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Research article

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Pectenocaris gen. nov., a new Brazilian Parastenocaridinae Chappuis, 1940, and Afrocaris gen. nov., a West African Fontinalicaridinae Schminke, 2010 (Copepoda, Harpacticoida, Parastenocarididae)

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Abstract. This study focuses on the description of a new Parastenocaridinae species belonging to a new genus from Brazil's Jalapão microregion and the establishment of a new genus for two West African Fontinalicaridinae species. Afrocaris gen. nov. and Pectenocaris gen. nov. differ in the morphology of the furca, with a gap between the outer setae I-III and the dorsal seta VII in Afrocaris gen. nov., and no gap between these elements in *Pectenocaris* gen. nov. The female genital field of *Pectenocaris* gen. nov. is rectangular and much broader than high than in other Parastenocaridinae. In Afrocaris gen. nov. the female endopod of the third percopod is short, ending in a small tip, without a distal fused spine as in *Pectenocaris* gen. nov. *Pectenocaris evilsoni* gen. et sp. nov. is the type species of a new Parastenocaridinae genus. The maxillula praecoxal arthrite of *Pectenocaris evilsoni* is armed with six elements, a unique character within the family. The fourth percopod of the male is heavily ornamented along the inner margin of the first and second exopodite, and cylindrical spinules with rounded tip are present on the basis, near the insertion of the short filiform endopod. The main characters supporting the new genus Afrocaris gen. nov. are the highly ornate inner margin of the first and second exopodites of the male fourth percopod and the short fourth percopod of the male endopod. The phylogenetic positions of Pectenocaris evilsoni gen. et sp. nov. and Afrocaris gen. nov. within their own subfamilies are challenging to ascertain due to the highly transformed male fourth percopod in *Pectenocaris evilsoni* gen. et sp. nov. and the two species of Afrocaris gen. nov. as well as the absence of an intermediate condition in species closely related to each of these genera or a clear synapomorphy for a more inclusive group within each subfamily, requiring further field and morpho/molecular systematic work.

Keywords. Africa, Central Brazil, mosses, neotropics, saturated substrate.

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Introduction

Recent decades have witnessed significant advancements in the taxonomy and high-level phylogenetics of the Parastenocarididae Chappuis, 1940 (Schminke 2010), marked by the introduction and phylogenetic classification of new genera from various global regions (Reid 1994; Galassi & De Laurentiis 2004; Schminke 2009, 2013; Cottarelli *et al.* 2010; Karanovic & Cooper 2011; Ranga Reddy *et al.* 2011, 2014; Corgosinho *et al.* 2012a, 2012b, 2017, 2021). The reestablishment of many of Jakobi's (1972) genera followed the influential work of Corgosinho & Martinez Arbizu (2005), which departed from Lang's (1948) traditional family group names and advocated for the reinstatement of Jakobi's (1972) nomenclature based on phylogenetic evidence. However, the literature occasionally exhibits hyperbole, with some genera being named without stringent phylogenetic justification (e.g., *Proserpinicaris* Jakobi, 1972 in Karanovic & Lee 2012; *Parastenocaris* Kessler, 1913 in Karanovic & Lee 2011), leading to polyphyletic taxa.

The phylogenetic framework and taxonomic classification of the Parastenocarididae remain dynamic. New species and genera have been frequently described, yet extensive areas of the globe, including Asia, the Western Pacific islands, Australia, Africa, South and Central America, remain underexplored or entirely unexplored. Our recent research has expanded the understanding of Brazil's Parastenocarididae fauna. Nonetheless, Brazil's vast size and status as a biodiversity hotspot (Myers *et al.* 2000) mean that our sampling, often limited to small-scale locales such as lengthy riverine sandy beaches, provides only a partial view of the actual local biodiversity. This is particularly true in less studied areas like the Amazonian lowlands and the Central Brazilian Plateau.

