductivity, alkalinity, pH, oxygen concentration, and lowest water temperature (Table 5). The shallow river and confined lagoon habitats of group C show the contrary, and the values of group B lay mostly in between except for oxygen concentration, which is similar for groups B and C.

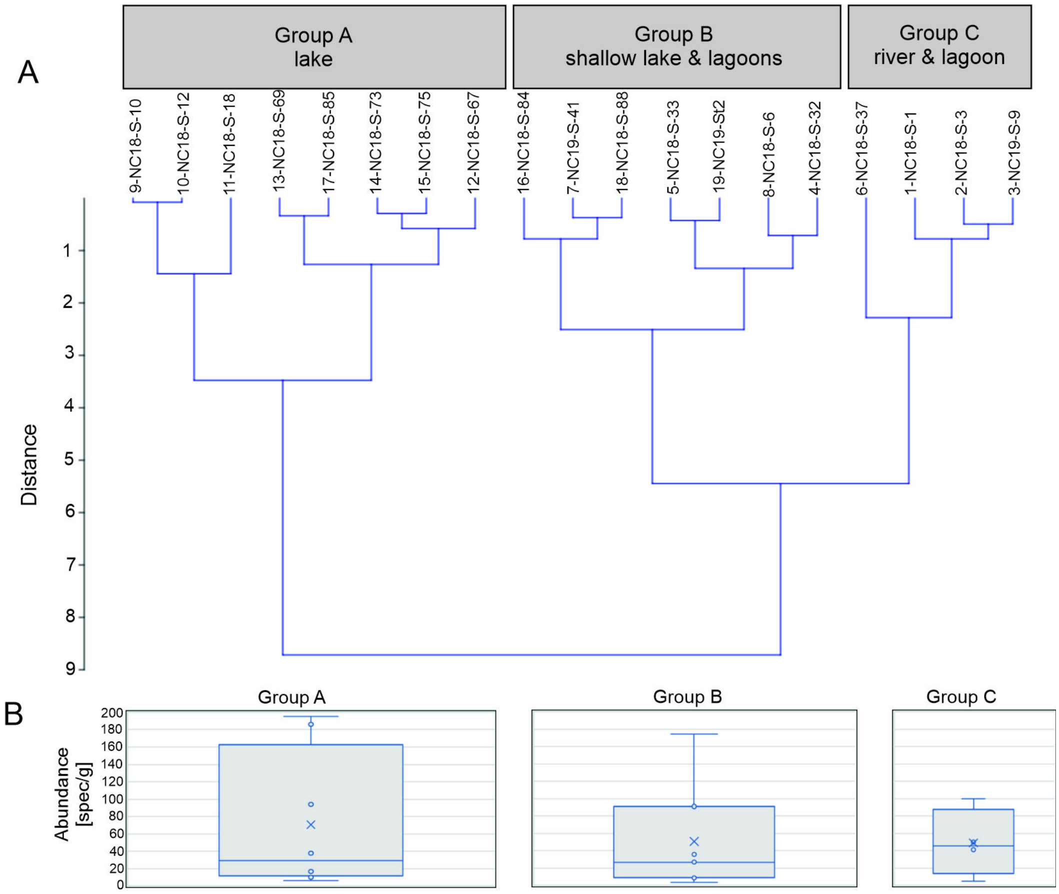

FIGURE 15. A) Classification of samples according to associated environmental factors (water depth, electrical conductivity, water temperature, and pH). Group A contains samples from the open lake, group B those from shallow waters, open lagoons and embayments, group C those from rivers and confined lagoons. B) The boxplots below the dendrogram show mean values (x) and variance of *Tonnacypris stewarti* abundance within the three groups of habitat types. For means and ranges of environmental factors see Table 5.

TABLE 5. Range, mean (m), and standard deviation (sd) of measured environmental factors within identified groups of habitats.

