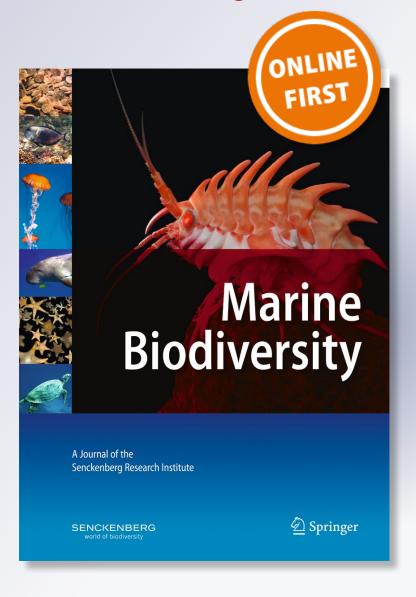
A new species of Halectinosoma Vervoort, 1962 (Copepoda: Harpacticoida) from Argentina, including a key to species with unusual leg armature patterns, notes on wrongly assigned taxa and an updated key to ectinosomatid genera

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#### ORIGINAL PAPER

### A new species of *Halectinosoma* Vervoort, 1962 (Copepoda: Harpacticoida) from Argentina, including a key to species with unusual leg armature patterns, notes on wrongly assigned taxa and an updated key to ectinosomatid genera

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**Abstract** Both sexes of a new brackish water species, Halectinosoma parejae sp. nov. (Harpacticoida: Ectinosomatidae), are described from the Bahía Blanca estuary (38°53'S, 62°07'W) in Buenos Aires Province. The species represents the first confirmed record of the genus in Argentinean waters and can be readily differentiated from its 68 valid congeners by its unique armature pattern on the swimming legs. A key to the 17 species displaying seta/spine formulae that diverge from the common plesiomorphic condition is provided, as well as an updated key to the genera of the Ectinosomatidae. The status of some species that had previously been assigned to the wrong genus has been re-evaluated. Pseudobradya lanceta Coull, 1986 is transferred to Halectinosoma Vervoort, 1962 as H. lancetum (Coull, 1986) comb. nov., while the closely related H. spinicauda Wells, 1961, H. pterinum Moore, 1974 and H. paraspinicauda Bodin, 1979 are removed from Halectinosoma and placed in Pseudobradya Sars, 1904 as P. spinicauda (Wells, 1961) comb. nov., P. pterina (Moore, 1974) comb. nov. and *P. paraspinicauda* (Bodin, 1979) comb. nov., respectively. The inadequately described H. littorale

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(Nicholls, 1939) is relegated to species inquirenda in Pseudobradya. The Japanese "population" of the Brazilian H. arenicola (Rouch, 1962) has been attributed distinct specific status as H. pseudarenicola sp. nov., while H. smirnovi (Chislenko, 1967) is reinstated as a valid species distinct from H. unicum Lang, 1965.

**Keywords** Buenos Aires Province · Ectinosomatidae · Meiofauna · Taxonomy

#### Introduction

The province of Buenos Aires (Argentina) has a 1220-km coastline, which has witnessed a long tradition of biological research (Miloslavich et al. 2011). However, the taxonomic literature on marine harpacticoid copepods from this region is remarkably scarce, being limited to a small number of contributions (e.g. Rouch 1962; Ramírez 1971; Sciberras et al. 2014). During an ongoing ecological survey of the meiobenthos in the Bahía Blanca estuary, one of the most abundant members of the copepod community proved to be an as yet undescribed species of Halectinosoma Vervoort, 1962.

Halectinosoma is one of the most diverse genera among the 22 valid genera included in the family Ectinosomatidae (Kihara and Huys 2009; Apostolov 2011), currently accommodating 68 species. The genus has been extensively studied and is the subject of three recent revisions. Clément and Moore (1995) resolved the taxonomic problems surrounding the group of Halectinosoma species that are morphologically similar to H. sarsi (Boeck, 1873). This was followed by a revision of the *herdmani* group of species, including a key for the identification of females of this species complex (Clément and Moore 2000). Finally, in a third paper, Clément and Moore (2007) focused on new species from the North Atlantic and Arctic regions. Despite these massive



contributions to the taxonomy of the genus, many additional unnamed species are known to exist. Species of *Halectinosoma* are often dominant members of marine harpacticoid communities and, yet, their identification at the species level is fraught with difficulty. Differences between species are often subtle and many descriptions are inadequate in modern terms and do not permit the accurate identification of species. The identification of species from very distant geographic localities must consequently be treated with circumspection.

Despite the cosmopolitan distribution and the ubiquitous occurrence of the genus, very few records are available from South America and only two of them can be considered reliable. Rouch (1962) described Ectinosoma (Halectinosoma) arenicola Rouch, 1962 from several sandy beaches in Recife, Pernambuco State, Brazil. The species was transferred to Halectinosoma by Lang (1965) and subsequently reported from a sandy beach on Kyushu in southern Japan by Itô (1973), but the validity of the latter record has been considered questionable (Clément and Moore 2000). Recently, Suárez-Morales and Fuentes-Reinés (2015) described a new species, H. arangureni from Laguna de Navío Quebrado, a brackish coastal lagoon system in northeastern Colombia. The record of *H. finmarchicum* (T. Scott, 1903) from Coroa do Avião in Pernambuco State (Wandeness et al. 1998) is doubtful. Clément and Moore (2000) demonstrated that the original description of H. finmarchicum by Scott (1903) has caused much confusion, as it was based on specimens of two different species. Consequently, they suggested to drop H. finmarchicum from classification and consider it a species inquirenda. Other doubtful records in Pernambuco State are those of Halectinosoma oblongum Kunz, 1949 from Ilha de Itamaracá by Gomes (2002) and from the Rio Formoso estuary by Vasconcelos (2003). The species was originally described from Helgoland (Kunz 1949); however, in view of the small differences separating many of the species of Halectinosoma, it cannot be assumed that the specimens from Germany and Brazil are conspecific. Other records of Halectinosoma from the Pernambuco coast (Gomes and Santos 2002; Santos et al. 1998, 2000; Souza-Santos et al. 2004) also require verification. Unidentified species of Halectinosoma have been reported by George and Schminke (1999) from the Straits of Magellan and the Beagle Channel in southernmost Chile, and from the northern littoral zone of São Paulo State, Brazil by Rocha et al. (2011), who differentiated no less than ten putative species. Nogueira et al. (2015) listed various harpacticoids associated with three members of the scleractinian coral genus Mussismilia Ortmann, 1890, including three unidentified species of Halectinosoma, but it is unlikely that they are genuine associates of these Brazilian endemic corals (Huys 2016).

In this paper, we describe both sexes of a new *Halectinosoma* species from the Bahía Blanca estuary and provide a key to species displaying divergent swimming leg

armature patterns and an updated key to genera of the family Ectinosomatidae. The status of some taxa that have been assigned to the wrong genus in the past is discussed.

