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## A new species of *Stylicletodes* Lang, 1936 (Copepoda: Harpacticoida: Cletodidae) from the East China Sea, including an updated key to species and synopsis of distribution records

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### Abstract

Both sexes of a new species, *Stylicletodes wellsii* **sp. nov.** (Harpacticoida: Cletodidae), are described from material collected from sediments in the East China Sea. The new species belongs to a species group whose members are characterized by an anal operculum that has a backwardly directed, median linguiform process and fifth legs that display naked or sparsely pinnate armature elements in both sexes. Within this group, *S. wellsii* **sp. nov.** is morphologically closest to *S. reductus* Wells, 1965 but differs primarily from its European congener in the armature pattern of P4 (both rami) and the female P5. Distribution records of all species are summarized and an updated identification key to the seven valid species in the genus is presented. Taxonomic issues related to the type species *S. longicaudatus* (Brady, 1880) are briefly discussed.

**Key words:** Crustacea, meiobenthos, taxonomy, morphology, East Asia

### Introduction

Members of the family Cletodidae T. Scott, 1905 are active mud-burrowers known mainly from shallow and sublittoral marine habitats, with some species occurring in the deep sea and brackish waters (Boxshall & Halsey 2004). In his revision of the Cletodidae, Lang (1936: 452, 467) recognized the synonymy between *Cletodes longicaudata* Brady, 1880 [see Huys (2009: 10) for the correct authorship of this species] and *Cletodes leptostylis* Sars, 1920 and argued that they could not be included in the genus *Cletodes* Brady, 1872. Consequently, he established the genus *Stylicletodes* Lang, 1936 and fixed *C. leptostylis* as the type species on Sars's (1920: 78) erroneous ground that the senior synonym *C. longicaudata* Brady, 1880 was a junior homonym of *C. longicaudata* Boeck, 1873. In reality Boeck (1873) had described *Enhydrosoma longicaudata* and hence Brady's (1880) binomen takes priority over *C. leptostylis*. This error was recognized by Lang (1948: 1328) who provided an extended diagnosis and added *Cletodes numidicus* Monard, 1935 to the genus. The latter was subsequently recognized as a synonym of *S. longicaudatus* (Por 1959; Lang 1965).

Species of the genus *Stylicletodes* are benthic and occur over a wide depth range from shallow water environments (Sars 1920; Monard 1935; Lang 1965) to the deep sea (Bodin 1968; Schriever 1986; George 1999, 2005; Willen 2004; Büntzow 2011; George *et al.* 2018). The genus currently comprises six valid species but only the type species, *S. longicaudatus* (Brady, 1880), has been recorded from a wide range of localities and from more than one oceanic basin (Table 1). The remaining species were all described from a single specimen and have a much more restricted distribution although this could be attributed to sampling bias. *Stylicletodes stylicaudatus* (Willey, 1935) was originally described (as *Cletodes stylicaudatus* Willey, 1935; transferred by Fiers 1996) from a single male

collected in Harrington Sound, Bermuda (Willey, 1935). The species has been recorded only three times since, *i.e.* from Castle Harbor Deep in Bermuda (Coull, 1970; Coull & Herman 1970 – as *Enhydrosoma stylicaudatum*), Punta Allen, Yucatán in Mexico (De Troch 2001) and Corpus Christi Bay, Texas (Burgess *et al.* 2005 – as *E. stylicaudatum*). *Stylicletodes verisimilis* Lang, 1965 was described from a single female obtained at 26 m depth in Monterey Bay, California (Lang 1965). The only other record of the species, also from California, is that by Montagna & Spies (1985) who collected it from the Isla Vista oil seep at 15 m depth in the Santa Barbara Channel. *Stylicletodes reductus* Wells, 1965 was described from a single female collected at 101 m depth in Loch Nevis on the west coast of Scotland (Wells, 1965). It was subsequently recorded in a marine cave near Marseille (NW Mediterranean) at a depth of only 15 m (Janssen *et al.* 2013) and from the southern Celtic Sea (J.M. Gee, unpublished data). An apparently morphologically similar species, *S. cf. reductus* was reported from Nha Trang Bay (Vietnam) in the South China Sea (Chertoprud *et al.* 2009) but not illustrated. Finally, Bodin (1968) added two deep-sea species from the Bay of Biscay, *S. minutus* Bodin, 1968 and *S. oligochaeta* Bodin, 1968, from 700 m and 1,200 m depth, respectively; each was based on a single female. *Stylicletodes oligochaeta* was subsequently recorded from the Straits of Magellan and the Beagle Channel in South America (George 1999, 2005) and the Anaximenes Seamount in the eastern Mediterranean where it co-exists with *S. minutus* (George *et al.* 2018). Baguley (2004) listed *S. aff. longicaudatus*, *S. aff. oligochaeta* and *S. aff. reductus* from the deep sea in the Northern Gulf of Mexico but the authenticity of these records remains to be confirmed.

The genus *Stylicletodes* appears to assume a cosmopolitan distribution. In the Pacific unidentified species have been recorded from South Korea (Kim *et al.* 2014; Karanovic *et al.* 2015), the Bohai Sea (Mu *et al.* 2002), the North-Western Pacific (Kuril-Kamchatka trench and abyssal plain) (Kitahashi *et al.* 2013; Schmidt *et al.* 2019), the Ryukyu Trench (Kitahashi *et al.* 2014), the New Ireland Fore-Arc system near Papua New Guinea (Willen 2004), Pauatahanui Inlet in New Zealand (Hicks 1986), the Santa Maria Basin (Fiers 1996) and San Diego Trough (Thistle & Eckman 1990) off California. Similar records are known from the Indian Ocean, including Nizampatnam Bay in the Bay of Bengal (Vijaya Bhanu *et al.* 2017) and Gazi Bay in Kenya (De Troch 2001). Atlantic records of unidentified species include those from the slope of Sergipe off northeastern Brazil (Vasconcelos 2008), the northeast Mid-Atlantic deep sea (Büntzow 2011), the Puerto Rico Trench (Schmidt *et al.* 2018), Svalbard (Kotwicki 2002), Madeira (Packmor & George 2016), the southern North Sea (Schückel *et al.* 2013), and the Ligurian Sea (Guidi-Guilvard *et al.* 2009) and northern Adriatic (Grego *et al.* 2014) in the Mediterranean.

Taxonomic studies on harpacticoid copepods from China are still scarce. Most cletodids from China have been recorded from the Bohai Gulf and the Yellow Sea. In this paper we describe a new species of the genus *Stylicletodes* obtained in sediment samples from the East China Sea, representing the first member of the family Cletodidae to be reported from this region.

**TABLE 1.** Records of *Stylicletodes longicaudatus* (Brady, 1880); depth in m; INT = intertidal; SUB = subtidal but depth unknown; – = no depth information available.

