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***Johnwellsia*, a new intertidal genus of Parastenheliidae (Copepoda, Harpacticoida) from the Taiwan Strait, China, including a review of the family and key to genera**

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Abstract

A new genus of Parastenheliidae, *Johnwellsia* **gen. nov.**, is proposed for its type and only species, *J. bipartita* **sp. nov.**, collected from Dadeji Beach in Xiamen, Taiwan Strait, China. The intricate taxonomic history of the family is reviewed with special emphasis on its type genus *Parastenhelia* Thompson & Scott, 1903. It is concluded that *P. hornelli* Thompson & Scott, 1903 is the type of the genus and that the widely adopted previous designation of *Harpacticus spinosus* Fischer, 1860 as type species of *Parastenhelia* is invalid. The taxonomic concept of *Parastenhelia* is restricted to the *hornelli*-group which includes four valid species: *P. hornelli*, *P. similis* Thompson & Scott, 1903, *P. oligochaeta* Wells & Rao, 1987, and *P. willemvervoorti* **sp. nov.**

The currently accepted concept of *Parastenhelia spinosa* as a highly variable cosmopolitan species is rejected. The genus *Microthalestris* Sars, 1905 (type: *Thalestris forficula* Claus, 1863) is resurrected to accommodate most *Parastenhelia* species that were previously placed in the *spinosa*-group. Two species, *Thalestris forficuloides* Scott & Scott, 1894 and *Parastenhelia antarctica* Scott, 1912, are reinstated as valid members of the genus which further includes *Parastenhelia gracilis* Brady, 1910, *Microthalestris littoralis* Sars, 1911, *P. costata* Pallares, 1982, *P. minuta* Pallares, 1982, *P. bulbosa* Gee, 2006 and five new species: *M. campbelliensis* **sp. nov.**; *M. polaris* **sp. nov.**; *M. santacruzensis* **sp. nov.**; *M. sarsi* **sp. nov.** and *M. variabilis* **sp. nov.** Both the type species, *Thalestris forficula*, and *Harpacticus spinosus* are considered *species inquirendae* in *Microthalestris*. Three new genera are proposed to accommodate the remaining *Parastenhelia* species. *Porirualia* **gen. nov.** contains *P. megarostrum* Wells, Hicks & Coull, 1982 (type) and *P. pyriformis* Song, Kim & Chang, 2003, and is the sistergroup of *Johnwellsia* **gen. nov.** *Parastenhelia aydini* Kuru & Karaytuğ, 2015 is placed in the monotypic genus *Karaytugia* **gen. nov.** while all species with penicillate elements on the antenna and P1 are transferred to *Penicillicaris* **gen. nov.**, including *Thalestris pectinimana* Car, 1884, which is removed from the synonyms of the *Parastenhelia spinosa* (Fischer, 1860) “complex”, and three new species: *P. maldivensis* **sp. nov.**, *P. penicillata* **sp. nov.**, and *P. sewelli* **sp. nov.**

The genus *Karllangia* Noodt, 1964 (type: *K. arenicola* Noodt, 1964) is relegated to a junior subjective synonym of *Thalestrella* Monard, 1935a (type: *T. ornatissima* Monard, 1935a). New or updated diagnoses for each genus, and differential diagnoses for species where appropriate, are provided. A key to the ten currently recognized genera in the Parastenheliidae is presented as well as keys to species for *Parastenhelia*, *Microthalestris*, *Thalestrella* and *Penicillicaris* **gen. nov.**

Key words: *Parastenhelia*, *Microthalestris*, *Thalestrella*, *Paraleptomesochra*, *Psammoleptomesochra*, *Foweya*, *Karaytugia* **gen. nov.**, *Penicillicaris* **gen. nov.**, *Porirualia* **gen. nov.**, sexual dimorphism, identification keys, species complex

Introduction

The taxonomic history of the Parastenheliidae (Copepoda, Harpacticoida) is long and intricate. The family currently accommodates 22 valid species in five genera: *Parastenhelia* Thompson & Scott, 1903; *Karllangia* Noodt, 1964; *Paraleptomesochra* Wells, 1967; *Psammoleptomesochra* Mielke, 1994a; and *Foweya* Gee, 2006. Thompson & Scott (1903: 263) proposed the type genus *Parastenhelia* for two new species, *Parastenhelia hornelli* Thompson & Scott, 1903 and *P. similis* Thompson & Scott, 1903, collected in Sri Lankan waters, but did not fix the type species. The genus was placed in the family “Harpacticidae” which at that time roughly corresponded with the present day concept of the order Harpacticoida. Lang (1934: 24) relegated *P. similis* to a junior subjective synonym of *P. hornelli* which he declared as the type of the genus (on p. 23: “... *P. hornelli*, die den Typus der Gattung ist”). For some inexplicable reason (but possibly because it is the oldest species name in the genus) Lang (1944: 13) subsequently designated *Harpacticus spinosus* Fischer, 1860 from Madeira as the type species, and his course of action has unfortunately been perpetuated in the literature [e.g. Vervoort (1964: 180), Apostolov & Marinov (1988: 134), Gee (2006: 2612), Kuru & Karaytuğ (2015: 121, 127)]. This subsequent fixation is invalid since *H. spinosus* was not originally included in the genus (ICZN Art. 69.2; Huys 2009). Sars (1905: 122) proposed the new genus *Microthalestris* for *Thalestris forficula* Claus, 1863 (type by monotypy) collected from Messina, Italy and, in a later account, added a second species, *M. littoralis* Sars, 1911, from several localities in Norway (Sars 1911: 369). Monard (1935a: 44) established the genus *Thalestrella* for a new species, *T. ornatissima* Monard, 1935a (type by monotypy), from Roscoff, Brittany. Both *Microthalestris* and *Thalestrella* were placed in the Thalestridae by their respective authors. Lang (1934: 22) relegated *M. littoralis* to a subspecies of *M. forficula* (Claus, 1863), transferred both to the genus *Parastenhelia* (effectively rendering *Microthalestris* a junior synonym of that genus) together with *P. hornelli*, *P. anglica* Norman & Scott, 1905 and *P. gracilis* Brady, 1910, and assigned the genus to the Thalestridae.

As part of his revision of the Thalestridae Lang (1936a: 52) introduced a subfamily classification, including a new subfamily, Parastenheliinae to accommodate *Parastenhelia*. Lang (1944: 13) raised the subfamily to full family status and transferred *Harpacticus spinosus* to *Parastenhelia*. In his monograph, Lang (1948: 586) gave a full list of synonyms for *P. spinosa* (Fischer, 1860), stated that three forms of the species had been reported in the literature, forma *typica* [for the junior synonym *P. forficula* (Claus, 1863)], forma *littoralis* (for *Microthalestris littoralis*), and forma *penicillata* (for *Microthalestris littoralis* var. *penicillata* Willey, 1935), and transferred *Thalestrella ornatissima* Monard, 1935a to the genus as *P. ornatissima* (Monard, 1935a). Lang (1948) abandoned the division in forms and recognized five valid species in *Parastenhelia*: *P. spinosa*, *P. hornelli*, *P. anglica*, *P. gracilis* and *P. ornatissima*. Since the publication of his monograph, two new forms of *P. spinosa* (*P. littoralis* forma *scotti* Sewell, 1940 and *P. spinosa* forma *bulgarica* Apostolov, 1968) in addition to eight new species have been added to the genus (Wells 2007; Kuru & Karaytuğ 2015): *P. reducta* Apostolov, 1975; *P. costata* Pallares, 1982; *P. minuta* Pallares, 1982; *P. megarostrum* Wells, Hicks & Coull, 1982; *P. oligochaeta* Wells & Rao, 1987; *P. pyriformis* Song, Kim & Chang, 2003; *P. bulbosa* Gee, 2006 (= upgraded *P. spinosa* forma *bulbosa* Wells, 1963a; ICZN Art. 45.5.1); and *P. aydini* Kuru & Karaytuğ, 2015. Krishnasway (1957) described a forma *krusadensis* of *P. hornelli* from Pamban Island between peninsular India and Sri Lanka. This form is so radically divergent in the P1 and antennary exopod that it cannot belong to the Parastenheliidae (Wells & Rao 1987: 62). Although the description is grossly inadequate for identification purposes it likely depicts a member of the Ameiridae. *Parastenhelia* (?) *tenuis* Brady, 1910, previously rejected as a member of *Parastenhelia* (Gurney 1927: 544) but considered *species incertae sedis* in the genus by Lang (1948: 592), was fixed as the type of a new genus, *Antarcticobradya* Huys, 1987 in the family Neobradyidae (Huys 1987: 140).

Noodt (1964: 143) established the genus *Karllangia* for its type and only species, *K. arenicola* Noodt, 1964, collected from coralline sand in the Red Sea, and placed it in the Ameiridae. Fiers (1990) and Mielke (1994b, 1997) expressed doubts about the familial assignment of *Karllangia* while Huys *et al.* (1996) remarked that both *Parastenhelia* and *Karllangia* are heterogeneous assemblages that might to a certain extent be related to each other. Willen (2000) moved the latter genus to the Parastenheliidae. The genus has seen the addition of four species and one subspecies since: *K. psammophila* Wells, 1967 from Inhaca Island, Mozambique (Wells 1967), *K. tertia* Kunz, 1975 from South Africa's Eastern Cape (Kunz 1975), *K. arenicola bengalensis* Wells & Rao, 1987 from the North Andaman and Car Nicobar Islands (Wells & Rao 1987), and two sympatric species, *K. obscura* Mielke, 1994b and *K. pulchra* Mielke, 1994b, from the Caribbean coast of Costa Rica (Mielke 1994b). Although Wells (1967) originally described *K. psammophila* as a separate species, he later (Wells & Rao 1987) reduced it to a subspecies of *K. arenicola* along with another form (*K. arenicola bengalensis*) and treated them as morphs of a polytypic species. Mielke (1994b) argued that *K. arenicola bengalensis* cannot be a subspecies of *K. arenicola* but must be regarded as a subspecies of *K. psammophila* or be given species rank. Wells (2007: 86) followed the latter course of action, upgrading it to *K. bengalensis*. Meanwhile Gee (2006) had already attributed specific status to *K. arenicola*, *K. bengalensis* and *K. psammophila*, based on differences in the first antennary segment of both sexes, the armature of the swimming legs and the ornamentation of the anal operculum. As a result of his revision of the genus, Gee (2006) (a) removed *K. tertia* (and *Parastenhelia anglica*) to a new genus *Foweya*, characterized by the sexually dimorphic inner basal spine of P1, the absence of sexual dimorphism on the P3 endopod and the most primitive swimming leg armature in the family, (b) placed *Parastenhelia reducta* Apostolov, 1975 as *incertae sedis* in *Karllangia*, and (c) transferred *Parastenhelia ornatissima* to this genus because of its sexually dimorphic antenna. The latter course of action has nomenclatural implications since *P. ornatissima* is the type species (by monotypy) of the genus *Thalestrella*, which was previously regarded as a junior synonym of *Parastenhelia* (see above). The generic name *Karllangia* must therefore sink as a junior synonym of *Thalestrella* which is resurrected here. The genus accommodates the following species: *Thalestrella ornatissima* Monard, 1935a [type]; *T. arenicola* (Noodt, 1964) **comb. nov.**; *T. psammophila* (Wells, 1967) **comb. nov.**; *T. reducta* (Apostolov, 1975) **comb. nov.**; *T. bengalensis* (Wells & Rao, 1987) **comb. nov.**; *T. obscura* (Mielke, 1994b) **comb. nov.**; and *T. pulchra* (Mielke, 1994b) **comb. nov.**

Mielke (1994a: 252) proposed the monotypic genus *Psammoleptomesochra* for a new species, *P. australis* Mielke, 1994a, from a beach slope on Chiloé Island in southern Chile and placed it in the *Leptomesochra* complex [*sensu* Lang (1965) and Wells (1967)] in the family Ameiridae. Bodin (1997) erroneously listed this species as *Paramesochra australis* in the Paramesochridae as well as under its correct original combination in the Ameiridae. Seifried (2003) noted that it must remain in the latter family as long as its position is unresolved since there is no

tangible evidence for assigning it to the Paramesochridae. Mielke (1994a) pointed out that *Psammoleptomesochra* is most closely related to the genus *Paraleptomesochra* (type species: *P. minima* Wells, 1967). Both genera diverge from the typical ameirid condition in the combination of the morphology of the rostrum, antennary exopod, mouthparts, P1 (position of inner seta on enp-1) and the presence of elaborate hyaline frills on the body somites. Based on this combination of characters Back & Lee (2013) transferred *Paraleptomesochra* and *Psammoleptomesochra* to the family Parastenheliidae.

A recent survey of the intertidal copepod fauna of Dadeji Beach in Xiamen, Taiwan Strait, China, resulted in the discovery of both sexes of a new representative of the Parastenheliidae which could not be assigned to any of the currently recognized genera in the family. The new genus and species, which is here described in detail, provided the impetus for the present review of the Parastenheliidae.

Material and methods

Specimens were collected in July 2010 from the gravelly sandy intertidal zone of Dadeji Beach, Xiamen, Taiwan Strait (24°26'30" N, 118°4'12" E), China. Sediment samples were collected to a depth of 20 cm by three PVC tube cores with an inner diameter of 2.4 cm (4.52 cm²), and subsequently fixed in 10% formalin. Meiofauna was extracted by decantation over a 31 µm sieve. Harpacticoids were sorted and preserved in 4% formalin.

Before dissection, the habitus was drawn from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid, and the parts individually mounted in lactophenol under coverslips, which were subsequently sealed with transparent neutral balsam. All drawings were prepared using a camera lucida mounted on an Olympus BX51 differential interference contrast microscope. Descriptive terminology follows that of Huys *et al.* (1996). Abbreviations used in text and figures are: *ae*, aesthetasc; *apo*, apophysis on male P3 endopod; *P1–P6*, first to sixth thoracic legs; *exp*, exopod; *enp*, endopod; *exp(enp)-1(-2,-3)*, the proximal (middle, distal) segment of a ramus. Body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. Scale bars in all illustrations are in µm. The type material is deposited in the Lab of Marine Benthos, Ocean University of China (OUCBL).

Systematics

Order Harpacticoida Sars, 1903

Family Parastenheliidae Lang, 1936a

Genus *Johnwellsia* gen. nov.

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Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P2–P3 endopods, P5–P6 and urosomal segmentation. Body fusiform; posterior margin of cephalothorax with plain hyaline frill; remaining somites (except P5-bearing somite and anal somite) with deeply divided, denticulodigitate, hyaline frills. Rostrum defined at base, large, reaching to halfway second segment of antennule; with parallel sides tapering sharply into pointed apex. Anal operculum semicircular, naked. Caudal ramus wider than long, without conspicuous spinular ornamentation; with seven setae, setae IV–V with fracture planes, not inflated at base in ♀.

Antennule slender, segment 1 elongate in both sexes; 9-segmented in ♀, segments 7–9 shortest, with aesthetascs on segments 4 and 9; haplocer and indistinctly 11-segmented in ♂ (segment 4 largely incorporated in segment 5), with geniculation between segments 7 and 8, and aesthetascs on segments 5 and 11; segmental homologies in ♂: I, II–VIII, IX–XII, XIII, XIV–XVII, XVIII, XIX–XX, XXI–XXII, XXIII, XXIV–XXV, XXVI–XXVIII. Antenna not sexually dimorphic; with completely fused allobasis lacking endopodal pinnate seta on abexopodal margin; exopod 2-segmented, proximal segment with two setae, distal segment with one lateral and three apical elements; free endopod without penicillate elements. Mandible with three elements on basis; endopod with two lateral and four apical setae; exopod rudimentary, represented by single seta on minute protuberance. Maxillary coxal epipodite

represented by one seta. Maxilla with three endites on syncoxa; endopod not completely discrete at base, with two setae. Maxilliped with two setae on syncoxa; basis with two setae, without longitudinal spinular row on palmar margin; endopod represented by claw with three accessory setae.

P1 inner basal spine not sexually dimorphic. P1 exopod 3-segmented, segments subequal in length; exp-2 with inner seta; exp-3 with two pinnate spines, one geniculate seta and one non-geniculate bipinnate seta. P1 endopod 2-segmented; enp-1 longer than exopod, with long, proximally inserted, pinnate inner seta, not extending to distal margin of segment, segment margins without area of reduced chitinization; enp-2 with one naked minute seta and two naked claws of different lengths. P2–P4 rami 3-segmented; inner seta of P2–P4 exp-1 of moderate size; distal inner seta of P3–P4 exp-3 reduced. P2 endopod ♂ 2-segmented; compound enp-2 with one inner seta (inner seta of ancestral enp-3 lost). P3 endopod ♂ 3-segmented; without inner seta (vs two in ♀) on enp-3, resulting in 1.1.021 pattern; outer spine not transformed into spinous apophysis. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	1.1.123	1.1.121 [♂: 1.121]
P3	1.1.323	1.1.221 [♂: 1.1.021]
P4	1.1.323	1.1.121

P5 ♀ endopodal lobe with five setae, outermost minute; inner margin without transverse striae; exopod moderately elongate, articulation with baseoendopod very narrow, with six elements. P5 ♂ endopodal lobe with two small elements, outer one shortest; exopod 2-segmented; exp-1 with short outer seta, exp-2 with three elements. Vestigial P6 ♀ represented by three setae. P6 ♂ with three setae.

Type and only species. *Johnwellsia bipartita* sp. nov. (by original designation herein).

Etymology. The genus is named in dedication to the late Prof. John J.B. Wells, in honour of his outstanding career in harpacticoid taxonomy, systematics and biogeography.

Johnwellsia bipartita sp. nov.

(Figs. 1–5)

urn:lsid:zoobank.org:act:142A465D-1E30-404B-9962-CCC7A10D3FE4

Type locality. China, Taiwan Strait, Xiamen, Dadeji Beach (24°26'30" N, 118°4'12" E); intertidal zone, gravelly sand.

Type material. Holotype adult female dissected on fifteen slides (OUCBL reg. no 2019.001). Paratypes are one adult male dissected on twelve slides (OUCBL reg. no 2019.002), ten female and ten male specimens preserved in 4% formalin (OUCBL reg. nos 2019.003–022), one female dissected on one slide (OUCBL reg. no 2019.023) and one male dissected on one slide (OUCBL reg. no 2019.024). All type specimens collected from the type locality by Dr Er Hua on 24 July 2010.

Etymology. The specific epithet is derived from the Latin *bi*, meaning two, and the past participle of *partire*, meaning to part, and refers to the 2-segmented condition of the male P5 exopod.

Description of female. Body length 505–530 µm (mean = 515 µm, *n* = 10), semicylindrical, widest at posterior margin of cephalothorax, tapering posteriorly without clear distinction between prosome and urosome (Fig. 1A–B). All somites with sensillae as illustrated, except for penultimate one. Conspicuous pores present on all somites. Rostrum (Fig. 1A–B) defined at base, elongated, triangular and with pointed tip; reaching to middle of antennular segment 2, with pair of subapical sensilla. Cephalothorax with plain hyaline frill; pedigerous somites bearing P2–P4 with distinctly incised hyaline frills dorsally; genital double-somite and abdominal somites 2–3 also with incised frills all around posterior margin; incised frills consisting of dentate lappets (Figs 1A–B, 2A). P4-bearing somite with transverse rows of minute spinules dorsally. P5-bearing somite with spinular row around dorsal and dorsolateral posterior margin. Genital and first abdominal somite forming elongate double-somite; original segmentation marked by dorsolateral and lateral, internal, transverse chitinous ribs; ornamentation consisting of two pairs of dorsolateral spinule rows in anterior half, and almost continuous spinular row posteriorly (interrupted dorsally, ventral spinules markedly shorter than lateral ones); with additional rows of minute spinules laterally and dorsally (Figs 1A–B, 2A). Second abdominal somite with ventral spinular row in anterior half and almost continuous row of spinules near

posterior margin (interrupted middorsally) (Figs 1A–B, 2A); with additional transverse rows of minute spinules ventrally and dorsally. Third abdominal somite with ventral row of spinules and additional transverse rows of minute spinules laterally and dorsally (Figs 1A–B, 2A). Anal somite with spinules either side of anal operculum and around ventral and lateral posterior margin (Figs 1A–B, 2A). Anal operculum (Fig. 1B) semi-circular, without ornamentation; anal frill with long hair-like extensions.

Caudal rami (Fig. 1C–E) slightly broader than long, with slightly oblique, transverse row of spinules on dorsal surface and wrapped around inner margin; with several spinules, laterally and ventrally, around bases of setae II–V; with seven setae; lateral and ventral surface with pore (Figs 1D–E, 2A). Seta I minute, positioned ventrally near outer margin (Fig. 1E); seta II naked, originating from outer margin; seta III long and naked, positioned at outer subdistal corner, slender; terminal setae IV–V long and bipinnate (Fig. 1A), with weakly developed fracture planes, seta IV about half as long as seta V; seta VI long and naked, originating from inner subdistal corner; seta VII tri-articulated at base, arising from dorsal surface (Fig. 1C).

Antennule (Fig. 2B–C) 9-segmented; segments 1–6 slender with segment 1 more elongate than in other parastenheliid genera; segments 7–9 short, in particular segment 7; all segments without spinular ornamentation; all setae naked; with aesthetasc on segments 4 and 9; apical acrothek consisting of aesthetasc and two setae. Armature formula as follows: 1-[1], 2-[10], 3-[6], 4-[3 + (1 + ae)], 5-[2], 6-[3], 7-[3], 8-[0], 9-[5 + acrothek].

Antenna (Fig. 2D). Basis and proximal endopodal segment completely fused, forming allobasis; abexopodal margin with two spinular tufts but no armature elements. Exopod 2-segmented; proximal segment with two setae, lateral one slender and naked, distal one long and unipinnate; distal segment with four setae: proximal one tiny and naked, apical margin with one unipinnate, spiniform element and two small naked setae. Endopod with sparse spinules along both lateral margins; lateral armature consisting of small naked element proximally and large unipinnate spine distally; distal armature consisting of one strong, unipinnate spine, four geniculate setae (longest one with large spinules around geniculation and fused at base to unipinnate seta) and one naked seta.

Mandible (Fig. 3A–B). Coxal gnathobase well developed, with complex cutting edge bearing several multicuspidate teeth, with strong tooth at ventral corner and short, unipinnate seta at dorsal corner. Basis elongate, with row of spinules on both anterior and posterior surfaces, with three setae near inner distal corner: one spiniform and unipinnate and two setiform and naked. Endopod elongate, 1-segmented; with two lateral and four terminal setae (two of which fused at base); exopod minute, represented by one tiny seta arising from small protuberance.

Maxillule (Fig. 3C). Praecoxal arthrite with seven spiniform elements around distal margin, with two long setae on anterior surface, and two short elements near inner margin. Coxal endite cylindrical, with four naked setae; coxal epipodite represented by one seta. Basis with three setae on single endite; rami fused to basis but clearly discernible. Endopod 1-segmented, with three naked, apical setae. Exopod 1-segmented, with one short, naked and one long, unipinnate seta apically.

Maxilla (Fig. 3D). Coxa with three endites, proximal endite bilobate with one naked seta on inner cusp and two naked setae on outer cusp; middle and outer endite each with two naked setae and one basally fused pinnate spine; allobasal endite drawn out into strong, unipinnate spine and three setae (one of which minute); endopod well-developed, 1-segmented, not completely discrete at base, with two naked setae.

Maxilliped (Fig. 3E). Armature of syncoxa as in male (see below; Fig. 5H). Basis with two short, naked setae along palmar margin and few spinules around outer margin. Endopod represented by well-developed, unipinnate claw and three accessory, naked setae near its base.

P1 (Fig. 3F). Intercoxal sclerite small, unadorned. Praecoxa (not illustrated) small, triangular, with spinule row on distal margin. Coxa with row of large spinules along outer margin and medial part of distal margin, and row of small spinules on anterior surface; with pore on anterior surface. Basis with unipinnate inner spine and bipinnate outer spine; with row of spinules near base of outer spine, along inner margin and around base of endopod. Exopod 3-segmented, segments subequal in length, proximal segment with row of spinules along outer margin and unipinnate spine at outer distal corner; middle segment with row of spinules along outer margin and two setules along inner margin, with unipinnate spine at outer distal corner and short, plumose seta at inner distal corner; distal segment with plumose, inner distal seta, unipinnate, geniculate outer distal seta, and two unipinnate outer spines. Endopod 2-segmented, prehensile; proximal segment much longer than exopod, with long, uniplumose seta arising from proximal fourth of segment; distal segment small, with few spinules, one minute inner seta and two slightly curved, naked spines apically.

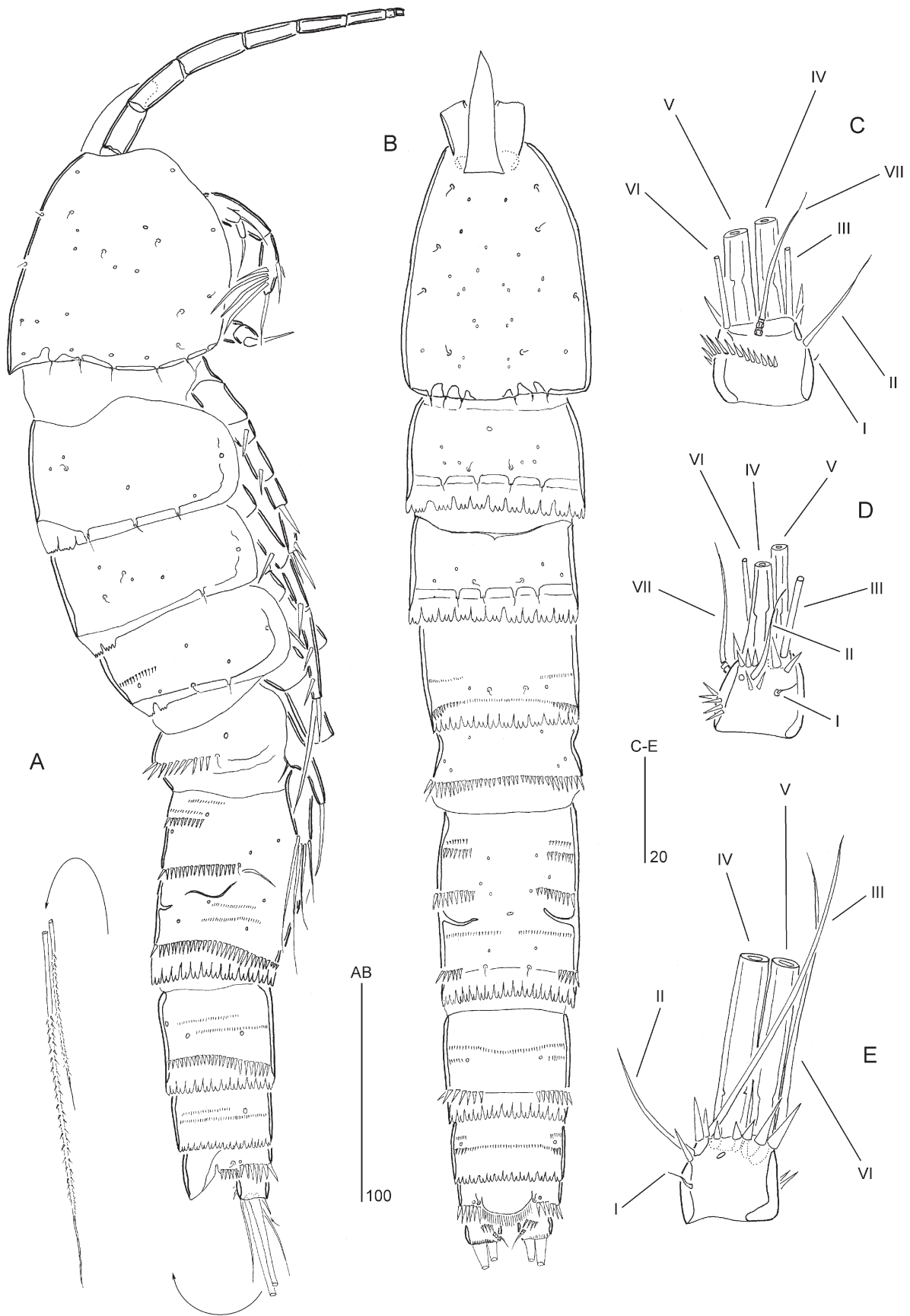


FIGURE 1. *Johnwellsia bipartita* gen. et sp. nov. (♀): A, habitus, lateral; B, same, dorsal; C, caudal ramus, dorsal; D, same, lateral; E, same, ventral.

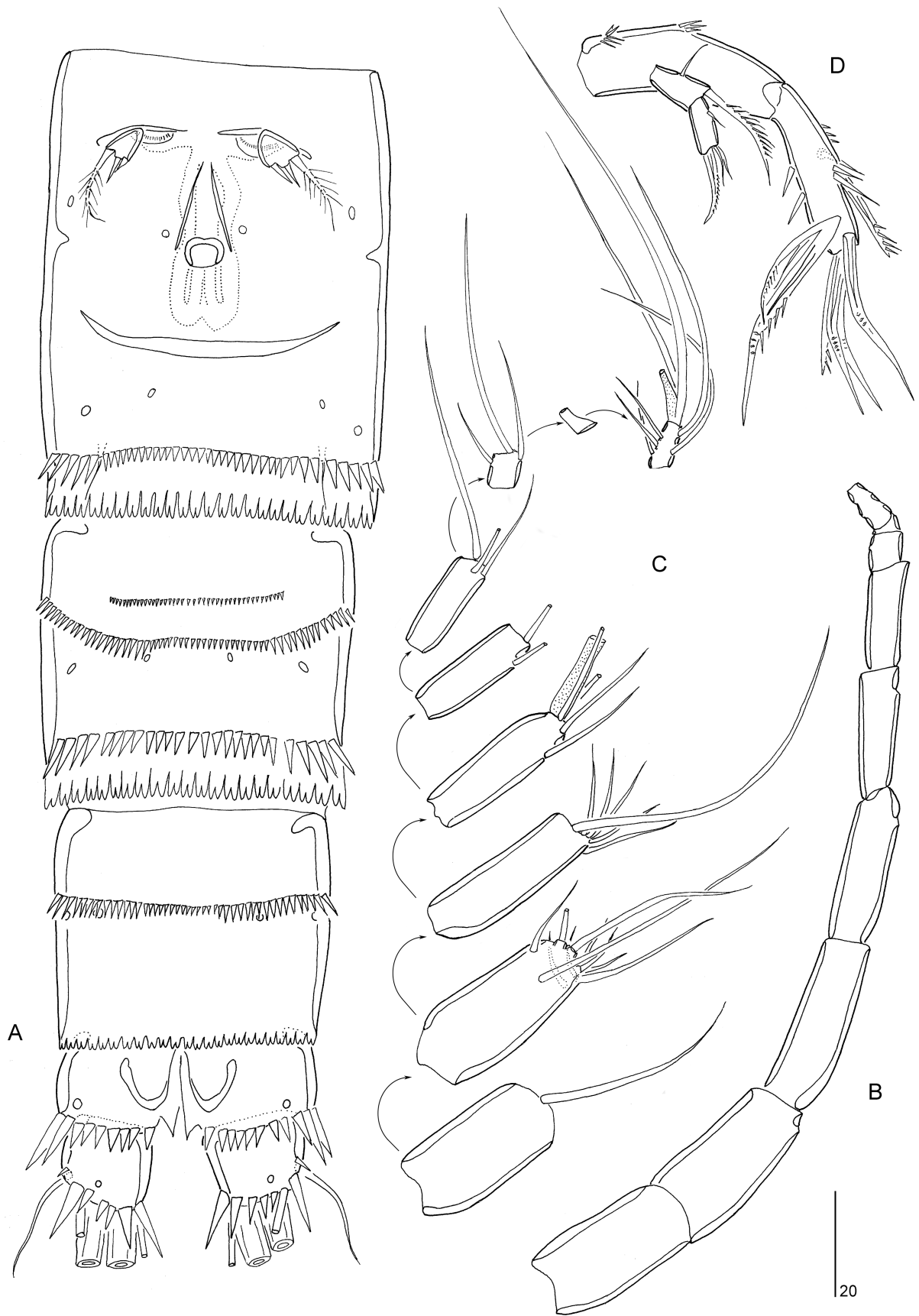


FIGURE 2. *Johnwellsia bipartita* gen. et sp. nov. (♀): A, urosome (excluding P5-bearing somite), ventral; B, antennule, ventral (armature omitted); C, antennule, ventral (disarticulated, showing armature); D, antenna.

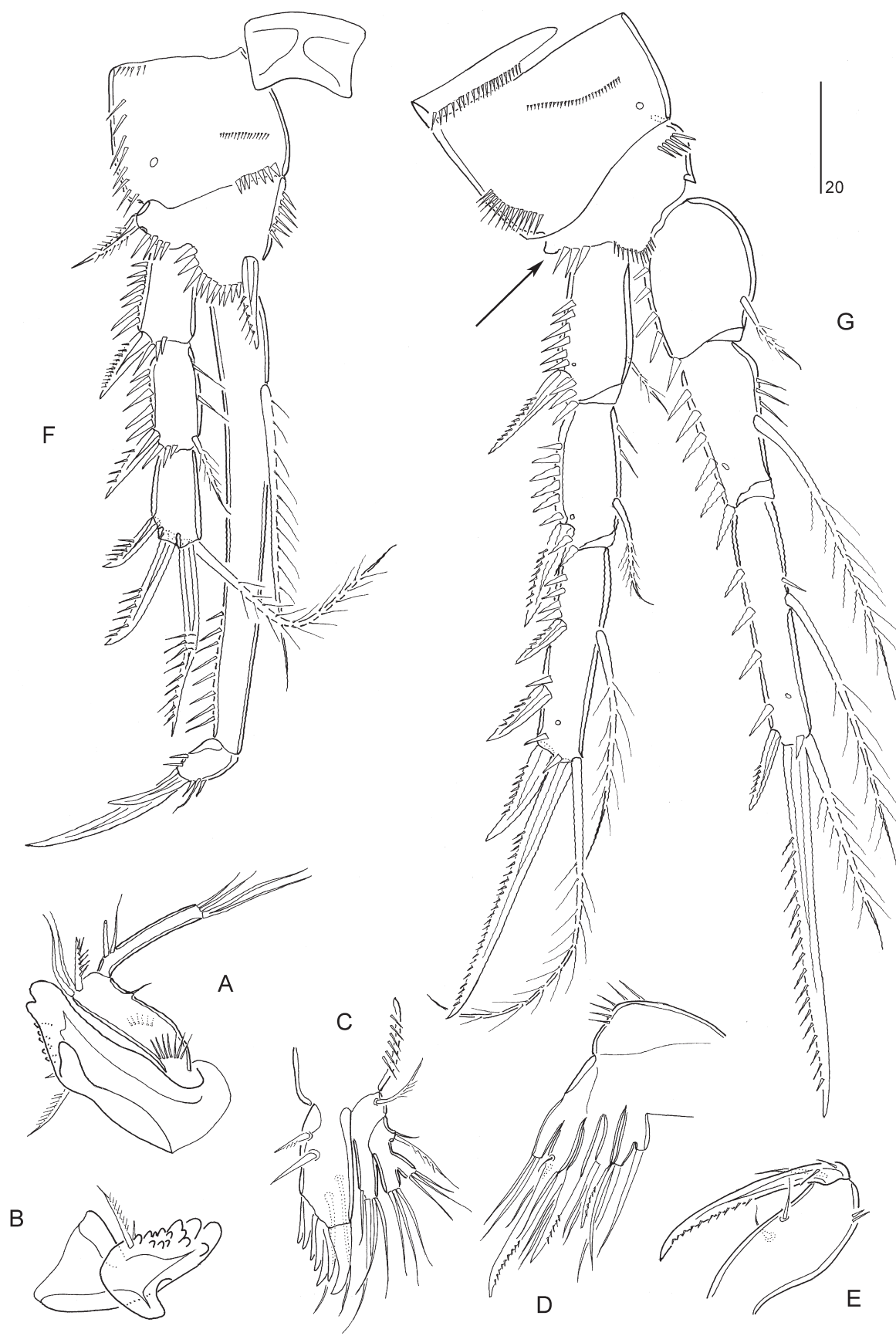


FIGURE 3. *Johnwellsia bipartita* gen. et sp. nov. (♀): A, mandible; B, mandibular coxa; C, maxillule; D, maxilla; E, maxilliped; F, P1, anterior (praecoxa omitted); G, P2, anterior (position of outer basal seta arrowed).