Convergence within the Parastenocarididae is anticipated and has been demonstrated by the phylogenetic analysis of the accepted genera of Parastenocaridinae Chappuis, 1940 of Corgosinho *et al.* (2017). Yet, addressing this hypothesis would require a thorough family-level phylogenetic analysis, incorporating both the reassessment of known species and the newly discovered ones, employing both classical and modern methods, including molecular phylogenetics. In Brazil, most of the known genera belong to the subfamily Fontinalicaridinae Schminke, 2010. To date, only three genera of Parastenocaridinae have been identified in Brazil: *Remaneicaris* Jakobi, 1972, *Eirinicaris* Corgosinho *et al.*, 2017, and *Parastenocaris* (with three undescribed species from the states of São Paulo and Paraná Corgosinho unpublished). This study introduces a novel genus and species of a fourth Parastenocaridinae, collected in the Jalapão's microregion, state of Tocantins, on the Central Brazilian Plateau. This new genus is distinguished by its male fourth pereiopod, which is highly modified and ornately internally, a trait we consider convergent with the one recorded in two African species of Fontinalicaridinae, *Parastenocaris nigerianus* Chappuis, 1959, and *P. kimi* Dumont, 1981, henceforth recognized as belonging to a new African genus, which we formally propose here.

Material and methods

The type material was collected both from saturated moss carpets covering a vertical sandstone wall next to Evilson's waterfall, and from moist organic substrate in shaded areas along the path taking to Escorrega Macaco waterfall, in the Jalapão region. The Jalapão microregion of eastern Tocantins is characterized by a diverse scenery. Its hydrography is characterized by the presence of several rivers, streams, waterfalls, and springs that originate from the Cerrado biome. Some of the main rivers are the Rio Novo, the Rio Preto, the Rio Sono, and the Rio Formoso. The region also has some eolian deposits that form the Jalapão Dunes, a unique feature in the region.

For description, entire specimens were examined in temporary lactic acid mounts prepared under a stereo microscope. Fragments of cover glass were used to support the cover glass of the preparations. By moving the cover glass slowly and carefully by hand, the whole animal or a particular appendage was placed in various positions, allowing the observation of morphological details. Drawings were made using a camera lucida on a light Nikon Eclipse 50i phase-contrast. After examination, specimens were returned and preserved in 70% ethanol. Illustrations were obtained with a scanning electron microscope Zeiss Sigma VP. In addition, for scanning electron microscopy (SEM), specimens of both sexes were prepared following protocols by Felgenhauer (1987) and Huys & Boxshall (1991). Following the successful capture of the SEM images, the stubs, which held the coated specimens, were returned to the Scanning Electron Microscope (SEM) facility for subsequent utilization.

The material is deposited in the Museu de Zoologia, Universidade de São Paulo, São Paulo (MZUSP).

The diagnosis of *Pectenocaris* gen. nov. represents its reconstructed ground pattern. For *Afrocaris* gen. nov., the diagnosis also includes the inferred ground pattern, which is reconstructed based on the fragmentary information available in the original descriptions of *Parastenocaris nigerianus* and *P. kimi*. The term "ground pattern" is used in the sense of "Grundmuster" (Ax 1984: 156) and refers to all plesiomorphies and autapomorphies present at the stem species of the genus in question.

The terms 'furca' and 'telson' are used according to Schminke (1976). Terminology and homologization of maxillary and maxillipedal structures follows Ferrari & Ivanenko (2008). Therefore, by the application of serial homology, the nomenclature of Huys & Boxshall (1991: 26, fig. 1.5.5) for maxilla is modified as follows: praecoxa of maxilla is recognized as syncoxa (praecoxa and coxa), coxa is considered as the basis, and the basis is recognized as the first endopodal segment with claw. Other morphological terms are used according to Huys & Boxshall (1991).

Abbreviations for morphological terms

А	=	antennule
A2	=	antenna
ae	=	aesthetasc
enp	=	endopod
enp1-3	=	endopodite 1–3
exp	=	exopod
exp1-3	=	exopodite 1–3
Fu	=	furca
Md	=	Mandible
Mx1	=	Maxillule
Mx2	=	Maxilla
Mxp	=	Maxilliped
P1-P5	=	legs 1–5

Results

Taxonomy

Class Maxillopoda Dahl, 1956 Subclass Copepoda Milne-Edwards, 1840 Order Harpacticoida Sars, 1903 Family Parastenocarididae Chappuis, 1940 Subfamily Parastenocaridinae Chappuis, 1940

Pectenocaris gen. nov. urn:lsid:zoobank.org:act:6F956703-BBF2-438D-A232-0C783005C5F7