Country/Region	Locality	Depth	Reference
Russia	Franz Josef Land, off East Glacier	SUB	Scott (1899) <sup>1,2</sup>
	White Sea	30–90	Kornev & Chertoprud (2008)
Iceland-Faroe Ridge	68°38'N 09°48'W and 63°30'N 07°34'W	600–1,000	Schriever (1986)
Norway	Svalbard, 76°24'N 33°43'E	183	Scott & Scott (1901) <sup>1</sup>
	Aust-Agder county, Risør	55	Sars (1920) <sup>3</sup>
Sweden	Gullmar Fjord	30–70	Lang (1948, 1965)
	Koster Fjord	200	Por (1964a)
	North Koster	110	Por (1964a)
	Skagerrak	100	Por (1964a)
Scotland	Firth of Forth, no locality specified	SUB	Scott (1902) <sup>1</sup>
	Firth of Forth, St Monans and Inchkeith	SUB	Scott (1906) <sup>1</sup>
	Firth of Clyde, Fairlie and Hunterstone	INT	Scott (1900) <sup>1</sup>
	Firth of Clyde, Portincross	13–53	Brady (1880) <sup>1</sup>

.....continued on the next page

**TABLE 1.** (Continued)

Country/Region	Locality	Depth	Reference
	Fladen Ground	146	Wells (1965)
	Loch Nevis	101	Wells (1965)
	Loch Creran	9	Saunders (2000)
England	Durham, Hartlepool	9	Brady (1880) <sup>1,4</sup>
	Cumbria, Solway coast	INT	Brady (1896) <sup>1</sup>
	Northumberland, Holy Island of Lindisfarne	INT	Brady (1904) <sup>1,5</sup>
	Northumberland, Craster	SUB	Moore (1973)
	Devon, Salcombe	–	Norman & Scott (1906) <sup>1</sup>
	Devon, near Eddystone Lighthouse	55	Norman & Scott (1906) <sup>1</sup>
	Cornwall, Whitsand Bay	–	Norman & Scott (1906) <sup>1</sup>
	Sussex coast, Mulberry and Brighton	INT–6	Venthams (2011)
Irish Sea	off Isle of Man	61–107	Moore (1979) <sup>6</sup>
Wales	Conwy, Llanfairfechan	INT	Thompson (1889, 1893) <sup>1</sup>
North Sea	no localities specified	SUB	Huys <i>et al.</i> (1992)
	no localities specified	SUB	Rossel & Martínez Arbizu (2019)
France	Charente-Maritime, La Rochelle region	INT	Bodin (1972, 1973, 1977)
	Pyrénées-Orientales, Le Racou	INT	Chappuis (1954) <sup>7</sup>
	Pyrénées-Orientales, Banyuls-sur-Mer	35	Soyer (1966) <sup>8</sup>
		30–40	Guille & Soyer (1969)
		SUB	Soyer (1971) <sup>9</sup>
		10–20	Bodiou (1976, 1982) <sup>8</sup>
Spain	Galicia, Ría de Ferrol	SUB	Candás <i>et al.</i> (2012)
Portugal	Madeira, Machico	2–3	Packmor & George (2016)
Montenegro	Budva	INT	Petkovski (1955) <sup>8</sup>
Mediterranean	Anaximenes Seamount	675–1,543	George <i>et al.</i> (2018)
Israel	Nahal Soreq [Nahal Rubin]	9	Por (1964b) <sup>8</sup>
Bulgaria	Black Sea coast	24	Marinov (1971)
		30–70	Apostolov & Marinov (1988)
Romania	Black Sea coast	16–94	Por (1959)
Ukraine/Georgia <sup>10</sup>	–	12–100	Griga (1963)
Ukraine	Crimean south coast	50–100	Kolesnikova (1983)
Tunisia	Cartaghe (Salammbô)	10	Monard (1935) <sup>11</sup>
Western Sahara <sup>12</sup>	offshore locality not specified	80	Marinov (1977)
NE Mid-Atlantic	Sedlo Seamount	773–886	Büntzow (2011)
	Seine Seamount	210	Büntzow (2011)
	deep sea, 26°33'W 40°11'N	2,720	Büntzow (2011)
U.S.A.	California, Santa Maria Basin	SUB	Fiers (1996), Fiers in Gómez (2000)
Mexico	Sinaloa, Ensenada de Pabellón lagoon	INT	Gómez (2000)
	Yucatán, Punta Allen	1–1.5	De Troch (2001)
Magellan Region	Magellan Straits	123–351	George (1999, 2005)
	Beagle Channel	219–320	George (1999, 2005)
	Patagonian continental slope	1,168	George (1999, 2005)
Argentina	Puerto Deseado, Sorrel, Cascajo	INT	Pallares & Hall (1974), Pallares (1975)

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**TABLE 1.** (Continued)

Country/Region	Locality	Depth	Reference
New Ireland Fore-Arc System	off Papua New Guinea, 03°19'S 152°35'E	1,610	Willen (2004) <sup>13</sup>
New Zealand	North Island, Wellington, Island Bay	INT-10	Hicks (1977a, b)

<sup>1</sup> as *Cletodes longicaudata* Brady, 1880.

<sup>2</sup> although Chislenko (1977: 272) lists the species in his table of harpacticoids from Franz Josef Land the record itself refers to Scott's (1899) work.

<sup>3</sup> as *Cletodes leptostylis* Sars, 1920.

<sup>4</sup> this record was originally published by Brady & Robertson (1878) who list the species as a *nomen nudum*.

<sup>5</sup> Lang (1948: 1328) claimed that Brady (1896) had recorded the species from Seaton Sluice in Northumberland but this is an error.

<sup>6</sup> depth data courtesy of C.G. Moore (pers. commn).

<sup>7</sup> as *Stylocletodes* [*sic*] *numidicus* (Monard, 1935). This spelling mistake was adopted by Delamare Deboutteville (1960: 229, 231, 406, 461, 478, 718).

<sup>8</sup> as *Stylicletodes numidicus* (Monard, 1935).

<sup>9</sup> Soyer recorded both *Stylicletodes longicaudatus* and *S. numidicus*.

<sup>10</sup> Griga (1963) obtained samples from the northeastern Black Sea between Yalta (Ukraine) and Batumi (Georgia) but did not specify the localities except that the species had been recorded from Crimea and the Caucasian region.

<sup>11</sup> as *Cletodes numidicus* Monard, 1935.

<sup>12</sup> formerly Spanish Sahara.

<sup>13</sup> as *Stylicletodes longicaudatus* "complex".

## Material and methods

Samples were collected in October 2014, and September and December 2016 in the East China Sea during sampling campaigns on board RV "Beidou" and "Kexue-III". Samples were fixed in 10% formalin and sieved through a 31 µm mesh. Specimens were extracted following the suspension-centrifugation method using Ludox® HS-40 (Burgess 2001; Rohal *et al.* 2018) and preserved in 75% alcohol. For their identification, the specimens were cleared in lactic acid and observed under a light microscope. Prior to dissection, the habitus was drawn and the whole body length was measured. Specimens were dissected in lactic acid and mounted on slides in lactophenol and subsequently sealed with nail-polish. Observations and drawings were made using a differential interference contrast microscope (Nikon Eclipse Ni) equipped with a drawing tube.