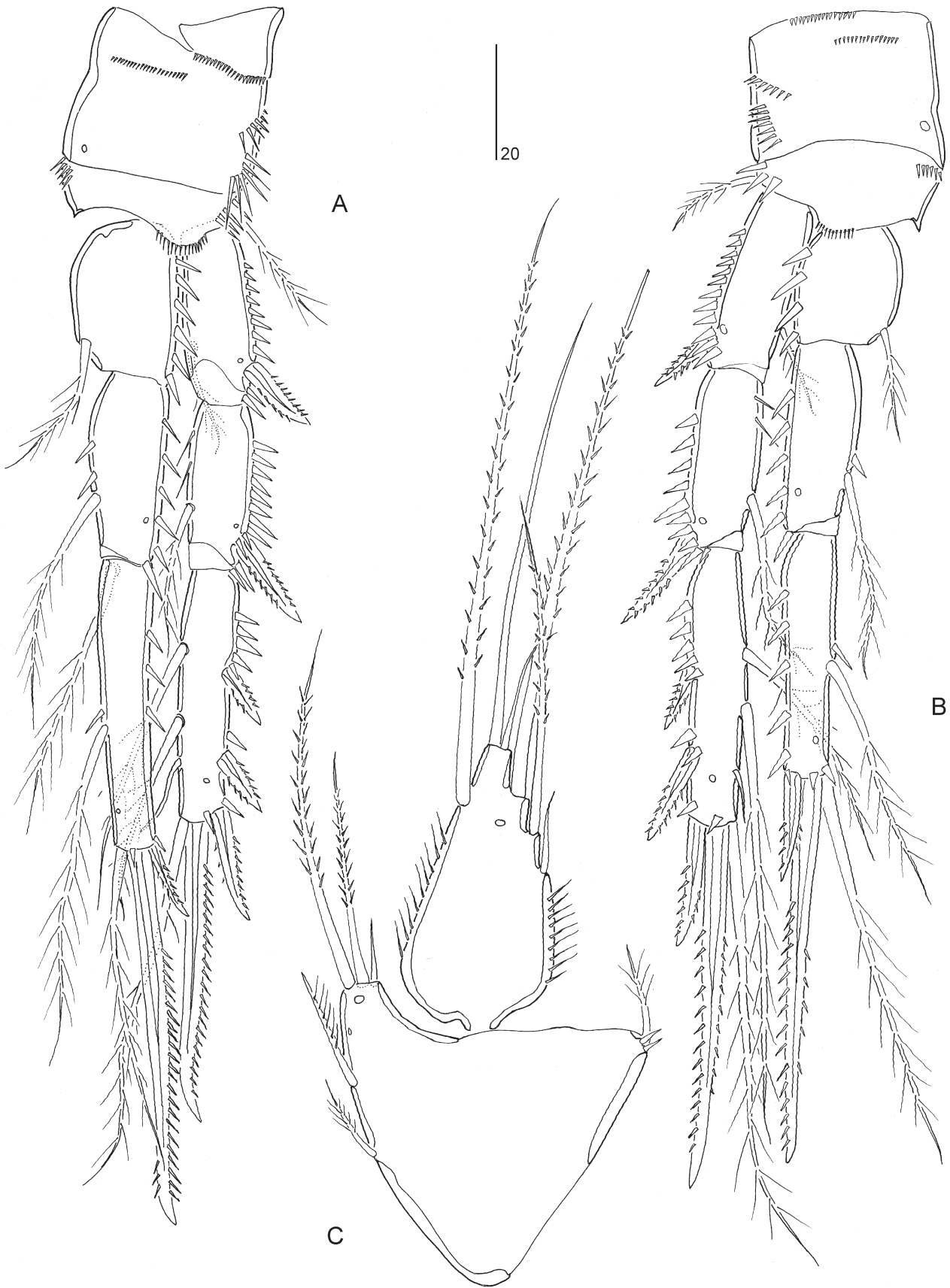


FIGURE 4. *Johnwellsia bipartita* gen. et sp. nov. (♀): A, P3, anterior; B, P4, anterior (praecoxa omitted); C, P5, anterior.



FIGURE 5. *Johnwellsia bipartita* gen. et sp. nov. (♂): A, antennule, ventral (armature omitted); B, antennule, ventral (disarticulated, showing armature); C, P2 endopod, anterior; D, P3 endopod, anterior; E, P4 endopod, anterior; F, P5, anterior; G, P6; H, maxilliped.

P2–P4 (Fig. 3G, 4A–B). Praecoxa triangular, with spinule row along distal margin; coxa with 1–2 row(s) of spinules along outer margin and row of tiny spinules on anterior surface; basis with row of spinules near proximal inner corner, row of fine setules distally between insertions of rami, and few spinules around base of outer seta, inner distal corner forming small, pointed process. Rami 3-segmented, slender; endopods about as long as (P2) or slightly shorter than (P3–P4) exopods; P2–P4 enp-3 longest, enp-1 widest and with convex inner margin. All segments with rows of large spinules along outer margin; with few spinules/setules on inner margin of exp-2, and enp-2 and -3; with anterior pore on all segments except for enp-1; distal inner seta on P3–P4 exp-3 very small. Armature formulae of P1–P4 as follows:

	exopod	endopod
P1	0.1.022	1.111
P2	1.1.123	1.1.121
P3	1.1.323	1.1.221
P4	1.1.323	1.1.121

P5 (Fig. 4C). Rami discrete and baseoendopods not fused medially. Endopodal lobe small, trapezoid; with five setae (four pinnate, one short and naked) and few spinules around base of outer basal seta; anterior surface with two pores. Exopod about two times longer than maximum width; basal portion articulating with baseoendopod very narrow; with row of setules along inner and outer margins; with six setae: one long, bipinnate, inner seta, two naked setae apically (one very long, other one short), and one short naked and two bipinnate setae along outer margin.

Genital field (Fig. 2A) with large midventral copulatory pore; paired genital apertures positioned anteriorly, each covered by vestigial P6 bearing three setae, inner two short, outer one long and plumose.

Description of male. Sexual dimorphism expressed in urosomal segmentation and ornamentation, antennule, endopods of P2–P4, P5 and P6. Body slightly smaller than female, length 415–460 μm (mean = 440 μm , $n = 10$).

Genital and first abdominal somites not fused. Urosomal ornamentation very similar to female, except for absence of transverse spinule row on ventral and lateral surfaces of penultimate somite.

Antennule (Fig. 5A–B) indistinctly 11-segmented, haplocer; segment 1 elongate; segment 4 largely incorporated into moderately swollen segment 5; geniculation located between segments 7–8 with four segments distal to it; segment 11 with surface suture along dorsal surface; aesthetasc on segments 5 and 11; all setae naked except for bipinnate seta on segment 1; armature formula as follows: 1-[1], 2-[10], 3-[8], 4-[2], 5-[4 + (1 + ae)], 6-[2], 7-[4 + 3 modified spines], 8-[1 + 2 modified spines], 9-[1], 10-[2], 11-[6 + (1 + ae)].

Maxilliped (Fig. 5H). As in female, syncoxa with two setae near inner distal corner.

P2 (Fig. 5C). Exopod as in female. Endopod 2-segmented; compound enp-2 with only one plumose inner seta, arising from proximal third of segment (homologue of inner seta of ♀ enp-2).

P3 (Fig. 5D). Exopod as in female. Enp-3 shorter than in female, without inner setae.

P4 (Fig. 5E). As in female except enp-3 slightly shorter.

Armature formulae of P1–P4 as follows:

	exopod	endopod
P1	0.1.022	1.111
P2	1.1.123	1.121
P3	1.1.323	1.1.021
P4	1.1.323	1.1.121

P5 (Fig. 5F). Baseoendopods fused medially, forming deeply incised transverse plate. Endopodal lobe with row of spinules along outer margin; with two short elements (inner one unipennate and spiniform, outer one naked and shorter than inner one); anterior surface with two pores; outer basal seta bipinnate and arising from short setophore. Exopod 2-segmented; exp-1 with row of spinules along outer margin and naked seta at outer distal corner; exp-2 with short naked seta at outer subdistal corner, long bipinnate seta apically and unipennate spine at inner subdistal corner; anterior surface of exp-2 with pore.

P6 (Fig. 5G) represented on each side by small plate closing off genital aperture; with three setae, middle seta about twice longer than other two, innermost one unipinnate.

Variability. In one dissected male the P2 enp-2 displayed two inner setae on one side.

Remarks. The new species cannot be placed in *Parastenhelia*, *Microthalestris*, *Karaytugia* **gen. nov.** or *Penicillicaris* **gen. nov.** since it does not display the sexual dimorphism on the P3 endopod (enp-3 with spinous apophysis; see Fig. 7A–F) that characterizes these four genera. The absence of sexual dimorphism in the male antenna also excludes the species from assignment to *Thalestrella* and the lack of a transformed inner base spine in the male P1 prevents it from being accommodated in *Foweya*, *Paraleptomesochra* or *Psammoleptomesochra*. *Johnwellsia bipartita* **sp. nov.** appears to be morphologically closest to two species that were previously assigned to *Parastenhelia*, *P. megarostrum* and *P. pyriformis*, but which will be transferred to a new genus *Porirualia* **gen. nov.** below. Both species and *J. bipartita* **sp. nov.** share the same sexual dimorphism on P3, involving the loss of setation elements on male enp-3. In members of *Porirualia* **gen. nov.** the proximal inner seta of enp-3 is lost in the male while the further derived state (involving the additional loss of the distal inner seta) is observed in *Johnwellsia* **gen. nov.** (Fig. 7G–I). Two additional synapomorphies supporting a sistergroup relationships between these genera are the modification of the distal seta on the mandibular basis into a short spine, and the reduction of the outermost endopodal element of the P5 in both sexes, being represented by a minute seta. *Johnwellsia* **gen. nov.** differs from *Porirualia* **gen. nov.** in the following characters: (a) rostrum reaching to middle of antennular segment 2 (*vs* very large, reaching to at least halfway the fourth antennular segment in the female); (b) antennule ♀ very slender with elongate segment 1 (*vs* more compact and segment 1 short); (c) antennary allobasis without abexopodal seta; (d) mandibular exopod rudimentary, represented by single seta on minute protuberance (*vs* 1-segmented with three setae); (e) maxillipedal basis with two setae (*vs* one seta); (f) P1 enp-1 inner seta long but not extending beyond distal margin of segment; (g) P2 endopod ♂ sexually dimorphic (2-segmented and distal inner seta of ♀ enp-3 lost in ♂; Fig. 6C); (h) P5 ♀ without series of transverse striae along inner margin of endopodal lobe; and (i) P5 exopod ♂ 2-segmented, with four elements in total (*vs* 1-segmented, with 5–6 elements). Species of both genera also differ in the shape of the female P5 exopod which is moderately elongate and shares a very narrow articulation with the baseopod in *Johnwellsia* **gen. nov.** (Fig. 4C). The 2-segmented P5 exopod in the male is an unusual condition in the family, being found only in *Parastenhelia willemvervoorti* **sp. nov.** and *Karaytugia aydini* (Kuru & Karaytuğ, 2015) **comb. nov.** (Vervoort 1964; Kuru & Karaytuğ 2015; Table 1 herein).

Review of parastenheliid genera

Parastenhelia Thompson & Scott, 1903

The description of two Sri Lankan species, *P. hornelli* and *P. similis*, by Thompson & Scott (1903) marked the start of the historical division of the genus into two groups, the *spinosa*-group, characterized by a distinctly elongate P1 exp-2, and the *hornelli*-group, which unites species with subequal segments in the P1 exopod. Various species have been added since then to either group, almost solely on the basis of P1 morphology, without considering other characters that could be of taxonomic or phylogenetic significance. Attempts to delimit species boundaries within *Parastenhelia* have historically been made by two opposing factions, *i.e.* lumpers (Lang 1948; Pesta 1959; Vervoort 1964; Wells & Rao 1987; Mielke 1974, 1990) versus splitters (Sewell 1940; Gee 2006; Kuru & Karaytuğ 2015). Proponents of the first school of thought were primarily influenced by Lang (1948) who basically considered *P. spinosa* an amalgam of forms in which the middle segment of the exopod of P1 is at least four times as long as broad. Wells & Rao (1987) pointed out that *P. spinosa*, as revised by Lang, is one of the most variable species of harpacticoids, and that no clearcut distinctions can be made between the various forms that he included. Unfortunately, the adoption of his system as the best approach to the complex taxonomy of the genus has generated tremendous confusion. An extreme example is presented by Vervoort's (1964) unwarranted recognition of extreme variability in specimens attributed to *P. spinosa* from the Caroline Islands. His grouping of two different forms – one with subequal exopodal segments in the P1 (*hornelli* type), the other with a distinctly elongate P1 exp-2 (*spinosa* type; note that his Fig. 70b depicts the exopod not the exopod as stated in the figure legend) – into *P. spinosa* defies any serious attempts to delimit species boundaries in the genus. As pointed out by Wells *et al.* (1982) the relative stability displayed by the proportions of the P1 exopodal segments in *P. spinosa* must invalidate Vervoort's inclusion of a form which by his own admission approaches *P. hornelli* in several respects.

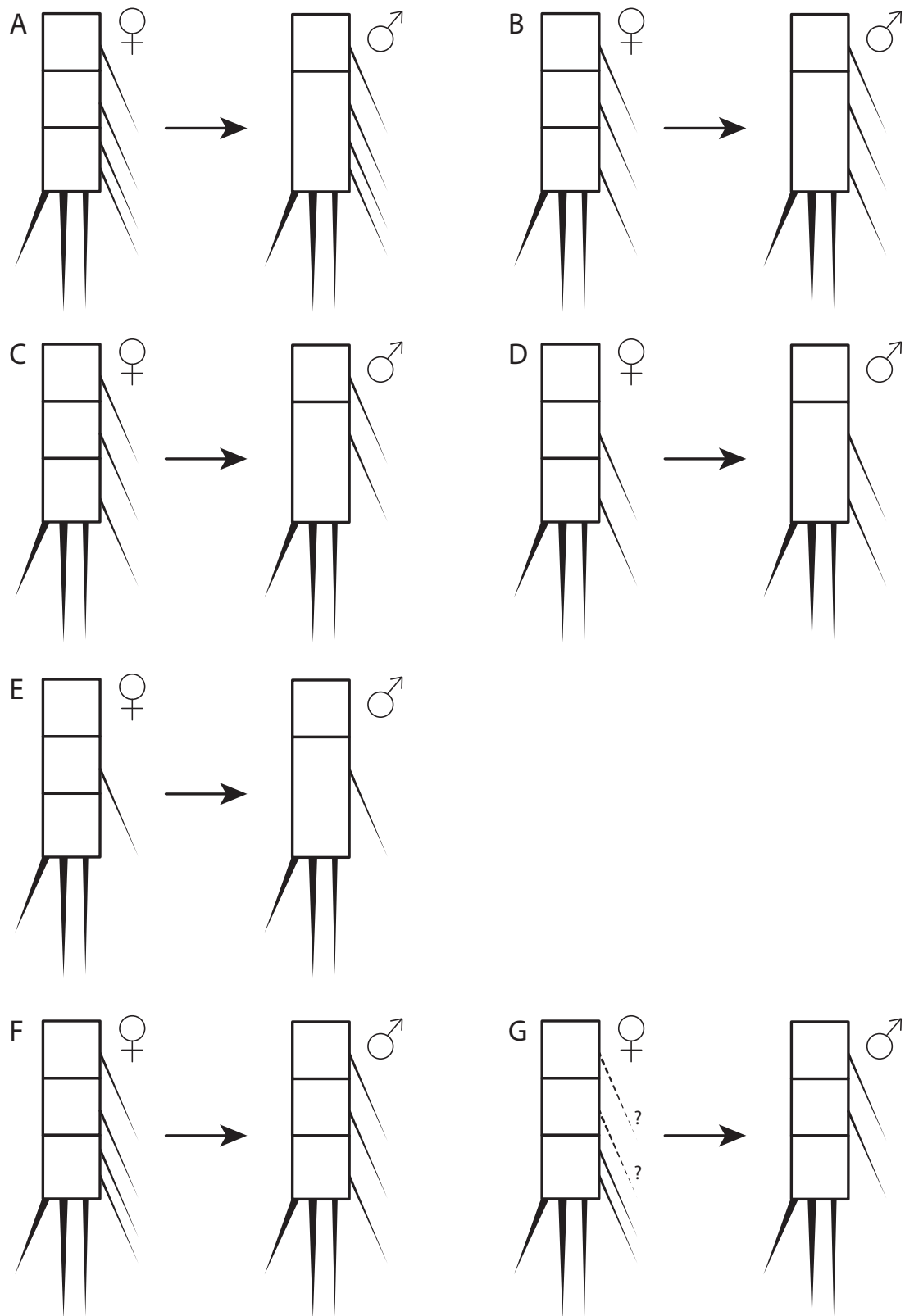


FIGURE 6. Sexual dimorphism of P2 (A–E) and P4 (F–G) endopodal segmentation and armature within the Parastheneliidae. A, *Foweya tertia* (Kunz, 1975); B, *Microthalestris costata* (Pallares, 1982) **comb. nov.**, *M. variabilis* **sp. nov.**, *Parasthenelia similis* Thompson & Scott, 1903, *P. willemvervoorti* **sp. nov.**, *Porirualia pyriformis* (Song, Kim & Chang, 2003) **comb. nov.**; C, *Johnwellisia bipartita* **sp. nov.**; D, *Parasthenelia hornelli* Thompson & Scott, 1903 *sensu* Apostolov (1973); E, *Parasthenelia oligochaeta* Wells & Rao, 1987; F, *Microthalestris bulbosa* (Gee, 2006) **comb. nov.**, *Parasthenelia willemvervoorti* **sp. nov.**; G, *Microthalestris minuta* (Pallares, 1982) **comb. nov.**, *Penicillicaris penicillata* **sp. nov.**

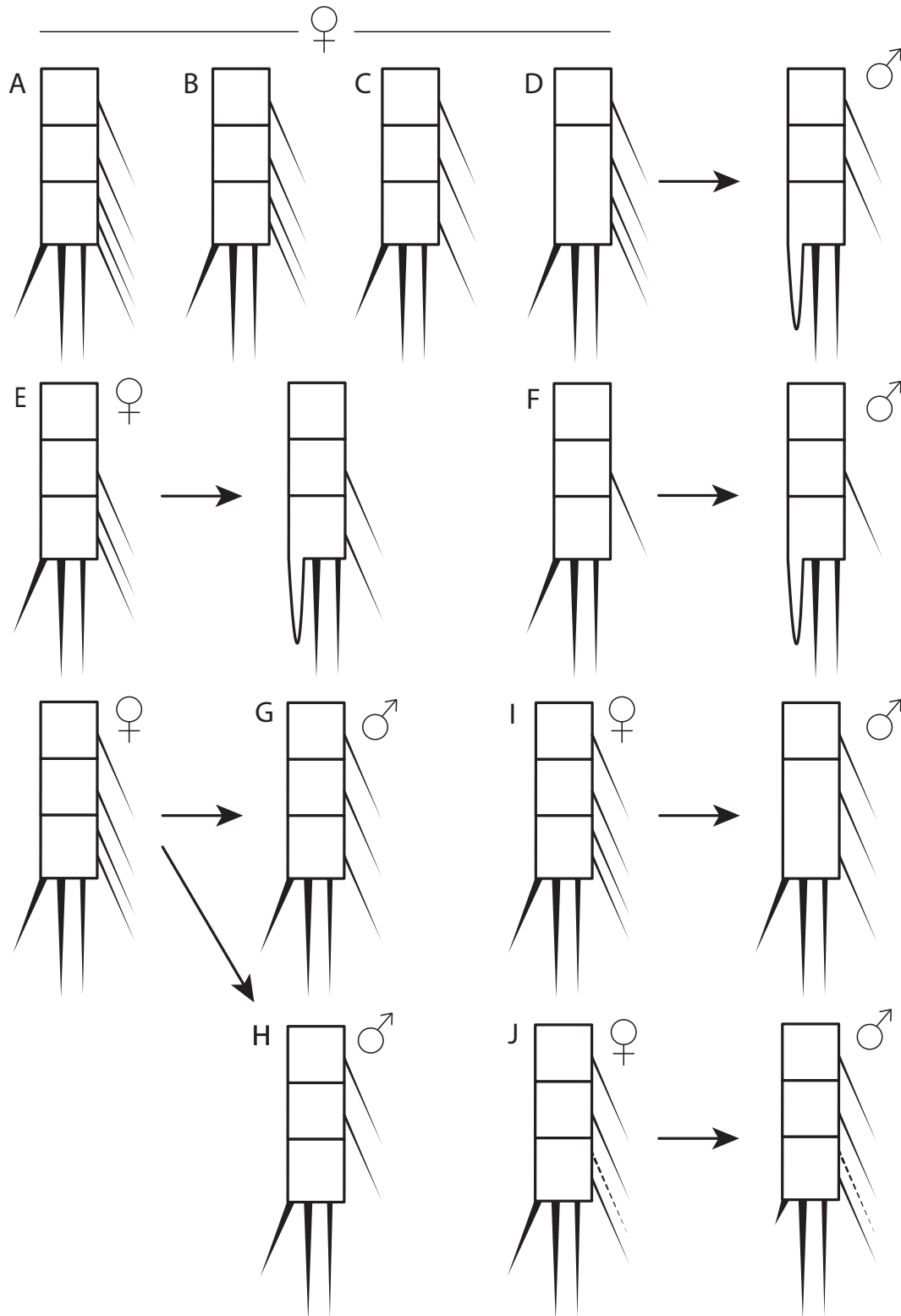


FIGURE 7. Sexual dimorphism of P3 endopodal segmentation and armature within the Parastenheliidae. A, *Microthalestris costata* (Pallares, 1982) **comb. nov.**; B, *Karaytugia aydini* (Kuru & Karaytuğ, 2015) **comb. nov.**, *Microthalestris campbelliensis* **sp. nov.**, *M. polaris* **sp. nov.**, *M. sarsi* **sp. nov.**, *Parastenhelia similis* Thompson & Scott, 1903, *P. willemvervoorti* **sp. nov.**, *P. hornelli* Thompson & Scott, 1903 *sensu* Apostolov (1973), *P. spinosa* (Fischer, 1860) *sensu* Marinov (1974), *Penicillicaris pectinimana* (Car, 1884) **comb. nov.**; C, *Microthalestris minuta* (Pallares, 1982) **comb. nov.**, *M. variabilis* **sp. nov.**; D, *Penicillicaris penicillata* **sp. nov.**; E, *Microthalestris bulbosa* (Gee, 2006) **comb. nov.**; F, *Parastenhelia oligochaeta* Wells & Rao, 1987; G, *Porirualia megarostrum* (Wells, Hicks & Coull, 1982) **comb. nov.**; H, *Johnwellsia bipartita* **sp. nov.**; I, *Porirualia pyriformis* (Song, Kim & Chang, 2003) **comb. nov.**; J, *Thalestrella* spp.

In his search of apomorphies that could define the genus *Parastenhelia* as a monophyletic lineage, Mielke (1990) highlighted the significance of the sexual dimorphism of the P3 endopod, involving the transformation of the outer spine on the distal segment into a fused apophysis and a reduction in the number of inner setae (to one in *P. bulbosa* and none in all other species) (Fig. 7). The absence of this character in *P. reducta* and *P. megarostrum* led him to claim that they do not belong to *Parastenhelia*. This view was corroborated by Gee (2006), who moved *P. reducta* as *species incertae sedis* to *Karllangia* (= *Thalestrella*) and suggested that both *P. megarostrum* and *P. pyriformis* should be assigned to one or more new genera, a course of action that is formalized here (see below).

Various authors have pointed out that a revision of the genus is hampered by the taxonomic confusion surrounding its alleged type species *P. spinosa* (Vervoort 1964; Wells & Rao 1987; Gee 2006; Kuru & Karaytuğ 2015). However, it has recently come to light that Lang's (1948) fixation of *P. spinosa* as the type was invalid since it was not originally included (ICZN Art. 69.2) and that *P. hornelli* had already been fixed as the type species by subsequent designation (Lang 1934: 24; Huys 2009: 96). This implies that any assessment of the monophyly of *Parastenhelia* must first centre on a review of *P. hornelli* (and allied species – *hornelli* group) since it provides the objective standard of reference for the application of the generic name it bears. Consequently, the genus is here restricted to a core group of four valid species which share a P1 exopod with three subequal segments in both sexes. Males of these species share a haplocer antennule with three segments distal to the geniculation, a 2-segmented P2 endopod (enp-2 and -3 forming a compound segment but total armature as in ♀) and a modified P3 endopod with spinous apophysis on enp-3 (Table 1; Figs 6–7).

Thompson & Scott (1903) described two *Parastenhelia* species from pearl oyster washings in the Gulf of Mannar off northwestern Sri Lanka: *P. hornelli*, which was represented by several females and males and was also found in general washings of dredged material in deep water off Galle (southwestern Sri Lanka), and *P. similis* of which only two females were recorded. The two species were considered morphologically similar with females being distinguished on the basis of proportional length differences in the antennular segments (the whole appendage being distinctly longer and more slender in *P. hornelli*), the morphology of the maxilliped, and the shape of the P5 exopod. Additional discrepancies are found in the P1 with the endopod being more slender, the inner seta of enp-1 distinctly longer, and the distal claws on enp-2 markedly longer (relative to the segment) in *P. hornelli*. Lang (1934) dismissed all these points and sank *P. similis* as a junior subjective synonym of *P. hornelli*. Since no variability in the antennule, P1 and P5 has so far been documented we regard these differences as sufficient justification to reinstate *P. similis* as a valid species.

Wells & Rao (1987) assessed the “*hornelli* group” based on material from Mozambique, the Andaman Islands and New Zealand. They redescribed both sexes of *P. hornelli* from specimens of Middle and South Andaman, recognized two distinct size morphs among the female specimens (small form about 630 µm; large form about 885 µm; all ♂♂ 650 µm) and opted for the interim solution to place specimens previously identified as this species by Noodt (1955a) and Apostolov (1973), as well as the material identified as *P. spinosa* by Vervoort (1964), in *P. hornelli*. Careful inspection of Wells & Rao's (1987) illustrations, however, shows that they were not dealing with *P. hornelli* but with *P. similis*. Evidence in support of this claim is found in the female morphology of the antennule (general facies and relative lengths of segments), maxilliped (palmar margin with conspicuous row of long spinules), P1 (length of endopod, inner seta of enp-1 and claws on enp-2), P5 exopod (exact shape and strong spinular ornamentation along inner and outer margins) and caudal rami (setae IV–V slightly swollen and irregularly shaped at base). The three differences between Thompson & Scott's (1903) type material of *P. similis* and Wells & Rao's (1987) specimens are (a) segmentation of female antennule (the minute segments 7–8 in Wells & Rao's Fig 52e are shown as completely fused in the original description), (b) absence of the small distal inner seta on P4 exp-3, and (c) absence of short inner seta on the endopodal lobe of P5, both of which are conceivable the result of imperfect observation. The records of *P. hornelli* from Odisha (formerly Orissa) in the Bay of Bengal (Rao 1989), Lakshadweep (Rao 1991) and Little Andaman (Rao 1993) are accompanied by very brief, mostly uninformative descriptions and must be considered as unconfirmed. Other Indian records from Bhitarkanika in Odisha (Chadha & Kar 1999), Kundugal channel (Krishnaswamy 1953) and Porites Bay (Krishnaswamy 1957) in Tamil Nadu, and the Andaman Islands (Rao 1993; Jayabarathi 2016; Jayabarathi *et al.* 2012, 2015; Pongener *et al.* 2018) are equally indeterminable.

Noodt (1955a) provides a brief redescription, completely lacking in illustrations, of two females from the Sea of Marmara in northwestern Turkey which he attributes to *P. hornelli*. He states that both P1 and P5 agree exactly in form and armature with the illustrations of Thompson & Scott (1903) but it is not clear which of the Sri Lankan

species he refers to. Since the shape of the exopod is different between *P. hornelli* and *P. similis*, Noodt's (1955a) statement that it is widening proximally towards the base of the endopod ("Insbesondere ist der Exp. P5 durch seine Erweiterung zur Basis hin typisch") may carry some significance since this feature is more expressed in *P. hornelli* (Thompson & Scott 1903: Plate VII, Fig. 8). Noodt's (1955a) report that the antennary exopod is 3-segmented must be an observational error since it is 2-segmented in the groundpattern in the Parastenheliidae (Willen 2000); he also states that the proximal segment bears one seta but does not disclose how many elements are present on the remaining segments. Noodt (1955a) presents the armature pattern of P2–P4, noting variability in the presence/absence of the inner seta on P2 exp-3. Although Wells & Rao (1987) pointed out that the pattern of P4 (exp: 1.1.223; enp: 1.1.221) is congruent with that given by Thompson & Scott (1903) (for both *P. hornelli* and *P. similis*) it remains to be confirmed whether the presence of only two inner setae on P3–P4 exp-3 in the Turkish specimens is genuine or reflects an oversight of the fine inner distal seta. Based on Noodt's description no positive statement can be made as to the validity of his identification and pending re-examination of the material (and discovery of the male) his record must be considered suspect. The unillustrated records of *P. hornelli* from two beaches (Cunda Beach and Altınova Beach) in the Aegean Sea (Karaytuğ & Sak 2006), in close proximity to the Sea of Marmara, possibly refer to the same species.

Although Vervoort (1964) voiced criticism of Lang's (1948) broad taxonomic concept of *P. spinosa*, he indirectly expressed the opinion that both *P. hornelli* and *P. ornatissima* may also fall within the range of this species. Among the material from Ifalik Atoll, Vervoort describes a male and a female which he assigns to *P. spinosa* while admitting that they approach *P. hornelli* in the structure of the P1 exopod, where the three segments have about the same length. Vervoort (1964) dismisses the significance of this difference by accepting Lang's (1948) view that it falls within the variability of *P. spinosa* – a concept that is mistakenly based on comparison of geographically separated and, most likely, non-conspecific populations. Since intrapopulation variability in the length of P1 exp-2 has never been recorded in any species so far, Vervoort's (1964) interpretation is rejected here. His material displays a number of distinct differences with both *P. hornelli* and *P. similis*: (a) P3–P4 exp-3 without inner seta; (b) in addition to the common sexual dimorphism expressed in the endopods of P2–P3, the male P4 endopod also differs from that of the female in having only one inner seta on enp-3; this type of sexual dimorphism has previously been observed in *Microthalestris littoralis f. penicillata* sensu Willey (1935) and *Parastenhelia bulbosa* (Gee 2006), and as a further derived state in *P. minuta* and *Penicillicaris penicillata* **sp. nov.** where both inner setae are lost in the male (Willey 1935; Pallares 1982; Fig. 6F–G herein); and (c) male P5 exopod 2-segmented; this condition was recently described in *P. aydini* (Kuru & Karaytuğ 2015) and in *Johnwellsia bipartita* **gen. et sp. nov.** (present account). Based on these differences it is obvious that Vervoort's (1964) material from stations 589 and 590 cannot be attributed to *P. spinosa* or to either of Thompson & Scott's (1903) species and must be assigned distinct specific rank (see below). Wells *et al.*'s (1982) claim that Vervoort's description and illustrations of the antenna are contradictory is irrelevant. His lateral habitus view (Fig. 68a) shows indeed the antennary exopod as 3-segmented under low magnification but the detailed drawing of the antenna (Fig. 68d) clearly reveals it as 2-segmented (as reiterated in the text: p. 186).

Apostolov (1973: 273, Fig. 9) reported two females and one male of *P. hornelli* on brown algae (*Cystoseira barbata*) near Tsarevo (formerly Michurin) along the Black Sea coast of Bulgaria. No text description was given, except for his statement that the male fits Thompson & Scott's (1903) original description perfectly. Apostolov (1973) provides illustrations of the male P2 endopod (similar to that illustrated by Thompson & Scott), P3 endopod (previously unknown) and P5. The latter differs significantly in that it is only 1-segmented and the armature elements all are very short, consequently ruling out the possibility that the Bulgarian material belongs to either *P. hornelli* or *P. similis*. Similar to Noodt's (1955a) specimens the antennary exopod is erroneously illustrated as 3-segmented causing Wells & Rao (1987) to suggest that both sets of specimens are conspecific. The female antennule and P5 exopod resemble their respective conditions as illustrated by Thompson & Scott (1903) for *P. hornelli*, the P4 also displays the same armature pattern (although confirmation of the exact number of inner setae on exp-3 is required in both), but the P1 endopod is comparatively longer and more slender. The only significant difference with Noodt's (1955a) material is found in the absence of the inner seta on P2 enp-1 (a condition that is mirrored in the male). In summary, Apostolov's (1973) Bulgarian specimens share several characters with *P. hornelli* from Sri Lanka but the 1-segmented condition of the male P5 exopod and deficiencies in the description of the antenna (and possibly P3–P4 exopods) prevent them from being assigned to the type species. Pending a re-examination of the Black Sea material, *P. hornelli* sensu Apostolov (1973) must be classified as indeterminate.

Apostolov & Pandourski (1999) reported one female and one male of *P. hornelli* from a littoral sandbank in

Livingston Island (South Shetlands archipelago), north of the Antarctic Peninsula (see also Pesce & Pandourski 2002: 134). The authors do not provide a text description but state that their material confirms the variability previously observed in this species and cite the different number of setae and spines on P3 exp-3 and enp-3 as an example. Although they do not cite the work it is likely that Apostolov & Pandourski (1999) used Wells & Rao's (1987) redescription of *P. hornelli* (= *P. similis*) as a reference for comparison. Their illustration of the female P3 endopod (they do not figure the exopod) shows three well developed inner setae on the distal segment which contradicts the condition in *P. similis* (Table 1). The female P5 exopod approaches the shape (although more truncated) of Thompson & Scott's (1903) *P. hornelli* while the length of the endopodal setae is different. The morphology of the male is said to be identical with *P. hornelli* but only the P2 endopod is illustrated; the proximal segment of this limb lacks the inner seta found in the type species. No information was given on the armature pattern of P2–P4 (except P3 endopod ♀) or the segmentation and setation of the male P6. Apostolov & Pandourski's (1999) description is too fragmentary to allow any conclusions to be made about its identity and consequently it must be classified as an indeterminable record of *P. hornelli*.

Based on Wells & Rao's (1987) report the only confirmed records of *P. similis* are from Sri Lanka (Thompson & Scott 1903), Inhaca Island in Mozambique (Wells 1967), northeastern New Zealand (Wells *et al.* 1982) and the Andaman Islands (Wells & Rao 1987). Authenticated records of *P. hornelli* remain restricted to the type populations from Galle and the Gulf of Mannar in Sri Lanka (Thompson & Scott 1903). This is in stark contrast with the previously assumed circum-subtropical distribution (Wells *et al.* 1982; Wells & Rao 1987) which included unconfirmed and (possibly) false records from the Aegean/Black Sea region (Noodt 1955a; Apostolov 1973), Barbados (Coull 1970a) and the U.S. Virgin Islands (Coull 1971a; Hartzband & Hummon 1974) in the Atlantic, and the east coast of Peninsular Malaysia (Zaleha *et al.* 2006) and the Caroline Islands (Vervoort 1964) in the Pacific. The armature pattern of P2–P4 given by Zaleha *et al.* (2006) shows that they were dealing with a different species. In addition to the unconfirmed Indian records mentioned above, *P. hornelli* has also been reported from Gazi Bay in Kenya (De Troch 2001 – as *P. cfr. hornelli*) and along the Pacific seaboard of North America including the Nanaimo River delta (Sibert 1981; Kask *et al.* 1982) and Fraser River estuary (Sibert *et al.* 1982; Bravender *et al.* 1993; Johansen & Reis 1994) in British Columbia, Padilla Bay (Simenstad *et al.* 1988) and Puget Sound (Simenstad *et al.* 1991) in Washington State and the Santa Barbara Channel in southern California (Spies *et al.* 1988). All these records are unillustrated and must be considered as unconfirmed and probably false. *Parastenhelia oligochaeta* has so far been recorded from the Andaman and Nicobar Islands (Chidyatapu, Mayabandar, Car Nicobar, Katchal and Great Nicobar Islands – Wells & Rao 1987) and from Bhitarkanika in Odisha, mainland India (Chadha & Kar 1999).

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P2–P3 endopods, P5–P6 and urosomal segmentation; occasionally P4 endopod and caudal ramus setae IV–V. Body subcylindrical, short; posterior margin of cephalothorax, somites bearing P2–P5 and remaining urosomites (except anal somite) with denticulodigitate hyaline frills. Rostrum defined at base, of moderate size, reaching at most to distal margin of second antennular segment; linguiform. Anal operculum semicircular, naked or bordered with fine spinules. Caudal ramus wider than long, without conspicuous spinular ornamentation on dorsal surface; with at least six setae (seta I possibly absent), setae IV–V slightly swollen at base in ♀ in some species (*P. similis*).

Antennule elongate and 8- or 9-segmented in ♀, segment 1 not elongate, segments 7–8 (when 9-segmented) shortest, with aesthetascs on segments 4 and 8 or 9; haplocer in ♂ but segmentation and segmental homologies unconfirmed, with three segments distal to geniculation, segment 5 swollen and with aesthetasc. Antenna not sexually dimorphic; proximal endopodal segment largely separated from basis or forming allobasis, with pinnate seta on abexopodal margin; exopod 2-segmented, proximal segment with two setae, distal segment with 1–2 lateral and three apical elements; distal endopodal segment without penicillate elements. Mandible with 2–4 elements on basis; endopod with eight setae; exopod 1-segmented with three setae or represented by single seta arising from minute knob. Maxillary coxal epipodite represented by one seta. Maxilla with three endites on syncoxa; endopod discrete, with 2–3 setae. Maxilliped with 2–3 setae on syncoxa; basis with 1–2 seta(e) on palmar margin; endopod represented by curved claw, accompanied by 1–2 accessory seta(e).

