



A new genus of Ectinosomatidae (Copepoda, Harpacticoida) from sublittoral sediments in Ubatuba, São Paulo State (Brazil), an updated key to genera and notes on Noodtiella Wells, 1965

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Abstract

Both sexes of a new genus and species of Ectinosomatidae (Copepoda, Harpacticoida) from sublittoral sediments collected on the inner continental shelf in Ubatuba, São Paulo State (Brazil) are described in detail. Chaulionyx gen. n. (type species: C. paivacarvalhoi sp. n.) differs from all known genera in the presence of a conspicuous bifid spine on the prehensile P1 endopod. It can be differentiated from other genera with a prehensile endopod (Halophytophilus Brian, 1919; Bradyellopsis Brian, 1925; Klieosoma Hicks & Schriever, 1985) by the presence of distinctive subrectangular middorsal pores on the urosomites and the unarmed male sixth legs. The genus Lineosoma Wells, 1965 is recognized as a paraphyletic taxon and relegated to a junior subjective synonym of Noodtiella Wells, 1965. Arenosetella pectinata Chappuis, 1954a is removed from its floating position in Ectinosomoides Nicholls, 1945, transferred to the genus Noodtiella as N. pectinata comb. n. and considered the senior subjective synonym of N. toukae Mitwally & Montagna, 2001. Dichotomous keys are provided for the identification of the 18 valid species of Noodtiella and the 21 valid genera of the family Ectinosomatidae. Halophytophilus aberrans Wells & Rao, 1987 is placed species incertae sedis in the family.

Keywords

Harpacticoida, Ectinosomatidae, Chaulionyx gen. n., Noodtiella, Lineosoma, taxonomy, generic key

Introduction

The harpacticoid family Ectinosomatidae is morphologically distinctive and arguably the most speciose group of copepods in marine meiobenthic communities. The taxonomic literature about this taxon is however, plagued by the scarcity of adequate species descriptions which poses a serious deterrent to most systematists and ecologists. In addition, the scale of variability exhibited by most described species is not well understood, males are frequently rare or completely unknown, distinctions between species and at least some genera are often debatable, and existing identification keys for the larger genera Ectinosoma Boeck, 1865, Halectinosoma Vervoort, 1962 and Pseudobradya Sars, 1904 are all essentially unreliable. The urgent need of revision of these genera is substantially hampered by the lack of type material and by the fact that some unverifiable descriptions undoubtedly contain important errors (Wells 2007). Recent work has demonstrated that some descriptions contain important observational errors and, consequently, some species have been attributed to the wrong genus (Clément and Moore 1995, 2000; Huys and Bodin 1997; Clément and Ólafsson 2001; Wells 2007). The recent recognition of species complexes (Clément and Moore 1995, 2000, 2007) reflects the previous ignorance of characters that have not been given the attention they deserved, such as mouthpart features and body ornamentation patterns. Hence the wide geographical distributions displayed by some ectinosomatids should not be uncritically accepted as the natural consequence of potentially transoceanic or equivalent long-distance dispersal since many of the published ectinosomatid records are probably incorrect.

The family Ectinosomatidae appears to have had a complex ecological radiation. The present day habitat utilization of most primitive genera suggests that it originated in the shallow marine environment where radiation, speciation and diversification appeared to be most successful. Most Ectinosomatidae are found in sublittoral marine sediments ranging from coarse sands to flocculent muds but literature data indicate that several independent freshwater incursions occurred during the evolutionary history of the family. Within the speciose, primarily marine genus Halectinosoma, at least four species have colonized freshwater habitats in Laurasia: H. abrau (Krićagin, 1878), H. concinnum (Akatova, 1935), H. japonicum (Miura, 1964) and H. uniarticulatum Borutzky, 1972. The genus Pseudectinosoma Kunz, 1935 appears to have descended from a coastal brackish water ancestor and primarily inhabits karstic springs, bores, wells, phreatic lakes and hyporheic habitats in Europe and Australia (Galassi et al. 1999; Karanovic 2006). A third freshwater incursion was reported by Karanovic and Pesce (2001) who described Rangabradya indica from subterranean waters in India. Various other ectinosomatid species have been recorded in low salinity habitats but at least for some of them the generic placement needs re-evaluation (e.g. Miura 1962, 1964; Štěrba 1968; Bruno and Cottarelli 1999; Bruno et al. 2003).

Although the majority of ectinosomatids have been described from the continental shelf and the intertidal zone, various species of *Halectinosoma*, *Bradya* Boeck, 1873 and *Parabradya* Lang, 1944 have secondarily radiated into the deep sea (Bodin 1968;

Seifried et al. 2007) and recent research (Gheerardyn et al. 2008) suggests that many other genera have achieved the same habitat shift. Others, such as species of Arenosetella Wilson, 1932, Glabrotelson Huys, 2009 and Noodtiella Wells, 1965 are found on the other end of the bathymetric spectrum, being frequently the only harpacticoids occurring in the infra- and supralittoral zones of sandy beaches (Mielke 1976). In beaches and sandy sublittoral habitats various genera have colonized the interstitial environment, either by adopting a cylindrical body shape (Arenosetella, Ectinosomoides Nicholls, 1945, Glabrotelson, Lineosoma Wells, 1965, Noodtiella, Oikopus Wells, 1967) or by simple miniaturization of the ancestral fusiform body (Signatidium Giesbrecht, 1881). Finally, some ectinosomatid lineages are no longer associated with the ancestral benthic habitat but have moved into the open pelagic or have abandoned their essentially free-living lifestyle. The holoplanktonic genus *Microsetella* Brady & Robertson, 1873 is known to attach and feed on discarded and occupied larvacean houses (Appendicularia) (Alldredge 1972; Ohtsuka et al. 1993) while other taxa have entered into associations with invertebrates. Examples of the latter include Peltobradya bryozoophila Médioni & Soyer, 1968, which appears to be associated with the bryozoan *Schizoma*vella linearis (Hassall, 1841) (Médioni and Soyer 1968), and an as yet undescribed genus which was found in the mucus coat surrounding the polychaete host Hydroides elegans (Haswell, 1883) (Huys unpubl.).

Excellent recent studies by Mielke (1979, 1981, 1986, 1987a-b) have contributed substantially to our knowledge of Central and South American Ectinosomatidae. However, the fauna along the vast Brazilian coastline remains poorly known (Reid 1998). Jakobi (1954) described three species of Pseudobradya and two species of Ectinosoma from Paraná State. Unfortunately, his descriptions are essentially inadequate and Lang (1965) suggested ranking all of them as species inquirendae while Wells (2007) listed them as species incertae sedis. The species described by Jakobi and Nogueira (1960) as Ectinosoma couceiroi is a likely synonym of E. dentatum Steuer, 1940 (Lang 1965: 17) and has thus far been recorded only from the Lagoa de Conceição in Santa Catarina State. Rouch (1962) described two new species, Noodtiella problematica and Halectinosoma arenicola, from sandy beaches in Pernambuco State and listed the first South American record of the allegedly cosmopolitan Arenosetella germanica Kunz, 1937. During the course of a meiofaunal survey off Ubatuba (São Paulo State) we discovered several new species of the Ectinosomatidae. One of these represented the most abundant harpacticoid copepod in the area and is described here as a representative of an as yet unknown genus, raising the number of valid genera in the family to twenty-one (Seifried et al. 2007; Wells 2007; Huys 2009).

Material and methods

Sediment samples were obtained during an ecological study of the meiofaunal diversity along the northern coast of São Paulo State as part of the interdisciplinary project "Utilização Racional do Ecossistema Costeiro da Região Tropical Brasileira: Estado

de São Paulo" conducted by the Departamento de Oceanografia Biológica – Instituto Oceanográfico da Universidade de São Paulo (IOUSP). Samples were collected at 12 stations along the inner continental shelf (15-53 m depth) between São Sebastião Island and Ubatumirim inlet, Ubatuba, in March and August, 1989. Description of the sampling methodology and physical and chemical analysis is given by Corbisier (1993). Coordinates and environmental parameters of the stations where the new genus occurred are compiled in Table 1.

Before dissection, the habitus was drawn from whole specimens temporarily mounted in glycerine. Adhesive plastic discs were used to support the coverslip in temporary mounts. Specimens were dissected in lactic acid and the dissected parts were mounted on slides in glycerine. Preparations were sealed with transparent nail varnish. All drawings were prepared using a camera lucida on a Zeiss Axioskop 2 Plus differential interference contrast microscope. Total body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: ae, for aesthetasc; P1–P6, for swimming legs 1-6; exp, enp and benp for exopod, endopod and baseoendopod, respectively; exp (enp)-1 (-2, -3) denotes the proximal (middle, distal) segments of a ramus. The term 'acrothek' denotes the trifid setal structure found on the apical margin of the distal antennulary segment (Huys and Iliffe 1998). Type material is deposited in the collections of the Museu de Zoologia, Universidade de São Paulo (MZUSP) and the Natural History Museum, London (NHM).

Three females and three males were prepared for scanning electron microscopy (SEM). Specimens were dehydrated through a series of graded acetone, critical-point

Table 1. Coordinates and environmental parameters of sampling sites where *Chaulionyx paivacarva-lhoi* gen. et sp. n. was recorded during the interdisciplinary project "Utilização Racional do Ecossistema Costeiro da Região Tropical Brasileira: Estado de São Paulo" (Departamento de Oceanografia Biológica – IOUSP). Stations were sampled across the inner continental shelf of São Paulo State between São Sebastião Island and Ubatumirim inlet, Ubatuba during March (V stations) and August 1989 (I stations). Lat. = latitude, Long. = longitude; Temp. = temperature; MZ = grain size; GS = sorting; Cogg = organic carbon.

| Station | Lat. | Long. | Depth | Temp. | MZ | GS | Sand | Silt | Clay | C | CaCO ₃ |
|---------|-----------|-----------|-------|-------|------|------|-------|-------|-------|------|-------------------|
| | (S) | (W) | (m) | (°C) | (Ø) | (φ) | (%) | (%) | (%) | (%) | (%) |
| 5V | 23° 40.8' | 44° 46.2' | 53 | 15.3 | 4.61 | 1.86 | 63.10 | 25.45 | 11.45 | 1.00 | 17.00 |
| 7V | 23° 31.2' | 44° 51.0' | 44 | 15.3 | 1.02 | 0.92 | 98.64 | 0.39 | 0.00 | 0.03 | 8.70 |
| 16V | 23° 45.5' | 44° 56.4' | 52 | 15.8 | 4.94 | 1.63 | 46.14 | 43.84 | 10.02 | 1.07 | 16.70 |
| 17V | 23° 41.4' | 44° 58.8' | 44 | 15.6 | 3.56 | 0.83 | 83.73 | 13.56 | 2.71 | 0.57 | 20.5 |
| 27V | 23° 46.2' | 45° 07.8' | 34 | 15.6 | 3.63 | 0.85 | 87.23 | 8.12 | 4.64 | 0.42 | 9.70 |
| 7I | 23° 31.2' | 44° 51.1' | 44 | 18.6 | 3.44 | 0.88 | 89.35 | 0.63 | 1.79 | 0.28 | 27.7 |
| 16I | 23° 45.7' | 44° 56.3' | 52 | 17.8 | 4.47 | 1.67 | 64.93 | 25.82 | 9.25 | 4.48 | 20.0 |
| 17I | 23° 41.4' | 44° 58.9' | 44 | 18.1 | 5.04 | 2.53 | 45.60 | 34.46 | 19.94 | 1.73 | 30.6 |
| 18I | 23° 37.2' | 45° 01.3' | 41 | 18.3 | 3.52 | 0.77 | 87.59 | 10.01 | 2.40 | 0.67 | 17.10 |
| 26I | 23° 50.5' | 45° 05.5' | 45 | 20.5 | 4.15 | 1.18 | 72.42 | 21.23 | 6.36 | 1.26 | 15.00 |
| 27I | 23° 46.3' | 45° 07.7' | 39 | 20.4 | 3.65 | 0.79 | 85.71 | 10.39 | 3.90 | 0.29 | 15.20 |

dried, mounted on stubs, sputter-coated with palladium and observed using a Philips XL 30 Field Emission Scanning Electron microscope.