Diagnosis

Parastenocarididae

Body elongated, vermiform, cylindrical, without clear demarcation between prosome and urosome. Fu cylindrical, with outer setae I-III and dorsal seta VII inserted in same transversal plane. Male A1 eightsegmented, ae on 5th and 8th segments. Female A1 seven-segmented, ae on 4th and 7th segments. Md, Mx2, Mxp as in other Parastenocarididae (exception: Mx2 of *Remaneicaris*; Corgosinho & Martínez Arbizu, 2005). Mx1 praecoxal arthrite armed with six elements, instead of four as figured in other species of the family (e.g., Remaneicaris insolitus Corgosinho et al., 2010). Setae on Mx1 and 2 transformed in hollow tubes. P1 and P2 characteristic of Parastenocarididae, without any unusual character. Male P3 with strongly ornated basis, with inner and outer rows of spinules; exp-1 thin and straight, with proximal and distal longitudinal spinular row, and inner proximal protuberance with a distal pore; apophysis sigmoidal, elongated, slightly bent inwards; thumb elongated, straight, slightly longer than apophysis. Female P3 enp almost as long as exp-1, spiniform. Male P4 exp-1 heavily ornamented along whole inner margin; exp-2 with row of spinules along last third of inner border and continuing on distal margin on anterior and lateral surfaces; basis with strong cylindrical spinules with rounded tip near the insertion of short filiform enp. P5 without sexual dimorphism, short, outer setae proximally inserted, with long spiniform inner process. Female P6 an unarmed and unornamented fused plate over genital field. Genital field is rectangular, much broader than high, occupying proximal third of genital double somite.

Etymology

The generic name is derived from the Latin noun '*pecten*', meaning 'comb', and refers to the comb formed by a row of long spinules along the inner margin of the first exp segment of leg 4 of the male.

Putative autapomorphies of Pectenocaris gen. nov.

1) Mx1 praecoxal arthrite armed with 6 elements; 2) setae of Mx1 and 2 transformed in hollow tubes; 3) Strong cylindrical spinules with rounded tip on male P4 basis, near insertion of filiform enp, and strong ornamentation (long spinules) on inner margin of male P4 exp-1 and 2; 4) male P3 exp-1 thin and straight, apophysis sigmoidal, elongated, slightly bent inwards; thumb elongated, straight, digitiform, slightly longer than apophysis.

Pectenocaris evilsoni gen. et sp. nov. urn:lsid:zoobank.org:act:51332A89-B62B-4CF1-B9ED-A8A3C5173DAC Figs 1–8

Etymology

The specific epithet honors Mr Evilson Machado da Fonseca, owner of the area where the type locality of the species is located.

Type material

Holotype

BRAZIL • ♂ (preserved in alcohol); State of Tocantins, Palmas, district of Taquaruçu de Cima, Taquaruçu Grande River, Tocantins River Basin; 10°13′51″ S, 48°07′18″ W; 5 Aug. 2019; Carlos E.F. da Rocha leg.; saturated moss and among decaying leaves besides Evilson's waterfall; MZUSP 45993.

Allotype

BRAZIL • \bigcirc (preserved in alcohol); same data as for holotype; MZUSP 45994.

Paratypes

BRAZIL • 46 $\bigcirc \bigcirc$, 37 $\bigcirc \bigcirc$ (preserved in alcohol); same data as for holotype; MZUSP 45995.



Fig. 1. *Pectenocaris evilsoni* gen. et sp. nov. **A**. Holotype, \bigcirc (MZUSP 45993), habitus, lateral view. **B**. Allotype, \bigcirc (MZUSP 45994), habitus, lateral view.

Other material examined

BRAZIL • 28 \Im , 29 \Im (preserved in alcohol); State of Tocantins, Palmas, district of Taquaruçu de Cima, Taquaruçu Grande River, Tocantins River Basin; 10°13′51″ S, 48°07′18″ W; 5 Aug. 2019; Carlos E.F. da Rocha leg.; saturated moss and decaying leaves besides Evilson's waterfall • 18 \Im , 8 \Im ; same data as for preceding; 10°18′00″ S, 48°07′57″ W; saturate substrate composed of mud and decaying leaves in a ditch besides the track leading to Escorrega Macaco waterfall.

Description

Male

Body length, measured from tip of rostrum to posterior margin of caudal rami, $330-347 \ \mu m$ in 10 specimens measured (average $337 \ \mu m$). Cephalothorax (Figs 1A, 2A, 8A) with large dorsal integumental window on posterior half. Genital somite and three subsequent urosomites each with transverse, narrow integumental window on anterior dorsal surface. Integumental pores and sensilla arrangement as shown in



Fig. 2. *Pectenocaris evilsoni* gen. et sp. nov., holotype, $\stackrel{\sim}{\bigcirc}$ (MZUSP 45993). **A**. Dorsal view of habitus. **B**. Ventral view of telson with furca and armature.