Descriptive terminology follows that of Huys *et al.* (1996). Abbreviations used in the text and figures are: *ae*, aesthetasc; *P1–P6*, first to sixth thoracic legs; *exp*, exopod; *enp*, endopod; *exp(enp)-1(-2,-3)*, the proximal (middle, distal) segment of a ramus. The type material was deposited in the Marine Biological Museum, Chinese Academy of Sciences, Qingdao, China (MBMCAS).

## Systematics

### Order Harpacticoida Sars, 1903

### Family Cletodidae T. Scott, 1905

### Genus *Stylicletodes* Lang, 1936

**Type species.** *Cletodes longicaudata* Brady, 1880 = *Stylicletodes longicaudata* (Brady, 1880) [by monotypy].

**Other species.** *Stylicletodes stylicaudatus* (Willey, 1935); *S. verisimilis* Lang, 1965; *S. reductus* Wells, 1965; *S. minutus* Bodin, 1968; *S. oligochaeta* Bodin, 1968.

***Stylicletodes wellsi* sp. nov.**

(Figs. 1–7)

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**Type locality.** East China Sea (29°31.002'N, 122°36.798'E); 25 m depth; silt.

**Type material.** Holotype: ♀ dissected on three slides (MBM189255). Paratypes: (a) 1 ♀ dissected on five slides (MBM189256), 1 ♂ (MBM189257) on three slides; from type locality; (b) 1 ♂ (MBM189258) partly dissected on two slides; from East China Sea (29°25.656'N, 122°58.998'E); 61 m depth; fine sand. All type specimens collected on 12 December 2016.

**Other material.** (a) 1 ♀ (MBM189259); from type locality; collected on 12 December 2016; (b) 1 ♀ (MBM189261); 29°25.656'N, 122°58.998'E; 61 m depth; fine sand; collected on 12 December 2016; (c) 1 ♀ (MBM189260); 28°52.998'N, 122°44.502'E; 66 m depth; silt; collected on 18 December 2016; (d) 1 ♂ (MBM189262); 31°40.2'N, 122°30'E; 28 m depth; silt; collected on September 2016; (e) 1 ♂ (MBM189263) DH4-5; 28°38.4'N, 124°37.8'E; 81 m depth; silt; collected on October 2014. All specimens collected in the East China Sea and preserved in 75 % ethanol.

**Etymology.** The species is named in honour of Professor John Berkeley James Wells, in recognition of his massive contributions to our knowledge of harpacticoid taxonomy and systematics.

**Description of female.** Total body length, measured from anterior margin of rostrum to posterior margin of caudal rami, ranging from 365 to 392 µm (mean = 377 µm;  $n = 4$ ).

Habitus (Fig. 1A, B) slender, curved ventrally in lateral aspect; P1-bearing somite fused to cephalosome forming cephalothorax. Without distinct demarcation between prosome and urosome. Rostrum fused to cephalothorax; triangular, ventrally recurved in lateral aspect, with two sensilla subapically. All somites with dorsal setules along posterior margin except for anal somite. Prosomites with pairs of papillary socles dorsally, each bearing one apical sensillum. Genital double-somite with vestigial P6 represented by two setae (outermost seta longer than innermost) in proximal half of genital somite (Fig. 1C); ventral surface relatively smooth, posterior margin with transverse row of strong spinules; genital field with large copulatory pore located near posterior margin. Genital double-somite and second abdominal somite with dorsolateral and ventrolateral papillary socles around posterior margin (Fig. 1A–C); ventral surface of second and third abdominal somites with transverse spinule row near posterior margin (Fig. 1C). Ventral surface of anal somite partially cleft medially (Fig. 1C); anal operculum (Fig. 1A, C) produced into long setular extension, flanked by two sensilla. Caudal rami (Fig. 1B; note that the rami in Fig. 1A are foreshortened because of the mounting position of the specimen) exceedingly narrow and elongated, about 13 times as long as wide; with one outer proximal seta, distally with three setae, inner margin with one seta near distal fifth of caudal ramus.

Antennule (Fig. 2A) five-segmented; surface of all segments smooth; fourth segment shortest; with aesthetasc on third segment; fifth segment with two spiniform setae along anterior margin, four apical setae, and three setae along posterior margin. Armature formula: 1-[1], 2-[4], 3-[3 + (1 + ae)], 4-[1], 5-[9].

Antenna (Fig. 2B). Surface of allobasis smooth; with one proximal and one subdistal abexopodal seta. Exopod one-segmented, with two setae, one subdistal and one distal. Free endopodal segment with longitudinal row of inner spinules proximally; some outer spinules subdistally; two outer subdistal spines laterally; one pinnate outer distal spine; one geniculate apical seta and three apical spines; and one inner distal spine.

Labrum (Fig. 1D) triangular, with few long spinules around pointed apex.

