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Research paper

A striking case of convergent evolution in two species of Cypricercinae (Crustacea, Ostracoda), with the description of a new genus and species from Brazil

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ABSTRACT

Neostrandesia striata gen. n. sp. n. is here described and constitutes an interesting case of convergent evolution with *Bradleytriebella lineata* (Victor and Fernando, 1981). Both cypricercine species look superficially similar, with comparable valve and carapace shapes and especially ornamentation, as in both species the valves are densely set with longitudinal ridges. However, examination of the limb chaetotaxy shows important differences, especially in the chaetotaxy of the maxillula-palp which shows reduced numbers of claws and setae, and in the first thoracopod, in which seta 'b' has taken a giant aspect in the new taxon. These, and other, differences merit the allocation of these two species to different genera and even tribes within the subfamily Cypricercinae.

1. Introduction

There are about 300 species and 62 genera of non-marine ostracods described from the Neotropics (Higuti & Martens in press). Approximately 62% of all species belong to the family Cyprididae (Martens et al. 2008). Within the Cyprididae, the subfamily Cypricercinae presently comprises 11 genera and 171 species worldwide, but mostly occur in the (sub-) tropics (Meisch et al. 2019). The taxonomy of the Cypricercinae has, for a long time, been confused, because there is a wide plasticity in shape, structure and size of the valves, making these structures rather unreliable in taxonomy. McKenzie (1982) pointed out that "Homeomorphy is a persistent joker in the taxonomic pack" and this is certainly true for the Cypricercinae. In such cases, soft part (limb) morphology is generally more conservative than valve morphology (with the exception of structures used during copulation, mostly in males) and most phylogenetic signal can be found in ostracod limbs. Unfortunately, in many of the descriptions of the older ostracod species and genera, also in the Cypricercinae, insufficient attention was given to the description of the chaetotaxy of the limbs.

The confusion in Cypricercine taxonomy was initially caused by the inability to provide good characters to distinguish between the oldest genera *Strandesia* Stuhlmann, 1888 and *Cypricercus* Sars, 1895. The type species of these genera have very different valves (high and rounded, with a helmet like dorsal expansion on the right valve in *Strandesia mercatorum* (Vavra 1895) and elongated without helmet in *Cypricercus cuneatus* Sars, 1895), but almost no structural differences in the soft part chaetotaxy (Savatenalinton & Martens 2009a). In addition, especially in *Strandesia s.l.*, dozens of species have been described that look very different from the type species.

The discovery of the variable Triebel's loop in the attachment of the caudal ramus (Rome 1969) was the first tool for the construction of a taxonomy for the subfamily. It allowed to transfer several genera from other subfamilies to the Cypricercinae and allowed the description of several new tribes and genera within this subfamily.

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Savatenalinton & Martens (2009b, 2010) provided the first revision at the levels of tribes and genera and suggested new characters that could bring taxonomic order in the group.

Convergent evolution in ostracod valves and carapaces is common and is most likely more common than is presently known. It is of course especially a problem in fossil ostracods, as no independent test on other characters (such as soft parts) is available to palaeontologists, except in some cases the geographic distribution and the stratigraphic age. One of the most striking cases of convergence in valve and carapace shape in extant non-marine ostracods is of course that of *Rudjakoviella prolongata* (Triebel 1962) from a Venezuelan Island and *Strandesia bicornuta* Hartmann, 1964 from southern India. In both species, the right valves have long and pointed anterior and posterior spines, but the soft part morphology shows that the two taxa are not at all closely related (see also Broodbakker 1983; Martens & George 1992). Other examples in freshwater ostracods are the dorsal hump on the right valves in both *Cyprinotus* Brady, 1886 and in *Strandesia* Stuhlmann, 1888, and the 'gigantic' valves in *Cypriconcha* Sars, 1926 and some Megalocypridinae.

Here, we provide another striking example of convergent evolution in cypricercine ostracods, namely between the circumtropical *Bradleytriebella lineata* (Victor & Fernando, 1981) and a new genus and species of the same subfamily, all from Brazilian floodplains.

2. Material and methods

2.1. Study area (see Fig. 1 and Table S1)

2.1.1. Araguaia River floodplain

The Araguaia River is located in central Brazil, and runs through four different states: Goiás, Mato Grosso, Pará and Tocantins (Morais et al. 2005). This river is 2.110 km long, is divided in upper, middle and lower Araguaia and has a drainage area of approximately 377,000 km^2. The climate of the tropical savanna ("Cerrado") has two well-distinct seasons, namely rainy season (between November and April) and dry season (May to October). Owing to extensive damages caused by farming activities, such as deforestation and subsequent erosions, the Araguaia River and its floodplain is considered a priority area for the conservation of biodiversity and is the object of political and environmental discussions (Latrubesse & Stevaux 2002; Latrubesse et al. 2009).

2.1.2. Amazon River floodplain

The Amazon River in South America is the second longest and has the largest drainage basin in the world, occupying more than 6.8 million km^2. During the rainy season, the water discharged in the Atlantic Ocean travels approximately 160 km out into the sea. Rainfall is evenly distributed spatially and temporally, ranging from 1500 to 2500 mm annually, for about 6 months a year (Goulding et al. 2003). The Amazon River and its tributaries are accompanied along their middle and lower courses by large fringing floodplains that cover an area of about 300,000 km^2. Every year the river rises more than nine meters, flooding the surrounding forests, known as *várzea* (Irion et al. 1997).

2.1.3. Upper Paraná River floodplain

The Paraná River is the tenth longest river in the world and has a drainage area covering 2.8×10^6 km^2. The first third of this basin is named Upper Paraná River and most of it runs within Brazil. The Upper Paraná River floodplain is located between the Porto Primavera Reservoir and the Itaipu Reservoir and is about 230 km long and 20 km wide. In this area, three conservation units were created: "Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná" (Environmental Protection Area), the "Parque Nacional de Ilha Grande" (National Park), and the "Parque Estadual do Ivinheima" (State Park). The floodplain, apart from the main channel of the Paraná River, also includes parts of the Ivinhema and Baía rivers (Agostinho et al. 2004).

2.2. Sampling

Sampling was done in November 2011 and March 2012 in the Araguaia River floodplain; in May 2012 in the Amazon floodplain and between 2004 and 2018 in the Upper Paraná River floodplain (Fig. 1). Ostracods were collected from the sediment-water interface (littoral) and from aquatic vegetation: *Azolla* sp., *Cabomba furcata* Schult. & Schult, *Eichhornia azurea* Kunth, *Eichhornia crassipes* (Mart.) Solms, *Egeria najas* Planch, *Limnobium* sp.; *Paspalum notatum* Flügge, *Pistia stratiotes* L., *Polygonum* sp., *Salvinia auriculata* Aubl, *Salvinia minima* Baker and *Utricularia foliosa* L (see Table S1). Littoral sampling was performed using a rectangular hand net (28 cm × 14 cm, mesh size ~160 μm). The floating and submerged vegetation was hand-collected, and the whole plants and/or roots were washed in a bucket (Campos et al. 2017). The material from the bucket was filtered in the net (mesh size 160 μm). All material was preserved in 70% ethanol, which was buffered with sodium tetraborate. Limnological variables, such as pH (pHmeter-Digimed), electrical conductivity (conductivimeter-Digimed), water temperature, and dissolved oxygen concentration (DO) were measured *in situ*, close to the aquatic macrophytes.