Figs 1A, 2A, 8A. Structure of all sensilla shown in Fig. 7F. Ventral surface of prosome among swimming legs smooth. Third urosomal somite (Figs 5G, 7A, 7C) with ventral flap distally, marking vestigial P6. Spermatophore (Figs 1A, 2A) Spermatophore ovoid, visible within body occupying pediger 5 and genital somite. Telson (Figs 1A, 2A, 2B, 8A) $1.2 \times as$ long as wide and twice the length of preceding somite; a dorsally produced backwards into pseudoperculum. Anal area with rows of setules (Fig. 7E). Fu (Figs 2B, 8A) twice as long as broad, setae I to III the shortest, grouped and sub-terminally inserted. SETA IV. Dorso-laterally placed, shorter than Fu, and sparsely uniserrate in distal half; seta V robust and



Fig. 3. *Pectenocaris evilsoni* gen. et sp. nov., holotype, ♂ (MZUSP 45993). **A**. Antennule. **B**. Antenna, arrow marking the hyaline frill. **C**. Mandible, arrow marking the oral broken seta. **C***. Mandible gnathobasis. **D**. Maxillula. **E**. Maxilla. **F**. Maxilliped. **G**. Labrum. **G***. Labium.

sparsely setulose, $6 \times$ length of caudal ramus; seta VI $1-1.2 \times$ length of caudal ramus, and with row of setules at base ventrally; seta VII almost as long as seta VI, implanted dorsally near inner margin of ramus, slightly below the insertion level of setae I–III (i.e., at about 0.6 length of ramus).

A1. Haplocer of 8 segments and armed as shown in Fig. 3A. Ae on segment 5 wider and longer than that on last segment. Armature formula 0, 6, 4, 2, 5+1+ae, 2+foliaceous spine, 1+ foliaceous spine, 7+ acrothek (2+ae).

A2 (Fig. 3B). Consisting of unarmed short coxa, basis with two transversal spinule groups, and onesegmented enp bearing 7 elements (two inner unipinnate spines, two distal inner spines also unipinnate, two distal geniculate setae, and one distal and outer unipinnate spines), and hyaline serrulate frill near apex on posterior surface (indicated by an arrow). Exopod reduced to knob with pinnate apical seta.

LABRUM AND LABIUM. As in Fig. 3G.

MD (Fig. 3C, C*). With coxa expanded into gnathobase with teeth. Palp uniramus, cylindrical, with two apical setae of same length implanted at base of sharp protrusion.

Mx1 (Fig. 3D). Comprised of praecoxal arthrite with spinule on inner surface, six robust, apically curved and unipinnate apical setaeand tubular seta on outer margin. Coxal endite bearing seta ending in pointed projection. Basis and enp merged together. Basal endite with three setae, two of them ending in pointed projection. Enp represented by seta implanted on tubercule. Exopod absent. All setae transformed in hollowed tube.

Mx2 (Fig. 3E). Allobasis with two endites; proximal endite with one seta; distal endite bearing three setae, the longest one comb-shaped, the remaining two os same lenght; proximal endopodal segment drawn out into denticulate claw; distal endopodal segment represented by two setae of subequal lengtht. Endites setae, and 2nd enp setae transformed in hollowed tubes. Claw of the proximal endopodal segment with subdistal pore.

MXP (Fig. 3F). Prehensile. Terminal segment with spinulose seta on tip.

P 1 (Fig. 4A), 2, 4. Biramous, with three-segmented exp. P1 (Fig. 4A) biramous. Coxa with two rows of spinules on anterior surface. Basis bearing gland pore and three rows of strong spinules on anterior surface. Exp three-segmented, with outer spine on proximal segment; second segment without spine but row of spinules at outer corner; and terminal segment with two spines and two geniculate setae apically. Enp 2-segmented; enp-1 slightly longer than exp-1 and 2 combined, with transversal row of four spinules internally, at approximate ²/₃ of enp length, and two groups (one proximal and one distal) of transversal spinules along outer margin; enp-2 with serrate outer spine and geniculate inner seta apically.

P2 (Fig. 4B). Coxa with two rows of spinules on anterior surface. Basis bearing row of spinules near the insertion of enp and exp, outer row of spinules, and outer pore. Exp with hyaline frills at inner corners of proximal and apical segments. Proximal segment with spine on distal outer corner and rows of spinules on outer margin and at outer corner. Median segment with apical spinules. Terminal segment armed with three elements: one short and unipinnate outer spine, one unipinnate outer distal seta shorter that bipinnate inner distal seta. Enp cylindrical, almost half length of exp-1, armed with seta implanted subterminally and directed towards middle line of body; apex blunt, bearing group of spinules.