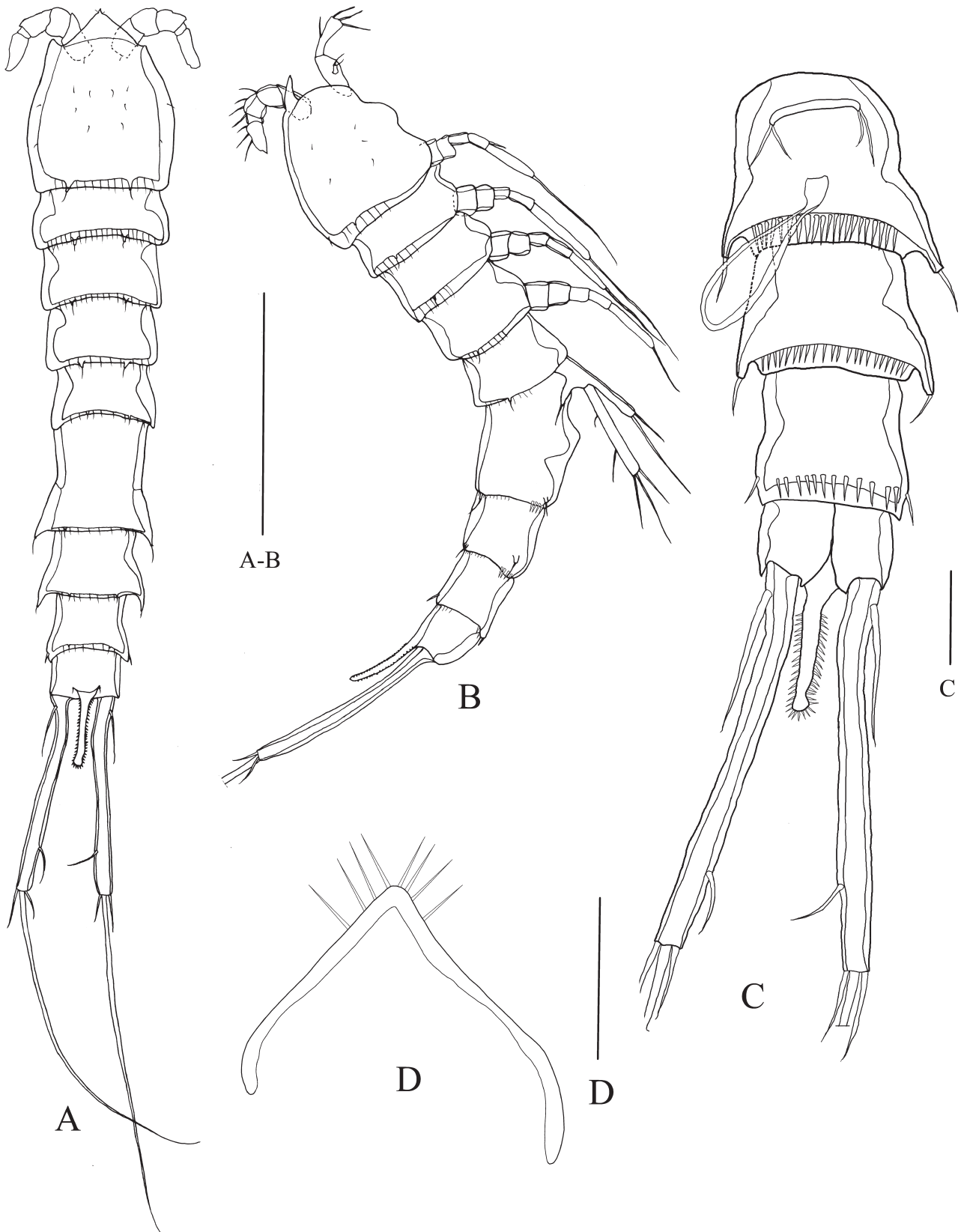
Mandible (Fig. 2C). Gnathobase elongate and narrow; with four teeth. Palp vestigial, represented by two slender setae.

Maxillule (Fig. 2D). Arthrite with five naked distal elements around distal margin; coxal endite with two setae; basis with two apical setae.

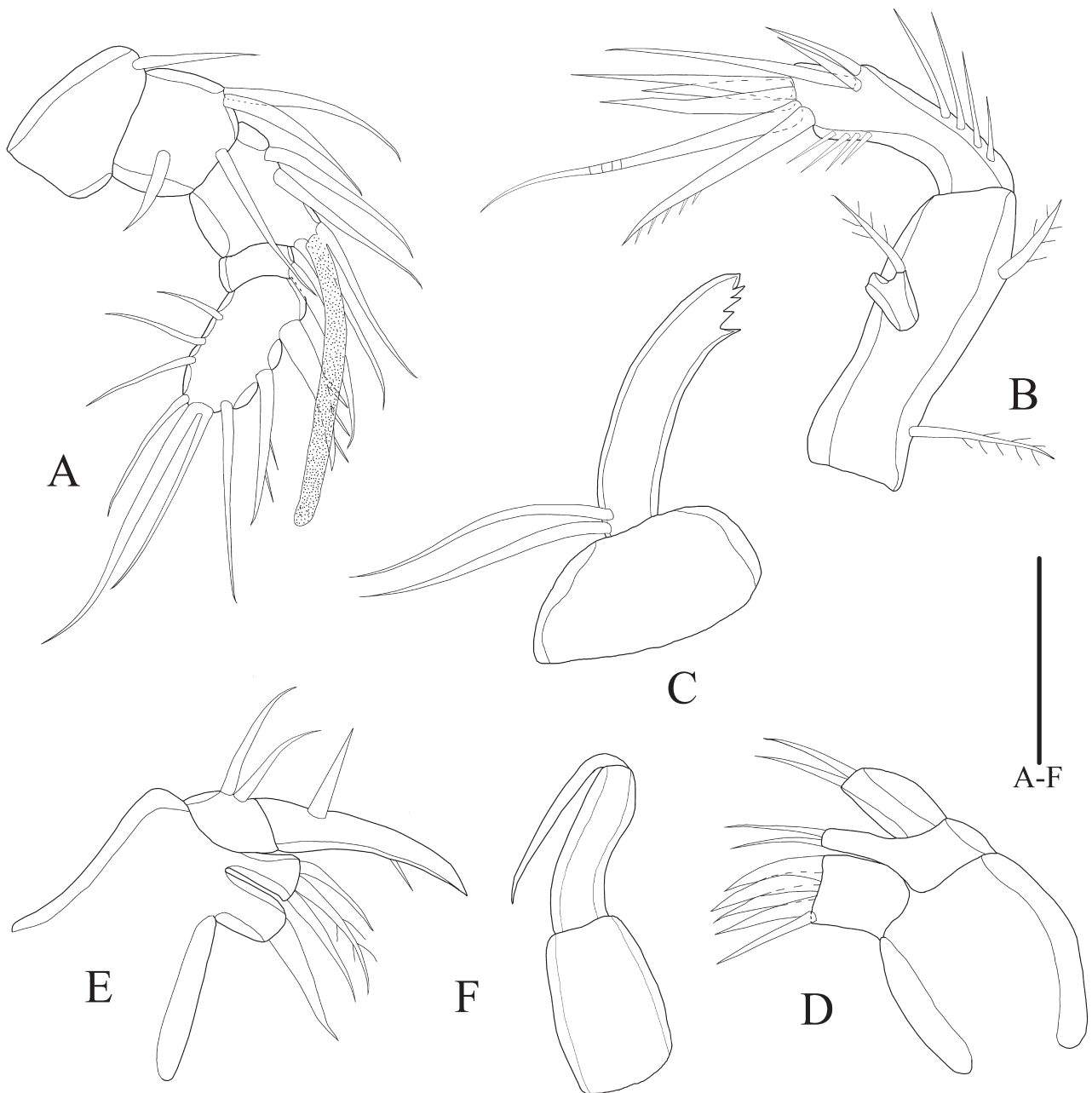
Maxilla (Fig. 2E). Syncoxa unornamented, with two endites, proximal endite with one strong seta; distal endite with one pinnate and two naked setae; allobasis with one strong claw bearing one seta; endopod represented by two slender setae.

Maxilliped (Fig. 2F) three-segmented, comprising of unarmed coxa and basis, and one-segmented endopod represented by distal claw.





**FIGURE 1.** *Stylicletodes wellsi* sp. nov. (♀): A, habitus, dorsal (holotype); B, habitus, lateral (paratype); C, urosome with spermatophore attached to genital field, ventral (paratype; P5-bearing somite omitted); D, labrum (paratype). Scale bars: A–B = 50 µm, C = 20 µm, D = 10 µm.



**FIGURE 2.** *Stylicletodes wellsi* sp. nov. (♀): A, antennule, ventral; B, antenna (missing apical seta indicated by arrow); C, mandible; D, maxillule; E, maxilla; F, maxilliped. A–C, D–G based on holotype; B, E–F based on paratype. Scale bars: 10  $\mu$ m.