Group	Water depth [m]	Conductivity [µS/cm]	Temperature [°C]	pH	O_2 [mg/l]	Alkalinity [mmol/l]
A: lake	8.0–60.7 m 35.4 sd 18.7	1305–1894 m 1659 sd 273	3.6–9.8 m 7.7 sd 2.1	9.0–11.2 m 9.6 sd 0.7	7.0–7.9 m 7.3 sd 0.3	14.0–18.2 m 17.0 sd 1.5
B: shallow lake & lagoon	0.1–11.5 m 2.7 sd 3.9	270–1292 m 1621 sd 220	11.1–18.9 m 14.4 sd 2.6	8.9–9.0 m 9.0 sd 0.0	4.6–6.9 m 6.1 sd 0.8	10.0–17.3 m 15.0 sd 2.5
C: river & lagoon	0.1–0.3 m 0.2 sd 0.1	149–270 m 211 sd 44	9.3–18.9 m 12.3 sd 3.9	8.0–9.0 m 8.4 sd 0.4	6.4–6.9 m 6.6 sd 0.2	1.3–2.9 m 2.0 sd 0.7

Discussion

Clarifications and taxonomic history of *Tonnacypris stewarti* on the Tibetan Plateau and in Afghanistan: Several studies have described and classified ostracod assemblages from lake surface sediments from the Tibet-Qinghai region (Daday 1908; Huang *et al*. 1982; Mischke *et al*. 2006; Wrozyna *et al*. 2009b; Xie *et al*. 2009;

Zhu *et al*. 2010; Schütt *et al*. 2010; Akita *et al*. 2016; Guo *et al*. 2016). In these studies, ostracods with a similar morphology to that of *T. stewarti* were given different names. Daday (1908) initially described males and females of *Herpetocypris stewarti* from Mang-tsa, a locality in the central part of the Tibetan plateau, however these specimens exhibit features consistent with the genus *Tonnacypris*, a genus reassignment was therefore made.

Interestingly, the females collected in the following decades during expeditions to Mongolia (Van der Meeren *et al*. 2009) presented similar morphological features to those found by Daday (1908). The limbs are identical among females from Mang-tsa (Daday 1908), Sichuan, Tibet (Peng *et al*. 2021), and Afghanistan (Hartmann 1964). Similarly, the males show uniformity across these regions (see details below). Following the re-description of a female specimen collected from Mongolia (Van der Meeren *et al*. 2009), initially assigned to *Tonnacypris estonica*, the present study contributes essential information regarding its taxonomic classification. The diagnostic generic features of *Tonnacypris* were critically reassessed, focusing predominantly on valve morphology, as well as chaetotaxy related to antennae, antennules, the first thoracopod, and the walking leg.

However, a detailed analysis and comparison of species with similar morphologies found on the Tibetan Plateau revealed that three taxa were in fact synonymous: *Eucypris gyirongensis*, *E. afghanistanensis*, and *Tonnacypris gyirongensis*. Consequently, they were added to the list of synonyms of the original description, which included specimens from the northern region of Estonia (Järvekülg 1960).

Moreover, the discovery of males and females from the Tibetan Plateau (Daday 1908; Peng *et al*. 2021) and Afghanistan (Hartmann 1964) served as fundamental evidence to confirm that the previously attributed names denote the same species, namely *Herpetocypris stewarti* (= *Tonnacypris stewarti*). This clarification now provides a solid basis for resolving the taxonomic puzzle associated with these species, contributing to a clearer understanding of their systematic position.

The swimming setae of A2 were described as short, the carapace reniform with setae on the surface, with an arched dorsal margin, the margins with multiple pore channels, and the valves of females ranging in length between 1200 and 1300 µm and in height between 600 and 650 µm. In contrast, male carapaces were slightly smaller in length (1000–1050 µm) and height (450–500 µm). Likewise, Daday (1908) described how the hemipenis presented a characteristic pyramidal shape, with a quadrangular accessory appendage consistent with that of males recorded in Lake Band-e Amir, Afghanistan (Hartman 1964), and Tibet (Peng *et al*. 2021).

Subsequently, Huang *et al*. (1982) recorded the presence of *Eucypris gyirongensis* valves in Pleistocene sediments from the southwestern Tibetan Plateau for the first time. Despite the absence of soft parts, after comparison with *Eucypris afghanistanensis* specimens (Hartmann 1964), *Eucypris gyirongensis* was identified and described as a new ostracod species. However, the kidney-shaped carapace and valve lengths of both species were similar (length 1000–1300 µm and height 500–620 µm, respectively). In addition, the measurements present ranges of carapace height and length similar to those recorded by Daday (1908) and in our study from Nam Co. Therefore, we consider *Eucypris gyirongensis* as another synonym.