P3 (Figs 4C, 6B). Consisting of coxa, basis and unisegmented exp (exp-1 and 2 fused); enp absent. Coxa with two spinules on outer margin. Basis bearing long outer seta, transversal row of long spinules near outer distal corner, curved row of spinules on anterior surface, and short row of spinules on posterior

surface. Exp long and narrow, with basal protuberance and two rows of outer spinules along posterior surface. Terminal apophysis sigmoidal, elongated, slightly bent inwards; thumb digitiform, tapering towards tip, straight, reaching past end of apophysis (Fig. 6B).

P 4 (Figs 4D, 6C–D). Coxa with row of spinules on anterior and posterior surfaces. Basis with outer seta, outer pore, and row of spinules between seta and exp. Exp three-segmented. Exp-1with spine at outer corner and three transversal rows of spinules; inner border with row of long, strong spinules, each one



Fig. 4. *Pectenocaris evilsoni* gen. et sp. nov., holotype, ♂ (MZUSP 45993). **A**. P1. **B**. P2. **C**. P3. **D**. P4. **E**. P5.

slightly curved backwards; all spinules equal in length, except for distal four spinules shorter than others and implanted on triangular expansion of exp-1. Exp-2 with row of spinules along last third of inner border, continuing on distal margin on anterior and lateral surfaces. Exp-3 with one outer unipinnate spine, $\frac{2}{3}$ the length of bipinnate inner distal seta, inner fringed hyaline frill at inner corner and row of



Fig. 5. *Pectenocaris evilsoni* gen. et sp. nov. **A**–**F**. Allotype, \bigcirc (MZUSP 45994). **A**. Antennule, P2–5 and genital double somite with genital field. **A**. Antennule. **B**. P2 coxa, basis, exp-1 and enp. **C**. P3. **D**. P4. **E**. P5. **F**. Ventral view of genital double somite with genital field. **G**. Holotype, \bigcirc (MZUSP 45993), P4–6 somites, ventral view.

spinules on outer corner. Enp reduced to filiform segment; row of curved and flattened robust spinules, with blunt tip implanted in front of it on anterior surface of basis.

P5 (Figs 4E, 7A, C). Not fused to intercoxal sclerite, represented by subtriangular plate extending into wide triangular medial process with pointed tip, and bearing four setaere; outermost basipodal seta about $1.6 \times$ as long as plate, and outer pore.



Fig. 6. *Pectenocaris evilsoni* gen. et sp. nov., SEM images. **A–D**. ♂, specimen 2. **E–F**. ♀, specimen 3. **A**. Mouth parts. **B**. P3. **C–D**. P4. **E–F**. P4 enp.

P6 (Fig. 7A, C). Vestigial, appearing as unarmed and unornamented fused plate.

Female

Body length, excluding caudal setae, varying from 365 to 390 μ m in 7 specimens measured (average 384 μ m). Integumental sensilla and pores distributed as shown in Fig. 1B. Cephalothorax with large



Fig. 7. *Pectenocaris evilsoni* gen. et sp. nov., SEM images. **A**, **C**. \Diamond , specimen 4. **A**. Ventral view of P5–6. **C**. ventral view of P5–6. **B**, **D–F**. \bigcirc , specimen 5. **B**. Ventral view of P5 and genital double segment with genital field. **D**. Ventral view of genital field. **E**. Detail of the anal region. **F**. Detail of sensilla cuticular insertion and morphology.



Fig. 8. *Pectenocaris evilsoni* gen. et sp. nov., SEM images. A. \Im , specimen 6, lateral habitus. B. \Im , specimen 7, lateral habitus.

dorsal integumental window on posterior half (Figs 1B, 8B). Genital double somite and two subsequent urosomites each with transverse narrow integumental window on anterior dorsal surface (Fig. 1B). Ventral surface of prosome smooth. Genital field rectangular, much broader than high with cuticular thickenings along transversal slit representing vestigial P6 forming design as shown in Fig. 7B, D. Anal somite and Fu as in male. None of females found carried egg sacs.

A1 (Fig. 5A) of 7 segments armed with 0, 4, 3, 2+ae, 1, 1, 7+ acrothek (2+ae). Ae on segments 4 longer than on segment 7.