P1 (Fig. 3A–B) slender. Intercoxal sclerite narrow, straight and naked. Coxa without ornamentation. Basis with two strong spinules around base of robust outer basal spine. Exopod three-segmented, all segments without armature along inner margin; first segment slightly shorter than second, each with one spinulose spine and several spinules along outer margin; distal segment about three times as long as second, with two spinulose apical setae, and two spinulose outer spines. Endopod two-segmented; proximal segment short, unarmed; distal segment about 8.4 times as long as proximal, with row of inner spinules subdistally; with one subdistal inner seta and one unipinnate seta apically.

P2 (Fig. 3C–D) slender. Intercoxal sclerite unornamented. Coxa almost square, without ornamentation. Basis with transverse row of spinules subdistally, with outer spine. Exopod three-segmented, all segments without armature along inner margin; first segment with spinules along distal and outer margins, and one spinulose outer spine; second segment about 1.5 times as long as first, with one spinulose spine and few spinules along outer margin; distal segment about 3.3 times as long as second, with row of spinules along inner margin, two spinulose apical setae and



two spinulose outer spines. Endopod two-segmented; proximal segment short, unarmed; distal segment about 16.7 times as long as proximal, with two strong spinules near inner subdistal margin, spinule row along outer margin, and two long, spinulose apical setae.

P3 (Fig. 4A) with smooth and wide intercoxal sclerite. Coxa smooth, almost trapezoidal. Basis with transverse row of spinules, with long outer seta (not shown in figure). Exopod three-segmented; first segment with outer and subdistal spinules and one spinulose outer spine; second segment as long as first, with one spinulose inner seta, and one spinulose spine and several spinules along outer margin; distal segment about 2.5 times as long as second, with two spinulose inner setae, two spinulose setae and one spinulose spine apically, and one spinulose outer spine. Endopod two-segmented; proximal segment short, unarmed; distal segment about 12.3 times as long as proximal, with two spinules along inner margin, long row of spinules along outer margin, and two naked apical setae.

P4 (Fig. 4B) slender. Intercoxal sclerite smooth and wide. Coxa smooth, slightly broader than long. Basis with row of subdistal spinules and long, sparsely plumose, outer seta. Exopod three-segmented; first segment with few subdistal spinules and one spinulose outer spine; second segment as long as first, with one spinulose inner seta and one spinulose outer spine; distal segment about 2.8 times as long as second, with one spinulose inner seta, two spinulose setae and one spinulose spine apically, and one spinulose spine and several spinules along outer margin. Endopod two-segmented; proximal segment short, unarmed; distal segment about 10.7 times as long as proximal, with several inner spinules long inner and outer margins, and one spinulose apical seta.

Armature formulae of P1–P4 as follows:

	Exopod	Endopod
P1	0.0.022	0.110
P2	0.0.022	0.020
P3	0.1.222	0.020
P4	0.1.222	0.010

P5 (Fig. 7C). Fifth legs not fused medially. Baseoendopod and exopod not fused, elongate, the former with outer basal seta. Endopodal lobe extending to almost halfway length of exopod; with four naked setae (one inner and three apical), median apical one reduced in length. Exopod long, about 12.5 times as long as greatest width; with three outer, one apical, and one subdistal inner seta; all setae naked.

**Description of male.** Total body length, measured from anterior margin of rostrum to posterior margin of caudal rami, ranging from 360 to 380  $\mu\text{m}$  (mean = 369  $\mu\text{m}$ ;  $n = 3$ ).

Habitus (Fig. 5A) generally as in female, except urosomites 2 and 3 not fused, and pro- and urosomites without setules dorsally; transverse spinular row on first abdominal somite shorter and abdominal spinulation sparser than in female.

Antennule (Fig. 5C) chirocer, five-segmented with geniculation between fourth and fifth segments; surface of all segments smooth; with aesthetasc on fourth and fifth segments. First segment with one naked seta; second segment with small plumose seta and five naked setae; third segment shortest; fourth segment swollen; apex of fifth segment recurved. Armature formula: 1-[1], 2-[6], 3-[6], 4-[2 + (1 + ae)], 5-[7 + (1 + ae)].

Antenna, mandible, maxillule, maxilla, maxilliped, and P4 as in female.

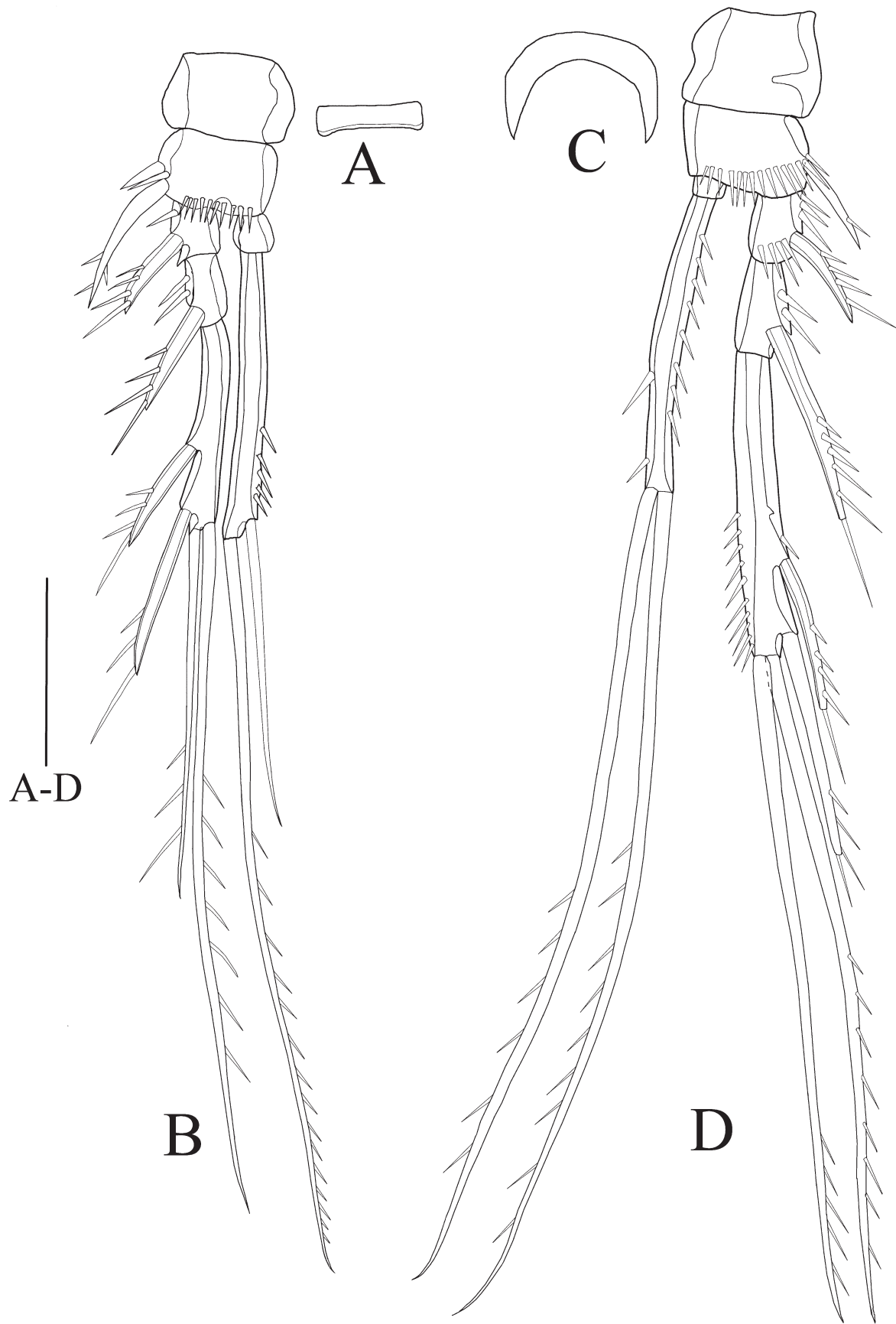
P1 (Fig. 6A). Intercoxal sclerite narrow, straight and naked. Praecoxa narrow, triangular, without ornamentation. Distal segment of endopod about seven times as long as proximal, with two spinules along inner margin. Otherwise as in female.