Wrozyna *et al*. (2009b) were the first to report this species from Nam Co (as *E. gyirongensis*). Juveniles and adults in surface sediment samples from the northwestern part of the lake were analyzed. However, it is important to clarify that the images of *E. gyirongensis* (= *T. stewarti)* in their publication (Plate 3, Figs. 1–2) correspond to two juvenile left valves of *Candona xizangensis*, which were also observed by Zhu *et al*. (2010, Fig. 3.12). The dorsal part of *C. xizangensis* is more rounded, and the posterior part is taller and triangular. Additionally, the inner posterior lamella is slightly thinner than that of *T. stewarti*, which is broader and covers more of the posterior region. The valve morphology of *T. stewarti* from Nam Co is similar to that of *Eucypris rischtanica* (see Li *et al*. 2010, Plate 1.4 and Plate 2.16), which was collected close to Lake Qinghai, northeastern Tibetan Plateau. The RV (1050 µm) and LV (1125 µm) illustrated by Li *et al*. (2010) represent adults, as evidenced by their valve shape and well-developed calcified inner lamella. These measurements closely align with the length range of *T. stewarti* specimens from Nam Co that we measured (Table 3). The fossil specimen of *Eucypris rischtanica* described and illustrated by Schneider in Mandelstam & Schneider (1963) shows the same size and morphology as our material from Nam Co. Thus, we regard *Eucypris rischtanica* Schneider 1963 as a younger synonym of *Tonnacypris stewarti* (Daday 1908). However, confirmation of this requires the study of Schneider's type material, which was not available to us.

From the morphological review and as discussed above, the individuals from Afghanistan are considered as *Tonnacypris stewarti* because they have a smooth carapace with multiple setae on the surface, they display an anteroventral peg in the calcified part of the lamella in the left valve—although sometimes the peg is inconspicuous—(Van der Meeren *et al*. 2009), the swimming setae of A2 are reduced, and the d2 setae are twice as long as the d1 in the second thoracopod. On the other hand, assignment to the genus *Eucypris* is ruled out, because it has been mentioned that representatives of this genus have an elliptical valve, the anterior surface of the valves is usually covered with warts, the d1 seta are three times longer than d2 in the second thoracopod, and the terminal segment of the palp of the Maxillula (Mx1) is distally cylindrical and curved (Meisch 2000; Karanovic 2012).

The distinction between *T. stewarti* and *T.* cf. *lutaria* is clear considering the size and the elongated carapace, in addition to the fact that the posterior angle of the valves is less pronounced in *T.* cf. *lutaria* (Martens *et al*. 1992). In proportion, *T.* cf. *lutaria* (left valve L = 2000, H = 990) is approximately twice as long as *T. stewarti* (L = 1078–1160 µm). Although it has been previously discussed that *T. stewarti* can present phenotypic plasticity, this has not yet been related to any environmental factor; the size of the species remains constant and does not exceed 1400 µm in length (Van der Meeren *et al*. 2009). This was confirmed by reviewing and analyzing previous records. For instance, the length of the female valves from Nam Co ranges from 1020 to 1256 µm, similar to the material from Sichuan (1160–1280 µm; Peng *et al*. 2021), Afghanistan (1033–1392 µm; Hartmann 1964), and Mongolia (1050–1330 µm; Van der Meeren *et al*. 2009). However, not all studies mention the morphological measurements, which are considered a necessary aspect of comparison between external characteristics for differentiation among species.

Based on the previously described characteristics, the identification of *T. estonica* (= *T. stewarti*) by Sohar & Meidla (2010) in Pandivere Upland, northern Estonia is likely incorrect, because the valves resemble *Tonnacypris glacialis*. The differences can be seen in the inner lamella, which is wider at the extremes, the posterior angle of the right valve is less pronounced, and *T. glacialis* is also much longer (1550–1920 µm) and higher (840 µm) (Griffiths *et al*. 1998; Fuhrmann 2012). Also, new sampling campaigns are required to clarify the possible geographical distribution of *T. stewarti* (= *T. estonica*) in Europe or determine whether it is restricted to the Asian continent.

Most individuals of *T. stewarti* from Nam Co had an inconspicuous anteroventral peg on the left valve. Similarly, the peg was not observed in valves from Lake Ngoring, northeastern Qinghai–Tibet Plateau (Li *et al*. 2021), although it is present in the specimens illustrated by Van der Meeren *et al*. (2009) and Peng *et al*. (2021) from Mongolia and Sichuan. This difference might be an intraspecific morphological variation.