P1 inner basal spine not sexually dimorphic. P1 exopod 3-segmented; exp-2 about as long as others, typically with short inner seta; exp-3 small, with two pinnate spines, one geniculate seta and one naked seta. P1 endopod 2-segmented; enp-1 elongate, about 1.3–1.5 times length of exopod, with long, pinnate, inner seta inserted in proximal third, segment margins without area of reduced chitinization; enp-2 very small, with one naked minute seta and two dentate claws. P2–P4 rami 3-segmented. P2 endopod ♂ 2-segmented; total number of spines/setae as

in ♀. P3 endopod ♂ 3-segmented; without inner setae on enp-3 and outer spine modified into spinous apophysis. P4 endopod ♂ occasionally with one less inner seta on enp-3 (*P. willemvervoorti* sp. nov.). Armature formula of P2–P4 as follows:

	exopod	endopod
P2	0–1.1.123	0–1.1.(0–1)21
P3	0–1.1.323	0–1.1.(0 or 2)21 [♂: 1.221 or 0.121]
P4	0–1.1.(2–3)23	0–1.1.(0 or 2)21

P5 ♀ endopodal lobe with five setae, outermost shortest; inner margin without transverse striae. P5 ♀ exopod elongate, with six elements. P5 ♂ endopodal lobe with two elements, outer one shortest; exopod 1-, 2- or 3-segmented, with 6–7 elements in total. Vestigial P6 ♀ represented by two minute setae. P6 ♂ with three setae.

Type species. *Parastenhelia hornelli* Thompson & Scott, 1903 (by subsequent designation; Lang 1934: 24).

Other species. *P. similis* Thompson & Scott, 1903; *P. oligochaeta* Wells & Rao, 1987; *P. willemvervoorti* sp. nov.

Species inquirendae. *Parastenhelia hornelli* Thompson & Scott, 1903 sensu Noodt (1955a), sensu Apostolov (1973), sensu Apostolov & Pandourski (1999) and sensu Zaleha *et al.* (2006).

Parastenhelia willemvervoorti sp. nov.

urn:lsid:zoobank.org:act:D4B6BA49-5E4C-4021-A57E-B6F4B35CA973

Original description. Vervoort (1964): 181, 184–188; Figs. 66a–b (♂ – from locality 590), 68a–c (♀ – from locality 589), 69a–f (♂ – from locality 590) [as *Parastenhelia spinosa*].

Type material. The dissected male specimen illustrated by Vervoort (1964: 181, 187) in his figures 66 (a–b) and 69 (a–f) and collected on 16 October 1953 is here designated as the holotype of *P. willemvervoorti* sp. nov. (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters listed in the diagnosis below and those mentioned and illustrated in Vervoort (1964) (ICZN Art. 13.1).

Type locality. Federated States of Micronesia, Caroline Islands, Ifalik (Ifaluk) Atoll; seaward reef about middle of Falarik. Vervoort (1964) collected males from two different stations (589 and 590). The male holotype came from station 590 (sand sample taken about 24 m from reef margin).

Differential diagnosis. *Parastenhelia*. Body length 290–470 µm in ♀, 270–650 µm in ♂. Rostrum as long as antennular segments 1–2 combined. Antennule 8-segmented in ♀; haplocer in ♂ but segmentation unconfirmed, with three segments distal to geniculation. Antenna with 2-segmented exopod bearing two setae on exp-1 and one lateral and three apical elements on exp-2. P1 exopod about 0.6 times length of endopod; exp-2 not elongate, slightly longer than exp-3. P1 enp-1 about 1.5 times length of exopod. P3–P4 exp-1 without inner seta, exp-3 with three inner setae. P2 endopod ♂ 2-segmented; enp-2 elongate, reaching apex of exopod, with additional inner seta [1.221 vs 1.1.121 in ♀]. P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]; P4 endopod ♂ 3-segmented, with only one inner seta on enp-3 [1.1.121 vs 1.1.221 in ♀]. Armature of P1–P4 – see Table 1. P5 ♀ with elongate exopod (about 2.5 times as long as wide), with six elements; armature of endopodal lobe unknown. P5 ♂ 2-segmented, with one outer seta on exp-1 and six elements on exp-2; endopodal lobe with two elements. P6 ♂ with three setae. Anal operculum smooth. Caudal ramus seta IV–V ♀ not swollen at base.

Etymology. The species is named after the late Prof. Willem Vervoort (12 June 1917 – 18 August 2010), eminent copepodologist, who discovered this species.

Key to species of *Parastenhelia* Thompson & Scott, 1903

1. P4 enp-1 without inner seta, enp-3 with three spines/setae (no inner setae); P2 endopod ♂ with armature formula 0.121 *P. oligochaeta* Wells & Rao, 1987.
- P4 enp-1 with inner seta, enp-3 with five spines/setae (two inner setae); P2 endopod ♂ with armature formula 1.221 2.
2. Antennule ♀ 8-segmented; P3–P4 exp-1 without inner seta; P5 exopod ♂ 2-segmented *P. willemvervoorti* sp. nov.

- Antennule ♀ 9-segmented ¹; P3–P4 exp-1 with inner seta ²; P5 exopod ♂ 1- or 3-segmented 3.
- 3. P1 enp-1 about six times length of enp-2; P5 exopod ♀ with straight or slightly convex inner margin
. *P. similis* Thompson & Scott, 1903.
- P1 enp-1 at least seven times length of enp-2; P5 exopod ♀ with slightly concave inner margin 4.
- 4. P5 exopod ♀ about three times as long as maximum width; P5 exopod ♂ 3-segmented . . . *P. hornelli* Thompson & Scott, 1903.
- P5 exopod ♀ about as 2.3 times as long as maximum width; P5 exopod ♂ 1-segmented. . . *P. hornelli* sensu Apostolov (1973).

¹ Thompson & Scott (1903) illustrate the antennule as 8-segmented in *P. similis* but Wells & Rao (1987) confirmed its 9-segmented condition.

² The condition of P3 exp-1 is unknown in *P. hornelli*.

***Microthalestris* Sars, 1905**

Various authors have reported on what they individually regard as *Parastenhelia spinosa* or varieties/species sharing some of its morphological characteristics, but recognise a wide range of variation in features such as segmentation of the female antennule, modification of the caudal ramus setae (particularly V), setation of the antennary exopod and endopod, relative proportions of P1 rami and form of their terminal elements, armature formulae of P2–P4, shape and armature of ♀ P5 exopod, and segmentation of ♂ P5 exopod. The magnitude of this variability, or the identity of differences which might represent true genetic discontinuity (and thus distinct species), is in many cases impossible to determine due to the inaccurate and/or incomplete descriptions and illustrations [especially the original description by Fischer (1860)] which have accompanied many published reports. The currently accepted concept of *P. spinosa* being a highly variable, cosmopolitan taxon has grown over time since 1860 by the gradual accumulation of differences observed in what were wrongly assumed to be geographically isolated populations of the same species. The historical review presented below aims at (a) pointing out some important misconceptions in the taxonomy of the species, (b) assigning distinct specific status to some of its radically divergent “populations”, and (c) formulating a working hypothesis and baseline for future comparisons and revisionary work.

Parastenhelia spinosa was first described as *Harpacticus spinosus* by Fischer [1860: 665–666, Table XXI (figures 51–53), XXII (figure 66)] from the island of Madeira [Lang (1948: 589) stated incorrectly that Fischer did not disclose the type locality] but the description is severely lacking in any real detail (8-segmented antennule, ovate female P5 with four spines on exopod and baseoendopod, caudal ramus seta V swollen at base) and only his illustration of the P1 provides the barest minimum to identify it as a member of the Parastenheliidae. The inaccuracies expressed in the few poorly rendered drawings (maxilliped, P1, female P5, caudal rami) and the lack of the male make the description virtually useless for comparative purposes. *Harpacticus spinosus* is placed in *Microthalestris* solely on account of its elongate P1 exp-2 but cannot be treated as anything more than a *species inquirenda* in this genus. Had Lang’s (1948) fixation of *H. spinosus* as the type of *Parastenhelia* been valid, this would have threatened stability and universality in the application of the name of the type species since its taxonomic identity cannot be determined from its name-bearing type. Although Lang (1936a: 21) considered the possibility that Fischer’s (1860) species was conspecific with *Parastenhelia forficula* var. *littoralis* (sensu Sars 1911) he recommended to set it aside on the grounds that it cannot be identified with any degree of confidence. Unfortunately, he changed his opinion by not only reinstating it as a valid species but also by illegitimately fixing it as the type of the genus (Lang 1944: 13; 1948: 586–588).

Claus (1863: 131–132, Plate XVII, figs 7–11) described *Thalestris forficula* Claus, 1863 as one of ten species assigned to his new genus *Thalestris* Claus, 1862 (type species by subsequent designation: *Thalestris longimana* Claus, 1863). The author reluctantly included *H. spinosus* in the genus as well as two other *Harpacticus* species previously described by Fischer (1860). His description of *T. forficula*, based on material from Messina (Sicily), included illustrations of the antennule of both sexes, P1, caudal rami and the female genital field. The most significant information that can be extracted from Claus’s (1863) concise description is the 8-segmented condition of the female antennule, the presence of an apophysis on the male P3 endopod, the modified caudal seta (V) displaying a basal swelling, and the length of the relatively short inner seta on P1 enp-1 which extends only to about 40% of the segment length. No information was given about the armature of P2–P5 in both sexes, or the segmentation of the male P5 exopod.

TABLE 1. Swimming leg armature formulae (P1–P5) of parastenheleid species (b = endopodal lobe of baseendopod; enp = endopod; e, exp = exopod; S = number of exopodal segments; – = missing data). *. *species inquirendae*; **. *species indeterminate* forms in need of thorough redescription. Genus abbreviations: *Pa.* = *Parastenhelita*, *Par.* = *Paraleptomexochra*, *Pe.* = *Penicilliaris*, *Po.* = *Porirualia*, *Ps.* = *Psammoleptomexochra*.

	P1		P2		P3		P4		P5 ♀		P5 ♂	
	exp	enp	exp	enp	exp	enp	exp	enp	e	b	e	b
<i>Parastenhelita</i> Thompson & Scott, 1903												
<i>Pa. hormelli</i> Thompson & Scott, 1903	0.0.022 ¹	1.111	—	—	—	—	1.1.223 ³	1.1.221	6	5	7	2
sensu Noodt (1955a) **	—	—	1.1.0–123	1.1.121	1.1.223	1.1.221	1.1.223	1.1.221	6	5	—	—
sensu Apostolov (1973) **	0.1.022	1.111	1.1.123	0.1.121 ⁴	1.1.223	1.1.221 ⁵	1.1.223	1.1.221	6	5	7	2
sensu Apostolov & Pandourski (1999) **	—	—	—	—	—	1.1.321	—	—	6	5	—	—
sensu Zaleha <i>et al.</i> (2006) **	—	—	0.1.123	1.1.121	0.1.223	1.1.221	0.1.323	1.1.221	—	—	—	—
<i>Pa. similis</i> Thompson & Scott, 1903 ⁶	0.1.022	1.111	1.1.123	1.1.121 ²	1.1.323	1.1.221 ⁵	1.1.323	1.1.221	6	5	6 ⁷	2
<i>Pa. oligochaeta</i> Wells & Rao, 1987	0.1.022	1.111	0.1.123	0.1.021 ⁸	0.1.323	0.1.021 ⁹	1.1.323	0.1.021	6	5	6	2
<i>Pa. willemervoorti</i> sp. nov. ¹⁰	0.0.022 ¹¹	1.111	1.1.123	1.1.121 ²	0.1.323	1.1.221 ⁵	0.1.323	1.1.221 ¹²	6	—	7	2
<i>Pa.</i> sp. sensu Zaleha <i>et al.</i> (2018) **	—	—	1.1.212	1.1.123	1.1.122	1.1.122	1.1.121	1.1.222	—	3	—	—
<i>Microthalestris</i> Sars, 1905												
<i>M. spinosa</i> (Fischer, 1860) comb. nov. *	0.?.022	? .011 ¹³	—	—	—	—	—	—	4	4	—	—
sensu Pesta (1959) **	0.1.022	1.111	—	—	0.1.223	—	—	—	6	5	—	—
sensu Marinov (1974)	0.1.022	1.111	0.1.123	0.1.121	0.1.223	1.1.221 ⁵	0.1.223	1.1.221	6	5	7	2
sensu Wells & Rao (1987) **	—	—	—	—	—	—	—	—	—	—	6	—
sensu Kornev & Chertoprud (2008) **	0.1.022	1.111	1.1.123	1.1.121	0.1.2–323	1.1.221	0.1.2–323	1.1.1–221	8	5	7	2
f. <i>bulgarica</i> Apostolov, 1968 ** ¹³	0.1.022	1.011 ¹³	0.1.123	0.1.121	1.1.223	—	0.1.223	1.1.221	6–7	5	7	2
<i>M. forficula</i> (Claus, 1863) comb. nov. *	0.1.022	1.111	—	—	—	—	—	—	—	—	—	—
sensu Wilson (1932b) **	0.1.022	1.111	—	—	—	—	—	—	8	5	7	2
<i>M. forficuloides</i> (Scott & Scott, 1894)	0.1.022	1.111	—	—	0.1.323	—	0.1.223	1.1.121	8	5	7	2
<i>M. littoralis</i> Sars, 1911	0.1.022	1.111	—	—	—	—	—	—	6	5	—	—
sensu Willey (1935) **	—	—	—	—	—	0.1.221	—	??.121	—	—	—	—
sensu Nicholls (1945) **	0.0.022 ¹¹	1.111	—	—	—	—	—	—	6	5	7	2
<i>M. gracilis</i> (Brady, 1910) comb. nov. ¹⁶	0.1.022	1.111	0.0.223	1.1.120	—	—	—	—	6	4	—	—
<i>M. antarctica</i> (Scott, 1912) comb. nov.	0.1.022	1.111	1.1.123	1.1.121	—	1.1.321 ¹⁷	1.1.223 ³	1.1.121	6	5	—	—
<i>M. costata</i> (Pallares, 1982) comb. nov. ¹⁸	0.1.022	1.111	1.1.123	1.1.121 ²	1.1.323	1.1.321 ⁵	1.1.323	1.1.221	6	5	7	2
<i>M. minuta</i> (Pallares, 1982) comb. nov.	0.1.022	1.111	1.1.123	1.1.021	1.1.223	1.1.121 ⁵	1.1.323	1.1.221 ¹⁹	6	5	7	2
<i>M. bulbosa</i> (Gee, 2006) comb. nov.	0.1.022	1.111	1.1.123	0.1.021	1.1.323	0.1.221 ²⁰	0.1.323	1.1.221 ¹²	6	5	7	2

.....continued on the next page

TABLE 1. (continued)

	P1		P2		P3		P4		P5 ♀		P5 ♂	
	exp	enp	exp	enp	exp	enp	exp	enp	e	b	e	S
<i>M. campbelliensis</i> sp. nov.	0.1.022	1.111	1.1.123	1.1.121	0.1.223	1.1.121	0.1.223	1.1.121	6	5	7	3
<i>M. polaris</i> sp. nov. ²¹	0.1.022	1.111	1.1.123	1.1.121	1.1.323	1.1.121	0.1.323	1.1.121	8	5	7	3
<i>M. santacrucensis</i> sp. nov.	0.1.022	1.111	—	—	0.0.123	—	—	—	6	5	6 ²²	1
<i>M. sarsi</i> sp. nov.	0.1.022	1.111	1.1.123	1.1.121	1.1.223	1.1.121	0.1.223	1.1.121	8	5	6	3
<i>M. variabilis</i> sp. nov. ²⁴	0.1.022	1.111	1.0.123	1.1.121 ²	1.0.223	1.1.121 ⁵	1.1.123	1.1.121	6	5	7	3
<i>Thalastrella</i> Monard, 1935a												
<i>T. ornaticissima</i> Monard, 1935a	0.1.022	1.111	0.1.223	1.1.121	0.1.223	1.1.121	0.1.223	1.1.221	6	5	4	1
<i>T. arenicola</i> (Noodt, 1964) comb. nov.	0.0.022	1.011 ¹³	0.1.223	1.1.121	0.1.223	1.1.121	0.1.223	1.1.221	6	5	4	1
<i>T. psammophila</i> (Wells, 1967) comb. nov.	0.1.022	1.111	0.1.223 ²⁸	1.1.121	0.1.323	1.1.121	0.1.323	1.1.221	5	5	4	1
<i>T. reducta</i> (Apostolov, 1975) comb. nov.	0.0.022	1.111	0.1.223	1.1.121	0.1.223	1.1.121	0.1.223	1.1.121	6	5	5	1
<i>T. bengalensis</i> (Wells & Rao, 1987) comb. nov.	0.1.022	1.111	0.1.223	1.1.121	0.1.323	1.1.121	0.1.323	1.1.221	5	5	4	1
<i>T. obscura</i> (Mielke, 1994b) comb. nov.	0.0.022	1.111	0.1.223	1.1.121	0.1.323	1.1.121	0.1.323	1.1.221	5	5	4	1
<i>T. pulchra</i> (Mielke, 1994b) comb. nov.	0.1.022	1.111	0.1.223	1.1.121	0.1.323	1.1.121	0.1.323	1.1.221	6	5	4	1
<i>Paraleptomesochra</i> Wells, 1967												
<i>Par. minima</i> Wells, 1967	0.022	1.011	1.1.121	1.0.010	1.1.121	1.0.010	1.1.121	1.0.010	6	3	4	1
<i>Par. wellsi</i> Rao, 1972	0.022	1.011	1.1.121	1.0.020	1.1.121	1.0.020	1.1.121	1.0.020	6	3	4	1
<i>Psammoleptomesochra</i> Mielke, 1994a												
<i>Ps. australis</i> Mielke, 1994a	0.0.022	1.111	0.0.022	0.0.021 ²⁶	0.0.022	0.0.021 ²⁶	0.0.122	1.0.021 ²⁶	6	4	5 ²⁷	1
Foweya Gee, 2006												
<i>F. anglica</i> (Norman & Scott, 1905)	0.1.022	1.111	1.1.223	1.1.221	1.1.323	1.1.321	1.1.323	1.1.221	6	5	6	1
<i>F. tertia</i> (Kunz, 1975)	0.1.022	1.111	1.1.223	1.1.221 ²⁸	1.1.323	1.1.321 ²⁹	1.1.323	1.1.221	6	5	5	1
<i>Johnwellisia</i> gen. nov.												
<i>J. bipartita</i> gen. et sp. nov.	0.1.022	1.111	1.1.123	1.1.121 ³⁰	1.1.323	1.1.221 ³¹	1.1.323	1.1.121	6	5	4	2
<i>Karayugia</i> gen. nov.												
<i>K. aydini</i> (Kuru & Karaytuð, 2015) comb. nov.	0.1.022	1.111	1.1.123	1.1.121	1.1.323	1.1.221 ⁵	0.1.323	1.1.121	6	5	5	2
<i>Penicillicaris</i> gen. nov.												
<i>Pe. pectinimana</i> (Car, 1884) comb. nov.	0.1.022	1.111	??.123	??.121	??.323	??.221 ⁵	??.223	??.1221	6(7)	5	7	1

.....continued on the next page

TABLE 1. (continued)

	P1		P2		P3		P4		P5 ♀			P5 ♂			
	exp	enp	exp	enp	exp	enp	exp	enp	e	b	e	b	e	b	S
<i>Pe. maldivensis</i> sp. nov.	0.0.022 ¹¹	1.111	—	—	—	—	0.1.223	1.1.121	6	5	7	2	1	—	—
<i>Pe. penicillata</i> sp. nov.	0.1.022	1.111	—	1.221	??.323	1.321 ^{5,32}	??.323	??.221 ¹²	6	5	7	2	1	—	—
<i>Pe. sewelli</i> sp. nov. ³³	0.1.022	1.011 ¹³	1.1.123	1.1.121	1.1.223	1.1.221 ⁵	—	??.221	6	5	7	2	1	—	—
<i>M. forficula</i> sensu Scott (1894a)**	0.1.012 ³⁴	1.011 ¹³	—	—	—	—	0.1.223	1.1.221	6	4 ³⁵	—	—	—	—	—
<i>M. littoralis</i> sensu Brian (1921)**	—	—	—	—	—	—	—	—	—	—	—	7	2	1	—
<i>M. littoralis</i> f. <i>scotti</i> sensu Sewell (1940)**	0.0.022 ¹¹	1.011 ¹³	—	—	—	—	—	—	6	5	—	—	—	—	—
<i>Portruadlia</i> gen. nov.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Po. megarostrum</i> (Wells, Hicks & Coull, 1982) comb. nov.	0.1.022	1.111	1.1.123	1.1.121	1.1.323	1.1.221 ¹²	1.1.323	1.1.221	6	5	6	2	1	—	—
<i>Po. pyriformis</i> (Song, Kim & Chang, 2003) comb. nov.	0.1.022	1.111	1.1.123	1.1.121 ²	1.1.223	1.1.221 ³⁶	0.1.223	1.1.221	6	5	5	2	1	—	—

¹ The absence of the inner seta on exp-2 requires confirmation.

² 2-segmented in ♂ (1.221); Thompson & Scott (1903) do not illustrate the inner seta on ♂ exp-1 in *Pa. hornelli* which is possibly an observational error (but see Apostolov 1973: Fig. 9–9).

³ The short, fine, distal inner seta on exp-3 is probably overlooked.

⁴ 0.221 in ♂.

⁵ 1.1.02 + apo in ♂.

⁶ Based on Wells & Rao's (1987) redescription of *Pa. hornelli* from Middle and South Andaman Islands. The original description of *Pa. similis* by Thompson & Scott (1903) lacks information on P2–P3 and figures P4 exp-3 with only two inner setae (the short distal one being overlooked).

⁷ Wells & Rao (1987) claim that exp-2 is unarmed and has only a long spinule. This observation is probably correct since in all other species with a 3-segmented exopod the inner seta arises from the distal corner and not from halfway along the inner margin.

⁸ 2-segmented in ♂ (0.121).

⁹ 0.1.02 + apo in ♂.

¹⁰ Note that the armature formulae given by Wells & Rao (1987: Table 4) for the exopod of P3 and both rami of P4 are incorrect.

¹¹ Both sexes were figured (Vervoort 1964: Figs 68c, 69a) without an inner seta on exp-2 which is probably an oversight. The same error probably applies to Sewell's (1940) descriptions of *Pa. littoralis* (Text-Fig. 26–G) and *Pa. littoralis* f. *scotti* (Text-Fig. 28–D).

¹² Armature pattern of exp-3 121 in ♂.

¹³ The vestigial seta was probably overlooked in the descriptions by Fischer (1860), Car (1884), Scott (1894a), Sewell (1940), Apostolov (1973) and Noodt (1964).

¹⁴ Armature formula of P1 and P4 based on Apostolov (1973) who also reported a different armature for the ♀ P5 exopod (six setae).

¹⁵ 1.1.12 + apo in ♂ P3 endopod.

¹⁶ Brady's (1910) description is grossly inadequate and incomplete; the setal counts presented here for P2 and P5 baseendopod are based on his illustrations (Textfig. VIII: Figs 3–4) and are most certainly incorrect, as well as his claim that the endopodal armature pattern for P2–P4 is [1.1.120].

- ¹⁷ Based on Lang's (1936a: Fig. 37) supplementary description (as *Pa. gracilis*).
- ¹⁸ Pallares (1982: 10) erroneously stated that P3–P4 exp-3 display a [333] pattern in the male; probably not having consulted Pallares's drawings of the male, Mielke (1990: 166) accepted this as an additional difference between the type population and his material collected from Bahía Lapataia near Ushuaia (Argentina).
- ¹⁹ Armature pattern of exp-3 021 in ♂.
- ²⁰ 0.1.12 + apo in ♂.
- ²¹ The single ♀ observed by Mielke (1974: 20) showed an aberrant setal pattern on one side of P2 exp-2 (with two inner setae) and P4 exp-3 (with inner seta).
- ²² There is confusion over the exact number of elements on the exopod. Pallares (1963) states that there are three outer, one inner and two apical elements but in a subsequent account (Pallares 1968: 65) explicitly states that there are seven without going into detail about their position. We have adopted Pallares's original observation pending re-examination of new material.
- ²³ Lang's (1936b: 24) only female displayed the atypical 121 pattern on exp-3.
- ²⁴ Mielke (1990) recorded a high degree of variability in the armature of P2–P4. Some specimens displayed (a) an inner seta on P2–P3 exp-2, (b) only one (instead of two) inner seta on P3 exp-3, (c) two (instead of one) inner setae on P4 exp-3, (d) two (instead of one) inner setae on P3–P4 exp-3, and/or (e) only two (instead of three) outer spines on P4 exp-3. One male lacked the inner seta on P4 exp-2.
- ²⁵ According to Wells (2007: 596) the original report of three inner setae on P2 exp-3 is wrong.
- ²⁶ The endopodal armature pattern differs from Mielke's (1994a: 257) in two aspects; the apical spiniform element on exp-3 is here considered as the homologue of the outer spine in other genera, and the two minute and fine setae originating from the inner corner of exp-3 are included in the formulae.
- ²⁷ Inner seta minuscule (Mielke 1994a: Fig. 4C).
- ²⁸ 2-segmented in ♂ (1.321).
- ²⁹ 1.1.321 in ♂; Kunz (1975) did not illustrate the ♀ condition but listed the armature formula of P3 endopod as 1.1.221 in his Table 5; Gee (2006) re-examined the type material and noted that the armature formula is as in *F. anglica*.
- ³⁰ 2-segmented in ♂ (1.121).
- ³¹ 1.1.021 in ♂.
- ³² Willey (1935) reported some specimens with a 3-segmented endopod in the ♀ (1.1.221).
- ³³ P3 endopod ♂ and P5 ♂ based on Vervoort's (1964) description of *Pa. spinosa* [partim]. According to Sewell (1940: Text-fig. 27H) P2 exp-1 lacks an inner seta but Vervoort shows a small inner element which is included in the armature formula here.
- ³⁴ Scott (1894a: Plate 12, Fig. 39) most likely overlooked the short inner seta on exp-3.
- ³⁵ Sewell (1940: 196) claims the proximal inner seta was overlooked in Scott's (1894a) description, bringing the total to five.
- ³⁶ 1.221 in ♂.

In a paper written in old Danish and completely lacking in illustrations, Boeck (1865: 266–267) described a new species, *Thalestris karmensis* Boeck, 1865, based on specimens collected from Karmøy in Norway; this species fell into oblivion until it was discussed by Sars (1905 – see below).

In a similar contribution, Boeck (1873: 56) provided a short unillustrated text description of *Dactylopus longipes* Boeck, 1873, obtained from 29 m depth in the Oslofjord in Norway. His female specimens were characterized by a 9-segmented antennule, a long and slender P1 exopod which is shorter than enp-1, a 2-segmented P1 endopod with a very long enp-1 which bears a seta in the proximal quarter of the inner margin, and a P5 exopod with eight elements. Based on this short description Lang (1936a: 31) would later synonymize *D. longipes* with *Thalestris forficula* which he had previously placed in *Parastenhelia* (Lang 1934: 24).

Thomson's (1883: 104–105; Plate X, Figs 16–21) material of *Thalestris forficula* from Otago Harbour in New Zealand agrees with the description of Claus (1863) in the 8-segmented condition of the female antennule and the basally inflated setae V on the caudal ramus but differs in size (1,000 vs 800 µm) and the morphology of P1. The female P5 bears six and five setae on the exopod and endopodal lobe, respectively. Lang (1934: 25) lists Thomson's record but does not appear to question its identity. In later accounts he accepts it as a record of either *Parastenhelia forficula* var. *littoralis* (Lang 1936a: 52) or *P. spinosa* (Lang 1948: 588).

Car (1884: 248–249, Plate XVIII, Figs 1–8) provided an illustrated description of a new species, *Thalestris pectinimana* Car, 1884, based on a single ovigerous female collected in the vicinity of Trieste, northeastern Italy. The author did not compare *T. pectinimana* with other congeners nor did he present a justification for its recognition as a distinct species. Illustrations were provided for the female in lateral aspect, antennule, antenna, maxilliped, distal segments of the P1 rami and P5. The species is characterized by the 8-segmented antennule, the large P5 with seven setae on the foliaceous exopod and five elements on the endopodal lobe, and the presence of distinct pectinate spines on the terminal segments of P1 exopod and endopod. No information was given on the armature of P2–P4. The species has not been recorded again since its original description. Pesta (1920: 590) listed it as a junior subjective synonym of *Phyllothalestris mysis* (Claus, 1863) but this was rejected by Lang (1936a: 49) who considered it a valid species of *Thalestris*. Lang (1948: 497, 588) revised his previous opinion and considered *T. pectinimana* conspecific with *Parastenhelia spinosa*, more specifically (based on P5 morphology) with the form described as *Microthalestris littoralis* f. *penicillata* by Willey (1935: 82). This claim is dubious since Willey did not describe the female P5 but only stated that it displays "... the fifth foot of *littoralis*". According to Sars's (1911: Suppl. Plate 11) description of *M. littoralis* the female P5 has only six setae on the exopod while *T. pectinimana* exhibits seven.

Scott (1894a: 100–101, Plate XII, Figures 33–41) recorded a single ovigerous female of *T. forficula* from a shore gathering in Accra (Ghana). The specimen is similar to Claus's (1863) material in the 8-segmented antennule and the basally swollen caudal ramus setae (V), however, is distinctly smaller (500 vs 800 µm). The most conspicuous feature is the presence of two strong pectinate claws on both P1 exp-3 and P1 enp-2. His illustration of P4 shows that it lacks the inner seta on exp-1 and has two inner setae on enp-3 (221). The female P5 has a reduced armature (if Scott's observations are correct), displaying six setae on the exopod and only four on the endopodal lobe. The latter observation was disputed by Sewell (1940: 196) who believed that the proximal inner seta of the endopodal lobe was overlooked.

Scott & Scott (1894: 142–144, Plate IX, Figs 4–9) described *Thalestris forficuloides* from mud near the low-water mark at Seafield in the vicinity of Leith, Firth of Forth, Scotland. An expanded description of the female and additional illustrations of the male were provided by Scott (1894b: 255–256, Plate X, Figures 13–25) based on specimens from the type locality (note that the mandible and maxillule were transposed in his Plate X). As the name suggests this species was considered close to *T. forficula*, displaying differences in the segmentation of the female antennule (9-segmented vs 8-segmented in *T. forficula*), the length of the P1 endopod, and some unspecified discrepancies in the "... proportional lengths of the other thoracic feet" (Scott & Scott 1894: 144).

Sars (1905: 122) proposed a new genus *Microthalestris* in the Thalestridae to accommodate *T. forficula* as its type and only species and stated that the forms recorded by Boeck (1865) as *Thalestris karmensis* and by Scott & Scott (1894) as *T. forficuloides*, both belong to *M. forficula* (Claus, 1863). His redescription of the latter (Sars 1905: 123–124, Plate LXXVI) corresponds exactly to the illustrations of Scott (1894b) in the segmentation of the antennule, morphology of P1, and the basally inflated caudal ramus seta (V), however, also shows a number of important differences with *T. forficuloides* including (a) P3 exp-1 with inner seta instead of without, (b) P3 exp-3 with two inner setae instead of three, (c) P5 exopod ♀ comparatively longer, and (d) P5 exopod ♂ 3-segmented instead of 1-segmented. Although Sars was not specific about the total number of setae on the male P5 exopod it

appears from his illustration that there are only six as opposed to the seven recorded in later descriptions. There is a hint of a short setal element among the spinular cluster on the outer margin of exp-1, however, the seta usually found in that position is typically very long (e.g. Chislenko 1967: Fig. 45; Mielke 1974: Fig. 9D). Lang's (1936b: 23, Fig. 52) observation of a similar condition in a male from the Øresund indicates that it is genuinely lost (or extremely reduced) rather than broken off during dissection. Although Lang (1934: 24) expressed doubts, primarily based on differences in antennular segmentation, about the conspecificity of Sars's (1905) Norwegian specimens of *M. forficula* and Claus's (1863) type material of *T. forficula*, he cited the former as a synonym of the new combination *Parastenhelia forficula* (Claus, 1863).

Sars (1911: 369–370, Supplement plate 11-1) added the new species *M. littoralis* Sars, 1911 to the genus which showed more or less the same distribution in Norway as *M. forficula*, including various localities along the south and west coasts and further northwards to the Trondhjem Fjord (Bejan). Sars (1911) only reported the female which differs from that of the type species in the more compact antennule (the number of segments was not disclosed), the longer and more slender P1, the number of exopodal setae on the P5 (six vs eight) and the normally developed seta V on the caudal ramus. Unfortunately, no information on the armature formula of P2–P4 was given which inevitably led to the incorrect assignment of various non-conspecific populations to this species.

Farran (1913) observed considerable variation in body size (500–850 µm) in his material of *M. littoralis* from Clare Island and Blacksod Bay, Co. Mayo (Ireland) (see also Farran *et al.* 1915; Southern 1915) which he viewed as a possible indication of the presence of a second species. All specimens agreed with Sars's (1905) description in the morphology of the female P5.

Pesta (1920: 591–593) summarized records of *Microthalestris* in the Adriatic, including *M. forficula* in the Venice Lagoon (Grandori 1912, 1914) and *M. littoralis* from the Palagruža (Pelagosa) archipelago (Steuer 1912).

Brian (1921: 77–80) reported *M. littoralis* from the Gulf of Genoa, illustrated naupliar stages I and III–V (Text figures 23–25; Plate VI, Fig. 3) and described copepodids III–V (Plate VIII, Figs 10–22). Dahms & Hicks (1996) pointed out that Brian's naupliar illustrations in reality refer to NIV–NVI. Brian's (1921) description reveals little information about the female except for the lateral aspect view of an ovigerous specimen (Plate III, Fig. 7), showing the presence of a single egg sac, and the ventral view of the abdomen (Plate V, Fig. 15) which shows that the caudal ramus seta V is not swollen at the base. His illustrations of the male (Plate IV, Fig. 9; Plate V, Fig. 5; Plate IX, Figs 9–14) document three characters of particular significance, (a) the presence of two penicillate spines on the antenna (already expressed in copepodid IV: his Plate VIII, Fig. 17), (b) the 3-segmented P3 endopod in the male bearing an inner seta on enp-1 and -2, in addition to the apophysis and two apical setae on enp-3, and (c) the 1-segmented condition of the male P5 exopod bearing seven setae. No information was provided on the segmentation of the female antennule or armature of the swimming legs and P5.

Monard (1927) retained *Microthalestris* in the Thalestridae as an “insufficiently described genus” (p. 157) in his *Synopsis universalis generum harpacticoidarum* but placed the closely related *Parastenhelia* in the Diosaccidae (= Miraciidae). He admitted that the latter genus may belong to the same family as *Microthalestris* on the basis of P1 morphology but was unable to make a firm recommendation for its exclusion from the Miraciidae because the number of egg sacs was apparently unknown [this being untrue since both Car (1884) and Brian (1921) had made cursory observations and illustrated a single egg sac].

Gurney (1927: 545) confirmed the presence of a single egg sac in a damaged female of an undescribed *Parastenhelia* species from Port Taufiq (Suez Port), located at the southern boundary of the Suez Canal in Egypt. He classified the genus in the Canthocamptidae.

Monard (1928: 348–349, Fig. XVIII–2) reported numerous specimens of *M. forficula* from Port-Vendres and Banyuls-sur-Mer on the French mediterranean coast and considered the species as extremely variable with *M. littoralis* definitely falling within its limits. Contrary to Sars (1905), Monard also appeared to support the concept that *M. forficula* assumes a cosmopolitan distribution by accepting doubtful records from New Zealand (Thomson 1883) and the Gulf of Guinea (Scott 1894a) as valid. The French material differs from the Norwegian specimens used in Sars's (1905) description in a number of significant aspects such as (a) the segmentation of the female antennule (eight vs nine), (b) antennary endopod with two penicillate elements, (c) caudal ramus setae IV–V with an inflated base (this also occurs in Claus's description of *T. forficula*), (d) claws on both rami of P1 distinctly shorter, (e) P3 exp-3 with three inner setae vs two, (f) P4 enp-3 with two inner setae vs one, (g) P5 exopod ♀ with six elements vs eight, and (h) P5 exopod ♂ 1-segmented vs 3-segmented. Monard (1928) also reported variability in the armature of the female P5 exopod with some (rare) specimens displaying seven elements, and variation in body

length (650–800 µm). Sewell (1940: 191) stated that Monard misidentified his specimens and was in reality dealing with *M. littoralis* sensu Sars (1911) but there is no justification for this claim.

Stephensen (1929) recorded *M. littoralis* from two localities in the Faroe Islands, *i.e.* off Trangisvaag (Suðuroy = Suderø), and between Streymoy (Strømø) and Eysturoy (Østerø). Lang (1948) re-examined Stephensen's material and confirmed the identity of the specimens from the latter site but confirmed that the male from Trangisvaag belongs to *Amonardia normani* (Brady, 1872) (Thalestridae).

Wilson (1932a) added the first North American record of *M. littoralis* from the plankton in Chesapeake Bay, Maryland, stating that he found both sexes. His record was not accompanied by any illustrations but the author seems to indicate that he accepts Brian's (1921) identification of the male of this species as correct. Wilson (1932b) subsequently recorded both *M. forficula* (Penzance Pond) and *M. littoralis* (Cuttyhunk Island between Buzzards Bay and Vineyard Sound) from the Woods Hole region, Massachusetts. The report of the first species included illustrations of P1, P5 of both sexes and male P3 endopod, all of which agree well with Sars's (1905) description except for the latter which shows an inner seta on the distal segment (only *P. bulbosa* shares this character; Table 1), and the male P5 which displays a long outer seta on the proximal segment. No information was given about the segmentation of the female antennule, swimming leg armature or the form of caudal ramus seta V. The North American specimens are distinctly smaller (♀♀: 400–500 µm; ♂♂: 350 µm) than their European counterparts. The authenticity of Wilson's (1932b) material of *M. littoralis* is indeterminable since the few illustrations provided are reproduced from Sars (1911). His text reveals that females (no males were found) correspond in the setation of the female and measure 500–600 µm. Interestingly, Wilson (1932b: 572) maintained *Parastenhelia* and *Microthalestris* as separate genera.