A2 and mouthparts as in male.

P1, P2 (Fig. 5B) and P5 (Fig. 5E) as in male.

P3 (Fig. 5 C) two-segmented exp. Enp protruded into blunt concave projection to accommodate spinule implanted at medium length.

P4 (Fig. 5D) coxa with curved row of short spinules. Basis with row of spinules on anterior surface, between insertion of outer seta and exp. Exp three-segmented; exp-1 with distal outer spine and three rows of spinules on the outer margin, and one inner distal row of spinules; exp-2 with distal row of spinules; exp-3 bearing one unipennate outer spine, distal inner bipinnate seta almost twice as long as outer spine, an inner distal hyaline frill, and two rows of spinules on apex. P4 basis with spinular row around enp insertion, with outer row of spinules, outer seta and outer pore; enp is short uni-segmented (³/₄ length of corresponding exp-1), and cylindrical with blunt tip, with two subapical, longitudinal spinules of same length.

Acompanying fauna

Copepoda Cyclopidae (*Paracyclops* sp., *Ectocyclops* sp. and *Metacyclops* sp.); Copepoda Canthocamptidae; Ostracoda (Darwinulidae and others); Acari (Hydrachnida and others); Mollusca (Gastropoda and Bivalvia); Tardigrada; Oligochaeta; and insect larvae.

Subfamily Fontinalicaridinae Schminke, 2010

Afrocaris gen. nov. urn:lsid:zoobank.org:act:2B1443DD-9EF7-4D21-833A-AC05B4270767

Diagnosis

Fontinalicaridinae; Fu elongated, with a gap between proximal distal outer setae I–III and dorsal seta VII. Female P3 enp short, with acuminate tip. Male P3 exp-1 strongly built, rectangular; apophysis (exp-2) bent inwards with acuminate or rounded tip (without distal spine); thumb short, not passing the distal margin of the apophysis. Male P4 highly ornamented along the inner margin of exp-1 and 2; ornamentation consisting of long spinules proximally and distally on the exp-1 and along the entire inner margin of exp-2; exp-1 as long as exp-2 and 3 combined; enp short, spiniform. P5 short, with long distal spiniform process on the inner margin; outer setae proximally inserted.

Etymology

The generic name refers to Africa, the continent in which the known species of the genus occur.

Type material

Afrocaris nigerianus (Chappuis, 1959) comb. nov. Geographical distribution: West Africa, Nigeria.

Other material examined

Afrocaris kimi (Dumont, 1981) comb. nov. Geographical distribution: West Africa, Guinea.

Putative autapomorphies of Afrocaris gen. nov.

1) Strong ornamentation (long spinules) on the inner margin of the male P4 exp-1 and 2; 2) short (spiniform or linguiform) male P4 enp.

Discussion

We describe a new genus of a Parastenocaridinae from the microregion of Jalapão, in the Brazilian Central Plateau, and we propose the establishment of a new genus to accommodate two West African species of Fontinalicaridinae. Given the shared biogeographical history of Africa and South America, which final separation have occurred around 90 mya (Thomaz Filho *et al.* 2000), and the superficial similarity between the species dealt with in this study, it is tempting to assign the three species to a single Neo/Afrotropical genus. The superficial similarities between the species composing both genera are baffling. The three species share practically the same strong ornamentation on the male exp-1 and 2 of the male P4, a reduced male P4 enp and a very similar P5.

Schminke (2010) proposed the establishment of two subfamilies within the Parastenocarididae, providing a list of species for each subfamily. Although Schminke (2010) did not refer to them as monophyletic unities, the available data constitute strong support of the monophyly of both subfamilies. Schminke (2010) listed seven characters which can be used to distinguish both subfamilies, namely 1) male A1; 2) P3 of female; 3) P3 of male; 4) P4 of male; 5) P5 of male and female; 6) genital field of female; 7) caudal rami morphology. However, it is not expected that all the typical conditions of each character, as discussed by Schminke (2010) for Parastenocaris brevipes Kessler, 1913 (Parastenocaridinae), and Fontinalicaris fontinalis (Schnitter & Chappuis, 1915) (Fontinalicaridinae) will occur in distinct species of each subfamily. The new genera are attributed to different subfamilies based on the characters: 2) P3 of female; and 7) furca morphology. In Afrocaris gen. nov., we hypothesize that the female P3 enp is short (apomorphic), ending in a small tip, not showing a distal fused spine as in Pectenocaris gen. nov. The evidence of a fusion is represented in other species of the family by a median spinule or spinule row demarcating the limit of the enp segment and the insertion of the distal fused spine; both characters occurring in Pectenocaris. Short P3 enp with distal acuminate tip has been described before for other Fontinalicaridinae such as Santaremicaris santaremensis Corgosinho et al., 2021 (Corgosinho et al. 2021), Murunducaris loyolai Corgosinho et al., 2008, M. noodti Corgosinho et al., 2008, and M. dactiloides (Kiefer, 1967) (Corgosinho et al. 2008). However, the female P3 enp of these species is proportionally shorter than what occurs within the Parastenocaridinae; moreover, there is no evidence of a proximal row of spinules marking the limit between the proximal enp and the distal fused spine. Pectenocaris and Afrocaris differ in the morphology of the furca, with a gap between the proximal outer setae I-III and the distal dorsal seta VII in Afrocaris a Fontinalicaridinae character (Schminke 2010), and no gap (apomorphy) between these elements in Pectenocaris, a character of the Parastenocaridinae (Schminke 2010).