P2 (Fig. 6B) as in female, except for distal segment of endopod slightly swollen medially, and with more spinules along inner margin.

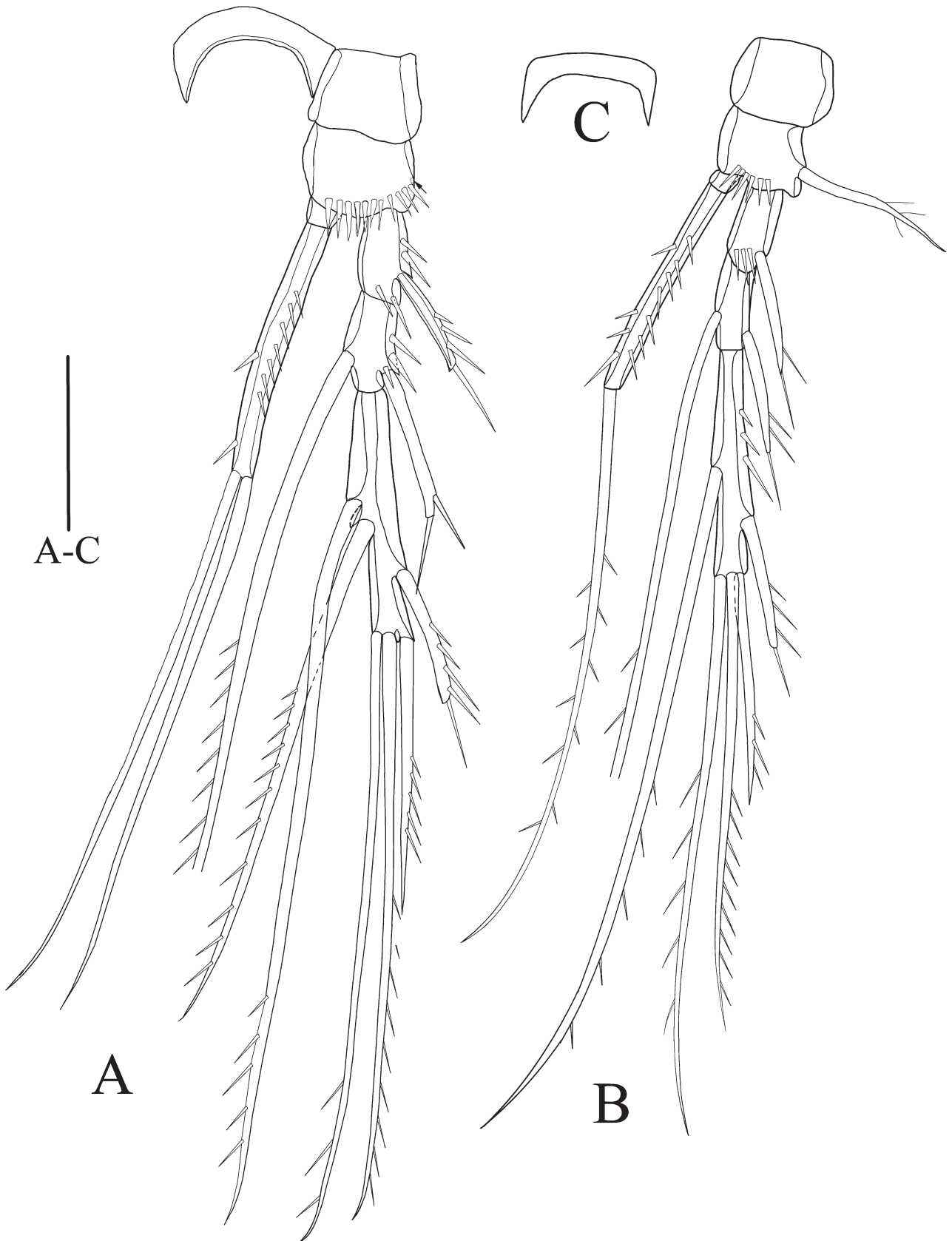
P3 (Fig. 7A) Coxa and basis as in female, except for fewer subdistal spinules on basis. Endopod sexually dimorphic, three-segmented; first segment as in female; second segment longest, with spiniform recurved apophysis arising from inner margin; third segment with two naked apical setae. Exopod three-segmented, first and second segments as in female; third segment with three inner setae, otherwise as in female.

P5 (Fig. 7B). Fifth legs not fused medially. Baseoendopod with outer basal seta and vestigial endopodal lobe bearing two naked setae apically and two spinules subdistally along inner margin. Exopod elongate, about 5.8 times as long as greatest width; with one outer, one subdistal inner and two apical setae.