Jakubisiak (1933: 115) recorded *M. littoralis* from the Isle of Šolta along the Dalmatian coast of Croatia and opposed Monard's (1928) view that this species must be subsumed under *M. forficula*, stating that it not only differs in the morphology of the female P5 but also in body size and the segmentation of the antennule.

Lang (1934) formally synonymized *Microthalestris* with *Parastenhelia* and transferred the latter to the Thalestridae based primarily on the similar position of the inner seta on P1 enp-2 and the reported presence of a single egg sac in members of the genus (*cf.* Gurney 1927: 545). Morphological comparisons between single species of these genera were also used as additional evidence in support of their synonymy, *e.g.* similarities were pointed out in the morphology of ♀ P5 (*P. hornelli* and *M. littoralis*), ♂ P5 (*P. hornelli* and *M. forficula*), P1 (*P. antarctica* and *M. forficula/littoralis*) and caudal ramus seta V (*P. similis* and *M. forficula*). Lang (1934: 25) relegated *M. littoralis* to a mere variety of *Parastenhelia forficula* (Claus, 1863), dismissing the most clearcut character that consistently separates these species (number of exopodal setae on ♀ P5) along most of the Norwegian coastline (Sars 1911) as of no significance. This course of action was based on the incongruous argument that differences had been reported between the widely disjunct "populations" of *T. forficula* (and *M. littoralis*) from New Zealand (Thomson 1883), Gulf of Guinea (Scott 1894a) and Ireland (Farran 1913). The first two sources contain incomplete and partly inaccurate descriptions (based on a single specimen in Scott's case) while the third is completely lacking in illustrations and by Farran's own account is probably based on an amalgam of two species. Lang's (1934) paper set the scene for his authoritarian stance in shaping a very broad, encompassing taxonomic concept of *Parastenhelia spinosa*, with the result that it has unjustly come to be regarded as a highly variable, cosmopolitan species. He further fuelled the controversy by assigning a pair in amplexus from Perseverance Harbour on Campbell Island in the southern Pacific to *P. forficula* var. *littoralis*. Differences in P1, P5 and caudal rami indicate that his subantarctic specimens belong to a different, as yet unnamed species (see below). Lang (1934) listed *T. karmensis* and *T. forficuloides* as synonyms of the typical *P. forficula*.

Monard (1935a: 43) recorded both *M. forficula* and *M. littoralis* from the Roscoff region (Brittany). The former displayed a 3-segmented P5 exopod in the male while females of the latter were excessively large (900 µm) compared to the Norwegian populations (590 µm; *cf.* Sars 1905). He continued to place *Parastenhelia* in the Miraciidae while maintaining *Microthalestris* and his newly established genus *Thalestrella* in the Thalestridae. During the same year, Monard (1935b: 47), adopting a different nomenclature, stated that he had found both the "typical" form and the *littoralis* variety of *Parastenhelia forficula* in Cartaghe (Salammbô), Tunisia and admitted having difficulties separating them. He reported variability in the number of segments in the female antennule (one specimen having seven!) and occasional left-right asymmetry in the setation of the female P5 exopod in some individuals. Without illustrations it is impossible to decide on the identity of his material.

Wiley (1935: 82–83) distinguished two forms in his material of *M. littoralis* from Harrington Sound in Bermuda.

One ovigerous female (500 µm) conformed to Sars's (1911) description in displaying 9-segmented antennules and unmodified caudal ramus setae. The endopods of P2–P4 of this *littoralis*-form are distinctly 3-segmented, have a constricted mobile articulation between enp-2 and enp-3 and the inner distal corner of enp-2 produced into a sharp spur beyond the insertion of the inner seta (his Fig. 121); the formula of P4 enp-3 is 121. Furthermore, the proximal inner seta of P4 exp-3 is longer than the second inner seta, which is comparatively short and only slightly thickened. All other specimens (♀♀: 500–700 µm; ♂♂: 400–500 µm) had 8-segmented antennules and forcipately curved caudal setae IV–V with swollen bases. Willey (1935: Figs 119–120, 122–126) assigned them to a separate *penicillata*-form, based on the presence of two penicillate spines amongst the apical armature elements of the antenna similar to those figured by Brian (1921) for *M. littoralis* from the Gulf of Genoa. In addition, both claws at the distal margin of P1 enp-2 are coarsely penicillate, and P1 exp-3 bears a slender inner seta, a geniculate seta, and two penicillate spines. In the *penicillata*-form P2–P3 enp-2 and -3 are more often indistinctly separated, without a functional articulation between them. Specimens with distinctly 3-segmented endopods of P2–P3 lack a spur at the inner distal corner of enp-2. The armature formula of P4 enp-3 is sexually dimorphic, being 221 in the female, and 121 in the male. On P3–P4 exp-3, the distal inner seta is excessively fine and curving outwards, and the proximal inner seta of P4 exp-3 is distinctly shorter than the middle one. Females of both forms share the typical P5 setation pattern of *M. littoralis* (six elements on the exopod, five on the endopodal lobe). Males of the *penicillata*-form have a 3-segmented P3 endopod with two apical setae and a spinous apophysis on enp-3, and a 1-segmented P5 exopod with seven elements.

Lang (1936b) recorded both *P. forficula* (one ♀, one ♂) and *P. forficula* var. *littoralis* (one ♀) from the Øresund between Zealand (Denmark) and Scania (Sweden) with all three specimens having been collected from different localities. His *P. forficula* specimens agree with Sars's (1911) description in the general facies of the P1 and P5 of both sexes but differs in the presence of only one inner seta on P3 enp-3 (instead of two) in the female; however, it must be noted that the latter observation was based on a single female and not accompanied by an illustration. Lang (1936b) assigned, except for his own record from Campbell Island (Lang 1934), several older records to *P. forficula* var. *littoralis* without giving any explanation. These include the reports of *Microthalestris littoralis* from Norway (Sars 1911), western Ireland (Farran 1913), the Gulf of Genoa (Brian 1917, 1921), Palagruža in Croatia (Steuer 1912), Chesapeake Bay (Wilson 1932a) and Cuttyhunk Island, Massachusetts (Wilson 1932b), of *Microthalestris forficula* from Banyuls-sur-Mer (Monard 1928), and of *Thalestris forficula* from New Zealand (Thomson 1883) and Ghana (Scott 1894a).

Lang (1936a) proposed a new subfamily Parastenheliinae within the Thalestridae and fixed *Parastenhelia* as its type and only genus. Contrary to his earlier opinion (Lang 1934: 24) he accepted the conspecificity of Claus's (1863) *T. forficula* and Sars's (1905) *M. forficula*, and assigned the previous records of *T. forficula* from Lille-Karajak fjord, western Greenland (Vanhöffen 1897) and of *M. forficula* from Woods Hole (Wilson 1932b) to *Parastenhelia forficula*. He maintained Sars's (1911) *M. littoralis* as a variety of *P. forficula*, made *Dactylopus longipes* a synonym of this species, but surprisingly made no mention of Fischer's (1860) *Harpacticus spinosus*. The two females of *P. gracilis* he reported from the Falkand Islands are here assigned to *P. antarctica* (see below).

Monard (1937: 59, 62, Fig. 3–E) collected material from Algiers and Bou Ismail (formerly Castiglione) in Algeria and assigned it to *P. forficula littoralis*. He figured the male P5 exopod as 1-segmented bearing a total of seven elements and based on his previous observations (Monard 1928, 1935a) prudently postulated that this character may be dimorphic among males.

In his review of the genus *Parastenhelia* Sewell (1940: 189–196) reassessed the great degree of reported variability in antennule segmentation, armature of P2–P4, segmentation of male P5 exopod, and shape of terminal caudal ramus setae. He forcefully opposed the views of Lang (1934, 1936a, 1936b) and Monard (1935b, 1937) for uncritically accepting the synonymy of *T. forficula*, *T. forficuloides* and *M. littoralis*, claiming that these authors and others before them had been dealing with a mixture of species. Sewell (1940) reinstated the latter two as valid species of *Parastenhelia* and maintained Willey's (1935) penicillate variety as a distinct form of *P. littoralis*. His material from seaweed washings in Addu Atoll, the southernmost atoll of the Maldives, revealed three different forms which he attributed to *P. littoralis*, *P. littoralis* f. *penicillata*, and a new form, *P. littoralis* f. *scotti*. Sewell's *P. littoralis* material (his Text-Fig. 26) is characterized by the following features: (a) body length 440–560 µm (♀), unknown (♂); (b) antennule ♀ 9-segmented; (c) antennary endopod with two penicillate spines; (d) P1 enp-1 very long, about 1.45 times length of exopod; enp-2 with two penicillate claws; exp-3 with three penicillate elements and one long seta; (e) P3 endopod ♂ 3-segmented, with armature formula [1.1.02 + apo]; (f) P4 exp-1 without inner

seta and exp-3 with seven elements; endopod with inner seta on exp-1 and -2, and four elements on enp-3; (g) P5 exopod ♀ elongate, about 3.7 times as long as maximum width, with six setae; endopodal lobe with five setae; (h) P5 exopod ♂ 1-segmented, with seven setae; and (i) caudal ramus seta V unmodified or only slightly swollen at the base. Despite the absence of information about female antennular segmentation, antennary morphology and swimming leg armature in *M. littoralis*, it is still obvious that Sewell's (1940) specimens do not belong to this species; this is best illustrated by the morphology of the P1 and the length:width ratio of the ♀ P5 exopod. The absence of the inner seta on P1 exp-2 is most likely based on an observational error. It is puzzling why Sewell listed *T. forficula* sensu Thomson (1883) and *M. forficula* sensu Monard (1928) as misidentified records of *P. littoralis* since both sets of specimens are significantly divergent from Sars's (1905) description.

Sewell's (1940: Text-Fig. 27) second form, based on females only and assigned to *P. littoralis* f. *penicillata*, is characterized by the following features: (a) body length 600 µm (♀), unknown (♂); (b) antennule ♀ 8-segmented; (c) antennary endopod with two penicillate spines; (d) P1 enp-1 long, about 1.15 times length of exopod; enp-2 with two penicillate claws; exp-3 with two pinnate claws and two (?) setae; (e) P2–P3 exp-3 with six and seven setae/spines, respectively, P2 exp-1 without inner seta; (f) P2–P4 enp-3 with four, five and five elements, respectively; (g) P5 exopod ♀ elongate, about three times as long as maximum width, with six setae; endopodal lobe with five setae; and (h) caudal ramus setae IV–V markedly swollen at the base (occasionally less pronounced in seta IV). According to Sewell (1940) there is no doubt that his material is identical to Willey's (1935) specimens from Bermuda but a comprehensive comparison is hampered by the lack of information on (a) relative segment lengths of P1, armature of P2, and setation and length:width ratio of the female P5 exopod in the Bermudian material, and (b) armature of P4 exopod, sexual dimorphism in P4 enp-3 setal pattern, and both segmentation and armature of the male P5 exopod in the Maldivian specimens. It is unclear whether the absence of the thin, outwardly curved, distal inner seta on P3 (and possibly P4) exp-3 in Sewell's (1940: Text-Fig. 27–I) specimens is genuine or due to an observational error; a minute notch along the distal portion of the inner margin appears to hint at its presence.

The final form, based on a single female (Text-Fig. 28), was described as a new variety, forma *scotti*, of *P. littoralis*. It is characterized by the following features: (a) body length 560 µm; (b) antennule 8-segmented; (c) antennary endopod without penicillate spines; (d) P1 enp-1 very long, about 1.33 times length of exopod and twice as long as exp-2; enp-2 with two pinnate claws; exp-3 with three claws and one seta; (e) P5 exopod large (reaching to middle of third abdominal somite), elongate-oval, about three times as long as maximum width (measured in proximal 1/3), with six setae all inserting in distal one-third; endopodal lobe with five setae; and (f) caudal ramus very broad (about 4.5 times as wide as long), seta V forming pyriform swelling at the base. Sewell (1940) considered this form identical with Scott's (1894a) ovigerous female of *T. forficula* from Ghana, primarily on account of the general shape of the P5 exopod and the modification of caudal seta V. Although both females are strikingly similar in these two characters and Sewell dismissed the absence of the proximal inner seta on the P5 endopodal lobe in Scott's specimen as an observational error, others demonstrate that they are clearly different. Such features are particularly related to the P1 (relative lengths of rami, armature of exp-3) and P5 (length:width ratio, size relative to urosome, position and length of setae). A comparison of the swimming legs is impossible since only the P4 was figured by Scott (1894a: Plate XII, Fig. 39) and no information was given by Sewell (1940) other than that they "... appear to resemble those of *P. littoralis*".

Lang (1944: 13) invalidly fixed *Harpacticus spinosus* as the type species of *Parastenhelia*.

Nicholls (1945: 3–4, Text fig. 2A–B) illustrated two forms of *P. forficula* from the reef fringing Leander Point at Port Denison near Dongarra in Western Australia. Both forms differ considerably in the shape of caudal ramus setae IV–V, P1 and female P5. Adopting the view of both Monard (1928) and Lang (1934, 1936a, 1936b) he considered *M. littoralis* a variety of *P. forficula*. Three females (720 µm), which were assigned to the "typical" form of *P. forficula*, display (a) distinctly basally swollen caudal setae IV–V, (b) a P1 in which exp-2 and enp-1 are extremely elongate, being much longer than in Sars's (1905) material from Norway, and (c) a P5 which is ovate in shape and shows the 6-element arrangement typical of *P. littoralis* instead of the eight setae/spines in typical *P. forficula*. Nicholls (1945: 4) himself regarded the identification of his material as provisional, suggesting it may represent a new species. The second form, described as *P. forficula* var. *littoralis* (♀♀: 630–670 µm.; ♂: 540 µm), exhibits unmodified caudal setae IV–V. Females differ slightly from Sars's (1911) description of *M. littoralis* in (a) the proportionally longer P1 exp-2 and enp-1, and (b) the P5 endopodal lobe which is narrower and less truncate. Nicholls (1945) claimed that the male P5 (1-segmented with seven elements) did not conform with the descriptions of Sars and Lang but this statement cannot be substantiated since Sars (1911) did not describe the male and Lang's (1934: Fig. 56) illustration of the P5 refers to a different species (see below).

Having previously claimed that *Harpacticus spinosus* was indeterminable (Lang 1936a: 21), Lang (1948: 311) stated that “Fischer’s illustrations of this species clearly show that it is the same species that Claus described as *Thalestris forficula* and which Lang (1934) subsequently placed in the genus *Parastenhelia*. That I make this identification without any reservation, is based on the fact that there is no other harpacticoid whose P1 and P5 are built in the way Fischer depicts” [our translation]. As a result of Lang’s groundless reinstatement of *H. spinosus* as a valid species it not only became the senior synonym of a whole string of species and forms previously considered as conspecific with *M. forficula* and *M. littoralis* but was also unjustly designated as the type species (*P. spinosa*) of *Parastenhelia*. Lang (1948) assembled arguments in favour of his very broad concept of *P. spinosa*, including all the species, forms and varieties that in the course of time had been described and he considered conspecific – mostly on dubious grounds. These include *Thalestris forficula*, *T. forficuloides*, *T. karmensis*, *T. pectinimana*, *Dactylopus longipes*, *Microthalestris littoralis* and *M. littoralis* f. *penicillata*. With regard to the latter Lang (1948: 586) stated emphatically that comparison with Fischer’s (1860) description of *Harpacticus spinosus* shows beyond doubt that both forms are identical. Since Fischer only illustrated, and quite inadequately, the maxilliped, P1, female P5 and the caudal ramus, it is inexplicable how Lang could have arrived at this conclusion because none of these appendages (except for the caudal ramus) was figured or described by Willey (1935). Given that Fischer’s (1860) illustrations do not inspire confidence in their accuracy it would not be extraordinary to state that there is no tangible evidence for synonymizing any of the other species/forms mentioned above with *H. spinosus*. Lang (1948: 586) suggests in his review that *M. forficula*, *M. littoralis* and *M. littoralis* f. *penicillata* should be regarded as three forms (forma *typica*, forma *littoralis* and forma *penicillata*, respectively) of *P. spinosa*, which however are not geographically or ecologically distinct. Separation of these forms was based on the shape and/or modification of caudal ramus setae IV–V, number of segments in the female antennule, presence/absence of penicillate spines on the antennary endopod, shape and ornamentation of the distal claws on P1 enp-2, number of setae on P3–P4 exp-3, P4 enp-3 (in both sexes where known) and P5 exopod ♀, and segmentation of P5 exopod ♂. Rather than exploring the possibility that *P. spinosa* may represent a species complex Lang claimed that it is impossible to keep the three forms distinct because a number of intermediate forms are known to exist and the combination of characters varies in every conceivable manner. Lang (1948: 587) underpinned his claim by shoehorning into *P. spinosa* every form and variety from geographically disparate locations such as Campbell Island (Lang 1934), the Woods Hole region (Wilson 1932b), Gulf of Guinea (Scott 1894a), Brittany (Monard 1935a), the Banyuls area (Monard 1928) and the Gullmar Fjord in Sweden (Lang 1948), irrespective of the morphological variation reported. Since Lang failed to recognize sibling species boundaries, which negatively affects studies on biodiversity, speciation and ecology, his attempt to present a unifying, deliberately broad, taxonomic concept of *P. spinosa* should be seen as an exercise in futility. Unfortunately, most subsequent workers have uncritically adopted this concept and even attempted to expand it (e.g. Vervoort 1964) rather than subjecting it to scrutiny [Gee (2006) and Kuru & Karaytuğ (2014) are notable exceptions]. The species is now widely viewed as assuming an allegedly cosmopolitan distribution, covering all continents and including records from the Arctic (Vanhöffen 1897; Scott 1899; Scott & Scott 1901; Sars 1909; Brotskaya 1962; Mielke 1974; Chislenko 1967, 1977; Chertoprud *et al.* 2005; Kornev & Chertoprud 2008; Dvoretzky & Dvoretzky 2010) and remote islands such as Tristan da Cunha (Wiborg 1964) and Moce Island, Fiji (Wells 1978).

Lang’s (1948) view was not generally accepted by some Irish workers who continued to separate “populations” of *P. spinosa* into forms or even species. Williams (1954) recorded both *Microthalestris forficula* and *M. littoralis* from pools at Ardglass (the latter also from similar habitats at Kilclief) in Co. Down, Northern Ireland. Roe (1958) reported both *P. spinosa* var. *littoralis* and *P. spinosa* var. *penicillata* in intertidal pools around Dalkey Island and The Muglins (lighthouse), Co. Dublin, Ireland. Both forms were subsequently obtained from littoral stone and seaweed washings and net sweepings in Lough Hyne (Ine), West Cork, Ireland (Roe 1960).

Noodt (1955b: 204) suggested that Sewell’s (1940) *Parastenhelia littoralis* f. *scotti* probably falls within the boundaries of Lang’s concept of *P. spinosa*.

Božić (1955: 5, 11, Plate 4, Figs 1–3) described *P. spinosa* from Kernic, west of Roscoff, Brittany and illustrated the female caudal ramus, antennary exopod and mandibular palp. Females display a 9-segmented antennule and a P5 with six setae on the exopod and five on the endopodal lobe. Males have a 3-segmented P5 exopod bearing seven elements. Božić (1955) reported sexual dimorphism in the shape of caudal ramus seta IV, being distinctly swollen and bulb-shaped in the female and unmodified in the male. In both sexes the inner terminal seta V was more or less normal at the base. The material was accorded distinct specific rank by Gee (2006 – see below).

Șerban (1959) reported *P. spinosa* from Agigea along the Romanian Black Sea coast, stating that his specimens

approached Willey's (1935) *penicillata* form because of the 1-segmented exopod in the male P5, a condition he attributed to neotenic development rather than variability. It is not clear whether his material displayed the penicillate spines on the antenna and P1 endopod. Pór (1960) subsequently recorded *P. littoralis* from Eforie and Agigea and advocated that *P. spinosa* (which he regarded as conspecific with *Microthalestris forficula*) and *P. littoralis* are separate species.

Pesta (1959: 128–129; Figs 66–69) collected both sexes of *P. spinosa* from algal washings at Sorrento in the Bay of Naples, Italy. Illustrations were provided for the P1, the female P5 and abdomen, and the male P3. Pesta accepted Lang's (1948) concept of *P. spinosa*, being a variable species containing three ill-defined and overlapping forms, and stated that the females in his material displayed the P5 armature of f. *littoralis* and the basally swollen caudal ramus seta V of f. *typica*, and that one of the males resembled f. *penicillata* in the structure of the P3 endopod. The body size of the male was erroneously given as 4.4 mm (it is more likely 440 µm). Among all the records that have been attributed to *P. spinosa*, Pesta's is probably the one that is most similar to Claus's (1863) original from Messina. Apart from being the one that is geographically closest to the type locality in Sicily, the Neapolitan female agrees with the original description in the relative proportions of the P1 rami, the degree of modification of caudal ramus seta V and the ovate shape of the P5. Except for the male P3 Pesta (1959) does not provide any information about the armature of the remaining swimming legs or the segmentation and setation of the male P5.

In his first paper on the harpacticoids from the Isles of Scilly Wells (1961) reported finding populations of *P. spinosa* containing a mixture of f. *typica*, f. *littoralis* and many females which were identical with Božić's (1955) unnamed form characterized by the bulbous base of caudal ramus seta IV. The species was found on all four principal islands (St Mary's, Tresco, St Martin's and St Agnes). Wells (1963a: 14) subsequently found the bulbous form in clean sandy substrates at two sites in the estuary of the River Exe and formally proposed to name it *P. spinosa* forma *bulbosa*. A second form, *P. spinosa* forma *littoralis* was also recorded from one of the stations in the estuary. Gee (2006: 2634–2643, Figs 14–19) re-examined Wells's (1963a) forma *bulbosa* based on new material from the Isles of Scilly and accorded it full specific rank (as *P. bulbosa*). Both Bodin & Boucher (1983) and Bodin (1988) had previously recorded the taxon from Nord-Finistère (Brittany) as *P. spinosa bulbosa*. Since neither satisfied the criteria of availability (ICZN Arts 11–18) they cannot claim authorship for the subspecific name (ICZN Art. 45.5.1). Wells's (1970: 261) record of *P. spinosa* from Port Hellick on St Mary's was also confirmed to be conspecific with *P. bulbosa* (Gee 2006).

Vervoort (1964: 182) found that most of his Ifaluk material, although showing great variability in body length, agreed with Lang's (1948) forma *typica* of *P. spinosa* (formerly *M. forficula*). No illustrations were given but Vervoort stated that the females were characterized by a 9-segmented antennule, normally developed spines on the antennary endopod, P1 exp-2 (Vervoort erroneously referred to as the "2nd endopodal segment") 4–5 times as long as wide with an inner seta near the apex, P4 exp-3 with one inner seta, P5 exopod with eight elements, and a slightly basally swollen caudal ramus seta V. Males displayed a 3-segmented P5 exopod bearing six setae. One female and one male of a different form (from his locality 592), which he claimed would formerly have been assigned to Willey's (1935) forma *penicillata*, were described in considerable detail (Vervoort 1964: 182–184, Figs 64c, 66c, 67, 68d, 70a–g). The female (520 µm) exhibits a fairly long 8-segmented antennule, two penicillate spines on the antennary endopod, P1 exopod with two penicillate spines on exp-3 (note that Vervoort had misinterpreted this ramus as the endopod), basally swollen caudal ramus setae IV–V, and a P5 exopod with six elements. No information was provided about the female armature of P2–P4 or P5 endopodal lobe but Vervoort did illustrate the exopods of P2–P3 and the endopod of P3 of the male (420 µm). His material is assigned distinct species status below.

Bodin (1964: 128, Plate III, Fig. 15) recorded specimens of *P. spinosa* f. *penicillata* in high abundance in the Marseille region, southern France. Females display eight segments in the antennule but the proportional segment lengths are different from those reported by Monard (1928) and Sewell (1940). The only illustration given is that of the male P3 endopod which differs from Willey's (1935) account in the absence of the inner seta on exp-1.

Chislenko (1967: 140–144, Figs 45–46) provided illustrations of both sexes and an aberrant specimen of *P. spinosa* from the White Sea. His material (♀: 550–800 µm, ♂: 400–420 µm) shows some similarities with Sars's (1905) illustrations of *M. forficula* (e.g. 9-segmented antennule and eight elements on P5 exopod ♀) but differs in the length:width ratio of the female P5. The P1 has a similar exopod:endopod length ratio but the rami are significantly longer in the White Sea specimens. The males among Chislenko's material display the full complement of seven elements on the P5 exopod while the outer seta is absent on the proximal exopodal segment in the Scandinavian populations of *M. forficula* (Sars 1905; Lang 1936b). Considerable variability was observed in the degree of the

basal swelling of caudal ramus seta V, including left-right asymmetry in the same specimen. In one female individual the P5 exopod on one side only had seven instead of the typical eight setae but the taxonomic significance of this aberration was dismissed. Chislenko (1967) drew particular attention to the structure of the female genital field, pointing out that the condition in the White Sea material differed significantly from that of Lang's (1934: Fig. 51) illustration of the structure in his forma *littoralis* but was more similar to Claus's (1863: Plate XVII, Fig. 11) approximate representation of that in the *typica* form. He expressed a sceptical attitude towards the recognition of forms or varieties in *P. spinosa*, claiming instead that a proper comparative analysis of the female genital field of these infrasubspecific taxa would confirm their specific status.

Apostolov (1968: 398, Plate 2, Figs 1–10) reported both sexes of *P. spinosa* from a sandy beach in Tsarevo (formerly Michurin), Bulgaria, provided a partial description, and assigned them to a new form, f. *bulgarica*. The Black Sea specimens are characterized by unmodified caudal ramus setae IV–V, the absence of the inner seta on P2 exp-1 and enp-1, and the presence of seven setae on the ♀ P5 exopod. The male displays a 1-segmented P5 exopod with seven elements and a bisetose endopodal lobe which is distinctly larger than in any other reported population. Apostolov (1968) illustrated sexual dimorphism in the setation of the antennary exopod but did not comment on it in the text. In a later paper Apostolov (1973: 270, 272–273, Fig. 8) recorded additional specimens from Tsarevo and supplemented his original descriptions of the female with illustrations of the genital field, P1, P2, P4, P5 and caudal rami. The latter two differ in some aspects (e.g. P5 exopod with only six setae) from his 1968 drawings, rendering future morphological comparison difficult.

Mielke (1974: 20–22, Fig. 9) reported on *Parastenhelia* specimens he collected in the intertidal zone at Longyearbyen in Svalbard. He assigned the material to *P. spinosa*, stating that it could not be attributed to any of the forms recognized so far. Illustrations were presented of the antennary exopod and P1 of the female, and the P3 endopod and P5 of the male. The female (590 µm) is characterized by a 9-segmented antennule, normally developed caudal ramus setae, and eight and five setae on the exopod and endopodal lobe of the P5, respectively. Males (420–510 µm) possess a characteristic, acutely recurved, spinous apophysis on the P3 endopod. Some aberrations were recorded in the armature of P2 enp-2 (one or two inner setae) and P4 exp-1 (with or without inner seta).

Marinov (1974: 80–82, Figs 1–2) provided a description of *P. spinosa* specimens collected from algal washings at Sozopol on the southern Bulgarian Black Sea coast. Females display an 8-segmented antennule, six and five elements on the P5 exopod and endopodal lobe, respectively, and what appear to be unmodified caudal ramus setae IV–V. The distal endopod segment of P1 bears two pinnate (or penicillate) claws while enp-1 is excessively long, measuring 2.2 times the length of exp-2. The inner seta on P4 enp-1 is exceptionally long, extending beyond the distal tip of the endopod. The male shows the typical modification on the P3 endopod [1.1.02 + apo] and a 1-segmented P5 exopod with seven elements. Marinov (1974) reported some aberrant specimens that had a 1-segmented exopod in P3–P4, each carrying two apical elements, and observed a malformation in one male exopod which carried only six setae. Due to its dubious taxonomic status Apostolov's (1968) forma *bulgarica* was dismissed from further consideration.

Chislenko (1977: 246, Fig. 6–1,2) collected two females (675–700 µm) of *P. spinosa* from washings of the demosponge, *Semisuberites cribrosa* (Miklucho-Maclay, 1870), in Franz Josef Land. He maintained that his specimens were morphologically similar to the material he described from the White Sea (Chislenko 1967) which is confirmed by the two illustrations presenting the genital field and the P5 (with eight elements on the exopod).

According to Wells & Rao (1987) specimens (two ♀♀, one ♂) of *P. spinosa* from the Andaman Islands appear to be morphologically most similar to Sewell's (1940) forma *scotti*, with eight segments in the female antennule, non-pectinate spines on the antennary endopod and a relatively short P1 exopod. The exopod of the male P5 is 3-segmented with six setae.

Gee (2006) stated that the Langian concept of *P. spinosa* as a very variable, cosmopolitan species is probably erroneous and a thorough reappraisal of this species is required. He convincingly demonstrated that *P. spinosa* var. *bulbosa* must be accorded distinct specific status as *P. bulbosa* and argued that Willey's (1935) forma *penicillata* displays several characteristics warranting its elevation to species level.

Kornev & Chertoprud (2008: 196–197) provided an illustrated description of a White Sea population which they identified as *P. spinosa*. It appears that most of the text and at least some of the illustrations are a verbatim account of Chislenko's (1967) description, including the substantial variation recorded in female body length. The authors do not specify whether the observed variability in P3–P4 armature is based on their White Sea material or on previous literature reports.

Kuru & Karaytuğ (2015) added a new species, *P. aydini*, from the eastern Mediterranean and Aegean coasts of Turkey and considered it morphologically closest to *P. spinosa*. The species is unique in the family by displaying a 2-segmented P5 exopod with a total of five setae in the male (a 2-segmented condition with different armature has been observed in *Johnwellsia bipartita* **gen. et sp. nov.** and *Parastenhelia willemvervoorti* **sp. nov.**). According to Kuru & Karaytuğ (2015), females of *P. aydini* differ from those of *P. spinosa* by the 9-segmented antennule, the reduction of the spinular rows around the outer margins of the bases of P1–P4, the presence of only four elements on P4 enp-3, ornamentation of the P5 baseoendopod and exopodal setae different, and the normally developed caudal ramus seta V. Males differ in the absence of a modified element on the seventh segment of the antennule (apparently present in *P. spinosa*), the notched apophysis on P3 enp-3 and the presence of only four setae on P4 enp-3. It is not clear which material of *P. spinosa* the authors used as their reference for comparison.

Zaleha *et al.* (2018) provided a short text description of a single ovigerous female of *Parastenhelia* sp. from sediment in seagrass bed in Sungai Pulai, Johor, Malaysia. The antennule was described as 8-segmented and the 2-segmented P1 endopod as being much longer than the exopod. However, the armature of P2–P4 and the endopodal lobe of P5 is radically divergent from any other species in the genus, casting serious doubts on the validity of their identification. Zaleha *et al.* (2010) had previously identified *Parastenhelia littoralis* from rockpool seaweeds and sediment in Pulau Besar, Melaka.

Cordell (2018: 117–118, Fig. 5) found several *Parastenhelia* specimens on debris, generated from the earthquake and tsunami that struck Japan on 11 March 2011, that landed in North America. The species was recorded on floating structures (docks, vessels, buoys) in several localities along the coasts of Washington and Oregon. While Cordell assigned the material to *P. spinosa* he acknowledged that they may be a different species within a larger species complex. Photographs were provided of the P1 and female urosome, showing that the caudal ramus seta V is somewhat swollen near the base. Although this character was observed in every female, Cordell (2018) mentioned that specimens he had previously examined from the northeast Pacific had almost no swelling at the base of this seta.

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P3 endopod, P5–P6 and urosomal segmentation; occasionally endopods of P2 and P4, and caudal ramus setae IV–V. Body subcylindrical, short; posterior margin of urosomites (except anal somite) typically with denticulodigitate hyaline frills. Rostrum defined at base, of moderate size, reaching at most to distal margin of second antennular segment; linguiform. Anal operculum semicircular, typically bordered with fine spinules. Caudal ramus wider than long, without spinular row on dorsal surface; with at least seven setae (seta I possibly absent); setae IV and/or V slightly swollen at base in ♀; seta IV ♀ with bulbous base in some species (*M. bulbosa* **comb. nov.**).

Antennule ♀ elongate and 9-segmented in ♀, segment 1 not elongate, segments 7–8 (when 9-segmented) shortest, with aesthetascs on segments 4 and 8 or 9. Antennule ♂ haplocer with four segments distal to geniculation but segmentation and segmental homologies unconfirmed for most species; in *M. bulbosa* **comb. nov.** segment 5 swollen and with aesthetasc, segmental homologies as follows: I, II–VIII, IX–XII, XIII, XIV–XVII, XVIII, XIX–XX, XXI–XXII, XXIII, XXIV–XXV, XXVI–XXVIII. Antenna not sexually dimorphic; proximal endopodal segment largely separated from basis or forming allobasis, with pinnate seta on abexopodal margin; exopod 2-segmented, proximal segment with 1–2 seta(e), distal segment with 1–2 lateral and three apical elements; distal endopodal segment without penicillate elements. Mandible with 3–4 elements on basis; endopod with eight setae; exopod 1-segmented with 2–5 setae. Maxillulary coxal epipodite represented by one seta. Maxilla with three endites on syncoxa; endopod discrete, with 2–3 setae. Maxilliped with 2–3 setae on syncoxa; basis with two setae on palmar margin; endopod represented by curved claw, accompanied by up to three accessory seta(e).

P1 inner basal spine not sexually dimorphic. P1 exopod 3-segmented; exp-2 elongate, about 2–2.5 times length of exp-1 and between two-thirds and 80% length of endopod, with inner seta; exp-3 very small, typically with two pinnate spines, one geniculate seta or claw, and one non-geniculate seta. P1 endopod 2-segmented; enp-1 elongate, longer than exopod, with well developed inner seta originating either from near end of proximal quarter of segment or from middle third of segment, segment margins without area of reduced chitinization; enp-2 very small, with one naked minute seta and two dentate claws (or one of claws replaced by geniculate seta/spine). P2–P4 rami 3-segmented. P2 endopod ♂ typically 3-segmented and not modified; occasionally 2-segmented but with same total number of spines/setae as in ♀ (*M. costata* **comb. nov.**, *M. variabilis* **sp. nov.**). P3 endopod ♂ 3-segmented; without inner setae on enp-3 and outer spine modified into spinous apophysis. P4 endopod ♂ occasionally with one (*M.*

bulbosa **comb. nov.**) or two (*M. minuta* **comb. nov.**) less(er) inner seta(e) on enp-3. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	1.0–1.123	0–1.1.(0–1)2(0–1)
P3	0–1.0–1.(1–3)23	0–1.1.(1–3)21 [♂: 0–1.0–1.02 + apo]
P4	0–1.1.(1–3)23	1.1.(1–2)21

P5 ♀ endopodal lobe with five setae; inner margin without transverse striae. P5 ♀ exopod elongate, with six or eight elements. P5 ♂ endopodal lobe with two elements, outer one shortest; exopod 1- or 3-segmented, with 6–7 elements in total. Vestigial P6 ♀ represented by three minute setae. P6 ♂ with three setae.

Type species. *Thalestris forficula* Claus, 1863 = *Microthalestris forficula* (Claus, 1863) **comb. nov.** (by monotypy; Sars 1905: 123) [*species inquirenda*].

Other species. *Thalestris forficuloides* Scott & Scott, 1894 = *M. forficuloides* (Scott & Scott, 1894) **comb. nov.**; *Parastenhelia gracilis* Brady, 1910 = *M. gracilis* (Brady, 1910) **comb. nov.**; *M. littoralis* Sars, 1911; *Parastenhelia antarctica* Scott, 1912 = *M. antarctica* (Scott, 1912) **comb. nov.**; *Parastenhelia costata* Pallares, 1982 = *M. costata* (Pallares, 1982) **comb. nov.**; *Parastenhelia minuta* Pallares, 1982 = *M. minuta* (Pallares, 1982) **comb. nov.**; *Parastenhelia bulbosa* Gee, 2006 = *M. bulbosa* (Gee, 2006) **comb. nov.**; *M. campbelliensis* **sp. nov.**; *M. polaris* **sp. nov.**; *M. santacruzensis* **sp. nov.**; *M. sarsi* **sp. nov.**; *M. variabilis* **sp. nov.**

Additional species inquirendae. *Harpacticus spinosus* Fischer, 1860; *Parastenhelia spinosa* (Fischer, 1860) sensu Pesta (1959), sensu Marinov (1974), sensu Wells & Rao (1987) and sensu Kornev & Chertoprud (2008); *Parastenhelia spinosa* f. *bulgarica* Apostolov, 1968; *Microthalestris forficula* (Claus, 1863) sensu Wilson (1932b); *Microthalestris littoralis* Sars, 1911 sensu Willey (1935) and sensu Nicholls (1945).

Species incertae sedis. *Thalestris karmensis* Boeck, 1865; *Dactylopus longipes* Boeck, 1873.

Formal recognition of species within the “*Parastenhelia spinosa* complex”

Within the formerly recognized “*Parastenhelia spinosa* complex”, intra-population/specimen variability has been recorded in the number of antennular segments, armature of P3–P4 exp-3, number of setae on the female P5 exopod and, to a lesser extent, the modification of caudal ramus setae IV–V, however, our general perception is that these reports are based on single and probably aberrant specimens, often displaying left-right asymmetry, or on observational errors. No such variability has been observed in antennary endopod armature, the ratio of P1 enp-1:exp-2 and the segmentation of the male P5 exopod. Based on these and other characters we have identified “populations” that had previously been mislabeled as *P. spinosa* and accorded them specific rank where justified. Similarly, species that were unjustly relegated to junior subjective synonyms of *P. spinosa* are reinstated whenever there is sufficient morphological evidence for this course of action. Note that in the differential diagnoses below the lengths of exopodal and endopodal segments of P1 are measured along the outer margin.