Similar to Peng *et al*. (2021), Li *et al*. (2021) accurately classified the material identified as *T. estonica* within the Qinghai-Tibet Plateau region. Unfortunately, they did not incorporate the information from Daday (1908) and Hartmann (1964). As a result, they were unaware that the same species (including males) had already been described prior to Järvekülg (1960) and later under different names (*Eucypris afghanistanensis*, *E. gyirongensis*, *T. gyirongensis*; Yang 1988; Mischke *et al*. 2006; Wrozyna *et al*. 2009b; Zhu *et al*. 2010; Peng *et al*. 2013; Guo *et al*. 2016; see Table 2). For this reason, we emphasize that it is only possible to ensure a reliable identification down to species level and to avoid taxonomic inconsistencies through the detailed examination of juveniles and adults, including measurements of length and height, the shape of valves and carapaces, and distinctive features such as the presence or absence of teeth and superficial reticulation (internal or external).

Sexual dimorphism and the importance of describing female genitals in *T. stewarti*: Regarding the limbs (A1, A2, T1, T2, T3, and CR), there was little variation among female individuals from Nam Co, Mang-tsa (Daday 1908), Sichuan (Peng *et al*. 2021), Afghanistan (Hartmann 1964), and Mongolia (Van der Meeren *et al*. 2009). However, notable sexual dimorphism is evident, particularly in males displaying a modified T1. Additionally, A2 exhibits modifications in the distal part, with z1 and z2 setae transformed into claw-like structures, and reductions in G1 and G3 (Peng *et al*. 2021). Most importantly, males from the Tibetan Plateau share similar characteristics with males from Afghanistan. Male hemipenis from Mang-tsa, (Tibet) (Daday 1908) and Afghanistan (Hartmann 1964) resemble those described by Peng *et al*. (2021) for the southwestern Tibetan Plateau (refer to Fig. 10A–C). The triangular lateral shield and a sub-triangular median shield with distal rounding indicate the conspecific nature of individuals from both regions as *T. stewarti*.

Compared to hemipenes, female genital lobes are less frequently used for interspecies identification (Cohen & Morin 1990). This could be attributed to the perception that they lack distinct internal features (Broodbakker 1982). In the structure referred to as the intersection, differentiation occurs primarily due to the presence of projections in the female lobes. Moreover, existing descriptions are limited in number and often lack detailed morphological comparation across species, underscoring the significance of their documentation (see Matzke-Karasz *et al*. 2017).

Sexual and asexual populations in the Palearctic region: Based on the comprehensive evidence generated by our investigation and similar studies, the populations from Nam Co identified as *Tonnacypris stewarti*, as well as those encountered in northern and western Mongolia (Van der Meeren *et al*. 2009), are considered as asexual populations because they lack male individuals. This contrast with the sexual populations observed in Afghanistan

(Hartmann 1964) as well as in the Sichuan and Tibet regions (Daday 1908; Peng *et al*. 2021). This distribution of asexual and sexual populations is referred to as geographic parthenogenesis (Tilquin & Kokko 2016; Horne & Martens 1999). This phenomenon has also been noted for species such as *Eucypris virens* (Jurine 1820), *Heterocypris incongruens* (Ramdohr 1808), and *Limnocythere inopinata* (Baird 1843). These records indicate the presence of both asexual and sexual populations distributed in Europe (Butlin *et al*. 1998, Horne & Martens 1999; Schmit *et al*. 2013b). For instance, populations with males were primarily recorded in Mediterranean Europe and North Africa, whereas asexual populations prevail in northern Scandinavia and in other regions worldwide, including North and South America, the Middle East, Asia, Australia, Greenland, and even remote islands like the Canaries, Azores, and Kerguelen (Schmit *et al*. 2013b). This pattern is thought to arise from post-glacial invasions of asexual species into the northern regions (Adolfsson *et al*. 2010; Horne & Martens 1999; Schmit *et al*. 2013b). It is even possible to find both reproduction strategies in one waterbody caused by spatial and environmental segregation, as in the temporary Lake Caracuel, Spain, where the parthenogenetic population of *E. virens* mainly inhabits the littoral zone, while the sexual population lives in the central area (Schmit *et al*. 2013a). Specifically, the sexual populations of *E. virens* were found to thrive in temporary pools characterized by unpredictable hydroperiods, while the asexual populations displayed a preference for more stable conditions without desiccation.