The female genital field of the species attributed to *Afrocaris* gen. nov. was not described by neither Chappuis (1959) or Dumont (1981). It is of striking importance to mention; however, that the genital field of the females of *Pectenocaris* gen. nov. is rectangular and much broader than high (Schminke 2010), a plesiomorphy which can also be observed in the basalmost Parastenocaridinae (*Remaneicaris* Jakobi, 1972), and some groundwater Ameiridae (see Lee & Huys 2002; Karanovic & Hancock 2009). The apomorphic condition occurs in fontinalicaridids, in which the genital field is U-shaped, or T-Shaped, as broad as high.

Pectenocaris evilsoni gen. et sp. nov. can be assigned to a new genus based on the set of characters not observed elsewhere within the Parastenocaridinae, and which we consider apomorphic:

1) Mx1 praecoxal arthrite armed with six apical elements and one outer tubular seta, instead of three distal elements and one anterior tubular seta as present proposed for the ground pattern of the family (Corgosinho et al. 2007). This is a unique character within the family; the additional elements clearly represent supernumerary elements. However, here we consider the supernumerary elements as the expression of silenced genes in the Parastenocarididae lineage, with the expression of a plesiomorphic condition in the Mx1 of *Pectenocaris* gen. nov. Such morphological event could be verified at smaller scale in *Remaneicaris*. Corgosinho (2007, unpublished data) revised the entire *Remaneicaris* genus and produced a morphological phylogenetic analysis for the genus (Corgosinho 2007). It was found that a derived group within *Remaneicaris*, closely related to *R. sanctiludovici* (Noodt, 1965), the plates covering the female genital field have one or two setae, a plesiomorphic character lost in the Parastenocarididae phylogenetic lineage, reappearing within *Remaneicaris* (Corgosinho 2007).

2) Male P3 with strongly ornamented basis, with inner and outer rows of spinules; exp-1 thin and straight, proximally and distally ornamented with a row of spinules, and with a proximal inner protuberance with a distal pore; apophysis sigmoidal, elongated, slightly bent inwards, with thin acuminate inner tip; thumb elongated, straight, slightly longer than apophysis. Such P3 morphology of the exp is unique within the Parastenocaridinae. It is superficially similar to the male P3 of *Kinnecaris* Jakobi, 1972 and *Monodicaris* Schminke, 2009 (Schminke 2008, 2009), but a detailed inspection fails to establish homologies, *Monodicaris* and *Kinnecaris* forming a clade within the Parastenocaridinae with *Parastenocaris* and *Eirinicaris*, all sharing the same furca construction (Corgosinho *et al.* 2017), whereas *Pectenocaris* gen. nov. occupies a phylogenetic position not yet possible to assess.