Results

Order HARPACTICOIDA Sars, 1903 Family ECTINOSOMATIDAE Sars, 1903

Chaulionyx gen. n.

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Diagnosis. Ectinosomatidae. Small-sized. Body fusiform, greatest width measured at posterior margin of cephalothorax; body somites strongly chitinized; hyaline frill of cephalic shield and somites bearing P2–P4 plain, that of other somites minutely serrate; no distinct surface ornamentation except for anterodorsal spinule rows on all body somites, ventral spinule rows on abdominal somites and large middorsal pores. Pseudoperculum weakly developed. Sexual dimorphism in antennule, P1, P5, P6, genital segmentation, abdominal ornamentation and caudal ramus.

Rostrum large, hyaline, broadly rounded, not defined at base. Antennule 5-segmented in female, 7-segmented in male with geniculation between segments 5 and 6. Antenna with 3-segmented exopod (formula 0-1-2); distal endopod segment with 2 lateral and 5 apical elements. Labrum with frontal spinous projection. Mandible with small gnathobase and biramous palp; basis with 3 setae, exopod minute with 3 setae, endopod with 3 lateral and 7 apical elements. Maxillule with well developed arthrite; coxa represented by a single seta; exopod bisetose with the lateral seta typically outwardly reflexed; basis and endopod fused, with 10 setae in total. Maxilla prehensile, robust; syncoxa with 3 endites (formula 4-1-3); allobasis with 3 lateral and 1 apical setae; endopod 2-segmented (ancestral segments 2-3 fused). Maxilliped stenopodial, 3-segmented, slender; syncoxa with 1 seta; endopod with 1 lateral and 3 terminal setae.

P1 with an inner and an outer seta on the basis; exopod 3-segmented; endopod prehensile, 2-segmented, enp-2 with bifid outer claw. P2–P4 with outer seta on basis; rami 3-segmented; inner seta of enp-2 distinctly short. Armature formula:

| | Exopod | Endopod |
|----|---------|---------|
| P1 | 0.1.122 | 1.321 |
| P2 | 1.1.222 | 1.1.221 |
| Р3 | 1.1.222 | 1.1.221 |
| P4 | 1.1.322 | 1.1.221 |

P5 of both sexes with separate exopod and baseoendopod; exopod with 1 surface and 3 marginal setae; endopodal lobe with 2 spines/setae.

Female gonopores fused forming a median genital slit, covered by the pair of P6 each bearing 1 long seta; midventral copulatory pore small.

Male P6 asymmetrical, unarmed; functional member represented by small operculum, other member fused to genital somite.

Caudal ramus short, with 7 setae; setae IV–V basally fused, without fracture planes. **Type and only species.** *Chaulionyx paivacarvalhoi* sp. n.

Etymology. The generic name is derived from the Greek *chaulios* (outstanding, prominent) and *onyx* (nail, claw), and refers to the modified, claw-like, bifid outer spine on the P1 endopod. Gender: feminine.

Chaulionyx paivacarvalhoi sp. n.

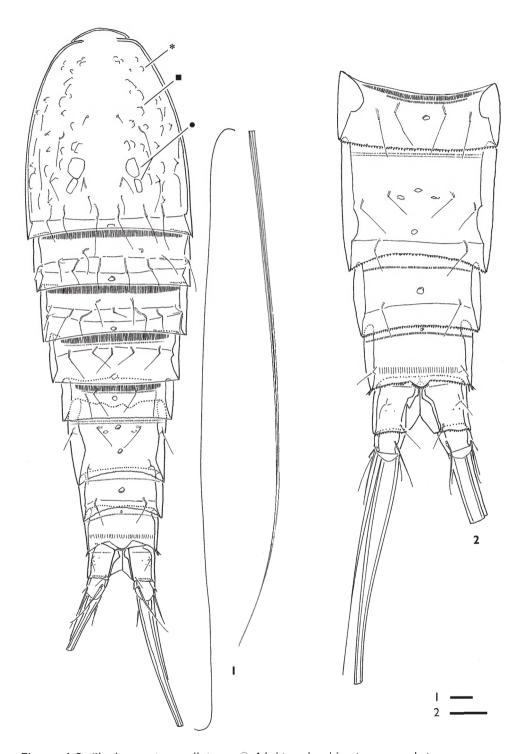
urn:lsid:zoobank.org:act:0075F457-E809-451D-9CFB-9B2B1BE2EF19 Figs 1-37

Type locality. Brazil, northern coast of São Paulo State, Ubatuba (23° 41.4' S, 44° 58.8' W), 44 m depth (station 17V in Table 1).

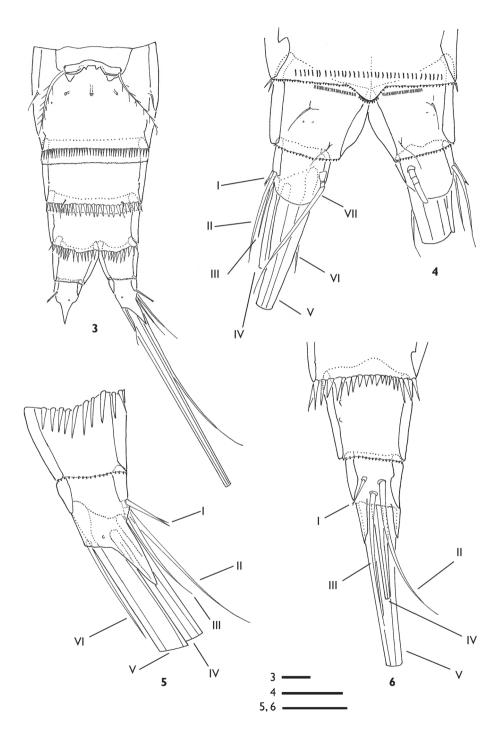
Material examined. Holotype female in ethanol (reg. no. MZUSP 16467). Undissected paratypes (in ethanol) deposited in MZUSP (reg. nos 16468, 19063-19065) are 1 female and 1 male from station 17V; 3 females and 1 male from station 16V, 2 males from station 16I, 1 female and 1 male from station 17I. Additional undissected paratypes (in ethanol) deposited in NHM are 2 males from station 17V (reg. nos 2009.1-2), 3 females from station 27V (reg. nos 2009.3-5) and 1 male from station 27I (reg. no 2009.6). Dissected paratypes and other material examined are retained in the personal collection of C.E.F. da Rocha (Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo). All material collected by T. Corbisier.

Description. FEMALE (Figs 1-21, 27-35). Body length 260-290 μ m (n = 4; mean = 275 μ m). Body (Fig. 1) fusiform, maximum width measured at posterior margin of cephalic shield; body somites gradually tapering posteriorly. Cephalic shield with minute integumental pits and numerous pores; paired chitinous patches present dorsally in posterior half (for examples of these integumental structures see labelling in Fig. 1 and accompanying legend). Body somites with thickly chitinized cuticle; pedigerous somites and second abdominal somite with large middorsal pore; genital double-somite with 2 pores. Sensillae long and fine, distributed as illustrated in Fig. 1. Hyaline frill of cephalic shield and somites bearing P2–P4 plain, partially concealing fine spinular rows located in anterior half of succeeding somite (Fig. 1); frills of urosomites minutely denticulate (Figs 1-2, 30-31).

Genital and first abdominal somites fused forming double-somite (Figs 1-3, 21); slightly longer than broad; posterior margin with continuous spinular row; original segmentation marked by sensilla, paired dorsal chitinous patches and a middorsal pore (Fig. 2). Second and third abdominal somites with a continuous row of coarse spinules around ventral posterior margin (Fig. 3). Penultimate somite with a small pseudoper-



Figures 1-2. Chaulionyx paivacarvalhoi sp. n. \bigcirc : **I** habitus, dorsal [* = integumental pit; \blacksquare = pore; \bullet = chitinous patch **2** urosome, dorsal. Scale bars = $10 \ \mu m$.



Figures 3-6. *Chaulionyx paivacarvalhoi* gen. et sp. n. ♀: **3** urosome, ventral [segment bearing P5 omitted] **4** caudal rami, dorsal **5** left caudal ramus, ventral **6** left caudal ramus, lateral. Scale bars = 10 µm.

culum (Figs 1-2, 30), dorsal surface and distal margin with rows of spinules (Figs 30, 32). Anal somite (Figs 1-4, 30) medially cleft; dorsal surface with paired anterior rows of minute spinules and pairs of sensilla and pores (Fig. 4); distal margin with small spinules (Fig. 33); anal operculum absent.

Caudal rami (Figs 4-6) about as long as wide, with 7 naked setae; bases of terminal setae covered by rounded membranous serrate extension dorsally (Figs 4, 30, 34) and an acuminate lappet ventrally (Fig. 5). Seta I minute, with bifid apex. Setae IV–V fused basally, without fracture planes. Seta V longest and swollen in proximal half. Seta VII tri-articulate at base.

Rostrum large (Figs 7, 27), ventrally deflected; broadly rounded, quadrangular; not defined at base but original demarcation marked by membranous areas bilaterally (Fig. 27); no sensilla discernible.

Antennule (Fig. 8) short, 5-segmented. Segment 1 with pinnate seta; segment 3 with conspicuous aesthetasc; distal segment long, with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[1 pinnate], 2-[7], 3-[6 + (1 + ae), 4-[1], 5-[5 + acrothek].