However, the driving factors behind the variation in reproduction type differ from region to region and remain unresolved (Meisch 2000; Schön *et al*. 2000). A possible explanation is that environmental conditions could influence reproductive strategies, with unstable or highly fluctuating environments promoting sexual reproduction (Schwalb 2003). In contrast, stable environments display asexual or parthenogenetic species, which reproduce more rapidly (Boomer *et al*. 2003; Fernandes Martins *et al*. 2008).

For instance, during the glacial periods of the late Pleistocene and the early Holocene in Europe, fluctuating temperatures (colder winters and warmer summers) likely allowed the persistence of sexually reproducing populations. Alternatively, the post-glacial invasion hypothesis proposes that parthenogenetic species were the first to colonize new, more stable environments in northern Europe (Horne & Martens 1999; Boomer *et al*. 2003; Külköylüoğlu *et al*. 2012; Schmit *et al*. 2013b). This highlights the role of temperature and hydro-chemical conditions in shaping and sustaining reproductive strategies, which can determine the establishment of sexual or asexual populations, irrespective of geographical separation or isolation (Horne & Martens 1999).

Nonetheless, in the case of *T. stewarti* from Nam Co, the possibility of encountering sexual populations cannot be ruled out, especially considering the identification of males by Daday (1908) and Peng *et al*. (2021) in regions adjacent to Nam Co. Hence, for a deeper understanding, future research should focus on extensive sampling across diverse aquatic habitats in the lake and surrounding areas, covering different seasons.

Valve ontogeny: In general, species within the family Cyprididae molt eight times before reaching adulthood during their life cycle (Meisch 2000; Smith & Martens 2000). The valve ontogeny of *T. stewarti* consists of eight juvenile stages and one sexually mature adult, according to Roessler (1983) and Baltanás *et al*. (2000). In this study, we present the first recorded ontogeny of *T. stewarti* valves, spanning from stage A-7 to adults, using valve material extracted from surface sediment samples of Nam Co. The valves of the first-stage juvenile (A-8) were notably absent in the analyzed sediment samples, likely due to their poor preservation. This observation confirms previous work by Boomer *et al*. (2003) highlighting the need for cultures in the laboratory, an accurate approach that allows all development stages, complete life cycles, and reproductive strategies to be acquired (Turpen & Angell 1971; Danielopol *et al*. 2002; Wang *et al*. 2021). Depending on the species and environmental conditions such as temperature, water salinity, and food availability, successful recording of the life cycle is possible. Therefore, such experiments are necessary for a more comprehensive understanding of ostracod biology on the Tibetan Plateau, particular in Nam Co.

The growth ratio pertains to the correlation between the average length and height of an instar in comparison to the previous growth stage (Brooks 1886; Watabe & Kaesler 2004). The mean growth ratio values for both right and left valves of juvenile and adult *T. stewarti* (RV = 1.224; LV = 1.230) align remarkably well with Brooks' rule for crustaceans, implying a growth ratio of 1.260. Our dataset exhibits a stronger adherence to Brooks' rule than the *Limnocythere inopinata* analysis by Wang *et al*. (2021) (with an average growth ratio of 1.180). These values closely resemble those reported for *L. inopinata* in the studies by Zhai *et al*. (2015) (1.224 for Lake Daihai, 1.238 for Lake Dali, 1.219 for Lake Hulun; Lake Dali data reused by Wang *et al*. 2021). Our results provide information for taxonomic identification, facilitating differentiation between species. This methodology has the potential to uncover species-specific growth patterns, particularly for closely related species where distinguishing factors may be subtle (Brooks 1886; Watabe & Kaesler 2004).

There are only a few publications detailing the ontogeny of ostracod species on the Tibetan Plateau. Developmental stages are known for four species: *Tonnacypris stewarti* (last eight stages, this study), *Fabaeformiscandona gyirongensis* (nine stages, Mao *et al*. 2021), *Leucocytherella sinensis* (last four stages, Fürstenberg *et al*. 2015), and *Limnocythere inopinata* (nine stages, Zhai *et al*. 2015 and Wang *et al*. 2021). The latter two species dominate the Tibetan assemblages, with *L. inopinata* exhibiting a widespread distribution throughout the Holarctic region (Wang *et al*. 2021).