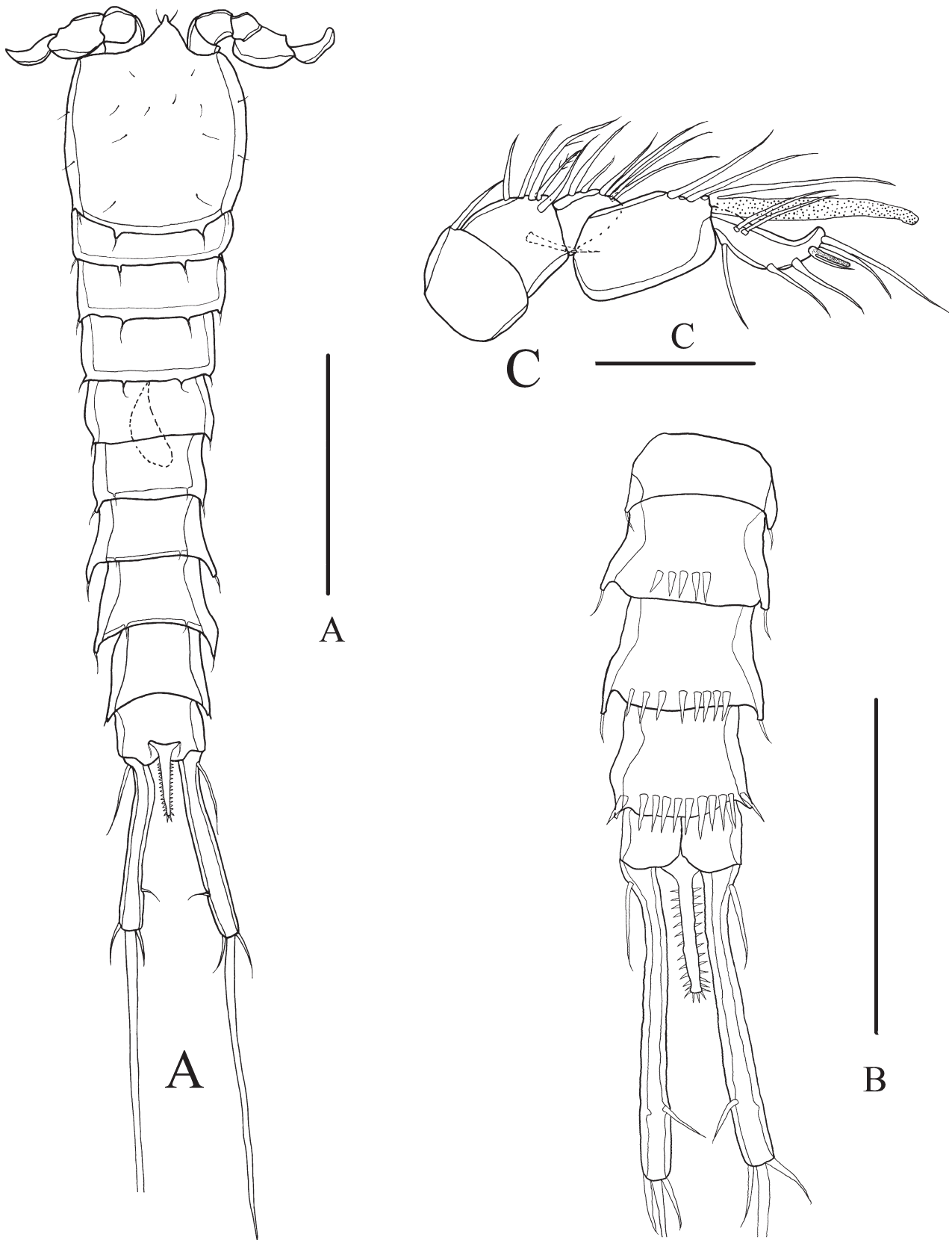
Sixth legs represented by unarmed flaps.



**FIGURE 3.** *Stylicletodes wellsi* sp. nov. (♀): A, coxa of P1, anterior; B, P1, anterior; C, coxa of P2, anterior; D, P2, anterior. A and C based on paratype; B and D based on holotype. Scale bar: 20µm.



**FIGURE 4.** *Stylicletodes wellsi* sp. nov. (♀): A, P3 including intercoxal sclerite, anterior (position of outer basal seta indicated by arrow); B, P4, anterior; C, coxa of P3, anterior. A–B based on holotype; C based on paratype. Scale bar: 20µm.



**FIGURE 5.** *Stylicletodes wellsi* sp. nov. (♂): A, habitus, dorsal; B, urosome, ventral; C, antennule. All based on paratype. Scale bars: A–B = 50 μm, C = 20μm.

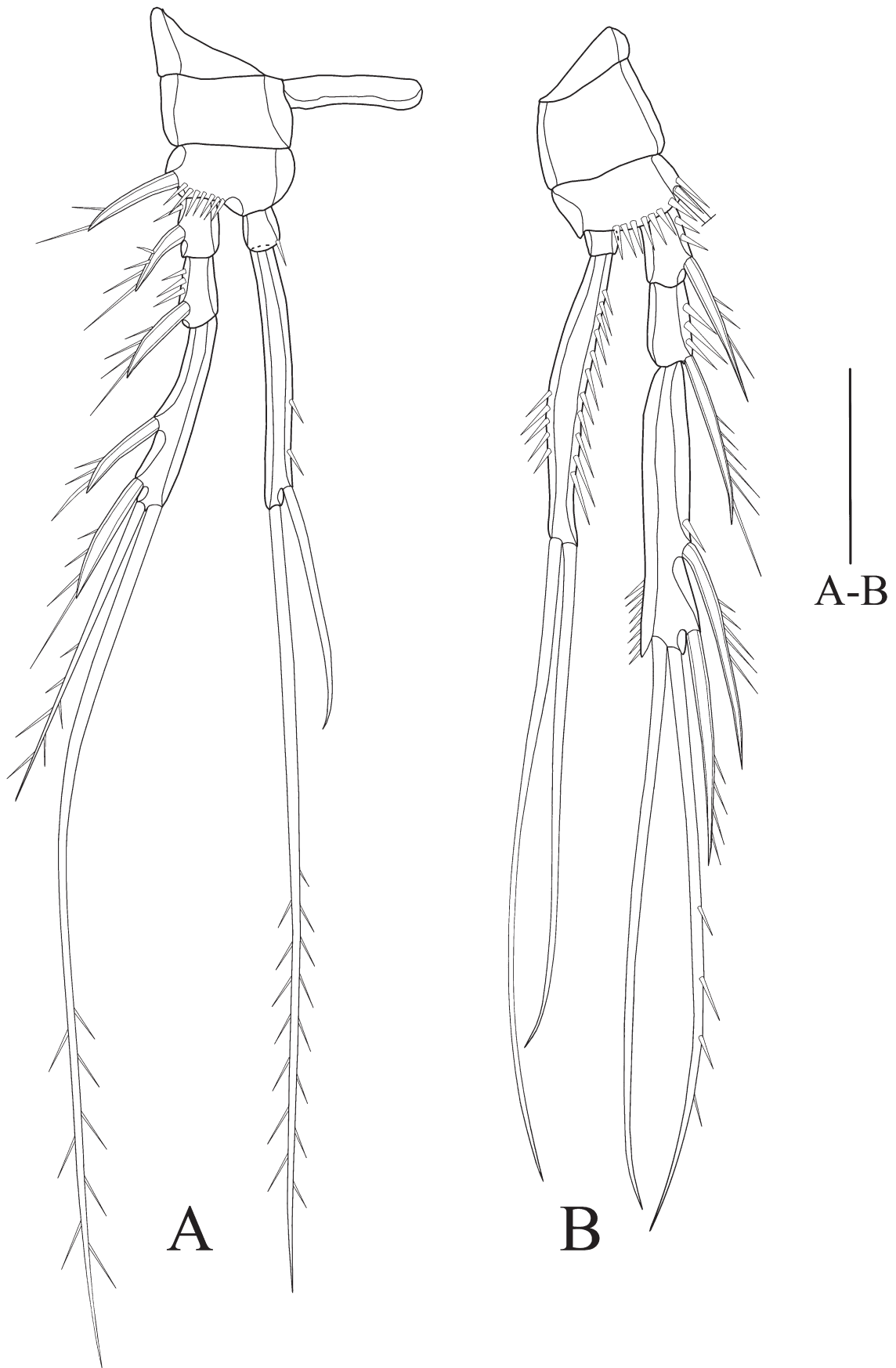


FIGURE 6. *Stylicletodes wellsi* sp. nov. (♂): A, P1, anterior; B, P2, anterior. All based on paratype. Scale bar = 20µm.