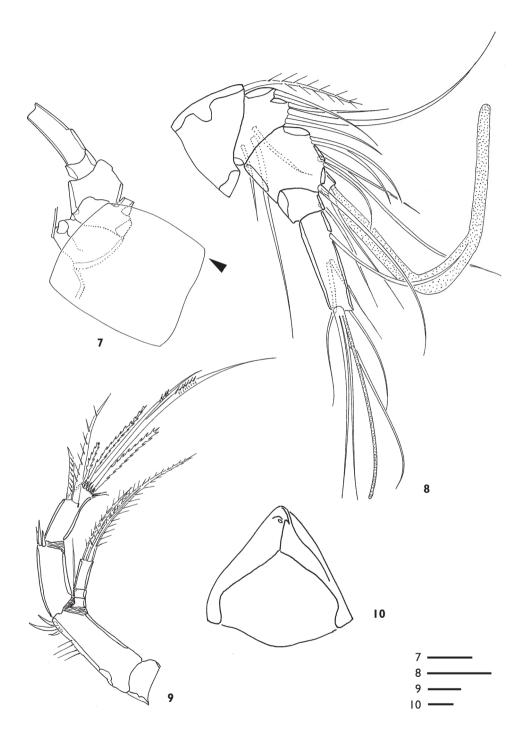
Antenna (Fig. 9) consisting of coxa, basis, 2-segmented endopod and 3-segmented exopod. Coxa small, indistinctly demarcated at base, without ornamentation. Basis unarmed; with some fine spinules along abexopodal margin and coarse spinules set near outer distal corner. Proximal endopod segment with a few coarse spinules near outer distal corner. Distal endopod segment with 2 unipinnate setae laterally; distal margin with spinule row and 5 elements, 2 of which are geniculate, others bipinnate. Exopod with small proximal and middle segments and elongate apical segment; exp-1 unarmed, exp-2 with short naked seta, exp-3 with 2 pinnate apical setae.

Labrum (Figs 10, 28) well developed, with frontal curved spinous projection bearing large anterior pore.

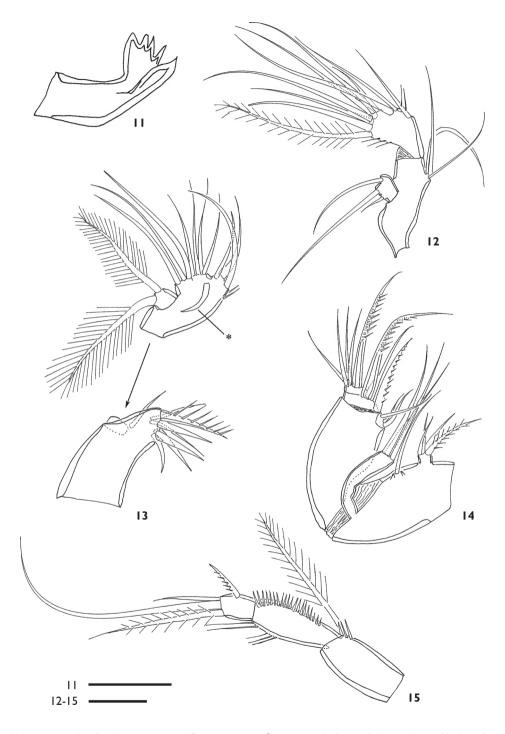
Mandible with small coxa (Fig. 11) and biramous palp (Fig. 12). Gnathobase reduced, with chitinized dorsal tooth and number of hyaline pointed projections. Basis elongate, with 3 lateral setae. Exopod small, 1-segmented, with 3 naked setae, outer one reduced. Endopod 1-segmented, with row of fine spinules along outer margin; armature consisting of 1 sparsely pinnate and 2 naked setae laterally and 1 bipinnate and 6 naked setae apically.

Maxillule (Fig.13) with fused praecoxa and coxa. Praecoxa with well developed arthrite bearing 4 spines and 1 seta around distal margin and 2 small setae on anterior surface; distalmost marginal spine with long spinules. Coxa represented by small seta on anterior surface near articulation with palp. Endopod incorporated into basis forming elongate segment; proximal basal endite a small protuberance bearing 3 setae; elements of distal basal endite (4) and endopod (3) forming group of 7 setae arranged around the distal margin; with cuticular reinforcement (indicated by asterisk in Fig. 13) on posterior surface; distal medial margin with characteristic spinules. Exopod a free small segment; with 1 apical and 1 backwardly directed plumose seta.

Maxilla (Fig. 14) prehensile, comprising syncoxa, allobasis and 2-segmented endopod with syncoxa and allobasis directed at a right angle. Syncoxa with 3 endites; proxi-



Figures 7-10. Chaulionyx paivacarvalhoi gen. et sp. n. \bigcirc : **7** rostrum (arrowed) and left antennule (armature omitted), dorsal **8** right antennule, dorsal **9** antenna **10** labrum. Scale bars = 10 μ m.



Figures 11-15. *Chaulionyx paivacarvalhoi* gen. et sp. n. ♀: **11** mandibular gnathobase **12** mandibular palp **13** maxillule [asterisk indicating cuticular reinforcement] **14** maxilla **15** maxilliped. Scale bars = 10 µm.

mal endite small, with 1 bipinnate and 3 naked setae; middle endite rudimentary, with 1 long naked seta; distal endite cylindrical and recurved, located in membranous area at syncoxa-allobasis joint, with 3 long naked setae. Allobasis robust, expanding in distal half; armed with 3 setae (2 small) near inner distal corner (derived from basis) and 1 strong pinnate seta on posterior surface (derived from incorporated endopod segment). Endopod with 1 geniculate pinnate claw and 1 naked seta on enp-1; enp-2 (representing fused middle and distal segments) with 1 geniculate pinnate claw and 4 naked setae.

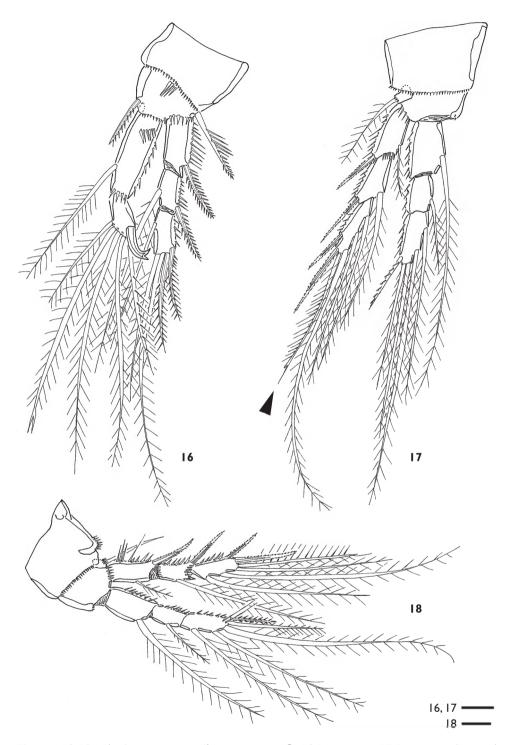
Maxilliped (Fig. 15) stenopodial and slender, comprising syncoxa, basis and 1-segmented endopod. Syncoxa with long pinnate seta and few spinules near distal corner. Basis unarmed; with long setules along outer margin and fine spinules along inner margin. Endopod with 1 short pinnate seta laterally and 1 short plus 2 longer (1 plumose) setae apically.

P1 (Fig. 16). Coxa with row of minute spinules along distal margin. Basis with rows of spinules on anterior surface and near insertion of exopod as illustrated; outer seta long, bipinnate and spiniform; inner spine unipinnate with spinules along outer margin. Exopod 3-segmented; with rows of spinules along outer margins; outer spines strong and bipinnate; exp-1 without inner seta; exp-2 with 1 inner plumose seta; exp-3 with 1 inner plumose seta, 2 plumose distal setae and 2 bipinnate outer spines. Endopod 2-segmented, prehensile; enp-1 elongate, with rows of spinules on anterior surface and along outer and distal margins, and 1 plumose inner seta inserted in distal third of segment; enp-2 with 3 plumose inner setae (middle one with bifid apex), 2 plumose distal setae, and 1 curved strong spine with bifid tip (Fig. 29).

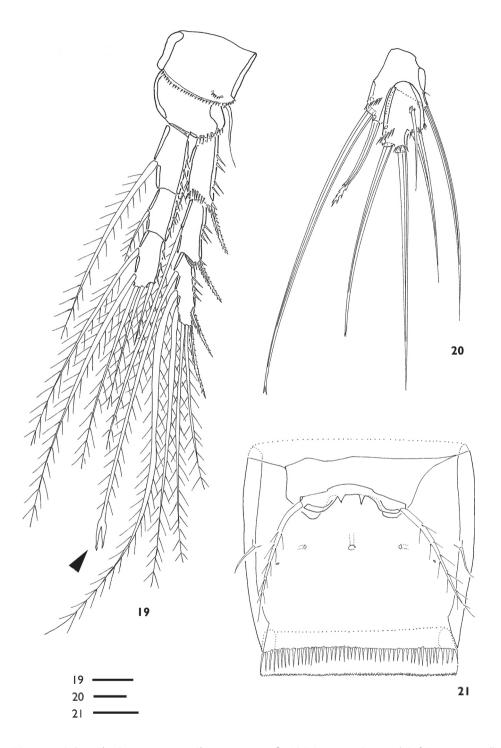
P2–P4 (Figs 17-19). Coxa with small spinules along distal margin. Basis with rows of spinules at base of exopod and around outer seta; outer seta plumose (P2) or naked (P3–P4). Exopod 3-segmented; with rows of spinules along outer margins; outer spines strong and bipinnate. Exp-1 with 1 reduced plumose inner seta; exp-2 with 1 plumose inner seta; exp-3 with 2 bipinnate outer spines, 2 plumose distal setae and 2 (P2–P3) or 3 (P4) plumose inner setae. P2 exp-3 outer distal seta plumose along outer margin and with apical flagellum (arrowed in Fig. 17). P4 exp-3 proximal inner seta with bifid apex; middle inner seta extremely well developed. Endopod 3-segmented; with rows of spinules along outer margins. Enp-1 with 1 plumose inner seta; enp-2 with 1 reduced plumose inner seta; enp-3 with 4 plumose setae (2 inner and 2 distal) and 1 bipinnate outer spine (P2–P3) or 1 plumose outer seta (P4). Armature formula of swimming legs as for genus.

P5 (Figs 20, 35). Baseoendopod outer expansion with 1 naked seta. Endopodal lobe with spinular row and small pore on anterior surface; with 2 naked setae, inner one very long (3.2 times longer than outer one) and with bifid apex, outer one with serrate apex. Exopod with 1 pore near distal inner margin and various spinule rows as figured; anterior surface with 1 naked seta; with 3 marginal setae, innermost one with bifid apex.