#### Materials and methods

The study area is a recreational beach along the north coast of the Bahía Blanca estuary (38°54′42.9″S, 62°04′31.4″W), one of the largest estuaries in Argentina. It extends over about 2300 km² and comprises several tidal channels, extensive tidal flats (1150 km²) with patches of low salt marshes and islands (410 km²) (Piccolo et al. 2009). This shallow estuary (mean depth 10 m) is under anthropogenic impact due to human settlement, wastewater discharge, commercial harbour activities and industries (Arias et al. 2010). Enrichment with inorganic nutrients and organic matter (Freije et al. 2008), and the hydrological dynamics, bring on eutrophication and increase water turbidity (Piccolo and Perillo 1990; Piccolo et al. 2009).

The collecting locality is situated in the middle fringe of the mid-littoral beach at Arroyo Pareja (38°53′S, 62°07′W), 3 km from Punta Alta city, in southwestern Buenos Aires Province (Fig. 1a, b). The substrate is silt-clayey with average values of 87% mud and 13% sand, and no evidence of net sediment accumulation (Pratolongo et al. 2010). A mostly homogeneous land-scape alternates with patches of the saltmarsh cordgrass *Spartina alterniflora* Loisel, which represents the dominant vegetation in the intertidal zone (Calvo-Marcilese and Pratolongo 2009). The macrobenthos is dominated by an association of *Laeonereis acuta* Treadwell, 1923 (Annelida, Nereididae) and *Heleobia australis* (d'Orbigny, 1835) (Gastropoda, Cochliopidae) (Elías 1985; Elías and Bremec 1986).

Samples were taken with 3-cm-diameter plastic corers (7.07 cm²) during low tide, within patches dominated by *Spartina alterniflora*. The samples were fixed in 4% formalin. The specimens were separated by elutriation and sieved with 40-, 125- and 225-µm-diameter sieves (Higgins and Thiel 1988). Drawings of the habitus were prepared using the "sandwich mounting method" (Huys and Boxshall 1991). Body length measurements were made in lateral aspect from the anterior margin of the rostrum to the posterior margin of the caudal rami along the dorsal curvature of the specimen.

Specimens were dissected in lactic acid and the dissected parts were mounted on slides in lactophenol. Preparations were sealed with transparent nail varnish. All drawings were prepared using a camera lucida mounted on a Leitz DMR differential interference contrast microscope. The descriptive terminology is adopted from Huys et al. (1996); the term "surface-seta insertion line" was used according Clément and Moore's (2000) definition. Abbreviations used in the text are: *ae*, aesthetasc; *P1*–*P6*, first to sixth thoracopod; *exp.*, exopod; *enp*, endopod; *exp.* (*enp*)-1 (2, 3) to denote the proximal (middle, distal) segment of a ramus. The term "acrothek"



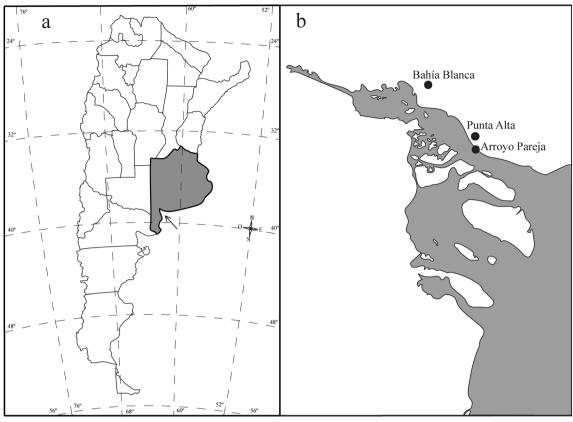


Fig. 1 a Map of Argentina with Buenos Aires Province in grey and sampling locality indicated by an arrow. b Map of Bahía Blanca estuary showing Arroyo Pareja (type locality); water in grey

denotes the trifid setal structure typically found on the apical margin of the distal antennulary segment (Huys and Iliffe 1998). Scale bars in the illustrations are in µm. Type specimens are deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Autonomous City of Buenos Aires, Argentina, and in the Natural History Museum (NHMUK), London, UK.

#### Results

Subclass **Copepoda** H. Milne Edwards, 1840

Order **Harpacticoida** G.O. Sars, 1903 Family **Ectinosomatidae** Sars, 1903

Genus *Halectinosoma* Vervoort, 1962

Type species: *Ectinosoma chrystalii* T. Scott, 1894 (cf. Opinion 2248; ICZN 2010).

Halectinosoma parejae sp. nov.

 three slides (MACN-In 40946), collected April 9, 2014; two adult ♂♂ dissected and mounted on four and six slides, respectively (MACN-In 40946), collected May 12, 2014; 10 ♂♂ preserved in ethanol (MACN-In 40946). *Paratypes deposited in NHMUK*: 10 ♀♀ and 10 ♂♂ preserved in ethanol (NHMUK-2017.48–57), collected April 9, 2014. All material collected by the senior author.

**Type locality**. Argentina, Buenos Aires Province; middle fringe of the mid-littoral beach at Arroyo Pareja (38°53′S, 62°07′W); silt-clayey sediment with *Spartina alterniflora* (Fig. 1).

Description of female (holotype). Body length 675 μm. Habitus fusiform (Fig. 2a). Colour of preserved specimens pale yellowish to colourless. Rostrum conical-triangular; about as long as wide; original demarcation from cephalothorax marked either side by membranous inserts; no sensillae were discernible (Fig. 2b). Cephalothorax gradually tapering anteriorly, representing one-third of total body length with four pairs of dorsal pores and straight, plain hyaline frill along posterior margin (Fig. 2a). Sensillar pattern on cephalothorax and body somites as illustrated (Figs. 2a and 3a–c). Somites bearing P2–P3 with several transverse rows of spinules dorsally; hyaline frill plain. Somite bearing P4 with transverse rows of spinules and incised hyaline frill. Somite bearing P5 with incised hyaline frill (Fig. 2a). Genital and first abdominal



Fig. 2 Halectinosoma parejae sp. nov., female holotype: a habitus, dorsal; b rostrum, dorsal; c antennule, ventral; d antenna with exopod shown in insert. Scale bars: 100 μm (a), 50 μm (b-d)



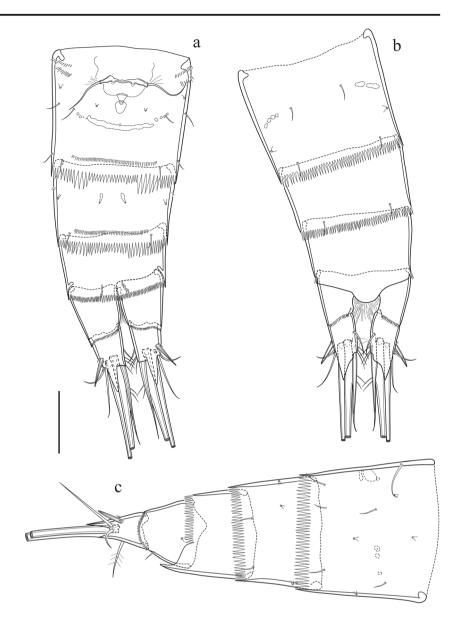
somite fused forming double-somite (Fig. 3a–c); original segmentation marked by sensillar pattern and by transverse internal chitinous stripe, which is unbroken midventrally (Fig. 3a), but represented by small patches of chitin dorsolaterally and, to a lesser extent, lateroventrally (Fig. 3b, c); number of patches variable. Genital double-somite with one pair of ventral, two pairs of lateroventral and one pair of dorsal pores and with rows of minute lateroventral spinules either side of genital slit, and a transverse row of spinules near ventral posterior margin; hyaline frill incised all around double-somite but it is uniform in length dorsally and laterally, while ventrally, the central part is shorter than the outer parts (Fig. 3a–c). Second abdominal somite with one pair of ventral, one pair of lateroventral and one pair of dorsolateral pores and with a