In this study, juvenile abundances were higher than those for adults. The results reflect a natural adult-to-juvenile ratio (1:7). However, the dynamic nature of the lake habitat could be a factor leading to incomplete records. Transport and deposition of juvenile valves away from their origin often hinders recordings, potentially indicating post-mortem transportation from rivers to the lake, resulting in a lower proportion of juveniles in samples from rivers and lagoons (Whatley 1988; Boomer *et al*. 2003). Similarly, the transportation of juveniles to deeper areas might influence the adult/juvenile ratio from littoral and sub-littoral areas to deeper zones. Thus, sampling across different sites is essential to establish sound knowledge on species distributions and taphonomic processes in Nam Co. For instance, Zhai *et al*. (2015) observed population structures and distribution patterns of *L. inopinata* in three lakes in northern China, correlating them with hydrodynamic gradients in each lake. Adult and pre-adult stages were preferentially deposited in the littoral zone, while juvenile stages were more abundant in deeper waters (10 m), a phenomenon referred to as "downslope transport". This pattern is driven by hydrodynamics influenced by wind, combined with environmental variables such as food availability, sediment type, and grain size (Zhai *et al*. 2013).

Furthermore, understanding different developmental stages of ostracod species allows their reliable use in paleolimnological inferences (Mao *et al*. 2021). For example, this approach could show the effect of environmental changes on population structure (life cycle period, adult/juvenile ratio, sizes, and growth rates), and valve morphology, as has been observed along salinity alterations (Fürstenberg *et al*. 2015).

Ecological aspects: Our cluster analysis based on results from Nam Co discerns three distinct environments, each with varying physico-chemical characteristics (Fig. 15). Samples from group A, located in deeper areas of the oligohaline and oligotrophic Nam Co, exhibit relatively high salinity and alkalinity, associated with high pH. Oxygen concentrations remain elevated due to the low trophic level of Nam Co. The vast water volume of the lake maintains stable conditions in its deeper waters, clearly distinguishing this habitat from the epilimnion and that of lagoons and rivers.

Group B samples are associated either with the epilimnion of Nam Co or with lagoons characterized by a good water exchange with the lake. Shallow water habitats are prone to stronger fluctuations of temperature and freshwater inflow. More marginal sampling positions of the lake and lagoons show similar effects for salinity. We expect higher productivity and coarser sediments within this group because of the shallow water depth. However, aquatic plants were scarce and present in low abundance in the sampling sites.

The physico-chemical parameters of the lagoons and rivers in group C are highly variable because of the small water volumes affected by seasonal temperatures and changes in inflow. Salinity is lower than in the other habitats. The dry season could even cause rivers and lagoons to run dry. The temporary character of some of the latter water bodies is a problem for aquatic organisms who must recolonize seasonally or need to have special survival strategies in these highly dynamic environments. *Tonnacypris stewarti* seems to be well adapted to these habitats, as shown by its wide distribution and relatively high abundance. The high abundances found in several samples collected from the profundal zone of Nam Co provide novel insights into the favored habitats of *T. stewarti*, which now extend to include oligohaline lake environments, a previously undocumented observation.

Tonnacypris stewarti, as investigated by us, is a potential bioindicator for cold, oligotrophic, and fresh to slightly brackish waters. Many ostracod species in Nam Co have typically been categorized as cold-water species, showing adaptability to different salinities (<5 ‰) (Wrozyna *et al*. 2009a). Our findings reveal that *T. stewarti* inhabits varying depths within Nam Co, ranging from shallow waters (<1.4 m) to depths of even 60 m. Interestingly, this species does not display a clear preference for a specific water depth, but it consistently lives in well-oxygenated waters (dissolved oxygen, 6–7 mg/l). Its presence and abundances have been mostly related to electrical conductivity levels, from low to high (31–160 µS/cm, Peng *et al*. 2021; 295–1222 µS/cm, Van der Meeren *et al*. 2009; and 149–1894 µS/cm, this study). Similarly, Wrozyna *et al*. (2009b), Frenzel *et al*. (2010), and Guo *et al*. (2016) highlight its presence in shallow, freshwater, and slightly brackish waters in the vicinity of macrophytes. Akita *et al.* (2016) noted its adaptability to salinities as high as 8.9 ‰ and a preference for flowing waters, including springs.