Microthalestris spinosa (Fischer, 1860) **comb. nov.** and *M. forficula* (Claus, 1863) **comb. nov.**

The original descriptions of two species that had previously been designated, validly or invalidly, as a type species (Sars 1905: 123; Lang 1944: 13), cannot be used as the basis for their identification. Fischer’s (1860) description of *Harpacticus spinosus* is grossly inadequate and renders the identification of the species indeterminable. Pending the collection of material from Madeira it must be set aside as a *species inquirenda* in *Microthalestris* since it does not qualify as a reference for morphological comparison with populations of *Microthalestris* (or *Parastenhelia*) spp. that have subsequently been assigned to it. The various morphs of *P. spinosa* described by Pesta (1959), Wells & Rao (1987) and Kornev & Chertoprud (2008) as well as Apostolov’s (1968) forma *bulgarica* are indeterminable (see Table 1 for armature formulae of P1–P5).

The allegedly cosmopolitan distribution of *Microthalestris spinosa* **comb. nov.** is a direct result of the inadequacy

of the original description and the adoption of Lang's (1948) excessively broad concept of the species. The great majority of the records below are probably false or indeterminable:

Iceland: Bay of Faxaflói (Ólafsson *et al.* 2001); Seltjarnarnes (Steinarsdóttir *et al.* 2003); Hvasshraun (Steinarsdóttir & Ingólfsson 2004).

Norway: Fanafjorden, south of Bergen (Dommasnes 1969).

Sweden: Øresund (Dahl 1948); Gullmarfjord (Lang, 1948); northern Øresund (Hagerman 1966).

Germany: Kiel Bay (Klie 1949; Anger & Scheibel 1976).

Scotland: St. Abbs (Moore 1973, 1974; Hicks 1980); Firth of Forth (Shiells 1983); Great Cumbrae Island (Preston & Moore 1988, 1990).

England: Wembury (Colman 1940) and Plymouth Sound (Wieser 1952) in Devon; Isles of Scilly (Wells 1961, 1970); Northumberland (Moore 1973, 1974).

Wales: Pembrokeshire (Crothers 1966); Anglesey and Menai Strait (Geddes 1972); north Wales (Lintas & Seed 1994); Holyhead Island (Jarvis & Seed 1996).

Isle of Man (Moore 1932; Bruce *et al.* 1963).

France: Bassin d'Arcachon (Renaud-Debyser 1963a, 1963b); Nord-Finistère (Brittany) (Le Guellec 1988).

Spain: Canary Islands, Tenerife (Noodt 1955b); River Ebro estuary (Sabater 1986).

Portugal: Azores (Chapman 1955; Chapman & Santler 1955).

Italy: Sorrento (Pesta 1959); Laguna di Lesina (Ceccherelli & Mistri 1990); Valle Smarlacca, northern Adriatic (Cristoni *et al.* 2004).

Montenegro: Budva (Petkovski 1955).

Romania: Agigea (Pintea & Klemens 1957; Şerban 1959).

Bulgaria: Gulf of Varna and Sozopol (Caspers 1951); Sozopol (Marinov 1974).

Black Sea (Sergeeva 2003).

Turkey: Datça-Bozburun Peninsulas, Muğla (Alper 2009; Alper *et al.* 2010); Dilek Peninsula, Aydın (Alper *et al.* 2015); Çatal and Kara Islands of Bodrum (Yıldız & Karaytuğ 2018).

Israel: Achziv, Caesarea (= Keisarya or Qaysaria) and Palamachim (Por 1964).

Russia: Kandalaksha Bay, White Sea (Kornev & Chertoprud 2008); Barents Sea (Dvoretzky & Dvoretzky 2010); Sea of Okhotsk (Chertoprud *et al.* 2015).

Mozambique: Inhaca Island (Wells 1967).

Andaman and Nicobar Islands: Aberdeen (Port Blair) and Mayabandar (Wells & Rao 1987); South Andaman (Jayabarathi 2016 – as *P. spinosa spinosa*).

China: South China Sea (Chertoprud *et al.* 2009).

Australia: Port Phillip Bay, Victoria (Walker-Smith 2003).

New Zealand: Island Bay, Wellington (Coull & Wells 1983); undisclosed locality (Webber *et al.* 2010).

Fiji: Moce Island (Wells 1978).

Bermuda: Baileys Bay and Trunk Island (Coull 1970b; Coull & Herman 1970).

Tristan da Cunha (Wiborg 1964).

Canada: Nanaimo Estuary (Kask *et al.* 1982); Lower Prospect, Nova Scotia (Johnson & Scheibling 1986, 1987a, 1987b).

U.S.A.: North Carolina continental shelf (Coull 1971b); central and northern California (Watkins 1983); Port Valdez, Prince William Sound (Cordell 2000; Hines & Ruiz 2001) and Kachemak Bay, Cook Inlet (Ruiz *et al.* 2006) in Alaska; Puget Sound (Haas *et al.* 2002), Elliot Bay (Toft & Cordell 2006; Toft *et al.* 2010), Crescent Bay and Freshwater Bay (Shaffer *et al.* 2020) in Washington State; recorded on Japanese tsunami-driven marine debris along west coast of North America from Alaska to California (Carlton *et al.* 2013, 2017; Cordell 2018; Gillman 2018; Miller *et al.* 2018).

Brazil: Porto de Galinhas (Sarmiento *et al.* 2009; Sarmiento & Santos 2012a, 2012b; Barroso *et al.* 2018) and Serrambi, Tamandaré, Rio Doce, Piedade and Paiva (Barroso *et al.* 2018) in Pernambuco State; Arraial do Cabo, Rio de Janeiro State (Sarmiento *et al.* 2012).

Similarly, Claus's (1863) description of *Thalestris forficula* is so inadequate that it is only recognizable as a *Microthalestris* by a figure of the P1. Although it should be classified as a species of doubtful identity needing further investigation (*species inquirenda*) and – as a designated type species – will not best serve stability and universality, this does not of itself invalidate Sars's (1905) type fixation. The following records of *Microthalestris*

forficula are considered indeterminable:

Iceland: Seydisfjord (Jespersen 1940; Klie 1941 – both as *Parastenhelia forficula*).

Faroe Islands: off Suðuroy and between Streymoy and Eysturoy (Stephensen 1929).

Northern Ireland: Ardglass, Co. Down (Williams 1954).

Germany: Kiel Bay (Klie 1929; Kunz 1935).

Scotland: Fairlie and Hunterston in the Firth of Clyde (Scott 1900 – as *Thalestris forficulus*); between Leith and Portobello, Firth of Forth (Scott 1906).

England: Plymouth region, Devon (Norman & Scott 1906; Marine Biological Association 1931, 1957).

Isle of Man: Port Erin and Port St Mary (Fraser (1936).

France: Roscoff, Brittany (Monard 1935a; Jakubisiak 1936).

Italy: Venice Lagoon (Grandori 1912, 1914; Pesta (1920).

Tunisia: Cartaghe (Salammbô) (Monard (1935b – as *Parastenhelia forficula*).

U.S.A.: Gulf of Maine (north of Georges Bank) (Bigelow 1926); Woods Hole (Wilson 1932b).

Australia: Port Denison, Western Australia (Nicholls 1945 – as *Parastenhelia forficula*).

New Zealand: Otago Harbour (Brady 1899 – as *Thalestris forficula*).

***Microthalestris forficuloides* (Scott & Scott, 1894) comb. nov.**

Thalestris forficuloides Scott & Scott, 1894

Scott & Scott (1894: 143) compared *T. forficuloides* with *T. forficula* and stated that both species are closely related but differed in the segmentation of the female antennule (9- vs 8-segmented), the proportional lengths of the antennular segments, and the relative size of the rami of P1. However, their claim (see also Scott 1894b: 256) that the two species also differed in the proportional length of the other swimming legs is unfounded since Claus (1863) neither described nor illustrated P2–P4. Sewell's (1940: 189) statement that the P4 has an additional seta on exp-3 and enp-3 in *T. forficuloides* is also incorrect. Comparison shows that the proportional length (relative to exp-1) of P1 enp-1 is virtually identical in both species but that the size of exp-2 is dissimilar (exp-1:exp-2 1.5 in *T. forficula* vs 2.2 in *T. forficuloides*). Differences can also be observed in the male antennule which is uncharacteristically elongate and slender in *T. forficula* (Claus 1863: Plate XVII, Fig. 9). Both species are similar in the morphology of caudal ramus seta V which displays a slight basal swelling posterior to the fracture plane. Based on the differences listed above, *T. forficuloides* is reinstated here as a valid species under the new combination *Microthalestris forficuloides* **comb. nov.**

Original description. Scott & Scott (1894): 142–144, 149; Plate IX, figs 4–9.

Additional description. Scott (1894b): 255–256; Plate X, figs 13–25.

Type locality. Scotland, Firth of Forth; mud near low-water mark at Seafield, in the vicinity of Leith.

Differential diagnosis. *Microthalestris*. Body length 730 µm in ♀, smaller in ♂. Antenna with 2-segmented exopod bearing one seta on exp-1 and two lateral and three apical elements on exp-2. P1 exopod about two-thirds length of endopod; exp-2 elongate, about twice as long as exp-1, and about 45% length of enp-1; insertion point of inner seta of enp-1 at 25% of inner margin length; exp-3 with two unipinnate spines and two geniculate setae; enp-2 with one minute seta, one geniculate seta and one geniculate claw. Armature pattern of ♀ P2–P4:

	exopod	endopod
P2	unknown	unknown
P3	0.1.323	unknown
P4	0.1.223	1.1.121

P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ with elongate exopod (about 2.4 times as long as maximum width), inner margin and proximal half of outer margin straight, with eight elements, proximal outer one long, outer apical one short; endopodal lobe with five elements, innermost one short. P5 ♂ exopod 1-segmented, with seven elements; endopodal lobe with two elements, outer one shortest. Armature of P6 ♂ unconfirmed. Caudal ramus seta V with slightly swollen proximal part.

Notes. Unconfirmed records of *M. forficuloides* include Inveraray and near Largabruach in Loch Fyne, Scotland by Scott (1897), Holy Island in Northumberland, England by Brady (1904) and Norman & Brady (1909 – as *M. forficula*) and the Isle of Man by Herdman (1897 – as *Thalestris forficuloides*).

Scott (1899) recorded *T. forficula* (= probably *Microthalestris polaris* **sp. nov.**; see below) dredged at 55 m depth off Cape Gertrude in Franz Josef Land and added, with a slight inclination, that *T. forficuloides* is probably to be regarded as merely a local form of the latter. This view was reiterated in a later paper reporting on the presence of the species (as “*T. forficulus*”) in Fairlie and Hunterston in the Firth of Clyde (Scott 1900). Scott (1906), accepting Sars’s (1905) synonymy, reported the species (as *M. forficula*) from pools near low-water between Leith and Portobello in the Firth of Forth but it is likely that his record referred to *T. forficuloides*. Norman & Scott (1906) recorded *M. forficula* from rock-pools at and above the high-water mark in Plymouth, Devon, listing *T. forficuloides* as a synonym, but the identity of this record remains indeterminable.

***Microthalestris littoralis* Sars, 1911**

Comparison of the various reports dealing with *M. littoralis* reveals the true state of confusion reigning in the genus. In Norway the species shows virtually the same distribution as *M. sarsi* **sp. nov.**, extending from the south coast northwards to the Trondhjem Fjord (Sars 1911). Several authors have reported on the sympatric occurrence of *M. littoralis* with other species but in the great majority of the cases the authenticity of the former is rendered doubtful by the absence of an adequate description or a definite statement of authority for the identification. For example, according to Wells (1961) three forms of *P. spinosa* (*typica*, *littoralis*, *bulbosa*) occur sympatrically in the Isles of Scilly while the latter two also coexist in the River Exe estuary (Wells 1963a). Both Monard (1935a) and Jakubisiak (1936) found that *M. littoralis* and *M. forficula* are sympatric in the Roscoff region in Brittany while Wilson (1932b) recorded both species from the Woods Hole region. Farran (1913) documented significant variation in female body size (500–850 µm) in his material of *M. littoralis* from Clare Island and Blacksod Bay in Ireland which he perceived as a possible indication of the presence of a second species. Lang’s (1934, 1936b, 1948) failure to recognize the sympatric occurrence of *Microthalestris* species and his subsequent proposal of an all-encompassing, highly variable species concept of *P. spinosa* are the primary reasons why most published records of both *M. littoralis* and *M. sarsi* **sp. nov.** cannot be accepted as accurate. Although most workers accepted Lang’s views and perpetuated the myth of a cosmopolitan morphologically plastic species, others advocated that *M. littoralis* deserved distinct species status (e.g. Willey 1935; Jakubisiak 1936; Sewell 1940; Nicholls 1945; Roe 1958, 1960; Pór 1960). Sars (1911) claimed that *M. littoralis* differed from his *M. forficula* (= *M. sarsi* **sp. nov.**) in the more compact antennule, the longer and more slender P1, the number of exopodal setae on the P5 (six vs eight) and the normally developed seta V on the caudal rami. Although the species was recorded from virtually all around the Norwegian coastline, no males were discovered by Sars (1911). Despite the absence of information on the armature formula of P2–P4, *M. littoralis* is reinstated here based on the differences listed above. The only reliable records of the species are those by Sars (1911).

Several authors have provided concise illustrated descriptions of what they believed to be *M. littoralis*. Brian’s (1921: 77–80) description of *M. littoralis* from the Gulf of Genoa included detailed illustrations of various developmental instars (naupliar stages I, III–V and copepodids III–V) while his descriptions of the adults are unfortunately not of a comparable standard. Little useful information is revealed about the morphology of the female except for the presence of a single egg sac and the normally developed caudal ramus seta V. The armature formula of P1–P5 is completely unknown although Brian (1921: 78) does mention that the distal endopodal segment of P3 has one spine and three plumose setae (“... una gracile spina e tre setole piumate...”). His description of the male shows the typical sexual dimorphism on the P3 endopod (bearing an inner seta on enp-1 and -2, and an apophysis and two apical setae on enp-3), and the 1-segmented condition of the male P5 exopod (bearing seven setae). The presence of two penicillate spines on the antenna (already expressed in copepodid IV: his Plate VIII, Fig. 17) provides evidence that Brian’s (1921) material does not belong to *Microthalestris*, representing instead a member of *Penicillicaris* **gen. nov.** (see below). Given its geographical proximity it may be conspecific with Car’s (1884) *Thalestris pectinimana*.

Wilson (1932b: 205) recorded ten females from Cuttyhunk Harbor, Massachusetts which he identified as *M. littoralis*. Unfortunately, the only drawings of the habitus in dorsal aspect and the P5 are adapted from Sars (1911), making it impossible to decide on the identity of his material. Lang’s (1934) illustrated record of *P. forficula* var.

littoralis from Campbell Island differs from *M. littoralis* in the morphology of the P1, female P5 and caudal ramus seta V and is here renamed as *M. campbelliensis* **sp. nov.** (see below).

Wiley (1935: 82–83) recorded one ovigerous female from Harrington Sound in Bermuda which according to the author agreed with Sars's (1911) description of *M. littoralis* in displaying 9-segmented antennules (although the segmentation was not disclosed by Sars) and unmodified caudal ramus setae. Much of Wiley's discussion centres around morphological differences in the antenna and swimming legs encountered between this "typical" specimen and his more abundant, sympatric, forma *penicillata*. The latter is here upgraded to species level and fixed as the type of *Penicillicaris* **gen. nov.** (see below) while the former is considered indeterminable based on the limited information presented by Wiley.

Monard's (1937: 59, 62, Fig. 3–E) description of *P. forficula littoralis* from Algeria, presenting a single illustration of the male P5 exopod, does not contain the bare minimum required for any meaningful statement on its identity.

Sewell (1940: 191–196) distinguished three different forms in his material of *Parastenhelia littoralis* obtained from seaweed washings in Addu Atoll, Maldives. The typical form, which he considered identical with Sars's (1911) *M. littoralis*, shows distinct differences with the original description in the female antennule, P1 and P5, unambiguously ruling out such conspecificity. The presence of penicillate spines on the antennary endopod and on exp-3 and enp-2 of P1 indicates that Sewell's (1940) material represents a member of *Penicillicaris* **gen. nov.** (see below). Given their morphological disparity, we cannot concur with the author that both *Thalestris forficula* sensu Thomson (1883) and *M. forficula* sensu Monard (1928) are misidentified records of *M. littoralis*.

Nicholls (1945: 4) provided illustrations of both sexes of *Parastenhelia forficula* var. *littoralis* from Port Denison in Western Australia. Females differ slightly from Sars's (1911) description of *M. littoralis* in (a) the proportionally longer P1 exp-2 and enp-1, and (b) the P5 endopodal lobe which is narrower and less truncate. Pending information on the antennule, antenna and swimming legs in both forms and on the male of *M. littoralis*, the Australian population is provisionally regarded as distinct from the Norwegian one.

Original description. Sars (1911): 369–370, Supplement plate 11, Fig. 1.

Type locality. Sars (1905) recorded material from several places on the south and west coasts of Norway, and in the Trondhjem Fjord. Since he did not specify which specimens the illustrations were based on, the type locality encompasses all of their respective places of origin (ICZN Art. 73.2.3).

Differential diagnosis. *Microthalestris*. Body length 600 µm in ♀, unknown for ♂. Antennule segmentation and antenna unconfirmed. P1 exopod about 80% length of endopod; exp-2 elongate, about twice as long as exp-1, and about half as long as enp-1; insertion point of inner seta of enp-1 at 25% of inner margin length; exp-3 with two unipinnate spines and two geniculate setae; enp-2 with one minute seta, one geniculate seta and one geniculate claw. Armature pattern of ♀ P2–P4 and ♂ P3 endopod unknown. P5 ♀ with elongate exopod (about three times as long as maximum width), inner margin and proximal two-thirds of outer margin straight, with six elements; endopodal lobe with five elements, innermost one short. P5–P6 ♂ unconfirmed. Caudal ramus seta V normally developed.

Notes. Most records of *M. littoralis* (either as a distinct species or as a form of *Parastenhelia forficula* or *P. spinosa*) are not accompanied by a description and must therefore remain indeterminable:

Sweden: Øresund (Lang 1936b – as *Parastenhelia forficula* var. *littoralis*).

Ireland: Clew Bay and Blacksod Bay, Co. Mayo (Farran 1913; Farran *et al.* 1915); Clare Island (Southern 1915); Dalkey Island and The Muggins, Co. Dublin (Roe 1958 – as *Parastenhelia spinosa* var. *littoralis*); Lough Hyne (Ine), Co. Cork (Roe 1960 – as *P. spinosa* var. *littoralis*).

Northern Ireland: Ardglass and Kilclief, Co. Down (Williams 1954).

England: Isles of Scilly (Wells 1961 – as *P. spinosa* forma *littoralis*); River Exe (Wells 1963a – as *P. spinosa* forma *littoralis*).

France: Roscoff, Brittany (Monard 1935a; Jakubisiak 1936).

Italy: Gulf of Genoa Brian (1917, 1921); Sardinia (Brian 1923a).

Croatia: Palagruža (Steuer (1912); Rovinj (Brian 1923b; Vátova 1928); Island of Šolta (Jakubisiak 1933).

Greece: Dodecanese Islands (Brian 1928a); Rhodes, Astypalaia, Tilos, Symi, Kos, Karpathos (Brian 1928b).

Algeria: Îlot de la Marine (Amirauté) and Bab-el-Oued (Monard 1936 – as *Parastenhelia* (*Microthalestris*) *forficula littoralis*); Algiers and Bou Ismaïl (Castiglione) (Monard 1937 – as *P. forficula littoralis*).

Ukraine: Yalta, Crimean Peninsula (Marcus & Pór 1960 – as *Parastenhelia littoralis*).

Bermuda: Harrington Sound (Wiley 1935).

U.S.A.: Chesapeake Bay (Wilson (1932a); Cuttyhunk Island (Wilson (1932b)).

India: Porites Bay off Krusadai Island, Tamil Nadu (Krishnaswamy 1957); Visakhapatnam coast (Sarma 1974a, 1974b, 1974c; Krishna Murty 1983) and Visakhapatnam Harbour (Sarma & Ganapati 1975) in Andhra Pradesh (all as *Parastenhelia littoralis*).

Andaman and Nicobar Islands: South Andaman (Jayabarathi 2016 – as *Parastenhelia spinosa littoralis*).

Malaysia: Peninsular Malaysia (Zaleha *et al.* 2010 – as *Parastenhelia littoralis*); Straits of Johor (Mahadi *et al.* 2014).

Australia: Port Denison, Western Australia (Nicholls 1945 – as *Parastenhelia forficula littoralis*).

***Microthalestris sarsi* sp. nov.**

urn:lsid:zoobank.org:act:23B221A4-6328-4AA6-9563-1344D0C0FBE1

Microthalestris forficula (Claus, 1863) *sensu* Sars (1905)

Parastenhelia spinosa (Fischer, 1860) *forma typica* [*sensu* Lang (1948)]

Although Lang (1934: 24) cursorily disputed the conspecificity of Sars's Norwegian and Claus's mediterranean material of *M. forficula*, he did not elaborate on the issue in later contributions that promoted his all-embracing concept of "*Parastenhelia spinosa*". Claus's description is of limited value for morphological comparison but illustrates two characters of significance ruling out conspecificity with the Nordic population, *i.e.* the segmentation of the female antennule and the proportional lengths of the rami of P1. Females of the type population display 8-segmented antennules whereas the Norwegian specimens have an additional segment. The rami of P1 are distinctly more elongate in the mediterranean material with exp-2 being 3.1 times as long as exp-1 (*vs* 2.1 in the Norwegian specimens) and about 80% the length of enp-1 (*vs* about 60%).

Sars (1905) treated *Thalestris karmensis* and *T. forficuloides* as synonyms of *M. forficula* but did not provide any justification. Although Sars and Boeck were contemporaries in the early stages of their careers it is unlikely that the former had the opportunity to examine Boeck's material of *T. karmensis* thirty years after his untimely death in 1873. Boeck (1865) did not present any illustrations and the essence of his concise description translates as follows: "The body is elongated, but the cephalothorax is somewhat inflated. The abdomen is short and wide, with rows of spinules around the posterior margin of the two middle somites. The caudal rami are wider than long. The antennules are short, with the second segment being about as long as the following two segments combined. The bases of the maxillipeds are oval and their claws very long. The first pair of swimming legs are elongated, with the endopod bearing a short seta at the end of the proximal quarter of the inner margin. The P1 exopod is shorter than the endopod; the middle segment has spinules along the outer margin, and a longer spine near its distal corner; the claws on exp-3 are very strong and several times longer than the segment. The oval exopod of P5 is longer than the endopodal lobe." Based on Boeck's (1865) description no positive statement can be made as to the validity of *T. karmensis* or its relationship to other parastenheliids. The little information that is given raises grave doubts that it belongs to *Microthalestris* at all or that it is a member of the Parastenheliidae. The species must be redescribed and pending this it is considered here as *species incertae sedis* in *Microthalestris*.

Microthalestris forficuloides is similar to Sars's material in P1 exopod/endopod length ratio, the position of the inner seta on P1 enp-1, the absence of the inner seta on P4 exp-1, the presence of only one inner seta on P4 exp-3, the maximum number of eight elements on the female P5 exopod, and the slightly swollen proximal part of caudal ramus seta V in the female, however, differs from it in the following suite of characters: (a) antennary exopod has one lateral seta on exp-1 and two lateral setae on exp-2 (*vs* two and one, respectively), (b) P3 exp-1 lacks the inner seta, (c) P3 exp-3 has three inner setae (*vs* two), (d) the female exopod is shorter (2.4 *vs* 2.8 times as long as maximum width), (e) the male exopod is 1-segmented (*vs* 3-segmented), and (f) the larger body size (♀♀: 730 µm *vs* 580 µm). On the basis of these morphological discrepancies, the previously suggested conspecificity with *M. forficuloides* can be ruled out and, consequently, Sars's (1905) form is here attributed distinct specific rank as *M. sarsi* sp. nov.

Lang (1948: 586) summarized earlier records attributed to *Parastenhelia spinosa* and stated that three forms of the species had been reported in the literature, *forma typica*, *forma littoralis* (for *Microthalestris littoralis*), and *forma penicillata* (for *M. littoralis* var. *penicillata* Willey, 1935). Although the diagnosis of his *forma typica* is clearly based on Sars's material of *M. forficula* (and not Claus's original description of the species), it is clear from

the contents of his work that he did not intend to propose it as new (in which case “*M. typica*” would have become an available and the valid name for Sars’s material). Lang (1948: 587) unambiguously revealed that the three forms had no taxonomic meaning by stating that “In Wirklichkeit is es unmöglich, die 3 Formen auseinanderzuhalten, den eine Menge Zwischenformen sind vorhanden, und die Merkmalkombinationen variieren in jeder denkbaren Weise”. Although the forma *typica* could be construed as a name proposed for an infrasubspecific entity, it remains unavailable since it was not adopted for a species or subspecies before 1985 (ICZN Art. 45.6).

Original description. Sars (1905): 123–124, Plate LXXVI.

Additional description. Lang (1936b): 23–25; Figs 50–52 (as *Parastenhelia forficula*).

Type material. The female specimen illustrated by Sars (1905: Plate LXXVI) is here designated as the holotype of *M. sarsi* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters listed in the diagnosis below and those mentioned and illustrated in Sars (1905) (ICZN Art. 13.1).

Type locality. Sars (1905) recorded material from several places on the south and west coasts of Norway, and in the Trondhjem Fjord. Since he did not specify which specimens the illustrations were based on, the type locality encompasses all of their respective places of origin (ICZN Art. 73.2.3).

Differential diagnosis. *Microthalestris*. Body length 580 µm in ♀, considerably smaller in ♂. Antenna with 2-segmented exopod bearing two setae on exp-1 and one lateral and three apical elements on exp-2. P1 exopod about two-thirds length of endopod; exp-2 elongate, about 2.1 times as long as exp-1, and about 60% length of exp-1; insertion point of inner seta of exp-1 at 25% of inner margin length; exp-3 with two unipinnate spines and two geniculate setae; exp-2 with one minute seta, one geniculate seta and one geniculate claw. Armature pattern of ♀ P2–P4:

	exopod	endopod
P2	1.1.123	1.1.121
P3	1.1.223	1.1.221
P4	0.1.223	1.1.121

P3 endopod ♂ 3-segmented, with apophysis on exp-3, armature pattern [1.1.02 + apo]. P5 ♀ with elongate exopod (about 2.8 times as long as maximum width), inner margin and proximal half of outer margin straight, with eight elements, proximal outer one long, outer apical one short; endopodal lobe with five elements, innermost one well developed. P5 ♂ exopod 3-segmented, with six elements (outer element of exp-1 absent or extremely reduced); endopodal lobe with two elements. Armature of P6 ♂ unconfirmed. Caudal ramus seta V with slightly swollen proximal part.

Etymology. The specific epithet is named after Georg Ossian Sars (20 April 1837 – 9 April 1927), eminent Norwegian copepodologist, who provided the first illustrated account of the species under the name *Microthalestris forficula* (Claus, 1863).

Notes. *Microthalestris sarsi* **sp. nov.** can readily be distinguished from other congeners that exhibit a 3-segmented exopod in the male by the absence (or possibly extreme reduction) of the outer seta on exp-1. Confirmation of this character in Lang’s (1936b) male of *Parastenhelia forficula* from the Øresund corroborates its conspecificity with *M. sarsi* **sp. nov.** Sars (1905) himself listed the records from the British Isles (Scott 1894b, 1897; Scott & Scott 1894 – all as *T. forficuloides*; Scott 1900 – as *T. forficulus*), the Bohuslän coast in Sweden (P.T. Cleve, unpubl. data), between Kolguev and Novaya Zemlya (Scott & Scott 1901 – as *T. forficulus*), Bear Island (Bjørnøya) and Hope Island, Svalbard (Scott & Scott 1901 – as *T. forficulus*), Franz Josef Land (Scott 1899 – as *T. forficula*), and the Arctic islands north of Grinnell Land, Canada (subsequently published by Sars 1909) as valid but considered the conspecificity of Scott’s (1894a – as *T. forficula*) record from the Gulf of Guinea questionable. It is now clear that at least the illustrated records of *T. forficuloides* (Scott 1894b; Scott & Scott 1894) are not conspecific with *M. sarsi* **sp. nov.** (see above) and that the Arctic records by Scott (1899), Scott & Scott (1901) and Sars (1909) may in reality refer to *M. polaris* **sp. nov.** (see below).

***Microthalestris polaris* sp. nov.**

urn:lsid:zoobank.org:act:2DD62715-A421-471B-A3A0-83EF1A166B81

Parastenhelia spinosa (Fischer, 1860) *sensu* Chislenko (1967, 1977), Mielke (1974)

Both *M. forficuloides* and *M. sarsi* **sp. nov.** display the maximum number of eight setae/spines on the female P5 exopod. This number has also been observed in females assigned to *M. forficula* by Wilson (1932b), and to *Parastenhelia spinosa* by Chislenko (1967, 1977), Mielke (1974) and Kornev & Chertoprud (2008). Wilson's (1932b) description is concise, illustrating only P1, P5 of both sexes and male P3 endopod. Differences in body size (distinctly smaller – see above), P1 endopod (proximal segment comparatively longer so that exp-2 is only about 40% the length of enp-1 and the insertion point of the inner seta of enp-1 is located at 17% of the inner margin length), male P3 endopod (with inner seta on enp-3), and the male P5 (with long outer seta on exp-1) rules out conspecificity of the Woods Hole material with *M. sarsi* **sp. nov.** Since information about the segmentation of the female antennule, swimming leg armature and morphology of caudal ramus seta V is completely lacking, Wilson's (1932b) material cannot be attributed distinct specific status at present and is therefore not considered any further. Conversely, the three illustrated reports based on material from Arctic localities (Chislenko 1967, 1977; Mielke 1974) contain sufficient information for a morphological comparison with *M. sarsi* **sp. nov.** Based on the descriptions by Chislenko (1967) and Mielke (1974), the Arctic specimens differ from the latter species in the following combination of characters: (a) antennary exopod with two lateral setae on exp-2 (*vs* one); (b) P1 exopod 75% length of endopod (*vs* two-thirds); (c) P3–P4 exp-3 with three inner setae (*vs* two); and (d) male P5 exopod with very long outer seta on exp-1 (*vs* absent or extremely reduced). They also can be distinguished from *M. forficuloides* by a number of features: (a) antennary exopod with two lateral setae on exp-1 (*vs* one); (b) P1 exopod 75% length of endopod (*vs* two-thirds); (c) P1 exp-2 2.5 times length of exp-1 and 55% length of enp-1 (*vs* twice and 45%, respectively); (d) P3 exp-1 with inner seta (*vs* absent); (e) P4 exp-3 with three inner setae (*vs* two); and (f) male P5 exopod 3-segmented (*vs* 1-segmented). Chislenko's (1977) illustrations of the female genital field and P5 (with eight elements on the exopod although its length:width ratio is slightly greater than in the White Sea females) appears to confirm the conspecificity of his Franz Josef Land material with the specimens he had previously reported from the White Sea (Chislenko 1967). Based on the morphological comparison above we are convinced that the Arctic material is sufficiently distinct from both *M. forficuloides* and *M. sarsi* **sp. nov.** to warrant the erection of a new species, which we name *M. polaris* **sp. nov.**

Original description. Mielke (1974): 20–22, Abb. 9.

Additional descriptions. Chislenko (1967: 140–144, Figs 45–46); Chislenko (1977: 246, Fig. 6–1, 2).

Type material. The female specimen illustrated by Mielke (1974: Abb. 9A–B) is here designated as the holotype of *M. polaris* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters listed in the diagnosis below and those mentioned and illustrated in Mielke (1974) (ICZN Art. 13.1).

Type locality. Svalbard archipelago, Spitsbergen, Longyearbyen; littoral zone.

Differential diagnosis. *Microthalestris*. Body length 550–800 µm in ♀, 400–420 µm in ♂. Antenna with 2-segmented exopod bearing two setae on exp-1 and two lateral and three apical elements on exp-2; armature of endopod unconfirmed but likely without penicillate spines. P1 exopod about 75% length of endopod; exp-2 elongate, about 2.5 times as long as exp-1, and about 55% length of enp-1; insertion point of inner seta of enp-1 at 25% of inner margin length; exp-3 with two unipinnate spines and two geniculate setae; enp-2 with one minute seta and two non-geniculate claws. Armature pattern of ♀ P2–P4:

	exopod	endopod
P2	1.1.123	1.1.121
P3	1.1.323	1.1.221
P4	0.1.323	1.1.121

P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ with elongate exopod (about 2.4 times as long as maximum width), inner margin and proximal half of outer margin straight, with eight elements, proximal outer one long, outer apical one short; endopodal lobe with five elements, innermost one well developed. P5 ♂ exopod 3-segmented, with seven elements, outer seta of exp-1 very long, longer than or as

long as outer basal seta; endopodal lobe with two elements. Armature of P6 ♂ unconfirmed. Caudal ramus seta V with slightly swollen proximal part.

Etymology. The species name is derived from the Latin *polaris*, meaning polar, and refers to the Arctic distribution of this species.

Notes. The species appears so far to be restricted to the Arctic Ocean and its marginal waterbodies such as the White Sea. It has been recorded from Kandalaksha Bay (Chislenko 1967), Svalbard (Mielke 1974) and Franz Josef Land (Chislenko 1977). Kornev & Chertoprud (2008: 196–197, Fig. 5.94–A, Б, B) also reported *P. spinosa* from the White Sea, including an aberrant specimen, and reproduced Chislenko's (1967) illustrations of the P1 and P5 of both sexes. They mentioned substantial variation in female body length (550–800 µm) but this is a verbatim account of Chislenko's (1967) measurements. It is also not clear whether the variability included in their armature formulae of P3–P4 (number of inner setae on P3–P4 exp-3 and P4 enp-3; Table 1) is based on their own observations of White Sea material or reflects variability reported in the literature. Since the authors provided no direct evidence that they were dealing with *M. polaris* **sp. nov.**, their record is at present to be considered as unconfirmed. This uncertainty is exacerbated by the fact that, despite the reported variability on other segments, the White Sea specimens appear to be consistent in the lack of the inner seta on P3 exp-1 (which is present in *M. polaris* **sp. nov.**).

Chislenko (1967) collected two females from washings of the demosponge, *Semisuberites cribrosa* (Esperiopsidae), in Franz Josef Land but this association is to be regarded as accidental (Huys 2016). Previous records of *Thalestris forficula* from Arctic localities may refer to *M. polaris* **sp. nov.** but in the absence of morphological or other compelling evidence they must remain unconfirmed. These include the records from Lille-Karajak fjord in western Greenland (Vanhöffen 1897), Cape Gertrude in Franz Josef Land (Scott 1899), between Kolguev and Novaya Zemlya (Scott & Scott 1901 – as *T. forficulus*), Bear Island (Bjørnøya) and Hope Island, Svalbard (Scott & Scott 1901 – as *T. forficulus*), the Arctic islands north of Grinnell Land, Canada (Sars 1909) and Seydisfjord in Iceland (Jespersen 1940; Klie 1941 – both as *Parastenhelia forficula*). Similarly, the Arctic records of *Parastenhelia spinosa* from Iceland (Ólafsson *et al.* 2001; Steinarsdóttir *et al.* 2003; Steinarsdóttir & Ingólfsson 2004), Kandalaksha Bay in the White Sea (Brotskaya 1962; Chertoprud *et al.* 2005) and from mesozooplankton in the Barents Sea (Dvoretzky & Dvoretzky 2010) require authentication before they can be considered conspecific with *M. polaris* **sp. nov.**

Parastenhelia gracilis* Brady, 1910 and other subantarctic records of *Parastenhelia

Microthalestris gracilis (Brady, 1910) **comb. nov.** belongs to a close-knit group of subantarctic species characterized by the position of the inner seta on P1 enp-1 which originates from the middle third of the segment. This subantarctic group includes *M. gracilis*, *M. antarctica* (Scott, 1912) **comb. nov.**, *M. costata* (Pallares, 1982) **comb. nov.**, *M. santacruzensis* **sp. nov.** and *M. variabilis* **sp. nov.** In all other members of the genus the inner seta of P1 enp-1 is situated further proximally, at around 25% the length of the inner margin of the segment. Interestingly, the latter condition is also displayed by *M. minuta* (Pallares, 1982) **comb. nov.** from Tierra del Fuego and *M. campbelliensis* **sp. nov.** from Campbell Island, suggesting the independent colonization of the subantarctic region by two different lineages. *Microthalestris gracilis* **comb. nov.** is known from a single female collected in the Baie de l'Observatoire (Observatory Bay) along the northern shore of the Golfe du Morbihan in the Kerguelen (Brady 1910: 513; Textfig. VIII). A second record by Jayabarathi (2016) from seagrass beds in South Andaman is highly questionable. The original description includes illustrations of the antennule, P1, P2, P5 and caudal rami but is deficient in many aspects. The armature is unknown for P3–P4 except for Brady's (1910) dubious claim that their distal endopodal segments have only three elements. The P2 is shown to have two inner setae on exp-3 which is also questionable. Since within the Parastenheliidae this condition is only found in members of *Thalestrella* and *Foweya* (Table 1) it may indicate that Brady's (1910) illustration is either based on an observational error or in reality refers to P3 or P4. Alternatively, the possibility that *P. gracilis* represents a member of *Foweya* cannot be excluded but this would require information on the male and the sexual dimorphism in this species. Another unusual feature of *P. gracilis* is the endopodal lobe of P5 which is remarkably small and displays only four setae. Lang's (1948) concept of *P. spinosa* grouped together all the various forms in which the middle segment of P1 exopod was at least four times as long as broad, with the exception of *P. gracilis* which was maintained as a distinct species mainly on the difference in the site of origin of the inner seta of P1 enp-2 and the shape of the female P5.