3) Male P4 exp-1 heavily ornamented along the whole inner margin; exp-2 with row of spinules along last third of inner border, extending on distal margin on anterior and lateral surfaces; basis with strong cylindrical spinules with rounded tip near the insertion of the short filiform endopod. This set of characters is not present elsewhere within the Parastenocaridinae, and clearly constitutes apomorphies for the new genus. A reduced P4 enp accompanied by basal spinules appears at least in the following Parastenocaridinae: A) European species: Parastenocaris vicesima Klie, 1935, P. karamani Chappuis, 1937, P. nolli Kiefer, 1938, P. hippuris Hertzog, 1938, P. husmanni Chappuis, 1953, P. rascana Petkovski, 1959, P. narentina Petkovski, 1959, P. lusitanica Noodt & Galhano, 1969, P. tyrrhenidis Cottarelli, 1970, Italicocaris italica (Chappuis, 1953), Minutacaris austriaca Kiefer, 1976, Simplicaris veneris (Cottarelli & Maiolini, 1980), S. lethaea Galassi & De Laurentiis, 2004. B) African species: Parastenocaris gracilis Chappuis, 1954, P. marlieri Chappuis, 1955, P. spinipes Wells, 1964, P. grassei Soyer, 1965, P. ursulae Schminke, 1971. Determining whether Pectenocaris evilsoni gen. et sp. nov. shares a closer relation to the African species (a more likely scenario) or the European species (a less likely scenario) is currently challenging, given the limitations of the available literature. Indeed, such high morphological transformations, as observed in the P4 of the new species, are of little help in the reconstruction of a phylogenetic analysis, without the help of intermediate character states, or a comprehension of a clear series of transformations. Hence, to address the phylogenetic position of Pectenocaris evilsoni, considerable collecting campaigns in Brazil, Africa, and even southern Europe are needed, followed by a coupled morphological and molecular taxonomic work.

Afrocaris gen. nov. is clearly a Fontinalicaridinae, as is evidenced by the morphology of the furca, with a gap existing between the proximal outer setae I–III and the distal dorsal seta VII. The female P3 enp is also of the Fontinalicaridinae type; short and unornamented (viz. *A. kimi* comb. nov.). *Afrocaris nigerianus* comb. nov. and *A. kimi* comb. nov. can be equally established as members of a new genus based on the highly ornate inner margin of the male P4 exp-1 and 2 and short male P4 enp.

It could be questioned that we cannot use the ground pattern principle to extrapolate the condition of the female P3 enp for both species of Afrocaris gen. nov., once this character is described only to Afrocaris *Kimi* comb. nov. We recognize that the use of ground patterns in taxonomic diagnosis presents several challenges, including increased uncertainty and the lack of direct observation. Taxonomic descriptions are hypotheses and relying on predicted characters - hypotheses within hypotheses - can weaken the robustness of these classifications. Evolutionary variability further complicates this approach, as assuming species will display the same characters as closely related taxa can be misleading. Despite these issues, ground patterns are justifiable if comparative phylogenetic methods are used, particularly when direct observation is not possible. This approach allows researchers to make educated guesses about unobserved characters, providing valuable insights into evolutionary histories and aiding in the description of new species from incomplete specimens. Within the Parastenocarididae, some characters are notably conservative. For example, the female P3 endopod (enp) exhibits different and very conservative morphologies within each subfamily. However, exceptions do occur, such as the loss of the female enp in some taxa like *Potamocaris* Dussart, 1979, where the subfamily ground pattern is represented by a short and blunt P3 end, whereas in the sister taxon Forficatocaris Jakobi, 1969 we can observe the presence of the P3 enp as it appears in the ground pattern of the Fontinalicaridinae. Note, however, that transformations are very consistent within different genera of Parastenocarididae, and closely related species, specially within the same genus, generally share the same character morphology for structures such as P1, P2 of both sexes, and P3 and P5 of females.

The phylogenetic position of this genus is not easy to determine either, in view of the same sort of highly transformed P4, and no intermediate condition in closely related species or even a clear synapomorphy for a more inclusive group. For the African Fontinalicaridinae, i.e., *Parastenocaris kabyla* Chappuis, 1954, *P. crassicaudis* Chappuis, 1955, *P. fossoris* Fryer, 1956, *P. matopoica* Wells, 1964, *P. jeanninei* Dumont, 1981, no conclusive result can be reached on their affinity with *Afrocaris* gen. nov. It is marginally possible that Dumont (1981) illustrated some kind of ornamentation on the inner margin of the male P4 exp-1 of *P. jeanninei*, which if present, could indicate a close proximity of this species with those belonging to *Afrocaris*.

Afrocaris kimi comb. nov. and *A. nigerianus* comb. nov. are similar in almost all aspects, which is indicative of a possible junior synonym of *A. kimi*. However, due to the presence of telson ornamentation in *A. nigerianus* which is missing in *A. kimi*, the absence of ornamentation on the male P3 outer margin of *A. nigerianus*, and the lack of evidence of variability within each species / population, it is not possible to proceed with the synonymyzation of both species' names. Additionally, there is a wide geographical gap between the type localities, which is an indication that these are closely related species instead of junior synonyms.

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