transverse row of spinules near ventral posterior margin; hyaline frill incised all around somite with the same shape as in genital double-somite (Fig. 3a–c). Penultimate somite with paired rows of spinules midventrally; posterior margin with incised lateroventral hyaline frill; sensillae absent on penultimate somite and on ventral/lateral surface of anal somite (Figs. 2a and 3a–c). Pseudoperculum well developed, unadorned and narrowly convex in shape (Fig. 3b). Anal somite deeply cleft medially; posterior margin with minutely incised hyaline frill; operculum absent (Fig. 3a–c).

Caudal ramus (Fig. 3a–c) slightly longer than maximum width and furnished with seven setae. Seta I spiniform, arising from ventral surface; with few spinules around its base. Setae II and III slender, closely set and issuing near distal outer corner,



Fig. 3 Halectinosoma parejae sp. nov., female holotype: a urosome, ventral; b urosome, dorsal; c urosome, lateral. Scale bar: 50 μm



seta III the more dorsal and accompanied by few spinules near its base. Setae IV–V well developed; smooth seta IV shorter (Fig. 2a) than bipinnate seta V; seta VI issuing from inner distal corner; well developed, as long as caudal ramus and anal somite combined; with few spinules along inner margin. Seta VII biarticulate at base; sparsely plumose; positioned near dorsal inner margin. Posterior edge of ramus terminating dorsally and ventrally with an acuminate lappet; inner margin of ramus with few spinules; ventral surface with pore.

Antennule (Fig. 2c). Short, robust, indistinctly 6-segmented; apical segment with incomplete suture on ventral surface running from posterior margin. Segment 1 longest and forming almost right angle with segment 2; with three ventral rows of minute spinules in proximal half and row of larger spinules near distal corner of posterior margin. Segment 3 with aesthetasc (length  $32 \mu m$ ) fused basally to long setae. All armature elements setiform

and smooth except for unipinnate spine near anterior margin of segment 2; all setae typically flaccid and with apical pore (not figured). Armature as follows: 1-[1], 2-[8+1 pinnate], 3-[7+(1+ae)], 4-[1], 5-[10+acrothek]. Acrothek consisting of 3 long swollen setae, distinctly fused at the base forming minute pedestal.

Antenna (Fig. 2d). Coxa well developed, without ornamentation. Basis longer than wide; outer margin with short row of strong spinules; distal half of abexopodal margin with row of long rigid setules, increasing in length towards endopod; insertion of exopod located far distally, near boundary with endopod. Endopod 2-segmented. Enp-1 longest, unarmed and without ornamentation. Enp-2 with few strong spinules near inner proximal corner and two surface rows of very large spinules; lateral armature consisting of two short pinnate spines; distal armature consisting of six pinnate spines of different length, outermost of which fused at base to sparsely



plumose seta. Exopod large, reaching beyond distal margin of enp-2; 3-segmented; exp.-1 forming virtually right angle with remaining segments; exp.-1 elongate, about as long as exp.-3 and with short unipinnate spine in distal quarter; exp.-2 slightly longer than wide, with strong unipinnate spine; exp.-3 with row of spinules in distal quarter and two massive spines, inner one longest and bipinnate.

Labrum (Fig. 4a) prominent and terminating in a median spinous projection.

Mandible (Fig. 4b, c). Coxa (Fig. 4b) strongly chitinised; gnathobase armed with one articulating spine at ventral corner, a strongly chitinised bidentate tooth medially and a dorsal extension with five pointed projections. Palp (Fig. 4c) biramous. Basis elongate; with few minute spinules near base of segment and with tuft of elongate setules along proximal inner margin; distal inner

sion with five pointed projections. Palp (Fig. 4c) birar elongate; with few minute spinules near base of segme tuft of elongate setules along proximal inner margin;

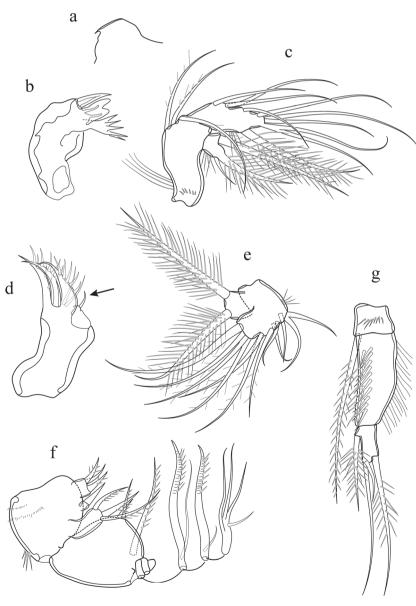
Fig. 4 Halectinosoma parejae
sp. nov., female holotype: a
labrum, lateral; b mandibular
gnathobase; c mandibular palp; d

maxillule, fused praecoxa and

coxa (coxal endite marked by arrow); **e** maxillulary palp; **f** 

maxilla, insert showing disarticulated endopod; **g** maxilliped. Scale bar: 50 μm margin with three sparsely pinnate setae, of which distal one characteristically crosses over the segment towards the outer margin. Endopod elongate; inner margin with five smooth setae; apex with four naked setae, of which outermost two fused at base; outer margin with strong multipinnate seta and few long spinules halfway along the segment margin. Exopod one-segmented, small, with few long spinules issuing from outer margin; with two strong multipinnate setae (apical one fused basally to segment) and one short, naked seta.

Maxillule (Fig. 4d, e). Praecoxa (Fig. 4d) a strongly chitinised segment; arthrite with three strongly curved, unipinnate spines, of which only middle one is articulating at base; posterior surface with two short naked setae. Coxa apparently incorporated in praecoxa; represented by vestigial endite with minute seta (marked by arrow in Fig. 4d). Palp bilobate; 1-segmented but





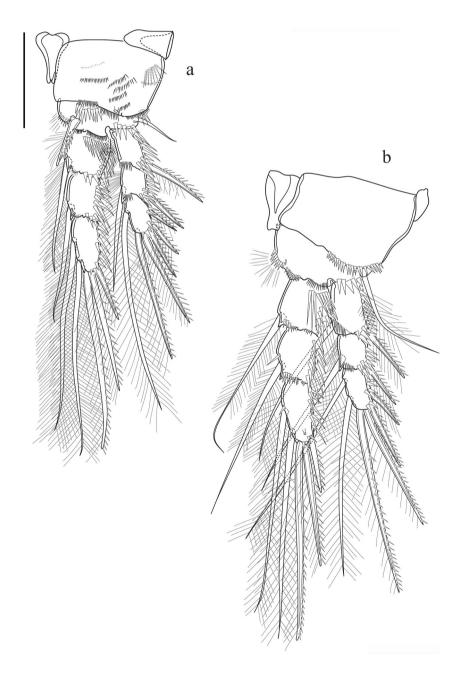
original boundary of exopod marked by suture on anterior surface. Basis with few spinules along inner margin; endites largely incorporated into segment, proximal endite represented by three naked setae (two of which fused at base), distal endite represented by one sparsely plumose and two naked setae. Endopodal lobe with two lateral setae; apical margin with four setae, outermost of which distinctly swollen; all elements sparsely plumose. Exopodal lobe with two strong multipinnate setae.