In western Mongolia, this species prefers oligotrophic environments, primarily springs, indicating its potential as an indicator of good water quality (Van der Meeren *et al*. 2009). Moreover, this species inhabits shallow waters with sandy substrate, sometimes in the presence of aquatic plants, with water temperatures of between 3.5 and 16.8 °C, pH of 6.9–9.1, electrical conductivity of 41–2670 µS/cm, and altitudes of 905–2571 m a.s.l. (Van der Meeren *et al*. 2009). In Lake Qinghai, *T. stewarti* is abundant in shallow waters and temporary pools with hydrophytes and pH values ranging from 6.1 to 8.3, and salinities of 0.28 g/l to 0.57 g/l, with a maximum value of 11.6 g/l (Li *et al*. 2010). Similarly, in the Himalayan region, *T. stewarti* was observed in sediments characterized by the presence of abundant aquatic plants, cold temperatures, and shallow waters (Kotlia *et al*. 1998; Shukla *et al*. 2002).

Synthesizing recent data and prior research, *T. stewarti* can be classified primarily as a freshwater species (environments with electrical conductivity below 1000 µS/cm). However, it also exhibits adaptability to slightly brackish conditions, typically with an electrical conductivity ranging up to 1000 or 2000 µS/cm. Also, it can be considered as an indicator of oligotrophic, cold, turbulent waters and shows a preference for macrophytes (Yang 1988; Van der Meeren *et al*. 2010; Akita *et al*. 2016). Following the ecological terms used in Meisch (2000), *T. stewarti* can be characterized as preferring freshwater, being oligothermophilic, meso- to polyrheophilic, and titanoeuryplastic.

Geographical distribution: According to our literature revision, *T. stewarti* has a Palearctic distribution (Fig. 16). We harmonized several synonyms of this species that were previously considered distinct, thereby expanding the recognized geographical range of *T. stewarti* (Zhu *et al*. 2010). In this study, *Tonnacypris stewarti* was found in Nam Co, and other habitats such as rivers and small lagoons. In addition, the species lives mainly in the littoral zone on the surface sediments of rivers and springs (Van der Meeren *et al*. 2009). Valves and living organisms have been found in Holocene and modern surface sediments from different Tibetan lakes, including Nam Co (living specimens, Wrozyna *et al*. 2009b; Xie *et al*. 2009; Schütt *et al*. 2010; Zhu *et al*. 2010), Mang-tsa, southern part of Tibetan Plateau (living specimens; Daday 1908), Tangra Yumco (living specimens, Akita *et al*. 2016), Taro Co (Guo *et al*. 2016), Pumoyum Co (Peng *et al*. 2013), Lake Ngoring (Li *et al*. 2021), Lake Donggi Cona (Mischke *et al*. 2010a); Qaidam Basin (Mischke *et al*. 2006); and Lake Qinghai (Li *et al*. 2010). It was also found in Ladakh, Northeastern India (Shukla *et al*. 2002), Lamayuru, Trans-Himalaya (Kotlia *et al*. 1998), and it has been reported in Estonia (Järvekülg 1960), Afghanistan (living specimens; Hartmann 1964), Mongolia (living specimens, Van der Meeren *et al*. 2009), and probably also in Kyrgyzstan, Uzbekistan (Mandelstam & Schneider 1963), as well as in the north-eastern regions of Poland (Sywula 1974). In addition, there is a report from Lake Balkhash (Kazakhstan) based on juvenile ostracods only; in the absence of descriptions of adults, this report should be considered with caution (Mischke *et al*. 2020).