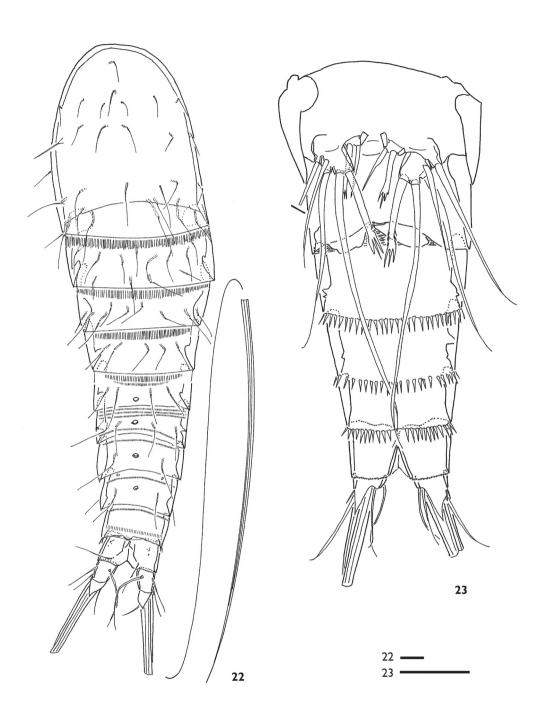
Genital field (Figs 3, 21) with relatively small midventral copulatory pore. Sixth pair of legs (Fig. 21) vestigial, fused medially forming a common plate that covers paired genital apertures (or median slit); each P6 with 1 plumose seta. Egg-sac single.



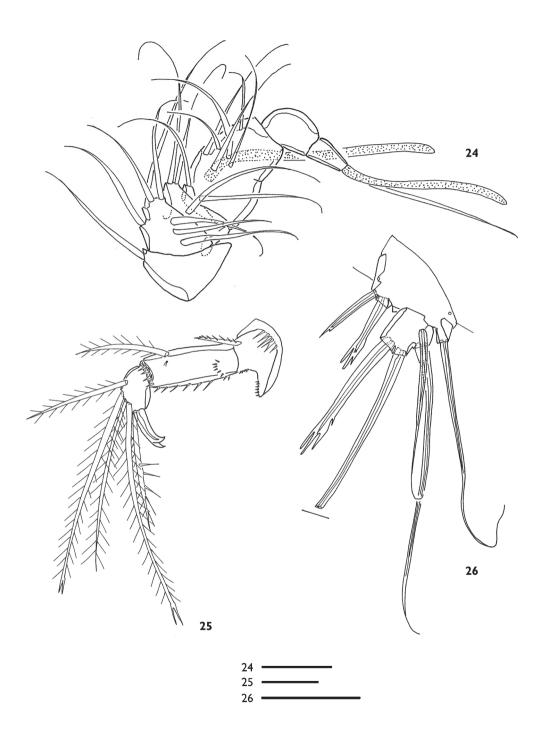
Figures 16-18. Chaulionyx paivacarvalhoi gen. et sp. n. \bigcirc : **16** P1, anterior; **17** P2, anterior [seta with apical flagellum arrowed] **18** P3, anterior. Scale bars = 10 μ m.



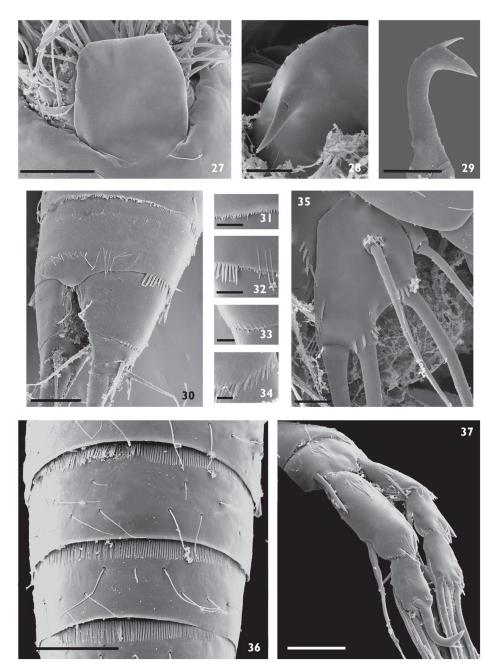
Figures 19-21. Chaulionyx paivacarvalhoi gen. et sp. n. \bigcirc : **19** P4, anterior [seta with bifid apex arrowed] **20** P5, anterior **21** genital double-somite. Scale bars = 10 μ m.



Figures 22-23. *Chaulionyx paivacarvalhoi* gen. et sp. n. \circlearrowleft : **22** habitus, dorsal **23** urosome, ventral. Scale bars = 10 µm.



Figures 24-26. Chaulionyx paivacarvalhoi gen. et sp. n. \lozenge : **24** antennule, dorsal **25** P1 basis and endopod, anterior **26** P5, anterior. Scale bars = $10 \mu m$.



Figures 27-37. Chaulionyx paivacarvalhoi gen. et sp. n. Scanning electron micrographs (\mathcal{Q} : 27-35; \mathcal{Z} : 36-37): 27 rostrum, dorsal 28 labrum, anterior 29 bifid outer spine on P1 enp-2 30 second abdominal somite (posterior margin), third abdominal somite, anal somite and caudal rami, dorsolateral 31 detail of serrate posterior margin of second abdominal somite 32 detail of posterior margin of third abdominal somite 33 posterior margin of anal somite 34 posterior margin of caudal ramus showing dorsal semicircular serrate extension 35 P5, anterior 36 prosomal ornamentation, dorsal 37 P1 endopod, anterior. Scale bars: 1 μm (34), 2.5 μm (33), 5 μm (28-29, 31-32, 35), 10 μm 27 (30, 37), 20 μm (36).

MALE. (Figs 22-26, 36-37). Body length 230-260 μm (n = 6; mean = 246 μm) (Fig. 22). Sexual dimorphism expressed in caudal ramus, antennule, P1, P5, P6, and in genital segmentation. Ornamentation of body (Figs 22-23, 36) generally as in female, except for small differences such as cephalic sensilla being longer and distributed differently, and pits, pores and chitin patches missing on the cephalic shield.

Caudal ramus (Fig. 23) with both dorsal and ventral posterior margin produced into triangular extension covering bases of setae IV–VI.

Antennule (Fig. 24), haplocer, 7-segmented; geniculation between segments 5 and 6; segment 5 elongated and incompletely divided. Setae and aesthetasc formula: 1-[1], 2-[7], 3-[3], 4-[1], 5-[7 + ae], 6-[0], 7-[1 + ae].

P1 (Figs 25, 37). Enp-2 wider than in female; outer distal spine with bifid apex.

P5 (Figs 23, 26) shorter than in female. Endopodal lobe small, with 2 short, stout setae, innermost with bifid apex, outer one with tridentate apex. Exopod short; with 1 seta on anterior surface and 3 marginal setae; inner distal seta with tridentate apex, outer distal seta very long.

P6 (Fig. 23) asymmetrical, without ornamentation.

Etymology. The new species is named in honour of Prof. João de Paiva Carvalho (Instituto Oceanográfico, Universidade de São Paulo) in recognition of his significant contributions to the taxonomy of Copepoda.

Discussion

The form of the maxilla is of high significance in assessing phylogenetic relationships within the family Ectinosomatidae. Two types can be distinguished on the basis of the shape and orientation of the allobasis. In the first type the maxilla is stenopodial (nonprehensile) with the syncoxa, allobasis and endopod arranged in a virtually rectilinear sequence. This arrangement is displayed in Ectinosoma, Halectinosoma, Rangabradya, Microsetella and the interstitial genera Arenosetella, Glabrotelson, Microsetella, Ectinosomoides and Oikopus. In the second type the syncoxa and allobasis are directed at a right angle, forming a prehensile limb. The articulation between these two segments is modified and typically displays a large membranous area around the medial distal surface of the syncoxa, facilitating flexure of the distal part of the maxilla. This prehensile type is found in all other ectinosomatid genera, including *Chaulionyx*, gen. n. Within this group (and the entire family) only three genera – in addition to Chaulionyx – display a prehensile P1 endopod: Halophytophilus Brian, 1919, Bradyellopsis Brian, 1925 and Klieosoma Hicks & Schriever 1985. Among this group, the primitive genus Klieosoma can be readily distinguished by the ancestral 3-segmented condition of the P1 endopod, bearing 4 (*K. spinosa* Hicks & Schriever, 1983) or 5 elements (*K. triarticula*tus (Klie, 1949)) on the distal segment, unlike the 2-segmented condition consistently reported for the other three genera. Chaulionyx differs from the remaining two genera in the presence of a conspicuous bifid claw (in addition to 5 well developed plumose setae) on the distal endopod segment of P1, the presence of distinctive subrectangular

middorsal pores on the urosomites (similar pores have thus far only been reported for *Ectinosoma*; cf. Huys and Bodin 1997) and the unarmed sixth legs in the male (in both *Bradyellopsis* and *Halophytophilus* the male P6 bears 1 seta). Descriptions of all species of *Bradyellopsis* (except *B. foliatus* Watkins, 1987) are incomplete (Wells 2007) but differ from *C. paivacarvalhoi* in the presence of a large spine (or spinous process) on segment 2 (and often segments 1 and 3) of the antennule, the rudimentary antennary exopod (at most a small segment with 1-3 setae), the spinous projections on the caudal rami and the detailed morphology of P1 enp-2. Species belonging to *Halophytophilus* can be distinguished from *C. paivacarvalhoi* by the presence of 3 outer spines on P1–P4 exp-3 but only 3 elements on P1 enp-2.

On the distinction between Noodtiella and Lineosoma

Wells (1965) proposed two new genera for interstitial ectinosomatids from the Canary Islands and Portugal, and England, respectively: *Noodtiella* Wells, 1965 (type species by original designation: *Sigmatidium*? *arenosetelloides* Noodt, 1958) and *Lineosoma* Wells, 1965 (type species by original designation: *Lineosoma iscense* Wells, 1965; since the gender of the genus is neuter the incorrect original spelling *iscensis* is amended here accordingly, cf. ICZN Art. 30.1.2). Both *Noodtiella* Wells, 1965 and *Noodtia* Lang, 1965 have the same name-bearing type, *S.*? *arenosetelloides* Noodt, 1958, and are therefore objective synonyms. The former takes precedence over the latter [see post-script in Lang (1965: 547)]. Wells (1965) remarked on the close similarity between *Noodtiella* and *Lineosoma* (e.g. in body shape, antennule, antenna, prehensile maxilla, P5) but considered the 2-segmented condition of the P1–P4 endopods in the former (as opposed to 3-segmented in *Lineosoma*) sufficient justification for the separation into two genera.

Wells (1967) description of *N. intermedia* rendered the distinction between *Noodtiella* and *Lineosoma* no longer tenable since his species displayed a 2-segmented P1 endopod but 3-segmented P2–P4 endopods. According to the author the segmentation pattern in *N. intermedia* can so readily be interpreted as intermediate between the two known conditions that, collectively, the species included in *Noodtiella* and *Lineosoma* form an evolutionary sequence. Consequently, Wells (1967) synonymised both genera, stating that *Noodtiella* Wells, 1965 (p. 30) has page priority over *Lineosoma* Wells, 1965 (p. 33) and the latter must sink as a junior subjective synonym of the former. This course of action was followed by Lindgren (1975) who added *N. enertha* (another species with 3-segmented P1–P4 endopods) to the genus.