2.3. Preparation and illustration of soft parts and valves

Ostracods were dissected using a stereomicroscope Olympus SZX16. Soft parts were separated from the valves using dissection needles; valves were stored dry in micropaleontological slides. Soft parts were put in a drop of glycerine for the dissection of the appendages and were covered with a cover-slip. The dissection was sealed using nail polish. Drawings were made using a camera lucida (Olympus U-DA) attached to the microscope (Olympus CX-41). Carapace and valves were illustrated and measured in different views (valves: internal, external, carapaces: ventral, dorsal, frontal) using Scanning Electron Microscopy (SEM) (Brussels lab, Philips XL30). The types and illustrated specimens are stored in the Museum of Zoology of the University of São Paulo (MZUSP) and the Royal Belgian Institute of Natural Sciences (IG - RBINS).

The chaetotaxy of the limbs follows the models proposed by Broodbakker & Danielopol 1982; Martens 1989 for the antenna and Meisch 2000 for the second and third thoracopod.

2.4. Size classes of several soft part features used in the text and in Table 2

Y-aesthetasc: short = distance between tip of Y and tip of segment is about length of Y; normal = distance between tip of Y and tip of segment is less than length of Y; Long = tip of Y reaching beyond tip of segment.

First thoracopod b-seta: long = average length about that of apical setae; giant = length >3 × average length of apical setae.

Caudal ramus: slender = Type E; stout = Type A - C (see Savatenalinton & Martens 2009b Fig. 2).

3. Results

Class OSTRACODA Latreille, 1806
Subclass PODOCOPA G. W. Müller, 1894
Order PODOCOPIDA Sars, 1866
Suborder CYPRIDOCOPINA Baird, 1845

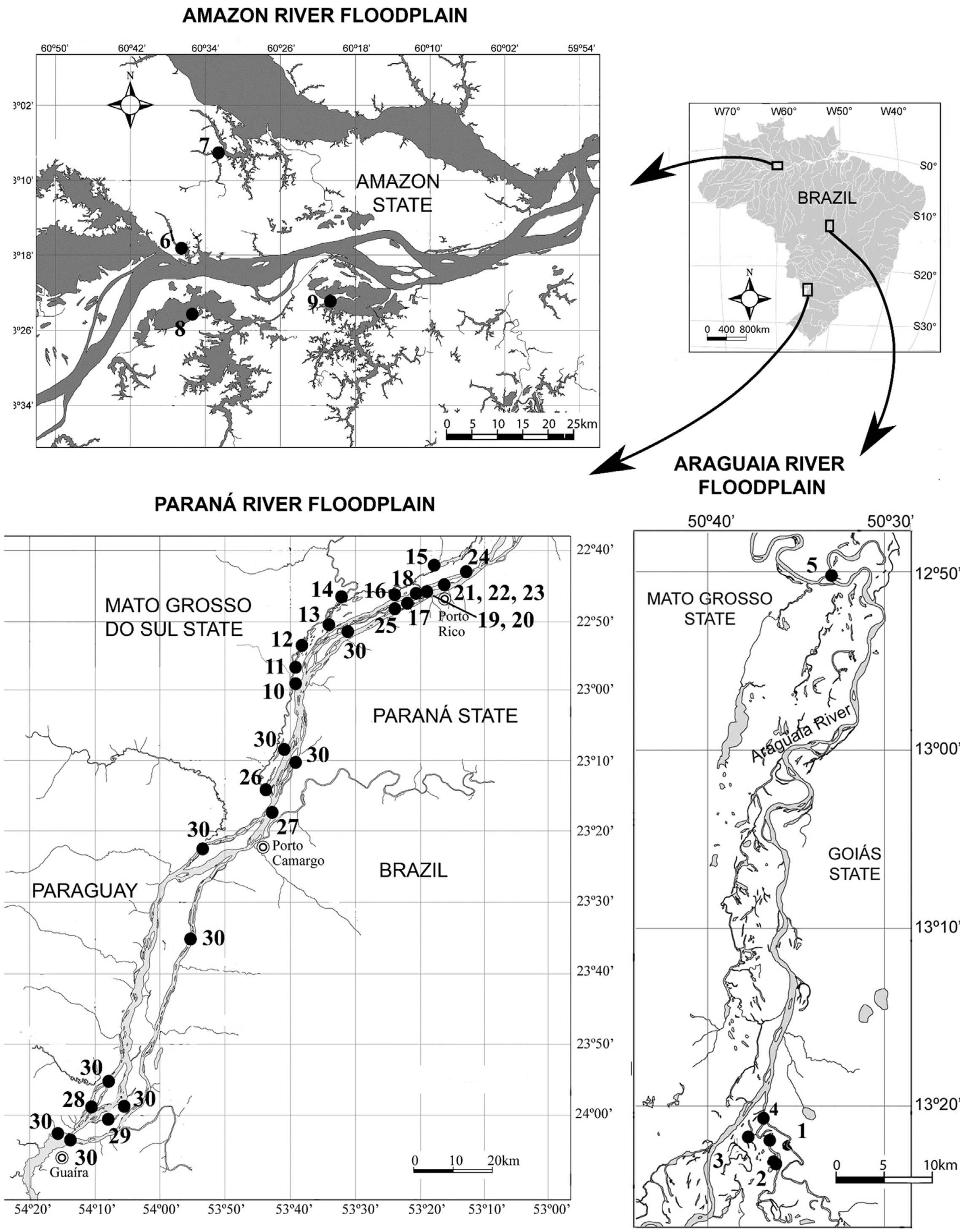

Fig. 1. Localities where *Neostrandesia striata* gen. n. sp. n. and *Bradleytriebella lineata* were recorded in the Araguaia, Amazon and Paraná rivers floodplains. See Table S1 for locality descriptions.

Superfamily CYPRIDOIDEA Baird, 1845
Family CYPRIDIDAE Baird, 1845
Subfamily CYPRICERCINAE McKenzie, 1971
Tribe Cypricercini McKenzie, 1971

3.1. Genus **Neostrandesia** gen. n.

3.1.1. Type species

Neostrandesia striata gen. n. sp. n. (here designated).

3.1.2. Etymology

Neostrandesia is closely related to *Strandesia s.s.* (for example in the same position of the Triebel's loop in the attachment of the caudal ramus), hence we combine 'Neo' (new) with the root 'Strandesia'.

3.1.3. Diagnosis

Right valve with an anterior inwardly displaced selvage. Antenna with aesthetasc Y of normal length, i.e. not reaching beyond

Table 1
Measurements (in μm) of specimens of *Neostrandesia striata* gen. n. sp. n. in the Araguaia and Amazon rivers floodplains, and *Bradleytriebella lineata* in the Upper Paraná River floodplain. Abbreviations used in the table: Left valve inner view (LVi), right valve inner view (RVi), carapace right lateral view (CpRl), carapace dorsal view (CpD), carapace ventral view (CpV).