Maxilla (Fig. 4f) non-prehensile, comprising syncoxa, allobasis and 3-segmented endopod. Syncoxa with two surface rows of minute spinules and few larger spinules near outer distal corner; with three endites, of which middle one markedly smaller; proximal endite with three short spines, two of them pinnate; middle

endite with one naked spine; distal endite cylindrical and recurved, located in membranous area at syncoxa–allobasis joint, with one spine and two pinnate setae. Allobasis robust, with strongly convex inner margin; armed with two setae along inner distal corner (derived from basis) and one strong pinnate seta on posterior surface (derived from incorporated endopod segment). Endopod condensed; enp-1 and -2 each with geniculate spine and naked seta (minute on enp-2); enp-3 with three basally fused setae and with a fourth shorter seta issuing from their common base; geniculate spines on enp-1 and -2 typically curved and pinnate in distal half.

Maxilliped (Fig. 4g) stenopodial and moderately slender; comprising syncoxa, basis and 1-segmented endopod. Syncoxa with long pinnate seta, reaching beyond apex of endopod, and

Fig. 5 Halectinosoma parejae sp. nov., female holotype: a P1, anterior; b P2, anterior. Scale bar: 50 μm





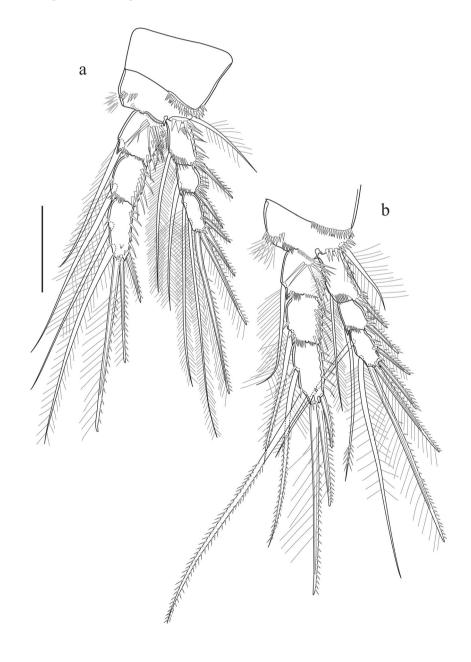
one surface row of spinules. Basis unarmed; with long setules along outer margin, double row of strong spinules on anterior surface, and single row of finer spinules along inner margin. Endopod with strong multipinnate seta laterally; apical armature consisting of one bipinnate and two naked setae.

Swimming legs (Figs. 5 and 6) with 3-segmented rami, endopods typically longer than exopods. Praecoxa represented by indistinct U-shaped sclerite wrapped around outer proximal corner of coxa (only illustrated for P1–P2; Fig. 5). Intercoxal sclerites narrow; without ornamentation. Coxae with anterior row of spinules around outer half of free distal margin. Bases with naked (P1) or plumose (P2–P4) outer seta issuing from outer corner; inner distal margin with spinules anteriorly and setular tuft posteriorly. First and second exopodal segments with anterior incised hyaline frill, near inner distal margin; inner distal corner of exp.-2 drawn

out into spinous process; outer margins of exopodal segments with spinular ornamentation as shown; inner margin of exp.-2 with setular row; outer and distal exopodal spines of all segments with outer spinules and inner setules; inner exopodal elements setiform and plumose except for inner seta of P4 exp.-2 being bipinnate in distal quarter (Fig. 6b). Endopodal segments with spinular ornamentation along outer margin as shown; anterior surface of enp-1 with row of very long spinules in addition to smaller ones; part of distal margin of enp-1 and -2 with incised hyaline frill on anterior surface; outer and distal spines of enp-3 with outer spinules and inner setules; inner element of enp-1 setiform and plumose.

P1 (Fig. 5a) with elaborate spinular ornamentation on anterior and posterior surfaces of coxa. Basis with strong inner spine, bearing outer spinules and inner setules. Inner setae of enp-2 and -3 plumose.

**Fig. 6** *Halectinosoma parejae* sp. nov., female holotype: **a** P3, anterior; **b** P4, anterior. Scale bar: 50 μm





P2–P4 enp-2 and -3 with inner setae either plumose (P2–P3) or bipinnate (P4); inner distal seta of P4 enp-3 extremely enlarged (Fig. 6b). Inner distal corner of P2–P4 enp-2 produced into small spinous process; P2–P4 enp-3 with anterior pore near distal margin.

Armature formulae as follows:

	Exopod	Endopod
P1	0.1.123	1.1.221
P2	1.1.222	1.1.221
P3	1.1.222	1.1.221
P4	1.1.222	1.1.221

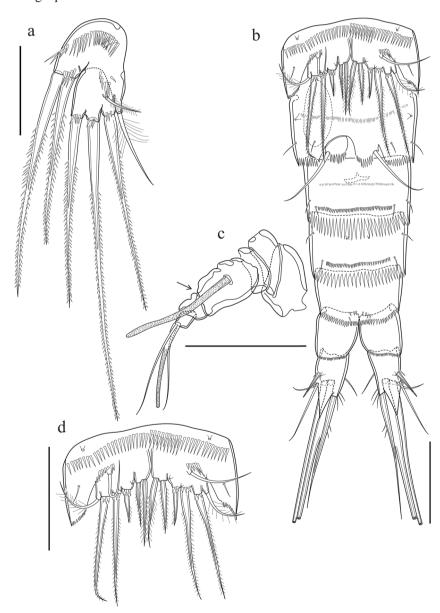
P5 (Fig. 7a). Exopod longer than wide and confluent with baseoendopod on anterior surface only. Baseoendopod slightly shorter than greatest width; with transverse row of large spinules

on anterior surface. Endopodal lobe very short, reaching proximal fifth of exopod; armed with two spinulose setae, outer one slightly shorter than inner one, not reaching beyond tip of innermost seta of exopod; with spinules at base of outer seta. Outer expansion with plumose basal seta. Exopod with three terminal setae each issuing from spinulose lobe: inner and outer setae subequal in length and distinctly shorter than middle seta; surface-seta plumose accompanied by a row of spinules at the insertion site.

Gonopores fused medially forming common genital slit (Fig. 3a), closed off by vestigial fused sixth legs bearing sparsely plumose outer seta on either side. Copulatory pore small, located midventrally in proximal half of genital double-somite. Ovigerous female bearing one egg sac.