Using the widely accepted distinction between *Sigmatidium* (P2–P4 endopods 3-segmented) and *Pseudectinosoma* (P2–P4 endopods 2-segmented) as an analogy, Kunz (1975) believed the separation on the same grounds between *Noodtiella* and *Lineosoma* was warranted and reinstated the latter as a valid genus (in which he included *N. intermedia*). However, the subsequent description of *N. gracile* Mielke, 1975, *N. frequentior* Mielke, 1979 and *N. mielkei* Wells & Rao, 1987 – all of which exhibit a

Table 2. Swimming leg armature formulae of the 18 valid *Noodtiella* species (P4-OS = outer spine of P4 exp-2 present/absent; P5-OS♀ = outer endopodal spine fused to baseoendopod in female/discrete at base). Segments with numerals in boldface refer to endopodal segments with posterior surface setae.

| | P1 | - | P | P2 | Ь | P3 | П | P4 | P4-0S | ₽5-0S |
|--|---------|---------|---------|---------|---------|---------|-----------------|---------|-------|----------|
| | exb | enp | exp | duə | exb | enp | exp | duə | | |
| N. iscensis (Wells, 1965), comb. n. a | 0.0.021 | 1.1.120 | 1.1.021 | 1.1.120 | 1.1.021 | 1.1.221 | 1.1.021 | 1.1.221 | ۸. | discrete |
| N. enertha Lindgren, 1975 b | 0.1.021 | 1.0.221 | 1.1.021 | 1.0.321 | 1.1.021 | 1.0.321 | 11.021 | 1.0.321 | + | fused |
| N. intermedia Wells, 1967 ° | 0.1.022 | 1.121 | 1.1.022 | 1.1.121 | 1.1.022 | 1.1.121 | 1 1.022 | 1.1.121 | ۸. | fused |
| N. chilensis (Mielke, 1987a), comb. n. | 0.1.022 | 1.120 | 1.1.022 | 1.0.220 | 1.1.022 | 1.0.220 | 1.0.220 1.1.022 | 1.0.220 | + | discrete |
| N. pectinata (Chappuis, 1954a), comb. n. d | 0.1.022 | 1.121 | 1.1.022 | 1.321 | 1.1.022 | 1.321 | 1.1.021 | 1.321 | + | fused |
| N. wellsi Apostolov, 1974 | 0.1.022 | 1.121 | 1.1.022 | 1.221 | 1.1.022 | 1.221 | 1.1.022 | 1.221 | + | discrete |
| N. ornamentalis Wells & Rao, 1987 ° | 0.1.022 | 1.121 | 1.1.022 | 1.221 | 1.1.022 | 1.221 | 1.1.022 | 1.221 | ۸. | fused |
| N. Iusitanica Wells, 1965 f | 0.1.021 | 1.121 | 1.1.021 | 1.221 | 0.1.021 | 1.221 | 0.1.021 | 1.221 | ۸. | fused |
| N. arenosetelloides (Noodt, 1958) | 0.1.022 | 1.121 | 1.1.022 | 1.121 | 1.1.022 | 1.121 | 1 1.022 | 1.121 | + | discrete |
| N. hoodensis Mielke, 1979 | 0.1.022 | 1.120 | 1.1.021 | 1.220 | 1.1.021 | 1.220 | 1.1.021 | 1.220 | 1 | discrete |
| N. tabogensis Mielke, 1981 | 0.1.022 | 1.120 | 1.1.021 | 1.220 | 1.1.021 | 1.220 | 1.0.021 | 1.220 | 1 | discrete |
| N. coquimbensis Miclke, 1987b | 0.1.022 | 1.120 | 1.1.021 | 1.220 | 1.1.021 | 1.220 | 1.1.021 | 1.220 | + | discrete |
| N. larinconadensis Mielke, 1987b | 0.1.022 | 1.120 | 1.1.021 | 1.220 | 1.1.021 | 1.220 | 0.1.021 | 1.220 | 1 | discrete |
| N. pacifica Mielke, 1987b | 0.1.022 | 1.120 | 0.1.021 | 1.220 | 0.1.021 | 1.220 | 1.1.021 | 1.220 | 1 | discrete |
| N. problematica (Rouch, 1962) 8 | 0.1.022 | 1.120 | 0.1.021 | 1.120 | 0.1.021 | 1.220 | 0.1.021 | 1.220 | 1 | discrete |
| N. frequentior Mielke, 1979 | 0.0.022 | 1.120 | 1.0.021 | 1.220 | 1.0.021 | 1.220 | 1.021 | 1.220 | ı | discrete |
| N. mielkei Wells & Rao, 1987 | 0.1.022 | 1.120 | 1.1.022 | 1.220 | 1.1.022 | 1.220 | 1.122 | 1.120 | + | fused |
| N. gracile Mielke, 1975 | 0.1.021 | 1.120 | 1.1.021 | 1.220 | 1.1.021 | 1.220 | 1.121 | 1.120 | ı | discrete |
| | | | | | | | | | | |

- Based on Huys et al. (1996). This species was originally described as Pararenosetella sp. by Wells (1963)
- Lindgren (1975) claimed this species is unique by the presence of two inner setae on P2–P4 enp-1; this is undoubtedly an observational error resulting from misinterpreting the setular tuft for a supernumerary seta. In addition, the author stated correctly that P2-P4 enp-2 has 6 setae but this is not reflected in his setal formula which gives 221 for these segments. Finally, his illustration of P1 showing no seta on enp-2 but a 221 armature pattern on enp-3 requires confirmation since it conflicts with the pattern observed in N. iscensis (a 1.1.121 formula for P1 endopod would be more likely).
- Wells (1967) showed an outer distal spine on P1 enp-2 but this is likely to be the distal portion of the artificially displaced inner seta. Wells and Rao (1987) pointed out that the original description is wrong in that P1 enp-2 bears four elements, not three.
- Mitwally and Montagna (2001) list the formula for P2–P4 enp-2 as 221 but do not take into account the posterior surface seta; the formula is here amended
- Wells and Rao's (1987) illustration of the P2 is likely to be incorrect; the distal endopod segment appears to be reversed although the spinule row marking the original subdivision is illustrated on the correct (outer) margin; given the close relationship to N. pertinata it is also conceivable that the authors overlooked the posterior surface seta on P2-P4 enp-2.
- The armature formula of P1 enp-2 is 121 according to Wells' (1965) Table I but the illustration of this appendage (his Fig. 9) shows 120 instead. Similarly, it Rouch (1962) lists the posterior surface seta of enp-2 for P3-P4 in his setal formula (and figures it for the P4) but not for P2; this loss requires confirmation appears that the P2 exopod is rotated 180 degrees in his Fig. 10 giving the false impression that there is no inner seta on enp-1.
 - N. problematica as an additional difference but this seta is reduced in N. pacifica and may well have been overlooked in Rouch' (1962) original description. It is and should not be used as a character to differentiate N. problematica from N. pacifica. Mielke (1987b) also used the absence of the inner seta on P4. conceivable that N. pacifica and N. problematica are conspecific.

2-segmented P4 exopod – once again casts doubt on the validity of this generic distinction, and Mielke (1987a) pointed out that *Lineosoma* in Kunz's (1975) sense was not diagnosed by an autapomorphy. This effectively renders the genus a paraphyletic group with respect to the species currently included in *Noodtiella*. Consequently, *Lineosoma* is here relegated to a junior subjective synonym of *Noodtiella*, adopting Wells' (1967) argument of page priority.

Chappuis (1954a) described two new species of Arenosetella, A. incerta (P1-P4 with 3-segmented endopods) and A. pectinata (P1-P4 with 2-segmented endopods) and presented illustrations of a fifth copepodid stage which he named "Arenosetella spec. juv.". These three forms co-occurred in the intertidal zone of Canet-Plage, which - in the absence of any habitus drawings in Chappuis' descriptions - made Lang (1965) suggest that "Arenosetella spec. juv." and A. pectinata represented the fourth and fifth copepodids of A. incerta, respectively. Conversely, Noodt (1958) surmised that Arenosetella pectinata Chappuis, 1954a was a valid species that may be assigned to the genus *Ectinosomoides*. Bodin (1997) listed the new combination *Ectinosomoides pectinatus* (Chappuis, 1954a) as a *species incerta* but incorrectly stated that Lang (1965) agreed with Noodt's (1958) opinion. Wells (2007) effectively listed A. pectinata as a synonym of A. incerta, claiming that the juvenile status of the former is corroborated by the different lines of circumstantial evidence highlighted by Lang (1965) (smaller body size, 2-segmented P2–P4 endopods with vestigial segment boundaries between enp-2 and enp-3) and Wells and Rao (1987) (juvenile condition of anal ornamentation). Copepodid V stages of Arenosetella lack the pseudoperculum and prominent anal hooks expressed in the adults but possess instead an arcuate anal operculum which bears a series of spinular extensions (Noodt 1952; Lang 1965; Wells and Rao 1987). This condition is also found in "Arenosetella spec. juv." and appears to reinforce Chappuis' (1954a) claim that this stage represents the last copepodid of A. incerta, however, it is radically different from that displayed in A. pectinata. Chappuis (1954a), in his description of the latter, stated "..., à la place de l'opercule anal, deux plaques symétriques se terminant chacune en 5 à 6 pointes". A similar raised pair of multidentate lamellae on the anal somite was described for two closely related species in the genus Noodtiella: N. ornamentalis Wells & Rao, 1987 and N. toukae Mitwally & Montagna, 2001. Based on this character and the apparent differences with Arenosetella, Wells and Rao (1987) suggested that N. ornamentalis may be placed in a genus separate from Noodtiella but refrained from formally naming and diagnosing it. However, N. ornamentalis displays all the diagnostic characters of Noodtiella and has exactly the same swimming leg setal formula as N. wellsi Apostolov, 1974, which lacks the multidentate lamellae (Table 2). Since removing this species, and the closely related N. pectinatal N. toukae, would render Noodtiella a paraphyletic taxon, they are here retained in the genus as representatives of a specialized lineage characterized by the conspicuous anal ornamentation. Mitwally and Montagna (2001) compared N. toukae with N. ornamentalis but naturally not with A. pectinata. Comparison with Chappuis' (1954a) description reveals complete congruence in the morphology of the swimming legs, fifth legs of both sexes and the anal somite between both Mediterranean forms. Consequently, A. pectinata is here removed from its uncertain position in Ectino*somoides* to the genus *Noodtiella* as *N. pectinata* comb. n., and *N. toukae* is relegated to a junior subjective synonym of the latter.