Species	Sex	Code	Valve	L (μm)	H (μm)	W (μm)
Neostrandesia striata gen. n. sp. n.	Female	MZUSP 39641	LVi	696	420	
	Female	MZUSP 39641	RVi	679	410	
	Female	MZUSP 39642	CpRl	683	414	
	Female	IG 34035	CpD	693		435
	Female	Specimen lost	CpV	675		432
Bradleytriebella lineata (Victor & Fernando 1981)	Female	MZUSP 39646	LVi	640	389	
	Female	MZUSP 39646	RVi	626	387	
	Female	MZUSP 39647	CpRl	640	385	
	Female	IG 34036	CpD	636		396
	Female	MZUSP 39648	CpV	629		396

Table 2
Comparative table among the character of genera from subfamily Cypricercinae, according to Furtos (1936), Würdig & Pinto (1990), George & Martens (1993a, b), Meisch (2000), Savatenalinton & Martens (2009b), and several new observations. Abbreviations used in the table: right valve (RV), antenna (A2), caudal ramus (CR), maxillula (Mx1), first thoracopod (T1).

Genera/Character	RV anterior selvage	A2 aesthetasc Y	Mx1 side-ways bristles	Mx1, first palp segment, setae	Mx1 2nd palp segment setae	T1, d-seta	T1, b-seta	CR	Triebel's loop
Bradleystrandesiini									
Bradleystrandesia	Present	Short	2	6 + 1	3 claws, 3 setae	Present	Long	Slender	Dorsal branch
Bradleytriebella	Absent	Normal	1	6 + 1	3 claws, 3 setae	Absent	Long	Slender	Dorsal branch
Spirocypris	Present	Short	2	6 + 1	3 claws, 3 setae	Present	Long	Slender	Dorsal branch
Cypricercini									
Bradleycypris	Present	Normal	1	6 + 1	3 claws, 3 setae	Present	Long/Abs	Slender	Main branch
Cypricercus	Present	Short	2	6 + 1	3 claws, 3 setae	Present	Long	Slender	Main branch
Pseudostrandesia	Absent	Normal	2	6 + 1	3 claws, 3 setae	Absent	Long	Slender	Main branch
Strandesia	Present	Short	2	6 + 1	3 claws, 3 setae	Present	Long	Slender	Main branch
***Neostrandesia* gen.n.**	**Present**	**Normal**	**2**	**4 + 1**	**1 claw, 3 setae**	**Present**	**Giant**	**Stout**	**Main branch**
Nealecypridini									
Astenocypris	Absent	Short	0	6 + 1	2 claws, 3 setae	Absent	Absent	Stout	Main branch
Diaphanocypris	Absent	Normal	2	5 + 1	2 claws, 3 setae	Absent	Absent	Stout	Main branch
Nealecypris	Absent	Normal	2	6 + 1	3 claws, 3 setae	Absent	Long	Stout	Main branch
Tanycypris	Absent	Normal	2	6 + 1	3 claws, 3 setae	Present	Long	Stout	Main branch

tip of segment. Maxillula first endite with 2 side-ways directed bristles. First segment of maxillula-palp with 4 + 1 setae; second segment of maxillula-palp distally with 1 claw and 3 setae. First thoracopod with long (gigantic) and stout b-seta; d-seta present. Attachment of caudal ramus slender; Triebel's loop situated in the main branch.

Remark: as this genus is thus far monospecific, it is difficult to judge which characters are diagnostic at the generic level and which at the specific level. It would be tempting to cite the external valves ornamentation in the generic diagnosis, but as this is a convergent character with another species in another genus, we refrain from doing so. Future findings of other species in *Neostrandesia* gen. n. will allow to amend the diagnosis.

3.1.4. *Differential diagnosis*

The characters by which the 12 genera in the Cypricercinae can be distinguished are listed in Table 2.

The genus is monospecific.

3.2. ***Neostrandesia striata*** *gen. n. sp. n.*

Figs. 2–4.

Bradleytriebella cf. *lineata* n. sp. in Pereira et al., 2017: 327, Table 2.

3.2.1. *Diagnosis*

Carapace subovate, with clear striations on the external surface; left valve anteriorly overlapping right valve. Left valve with internal marginal groove along the anterior, ventral and posterior margin. Right valve with marginally inwardly displaced selvage, anterior valve margin crenulate because of ending striations. Antenna with natatory setae not reaching beyond tips of apical claws. Second thoracopod with seta d1 almost twice as long as d2. Caudal ramus stout, its attachment with an oval Triebel's loop in the main branch.

3.2.2. *Type locality*

Araguaia River floodplain, Lake Crixas IV in *U. foliosa*. Coordinates: 13°20′ 3.4″S, 050°36′37.7″, Brazil.

3.2.3. *Type material*

Holotype: A female, with soft parts dissected in glycerine in a sealed slide and with valves stored dry in a micropaleontological slide (MZUSP 39637).

Paratypes: Four females dissected and stored as the holotype (MZUSP 39638, MZUSP 39639, IG 34034, MZUSP 39640). Three females stored dry in micropaleontological slides (MZUSP 39641, MZUSP 39642, IG 34035).

3.2.4. *Other material investigated*

A female stored dry in micropaleontological slide (MZUSP 39644) from Crixas III Lake (ARA52) of Araguaia floodplain. A female dissected with soft parts in glycerine in a sealed slide and with valves stored dry in a micropaleontological slide (MZUSP 39643) from Jutai Lake (AMA76) of Amazon floodplain. See Table S1 for further details.