**Description of male**. Body length 454  $\mu$ m. Markedly smaller than in female. Sexual dimorphism expressed in antennule, P5, P6 and in urosomal segmentation.

Fig. 7 Halectinosoma parejae sp. nov., female holotype (a), male paratype (b–d): a P5, anterior; b urosome, ventral; c antennule, armature omitted and geniculation marked by arrow; d P5, anterior. Scale bars: 50 μm





Ornamentation of body generally as in female, except for small differences such as genital somite with transverse spinule row and one pair of lateroventral pores on ventral surface; first abdominal somite with additional spinule row on ventral surface and hyaline frill with a central part longer than outer parts, while female with hyaline frill shorter in central part than outer parts; second abdominal somite with two pores and four sensillae ventrally and uniform hyaline frill, while female with four pores and two sensillae ventrally and hyaline frill shorter in central part than outer parts (compare Figs. 3a and 7b).

Antennule (Fig. 7c) short, 6-segmented; haplocer, with geniculation located between segments 4 and 5 (marked by arrow). All segments except apical one strongly chitinised. Segment 4 with long aesthetasc (length 51  $\mu$ m), not fused at base to seta. Apical segment with apical acrothek consisting of two slender setae and one aesthetasc (length 75  $\mu$ m).

P5 (Fig. 7d). Baseoendopod and exopod fused forming common plate which is confluent with somite. Endopodal lobe armed with two pinnate setae, outer one slightly shorter than inner one. Outer small setophore with a slender plumose basal seta. Exopodal lobe with three pores; with one short inner and two long pinnate spines around stepped free margin, each issuing from a spinulose lobe; base of smooth surface-seta covered by short row of spinules.

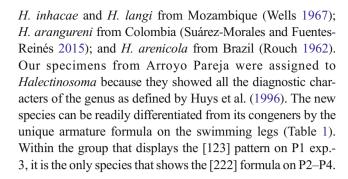
P6 (Fig. 7b). Sixth pair of legs asymmetrical with either left or right P6 fused to ventral wall of genital somite, other member articulating and closing off single functional gonopore; each P6 represented by a small oval plate with deeply incised free margin and one smooth seta at outer distal corner. Spermatophore elongate-oval; about 2.5 times as long as wide; length  $40~\mu m$ .

Variability. Only one out of 20 dissected female specimens lacked the inner seta on the proximal exopodal segment of P4. The specimen was included in the type series as a paratype. Body length varied between 641 and 759  $\mu$ m (n=10; mean = 688  $\mu$ m, standard deviation = 40  $\mu$ m) in females and between 444 and 528  $\mu$ m (n=10; mean = 479  $\mu$ m, standard deviation = 25  $\mu$ m) in males. Some variability was observed in the number of dorsolateral chitinous patches forming part of the transverse internal chitinous stripe of the female genital double-somite.

**Etymology**. The new species is named in honour of Joaquín Fernández Pareja, a pioneer during the 1823 expedition leading to the foundation of Bahía Blanca city in 1828.

#### **Discussion**

With the description of *Halectinosoma parejae* sp. nov., the number of valid species in this genus has risen to 69. Only eight species have their type locality in the Southern Hemisphere: *H. hydrofuge* and *H. otakoua* from New Zealand (Wells et al. 1982); *H. fusiforme*, *H. fusum*,



# Some notes on species with incorrect generic assignment

A number of species have been removed from *Halectinosoma* or are considered as having a doubtful taxonomic status. Huys and Bodin (1997) and Seifried (1997) remarked that H. porosum Wells, 1967 displayed the diagnostic features of Ectinosoma Boeck, 1865 and, consequently, reassigned it to this genus as E. porosum (Wells, 1967). Re-examination of the mouthparts of *Halectinosoma arcticum* (Olofsson, 1917) prompted Clément and Ólafsson (2001) to remove the species from its uncertain position in Halectinosoma to Pseudobradya Sars, 1904. Karanovic and Pesce (2001) argued that H. uniarticulatum Borutzky, 1972 cannot belong to Halectinosoma or be placed with confidence in any other known genus in the family; pending careful re-examination, Wells (2007) subsequently ranked it species incertae sedis in the Ectinosomatidae. Clément and Moore (2000, 2007) concluded that Ectinosoma finmarchicum T. Scott, 1903 was based on a composite of two species, H. elongatum Sars, 1904 and H. angulifrons Sars, 1919, and should be discarded. Wells (2007) considered it a species inquirenda, but since the taxonomic identity of E. finmarchicum cannot be determined from its existing name-bearing type, it is here ranked as a nomen dubium. Lang (1965) transferred Ectinosoma japonica Miura, 1964 to Halectinosoma but noted the incompleteness of the description of the female, and the discrepancies between the text and the illustrations. According to Karanovic and Pesce (2001), this species requires detailed re-examination and should be excluded from Halectinosoma if the original description turns out to be correct. Wells (2007) considered it a species inquirenda in Halectinosoma. Likewise, Ectinosoma (H.) sp. sensu Bodin (1964) from the Gulf of Marseille, southern France, is removed from the genus and considered species incertae sedis in the Ectinosomatidae. Without any additional information on the cephalic appendages and swimming legs, it is impossible to decide on the generic assignment of this species.

Coull (1986) noted two unique features that differentiated his new species *P. lanceta* from its congeners in *Pseudobradya*: (a) the morphology of the P5 of both sexes,



including shape, size and the presence of lancet-shaped spines on the exopod and endopodal lobe, and (b) the presence of four setae (instead of three) on the maxillipedal endopod. Recent redescriptions of members of *Pseudobradya* (e.g. Huys et al. 1996; Clément and Ólafsson 2001; Suárez-Morales and Fuentes-Reinés 2015) have shown that the pattern and number (one outer, one inner, two apical and usually fused basally) of armature elements on the maxillipedal endopod in this genus are essentially the same as those in *Halectinosoma*, and that the second apical seta has generally

been overlooked in earlier descriptions. Coull's (1986) decision to place *P. lanceta* in *Pseudobradya* was based solely on the presence of a 3-segmented maxillary endopod, a character of doubtful significance. In reality, comparison with the morphologically very similar *Halectinosoma arenicola* Rouch, 1962 shows that it was assigned to the wrong genus and must be transferred to *Halectinosoma* as *H. lancetum* (Coull, 1976) comb. nov. Both species have the lancet-shaped spines on the P5 and resemble each other in the shape of the rostrum and maxilliped. The only differences that can be deduced from

Table 1 Swimming leg armature formulae of *Halectinosoma* species<sup>a</sup>. Divergent patterns indicated in **bold** 