A dichotomous key to the 18 valid species of *Noodtiella* is presented below. Swimming leg setal formulae for these species are compiled in Table 2.

| 1 | P1 endopod 2-segmented |
|--|---|
| _ | P1 endopod 3-segmented |
| 2 | P2–P4 endopod 2-segmented |
| _ | P2–P4 endopod 3-segmented |
| 3 | P4 exopod 2-segmented |
| _ | P4 exopod 3-segmented |
| 4 | P2-P3 exp-3 with 4 setae/spines; P4 exp-2 with 5 setae/spines mielkei |
| _ | P2–P3 exp-3 with 5 setae/spines; P4 exp-2 with 3 or 4 setae/spines5 |
| 5 | P1 exp-2 with inner seta; P1 exp-3 with 3 elements; P3 exp-2 with inner seta; |
| | P4 exp-2 with 4 setae/spines gracile |
| _ | P1 exp-2 without inner seta; P1 exp-3 with 4 elements; P3 exp-2 without |
| | inner seta; P4 exp-2 with 3 setae/spines |
| 6 | P1 enp-2 with 3 elements |
| _ | P1 enp-2 with 4 elements |
| 7 | P4 exp-2 with outer spine |
| _ | P4 exp-2 without outer spine |
| 8 | P2–P3 exp-1 without inner seta9 |
| _ | P2–P3 exp-1 with inner seta |
| 9 | P4 exp-1 with short inner seta |
| _ | P4 exp-1 without inner setaproblematica |
| | |
| 10 | P4 exp-1 with inner seta |
| 10 - | P4 exp-1 without inner seta |
| 10 - 11 | * |
| _ | P4 exp-1 without inner seta |
| _ | P4 exp-1 without inner seta |
| _ | P4 exp-1 without inner seta |
| _ | P4 exp-1 without inner seta. P4 exp-2 with inner seta; P5 exopod with 3 setae in female and 4 setae in male. **Modensis** P4 exp-2 without inner seta; P5 exopod with 2 setae in female and 3 setae in male. **Labogensis** P1 exp-2 with inner seta; female P5 with outer endopodal spine fused to |
| - 11 - | P4 exp-1 without inner seta |
| - 11 - | P4 exp-1 without inner seta: P5 exopod with 3 setae in female and 4 setae in male |
| - 11 - | P4 exp-1 without inner seta: P5 exopod with 3 setae in female and 4 setae in male |
| - 11 - | P4 exp-1 without inner seta: P4 exp-2 with inner seta; P5 exopod with 3 setae in female and 4 setae in male |
| - 111 - 12 | P4 exp-1 without inner seta: P5 exopod with 3 setae in female and 4 setae in male. In male male male male male male male male |
| - 111 - 12 | P4 exp-1 without inner seta: P5 exopod with 3 setae in female and 4 setae in male |
| - 111 - 12 | P4 exp-1 without inner seta: P5 exopod with 3 setae in female and 4 setae in male |
| - 111 - 12 | P4 exp-1 without inner seta. P4 exp-2 with inner seta; P5 exopod with 3 setae in female and 4 setae in male. P4 exp-2 without inner seta; P5 exopod with 2 setae in female and 3 setae in male. P4 exp-2 without inner seta; P5 exopod with 2 setae in female and 3 setae in male. P5 exp-2 with inner seta; female P5 with outer endopodal spine fused to baseoendopod. P1 exp-2 without inner seta; female P5 with outer endopodal spine not fused to baseoendopod. P1 exp-2 with 4 elements; P4 enp-2 with inner seta; female P5 with outer endopodal spine fused to baseoendopod. P1 enp-2 with 3 elements; P4 enp-2 without inner seta; female P5 with outer endopodal spine not fused to baseoendopod. P1 enp-2 with 3 elements; P4 enp-2 without inner seta; female P5 with outer endopodal spine not fused to baseoendopod. Chilensis P1-P4 exp-3 with 3 elements. Chilensis Iusitanica |
| - 111 - 12 - 13 - 14 - | P4 exp-1 without inner seta: P5 exopod with 3 setae in female and 4 setae in male |
| - 111 - 12 - 13 | P4 exp-1 without inner seta. P4 exp-2 with inner seta; P5 exopod with 3 setae in female and 4 setae in male. P4 exp-2 without inner seta; P5 exopod with 2 setae in female and 3 setae in male. P4 exp-2 without inner seta; P5 exopod with 2 setae in female and 3 setae in male. P5 exp-2 with inner seta; female P5 with outer endopodal spine fused to baseoendopod. P1 exp-2 without inner seta; female P5 with outer endopodal spine not fused to baseoendopod. P1 exp-2 with 4 elements; P4 enp-2 with inner seta; female P5 with outer endopodal spine fused to baseoendopod. P1 enp-2 with 3 elements; P4 enp-2 without inner seta; female P5 with outer endopodal spine not fused to baseoendopod. P1 enp-2 with 3 elements; P4 enp-2 without inner seta; female P5 with outer endopodal spine not fused to baseoendopod. Chilensis P1-P4 exp-3 with 3 elements. Chilensis Iusitanica |

Key to the Genera of Ectinosomatidae

The genus *Tetanopsis* Brady, 1910 (type species: *T. typicus*) is included in the key below based on its allegedly 1-segmented antennary exopod, however, it should be recognized that its status is currently doubtful (Huys et al. 1996; Wells 2007) as well as the grounds for subsequently allocating *T. medius* Perkins, 1956, *T. smithi* Perkins, 1956 and *Arenosetella mediterranea* Chappuis, 1954b to this genus (Perkins 1956; Lang 1965).

The antennary exopod of *Ectinosomoides* was claimed to be entirely absent (Nicholls 1945) and this character was adopted by Wells (2007: 381) in his tabular keys. Huys et al. (1996: 158) scored the exopod as 3-segmented in their dichotomous key and this condition has been confirmed by re-examination of the single female of *E. longipes* Nicholls, 1945 found among the type material of *Neoleptastacus spinicaudatus* Nicholls, 1945 (cf. Sak et al. 2008: 435).

Nicholls (1935) established the genus *Hastigerella* for a new species *Hastigerella palpilabra* Nicholls, 1935 but McLachlan and Moore (1978: 198) relegated it to a junior synonym of *Ectinosoma tenuissima* Klie, 1929 and – based on their assertion that Nicholls (1935) had overlooked the anal claws – transferred this species to *Arenosetella*. They retained *Hastigerella* as a valid generic name and illegitimately designated *Ectinosoma leptoderma* Klie, 1929 as the new type species (ICZN Art. 61.1.3). Huys (2009) pointed out that adopting McLachlan and Moore's (1978) synonymy of *H. palpilabra* would render *Hastigerella* a junior subjective synonym of *Arenosetella* and therefore an invalid name. He proposed a new name, *Glabrotelson* (type species: *Hastigerella mehuinensis* Mielke, 1986), for the orphaned taxonomic grouping equivalent to *Hastigerella sensu* McLachlan and Moore (1978).

Seifried et al.'s (2007) course of action to upgrade the subgenus *Bradya* (*Parabradya*) to full generic rank appears premature since this leaves *Bradya* (now equivalent to its nominotypical subgenus) with only one questionable autapomorphy and hence a potentially paraphyletic status. The authors considered the maxillipedal endopod being fused to the basis at an angle as sufficient evidence to warrant separate generic status for the nominotypical subgenus *Bradya*. However, as the authors admitted themselves the fusion is not complete in some as yet undescribed *Bradya* species. Both *Bradya* and *Parabradya* are retained here as valid genera but an in-depth study of all species accommodated in the former genus is required before the validity of this separation can be confirmed. Lang (1936) showed 5 setae on the exopodal lobe of the female P5 in *Parabradya confluens* (Lang, 1936). This is a very unusual condition not found in any other extant member of the Ectinosomatidae (see also

Seifried et al. 2007) and would require re-examination of the type material before it can be used for identification.

As has been pointed out by Karanovic and Pesce (2001), Vervoort (1962: 399) explicitly fixed *Ectinosoma sarsii* Boeck, 1873 as type species of the subgenus *Ectinosoma* (*Halectinosoma*) but Lang (1965: 11), who upgraded *Halectinosoma* to generic status, did not mention Vervoort's (1962) designation. A comparison of the diagnoses of the two subgenera given in Lang (1944: 6) shows that *Halectinosoma* is distinguished from *Ectinosoma* on the basis of the setation of the exopod of leg 5. Therefore, the generic name *Halectinosoma* is available from Vervoort (1962), who cited (p. 255) that page in Lang (1944) in this connection and designated a type species (Huys 2008, 2009).

Wells and Rao (1987) placed their new species Halophytophilus aberrans with some diffidence in the genus Halophytophilus because it showed significant differences with its congeners in the non-prehensile P1 endopod and the armature of the P2-P4 endopods, in addition to discrepancies in the accessory ornamentation of the swimming legs and abdomen, and in the P5 and the caudal rami. The authors believed that there was a case for proposing a new subgenus for this species while Huys et al. (1996) surmised that it may belong to a separate genus. Bodin (1997) and Wells (2007) placed H. aberrans in the genus Klieosoma without giving any factual justification for this course of action. Gheerardyn et al. (2008) did not consider the species in their review of the genus Halophytophilus. It has now come to our attention that Wells and Rao's (1987) setal formula of P4 contradicts their illustration. In their description the authors stated that P2-P4 exp-1 lacks an inner seta while their Fig. 28f clearly shows a well developed seta on this segment in leg 4. Huys et al. (1996) constructed their generic key on the assumption that this seta was absent in all swimming legs and hence H. aberrans may have keyed out to the wrong couplet. Without any illustrations of the maxilla (although Wells and Rao did state that the mouthparts were as in H. simplex Wells & Rao, 1987) and P2-P4 it is impossible to decide which genus H. aberrans belongs to and, consequently, it is here considered species incertae sedis in the Ectinosomatidae. A dichotomous key to the 21 valid genera in the Ectinosomatidae is given below.