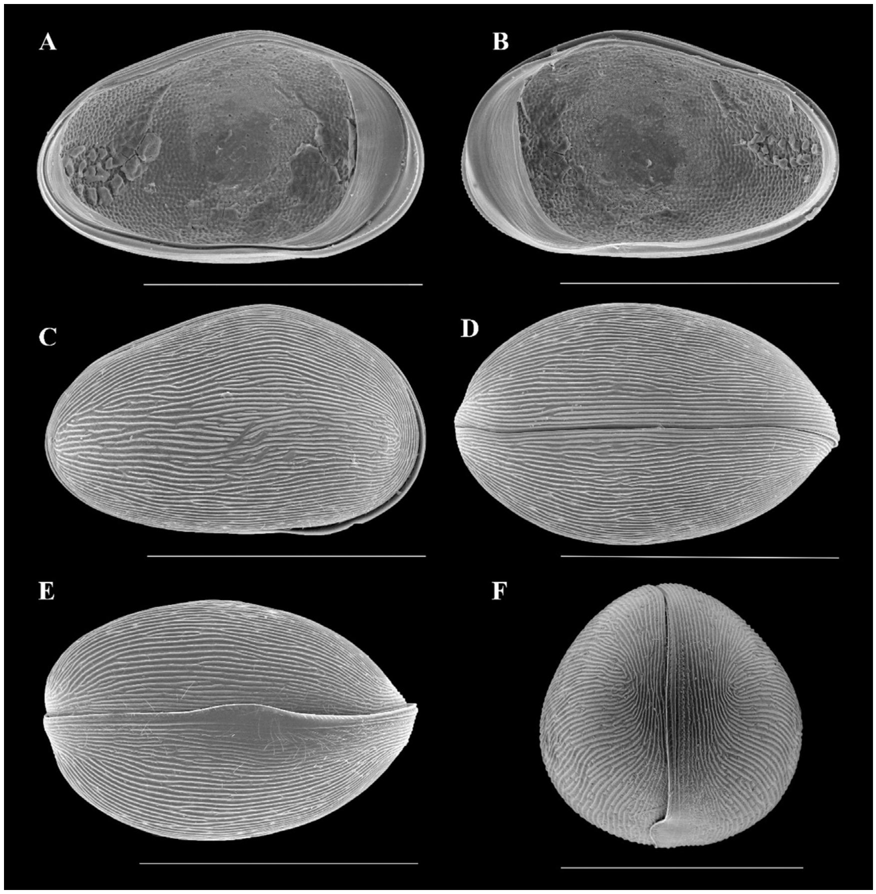

Fig. 2. Carapace and valves of *Neostrandesia striata* gen. n. sp. n. (A) Left valve inner view (MZUSP 39641); (B) Right valve inner view (MZUSP 39641); (C) Carapace right lateral view (MZUSP 39642); (D) Carapace dorsal view (IG 34035); (E) Carapace ventral view (Specimen lost); (F) Carapace frontal view (IG 34035).

3.2.5. Other localities

See Table S1 for further details.

3.2.6. Etymology

The species is named after the most striking characteristic, namely the external valve ornamentation which consist of longitudinal ridges from the anterior to the posterior part of the valves.

3.2.7. Differential diagnosis

N. striata gen. n. sp. n. can be distinguished from other species in the subfamily amongst other characters by a combination of the striation on the external surface of the carapace and the presence of a gigantic b-seta (c. twice the length of d-seta) on the first thoracopod. It has a similar appearance to *B. lineata*, yet the two species are distantly related, with the morphological similarity resulting from convergent evolution (see discussion).

3.2.8. Description of female

Left valve in inner view (Fig. 2A) with calcified inner lamella wide along anterior margin, narrower along posterior margin, and absent along ventral margin; with characteristic "*Strandesia*" inner groove present along the anterior, ventral and posterior margins. Right valve in inner view (Fig. 2B) with calcified inner lamella as in left valve, anterior selvage very slightly inwardly displaced, posterior and postero-ventral selvage more widely inwardly displaced; anterior valve margin crenulate owing to ending striations, posterior selvage partly crenulate. Greatest height in both valves situated well in front of the middle.

Carapace in left lateral view (Fig. 2C) sub-ovate, with striations on the surface from posterior to anterior margin. Carapace in dorsal view (Fig. 2D), sub-ovate, with striations; left valve overlapping right valve anteriorly and posteriorly, at the former edge asymmetrically so. Carapace in ventral view (Fig. 2E) with striations; left valve overlapping right valve with a flap slightly anteriorly to the middle. Carapace in frontal view (Fig. 2F), with striations; valves almost symmetrical.

Antennula as typical of the subfamily (not illustrated).

Antenna (Fig. 3A, B) with 5 segments, first two forming the protopodite, and distal three segments forming the endopodite. First segment (PrI) with 2 ventral setae (1 longer; 1 shorter, with the latter about 3/4 of the length of the longer seta). Second segment (PrII) with 1 long distal seta. Exopodite reduced to a small plate, with 1 long and 2 unequal short setae. First endopodal (EnI) segment with 1 ventral aesthetasc Y, 1 long apical seta (reaching the last segment) one group of 5 long and 1 short swimming setae (the 5 long setae not reaching beyond the tips of the apical claws; the shortest reaching the middle of third segment). Second endopodal (EnII) segment undivided, with 2 unequal but long dorsal setae and a group of 4 unequal long ventral setae (the longer one reaching the middle of G2); apically with 3 claws (G1, G2 and G3) and 3 setae (z1, z2 and z3). Terminal segment (Fig. 3B) (EnIII) with 2 claws (GM and Gm), an aesthetasc y3 with an accompanying seta, fused over a short distance, and a short g-seta.

Mandibula as typical of the subfamily (not illustrated).

Maxillula (Fig. 3C - chaetotaxy not complete) consisting of 3 masticatory lobes (Endites), a 2-segmented palp and a large respiratory plate (the latter not illustrated). Basal segment of palp with