Scott (1912: 561; Plate IV, figs. 25–33) described a second subantarctic species, *P. antarctica*, from Scotia Bay (60°43'42" S, 44°38'33" W) in the South Orkney Islands and compared the female (males are unknown) with *P. gracilis*. Gurney (1927: 544) suggested that *P. antarctica* appeared to be identical with *P. gracilis* and Lang (1934: 23) formally treated them as synonyms but neither author gave a justification for this claim. This course of action appears premature since significant differences can be observed in the morphology of P1 (length of exopod, in particular exp-2; length of claws on enp-2) and P5 (shape of exopod), both of which were dismissed as irrelevant by Lang (1934, 1936a, 1948). Although an unusual degree of intra-individual and intra-population variability has been recorded in the armature patterns of P2–P4 in some species of *Parastenhelia* (e.g. Mielke 1974, 1990) such variability is not expressed in the morphology of either P1 or P5. Lang (1936a: 53; Figs 36–37) reported two females from Berkeley Sound, Port Louis in the Falkland Islands which he attributed to *P. gracilis*. His illustration of the P1 leaves no doubt that he was dealing with the geographically closer *P. antarctica* since it is fully compatible in the relative lengths of its rami, exp-2 and claws on exp-3 with Scott's (1912) original description. Thomson (1883, 1913) recorded numerous *Thalestris*-like specimens from Otago Harbour, Dunedin in the South Island of New Zealand and assigned them to Claus's (1863) *T. forficula* [see also Brady (1899) who found it abundantly in the same location]. Lang (1934, 1936a) initially listed Thomson's record under the synonymy of *Parastenhelia forficula* var. *littoralis* and subsequently, again without giving any specific justification, classified it as conspecific with *P. spinosa* (Lang 1948). Wells *et al.* (1982) suggested that the Otago Harbour material may belong to *P. megarostrum* but were unable to make a firm recommendation for this assignment on morphological grounds (see below). Thomson's (1883) illustrations (Plate X, figs 16–21) show several similarities with the original description of *P. antarctica*, including (a) the general outline and proportional segmental lengths of the female antennule; (b) P1 exopod with elongate exp-2; (c) P1 endopod showing similar L:W ratio for enp-1; claws on enp-2 elongate as in *P. antarctica*; and (d) female P5 setation and general shape of exopod. Based on these similarities we consider it likely that Thomson's (1883) *T. forficula* belongs to *P. antarctica*, the only main difference being the position of the inner seta on P1 enp-1 which inserts more distally. The female antennule of Thomson's specimens was described as 8-segmented but reinterpretation of his illustration (Plate X, fig. 17) suggests it has nine segments (as in *P. antarctica*). The presence of four setae on the proximal segment indicates that it represents the second segment and that the real first segment was not observed or lost during dissection. The aesthetasc that originates from a ventral pedestal of the fourth segment is shown to insert on the anterodistal corner of this segment (in reality the fifth) in Thomson's drawing; this can be explained by assuming that the author observed the antennule in dorsal aspect. Based on the arguments above, *Microthalestris antarctica* (Scott, 1912) **comb. nov.** is here reinstated as a valid species. It is very close to *M. costata* **comb. nov.** in the morphology of the P1 and the foliaceous ♀ P5 exopod but differs from it in the armature of the distal endopodal segment of P4 (Table 1).

***Microthalestris campbelliensis* sp. nov.**

urn:lsid:zoobank.org:act:F47DAF34-B635-46E1-8FE4-AACFEF43218E

Microthalestris forficula (Claus, 1863) var. *littoralis* sensu Lang (1934)

Differences in the morphology of the P1, female P5 and caudal ramus indicate that Lang's (1934) material is not conspecific with *M. littoralis* and deserves distinct specific rank. It differs from all its subantarctic congeners in the armature of P2–P4, including *M. minuta* **comb. nov.** with which it shares the proximal position of the inner seta on P1 enp-1.

Original description. Lang (1934): 25–27, Figs 49–56.

Type material. The dissected male specimen illustrated by Lang (1934: Figs 52–56) is here designated as the holotype of *P. campbelliensis* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters mentioned in the diagnosis below and those illustrated in Lang (1934) (ICZN Art. 13.1).

Type locality. New Zealand, Campbell Island group, Campbell Island (Motu Ihupuku); Perseverance Harbour (South Harbour); 40 m depth.

Differential diagnosis. *Microthalestris*. Body length unknown. Antenna with 2-segmented exopod, armature unconfirmed; bearing two setae on exp-1 and two lateral and three apical elements on exp-2; armature of endopod unconfirmed but likely without penicillate spines. P1 exopod about 70% length of endopod; exp-2 elongate, about

2.1 times as long as exp-1, and about 55% length of enp-1; insertion point of inner seta of enp-1 at 20% of inner margin length; exp-3 with four elongate setiform elements; enp-2 with one minute seta and two non-geniculate claws. Armature pattern of ♀ P2–P4: see top of next page.

P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ with elongate exopod (about three times as long as maximum width), inner margin and proximal half of outer margin slightly convex, with six elements, outer ones about equally long, outer apical one shorter than inner apical one; endopodal lobe with five elements, innermost one short. P5 ♂ exopod 3-segmented, with seven elements, outer seta of exp-1 very long, longer than outer basal seta; endopodal lobe with two elements. Armature of P6 ♂ unconfirmed. Caudal ramus seta V with slightly swollen proximal part.

	exopod	endopod
P2	1.1.123	1.1.121
P3	0.1.223	1.1.221
P4	0.1.223	1.1.121

Etymology. The species name alludes to Campbell Island (Motu Ihupuku), an uninhabited subantarctic island of New Zealand, where the type locality is situated.

Note. Although Lang (1934: 26) claimed his material consisted solely of a pair *in amplexus* the condition of the caudal ramus (Fig. 49) was figured in two different females. The species is so far only known from the type locality.

***Microthalestris santacruzensis* sp. nov.**

urn:lsid:zoobank.org:act:6A60E30B-3CF6-4E72-915D-0EF22C6BD66B

Parastenhelia antarctica Scott, 1912 *sensu* Pallares (1963, 1968)

Pallares (1963, 1968) recorded both sexes of a *Parastenhelia* species from the Río Deseado, Santa Cruz in Argentina. Although the material was attributed to *P. gracilis* it is radically divergent from both this species and *P. antarctica* in the shape of the female P5 exopod. In the Argentine specimens the inner margin and the proximal two-thirds of the outer margin are virtually straight while in both *P. gracilis* and *P. antarctica* they are distinctly convex. Additional differences can be observed in the length of some of its elements, in particular the proximal outer seta of the exopod which is clearly longer and the inner element on the endopodal lobe which is minute. Pallares (1968) states that the male P5 exopod has seven elements but does not figure the limb nor discloses the number of segments; however, in her Ph. D. dissertation (Pallares 1963) she stated “Exopodo con tres sedas externas, una interna y dos largas apicales” suggesting that all elements originate from a single segment and the total is six rather than seven. The Argentine material differs from all species currently assigned to *Parastenhelia* in the reduced armature formula of the swimming legs. Pallares (1968) only illustrates the male P3 and gives no information in the text about P2 and P4; however, the absence of inner setae on P2 exp-1 and -2 in conjunction with the presence of only one inner seta on exp-3 differentiates the Río Deseado specimens from all known members of the genus. They further differ from *P. gracilis* in the length of the P1 exopod (exp-2 being distinctly longer) and the shape of caudal ramus seta V (swollen at the base). Although generally accepted as the first and only illustrated report of the male of *P. gracilis* (Mielke 1990; Bodin 1997; Wells 2007) there is no doubt that Pallares’s (1968) description deals with a different, as yet undescribed, species for which we coin the name *P. santacruzensis* **sp. nov.** Pallares (1975), in a subsequent report on littoral harpacticoids from Tierra de Fuego, recorded *P. gracilis* from Bahía Cook on Isla de Los Estados (Tierra del Fuego) but the authenticity of this record remains to be confirmed.

Original description. Pallares (1968): 63–65, Plate XIX.

Type material. Pallares’s (1968) original material no longer exists (M. Sciberras, pers. commn). The dissected male specimen illustrated by Pallares (1968: 64) in her Plate XIX is here designated as the holotype of *P. santacruzensis* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters listed in the diagnosis below and those mentioned and illustrated in Pallares (1968) (ICZN Art. 13.1).

Type locality. Pallares (1968) collected material from a number of localities in the Deseado River, Santa Cruz Province, Argentina: Punta Cavendish, Dos Hermanas, Punta Guanaco, Restinga Chaffers, Isla Quiroga and Bahía

Uruguay. Since Pallares (1968) did not specify which specimens she based her illustrations on, the type locality encompasses all of their respective places of origin (ICZN Art. 73.2.3).

Differential diagnosis. *Microthalestris*. Body length 890 µm in ♀, 700 µm in ♂. Antennule 9-segmented and haplocer in ♂. Antenna with 2-segmented exopod bearing two setae on exp-1 and one lateral and three apical elements on exp-2; endopod without penicillate spines. P1 exopod about 0.8 times length of endopod; exp-2 elongate, about 2.5 times as long as exp-1. P3 exopod armature pattern [0.0.123]; endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ with elongate exopod (about 3.2 times as long as wide), inner margin and proximal two-thirds of outer margin straight, with six elements, proximal outer one long, outer apical one minute; endopodal lobe with five elements, innermost one minute. P5 ♂ with six elements on 1-segmented exopod; endopodal lobe with two elements. P6 ♂ with three setae. Anal operculum smooth. Caudal ramus seta V with swollen base.

Etymology. The species is named after the Santa Cruz Province, located in the southern part of Argentina where the type locality is located.

***Microthalestris variabilis* sp. nov.**

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Parastenhelia ? *costata* Pallares, 1982 sensu Mielke (1990)

Based solely on P1 morphology *P. gracilis* appears morphologically close (and potentially conspecific) with *P. costata*, another Argentine species originally described from Bahía Thetis on the east coast of Tierra de Fuego (Pallares 1982: 9–11; Plates I–II) and which occurs sympatrically with *M. minuta* **comb. nov.** (Pallares 1982: 12–14; Plate III). Bick & Arlt (2013) recorded both species in considerable numbers from a soft-bottom area in Maxwell Bay (King George Island, South Shetlands) but it is not clear how they distinguished them. Mielke (1990) reported a second population on Isla Grande Tierra del Fuego from Bahía Lapataia near Ushuaia which he tentatively attributed to *P. costata*. An exceptionally high degree of variability in the armature of P2–P4 was observed in a relatively small sample (13 ♀♀, 6 ♂♂), causing Mielke (1990) to suggest that both Tierra del Fuego species, *P. costata* and *P. minuta* represented populations of the same species. Accepting this view would unnecessarily blur the species boundaries in *Microthalestris* even further and, considering the recent progress that has been made (e.g. Gee 2006), be a retrograde step in the revision of the genus. Mielke's (1990) specimens differ from the *P. costata* type population in the smaller body size [580–780 µm (♀), 420–560 µm (♂) vs 789–960 µm (♀), 600–706 µm (♂)], the shape of caudal ramus seta IV (with bulbous swelling near the base), the presence of only one or two inner setae (instead of three) on P3–P4 exp-3, the length of the inner seta on the male P3 enp-2, and the weakly developed endopodal lobe of the male P5, reaching barely beyond the proximal exopod segment (vs reaching well beyond the middle exopod segment). The female P5 differs in the shape of the exopod which is rounder in the type population and shows a wider spacing between the proximal and middle outer setae, and in the length of the proximal inner seta of the endopodal lobe which is distinctly shorter in Mielke's (1990) females. Based on this suite of differences we elect to attribute separate specific status to the Bahía Lapataia material rather than treating it as a population of *P. costata*.

Original description. Mielke (1990): 158–164, Figs 1–5.

Type material. The dissected female specimen illustrated by Mielke (1990: Figs 1–3, 4A, 5) is here designated as the holotype of *P. variabilis* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters mentioned in the diagnosis below and those illustrated by Mielke (1990) (ICZN Art. 13.1).

Type locality. Argentina, Province of Tierra del Fuego, Antarctica and South Atlantic Islands; Isla Grande Tierra del Fuego, Bahía Lapataia near Ushuaia.

Differential diagnosis. *Microthalestris*. Body length 580–780 µm in ♀, 420–560 µm in ♂. Antenna with 2-segmented exopod bearing two setae on exp-1 and two lateral and three apical elements on exp-2; endopod without penicillate spines. P1 exopod about 70% length of endopod; exp-2 elongate, about 1.8 times as long as exp-1, and about 40% length of enp-1; insertion point of inner seta of enp-1 at 40% of inner margin length; exp-3 with two unipinnate spines and two geniculate setae; enp-2 with one minute seta, one geniculate and one non-geniculate claw. Armature pattern of ♀ P2–P4:

	exopod	endopod
P2	1.0.123	1.1.121
P3	1.0.223	1.1.121
P4	1.1.123	1.1.121

P2 endopod ♂ 2-segmented (enp-2 and -3 forming compound segment), armature pattern [1.221]. P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ with ovate exopod (about 1.9 times as long as maximum width), with six elements, distal outer one longest, outer apical one short and naked; endopodal lobe with five elements, innermost one well developed. P5 ♂ exopod 3-segmented, with seven elements, outer seta of exp-1 long and naked; endopodal lobe with two short spiniform elements. Armature of P6 ♂ unconfirmed. Caudal ramus seta V normally developed, seta IV with bulbous swelling near base.

Etymology. The species name alludes to the high level of variability observed in the swimming leg armature.

Key to species of *Microthalestris* Sars, 1905

As pointed out above, Brady's (1910) description of *M. gracilis* is rudimentary, his illustrations are far from precise and the armature formula of P2–P5 is misleading. The species is consequently omitted from the key and the reader is advised to consult the original description. The same applies to *M. littoralis* which is only known from the female and for which no information on swimming leg armature exists.

1. P3–P4 exp-1 without inner seta, exp-3 with eight and seven spines/setae, respectively; P5 ♀ exopod with elements; P5 exopod ♂ 1-segmented with seven elements *M. forficuloides* (Scott & Scott, 1894).
– These characters not combined 2.
2. P2–P3 enp-1 without inner seta; P3 endopod ♂ with inner seta on enp-3 [0.1.12 + apo]; caudal ramus seta IV with distinctly bulbous, basal swelling. *M. bulbosa* (Gee, 2006) **comb. nov.**
– P2–P3 enp-1 with inner seta; P3 endopod ♂ without inner seta on enp-3 [1.1.02 + apo]; caudal ramus seta IV not modified 3.
3. P3 exp-3 armature 0.0.123; P5 exopod ♀ with six elements, inner margin and proximal two-thirds of outer margin virtually straight; P5 exopod ♂ 1-segmented, with six elements *M. santacruzensis* **sp. nov.**
– These characters not combined 4.
4. P3 enp-3 with one inner seta 5.
– P3 enp-3 with two inner setae 6.
– P3 enp-3 with three inner setae 8.
5. P2–P3 exp-2 with inner seta; P2 enp-3 without inner seta; P4 exp-3 with three inner setae; P4 enp-3 ♀ with two inner setae (021 in ♂); P5 exopod ♂ 1-segmented. *M. minuta* (Pallares, 1982) **comb. nov.**
– P2–P3 exp-2 without inner seta; P2 enp-3 with inner seta; P4 exp-3 with one inner seta; P4 enp-3 with one inner seta in both sexes; P5 exopod ♂ 3-segmented. *M. variabilis* **sp. nov.**
6. P3 exp-1 without inner seta; P5 exopod ♀ with six elements *M. campbelliensis* **sp. nov.**
– P3 exp-1 with inner seta; P5 exopod ♀ with eight elements 7.
7. P3–P4 exp-3 with three inner setae; P5 exopod ♂ with seven elements *M. polaris* **sp. nov.**
– P3–P4 exp-3 with two inner setae; P5 exopod ♂ with six elements, outer seta of exp-1 absent or extremely reduced
. *M. sarsi* **sp. nov.**
8. P4 enp-3 with one inner seta *M. antarctica* (Scott, 1912) **comb. nov.**
– P4 enp-3 with two inner setae *M. costata* (Pallares, 1982) **comb. nov.**

Unidentified species of *Parastenhelia*/*Microthalestris*

Unidentified species of *Parastenhelia* (most likely *Microthalestris*) have been reported from the Isles of Scilly, U.K. (Gee & Warwick 1994), the Venice Lagoon, Italy (Villano & Warwick 1995), Greece (Willen 2000; Sevastou 2005), hydrothermal vents on Jan-Mayen Ridge (Fricke *et al.* 1989) and Mohn Ridge (Schander *et al.* 2010) in the North Atlantic, Dry Tortugas, Florida (Pearse 1934 – as *Microthalestris* sp.), La Jolla, California (Gunnill 1982, 1983), the Galápagos Archipelago (Mielke 2003), Arraial do Cabo, Rio de Janeiro (Sarmiento *et al.* 2009) and Sergipe (Vasconcelos 2008) in Brazil, King George Island, South Shetland Islands (Bick & Arlt 2013), Zanzibar (Callens *et al.* 2012; Gheerardyn 2007; Gheerardyn *et al.* 2008), St Croix Island, South Africa (Beckley 1982), Point Calimere, southeastern India (Jayalakshmi *et al.* 2016), South Andaman (Jayabarathi 2016), peninsular Malaysia (Zaleha *et*

al. 2006, 2018), Dolsan Island, South Korea (Yu & Suh 2012; Yu *et al.* 2003), northern East Sea (Chertoprud *et al.* 2015), Momo Island (Iwasaki 1995a, 1995b) and Otsuchi Bay (Kim & Shirayama 1996) in Japan, Port Phillip Bay, Australia (Jenkins *et al.* 2002; Walker-Smith 2003), New Zealand (Webber *et al.* 2010), Baie de Sainte Marie, New Caledonia (Huys *et al.* 2009) and Fiji (Willen 2000).

Thalestrella Monard, 1935a

Karllangia Noodt, 1964

Monard (1935a: 45) described *Thalestrella ornatissima* as the type species of his new genus *Thalestrella*, based on females dredged from sand near Roc'h Iliévec in the Roscoff area (Brittany). Lang (1944, 1948) rejected the validity of *Thalestrella* and transferred *T. ornatissima* to *Parastenhelia*, claiming a close relationship with *P. anglica* and *P. hornelli*. Gee (2006) recently assigned the species to *Karllangia*, repeatedly stating that the original description was based on only a single female but there is no evidence for that in Monard's (1935a) paper.

Mielke (1994b: 152) recognized two evolutionary lineages within *Karllangia*, the more primitive branch comprising *K. arenicola arenicola* and *K. tertia*, and the more advanced one represented by *K. psammophila*, *K. arenicola bengalensis* and both Costa Rican species (*K. obscura*, *K. pulchra*). As pointed out by Gee (2006) the outstanding problem within the genus *Karllangia* is the fact that its type species, *K. arenicola*, apparently does not display the most important synapomorphy that supports the common ancestry of the remaining species (including the type species of *Thalestrella*). This character state which distinguishes *Karllangia* from other members of the Parastenheliidae is the modification of the male antenna (allobasal seta much more plumose, exp-1 smaller and with only one strong, plumose seta, exp-2 broader with more strongly plumose setae than in ♀). The original description by Noodt (1964) of *K. arenicola* from coralline sands on the Egyptian coast of the Red Sea does not mention any sexual dimorphism in the male antenna which could be attributed to either an observational error or to genuine absence. This ambiguity surrounding the type species has now been removed by synonymizing *Karllangia* with its senior subjective synonym *Thalestrella*. The presence of antennary sexual dimorphism in its type species, *T. ornatissima*, has been demonstrated by Gee (2006) who confirmed a number of additional genus-level apomorphies in the species, including the compressed appearance of the distal antennular segments in the female, the presence of only three setae on exp-2 of the antenna, two setae on the mandibular exopod, and one seta on the maxillipedal syncoxa; the absence of the inner seta on P2–P4 exp-1; and, a male P5 exopod with only four setae. Additional apomorphies which were not observed by Gee (2006) include (a) male antennule subchirocer, compound segment 5 (XIV–XX) swollen; (b) the male antennule with only three segments distal to the geniculation (XXI–XXIII, XXIV–XXV, XXVI–XXVIII); (c) ventral surface of segment 2 of male antennule with characteristic, backwardly directed, spiniform element, either displaying a serrate or flagellate tip (Wells & Rao 1987: Fig. 110b; Mielke 1994b: Fig. 6A); and (d) outer spine on P3 exp-3 reduced in size in ♂ (Mielke 1994b: Fig. 6C; Gee 2006: Fig. 5C; Fig. 7 herein).

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P3 exp-3 outer spine, P5–P6 and urosomal segmentation. Body subcylindrical; posterior margin of cephalothorax (typically) and all somites (except anal somite) typically with deeply divided, denticulodigitate or lobate, hyaline frills (plain in *T. obscura* **comb. nov.** and possibly *T. arenicola* **comb. nov.**). Rostrum defined at base, of moderate size, reaching at most to end of second segment of antennule; linguiform. Anal operculum semicircular, variously ornamented; usually bordered with fine spinules or denticles. Caudal ramus at most as wide as long, with dorsal spinular row; with seven setae, setae IV–V not basally inflated in ♀.

Antennule ♀ compact, 8- or indistinctly 9-segmented; segment 1 not elongate, distal four or five segments small with combined length only slightly longer than segment 4; with aesthetascs on segments 4 and 8 (or 9). Antennule ♂ subchirocer, 7-, 8- or indistinctly 9-segmented; ventral surface of segment 2 with characteristic, backwardly directed, spiniform element; with geniculation between segments 5 and 6 (or 6 and 7 when indistinctly 9-segmented) and 2–3 segments distal to geniculation; compound segment 5 (XIV–XX) swollen, occasionally subdivided dorsally by transverse surface suture; with aesthetasc on segments 5 and 7 or 8; segmental homologies of 8-segmented antennule: I, II–VIII, IX–XII, XIII, XIV–XX, XXI–XXIII, XXIV–XXV, XXVI–XXVIII. Antenna sexually dimorphic. Female antenna with proximal endopodal segment largely fused to basis forming allobasis, with

short pinnate seta on abexopodal margin; exopod 2-segmented (or segments partially fused), proximal segment with 1–2 setae, distal segment with one lateral and two apical elements (surrounded at base by serrate hyaline frill); distal endopodal segment without penicillate elements. Male antenna with enlarged, highly plumose seta on allobasis; exopodal segments of different size, with only one seta on proximal segment and all lateral setae enlarged and highly plumose. Mandible with three elements on basis; endopod with eight setae; exopod 1-segmented, with 2–4 setae. Maxillulary coxal epipodite represented by one seta. Maxilla with three endites on syncoxa; endopod discrete, with 4–5 setae. Maxilliped with one seta on syncoxa; basis with 0–2 setae on palmar margin; endopod represented by pinnate claw, accompanied by one accessory seta.

P1 exopod 3-segmented; segments subequal; exp-2 with or without inner seta; exp-3 with two pinnate spines and one geniculate spine and one (non-)geniculate seta. P1 endopod 2-segmented; enp-1 elongate, about twice as long as exopod, with well developed, pinnate inner seta originating from proximal half in a region of reduced chitinization of segment wall; enp-2 very small, with one naked minute seta and two unipinnate claws, longest of which geniculate. P2–P4 rami 3-segmented; outer spine of P3 enp-3 ♂ reduced in size. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	0.1.223	1.1.121
P3	0.1.(2–3)23	1.1.(1–2)21
P4	0.1.(2–3)23	1.1.(1–2)21

P5 ♀ endopodal lobe triangular, with five setae; inner margin without transverse striae; exopod elongate (2–5 times longer than wide), with 5–6 elements. P5 ♂ endopodal lobe with two elements; exopod 1-segmented, with 4–5 elements. Vestigial P6 ♀ represented by 2–3 short setae. P6 ♂ with three setae/spines.

Type species. *Thalestrella ornatissima* Monard, 1935a (by monotypy).

Other species. *Karllangia arenicola* Noodt, 1964 = *T. arenicola* (Noodt, 1964) **comb. nov.**; *K. psammophila* Wells, 1967 = *T. psammophila* (Wells, 1967) **comb. nov.**; *Parastenhelia reducta* Apostolov, 1975 = *T. reducta* (Apostolov, 1975) **comb. nov.**; *K. arenicola bengalensis* Wells & Rao, 1987 = *T. bengalensis* (Wells & Rao, 1987) **comb. nov.**; *K. obscura* Mielke, 1994b = *T. obscura* (Mielke, 1994b) **comb. nov.**; *K. pulchra* Mielke, 1994b = *T. pulchra* (Mielke, 1994b) **comb. nov.**

Species inquirenda. *Parastenhelia ornatissima* (Norman & Scott, 1905) sensu Por (1964).

***Thalestrella ornatissima* Monard, 1935a**

Parastenhelia anglica (Norman & Scott, 1905) sensu Wells (1961)
Karllangia ornatissima (Monard, 1935a) Gee (2006)

Original description. Monard (1935a): 45–46; Figs 87–96.

Additional descriptions. Wells (1961): 267–268; Fig. 2B. Gee (2006): 2613–2621; Figs 1–6.

Type locality. France, Brittany, Roscoff area; near Roc’h Iliévec; dredged from sand.

Notes. Por (1964) recorded seven females (400 µm) of *Parastenhelia ornatissima* from detritus-laden littoral sand in Achziv, northern Israel (Levantine coast). He provided illustrations (Plate 11; figs 95–96) of the female P5 and the posterior half of the abdomen in dorsal aspect. Bodin (1968) reported both sexes in a midlittoral sand sample from Banc du Bûcheron (Ile de Ré) near La Rochelle, but gave no morphological details, while Soyer (1971) subsequently recorded it from Banyuls-sur-Mer. Gee (2006) recorded *T. ornatissima* **comb. nov.** as the most abundant species in the harpacticoid community at low tide level on St Martin’s Flat in the Isles of Scilly (only one specimen was found near the high-water mark, cf. Gee 2009). His detailed study of the previously undescribed male confirmed that this species has a sexually dimorphic antenna and belongs in the genus *Karllangia* (= *Thalestrella*). Differences with Monard’s (1935a) description were dismissed as of no significance and attributed to the author’s imprecision in observing the minutiae of the mouthparts and, more importantly, the correct setation of the P4 exopod (two inner setae on exp-3 instead of three in the Scillonian material). Conversely, Por’s (1964) specimens, which allegedly share the same armature on P4 exp-3 as Monard’s material, were considered a potentially different

species. In reality, Por did not illustrate leg 4 nor did he provide a setal formula, stating only that “Antennae, mouthparts and swimming legs are typical”. The only two discrepancies observed between Monard’s type material and the specimens from the Israeli coast are related to the anal operculum, which has fewer (7) and larger spinous projections, and the P5, which has slightly shorter setae (particularly on the endopodal lobe). These characters, together with the length:width ratio of the P5 exopod (shorter compared to the specimens from the Isles of Scilly), are known to show a certain level of variability and do not warrant the proposal of a new species for the Levantine material, at least not until it has been subjected to thorough re-examination. Gee (2006) showed that the specimens from the sand flats of Tresco and St. Martins (Isles of Scilly), previously identified by Wells (1961) as *Parastenhelia anglica*, are conspecific with *T. ornatissima* **comb. nov.** This claim was primarily based on the abundance and location data of the material, in conjunction with the description of the male P5 given in Wells (1961).

Thalestrella ornatissima **comb. nov.** shares the presence of the inner seta on P1 exp-2 with *T. bengalensis* **comb. nov.**, *T. psammophila* **comb. nov.** and *T. pulchra* **comb. nov.** but differs from these species in the presence of only two outer spines on P3 exp-3.

The only other records of the type species are those by Willems *et al.* (2008) who obtained it from sandy shell gravel at 17–23m depth in the Koster-area, Swedish west coast, and by Alper & Sak (2018) who collected it in the mediolittoral zone of the Sarımsaklı coast (Balıkesir) in northwestern Turkey. A potentially morphologically close species was recorded under the name *P. cf. ornatissima* from the northern Gulf of Mexico (Thistle 2003; Thistle *et al.* 1995a, 1995b; Suderman & Thistle 1998).

***Thalestrella arenicola* (Noodt, 1964) comb. nov.**

Karllangia arenicola Noodt, 1964

Original description. Noodt (1964): 143–146; Plate 10 (Figs 97–111).

Type locality. Egypt, Red Sea coast near Hurghada; 2–4 m depth, coralline sand.

Notes. As suggested by Gee (2006: 2645) the sexual dimorphism of the antenna was probably overlooked by Noodt (1964) due to the small size of the species. Other discrepancies which are probably attributable to observational errors include (a) the absence of well developed, deeply incised hyaline frills on the body somites (although plain frills have also been observed in *T. obscura* **comb. nov.**); (b) the indistinctly 3-segmented antennary exopod in the female, displaying an incomplete suture dividing the distal segment, (c) the absence of the minute seta on P1 exp-2, (d) the presence of only one seta on P5 endopodal lobe ♂ (the minute outer seta was probably overlooked), and (e) the absence of a conspicuous dorsal spinular row on the caudal ramus. The inner seta of P1 exp-1 is exceptionally long compared to other congeners. *Thalestrella arenicola* **comb. nov.** shares the presence of only two segments distal to the geniculation in the male antennule with *T. bengalensis* **comb. nov.** and *T. reducta* **comb. nov.**, the absence of the inner seta on P1 exp-2 with *T. obscura* **comb. nov.** and *T. reducta* **comb. nov.**, and the presence of only two inner setae on P3 exp-3 with *T. ornatissima* and *T. reducta* **comb. nov.**

Thalestrella arenicola has not been recorded again since its original description (Noodt 1964). Rao (1980) listed “*Karllangia arenicola* [sic] Noodt ?” from an unspecified locality in the Andaman and Nicobar Islands; in all likelihood this record refers to *T. bengalensis*. Colangelo *et al.* (2001) reported on a species, “*Karllangia* cfr. *arenicola*”, collected from a shallow hydrothermal seepage site off the Island of Panarea (Aeolian Islands) in the Tyrrhenian Sea.

***Thalestrella psammophila* (Wells, 1967) comb. nov.**

Karllangia psammophila Wells, 1967

Original description. Wells (1967): 292–294; Text-fig. 52.

Type locality. Mozambique, Inhaca Island; Ilha dos Portuguesos (Elephant Isle); intertidal zone, clean sand.

Notes. *Karllangia psammophila* was originally described as a distinct species (Wells 1967: 292) but subsequently relegated by Wells & Rao (1987: 132) to a subspecies of *K. arenicola* along with another form (*K. arenicola bengalensis*) they described from material collected in the Andaman and Nicobar Islands. Wells & Rao claimed that

K. arenicola was identical to *K. psammophila* in every single aspect except for the lack in both sexes of an attenuated outer distal corner on the posterior margin of the first antennular segment. However, Gee (2006) reinstated the latter and *K. arenicola bengalensis* to full species status based on significant differences in the armature of the swimming legs and the ornamentation of the anal operculum. The author also examined paratype specimens of *K. psammophila*, revealing oversights in Wells's (1967) description of the antenna (abexopodal margin of allobasis with seta; ♀ exopod with two setae on exp-1 and one lateral and two distal setae on exp-2), mandible (basis with three setae; exopod small, with two setae) and maxilliped (syncoxa with one seta; basis with two setae on palmar margin), and suspected that similar corrections apply to *K. bengalensis*.

Thalestrella psammophila shares the presence of only five elements on the female P5 exopod with *T. obscura* **comb. nov.** and *T. bengalensis* **comb. nov.**, however, it differs from the former in the presence of well developed, denticulodigitate hyaline frills on the body somites and the presence of an inner seta on P1 exp-2, and from the latter by the attenuated outer corner of the proximal antennular segment in both sexes, the second outer seta of the female P5 exopod being distinctly longer (*vs* shorter) than the proximalmost seta, and the proximal outer seta of the male P5 exopod distinctly shorter (*vs* longer) than the segment.

***Thalestrella reducta* (Apostolov, 1975) comb. nov.**

Parastenhelia reducta Apostolov, 1975

Original description. Apostolov (1975): 172–175; Fig. 3.

Type locality. Bulgaria, Burgas Province; Tsarevo (formerly Michurin) and Lozenets; sandy bottom, 5 m depth.

Notes. Gee (2006) transferred *Parastenhelia reducta* as *species incertae sedis* to *Karllangia*, based on the female antennule with distinctly compressed distal segments, the maxillipedal syncoxa with only one seta, and the reduced armature and absence of sexual dimorphism of P2–P4. The generic assignment of this species, known only from a single female and male from shallow sandy sediments along the Bulgarian Black Sea coast (Apostolov 1975), was tentative since the male P5 exopod exhibits five setae (instead of four in the remaining *Karllangia* species) and, according to the original text description the antenna lacks sexual dimorphism. Armature patterns on the fifth legs are known to vary in many harpacticoid genera and small differences in setal numbers are therefore likely to be of less significance in delimiting their diagnostic boundaries. We concur with Gee (2006) that the hirsute bulbous structure in Apostolov's Figure 3h, partly concealed by the second segment of the male antennule, is conceivably the modified antennary exopod. Although a re-examination of Apostolov's (1975) specimens would be desirable, there appears to be no reason to question its generic assignment. *Parastenhelia reducta* is here removed from the *incertae sedis* category of *Karllangia* and reinstated as a valid species of *Thalestrella*. Por's (1964) specimens of *T. ornatissima*, the geographically closest record of the genus, agree with *T. reducta* **comb. nov.** in the length:width proportions of the female P5 exopod but conspecificity can be ruled out on the basis of differences in the anal operculum and caudal ramus length (as measured in dorsal aspect).

Thalestrella reducta **comb. nov.** can readily be distinguished from its congeners by the reduced armature on P3–P4 (P4 exp-3 with two inner setae *vs* three, P3–P4 exp-3 with one inner seta *vs* two) and the presence of six elements on the male P5 exopod. Apostolov (1975) did not figure the deeply incised hyaline frills on the body somites, however, his illustration (Fig. 3a) of the urosome showing the long pleural extensions (probably an optical section of the frills) indicates their presence. *T. reducta* is the only species in the genus that displays four setae on the mandibular exopod.

***Thalestrella bengalensis* (Wells & Rao, 1987) comb. nov.**

Karllangia arenicola bengalensis Wells & Rao, 1987

Original description. Wells & Rao (1987): 131–132; Fig. 110; Table 7.

Type locality. Andaman and Nicobar Islands: North Andaman, Mayabandar, Seaward Bay (12°52'06"N,

92°56'48"E); algal sand rich in detritus; fine to medium sand with a small amount of shell gravel; taken from surface to 20 cm deep between low and half-tide levels.

Notes. Wells & Rao (1987: 132, 218; Table 7) considered their specimens to be more or less intermediate between *K. arenicola* s.str. and *K. psammophila*. They considered all three of them as morphs of a single polytypic species and granted subspecific status to each of these potentially allopatric "populations". Gee (2006: 2644) re-examined material of *K. psammophila* and, consequently, reversed the situation by resurrecting them as valid species. According to Wells & Rao (1987: Fig. 110c) the female antennary exopod of *T. bengalensis* **comb. nov.** differs from the typical condition in bearing only one lateral seta on exp-2.

In addition to the type locality, the species was also recorded from the Sawai Bay of Car Nicobar Island (Wells & Rao 1987).

***Thalestrella obscura* (Mielke, 1994b) comb. nov.**

Karllangia obscura Mielke, 1994b

Original description. Mielke (1994b): 148, 150–152; Figs 7–8.

Type locality. Costa Rica, beach slope of Manzanillo (Caribbean coast).

Notes. *Thalestrella obscura* **comb. nov.** occurs sympatrically with *T. pulchra* **comb. nov.** at the type locality. It differs from the latter by the absence of well developed denticulodigitate hyaline frills on the abdominal somites and the inner seta on P1 exp-2, and by the presence of a tuft of very long setules on the male antennary allobasis near the articulation with the exopod, and only five elements on the female P5 exopod.

***Thalestrella pulchra* (Mielke, 1994b) comb. nov.**

Karllangia pulchra Mielke, 1994b

Original description. Mielke (1994b): 142–149; Figs 1–6.

Type locality. Costa Rica, beach slope of Manzanillo (Caribbean coast).

Note. See *T. obscura* **comb. nov.** for differentiating characters.

Key to species of *Thalestrella* Monard, 1935a

A dichotomous key to the six valid species of *Thalestrella* was provided by Gee (2006) which is updated below to include *T. reducta* **comb. nov.** and to rectify a mistake in his couplet 3 (*T. obscura* **comb. nov.** has only five setae on P5 exopod ♀). Additional unidentified species have been recorded from Papua New Guinea (Willen 2000), the Galápagos Archipelago (Mielke 2003), Zanzibar (Gheerardyn 2007; Gheerardyn *et al.* 2008; Callens *et al.* 2012) and possibly Heron Island (Iwasaki 1994), indicating a circum(sub)tropical distribution of the genus.