| 1 | Body cylindrical with cephalothorax rectangular in dorsal aspect; body approximately the same width throughout its length |
|---|---|
| _ | 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 |
| _ | Body with dorsoventrally depressed prosome, clearly wider than urosome |
| | |
| 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 | Endopods P2–P4 2-segmented <i>Ectinosomoides</i> Nicholls, 1945 |
| _ | Endopods P2–P4 3-segmented |

| 4 | Anal somite with dorsal armature of claws, lappets or spiniform processes |
|-----|--|
| | around anal opening; P5 exopod with 3 marginal and 1 surface seta |
| | |
| _ | Anal somite without such ornamentation5 |
| 5 | Antennary exopod 1-segmented |
| _ | Antennary exopod 3-segmented |
| 6 | Female P5 with foliaceous setae on exopod and baseoendopod, exopod with |
| O | 3 marginal and no surface setae; male P5 exopod with 4 normal marginal |
| | setae |
| | P5 with normal setae on exopod and baseoendopod in both sexes, exopod |
| _ | |
| | with 3 marginal and typically a surface seta [absent in Hastigerella noodti |
| 7 | Soyer, 1974 = <i>G. soyeri</i> (Bodin, 1976)] |
| 7 | P1–P4 endopods 2-segmented |
| _ | P1 endopod 2- or 3-segmented, P2–P4 endopods 3-segmented |
| 8 | P1 endopod prehensile |
| _ | P1 endopod not prehensile |
| 9 | P1 endopod 2-segmented |
| _ | P1 endopod 3-segmented |
| 10 | P1–P2 exp-3 with 2 outer elements |
| _ | P1–P2 exp-3 with 3 outer elements |
| 11 | Antennule with large spine on segment 2 (and often segments 1 and 3); an- |
| | tennary exopod rudimentary, with 1-3 small setae; P1 enp-2 with 4 elements |
| | (1-2 pinnate and claw-like) |
| _ | Armature elements on antennulary segments 1-3 setiform; antennary exopod |
| | well developed and 3-segmented; P1 enp-2 with 6 elements (outer one bifid |
| | and claw-like) |
| 12 | Maxilla prehensile, with syncoxa and allobasis forming right angle; P5 exo- |
| | pod poorly developed, short, fused to baseoendopod in female and distinct in |
| | male, with 3 marginal and no surface setae; body very small (< 300 µm) |
| | Signatidium Giesbrecht, 1881 |
| | These characters not combined 13 |
| 13 | P5 exopod and baseoendopod fused, forming a single plate in both sexes |
| 13 | 17 exoport and basedendoport fused, forming a single plate in both sexes |
| | |
| 1 / | P5 exopod and baseoendopod at least partly discrete |
| 14 | P1–P4 exp-3 with 5, 6, 6, 6 elements, respectively; male P6 unarmed; body |
| | of female small (< 400 μm); continental groundwater |
| | |
| _ | P1-P4 exp-3 with 6, 7, 8, 8 elements, respectively; male P6 with 2 setae; |
| | body of female large (≥ 1200 μm); marine, usually deepwater |
| | |
| 15 | Integument of somites with distinctive subrectangular pores; P5 exopod with |
| | 4 marginal setae Ectinosoma Boeck, 1865 |
| | |

| _ | Integument of somites without distinctive subrectangular pores; P5 exopod |
|----|---|
| 16 | with 3 marginal setae and 1 seta on anterior surface |
| | each terminating in 2-3 setae; antennary exopod without lateral spines |
| | |
| _ | These characters not combined |
| 17 | Third segment of female antennule 3 times as long as wide; mandibular endopod with one strong seta laterally; P1–P4 exp-3 with 2 outer spines; plank- |
| | tonic (occasionally in sediment) Microsetella Brady & Robertson, 1873 |
| _ | These characters not combined |
| 18 | Body comparatively robust with prosome-urosome separation usually dis- |
| | tinct (exception: B. kurtschminkei Seifried & Martínez Arbizu, 2008 with |
| | dorsoventrally flattened habitus); antenna with 2 setae on proximal exopod |
| | segment and 1 seta on proximal endopod segment; mandibular exopod with |
| | at least 5 setae; maxilliped robust with short endopod usually fused at an |
| | angle with basis and bearing 4 conspicuous setae Bradya Boeck, 1973 |
| _ | Body comparatively slender with no sharp separation between prosome and |
| | urosome; antenna with less than 2 setae on proximal exopod segment (except |
| | Pseudobradya ambigua Sars, 1920 with 2) and no seta on proximal endopod |
| | segment; mandibular exopod generally with fewer than 5 setae; maxilliped |
| | usually slender and straight with discrete endopod bearing 1 small and 4 |
| | conspicuous setae |
| 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 segmen- |
| | tation difficult to discern; reduced to a a narrow 3-segmented cylinder in P. |
| | leptognatha Sars, 1920); maxilliped short and robust |
| | |
| _ | Antennule without pigment spot; maxilla with at most a slight angle between |
| | syncoxa and allobasis, the latter generally attenuating distally, endopod 3-seg- |
| | mented but always small, its morphology not clearly discernible; maxilliped |
| | generally slender |

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References

- Akatova N (1935) Drei neue Copepoden-Arten aus dem Kaspi See. Zoologischer Anzeiger 111: 319-326.
- Alldredge AL (1972) Abandoned larvacean houses: a unique food source in the pelagic environment. Science 177: 885-887.
- Apostolov A (1974) Copépodes Harpacticoïdes de la mer Noire. Travaux du Muséum d'Histoire naturelle "Gr. Antipa" 15: 131-139.
- Bodin P (1968) Copépodes Harpacticoïdes des étages bathyal et abyssal du golfe de Gascogne. Mémoires du Muséum national d'Histoire naturelle de Paris, n. ser. (A)55(1): 1-107.
- Bodin P (1976) Catalogue des nouveaux Copépodes Harpacticoïdes marins. Additif no. 3. Brest, Laboratoire d'Océanographie Biologique, Université de Bretagne occidentale, 45 pp.
- Bodin P (1997) Catalogue of the new marine harpacticoid copepods (1997 edition). Documents de Travail, Institut royal des Sciences naturelles de Belgique 89: 1-304.
- Boeck A (1865) Oversigt over de ved Norges Kyster jagttagne Copepoder henhörende til Calanidernes, Cyclopidernes og Harpactidernes Familier. Forhandlinger i Videnskabsselskabet i Kristiania 1864: 226-282.
- Boeck A (1873) Nye Slaegter og Arter af Saltvands-Copepoder. Forhandlinger i Videnskabsselskabet i Kristiania 1872: 35-60.
- Borutzky EV (1972) Copepoda Harpacticoida gruntovykh vod poberezhya oz. Issyk-kul i yuzhnoi chasti Kuzylkumov. Copepoda Harpacticoida from subterranean water of the shore of Issyk-kul and southern Kisulkum. In: Fauna gruntovykh vod srednei Azii. Trudy zoologicheskogo Instituta, Akademiia nauk SSSR 51: 98-119.
- Brady GS (1910) Die marinen Copepoden der Deutschen Südpolar Expedition 1901-1903. I. Ueber die Copepoden der Stämme Harpacticoida, Cyclopoida, Notodelphyoida und Caligoida. Deutsche Südpolar-Expedition 11 (= Zoologie 3): 497-594.
- Brady GS, Robertson D (1873) Contributions to the study of the Entomostraca. No. VIII. On marine Copepoda taken in the west of Ireland. Annals and Magazine of natural History (4)12: 126-142.
- Brian A (1919) Descrizione di una nuova forma di Copepodo neritico della famiglia Ectinosomidae Sars, vivente tra le alghe del litorale di Quarto dei Mille. Atti della Società ligustica di Scienze Naturali e Geografiche 29: 71-78.
- Brian A (1925) Descrizione di un nuovo genere di Copepodo arpacticoide dell'Adriatico. Atti della Società ligustica di Scienze Naturali e Geografiche n. ser. 4: 116-121.
- Bruno MC, Cottarelli V (1999) New records of harpacticoids (Crustacea, Copepoda) from subterranean fresh and brackish waters of Greece. Contributions to the Zoogeography and Ecology of the Eastern Mediterranean Region 1: 305-315.
- Bruno MC, Reid JW, Perry SA (2003) Checklist and identification key for free-living copepod crustaceans in freshwater habitats of Everglades National Park and adjacent areas, Florida, U.S.A., with notes on their ecology. Florida Scientist 66: 23-42.
- Chappuis PA (1954a) Harpacticides psammiques récoltés par Cl. Delamare-Deboutteville en Méditerranée. Vie et Milieu 4: 254-276.
- Chappuis PA (1954b) IV. Copépodes psammiques des plages du Roussillon. In: Chappuis PA, Delamare Deboutteville Cl. (avec la collaboration de Balazuc, J. & Ruffo, S.) (Eds),

- Biospeologica LXXIV. Recherches sur les Crustacés souterrains (première série). Archives de Zoologie expérimentale et générale 91: 35-50.
- Clément M, Moore CG (1995) A revision of the genus *Halectinosoma* (Harpacticoida: Ectinosomatidae): a reappraisal of *H. sarsi* (Boeck) and related species. Zoological Journal of the Linnean Society 114: 247-306.
- Clément M, Moore CG (2000) A revision of the genus *Halectinosoma* (Harpacticoida: Ectinosomatidae): the *H. herdmani* (Scott & Scott) group of species. Zoological Journal of the Linnean Society 128: 237-267.
- Clément M, Moore CG (2007) Towards a revision of the genus *Halectinosoma* (Copepoda, Harpacticoida, Ectinosomatidae): new species from the North Atlantic and Arctic regions. Zoological Journal of the Linnean Society 149: 453-475.
- Clément M, Ólafsson E (2001) A redescription of the common harpacticoid *Pseudobradya* arctica (Olofsson, 1917) comb. nov. (Crustacea, Copepoda) from the Baltic Sea with ecological notes. Sarsia 86: 221-228.
- Corbisier TN (1993) Meiofauna da plataforma continental interna do litoral norte de São Paulo verão/89. Publicação Especial do Instituto Oceanográfico 10: 123-135.
- Galassi DMP, Dole-Olivier M-J, De Laurentiis P (1999) Phylogeny and biogeography of the genus *Pseudectinosoma*, and description of *P. janineae* sp. n. (Crustacea, Copepoda, Ectinosomatidae). Zoologica Scripta 28: 289-303.
- Gheerardyn H, Seifried S, Vanreusel A (2008) A new species of *Halophytophilus* Brian, 1919 (Copepoda: Harpacticoida: Ectinosomatidae) from cold-water corals in the Porcupine Seabight (NE Atlantic). Zootaxa 1761: 1-16.
- Giesbrecht W (1881) Vorläufige Mitteilung aus einer Arbeit über die freilebenden Copepoden des Kieler Hafens. Zoologischer Anzeiger 4: 254-258.
- Hassall AH (1841) Supplement to a catalogue of Irish zoophytes. Annals and Magazine of Natural History 7: 276-287, 363-373.
- Haswell WA (1883). On some new Australian tubicolous annelids. Proceedings of the Linnean Society of New South Wales 7: 633-638.
- Hicks GRF, Schriever G (1983) A new genus and species of Ectinosomatidae (Copepoda, Harpacticoida) based on the original material of Dr. h.c. Walter Klie. Mitteilungen aus dem zoologischen Museum der Universität Kiel 2(1): 1-7.
- Hicks GRF, Schriever G (1985) *Klieosoma* nom. nov., a replacement name for *Kliella* Hicks & Schriever, 1983 (Copepoda, Harpacticoida, Ectinosomatidae). Crustaceana 49 (notes and news): 100-101.
- Huys R (2008) Case 3470. Halectinosoma Vervoort, 1962 (Crustacea, Copepoda, Harpacticoida): proposed conservation of usage by designation of Halectinosoma chrystalii Scott, 1894 as the type species and by giving it precedence over Pararenosetella Lang, 1944. Bulletin of zoological Nomenclature 65: 276-281.
- Huys R (2009) Unresolved cases of type fixation, synonymy and homonymy in harpacticoid copepod nomenclature (Crustacea: Copepoda). Zootaxa (in press).
- Huys R, Bodin P (1997) First record of Acanthocephala in marine copepods. Ophelia 46(3): 217-231.
- Huys R, Gee JM, Moore CG, Hamond R (1996) Marine and brackish water harpacticoid copepods. Part 1. In: Barnes RSK, Crothers JH (Eds), Synopses of the British Fauna (New Series), 51: i–viii, 1-352. Field Studies Council, Shrewsbury.