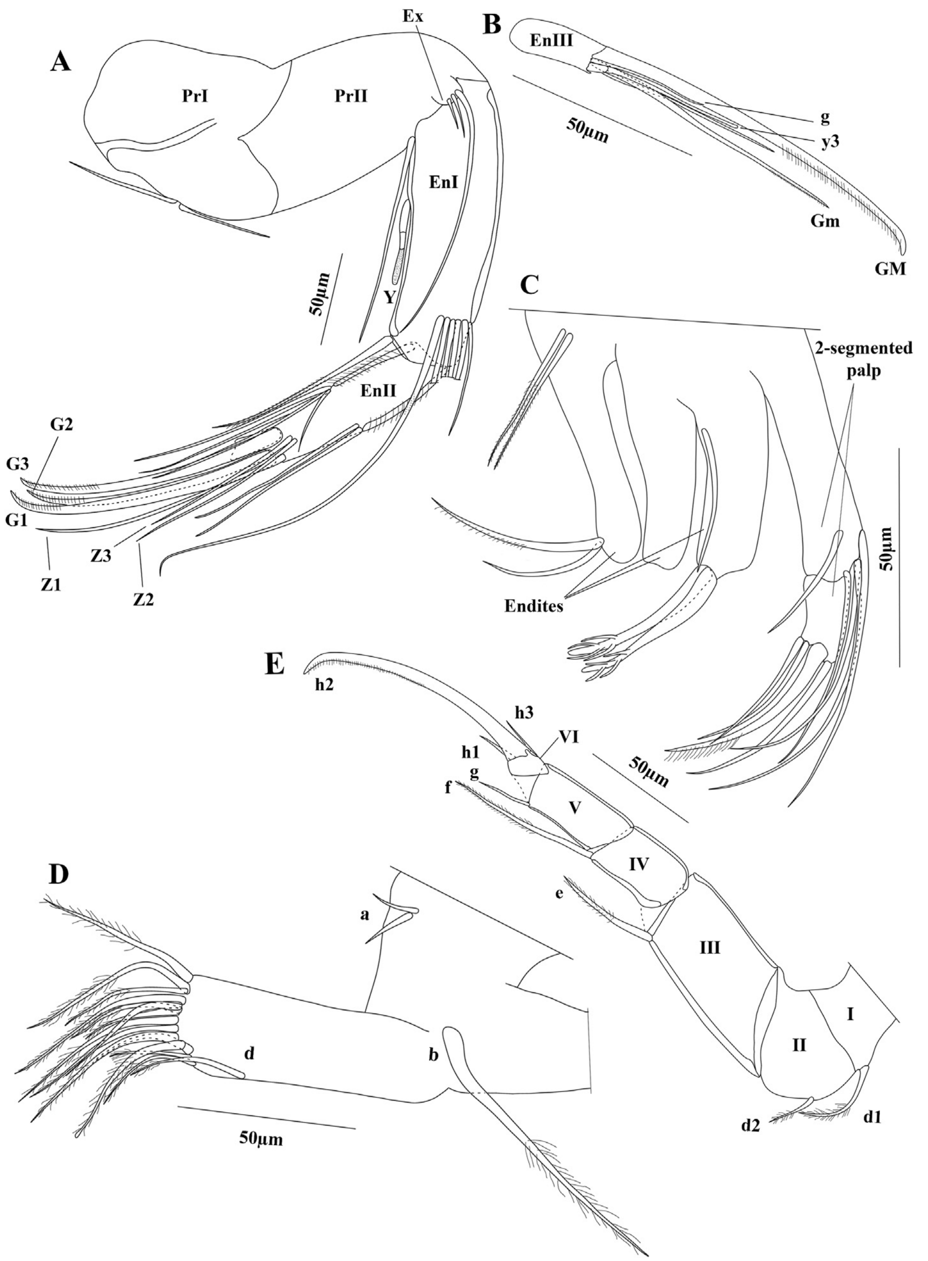

Fig. 3. Limbs of *Neostrandesia striata* gen. n. sp. n. (A) Antenna without last segment: Protopodite (PrI); Protopodite II (PrII); Endopodite I (EnI); Endopodite II (EnII); Exopodite (Ex) (MZUSP 39639); (B) Antenna last segment: Endopodite III (EnIII) (MZUSP 39639); (C) Maxillula (MZUSP 39637); (D) First thoracopod (IG 34034); (E) Second thoracopod: First segment (I); Second segment (II); Third segment (III); Fourth segment (IV); Fifth segment (V); Sixth segment (VI) (MZUSP 39638).

4 unequal long apical setae, and 1 short subapical seta. Terminal palp-segment with 1 claw and 3 setae. Third endite with 2 large bristles serrated, tips of teeth rounded and with long subapical seta. Two sideways-directed bristles on first endite, the shorter ca. 2/3 of the length of the longer one, both weakly hirsute.

First thoracopod protopodite (Fig. 3D) with 2 short a-setae, 1 stout and hirsute b-seta (ca. 2× the length of d-seta) and 1 long d-seta. Apically with 10 hirsute setae, subapically with a group of 4 hirsute setae. Endopodite with 3 unequal long hirsute setae (not illustrated here).

Second thoracopod (Fig. 3E) with 5 segments. First segment (I) with seta d1 long. Second segment (II) with seta d2 shorter, ca. half of the length of d1. Third segment (III) with 1 subapical hirsute seta (e). Fourth segment (IV) with 1 long apical hirsute seta (f). Fifth segment (V) with 1 short seta (g) reaching the end of the sixth segment. Sixth segment (VI) with 1 apical claw (h2) and 2 setae (1 subapical (h1) and 1 apical).

Third thoracopod (Fig. 4A-chaetotaxy not complete) with 3 segments. First segment with 3 long setae (d1, d2, dp) (not illustrated here). Second segment, longer than wide, with 1 subapical seta (e). Second segment longer than wide, with 1 subapical seta (f). Third segment, also longer than wide, with 1 lateral, hirsute seta (g); distal part of the third segment fused with 4th segment into a modified pincer, with 1 apical comb-like seta (h2), 1 small recurved seta, 1/5 of the length of the comb like seta and one longer and distally hirsute seta (h3). Small tooth-like structures present at the basis of the comb-like seta.

Caudal ramus (Fig. 4B) slender and curved, with ventral margin weakly serrated. Proximal and distal claws also weakly serrated. Proximal claw (pc) 2/3 of the length of distal claw (dc). Proximal seta (ps) 1/4 of the length of distal seta (ds).

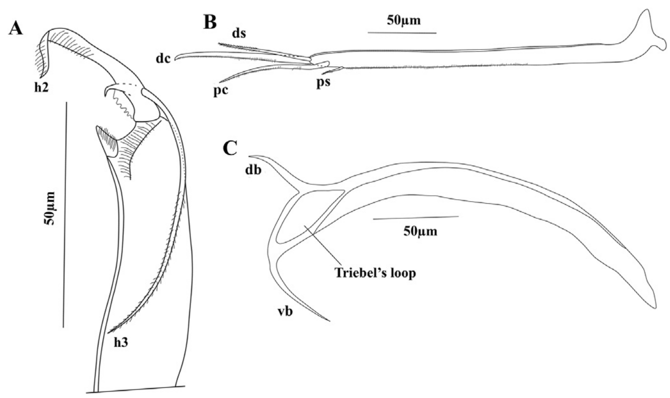

Fig. 4. Limbs of *Neostrandesia striata* gen. n. sp. n. (A) Third thoracopod pincer (MZUSP 39637); (B) Caudal ramus: Proximal claw (pc); Distal claws (dc); Proximal seta (ps); Distal seta (ds) (MZUSP 39637); (C) Caudal ramus attachment: Ventral branch (vb); Dorsal branch (db); Triebel's loop (MZUSP 39639).

Caudal ramus attachment (Fig. 4C) stout, with oval Triebel's loop in the main branch. Both ventral (vb) and dorsal branches (db) well-developed.

Male unknown.

3.2.9. Measurements

See Table 1.

3.2.10. Ecology and distribution

N. striata gen. n. sp. n. was recorded in association with several species of macrophytes in Araguaia River and Amazon floodplains. The range of water temperature recorded in these lakes was 27.6–32.1 °C, whereas the pH range was 6.5–6.8, i.e. slightly acid. Electrical conductivity and dissolved oxygen ranges were 39.1–69.7 $\mu S\ cm^{-1}$ and 1.05–4.01 mg. L^{-1}, respectively (see Table S1).

3.3. *Genus Bradleytriebella* Savatenalinton & Martens, 2009b

3.3.1. Type species

Bradleytriebella tuberculata (Hartmann 1964).

3.3.2. Other species

Bradleytriebella trispinosa (Pinto & Purper 1965); *B. lineata* (Victor & Fernando, 1981).

3.3.3. Diagnosis

See Savatenalinton & Martens (2009b).

3.4. ***Bradleytriebella lineata*** (Victor & Fernando, 1981)

Figs. 5–7.

Strandesia lineata in Victor & Fernando, 1981: 487, fig. 91–102.

Paracypretta amati in Martens, 1984: 154, fig. 54–68.

Strandesia biwaensis in Okubo, 2004: 36, Fig. 18.

Bradleystrandesia gr. *amati* n.sp. in Higuti et al., 2007:1934, Table 2.

Bradleystrandesia gr. *amati* n.sp. in Higuti et al., 2009:664, Table 1.

Bradleystrandesia gr. *amati* n.sp. in Higuti et al., 2010: 267, Table 2.

B. lineata in Savatenalinton & Martens, 2010: 70, Fig. 46.

3.4.1. Diagnosis

Carapace in lateral view subtriangular, with striations and setae on the external surface; greatest height situated well in front of the middle; left valve anteriorly and ventrally overlapping right valve; anterior and posterior margin rounded. Left valve with internal groove. Antenna with a long aesthetasc Y, reaching beyond tip of segment. First thoracopod with b and a -setae. Second thoracopod with seta d1 narrow and twice as long as d2. Caudal ramus slender, its attachment with Triebel's loop in the dorsal branch.