1. P3 exp-3 with two inner setae2.
- P3 exp-3 with three inner species4.
2. P4 exp-3 with two inner setae; P3–P4 exp-3 with one inner seta; P5 exopod ♂ with five setae
..... *T. reducta* (Apostolov, 1975) **comb. nov.**
- P4 exp-3 with three inner setae; P3–P4 exp-3 with two inner setae; P5 exopod ♂ with four setae3.
3. P1 exp-2 without inner seta; P5 exopod ♀ about three times as long as maximum width; P5 exopod ♂ semicircular; anal operculum without spinous projections but fringed by small setules/spinules *T. arenicola* (Noodt, 1964) **comb. nov.**
- P1 exp-2 with inner seta; P5 exopod ♀ about five times as long as maximum width; P5 exopod ♂ about twice as long as wide; anal operculum with 6–8 conspicuous spinous projections *T. ornatissima* Monard, 1935a.
4. Antennule ♀ 8-segmented; P3 exp-3 without sexual dimorphism; P5 exopod ♀ with five setae; anal operculum with about 40 setules5.
- Antennule ♀ 9-segmented; outer spine of P3 exp-3 very reduced in ♂; P5 exopod ♀ with six setae; anal operculum with about 12–25 spinules6.
5. Outer corner of proximal antennary segment attenuated; second outer seta of P5 exopod ♀ distinctly longer than proximalmost; proximal outer seta of P5 exopod ♂ distinctly shorter than segment *T. psammophila* (Wells, 1967) **comb. nov.** ¹

- Outer corner of proximal antennular segment normal; second outer seta of P5 exopod ♀ very short, distinctly shorter than proximalmost; proximal outer seta of P5 exopod ♂ distinctly longer than segment *T. bengalensis* (Wells & Rao, 1987) **comb. nov.**
- 6. Hyaline frills of abdominal somites plain; P1 exp-2 without inner seta; P5 exopod ♀ with five setae *T. obscura* (Mielke, 1994b) **comb. nov.**
- Hyaline frills of abdominal somites lobate; P1 exp-2 with inner seta; P5 exopod ♀ with six setae *T. pulchra* (Mielke, 1994b) **comb. nov.**

¹According to Wells (1967: Text-fig. 52M) P2 exp-3 has three inner setae which is a unique condition within the genus. The extreme distal position of the third inner seta, originating from the inner distal corner suggests that Wells observed an aberrant specimen with a supernumerary element on the P3 exopod. Gee (2006) re-examined the type material from Inhaca Island and made some corrections to the original description but did not comment on this character state. Although he stated that there are "...significant differences in the setation of the swimming legs ... to warrant specific status for both these forms" he refrained from using them in his key. Wells & Rao (1987: 218, Table 7) used it as a character to differentiate both subspecies but Wells (2007: 596) pointed out that his original observation was probably wrong, an opinion that is adopted here.

***Paraleptomesochra* Wells, 1967**

The justification for the proposal of this genus (Wells 1967: 300) was based exclusively on the 2-segmented condition of the P1 exopod in the type species *P. minima* Wells, 1967. Additional apomorphic character states shared with its congener, *P. wellsii* Rao, 1972, included the 8-segmented condition of the ♀ antennule, the presence of a modified distal element ("... expanded, bifid, hyaline structure...") on exp-2 of the antenna, proximal endopodal segment of antenna without allobasis, reduction of the mandibular exopod (absent or represented by short seta), mandibular basis with only two setae; maxilliped with reduced armature (at most one seta on syncoxa, none on basis), inner basal spine of ♂ P1 modified (with recurved tip), various reductions in the armature of P2–P4 (Tables 1–2), P5 endopodal lobe ♀ with only three elements, and P5 exopod ♂ with only four elements. The modification of the inner basal spine of P1 is shared with *Psammoleptomesochra* and *Foweya*; however, in members of the latter genus the inner spine is not recurved but typically straight, bifid apically, and carrying a flagellate extension at its tip (cf. Gee 2006: Figs 10D, 13A). It is conceivable that, within the Parastenheliidae, *Paraleptomesochra* is most closely related to *Psammoleptomesochra* (Mielke 1994a).

Both species of *Paraleptomesochra* are small-sized (♀: 274–336 µm; ♂: 276–315 µm) and exclusively known from sandy beaches. Rao (1980: 166) listed a species under the name "*Paraleptomesochra africana* (Kunz)" but this is a *lapsus calami* referring to *Praeleptomesochra africana* (Kunz, 1951) (family Ameiridae) (cf. Dev Roy & Venkataraman 2018). Finally, as yet unidentified species of *Paraleptomesochra* have been reported from shallow depths off the coast of northwestern Florida (Suderman & Thistle 1998) and from Heron Reef, Great Barrier Reef (Iwasaki 1994).

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P1 inner basal spine, P5–P6 and urosomal segmentation. Body cylindrical, short; posterior margin of prosomites and urosomites (except anal somite) with denticulodigitate hyaline frills. Rostrum fused at base, small, pointed. Anal operculum semicircular, bordered with fine setules. Caudal ramus about as long as wide, with dorsal spinular row; with at least six setae, setae IV–V not basally inflated in ♀.

Antennule ♀ elongate and 8-segmented in ♀, segment 1 not elongate, segments 6–7 shortest, with aesthetascs on segments 4 and 8. Antennule ♂ haplocer with three segments distal to geniculation; segmentation partly unconfirmed but probably at least 9-segmented with segmental homologies as follows: I, II–VIII, IX–XII, XIII, XIV–XVIII, XIX–XX, XXI–XXIII, XXIV–XXV, XXVI–XXVIII. Antenna not sexually dimorphic; proximal endopodal segment completely separated from basis, without seta on abexopodal margin; exopod 2-segmented, proximal segment with two setae, distal segment with 1–2 lateral and two apical elements (one of which enlarged, hyaline and bifid); distal endopodal segment without penicillate elements. Mandible with two elements on basis; endopodal armature unconfirmed; exopod absent or represented by a short seta. Maxillulary coxal epipodite unconfirmed. Maxilla with three endites on syncoxa; endopod unconfirmed. Maxilliped with 0–1 setae on syncoxa; basis without armature on palmar margin; endopod represented by claw without accessory setae.

P1 inner basal spine sexually dimorphic (recurved in ♂). P1 exopod 2-segmented; exp-2 slightly longer than

exp-1, with two distal and two outer pinnate elements. P1 endopod 2-segmented; enp-1 elongate, at most slightly longer than exopod, with short inner seta, segment margins probably without area of reduced chitinization; enp-2 very small, with one outer distal spine and one inner distal geniculate seta. P2–P4 rami 3-segmented; enp-2 and -3 without inner seta(e); inner seta of P2–P3 exp-1 reduced in size, absent in P4. P2–P3 endopods ♂ without sexual dimorphism. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	1.1.121	1.0.0(1–2)0
P3	1.1.121	1.0.0(1–2)0
P4	1.1.(1–2)21	1.0.0(1–2)0

P5 ♀ endopodal lobe with three setae (one inner, two distal); inner margin without transverse striae. P5 ♀ exopod ovate, with six elements. P5 ♂ endopodal lobe with 1–2 elements; exopod 1-segmented, with four elements. Vestigial P6 ♀ represented by one seta. P6 ♂ with two setae.

Type species. *Paraleptomesochra minima* Wells, 1967 (by original designation).

Other species. *P. wellsi* Rao, 1972.

Notes. Both Wells (1967) and Rao (1972) state that the rostrum is fused to the cephalothorax which, if correct, would be a unique condition in the family. The segmental homologies of the haplocer male antennule are unconfirmed although Rao (1972) describes it as 7-segmented with the sixth segment partially divided by an indistinct suture in *P. wellsi*. The description of the armature on the caudal ramus (with four setae in *P. minima*, five in *P. wellsi*) is almost certainly incorrect. The presence/absence of the coxal epipodite of the maxillule is unconfirmed since neither Wells (1967) nor Rao (1972) describe the appendage. Similarly, it is not clear whether the maxillary endopod is expressed or the maxillipedal claw has any accessory elements.

Paraleptomesochra minima Wells, 1967

Original description. Wells (1967): 297–300; Text-fig. 54.

Type locality. Mozambique, Inhaca Island; Ilha dos Portuguesos (Elephant Isle); intertidal zone, clean sand.

Notes. The species differs from its congener *P. wellsi* primarily in the armature of P4 exp-3 (121 vs 221), P2–P4 enp-3 (one apical element vs two) and the endopodal lobe of the male P5 (two setae vs one). Additional differences include the caudal ramus which is slightly longer than wide in *P. minima* (vs as long as wide), the length of P1 enp-2 which is longer in *P. wellsi* (and the position of its inner seta being more proximal), the morphology of the setae on P1 exp-2 and the inner distal seta of P2–P4 exp-3 which are characterized by a row of stiff pinnules near the apex in *P. wellsi*, and the shape of the male P5 exopod (trapezoid vs oval).

Wells (1967: Text-fig. 54F) shows three setae on the mandibular basis with the two proximal ones at a considerable distance from the distal one. It is conceivable that the short proximal “setae” are ornamentation elements similar to those described and figured by Mielke (1994b: Figs 2D, 8A) for *Thalestrella pulchra* and *T. obscura*. Rao (1972: 4F) illustrated similar (but more) setules in his description of *P. wellsi* in addition to two distal setae. Wells (1967) also described the mandibular endopod as 2-segmented but this is unlikely; the exopod is apparently lacking but represented by a seta in *P. wellsi*. The absence of the seta on the maxillipedal syncoxa (present in *P. wellsi*) requires confirmation.

Although Rao (1972) had previously described *P. wellsi* from mainland India, both Rao (1975) and Wells & Rao (1987) attributed their material from the Andaman and Nicobar Islands (Middle and South Andaman, Car Nicobar Island) to the geographically much more distant *P. minima*. The latter was subsequently recorded from the littoral zone of Lakshadweep (formerly known as the Laccadive, Minicoy and Aminidivi Islands) (Rao & Misra 1983; Rao 1991) and Little Andaman (Rao 1993).

TABLE 2. Differentiating characters between genera of Parastheneliidae (apo = spinous apophysis; dis = distal; benp = baseendopod; enp = endopod; exp = exopod; lat = lateral).

Character	<i>Parasthenelia</i>	<i>Microthalestris</i>	<i>Thalestrella</i>	<i>Paraleptomesochra</i>	<i>Psammoleptomesochra</i>	<i>Foweya</i>	<i>Johnwellisia</i>	<i>Karayugia</i>	<i>Penicilliaris</i>	<i>Porirualia</i>
Rostrum	short	short	short	short	short	short	short	short	short	large
Antennule segment 1	short	short	short	short	short	short	elongate	short	short	short or elongate
Antennule ♀ segmentation	8- or 9-segmented	9-segmented	8- or 9-segmented ¹	8-segmented	9-segmented	9-segmented	9-segmented	9-segmented	8- or 9-segmented	9-segmented
Antennule ♂ type	haplocer	haplocer	subchirocer	haplocer	haplocer	subchirocer	haplocer	haplocer	haplocer	haplocer
Antennule ♂ number of segments distal to geniculation	three	four	2-3	three	unknown	three	four	Four	four	four
Antenna abexopodal seta	present	present	present	absent	present	present	absent	present	present	present
Antenna sexual dimorphism	absent	absent	present	absent	absent	absent	absent	absent	absent	absent
Antenna lateral spines of enp-2	unmodified	unmodified	unmodified	unmodified	unmodified	unmodified	unmodified	unmodified	unmodified	unmodified
Antenna armature exp	2; 1-2 lat + 3 dis	1-2; 1-2 lat + 3 dis	1-2; 1 lat + 2 dis ²	2; 1 lat + 2 dis	2; 2 dis	2; 2 lat + 3 dis	2; 1 lat + 3 dis	2; 2 lat + 3 dis	2; 1-2 lat + 3 dis	2; 2 lat + 2-3 dis
Mandible armature basis	2-4	2-4	3	1-2	2	3	3	3	2	3-4
Mandible armature exp	1-segmented with 3 setae or seta on minute knob	1-segmented with 2-5 setae	1-segmented with 2-4 setae	seta arising from basis or absent	minute seta arising from basis	1-segmented with 4 setae	minute seta on small process	1-segmented with 2 setae	1-segmented with 2 setae	1-segmented with 3 setae
Maxillule coxal epipodite	present	present	present	unconfirmed	absent	present	present	present	unconfirmed	present
Maxilliped syncoxal setae	2-3	2-3	1	0-1	1	3	2	2	0-1	2
Maxilliped basal setae	1	1-2	0 or 2	0	0	2	2	2	1	1
P1 inner basal spine ♂ modified	no	no	no	yes	yes	yes	no	no	no	no
P1 exp segmentation	3-segmented	3-segmented	3-segmented	2-segmented	3-segmented	3-segmented	3-segmented	3-segmented	3-segmented	3-segmented
P1 exp segment proportions	subequal	exp-2 >>>	subequal	subequal	subequal	exp-2 >	subequal	exp-2 >>>	exp-2 >>>	subequal
P1 emp-1 thinner cuticle area	absent	absent	present	absent	present	present	absent	absent	absent	absent
P1 penicillate elements exp/emp	absent	absent	absent	absent	absent	absent	absent	absent	present	absent
P2 exp-3 number of inner setae	1	1 ³	2	1	0	2	1	1	1	1
P2 exp-3 number of outer spines	3	3	3	1	2	3	3	3	3	3
P2 emp-3 ♀ number of inner setae	0-1	0-1	1	0	0	2	1	1	1	1
P2 emp ♂ armature	1.221 or 0.121	1.1.(1-2)21 or (0-1).1.021	1.1.121	1.0.0(1-2)0	0.0.0.10	1.321	1.121	1.1.121	1.1.121	1.1.121 or 1.221

P3 exp-1 inner seta	absent/present	absent/present	absent	present	absent	present	present	present	present	present	present	present
P3 exp-3 number of elements	(7?)–8	6–8	7–8	4	4	8	8	8	7–8	8	7–8	7–8
P3 exp-2 ♀ inner seta	present	present	present	absent	absent	present	present	present	present	present	present	present
P3 exp-3 ♀ number of inner setae	0 or 2	1–3	1–2	0	0	3	2	2	2 ⁴	2	2 ⁴	2
P3 exp-3 ♀ outer spine	present	present	present	absent	present	present	present	present	present	present	present	present
P3 exp ♂ spinous apophysis	present	present	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
P3 exp ♂ armature	0–1.1.02 + apo	0–1.1(0–1)2 + apo	1.1.(1–2)21	1.0.0(1–2)0	0.0.010	1.1.321	1.1.021	1.1.02 + apo	1.1.02 + apo	1.1.02 + apo	1.1.02 + apo	1.1.121 or 1.221
P4 exp-3 number of elements	7–8	6–8	7–8	4–5	5	8	8	8	7–8	8	7–8	7
P4 exp-2 ♀ inner seta	present	present	present	absent	absent	present	present	present	present	present	present	present
P4 exp-3 ♀ number of inner setae	0 or 2	1–2	1–2	0	0	2	1	1	1–2	1	1–2	2
P4 exp-3 ♀ outer spine	present	present	present	absent	present	present	present	present	present	present	present	present
P5 exp ♀ number of elements	6	6 or 8	5–6	6	6	6	6	6	6	6	6	6
P5 exp ♀ number of elements	5	5 ³	5	3	4	5	5	5	5	5	5	5
P5 exp ♀ inner margin striae	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
P5 exp ♂ number of segments	1, 2 or 3	1 or 3	1	1	1	1	2	2	1	2	1	1
P5 exp ♂ number of elements	6–7	6–7	4–5	4	5	5–6	4	5	7	5	7	5–6
Caudal ramus setae IV–V ♀	V occasionally swollen	V usually and IV occasionally modified	IV occasionally not modified	not modified	not modified	not modified	not modified	not modified	not modified	not modified	IV–V usually modified	not modified

¹ Occasionally indistinctly 9-segmented with apical segment showing partial surface suture (Gee 2006: Fig. 3A–B).

² ♀ condition; exopodal segments in ♂ are of different size with only one seta on proximal segment and all lateral setae enlarged and highly plumose. Note also that Apostolov 1975: Fig. 3i) gives a divergent formula (1. 2 lat + 2 dis) for *K. reducta* which requires confirmation. Similarly, Noodt (1964: Fig. 104) shows an indistinctly 3-segmented exopod with a suture dividing the distal segment, resulting in a formula 1.1.2 dis; this is likely to be based on an observational error.

³ Brady (1910: Textfig. VIII, Fig. 3) reports two inner setae in *M. gracilis* but given the inadequacy of the rest of his description this observation is to be considered questionable.

⁴ Three inner setae in *Pe. penicillata* sp. nov. due to failure of separation of exp-2 and exp-3 [1.321].

⁵ Brady's (1910: Textfig. VIII, Fig. 3) dubious report of four setae requires confirmation.

Paraleptomesochra wellsii Rao, 1972

Original description. Rao (1972): Fig. 4.

Type locality. India, Andhra Pradesh, Visakhapatnam (formerly Waltair), 17°43'30"N 83°20'30"E; intertidal zone, fine and medium sand, 10–30 cm below surface near half-tide level.

Notes. Rao (1972) describes the male antennule as 7-segmented with the sixth segment being partly subdivided. The segmentation pattern is here provisionally reinterpreted as 9-segmented due to segment 4 (XIII) having been overlooked and the three segments distal to the geniculated accepted here as fully discrete. Rao's (1972: Fig. 4D) illustration of two aesthetascs originating from the swollen segment 5 must be attributed to an observational error.

The species was subsequently recorded from two localities (Konark = Konarak, Puri) in Odisha (formerly Orissa) in the Bay of Bengal (Rao 1989).

Psammoleptomesochra Mielke, 1994a

Mielke (1994a: 258) placed *Psammoleptomesochra* in the “*Leptomesochra*-complex”, an artificial group of genera in the Ameiridae (Lang 1965; Wells 1967), and recognized a certain closeness with *Parapseudoleptomesochra reducta* Rao, 1972 (now type species of *Raoleptomesochra* Karanovic, 2004) and particularly *Paraleptomesochra*. *Psammoleptomesochra* displays many autapomorphic character states including, (a) antennary exopod without lateral setae on exp-2; (b) mandibular basis with two setae; (c) mandibular exopod vestigial, represented by minute seta; (d) coxal epipodite on maxillule absent; (e) maxillipedal basis without setae; (f) P1 exp-2 without inner seta; (g) P2 exp-3 without inner setae; and (h) P2–P4 enp-3 with reduced distal setae (represented by two setules).

Psammoleptomesochra shares the area of reduced chitinization on the elongate P1 enp-1 with *Paraleptomesochra* and *Foweya*, while the sexual dimorphism of the inner basal spine on P1 is also displayed in *Foweya* and *Thalestrella*. *Paraleptomesochra* has many reductions in common with *Psammoleptomesochra* including the loss of setation elements on the mandibular basis and exopod, maxillipedal syncoxa and basis, P2–P4 and endopodal lobe of ♀ P5 (Table 2). In both genera the armature of P2–P4 is strongly reduced but not all setal losses are evidence for their common ancestry. For example, as a result of convergent evolution, both genera display only four elements on P3 exp-3 but in the former the pattern consists of one inner, two distal and one outer element(s) [121] while in the latter there are two distal and two outer elements [022].

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P5–P6 and urosomal segmentation. Body subcylindrical; posterior margin of cephalothorax and all somites (except anal somite) with deeply divided, denticulodigitate, hyaline frills. Rostrum defined at base, small, reaching to proximal third of second segment of antennule; linguiform with rounded apex. Anal operculum semicircular, bordered with few (around six) strong spinules. Caudal ramus about twice as long as wide, with dorsal oblique row of spinules; with six setae, setae II–III short, pinnate and spiniform, setae IV–V not swollen at base.

Antennule short and 9-segmented in ♀, segment 1 not elongate, segments 7–8 shortest, with aesthetascs on segments 4 and 9; haplocer in ♂, segmentation, position of geniculation and segmental homologies unconfirmed. Antenna with basis; proximal endopodal segment with short abexopodal seta; distal endopodal segment without penicillate elements; exopod 2-segmented, proximal segment with two lateral setae, distal segment with two apical elements. Mandible with two elements on basis; endopod with two lateral and 5–6 apical setae; exopod vestigial, represented by short seta. Maxillary coxal epipodite absent. Maxilla with three endites on syncoxa; endopod discrete, with three setae. Maxilliped with one seta on syncoxa; basis without seta(e) but with short longitudinal spinular row on palmar margin; endopod represented by claw with one accessory seta.

P1 inner basal spine sexually dimorphic, recurved in ♂. P1 exopod 3-segmented, segments subequal in length; exp-2 without inner seta; exp-3 with two pinnate spines and two geniculate setae. P1 endopod 2-segmented; enp-1 longer than exopod, with well developed, pinnate inner seta arising from area of reduced chitinization in middle third of segment; enp-2 with one naked minute seta and two claws (one geniculate, one non-geniculate). P2–P4 rami 3-segmented; endopods short, at most as long as exp-1 and -2 combined; inner distal element of P2–P4 exp-3 setiform and thin; endopodal segments without inner setae except for P4 enp-1 bearing long pectinate seta; P2–P4 enp-3 with two vestigial distal setae and one outer spine. P2–P4 endopods ♂ without sexual dimorphism. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	10.0.022	0.0.021
P3	0.0.022	0.0.021
P4	0.0.122	1.0.021

P5 ♀ endopodal lobe with four elements, innermost spiniform; inner margin without transverse striae; exopod elongate, with six naked setae. P5 ♂ endopodal lobe with two elements, outer one shortest; exopod 1-segmented, with five elements, inner one vestigial. Vestigial P6 ♀ represented by two setae. P6 ♂ with two setae and one spine (innermost element).

Type and only species. *Psammoleptomesochra australis* Mielke, 1994a (by original designation).

Type locality. Chile, Los Lagos Region, Chiloé archipelago, southeastern coast of Isla Chiloé, Quellón Viejo; sandy beach.

Original description. Mielke (1994a): 252–258; Figs 1–4.

Notes. The endopodal armature pattern adopted herein differs from Mielke's (1994a: 257) formula in two aspects: the apical spiniform element on enp-3 is here considered as the homologue of the outer spine in other genera, and the two minute and fine setae originating from the inner corner of enp-3 are included in the formula as distal elements (Table 1). Mielke (1994a) observed variability in the armature of the P5 endopodal lobe (with 2–3 apical setae) in the female and the P5 exopod (distal seta on outer margin variable in length) in the male.

Foweya Gee, 2006

Gee (2006) recognized the close resemblance between *Parastenhelia anglica* and *Karllangia tertia* and removed both species from their respective genera and placed them in a newly proposed genus *Foweya*. Both *Foweya anglica* (Norman & Scott, 1905) and *F. tertia* (Kunz, 1975) exhibit the narrowing of the outer cuticle of P1 enp-1 at around the insertion level of the inner seta (shared with *Thalestrella* and *Psammoleptomesochra*), the bifid, sexually dimorphic inner spine on the P1 basis in the male (shared with *Paraleptomesochra* and *Psammoleptomesochra*), the 10-segmented male antennule with only three segments distal to the articulation, the absence of sexual dimorphism in the endopod of P3 (shared with *Thalestrella*, *Paraleptomesochra* and *Psammoleptomesochra*), and the most primitive swimming leg armature formula within the family, including two inner setae on P2 exp-3 and enp-3 and three inner setae on P3 enp-3. Gee (2006) confirmed that the specimens, previously identified as *Parastenhelia anglica* from St. Agnes, St. Mary's and Tresco (Isles of Scilly) by Wells (1961, 1970) and from Namibia by Kunz (1963), are conspecific with *Thalestrella ornatisissima* (type locality: Roscoff, Brittany), and *Foweya tertia* (type locality: Eastern Cape, South Africa), respectively.

Males of the two known *Foweya* species can be differentiated by the segmentation of the P2 endopod (3-segmented in *F. anglica*, 2-segmented in *F. tertia*) and the morphology of the fifth legs (with five exopodal setae in *F. tertia* vs six in *F. anglica*; endopodal lobe relatively weakly developed and both setae equally long in *F. tertia* vs well developed lobe and outer endopodal seta distinctly longer than inner one in *F. anglica*). Females (and males) can be distinguished by the ornamentation of the anal operculum (with approximately 30 small, closely set denticles in *F. anglica* vs numerous very fine spinules in *F. tertia*).

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P1 inner basal spine, P5–P6 and urosomal segmentation; occasionally in segmentation of P2 endopod. Body subcylindrical, short; posterior margin of cephalothorax and somites bearing P2–P5 with plain hyaline frills; remaining urosomites (except anal somite) with denticulodigitate hyaline frills. Rostrum defined at base, of moderate size, reaching at most to end of second segment of antennule; linguiform. Anal operculum semicircular, bordered with fine spinules or denticles. Caudal ramus wider than long, with dorsal spinular row; with seven setae, setae IV–V not basally inflated in ♀.

Antennule elongate and 9-segmented in ♀, segment 1 not elongate, segments 5–8 shortest, with aesthetascs on segments 4 and 9; haplocer and 10-segmented with three segments distal to geniculation in ♂, with geniculation between segments 7 and 8, segments 5–7 swollen and with aesthetasc on segment 5; segmental homologies in ♂: I, II–VIII, IX–XII, XIII, XIV–XVI, VII–XVIII, XIX–XX, XXI–XXIII, XXIV–XXV, XXVI–XXVIII. Antenna not sexually dimorphic; proximal endopodal segment largely fused to basis forming allobasis, with pinnate seta on abexopodal margin; exopod 2-segmented, proximal segment with two setae, distal segment with two lateral and

three apical elements; distal endopodal segment without penicillate elements. Mandible with three elements on basis; endopod with eight setae; exopod 1-segmented, with four setae. Maxillary coxal epipodite represented by one seta. Maxilla with three endites on syncoxa; endopod discrete, with 4–5 setae. Maxilliped with three setae on syncoxa; basis with two setae on palmar margin; endopod represented by pinnate claw, accompanied by two accessory setae.

P1 inner basal spine sexually dimorphic (with bifid tip in ♂). P1 exopod 3-segmented; exp-2 only slightly longer than exp-1, with inner seta; exp-3 small, with two pinnate spines and two geniculate setae. P1 endopod 2-segmented; enp-1 elongate, almost twice as long as exopod, with moderately long, pinnate inner seta originating from proximal third (at 35% of ramus length in a region of reduced chitinization of segment wall); enp-2 very small, with one naked minute seta and two unipinnate claws. P2–P4 rami 3-segmented (except P2 endopod ♂ occasionally 2-segmented); P3 endopod ♂ not sexually dimorphic. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	1.1.223	1.1.221 [♂: 1.1.221 or 1.321]
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221

P5 ♀ endopodal lobe with five setae; inner margin without transverse striae; exopod elongate, with six elements. P5 ♂ endopodal lobe with two elements; exopod 1-segmented, with 5–6 elements. Vestigial P6 ♀ represented by three short setae. P6 ♂ with three setae.

Type species. *Parastenhelia anglica* Norman & Scott, 1905 = *Foweya anglica* (Norman & Scott, 1905) (by original designation).

Other species. *Karllangia tertia* Kunz, 1975 = *Foweya tertia* (Kunz, 1975).

***Foweya anglica* (Norman & Scott, 1905)**

Parastenhelia anglica Norman & Scott, 1905

Parastenhelia anglica was first described by Norman & Scott (1905: 289) and subsequently illustrated by the same authors (Norman & Scott 1906: 148) from one or two female specimens dredged outside Fowey harbour, Cornwall. The species was not reported again until Wells (1963b) obtained it on a low spring tide from coarse shell gravel at Angus Rock in Strangford Lough, Northern Ireland. Ventham (2011) reported *F. anglica* from gravel/mudstone material collected at 21.2 m depth along the Sussex coast. Noli *et al.* (2018) recorded the species from fine littoral sands in Porto Frailis along the eastern coast of Sardinia (Ogliastra region). Finally, Packmor & George (2018) added another record from the littoral zone at Ponta Delgada in Madeira. Jayabarathi (2016) claimed to have found *F. anglica* (or *F. angelica* [*sic*]) in South Andaman but the authenticity of this record is doubtful.

Original description. Norman & Scott (1905): 289–290 (♀ only).

Additional descriptions. Norman & Scott (1906): 148–150; Plate X (Figs 10–11), Plate XIII (Figs 4, 9), Plate XIV (Fig. 6), Plate XVI (Fig. 4), Plate XVII (Fig. 4), Plate XXI (Fig. 2). Gee (2006): 2623–2631; Figs 7–11.

Type locality. England, south Cornwall, Fowey; dredging outside of Fowey harbour; 7.3–9.1 m.

***Foweya tertia* (Kunz, 1975)**

Parastenhelia anglica Norman & Scott, 1905 sensu Kunz (1963)

Karllangia tertia Kunz, 1975

Foweya tertia appears so far to be restricted to southern Africa. In addition to the type locality in the Eastern Cape, Kunz (1963) had previously recorded it (as *P. anglica*) from a sandy littoral substrate in an undisclosed locality (possibly Lüderitz Bay) in Namibia. Colangelo *et al.* (2001) reported *Karllangia tertia* from a shallow hydrothermal vent site off the Island of Panarea in the Tyrrhenian Sea but this record may refer to a different species.

Original description. Kunz (1975): 198–200; Figs 154–176.

Additional descriptions. Kunz (1963 – as *P. anglica*): 41–43; Figs 38–48. Gee (2006): 2631–2634; Figs 12–13.

Type locality. South Africa, Eastern Cape, off East London; shell gravel in tidal pools on a reef.

***Karaytugia* gen. nov.**

urn:lsid:zoobank.org:act: 3541F2B6-4847-4ECE-B77A-C4D55732718F

Kuru & Karaytuğ (2015) described a new species, *Parastenhelia aydini*, from a Turkish beach in the Eastern Mediterranean and considered it morphologically most similar to *Pa. spinosa*. The authors refer to their unpublished observations but it is not clear which “population” they identified as *Pa. spinosa*. They differentiated *Pa. aydini* from the latter by the combination of the following characters: (a) ♀ antennule 9-segmented; (b) spinular rows near outer margin of P1–P4 bases significantly reduced; (c) P4 enp-3 with four setae in both sexes; (d) ornamentation of endopodal and exopodal setae of ♀ P5 different; (e) caudal ramus seta V of ♀ not swollen near the base; (f) modified element on the seventh segment of ♂ antennule not present; (g) apophysis on ♂ P3 enp-3 notched; and (h) ♂ P5 exopod 2-segmented, five setae in total.

Unique characters displayed by *Pa. aydini* include (a) the modification of the endopodal claw on the maxilliped; the distal half does not taper to a sharp tip as in other members of the family, forming instead a spatulate structure fringed with a series of densely arranged serrations around the inner margin and rounded apex; (b) P1 exp-3 with one very long naked seta and three claws of different lengths, the longest one being 0.8 times the length of exp-2; (c) P1 enp-2 claws radically divergent in size, with large one nearly three times longer than short one; (d) inner seta of P2–P3 enp-1 reduced; (e) spinous apophysis on ♂ P3 endopod with foot-shaped tip; and (f) ♂ P5 exopod 2-segmented, with one very long outer seta on exp-1 and four elements on exp-2; the only other species in the Parastenheliidae that display a 2-segmented exopod are *Parastenhelia willemvervoorti* **sp. nov.** and *Johnwellsia bipartita* **gen. et sp. nov.** which have six short elements, and one spine and two setae, respectively, on exp-2. Based on this combination of apomorphic character states, *Pa. aydini* is here fixed as the type species of a new genus, *Karaytugia* **gen. nov.**

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P2–P3 endopods, P5–P6 and urosomal segmentation. Body subcylindrical, short; posterior margin of cephalothorax and somites bearing P2–P5 with plain hyaline frills; remaining urosomites (except anal somite) with serrate hyaline frills. Rostrum defined at base, of moderate size, reaching to about halfway second segment of antennule; elongate triangular. Anal operculum semicircular, bordered with fine spinules. Caudal ramus wider than long, with conspicuous spinular ornamentation; with seven setae, setae IV–V not basally inflated in ♀.

Antennule elongate and 9-segmented in ♀, segment 1 not elongate, segments 7–8 shortest, with aesthetascs on segments 4 and 9; haplocer and 11-segmented in ♂, with geniculation between segments 7 and 8, segment 5 swollen and with aesthetasc; segmental homologies in ♂: I, II–VIII, IX–XII, XIII, XIV–XVII, XVIII, XIX–XX, XXI–XXII, XXIII, XXIV–XXV, XXVI–XXVIII. Antenna not sexually dimorphic; proximal endopodal segment largely separated from basis, with pinnate seta on abexopodal margin; exopod 2-segmented, proximal segment with two setae, distal segment with two lateral and three apical elements; distal endopodal segment without penicillate elements. Mandible with three elements on basis; endopod with eight setae; exopod 1-segmented, with two setae. Maxillulary coxal epipodite represented by one seta. Maxilla with three endites on syncoxa; endopod discrete, with three setae. Maxilliped with two setae on syncoxa; basis with two setae and longitudinal spinular row on palmar margin; endopod represented by conspicuously serrated claw, accompanied by three accessory setae.

P1 inner basal spine not sexually dimorphic. P1 exopod 3-segmented; exp-2 much longer than others, nearly three times as long as exp-1 and about half as long as enp-1, with short inner seta; exp-3 small, with two pinnate spines, one geniculate seta and one naked seta. P1 endopod 2-segmented; enp-1 elongate, about 1.5 times length of exopod, with short, proximally inserted, pinnate inner seta, segment margins without area of reduced chitinization; enp-2 very small, with one naked minute seta and two dentate claws. P2–P4 rami 3-segmented; inner seta of P2–P3 exp-1 reduced in size, absent in P4. P2–P3 endopods ♂ 3-segmented. P2 slightly more robust in ♂. P3 endopod ♂ without inner setae (*vs* two in ♀) on enp-3 and outer spine modified into apically truncated spinous apophysis. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	1.1.123	1.1.121
P3	1.1.323	1.1.221 [♂: 1.1.02 + apo]
P4	0.1.323	1.1.121

P5 ♀ endopodal lobe with five setae, outermost well developed, innermost shortest; inner margin without transverse striae. P5 ♀ exopod elongate, with six elements. P5 ♂ endopodal lobe with two elements, outer one shortest; exopod 2-segmented, with one long outer seta on exp-1 and four elements on exp-2. Vestigial P6 ♀ represented by three minute setae. P6 ♂ with three setae.

Etymology. The genus name is dedicated to Prof. Süphan Karaytuğ (Mersin University, Turkey), in recognition of his contributions to the harpacticoid fauna of Turkey, and under whose mentorship the next generation of harpacticoid experts in his home country emerged. Gender: feminine.

Type and only species. *Parastenhelia aydini* Kuru & Karaytuğ, 2015 = *Karaytugia aydini* (Kuru & Karaytuğ, 2015) **comb. nov.** (by original designation herein).

Karaytugia aydini (Kuru & Karaytuğ, 2015) **comb. nov.**

Parastenhelia aydini Kuru & Karaytuğ, 2015

Original description. Kuru & Karaytuğ (2015): 121–127; Figs 1–8.

Type locality. Turkey, Kızkalesi, Mersin (36°27.473' N, 34°08.647' E); sand at 0.3 m depth adjacent to rocky shore.

Notes. Kuru & Karaytuğ (2015) observed slight sexual dimorphism in the ornamentation of caudal ramus seta III (naked in ♀, minutely bipinnate in ♂). This observation needs confirmation based on a larger sample since only two males were examined. The authors also claim that the male antennule is 11-segmented and present the armature pattern as follows: 1-[1], 2-[10], 3-[5], 4-[6], 5-[3], 6-[1+ (1 + ae)], 7-[1 + 6 modified], 8-[1 + 2 modified], 9-[1], 10-[4], 11-[6 + acrothek]. The presence of four segments (their segments 8–11) distal to the geniculation is correct, however, the segmentation pattern proximal to the geniculation is ambiguous even though the authors illustrated it from different angles (their Fig. 7B–E). Comparison with the ancestral male harpacticoid pattern (as in *Hamondia superba* Huys, 1990: cf. Huys & Boxshall 1991) clarifies the homologies of the proximal segments in *K. aydini* **comb. nov.** and reveals some observational errors in the original description. The homologies between actual segments (indicated in Arabic numerals) and ancestral segments (in Roman numerals) in the male groundpattern of the Harpacticoida are as follows (Huys & Boxshall 1991: 115, Fig. 2.4.4): 1-[I], 2-[II], 3-[III–VIII], 4-[IX–XII], 5-[XIII], 6-[XIV–XVI], 7-[XVII], 8-[XVIII], 9-[XIX–XX], 10-[XXI–XXII], 11-[XXIII], 12-[XXIV], 13-[XXV], 14-[XXVI–XXVIII]. In this ancestral 14-segmented pattern the large aesthetasc is situated on segment 6 (and on segment 4 in the female), however, in all members of the Parastenheliidae segment 2 is not expressed as a discrete segment, forming instead a compound segment [II–VIII] and making the aesthetasc originate from actual segment 5. According to Kuru & Karaytuğ (2015) the aesthetasc arises from segment 6 in *K. aydini* **comb. nov.** This condition is extremely unlikely and is further exacerbated by the fact that ancestral segment XIII (= segment 4 in the parastenheliid groundpattern), which is expressed as a U-shaped bisetose sclerite in most male harpacticoids, was overlooked (although there is a hint of it in their Fig. 7D), thus effectively shifting the position of the aesthetasc even further to segment 7. Their alleged sixth segment (their Fig. 7C–D) shown to carry this sensory structure is in reality the cylindrical pedestal of segment 5 [= XIV–XVII] which partly conceals the real segment 6 [= XVIII] in ventral aspect. Finally, their segment 7 is a compound double segment homologous to ancestral segments XIX–XX. Kuru & Karaytuğ (2015) claim that the armature for this segment is “1 + 6 modified” but this is almost certainly based on an observational error. Male harpacticoids typically display two spiniform elements on the anterior surface and one seta at the anterodistal corner (cf. Huys & Boxshall 1991: Fig. 115) and the same pattern is expressed in *K. aydini* **comb. nov.**, the supernumerary elements being spinules. Similar spinular or setular ornamentation elements have been recorded on the same antennular segment in many other harpacticoids such as in *Neobradya pectinifera* Scott, 1892 (Huys 1987: Fig. 1B).