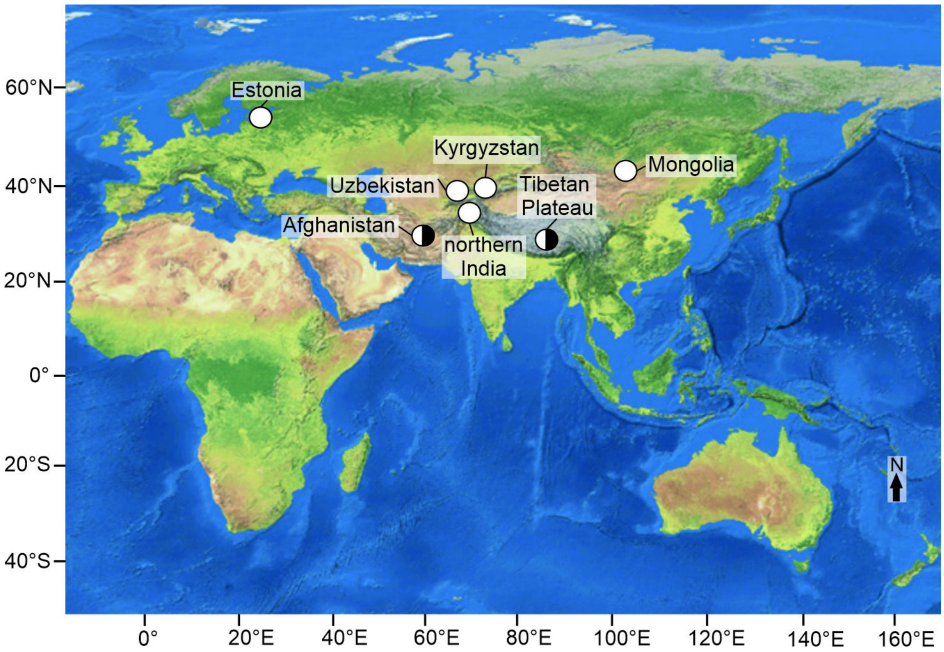

FIGURE 16. Palearctic distribution of *Tonnacypris stewarti*, from Estonia to Mongolia. For references see text about geographical distribution. On the map, the populations are differentiated into asexual (just females; white circle) and sexual (females and males; black and white circle).

Conclusions

Our study clarified the taxonomic status of *T. stewarti* by identifying seven synonyms (*Herpetocypris stewarti*, *Ilyodromus estonicus*, *Eucypris afghanistanensis*, *E. gyirongensis*, *E. rischtanica*, *Tonnacypris gyirongensis*, and *Tonnacypris estonica*). Based on our detailed morphological study, future studies should start using the name *Tonnacypris stewarti* (Daday 1908) instead of *Eucypris afghanistanensis* Hartmann 1964, *Tonnacypris gyirongensis* (Yang 1982) in Huang *et al*. (1982), and *Tonnacypris estonica* (Järvekülg 1960). The potential of considering the anatomy of ostracod female genitals for species identification is proven here, as those of *T. stewarti* from Nam Co, Taro Co, Mang-tsa (Tibetan Plateau) and Afghanistan presented the same shape and structure. We specifically recognized that the structure referred to as the intersection of the female genital lobes is distinguishable. Therefore, we strongly recommend more detailed studies to distinguish between species, especially in parthenogenetic populations. Seven juvenile stages were identified in Nam Co, of which a reticulation pattern was observed to emerge in the valves of juveniles A-7, A-6, and A-5. Our detailed morphological descriptions and SEM photographs of juvenile stages A-7 to A-1 improve the identification of juveniles for future paleoecological studies, as it will be easier and more precisely possible to evaluate the dynamics of the aquatic system concerning the presence of juvenile organisms. The ostracod populations from Nam Co are considered asexual, as are those from western Mongolia. The existence of sexual populations from Mang-tsa, Linzhi (Tibetan Plateau), and Afghanistan suggests that *T. stewarti* is a species with geographical parthenogenesis. However, additional data is required from different latitudes to determine the distribution pattern of both the sexual and asexual populations, more specifically, to establish whether the asexual populations are distributed further north than the sexual ones. This type of distribution pattern was not observed in the records of *T. stewarti* from the Tibetan Plateau.

T. stewarti (Daday 1908) has a wide distribution in the Palearctic region (Estonia, northern India, Afghanistan, Mongolia, and Tibetan Plateau). Likewise, it would be necessary to take samples from lakes in northern Estonia and its surrounding areas, where *T. stewarti* (= *Ilyodromus estonicus* Järvekülg 1960) was recorded 60 years ago, in order to verify its presence in Europe. This species is associated with cold, well-oxygenated, freshwater to oligohaline habitats and prefers the presence of aquatic plants.

Here, we demonstrate how species misidentifications can result from relying solely on valves deposited in sediment cores and surface sediments, and not also using living material with well-preserved soft parts. Additional use of the latter allows synonyms to be avoided, making it possible to study species exchanges and changes of biodiversity over time.

Authorship contribution statement

Mauricio Bonilla: Conceptualization, Formal analysis, Investigation, Data curation, Writing—original draft. **Paula Echeverría-Galindo**: Conceptualization, Methodology, Investigation, Resources, Writing—review & editing. **Peter Frenzel**: Methodology, Supervision, Visualization, Writing—review & editing. **Liseth Pérez**: Conceptualization, Supervision, Visualization, Methodology, Writing—review & editing. **Nicole Börner**: Methodology, Resources, Writing—review & editing. **Katharina Dulias**: Writing—review & editing. **Junbo Wang**: Supervision, Methodology, Writing—review & editing. **Antje Schwalb**: Conceptualization, Funding acquisition, Resources, Writing—review & editing.

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