3.4.2. Type locality and material

Recorded in Mindanao, Philippines by Victor & Fernando, 1981 in roadside ditches, ponds, a lake and a washing pool.

3.4.3. Material examined

Three females dissected with soft parts in glycerine in a sealed slides and valves stored dry in micropaleontological slides (MZUSP 39646, IG 34037 and MZUSP 39645). Three females with carapace stored dry in micropaleontological slides (MZUSP 39647, IG 34036, MZUSP 39648).

3.4.4. Differential diagnosis

Bradletriebella lineata can be distinguished from other species from this genus by the striation on the external surface of the carapace. Although it has a similar appearance to *N. striata* gen. n. sp. n. the former one has a weak striation and a long aesthethasc Y on the antenna. Such morphological similarities result from convergent evolution (see discussion).

3.4.5. Redescription of female

Left valve in inner view (Fig. 5A) with calcified inner lamella wide along anterior margin, narrower along posterior margin, and absent along ventral margin; with inner groove present along the anterior, ventral and posterior margins. Right valve in inner view (Fig. 5B) with calcified inner lamella as in left valve. Greatest height in both valves situated well in front of the middle.

Carapace in left lateral view (Fig. 5C) subtriangular, with striations and setae on the surface; left valve overlapping right valve anteriorly and ventrally. Carapace in dorsal view (Fig. 5D), subovate, with striations; left valve overlapping right valve anteriorly. Carapace in ventral view (Fig. 5E) with striations; left valve overlapping right valve with a flap slightly anteriorly to the middle.

Antennula as typical of the subfamily (not illustrated).

Antenna (Fig. 6A-B) with 5 segments, first two forming the protopodite, and distal three segments forming the endopodite. First segment (PrI) with 2 ventral setae (1 longer; 1 shorter, with the latter about 3/4 of the length of the longer seta). Second segment (PrII) with 1 long distal seta. Exopodite (Ex) reduced to a small plate, with 1 long and 2 unequal short setae. First endopodal (EnI) segment with 1 long ventral aesthetasc Y, 1 long apical seta and one group of 5 long and 1 short swimming setae (the 5 long setae not reaching beyond the tips of the apical claws; the shortest reaching the middle of third segment). Second endopodal (EnII) segment undivided, with 2 unequal but long dorsal setae and a group of 4 unequal long ventral setae (the longer one almost reaching the tip of G3); apically with 3 claws (G1, G2 and G3) and 3 setae (z1, z2 and z3). Terminal segment (Fig. 6B) (EnIII) with 2 claws (GM and Gm), an aesthetasc y3 with an accompanying seta, fused over a short distance, and a short g-seta.

Mandibula as typical of the subfamily (not illustrated).

Maxillula (Fig. 6C - chaetotaxy not complete) consisting of 3 masticatory lobes (Endites), a 2-segmented palp and a large respiratory plate (the latter not illustrated). Basal segment of palp with 4 unequal long apical setae, and 1 short subapical seta. Terminal palp-segment with 3 claws and 3 setae. Third endite with 2 large

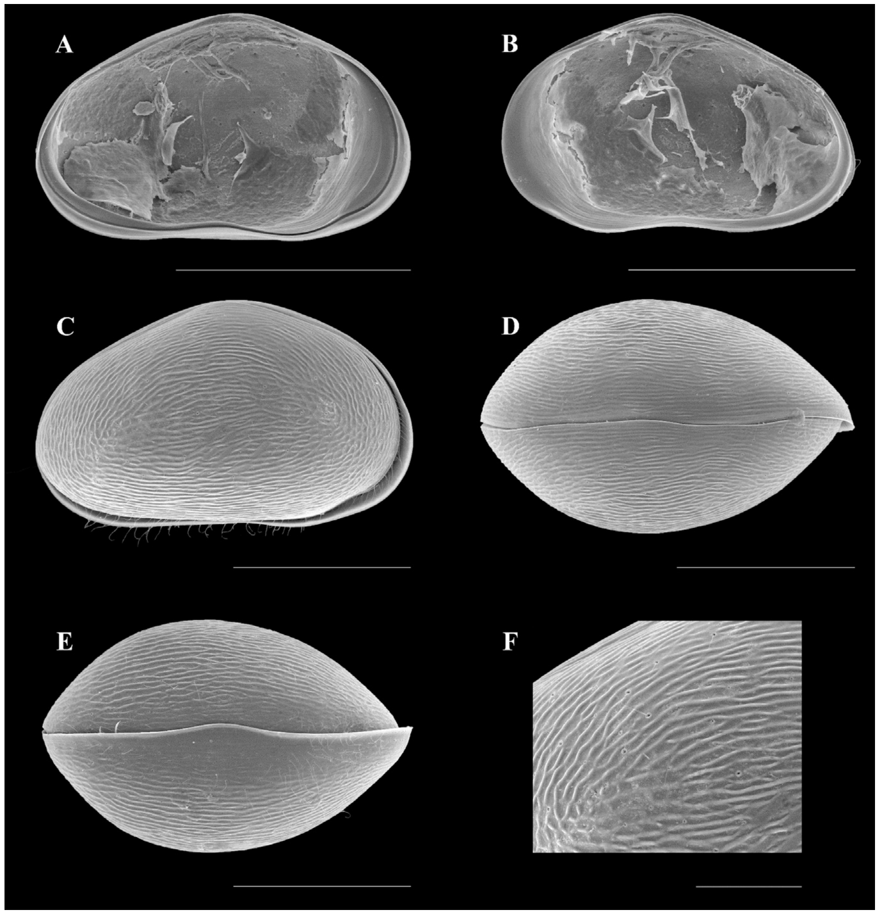

Fig. 5. Carapace and valves of *Bradleytriebella lineata*. (A) Left valve inner view (MZUSP 39646); (B) Right valve inner view (MZUSP 39646); (C) Carapace right lateral view (MZUSP 39647); (D) Carapace dorsal view (IG 34036); (E) Carapace ventral view (MZUSP 39648); (F) Carapace right lateral view, detail of the carapace surface (MZUSP 39647).

bristles serrated, tips of teeth rounded and with long subapical seta. One sideway-directed bristles on first endite, the shorter ca. 2/3 of the length of the longer one, both weakly hirsute.

First thoracopod protopodite (Fig. 6D) with 2 short a-setae, 1 b-seta. Apically with 10 hirsute setae, subapically with a group of 4 hirsute setae. Endopodite with 3 unequal long hirsute setae (not illustrated here).

Second thoracopod (Fig. 6E) with 5 segments. First segment (I) with seta d1 long and narrow. Second segment (II) with seta d2 shorter, ca. half of the length of d1. Third segment (III) with 1 subapical hirsute seta (e). Fourth segment (IV) with 1 long apical hirsute seta (f). Fifth segment (V) with 1 short seta (g) reaching the end of the sixth segment. Sixth segment (VI) with 1 apical claw (h2) and 2 setae (1 subapical (h1) and 1 apical).