	P1		P2		Р3		P4	
	exp.	enp	exp.	enp	exp.	enp	exp.	enp
Typical condition <sup>b</sup>	0.1.123	1.1.221	1.1.223	1.1.221	1.1.323	1.1.221	1.1.323	1.1.221
H. fusum Wells, 1967	0.1.123	1.1.221	1.1.223	1.1.221	1.1.223	1.1.221	1.1.223	1.1.221
H. hydrofuge Wells, Hicks & Coull, 1982	0.1.123	1.1.221	1.1.223	1.1.221	1.1.223	1.1.221	1.1.223	1.1.221
H. distinctum (Sars, 1920)	0.1.123	1.1.221	1.1.223	1.1.221	1.1.223	1.1.221	1.1.223	1.1.221
H. gothiceps (Giesbrecht, 1881)	0.1.123	1.1.221	1.1.223	1.1.221	1.1.222	1.1.221	1.1.322	1.1.221
H. paragothiceps Clément & Moore, 2007	0.1.123	1.1.221	1.1.223	1.1.221	1.1.222	1.1.221	1.1.322	1.1.221
H. erythrops (Brady, 1880)	0.1.123	1.1.221	1.1.123	1.1.221	1.1.122	1.1.221	1.1.122	1.1. <b>121</b>
H. unicum Lang, 1965	0.1.123	1.1.221	1.1.222	1.1.221	1.1.322	1.1.221	1.1.322	1.1.221
H. smirnovi (Chislenko, 1967)	0.1.123 <sup>c</sup>	1.1.221 <sup>c</sup>	1.1.222	1.1.221	1.1.322	1.1.221	1.1.322	1.1.221
H. parejae sp. nov.	0.1.123	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221
H. islandicum Apostolov. 2007	0.1.122	1.1.221	1.1.222	1.1.221	1.1.322	1.1.221	1.1.222	1.1.221
H. oblongum (Kunz, 1949)	$0.1.122^{d}$	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221
H. curticorne (Boeck, 1873)	0.1.122	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221
H. abyssicola Bodin, 1968	0.1.122	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221
H. arangureni Suárez-Morales & Fuentes-Reinés, 2015	0.1.122	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221
H. langi Wells, 1967	0.1. <b>122</b> <sup>e</sup>	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221	1.1.222	1.1.221
H. gracile (Scott & Scott, 1896)	0.1.122	1.1.221	Unknown	Unknown	Unknown	Unknown	1.1. <b>122</b>	1.1.221
H. tenuireme (Scott & Scott, 1896)	0.1. <b>122</b>	1.1. <b>220</b>	0.1.222	1.1.220	0.1.222	1.1.220	<b>0</b> .1. <b>222</b>	1.1.220

<sup>&</sup>lt;sup>a</sup> The following species have been regarded problematic or of doubtful status due to their deficient or incomplete original descriptions and were consequently excluded for further comparison: *H. sarsi* Boeck, 1873 – *species incertae sedis* (Clément and Moore 1995); *H. spinipes* (Brady, 1880) – *species dubia* (Clément and Moore 1995); *H. finmarchicum* (T. Scott, 1903) – *nomen dubium* (this study); *H. wiesei* (Smirnov, 1932) – species *incertae sedis* (Wells 2007); *H. japonicum* (Miura, 1964) – *species inquirenda* (Wells 2007); *H. limnophilum* (Štěrba, 1968) – species *incertae sedis* (Wells 2007); *H. uniarticulatum* Borutzky, 1972 – *species incertae sedis* (Wells 2007). Both *H. longicorne* (Scott & Scott, 1896) and *H. concinnum* (Akatova, 1935) were not included because the armature formulae of at least P2–P3 are unknown



b This swimming leg armature pattern is the ancestral condition in the genus, currently being shared by the following 49 valid species: *H. abrau* (Kričagin, 1877); *H. chrystalii* (T. Scott, 1894); *H. armiferum* (Scott & Scott, 1896); *H. herdmani* (Scott & Scott, 1896); *H. brevirostre* (Sars, 1904); *H. elongatum* (Sars, 1904); *H. mixtum* (Sars, 1904); *H. neglectum* (Sars, 1904); *H. brunneum* (Brady, 1905); *H. angulifrons* (Sars, 1919); *H. proximum* (Sars, 1919); *H. clavatum* (Sars, 1920); *H. tenerum* (Sars, 1920); *H. arenicola* (Rouch, 1962); *H. canaliculatum* (Por, 1964); *H. diops* (Por, 1964); *H. inopinatum* (Por, 1964); *H. kunzi* Lang, 1965; *H. longisetosum* Lang, 1965; *H. ornatum* Lang, 1965; *H. similidistinctum* Lang, 1965; *H. fusiforme* Wells, 1967; *H. inhacae* Wells, 1967; *H. gascognense* Bodin, 1968; *H. dimorphum* Coull, 1970; *H. cooperatum* Bodin, Bodiou & Soyer, 1971; *H. monardi* Soyer, 1972; *H. paradistinctum* Soyer, 1972; *H. travei* Soyer, 1972; *H. valeriae* Soyer, 1972; *H. winonae* Coull, 1975; *H. perforatum* Itô, 1981; *H. otakoua* Wells, Hicks & Coull, 1982; *H. lancetum* (Coull, 1986) comb. nov.; *H. argyllensis* Clément & Moore, 1995; *H. chislenki* Clément & Moore, 1995; *H. denticulatum* Clément & Moore, 1995; *H. pseudosarsi* Clément & Moore, 2000; *H. bitannicum* Clément & Moore, 2000; *H. huysi* Clément & Moore, 2000; *H. mandibularis* Clement & Moore, 2007; *H. latisetifera* Clement & Moore, 2007; *H. mandibularis* Clement & Moore, 2007; *H. foveolata* Kim, Jung & Yoon, 2017; *H. pseudarenicola* sp. nov.

<sup>&</sup>lt;sup>c</sup> Chislenko (1967) did not describe leg 1; observations based on Letova's (1982) partial redescription

<sup>&</sup>lt;sup>d</sup> Kunz (1949) described the pattern as 0.1.212

<sup>&</sup>lt;sup>e</sup> Wells (1967) erroneously lists the formula as 0.1.123

Rouch's (1962) concise description of *H. arenicola* and Coull's (1986) illustrations of *H. lancetum* relate to the antennary exopod (proximal segment with small seta), P5 (differences in relative lengths of setae/spines) and caudal rami (inner margin distinctly concave). *Halectinosoma lancetum* is also closely related to the species identified by Itô (1973) as *H. arenicola* (= *H. pseudarenicola* sp. nov.; see below) with which it shares the elongate rectangular rostrum, the unusually slender, elongate antennule (not figured by Rouch (1962), the shape of the maxilliped (with distinctly convex outer margin) and the enlarged spines on the P5. Both species differ primarily in body size, the shape and length of the elements on the P5 in both sexes, and the ventral surface ornamentation of the posterior half of the female genital double-somite.