- Huys R, Iliffe TM (1998) Novocriniidae, a new family of harpacticoid copepods from anchihaline caves in Belize. Zoologica Scripta 27: 1-15.
- Jakobi H (1954) Harpacticoida (Cop. Crust.) da microfauna do substrato areno-lodoso do "Mar de Dentro" (Ilha do Mel Baía de Paranagúa Brasil). (Harpacticiden der Mikrofauna aus sandig-schlammigem Grund im "Mar de Dentro" (Ilha do Mel Baía de Paranagúa Brasil)). Dusenia 5: 209-232.
- Jakobi H, Nogueira MH (1960) Descrição de uma nova espécie de *Ectinosoma* encontrada em aguas salobras da Ilha de Santa Catarina. (Copepoda-Harpacticoidea). Boletim da Universidade do Paraná, Zoologia 5: 1-10.
- Karanovic T (2006) Subterranean copepods (Crustacea, Copepoda) from the Pilbara region in Western Australia. Records of the Western Australian Museum Supplement 70: 1-239.
- Karanovic T, Pesce GL (2001) A new genus and species of the family Ectinosomatidae (Crustacea: Copepoda: Harpacticoida) from the groundwaters of India. Annales de Limnologie 37(4): 281-292.
- Klie W (1929) Die Copepoda Harpacticoida der südlichen und westlichen Ostsee mit besonderer Berücksichtigung der Sandfauna der Kieler Bucht. Zoologische Jahrbücher, Systematik 57: 329-386.
- Klie W (1949) Harpacticoida (Cop.) aus dem Bereich von Helgoland und der Kieler Bucht. 1. Kieler Meeresforschungen 6: 90-128.
- Krićagin N (1878) Otchet' ob' ekskursii na Sv. Bereg" Chernago morya sovershennoi po porucheniyu Kievskago obshchestva estestvois'pyta'telei letom' 1874 g. [Report on an excursion to the northeastern shore of the Black Sea carried out in the summer of 1874 on the instructions of the Kiev Society of Naturalists]. Zapiski Kievskago Obshchestva Estestvoispÿtateleĭ 5(1): 1-56. [In Ukrainian].
- Kunz H (1935) Zur Oekologie der Copepoden Schleswig-Holsteins und der Kieler Bucht. Schriften der Naturwissenschaftlichen Vereins für Schleswig-Holstein 21: 84-132.
- Kunz H (1937) Zur Kenntnis der Harpacticoiden des Küstengrundwassers der Kieler Förde. (Studien an marinen Copepoden. I). Kieler Meeresforschungen 2: 95-115.
- Kunz H (1975) Harpacticoiden (Crustacea, Copepoda) aus dem Küstengrundwasser der französischen Mittelmeerküste. Zoologica Scripta 3: 257-282.
- Lang K (1936) Die während der schwedischen Expedition nach Spitzbergen 1898 und nach Grönland 1899 eingesammelten Harpacticiden. Kungliga Svenska Vetenskapsakademiens Handlingar (3)15(4): 1-55.
- Lang K (1944) Monographie der Harpacticiden (Vorläufige Mitteilung). Almqvist & Wiksells Boktryckeri Ab, Uppsala, 39 pp.
- Lang K (1965) Copepoda Harpacticoida from the Californian Pacific coast. Kungliga Svenska Vetenskapsakademiens Handlingar (4)10(2): 1-560.
- Lindgren EW (1975) Six meiobenthic Harpacticoida (Crustacea, Copepoda) from North Carolina beaches. Cahiers de Biologie marine 16: 445-473.
- McLachlan A, Moore CG (1978) Three new species of Harpacticoida (Crustacea, Copepoda) from sandy beaches in Algoa Bay, South Africa, with keys to genera *Arenosetella*, *Hastige-rella*, *Leptastacus* and *Psammastacus*. Annals of the South African Museum 76(4): 191-211.
- Médioni A, Soyer J (1968) Copépodes Harpacticoïdes de Banyuls-sur-Mer. 6. Nouvelles formes associées à des Bryozoaires. Vie et Milieu (A)18: 317-343.

- Mielke W (1975) Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt. Mikrofauna des Meeresbodens 52: 1-134.
- Mielke W (1976) Ökologie der Copepoda eines Sandstrandes der Nordseeinsel Sylt. Mikrofauna des Meeresbodens 59: 1-86.
- Mielke W (1979) Interstitielle Fauna von Galapagos. XXV. Longipediidae, Canuellidae, Ectinosomatidae (Harpacticoida). Mikrofauna des Meeresbodens 77: 1-106.
- Mielke W (1981) Interstitielle Ectinosomatidae (Copepoda) von Panama. Mikrofauna des Meeresbodens 85: 1-45.
- Mielke W (1986) Copépodos de la meiofauna de Chile, con descriptión de dos nuevas especies. Revista Chilena de Historia natural 59: 73-86.
- Mielke W (1987a) Zwei Spezies der Gattungen *Noodtiella* und *Lineosoma* (Copepoda) von Chile. Crustaceana 53: 152-159.
- Mielke W (1987b) Interstitielle Copepoda von Nord- und Süd-Chile. Microfauna Marina 3: 309-361.
- Mitwally HM, Montagna PA (2001) Egyptian interstitial Copepoda Harpacticoida with the description of two new species and one subspecies. Crustaceana 74: 513-544.
- Miura Y (1962) Three new harpacticoid copepods from the subterranean waters of Shikoku in Japan. Japanese Journal of Zoology 13: 267-274.
- Miura Y (1964) Subterranean harpacticoid copepods from a driven well in Japan. Japanese Journal of Zoology 14: 133-141.
- Nicholls AG (1935) Copepods from the interstitial fauna of a sandy beach. Journal of the marine biological Association of the United Kingdom, new series 20: 379-405.
- Nicholls AG (1945) Marine Copepoda from Western Australia. IV. Psammophilous harpacticoids. Journal of the Royal Society of Western Australia 29: 17-24.
- Noodt W (1952) Marine Harpacticiden (Cop.) aus dem eulitoralen Sandstrand der Insel Sylt. Abhandlungen der mathematisch-naturwissenschaftlichen Klasse. Akademie der Wissenschaften und der Literatur in Mainz 1952(3): 105-142.
- Noodt W (1958) Die Copepoda Harpacticoidea des Brandungsstrandes von Teneriffa (Kanarische Inseln). Abhandlungen der mathematisch-naturwissenschaftlichen Klasse. Akademie der Wissenschaften und der Literatur in Mainz 1958(2): 53-116.
- Ohtsuka S, Kubo N, Okada M, Gushina K (1993) Attachment and feeding of pelagic copepods on larvacean houses. Journal of Oceanography 49: 115-120.
- Perkins EJ (1956) The harpacticoid genus *Tetanopsis* Brady, with a description of *Tetanopsis smithi*, sp. n. and *Tetanopsis medius*, sp. n. Annals and Magazine of natural History (12)9: 497-504.
- Reid JW (1998) Maxillopoda Copepoda. Harpacticoida. In: Young PS (Ed.), Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro. pp. 75-127 (Série Livros n. 6).
- Rouch R (1962) Harpacticoïdes (Crustacés Copépodes) d'Amérique du Sud. Biologie de l'Amérique Australe 1: 237-280.
- Sak S, Huys R, Karaytuğ S (2008) Disentangling the subgeneric division of Arenopontia Kunz, 1937: resurrection of Psammoleptastacus Pennak, 1942, re-examination of Neoleptastacus spinicaudatus Nicholls, 1945, and proposal of two new genera and a new generic classification (Copepoda, Harpacticoida, Arenopontiidae). Zoological Journal of the Linnean Society 152: 409-458.

- Sars GO (1903) Copepoda Harpacticoida. Parts I & II, Misophriidae, Longipediidae, Cerviniidae, Ectinosomidae (part). An account of the Crustacea of Norway, with short descriptions and figures of all the species 5: 1-28 + pls. 1-16.
- Sars GO (1904) Copepoda Harpacticoida. Parts III & IV. Ectinosomidae, Harpacticidae (part). An account of the Crustacea of Norway, with short descriptions and figures of all the species 5: 29-56 + pls. 17-32.
- Sars GO (1910) Copepoda Harpacticoida. Parts XXIX & XXX. Tachidiidae (concluded), Metidae, Balaenophilidae, supplement (part). An account of the Crustacea of Norway, with short descriptions and figures of all the species 5: 337-368 + pls. 225-230 + supplement pls. 1-10.
- Sars GO (1920) Copepoda Supplement. Parts III & IV. Harpacticoida (continued). An account of the Crustacea of Norway, with short descriptions and figures of all the species 7: 25-52, pls. 17-32.
- Seifried S, Plum C, Schulz M (2007) A new species of *Parabradya* Lang, 1944 (Copepoda: Harpacticoida: Ectinosomatidae) from the abyssal plain of the Angola Basin. Zootaxa 1432: 1-21.
- Soyer J (1974) Contribution à l'étude des Copépodes Harpacticoïdes de Méditerranée occidentale. 9. Le genre *Hastigerella* Nicholls (Ectinosomidae Sars, Olofsson). Systématique, écologie. Vie et Milieu (B)24: 175-192.
- Štěrba O (1968) Neue Harpacticoidea (Crustacea, Copepoda) aus dem asiatischen Teil der Paläarktis. Zoologischer Anzeiger 180: 50-68.
- Steuer A (1940) Über eine neue Ectinosoma-Art (Copepoda Harpacticoida) aus dem Mittelmeer. Zoologischer Anzeiger 132: 124-130.
- Vervoort W (1962) Report on some Copepoda collected during the Melanesia Expedition of the Osaka Museum of Natural History. Publications of the Seto marine biological Laboratory 10: 393-470.
- Watkins RL (1987) Description of new species of *Bradyellopsis* and *Perissocope* (Copepoda: Harpacticoida) from the California coast with revised keys to the genera. Journal of crustacean Biology 7: 380-395.
- Wells JBJ (1963) Copepoda from the littoral region of the estuary of the River Exe (Devon, England). Crustaceana 5: 10-26.
- Wells JBJ (1965) Two new genera of harpacticoid copepods of the family Ectinosomidae. Revista de Biologia, Lisboa 5(2-3): 30-35.
- Wells JBJ (1967) The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. Transactions of the Royal Society of Edinburgh 67(7): 189-358.
- Wells JBJ (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). Zootaxa 1568: 1-872.
- Wells JBJ, Rao GC (1987) Littoral Harpacticoida (Crustacea: Copepoda) from Andaman and Nicobar Islands. Memoirs of the zoological Survey of India 16(4): 1-385.
- Wilson CB (1932) The copepods of the Woods Hole region, Massachusetts. Bulletin of the United States National Museum 158: 1-635.