Third thoracopod (Fig. 7A-chaetotaxy not complete) with 3 segments. First segment with 3 long setae (d1, d2, dp) (not illustrated here). Second segment, longer than wide, with 1 subapical seta (e). Second segment longer than wide, with 1 subapical seta (f). Third segment, also longer than wide, with 1 lateral, hirsute seta (g); distal part of the third segment fused with 4th segment into a modified pincer, with 1 apical comb-like seta (h2), 1 small recurved seta, 1/5 of the length of the comb like seta and one longer and distally hirsute seta (h3). Small tooth-like structures present at the basis of the comb-like seta.

Caudal ramus (Fig. 7B) slender and curved, with ventral margin weakly serrated. Proximal (pc) and distal claws (dc) also weakly serrated. Proximal claw 2/3 of the length of distal claw. Proximal seta (ps) 1/4 of the length of distal seta (ds).

Caudal ramus attachment (Fig. 7C) slender, with oval Triebel's loop in the middle of dorsal branch (db). Ventral branch (vb) long with swollen end.

Male unknown.

3.4.6. Measurements

See Table 1.

3.4.7. Ecology and distribution

B. lineata was recorded associated with several species of macrophytes and in the sediment (littoral) in the upper Paraná River floodplain (22°20′- 24°10′S and 53°00′-54°20′W). This species was widely distributed across 21 different environments such as rivers, channels, lakes and backwater. It has a high environmental plasticity as it was recorded in Brazilian floodplains with a temperature range of 15.3–35.1 °C, whereas the electrical conductivity range was 16.3–73.7 $\mu S\ cm^{-1}$, pH between 3.1 and 10.2 and the dissolved oxygen range was 0.8–15.1 mg. L^{-1} (see Table S1).

4. Discussion

With the present descriptions of *N. striata* gen. n. sp. n. the number of Brazilian *Cypricercinae* species increased to 18, and worldwide to 172 species in 12 genera. However, for several of these species either their generic assignment or even their status as valid species remains uncertain. This is especially true for the Brazilian species described by Tressler (1950); their taxonomic

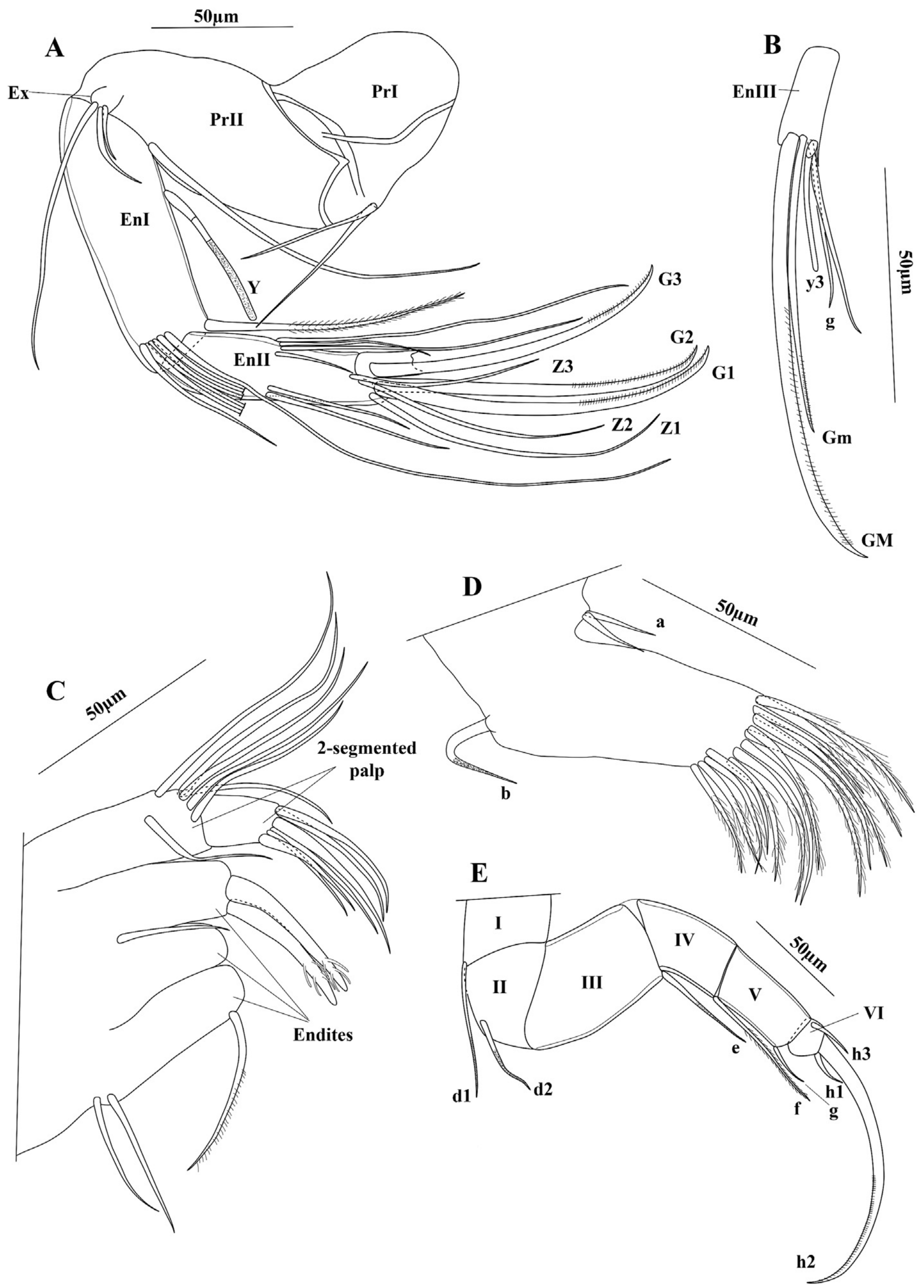

Fig. 6. Limbs of *Bradleytriebella lineata*. (A) Antenna without last segment: Propodite (PrI); Protopodite II (PrII); Endopodite I (EnI); Endopodite II (EnII); Exopodite (Ex) (MZUSP 39645); (B) Antenna last segment: Endopodite III (EnIII) (MZUSP 39645); (C) Maxillula (MZUSP 39646); (D) First thoracopod (MZUSP 39646); (E) Second thoracopod: First segment (I); Second segment (II); Third segment (III); Fourth segment (IV); Fifth segment (V); Sixth segment (VI) (MZUSP 39646).

position will be discussed elsewhere. In addition, several other new species are already recognized (Ferreira et al. in press).