The type species was also collected from Denizy-ıldızı beach in Urla (İzmir Province) in the Aegean Sea (Kuru & Karaytuğ 2015).

***Penicillicaris* gen. nov.**

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Ever since the discovery and description of *Thalestris pectinimana* Car, 1884, the presence of penicillate elements on the antennary endopod and the distal exopodal and endopodal segments of P1 in various related forms (Scott 1894a; Brian 1921; Monard 1928; Willey 1935; Sewell 1940; Bodin 1964; Vervoort 1964) has been uncritically accepted as part of the documented variability allegedly displayed by *Parastenhelia spinosa* (Lang 1948 and others) and unfortunately did not receive the attention it deserved. Sewell (1940) for example, claimed that Monard's (1928) penicillate form from Banyuls-sur-Mer referred to *Parastenhelia littoralis* while his own material from Bermuda listed under the latter name cannot possibly be conspecific with the species described by Sars (1911). A new genus, *Penicillicaris* gen. nov., is proposed here to accommodate four forms that had previously been subsumed in the *Parastenhelia spinosa* complex and are attributed full species rank. Another three forms are placed with reservations in the genus as *species inquirendae*: *Microthalestris forficula* (Claus, 1863) sensu Scott (1894a), *M. littoralis* Sars, 1911 sensu Brian (1921) and *M. littoralis* Sars, 1911 f. *scotti* sensu Sewell (1940).

A number of records refer to the penicillate form but are not accompanied by illustrations. Such indeterminable records include those from Visakhapatnam (formerly Waltair), Andhra Pradesh in India (Krishnaswamy 1957 – as *Parastenhelia littoralis* f. *penicillata* [sic]), Dalkey Island and The Muglins, Co. Dublin (Roe 1958) and Lough Hyne (Ine), Co. Cork (Roe 1960; Sloane *et al.* 1961) in Ireland (all *P. spinosa* f. *penicillata*), and Rovinj in Croatia (Zavodnik 1969 – as *P. spinosa* var. *penicillata*).

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P3 endopod, P5–P6 and urosomal segmentation; occasionally in P4 endopod (*Pe. penicillata* sp. nov.). Body subcylindrical; condition of hyaline frills of cephalothorax and somites unconfirmed. Rostrum defined at base, reaching at most to halfway second segment of antennule; linguiform. Anal operculum semicircular, bordered with fine setules. Caudal ramus wider than long, without conspicuous spinular ornamentation; with at least six setae, setae IV–V typically inflated at base in ♀.

Antennule ♀ slender and typically 8-segmented (occasionally 9-segmented), with aesthetascs on segments 4 and 8 (or 9). Antennule ♂ haplocer and presumably 10-segmented; with geniculation between segments 6 and 7, and four segments distal to geniculation; segment 5 swollen and with aesthetasc; segmental homologies in ♂: I, II–VIII, IX–XII, XIII, XIV–XVIII, XIX–XX, XXI–XXII, XXIII, XXIV–XXV, XXVI–XXVIII. Antenna not sexually dimorphic; allobasis completely fused or partially divided, with endopodal pinnate seta on abexopodal margin; exopod 2-segmented, proximal segment with two setae, distal segment with 1–2 lateral and three apical elements; free endopod with two penicillate elements. Mandible with 2 elements on basis; endopod with two lateral and 3–4 apical setae; exopod 1-segmented, with two setae. Maxillary coxal epipodite and maxilla unconfirmed. Maxilliped with 0–1 seta(e) on syncoxa; basis with one seta on palmar margin; endopod represented by claw with unconfirmed number of accessory setae.

P1 inner basal spine not sexually dimorphic. P1 exopod 3-segmented; exp-2 elongate and much longer than others, with inner seta; exp-3 with two penicillate spines, a geniculate seta or additional penicillate spine, and one non-geniculate seta. P1 endopod 2-segmented; enp-1 longer than exopod, with short, proximally inserted, pinnate inner seta, inner segment margin without area of reduced chitinization; enp-2 with one naked minute seta and two penicillate claws. P2–P4 rami typically 3-segmented, P2–P3 endopods ♀ occasionally 2-segmented (*Pe. penicillata* sp. nov.); inner seta of P2–P4 exp-1 reduced in size. P3 endopod ♂ 3-segmented; enp-3 with spinous apophysis and no inner setae. P4 endopod ♂ occasionally without inner setae on enp-3 [1.1.021; in *Pe. penicillata* sp. nov.]. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	1.1.123	1.1.121 or 1.221
P3	1.1.(2–3)23	1.1.221 or 1.321 [♂: 1.1.02 + apo]
P4	0–?1.1.(2–3)23	1.1.(1–2)21

P5 ♀ endopodal lobe with five setae; inner margin without series of transverse striae. P5 ♀ exopod elongate, with six elements. P5 ♂ endopodal lobe with two elements, outer one typically shortest; exopod 1-segmented, with seven elements. P6 unconfirmed in both sexes.

Etymology. The generic name is derived from the Latin *penicillus*, meaning paintbrush, and the Greek suffix *-caris*, meaning shrimp, and refers to the presence of penicillate spines on the antennary endopod and both rami of the first swimming leg. Gender: feminine.

Type species. *Thalestris pectinimana* Car, 1884 = *Penicillicaris pectinimana* (Car, 1884) **comb. nov.** (by original designation herein).

Other species. *P. maldivensis* **sp. nov.**; *P. penicillata* **sp. nov.**; *P. sewelli* **sp. nov.**

Species inquirendae. *Microthalestris forficula* sensu Scott (1894a); *M. littoralis* Sars, 1911 sensu Brian (1921); *M. littoralis* Sars, 1911 f. *scotti* sensu Sewell (1940).

***Penicillicaris pectinimana* (Car, 1884) comb. nov.**

Thalestris pectinimana Car, 1884

Microthalestris forficula (Claus, 1863) sensu Monard (1928)

Parastenhelia spinosa (Fischer, 1860) f. *penicillata* sensu Bodin (1964)

Lang (1948: 497, 588) considered *Thalestris pectinimana* a junior subjective synonym of *Parastenhelia spinosa* and, based on P5 morphology, identified it with the form previously described as *Microthalestris littoralis* f. *penicillata* by Willey (1935). Although Car's (1884) illustrations are fragmentary, comparison with Monard's (1928) description of his *Microthalestris forficula* material from Banyuls-sur-Mer leaves little doubt that both belong to the same species. Evidence in support of this conspecificity is found in the 8-segmented ♀ antennule, the surface ornamentation of the maxillipedal basis, ornamentation of elements on P1 enp-2 and the foliaceous P5 ♀. It is conceivable that Bodin's (1964: 128) material of *Parastenhelia spinosa* var. *penicillata* from Marseille also belongs to this species. Other Mediterranean records from the Gulf of Genoa (Brian 1921 – as *Microthalestris littoralis*) and Rovinj in Croatia (Zavodnik 1969 – as *P. spinosa* var. *penicillata*) potentially refer to *Pe. pectinimana* **comb. nov.** but must remain indeterminable in the absence of compelling morphological evidence.

Original description. Car (1884): 248–249; Plate XVIII, Figs 1–8.

Additional descriptions. Monard (1928): 348–349; fig. XVIII (as *Microthalestris forficula*). Bodin (1964): 128–129; Plate III, fig. 15 (as *Parastenhelia spinosa* var. *penicillata*).

Type locality. Italy, Trieste (Adriatic); plankton.

Differential diagnosis. *Penicillicaris*. Body length 650–800 µm [according to Monard (1928) but sex not specified; sometimes markedly smaller (350 µm!)]. Antennule 8-segmented in ♀. Antenna with 2-segmented exopod bearing two setae on exp-1 and two lateral and three apical elements on exp-2. Mandibular armature unconfirmed. Maxilliped with one seta on syncoxa and basis. P1 exp-3 with two penicillate spines, one geniculate seta and one short non-geniculate seta. P1 enp-1 about 1.15 times length of exopod. Armature pattern of ♀ P2–P4:

	exopod	endopod
P2	?.?.123	?..1.121
P3	?.?.323	?..1.221
P4	?.?.223	?..?.221

P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ exopod about 2.15 times as long as maximum width; inner and outer margins gradually converging towards apex; with 6–7 elements. P5 endopodal lobe ♀ short, extending to about proximal fifth of exopodal length. P5 exopod ♂ 1-segmented, elongate–oval; with seven elements. P5 endopodal lobe ♂ extending to insertion point of proximal inner seta of exopod; with two elements. Caudal ramus setae IV–V of ♀ inflated near base (forcipate type).

Notes. Car (1884) was the first to note the presence of a single egg sac in a member of the Parastenheliidae. Monard (1928) observed variability in the number of setae on the P5 exopod of the female, with six elements being

the typical condition and seven (as in Car's description) the rare one. The species is so far restricted to the western Mediterranean (Banyuls-sur-Mer, Marseille, Trieste).

***Penicillicaris maldivensis* sp. nov.**

urn:lsid:zoobank.org:act:54CA1F70-8A1B-4FE7-A1F5-38AF975509B5

Microthalestris littoralis Sars, 1911 sensu Sewell (1940)

This is the first of three sympatric forms encountered by Sewell (1940) in seaweed washings from Addu Atoll in the Maldives. The species differs from its congeners by the armature of P1 exp-3 which consists of three penicillate spines and one long non-geniculate seta (vs two penicillate spines, one geniculate and one non-geniculate setae). The endopod is also much longer than in *Pe. pectinimana* **comb. nov.** and *Pe. sewelli* **sp. nov.** (unknown in *Pe. penicillata* **sp. nov.**), enp-1 being 1.5 times longer than the exopod (vs. 1.15 times). Females can be distinguished by the 9-segmented condition of the antennule (vs 8-segmented), the absence of modified (forcipate) caudal ramus setae IV–V and the elongate P5 exopod (3.8 times as long as maximum width vs at most three times – unknown in *Pe. penicillata* **comb. nov.**).

Original description. Sewell (1940): 191–193; Text-fig. 26A–K.

Type material. The dissected female specimen illustrated by Sewell (1940: Text-fig. 26A, C, E–G, I–J) is here designated as the holotype of *P. maldivensis* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters mentioned in the diagnosis below and those discussed and illustrated by Sewell (1940) (ICZN Art. 13.1).

Type locality. Maldivian archipelago, Addu Atoll; seaweed washings.

Differential diagnosis. *Penicillicaris*. Body length 440–560 µm in ♀, unknown for ♂. Antennule 9-segmented in ♀; with four segments distal to geniculation in ♂. Antenna with 2-segmented exopod bearing two setae on exp-1 and one lateral and three apical elements on exp-2. Mandible with two setae on basis; exopod 1-segmented, with two setae. Maxillipedal armature unconfirmed. P1 exp-3 with three penicillate spines and one long non-geniculate seta. P1 enp-1 about 1.5 times length of exopod. Armature pattern of ♀ P2–P4:

	exopod	endopod
P2	unknown	unknown
P3	unknown	unknown
P4	0.1.223	1.1.121

P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ exopod elongate, about 3.8 times as long as maximum width; proximal half of inner and most of outer margin parallel; with six elements. P5 endopodal lobe ♀ short, extending to about proximal quarter of exopodal length. P5 exopod ♂ 1-segmented, elongate–oval; with seven elements. P5 endopodal lobe ♂ extending to insertion point of proximal inner seta of exopod; with two elements. Caudal ramus setae IV–V of ♀ not inflated near base.

Etymology. The species name refers to the Republic of the Maldives where the type locality is located.

Notes. Sewell's (1940) illustration of the P3 endopod (his Text-fig. 26H) was inadvertently mislabelled as the P2 endopod. The absence of the inner seta on P1 exp-2 (his Text-fig. 26G) is probably based on an observational error.

***Penicillicaris penicillata* sp. nov.**

urn:lsid:zoobank.org:act:0C7D1809-6DBA-49D8-8330-188442A571E2

Microthalestris littoralis Sars, 1911 f. *penicillata* Willey, 1935

Since Willey (1935) expressly gave his material infrasubspecific rank, and the content of his work unambiguously reveals that the name “*penicillata*” was proposed for a form, it is deemed to be infrasubspecific and therefore not

regulated by the Code (Art. 45.6.4). Since it was not adopted by another author for a species or subspecies before 1985 it remains permanently unavailable. Willey's (1930) form is here elevated to species rank and established as a new name with the current authorship and date.

Original description. Willey (1935): 82–83; Figs 119–120, 122–126.

Type material. The dissected female specimen illustrated by Willey (1935: Figs 119–120, 122–124) is here designated as the holotype of *P. penicillata* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters mentioned in the diagnosis below and those discussed and illustrated by Willey (1935) (ICZN Art. 13.1).

Type locality. Bermuda, Trunk Island, Harrington Sound; washings of black seaweeds.

Differential diagnosis. *Penicillicaris*. Body length 500–700 µm in ♀, 400–500 µm in ♂. Antennule 8-segmented in ♀. Antennary exopod and mouthparts unconfirmed. P1 exp-3 with two penicillate spines, one geniculate seta and one well developed non-geniculate seta. Relative length of P1 enp-1 unconfirmed. P2–P3 endopods ♀ with enp-2 and enp-3 more often very imperfectly separated, without mobile articulation between them (when distinctly 3-segmented no spur at inner distal corner); P4 endopod ♂ with armature pattern [1.1.021] (both inner setae of ♀ not expressed in ♂). Armature pattern of ♀ P2–P4:

	exopod	endopod
P2	unknown	unknown
P3	??.323	1.321
P4	?1.323	??.221

P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ with six elements on exopod; shape and length of exopod and endopodal lobe unconfirmed. P5 exopod ♂ 1-segmented, oval; with seven elements. P5 endopodal lobe ♂ extending to insertion point of proximal inner seta of exopod; with two elements. Caudal ramus setae IV–V of ♀ inflated near base (forcipate type).

Etymology. The species named is derived from the Latin *penicillus*, meaning paintbrush, and refers to the presence of penicillate elements on the antennary endopod and both rami of the first swimming leg.

Notes. Willey (1935) inadvertently used two different spellings for his new form which he introduced as *penicillata* (p. 82) but was cited later in the paper on three occasions as *penicillata*. Unfortunately, some authors (e.g. Krishnaswamy 1957: 33) adopted the incorrect spelling *penicillata*. According to Willey (1935) the new species is unique in the morphology of the female P2–P3 endopods which seem to lack a functional articulation between enp-2 and enp-3 in most specimens. His discovery of an additional hair-like seta on the distal exopodal segment of P3–P4 means that some caution should be exercised when using previously reported armature patterns to identify other species since some may be incorrect. *Penicillicaris penicillata* **sp. nov.** is so far the only member of the genus that displays sexual dimorphism on the P4 endopod with both inner setae of enp-3 in the female not being expressed in the male, resulting in an armature pattern [1.1.021].

Penicillicaris sewelli **sp. nov.**

urn:lsid:zoobank.org:act:5F142B2D-CDF6-4109-AA29-3B93121663FC

Microthalestris littoralis Sars, 1911 f. *penicillata* sensu Sewell (1940)

Microthalestris littoralis Sars, 1911 f. *penicillata* sensu Vervoort (1964)

The second form reported by Sewell (1940: 193) is only known from the female. Although the author claimed that his Indian Ocean form was identical with Willey's (1935) Atlantic form *penicillata* we consider it more likely that it is conspecific with Vervoort's (1964) material from Ifalik Atoll in the Pacific which also includes the male.

Original description. Sewell (1940): 193–195; Text-fig. 27A–J (♀ only).

Additional description. Vervoort (1964): 177, 181–184, 189; Figs 64c, 66c, 67, 68d, 70a–g.

Type material. The female specimen illustrated by Sewell (1940: Text-fig. 27A–J) is here designated as the holotype of *P. sewelli* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters mentioned in the diagnosis below and those discussed and illustrated by Sewell (1940) (ICZN Art. 13.1).

Type locality. Maldive archipelago, Addu Atoll; seaweed washings.

Differential diagnosis. *Penicillicaris*. Body length 520–600 µm in ♀, 420 µm in ♂. Antennule 8-segmented in ♀. Antenna with 2-segmented exopod bearing two setae on exp-1 and two lateral and three apical elements on exp-2. Mandible with two setae on basis; exopod 1-segmented, with two setae. Maxillipedal syncoxa unarmed; basis with one seta on palmar margin. P1 exp-3 with two penicillate spines, one geniculate seta and one short non-geniculate seta. P1 enp-1 about 1.15 times length of exopod. Armature pattern of ♀ P2–P4:

	exopod	endopod
P2	1.1.123	1.1.121
P3	1.1.223	1.1.221
P4	————	???.221

P3 endopod ♂ 3-segmented, with apophysis on enp-3, armature pattern [1.1.02 + apo]. P5 ♀ exopod about three times as long as maximum width; inner margin and proximal two-thirds of outer margin parallel; with six elements. P5 endopodal lobe ♀ extending to about proximal third of exopodal length. P5 exopod ♂ 1-segmented, elongate–oval; with seven elements. P5 endopodal lobe ♂ well developed, trapezoidal, extending slightly beyond insertion point of proximal inner seta of exopod; with two elements. Caudal ramus setae IV–V of ♀ inflated near base (forcipate type).

Etymology. The species is dedicated to Robert Beresford Seymour Sewell, leader of the John Murray Expedition (1933–1934) to the Indian Ocean, during which it was collected.

Notes. Sewell (1940: Text-fig. 27G) illustrates an inner seta in the proximal quarter of P1 exp-2 but this, in addition to the alleged absence of the short seta on both exp-3 and enp-2 of this limb, must be based on observational errors. Vervoort (1964) misinterpreted the exopod as the endopod in both sexes in his text (pp. 182, 194) and illustration (Fig. 70b); the inner seta on exp-2 was almost certainly overlooked. According to Sewell (1940: Text-fig. 27H) P2 exp-1 lacks an inner seta but Vervoort shows a small inner element which is included in the armature formula here. The only significant difference between the Maldivian and Pacific populations appears to be the armature of the antennary exopod. According to Sewell (1940) the proximal segment has one minute and one long seta, and the distal segment has two lateral and three distal setae. Vervoort's (1964: 70g) illustration of the antenna appears to indicate that the proximal segment has two long setae and the distal segment only one lateral in addition to the three distal ones. It is conceivable that this discrepancy is the result of an incorrectly observed segment boundary, causing the proximal inner seta of exp-2 to erroneously originate from exp-1, combined with the oversight of the minute proximal element on exp-1. In addition to the type locality in the Maldives, the species has also been recorded from the Caroline Islands (Federated States of Micronesia).

Key to species of *Penicillicaris* gen. nov.

The swimming leg armature is incompletely known for all species (Table 1). Willey (1935: Fig. 123) noted that in *Pe. penicillata* **sp. nov.** the distal exopodal segment of P3–P4 has three inner setae, the distal one of which is "... an excessively fine hair curving outwards...". It is conceivable that this element has been overlooked in earlier descriptions and thus caution is required when using this key (see couplet 3). Any identification made must be checked against the original description(s).

1. Antennule ♀ 9-segmented; P1 exp-3 with three penicillate spines and one long non-geniculate seta; caudal ramus setae IV–V not modified in ♀ *P. maldivensis* **sp. nov.**
- Antennule ♀ 8-segmented; P1 exp-3 with two penicillate spines, one geniculate seta and one shorter non-geniculate seta; caudal ramus setae IV–V with swollen bases in ♀ 2.
2. P2–P3 endopods ♀ with enp-2 and enp-3 more often very imperfectly separated, without mobile articulation between them (when distinctly 3-segmented no spur at inner distal corner); P4 endopod ♂ with armature pattern [1.1.021] (both inner setae of ♀ not expressed in ♂) *P. penicillata* **sp. nov.**
- These characters not combined 3.
3. P3 exp-3 with seven elements; P5 exopod ♀ about three times longer than maximum width, inner and outer margins mostly parallel; P5 endopodal lobe ♀ reaching to about one third of exopodal length *P. sewelli* **sp. nov.**
- P3 exp-3 with eight elements; P5 exopod ♀ about 2.15 times longer than maximum width, inner and outer margins gradually

converging towards apex; P5 endopodal lobe ♀ reaching to about one fifth of exopodal length
..... *P. pectinimana* (Car, 1884) **comb. nov.**

***Porirualia* gen. nov.**

urn:lsid:zoobank.org:act:BE15D3D2-7B7E-40A0-ABE7-B5EF1F7F12AA

Wells *et al.* (1982) placed *Parastenhelia megarostrum* in close proximity to *Pa. anglica*, *Pa. ornatissima*, *Pa. reducta* and *Pa. hornelli*, all of which share a 3-segmented P1 exopod with segments of subequal proportions. Based on the 9-segmented antennule in the female, the position and length of the inner seta on P1 enp-1, the shape of the female P5 and armature of the male P5 exopod, they placed it closest to *Pa. hornelli*. Although the *hornelli*-complex was far from resolved at the time, Wells *et al.* (1982) considered distinct species status for *Pa. megarostrum* warranted because it displayed characters reflecting considerable conservatism in the genus, such as the massive size of the rostrum, the length/width ratio of P1 enp-2, the relative position of the setae on the female P5 exopod, abdominal ornamentation, and relative proportions of the exopodal setae on the male P5 exopod. They also attached considerable significance to the distinctive bulbous genital field in the female, which was regarded as an effective isolating factor in the mate recognition of this species.

Song *et al.* (2003) considered *Pa. pyriformis* most closely related to *Pa. hornelli* and *Pa. megarostrum* based on the shared presence of subequal segments in the P1 exopod, the position and length of the inner seta on P1 enp-1 and the 9-segmented antennule in the female. They also recognized a certain resemblance with *Pa. oligochaeta*, based on the length and location of the inner seta of P1 enp-1, but the latter species differs in the ornamentation of the anal operculum, armature of ♀ P2–P4, segmentation and armature of ♂ P2–P3 endopods and the presence of six elements on the male P5 exopod.

Both Mielke (1990) and Gee (2006) have suggested removing *Pa. megarostrum* and/or *Pa. pyriformis* from *Parastenhelia* because they lack the characteristic sexual dimorphism on the male P3 endopod that defines this genus. Neither species can be accommodated in *Thalestrella* because they do not exhibit the sexual dimorphism on the antenna that is typical for this genus nor can they be assigned to *Foweya* since the males lack the modified inner basal spine of P1. Both genera are also characterized by an area of reduced cuticle thickness on the P1 endopod which is not expressed in *Pa. megarostrum* or *Pa. pyriformis*. In accordance with earlier views (Mielke 1990; Gee 2006), both species are here transferred to a new genus, *Porirualia* **gen. nov.**, based on the following suite of apomorphic character states: (a) rostrum very large, reaching to at least halfway the fourth antennular segment in the female; (b) P1 enp-1 inner seta very long, extending beyond distal margin of segment; and (c) P5 ♀ with series of transverse striae along inner margin of endopodal lobe; these striae are internal chitinous reinforcements and are more strongly developed in *Pa. megarostrum* (Wells, Hicks & Coull, 1982) **comb. nov.** than in *Pa. pyriformis* (Song, Kim & Chang, 2003) **comb. nov.** The new genus shares a sistergroup relationship with *Johnwellsia* **gen. nov.** based on the following synapomorphies: (a) distal seta on the mandibular basis modified into short spine; (b) P3 endopod ♂ with only one inner seta on distal segment (homologue of proximal inner seta of ♀ enp-3 not expressed in ♂; Fig. 7G–I); and (c) outermost element of P5 endopodal lobe reduced, represented by minute seta in both sexes.

There is controversy over the segmentation of the male antennule. Both Wells *et al.* (1982) and Song *et al.* (2003) describe it as 9-segmented although the latter authors figure ten segments. The antennule is here reinterpreted as 10-segmented with the geniculation positioned between segments 6 and 7. The small bisetose segment 4 (= ancestral segment XIII; figured but not counted by Song *et al.* 2003) was overlooked by Wells *et al.* (1982). The apical segment in *Pa. megarostrum* **comb. nov.** was described as unarmed, displaying a row of fine marginal hairs; it is unlikely that this observation is correct.

Diagnosis. Parastenheliidae. Sexual dimorphism in antennule, P2–P3 endopods, P5–P6 and urosomal segmentation. Body fusiform; posterior margin of cephalothorax and all somites (except anal somite) with deeply divided, denticulodigitate, hyaline frills. Rostrum defined at base, very large, reaching to at least halfway fourth segment of antennule; with parallel sides tapering sharply into rounded apex. Anal operculum semicircular, bordered with fine setules. Caudal ramus wider than long, without conspicuous spinular ornamentation; with six setae, seta V slightly inflated at base in ♀.

Antennule short and 9-segmented in ♀, segment 1 not elongate, segments 7–8 shortest, with aesthetascs on segments 4 and 9; haplocer and 10-segmented in ♂, with geniculation between segments 6 and 7, segment 5 swollen and with aesthetasc; segmental homologies in ♂: I, II–VIII, IX–XII, XIII, XIV–XVIII, XIX–XX, XXI–XXII, XXIII,

XXIV–XXV, XXVI–XXVIII. Antenna not sexually dimorphic; allobasis completely fused or partially divided, with endopodal pinnate seta on abexopodal margin; exopod 2-segmented, proximal segment with two setae, distal segment with two lateral and 2–3 apical elements; free endopod without penicillate elements. Mandible with 3–4 elements on basis, distal one enlarged and spiniform; endopod with two lateral and three apical setae; exopod 1-segmented, with three setae. Maxillulary coxal epipodite represented by one seta. Maxilla with three endites on syncoxa; endopod discrete, with 2–3 setae. Maxilliped with two setae on syncoxa; basis with one seta and longitudinal spinular row on palmar margin; endopod represented by claw with one accessory seta.

P1 inner basal spine not sexually dimorphic. P1 exopod 3-segmented, segments subequal in length; exp-2 with inner seta; exp-3 with two pinnate spines, one geniculate seta and one naked seta. P1 endopod 2-segmented; enp-1 longer than exopod, with long, proximally inserted, pinnate inner seta extending almost to distal margin of enp-2, inner segment margin without area of reduced chitinization; enp-2 with one naked minute seta and two pinnate claws. P2–P4 rami 3-segmented; inner seta of P2–P4 exp-1 reduced in size. P2–P3 endopods ♂ 2- or 3-segmented. Apical setae of P2 enp-3 ♂ occasionally shorter than in ♀. P3 endopod ♂ with only one inner seta (vs two in ♀) on enp-3, resulting in 1.1.121 or 1.221 (when ♂ endopod 2-segmented) pattern; without spinous apophysis. Armature formula of P2–P4 as follows:

	exopod	endopod
P2	1.1.123	1.1.121 [♂: 1.1.121 or 1.221]
P3	1.1.2–323	1.1.221 [♂: 1.1.121 or 1.221]
P4	1.1.2–323	1.1.221

P5 ♀ endopodal lobe with five setae, outermost minute; inner margin with series of transverse striae. P5 ♀ exopod elongate, with six elements. P5 ♂ endopodal lobe with two elements, outer one minute; exopod 1-segmented, with 5–6 elements. Vestigial P6 ♀ represented by 1–2 minute seta(e). P6 ♂ with three setae.

Etymology. The generic name alludes to the type locality of its type species, Pauatahanui Inlet in Porirua Harbour, Wellington. Gender: feminine.

Type species. *Parastenhelia megarostrum* Wells, Hicks & Coull, 1982 (by original designation herein) = *Porirualia megarostrum* (Wells, Hicks & Coull, 1982) **comb. nov.**

Other species. *Parastenhelia pyriformis* Song, Kim & Chang, 2003 = *Po. pyriformis* (Song, Kim & Chang, 2003) **comb. nov.**

***Porirualia megarostrum* (Wells, Hicks & Coull, 1982) comb. nov.**

Parastenhelia megarostrum Wells, Hicks & Coull, 1982

Original description. Wells *et al.* (1982): 159–164; Figs 5–6; Table 2.

Type locality. New Zealand, North Island, Wellington; Porirua Harbour, Pauatahanui Inlet (since renamed to Te Awarua-o-Porirua Harbour); intertidal beach some 200 m north-east of the State Highway 1 bridge; fine sand with some silt.

Differential diagnosis. This coincides with Wells *et al.*'s (1982) excellent description of *Parastenhelia megarostrum*. See below for differences with its only congener, *Po. pyriformis* **comb. nov.**

Notes. Wells *et al.* (1982) remarked that, despite discrepancies in his illustrations, based on locality and collection details, it appears that Thomson's (1883) *Thalestris forficula* is conspecific with *Po. megarostrum* **comb. nov.** This claim is considered highly unlikely for a variety of reasons: (a) Thomson's female specimens are significantly larger (1 mm vs 665 µm); (b) there is no mention of the large rostrum which is one of the most conspicuous characters of *Po. megarostrum* **comb. nov.**; (c) the antennule is more slender; (d) P1 exp-2 is elongate, about 2.5 times the length of exp-1 (vs subequal to exp-1); and (e) P1 enp-1 is comparatively longer and its inner seta shorter. Thomson (1883) also stated that the central caudal setae (seta V) are "... swollen just beyond their basal articulation, and marked along the greater part of their length with annular articulations" while in *Po. megarostrum* **comb. nov.** all caudal ramus setae are unmodified. As stated above it is conceivable that *T. forficula* sensu Thomson (1883) is conspecific with *Microthalestris antarctica* **comb. nov.**

Porirualia megarostrum **comb. nov.** is so far endemic to New Zealand where it is found on fine silty intertidal

sandbanks in practically all of the country's major estuarine and harbour systems (Wells *et al.* 1982; Wells & Hicks in Dahms & Hicks 1996). Additional records from Porirua Harbour, including Pauatahanui Inlet, have been added by Hicks (1984, 1985, 1986, 1988, 1989, 1991, 1992), Iwasaki *et al.* (1993, 1999) and Blaschke *et al.* (2010). On the North Island it has been recorded at localities extending northward from Wellington to Kaipara Harbour on the west coast and to Doubtless Bay on the east, occurring sympatrically with *Parastenhelia hornelli* in Whangateau Harbour (Wells *et al.* 1982). The species has also been reported from the South Island, including Portobello Harbour (Otago Harbour) (Stringer *et al.* 2012a), Papanui Inlet (Otago Peninsula) (Leduc & Probert 2011; Leduc *et al.* 2009) and Okains Bay, Canterbury (Stringer *et al.* 2012b). Dahms & Hicks (1996) described all six nauplius stages of *Po. megarostrum* **comb. nov.** while Dahms (1993) provided details on the copepodid development of this species. Field experiments employing emergence traps indicate that adults do not swim or have only poorly developed swimming ability (Hicks 1986) while nauplii and copepodids are passively mobile, being transported by shifting sandgrains they cling on (Hicks 1988) or resuspended by tidal bottom shear currents (Hicks 1992). Nauplii have never been observed actively swimming (Dahms & Hicks 1996). *Porirualia megarostrum* **comb. nov.** is the most abundant epibenthic metazoan on Mana Bank in Pauatahanui Inlet and the dominant food source for young flatfish (Hicks 1984). Study of flat fish predation on copepods at this site indicated that although predation was high, there was little impact on overall abundance of the copepod (Hicks 1985).

***Porirualia pyriformis* (Song, Kim & Chang, 2003) comb. nov.**

Parastenhelia pyriformis Chang, Kim & Chang, 2003

Original description. Song *et al.* (2003): 221–227; Figs 1–4; Table 1.

Type locality. South Korea, Jeju Island, Sehwa Beach (33°28'07" N, 126°54'43" E); shallow sublittoral zone.

Differential diagnosis. This coincides with Song *et al.*'s (2003) description of *Parastenhelia pyriformis*.

Notes. Song *et al.* (2003) added a second record from Seungbong Island in the Yellow Sea where it was found to be associated with macroalgae (*Zostera japonica*) on sandy bottoms (see also Song *et al.* 2012).

The two species can be distinguished, in both sexes, by (a) rostrum size (reaching to distal margin of segment 5 of the antennule in *Po. megarostrum* vs halfway segment 4 in *Po. pyriformis*), (b) antennary morphology (allobasis partially divided by surface suture and exp-2 with four setae/spines vs allobasis without trace of original segmentation and exp-2 with five elements, *i.e.* with additional apical seta), (c) armature of mandibular basis (with one spine and three setae vs one spine and two setae), (d) length:width ratio of P1 enp-2 (2.2 vs 1.3), and (e) armature of P3–P4 exp-3 (distal inner seta present and short vs absent). In addition, females can be differentiated by the proportional segment lengths in the antennule (segment 1 longest in *Po. megarostrum* vs segment 2 longest and entire appendage more slender in *Po. pyriformis*) and P5 morphology (L:maximum W ratio 2.2 and distal outer seta longest in *Po. megarostrum* vs 3.25 and inner distal seta longest in *Po. pyriformis*). Males differ in the segmentation of P2–P3 endopods (3-segmented vs 2-segmented) and the number of elements on the P5 exopod (six vs five).

Key to genera of Parastenheliidae

1. P3–P4 exp-3 with 4–5 elements; P3–P4 enp-2 ♀ without inner seta 2.
– P3–P4 exp-3 with 6–8 elements; P3–P4 enp-2 ♀ with inner seta 4.
2. Antennule ♀ 8-segmented; proximal endopodal segment of antenna without abexopodal seta; P1 exopod 2-segmented; P1 endopod without area of thin cuticle near insertion of inner seta *Paraleptomesochra* Wells, 1967.
– Antennule ♀ 9-segmented; proximal endopodal segment of antenna with abexopodal seta; P1 exopod 3-segmented; P1 endopod with area of thin cuticle near insertion of inner seta *Psammoleptomesochra* Mielke, 1994a.
3. P1 inner basal spine sexually dimorphic; P2 enp-3 with two inner setae *Foweya* Gee, 2006.
– P1 inner basal spine not sexually dimorphic; P2 enp-3 with 0–1 inner seta(e) 4.
4. P1 exopodal segments subequal 5.
P1 exp-2 much longer than exp-1 and -3 8.
5. Antennule ♀ with segments distal to aesthetasc-bearing (4th) segment significantly compressed; antennule ♂ with characteristic backwardly directed spiniform element on second segment, either displaying a serrate or flagellate tip; antenna sexually dimorphic, in ♂ with abexopodal seta of allobasis and lateral setae of exopodal segments enlarged and highly plumose; distal segment of antennary exopod with three elements; maxillipedal syncoxa with only one seta; P2 exp-3 with two inner setae;

- outer spine on P3 enp-3 ♂ reduced in size *Thalestrella* Monard, 1935a.
- Antennary segments ♀ distal to aesthetasc-bearing (4th) segment not displaying compressed appearance; antennule ♂ without such modified element on second segment; antenna without sexual dimorphism; distal segment of antennary exopod with at least four elements; maxillipedal syncoxa with 2–3 setae; P2 exp-3 with one inner seta; outer spine of P3 enp-3 ♂ not sexually dimorphic 6.
6. Rostrum very large, reaching at least to halfway 4th segment of antennule; distal element on mandibular basis enlarged and spiniform; P5 baseopod ♀ with transverse striae along inner margin of endopodal lobe, outermost seta minute; P3 endopod ♂ with three inner setae *Porirualia* **gen. nov.**
- Rostrum much smaller, reaching at most to distal margin of 2nd segment of antennule; distal element on mandibular basis setiform; P5 baseopod ♀ without transverse striae along inner margin of endopodal lobe, outermost seta well developed; P3 endopod ♂ with 1–2 inner seta(e) 7.
7. Antennary allobasis without abexopodal seta; antenna with one lateral element on exp-2; maxillipedal basis with two setae; P3 endopod ♂ without spinous apophysis on enp-3; P5 exopod ♂ with four elements *Johnwellsia* **gen. nov.**
- Antennary allobasis with abexopodal seta; antenna with two lateral elements on exp-2; maxillipedal basis with one seta; P3 endopod ♂ with spinous apophysis on enp-3; P5 exopod ♂ with 6–7 elements *Parastenhelia* Thompson & Scott, 1903
8. Lateral spines of distal segment of antennary endopod penicillate; P1 exp-3 and enp-2 with penicillate elements *Penicillicaris* **gen. nov.**
- Lateral spines of distal segment of antennary endopod pinnate; elements of P1 exp-3 and enp-2 non-penicillate 9.
9. Endopodal claw of maxilliped spatulate, fringed with series of densely arranged serrations around inner margin and rounded apex; P5 exopod ♂ 2-segmented, with five elements *Karayutgia* **gen. nov.**
- Endopodal claw of maxilliped tapering gradually and ending in pointed tip, without serrations around inner margin; P5 exopod ♂ 1- or 3-segmented, with 6–7 elements *Microthalestris* Sars, 1905.

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