Three species that were previously placed in *Halectinosoma* are here assigned to *Pseudobradya: H. spinicauda* (Wells, 1961) from the Isles of Scilly, H. pterinum Moore, 1974 from the Isle of Man and H. paraspinicauda Bodin (1979) from La Rochelle, France. Moore (1974) himself pointed out that the mouthparts of his new species H. pterinum were more similar to those of Pseudobradya pulchera Lang, 1965 than to other species of Halectinosoma. Bodin (1979) also originally assigned his species to the genus Halectinosoma and remarked on the striking similarity with H. spinicauda and H. pterinum, particularly in the shape and ornamentation of the female P5, and the modification of caudal ramus setae III and VI into pinnate spines. All three species are here formally allocated to Pseudobradya based on the morphology of the mandibular gnathobase, maxilla and maxilliped. Pseudobradya paraspinicauda (Bodin, 1979) comb. nov. differs from P. spinicauda (Wells, 1961) comb. nov. primarily in the following characters: (a) the proximal antennary exopod segment is unarmed instead of displaying a small seta, (b) P3-P4 exp.-3 has three inner setae instead of two, (c) the middle and distal inner elements of P4 exp.-3 are setiform instead of spiniform, (d) the inner exopodal seta of the female P5 is shorter and its outer endopodal spine is more robust and (e) the caudal rami are distinctly shorter in P. paraspinicauda. Features differentiating P. pterina (Moore, 1974) comb. nov. from the latter include: (a) the presence of a pigmentary patch on the first antennulary segment, (b) proximal antennary exopod segment with a small seta instead of being unarmed, (c) maxillipedal syncoxa with a very long seta extending far beyond the distal margin of the endopod (instead of two short setae), (d) the inner exopodal seta of the female P5 is longer than the middle one (instead of shorter) and the outer endopodal element is setiform and slender (instead of spiniform and robust) and (e) the caudal rami are distinctly longer.

Nicholls' (1939) description of *Ectinosoma littoralis* is incomplete and probably incorrect (e.g. according to his armature formula, P3 exp.-2 lacks the inner seta). Lang (1965) transferred the species to *Halectinosoma* as *H. littorale*; however, the morphology of the mandibular gnathobase, maxilla and maxilliped suggest that it should be removed to

*Pseudobradya*. The species is here formally placed in that genus as *species inquirenda*.

## Taxonomic status of *H. smirnovi* (Chislenko, 1967) and *H. arenicola* (Rouch, 1962) sensu Itô (1973)

Bodin (1971, 1997) considered the possibility that *H. smirnovi*, originally described from the White Sea (Chislenko 1967), is merely a junior synonym of *H. unicum* Lang, 1965 from the Californian coast, while other authors (Coull 1975; Apostolov 2007) effectively considered them as conspecific. The species does not feature in Wells' (2007) tabular keys. A proper justification for this course of action has never been provided and the species, which has been redescribed by Letova (1982), is here reinstated.

Rouch (1962) provided a brief first description of H. arenicola from a Brazilian beach, while Itô (1973) presented a subsequent detailed description of material, ascribed to H. arenicola, from a Japanese sandy beach. As pointed out by Clément and Moore (2000), the Japanese material has strong similarities with the original description in some respects, but there are also distinct differences: (a) cephalothorax with large bright-red dorsal spot near the anterior margin in the Japanese material (absent in the type material), (b) proximal segment of antennary exopod without the small seta illustrated by Rouch (1962), (c) inner margin of caudal ramus straight (distinctly concave in the type material) and (d) the shape of endopodal spines  $(\mathcal{L})$  and relative length of exopodal elements (both sexes) of P5 are different. Clément and Moore (2000) noted that, in view of the small morphological details that differentiate many of the species of *Halectinosoma*, it cannot be assumed that the specimens from Brazil and Japan are conspecific. Their recommendation is followed here and, pending a more detailed examination of material from the type locality in Recife, Itô's (1973) material is attributed separate specific status as Halectinosoma pseudarenicola sp. nov. Zaleha (2001) recorded the H. arenicola from peninsular Malaysia and figured ventral views of the urosome for both sexes; it is conceivable that she was dealing with *H. pseudarenicola* sp. nov. The species is closely related to both H. lancetum and H. arenicola (see above for a discussion of the main differences). Itô (1973) pointed out some minor differences in the endopod of the maxilliped and maxilla between his material and Rouch's (1962) illustrations of *H. arenicola*, but these are most likely attributable to deficiencies in the latter. The frontal portion of the cephalothorax has a large bright-red spot which looks different from a typical nauplius eye but may have a photosensitive function (Itô 1973). No morphological variability was observed. The female specimen figured by Itô (1973: figs 5, 6(1-8) and 7) is here designated as the holotype in accordance with International Commission on Zoological Nomenclature (ICZN) Arts 72.5.6 and 73.1.4.



# Key to species of *Halectinosoma* with divergent armature patterns in P1–P4

Fifty species of *Halectinosoma* differ from *H. parejae* sp. nov. by displaying the ancestral number of armature elements on legs 1–4 (Table 1); nine of them were re-examined in detail by Clément and Moore (1995, 2000) and another 13 species were newly described by Clément and Moore (1995, 2000, 2007). The key below allows the identification of 17 species of *Halectinosoma* whose swimming legs diverge from the plesiomorphic condition (Table 1).

- 1 P1 exp.-3 with three outer spines [formula 123] 2.
- P1 exp.-3 with two outer spines [formula 122] 10.
- 2 P3–P4 exp.-3 with three outer spines 3.
- P3–P4 exp.-3 with two outer spines 5.
- 3 Innermost seta of  $\bigcirc$  P5 exopod reduced *H. distinctum* (Sars, 1920).
  - Innermost seta of  $\bigcirc$  P5 exopod well developed 4.
- 4 First exopodal segment of antenna without armature *H. fusum* Wells, 1967.
- First exopodal segment of antenna with one seta *H. hydrofuge* Wells, Hick & Coull, 1982.
  - 5 P2 exp.-3 with three outer spines 6.
  - P2 exp.-3 with two outer spines 8.
- 6 P2–P4 exp.-3 with one inner seta; P4 enp-3 with one inner seta *H. erythrops* (Brady, 1880).
- P2-P3 exp.-3 with two inner seta, P4 exp.-3 with three inner setae; P4 enp-3 with two inner setae 7.
- 7 Cephalothorax with a pigmented patch *H. gothiceps* (Giesbrecht, 1881).
- Pigmented patch on cephalothorax absent
   H. paragothiceps Clément & Moore, 2007.
  - 8 P3-P4 exp.-3 with three inner setae 9.
  - P3-P4 exp.-3 with two inner setae *H. parejae* sp. nov.
- 9 Inner part of  $\bigcirc$  P5 endopodal lobe produced into globular extension *H. unicum* Lang, 1965.
- Distal margin of  $\mathcal{P}$  P5 endopodal lobe virtually straight *H. smirnovi* (Chislenko, 1967).
  - 10 P1-P4 enp-3 with outer spine 11.
- P1–P4 enp-3 without outer spine *H. tenuireme* (Scott & Scott 1896)
  - 11 P4 exp.-3 with two inner setae 12.
- P4 exp.-3 with one inner seta *H. gracile* (Scott & Scott, 1896).
  - 12 P3 exp.-3 with two inner setae 13.
- P3 exp.-3 with three inner setae *H. islandicum* Apostolov, 2007.
- 13 Inner seta of  $\stackrel{\frown}{\hookrightarrow}$  P5 endopodal lobe about four times as long as outer one *H. abyssicola* Bodin, 1968.
- Setae of  $\stackrel{\bigcirc}{\hookrightarrow}$  P5 endopodal lobe subequal or inner seta slightly longer than outer one 14.
  - 14 First exopodal segment of antenna unarmed 15.
  - First exopodal segment of antenna with one seta 16.