4.1. Convergent evolution between N. striata gen. n. sp. n. and B. lineata

The present paper reports on two ostracod species from Brazilian floodplains which show a striking case of convergent evolution. Both species look almost identical in external view: broadly rounded anterior and more pointed posterior margins and rounded dorsal margin with the greatest height situated well in front of the middle, and with, most markedly, the external valve surface densely set with ridges. There are small differences in valve and carapace shape. For example, in dorsal view the anterior left/right overlap is more pronounced in *B. lineata*, while the posterior overlap is more asymmetrical in *N. striata* gen. n. sp. n (see also illustrations of *B. lineata* in Martens, 1984), but such differences in valve morphology would normally be considered as either intraspecific variability or as differences between closely related species. The only structural difference in the valves between the two species is the presence of anterior sub-marginal selvages in both valves in *N. striata* gen. n. sp. n., which are absent in *B. lineata.* The anterior selvage on the right valve is present in most genera in the Cypricercinae, except in *Bradleytriebella* and in the genera of the Nealecypridini. However, examination of soft parts in both species show other important differences. All

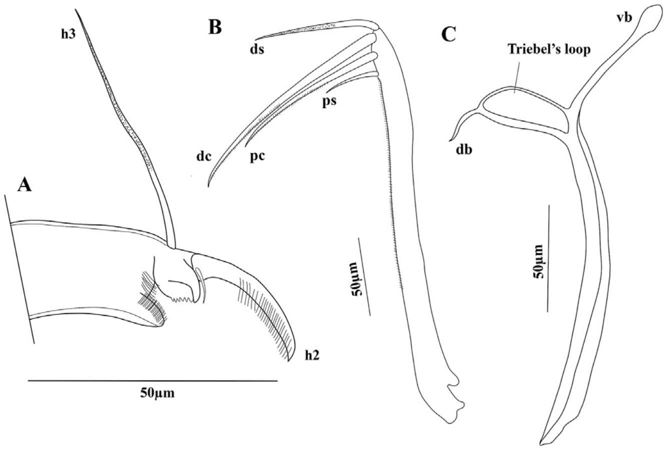

Fig. 7. Limbs of *Bradleytriebella lineata*. (A) Third thoracopod pincer (MZUSP 39646); (B) Caudal ramus: Proximal claw (pc); Distal claws (dc); Proximal seta (ps); Distal seta (ds) (MZUSP 39645); (C) Caudal ramus attachment: Ventral branch (vb); Dorsal branch (db); Triebel's loop (MZUSP 39646).

characters and character states discussed below are summarized in Table 2.

The specimens illustrated as species *Strandesia* spec. in Karanovic (2012, Fig. 112C–E) also have a general shape and external valve ornamentation as in the two species (re-) described here. However, the marginal valve structure of the left valve seems different while also the valves are higher in lateral view and the anterior left/right overlap in dorsal and ventral views is more pronounced. It could thus constitute a third species in the present cluster of species with convergent morphologies.

4.1.1. Aesthetasc Y on antenna

The length of the aesthetasc Y can be quite variable, even in congeneric species. The size-classes used in Table 2 (see also Material and Methods) therefore apply to the type species of the 12 genera. *B. tuberculata* (Hartmann 1964) also has a 'normal' type of aesthetasc Y (Savatenalinton & Martens 2009b) so that within the Cypricercinae only *B. lineata* appears to have a "long" aesthetasc Y, i.e. which reaches beyond the tip of the segment (Fig. 6A). The length of the aesthetasc is often correlated to the habitat of the ostracod species, and longer aesthetascs are believed to be linked to an interstitial mode of life, at least in Candoninae (Danielopol 1973). However, *B. lineata* is a common species in the pleuston of floating plants in the Paraná River floodplain (see Table S1) and has not been recorded interstitially yet. The causality of this unusually long aesthetasc Y in this species remains thus far unknown. It is furthermore noteworthy that North African specimens of this species also have a long aesthetasc Y, but less so than in the Brazilian specimens (Martens 1984). In addition, there is some variation between specimens in the same Sudanese population, where this aesthetasc either almost reaches the tip of the segment or fully reaches it (Martens 1984), but never surpasses it as in the present Brazilian specimens.

4.1.2. Sideways-directed bristles

Nearly all genera in the Cypricercinae have two sideways-directed bristles on the first endite of the maxillula, also *B. tuberculata*, the type species of *Bradleytriebella*. It is thus surprising that *B. lineata* has only one such bristle. *Bradleycypris* also has only one bristle there, whereas *Astenocypris* seems to have no sideway directed bristles (this character checked on specimens used by George & Martens 1993b).

4.1.3. Chaetotaxy of maxillula first palp segment

This is normally a very conservative feature, comprising of 6 long apical setae and 1 shorter subapical seta. As is apparent from Table 2, this chaetotaxy appears in nearly all cypricercine genera. Only *Diaphanocypris meridana* (Furtos 1936) has 5 + 1 setae there, and *N. striata* gen. n. sp. n. has only 4 + 1 setae there, which sets it aside within the Cypricercinae.

4.1.4. Chaetotaxy of maxillula second palp segment

Also this configuration is normally most conservative with 3 apical claws and 3 apical setae, and Table 2 again shows that most genera in the Cypricercinae adhere to this scheme. Here, both *D. meridana* and *Astenocypris papyracea* (Sars 1903) have 2 claws and 3 setae, while *N. striata* gen. n. sp. n., has 1 claw and 3 setae. This reduction in the chaetotaxy of the maxillula in these genera is remarkable, and given that they belong to two different tribes, most likely again constitutes a case of convergent evolution.

4.1.5. Seta 'd' on first thoracopod

The presence or absence of seta "d" on first thoracopod has been important in delimiting genera within the Cypricercinae (see Savatenalinton & Martens 2009b), but as becomes clear from Table 2 rather forms a mosaic within the subfamily, as the presence or absence is not congruent with the grouping of genera in tribes. This is a pattern inconsistent with the neighboring seta 'c' on this limb, which occurs in all genera of the Eucypridini (and indeed defines the tribe) and has thus far been found nowhere else in the Cyprididae (Martens 1989).

4.1.6. Seta 'b' on first thoracopod

This seta is normally very conservative in the family Cyprididae and is nearly always present with length similar to the average length of the apical setae of the basipodite of this limb. The plasticity of this seta (presence, absence) in the Cypricercinae is thus remarkable. Its appearance as a giant seta (more than 3 times longer than 'normal' and much stouter) in *N. striata* gen. n. sp. n. is even more unexpected. The potential function of this giant seta remains as yet unknown. In addition, it appears that there can be an asymmetry in this feature, as was observed in several specimens and species of *Bradleycypris* (unpubl. results), hence the double entry in Table 2.

4.1.7. Caudal ramus and Triebel's loop

The relevance of this ramus and the shape and position of the Triebel's loop in Cypricercinae has already been discussed in detail by Savatenalinton & Martens (2009b) and needs no further elaboration here.

4.2. The taxonomic position of *N. striata* gen. n. sp. n.

Within the Cypricercinae, *N. striata* gen. n. sp. n. occupies a somewhat special position, especially because of the reduction in the chaetotaxy of the maxillula-palp and the giant aspect of the "b" seta on the first thoracopod. However, because of the shape of the Caudal Ramus and the position of the Triebel's loop, we lodge the new genus in the Tribe Cypricercini.

Table 2 nevertheless shows that the distribution of several characters and character states over the different genera and tribes follows a rather mosaic pattern, and this does not strengthen the value of the present tribes. Future comparative morphological analyses of a larger set of species will test if the present assignment of the new genus to the Cypricercini is correct, or if the new genus needs a separate tribe, or indeed whether or not the present classification of 12 genera in three tribes can be maintained.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcz.2019.06.007.

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