- 15 Antennule with darkly pigmented patch on first segment *H. curticorne* (Boeck, 1873).
- Antennule without such pigmented patch on first segment *H. langi* Wells, 1967.
- 16 Setae of  $\stackrel{\bigcirc}{+}$  P5 endopodal lobe considerably shorter than exopodal setae *H. oblongum* (Kunz, 1949).
- Setae of  $\bigcirc$  P5 endopodal lobe subequal or slightly shorter than exopodal setae *H. arangureni* Suárez-Morales & Fuentes-Reinés, 2015.

#### Updated key to genera of Ectinosomatidae

The recent discovery of the new genus *Pontobradya* Apostolov, 2011 from 2350 to 2974 m depth off the coast of Iceland requires an update of Kihara and Huys' (2009) generic key. The key below is applicable to both sexes of members of the 22 currently recognised valid genera in the Ectinosomatidae.

- 1. Body cylindrical with cephalothorax rectangular in dorsal aspect; body approximately the same width throughout its length 2.
- Body fusiform with cephalothorax sub-triangular in dorsal aspect; greatest body width usually at posterior margin of cephalothorax; urosome gradually tapering towards the posterior end 7.
- Body with dorsoventrally depressed prosome, clearly wider than urosome 20.
- 2. Antennary exopod 2-segmented; maxilla prehensile, with major articulation between elongate syncoxa and elongate allobasis *Noodtiella* Wells, 1965.
- Antennary exopod 1- or 3-segmented; maxilla not prehensile, with at most a slight angle between syncoxa and allobasis 3.
- 3. Endopods P2–P4 2-segmented *Ectinosomoides* Nicholls, 1945.
  - Endopods P2-P4 3-segmented 4.
- 4. Anal somite with dorsal armature of claws, lappets or spiniform processes around anal opening; P5 exopod with three marginal and one surface seta *Arenosetella* Wilson, 1932.
  - Anal somite without such ornamentation 5.
  - 5. Antennary exopod 1-segmented *Tetanopsis* Brady, 1910.
  - Antennary exopod 3-segmented 6.
- 6. Female P5 with foliaceous setae on exopod and baseoendopod, exopod with three marginal and no surface setae; male P5 exopod with four normal marginal setae *Oikopus* Wells, 1967.
- P5 with normal setae on exopod and baseoendopod in both sexes, exopod with three marginal and typically a surface seta [absent in *Hastigerella noodti* Soyer, 1974 = *Glabrotelson soyeri* (Bodin, 1976)] *Glabrotelson* Huys in Kihara & Huys, 2009.



- 7. P1–P4 endopods 2-segmented *Pseudectinosoma* Kunz, 1935.
- P1 endopod 2- or 3-segmented, P2-P4 endopods 3-segmented 8.
  - 8. P1 endopod prehensile 9.
  - P1 endopod not prehensile 12.
  - 9. P1 endopod 2-segmented 10.
- P1 endopod 3-segmented Klieosoma Hicks & Schriever, 1985.
  - 10. P1–P2 exp.-3 with two outer elements 11.
- P1–P2 exp.-3 with three outer elements *Halophytophilus* Brian, 1919.
- 11. Antennule with large spine on segment 2 (and often segments 1 and 3); antennary exopod rudimentary, with 1–3 small setae; P1 enp-2 with four elements (1–2 pinnate and claw-like) *Bradyellopsis* Brian, 1925.
- Armature elements on antennulary segments 1–3 setiform; antennary exopod well developed and 3-segmented; P1 enp-2 with six elements (outer one bifid and claw-like) *Chaulionyx* Kihara & Huys, 2009.
- 12. Maxilla prehensile, with syncoxa and allobasis forming right angle; P5 exopod poorly developed, short, fused to baseoendopod in female and distinct in male, with three marginal and no surface setae; body very small ( $< 300 \mu m$ ) *Sigmatidium* Giesbrecht, 1881.
  - These characters not combined 13.
- 13. P5 exopod and baseoendopod fused, forming a single plate in both sexes 14.
  - P5 exopod and baseoendopod at least partly discrete 15.
- 14. P1–P4 exp.-3 with 5, 6, 6, 6 elements, respectively; male P6 unarmed; body of female small (<  $400 \mu m$ ); continental groundwater *Rangabradya* Karanovic & Pesce, 2001.
- P1–P4 exp.-3 with 6, 7, 8, 8 elements, respectively; male P6 with two setae; body of female large ( $\geq$  1200  $\mu$ m); marine, usually deepwater *Parabradya* Lang, 1944.
- 15. Integument of somites with distinctive subrectangular pores; P5 exopod with four marginal setae *Ectinosoma* Boeck, 1865.
- Integument of somites without distinctive subrectangular pores; P5 exopod with three marginal setae and one seta on anterior surface 16.
- 16. Mandible with rudimentary gnathobase, elongate basis and filiform rami, each terminating in 2–3 setae; antennary exopod without lateral spines *Ectinosomella* Sars, 1910.
  - These characters not combined 17.
- 17. Third segment of female antennule three times as long as wide; mandibular endopod with one strong seta laterally; P1–P4 exp.-3 with two outer spines; planktonic (occasionally in sediment) *Microsetella* Brady & Robertson, 1873.
  - These characters not combined 18.
- 18. Body comparatively robust with prosome–urosome separation usually distinct (exception: *Bradya kurtschminkei* Seifried & Martínez Arbizu, 2008 with dorsoventrally flattened habitus); antenna with two setae on proximal exopod

- segment and one seta on proximal endopod segment; mandibular exopod with at least five setae; maxilliped robust with short endopod usually fused at an angle with basis and bearing four conspicuous setae *Bradya* Boeck, 1873.
- Body comparatively slender with no sharp separation between prosome and urosome; antenna with less than two setae on proximal exopod segment (except *Pseudobradya ambigua* Sars, 1920 with two) and no seta on proximal endopod segment; mandibular exopod generally with fewer than five setae; maxilliped usually slender and straight with discrete endopod bearing one small and four conspicuous setae 19.
- 19. Antennule with or without dark pigment spot within the proximal three segments; maxilla prehensile, allobasis usually truncate distally and carrying 3-segmented endopod (although endopod sometimes very small and segmentation difficult to discern; reduced to a narrow 3-segmented cylinder in *P. leptognatha* Sars, 1920); maxilliped short and robust *Pseudobradya* Sars, 1904.
- Antennule without pigment spot; maxilla with at most a slight angle between syncoxa and allobasis, the latter generally attenuating distally, endopod 3-segmented but always small, its morphology not clearly discernible; maxilliped generally slender *Halectinosoma* Vervoort, 1962.
- 20. P1 endopod 3-segmented; ♀ P5 exopod with four marginal elements *Pontobradya* Apostolov, 2011.
- P1 endopod 2-segmented; ♀ P5 exopod with three marginal elements and one surface-seta *Peltobradya* Médioni & Soyer, 1968.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

**Field study** Permits and approval of field or observational studies have been obtained by the authors.



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