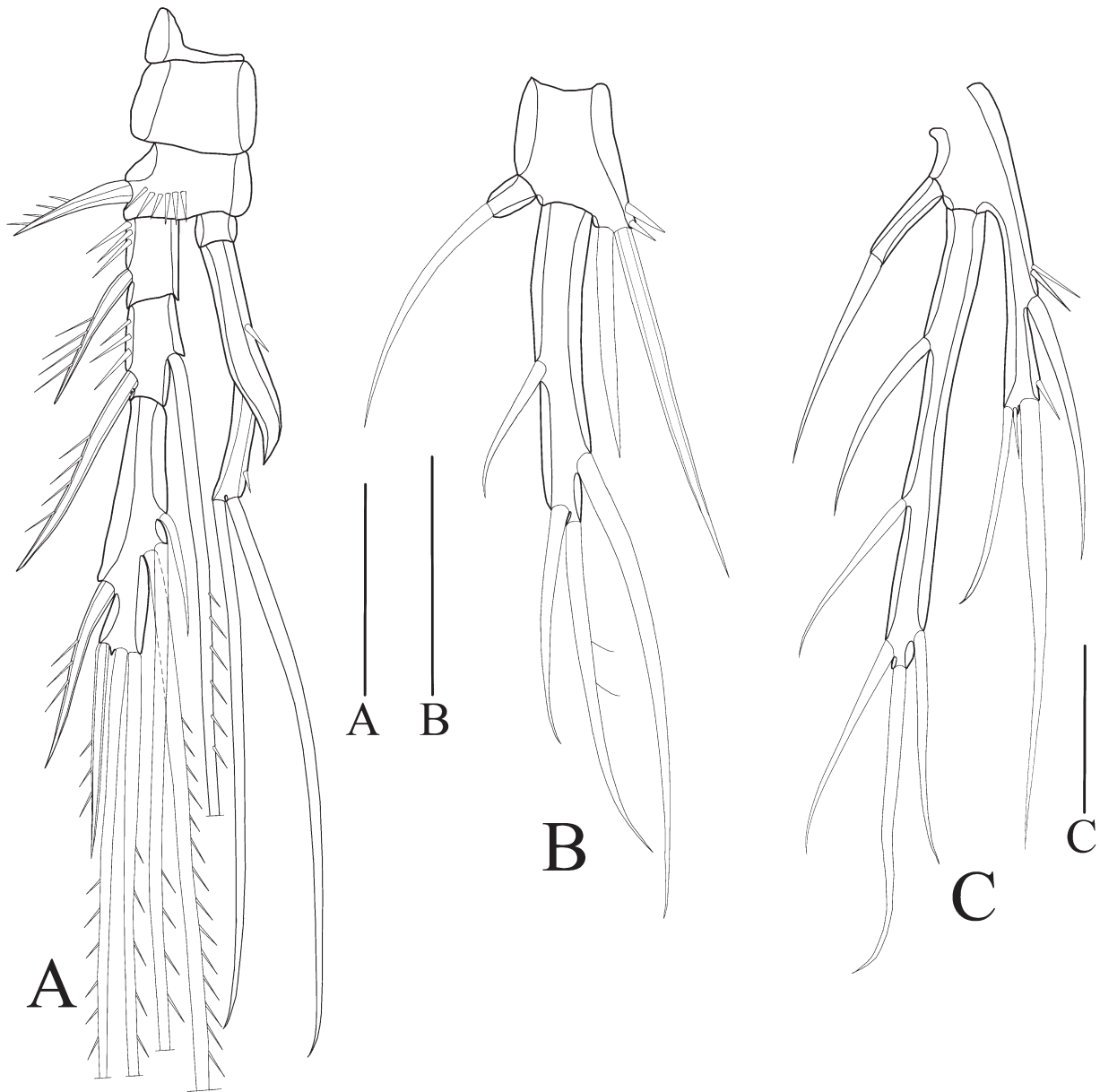


FIGURE 7. *Stylicletodes wellsi* sp. nov.: A, P3 ♂, anterior; B, P5 ♂, anterior, C, P5 ♀, anterior. Scale bars: 20µm.

## Discussion

Morphological comparison in the genus *Stylicletodes* is hampered by the fact that (a) most species are known from one sex only, either the female (*S. minutus*, *S. oligochaeta*, *S. reductus*, *S. verisimilis*) or the male (*S. stylicaudatus*), (b) some original descriptions lack sufficient detail for such comparison (*S. reductus*, *S. stylicaudatus*), and (c) virtually nothing is known about intraspecific variability since five out of six species were described on the basis of one individual. The notable exception is the type species *S. longicaudatus* which has been the subject of excellent redescrptions (Lang 1965; Gómez 2000), is known from both sexes and a considerable number of specimens, and allegedly assumes a wide geographical distribution (Table 1). In his critical assessment of previous distribution records of *S. longicaudatus*, Gómez (2000) casted doubt on its reported amphi-atlantic distribution, stating that this supposition appears to be founded primarily on inadequate descriptions that fail to reveal information on characters of diagnostic significance. Such characters include the antennulary armature, relative size of the antennary allobasis and free endopodal segment, position of origin of the antennary exopod, proportional lengths of the rami of P1–P4, and detailed morphology of the female genital field. Lang (1965) reported considerable variability in a small sample



(3 ♀♀, 1 ♀ urosome, 2 ♂♂) of *S. longicaudatus* from the Gullmar Fjord in Sweden. The four females displayed different combinations of body length (470–840 µm), rostral morphology, relative length of antennular segments 2–3 and P1 exopod/endopod, shape of P1–P4 exp-3, length of P5 exopod and caudal ramus length and left/right asymmetry. Lang (1965) used this “intraspecific variability” to justify Por’s (1959) earlier course of action to synonymize *S. numidicus* (Monard, 1935) with *S. longicaudatus*. The authenticity of Lang’s (1965) Gullmar Fjord material was disputed by Gómez (2000) who claimed that both females and males represented an amalgam of different species, suggesting the presence of sympatric, as yet undescribed, members in the genus and that the relegation of *S. numidicus* as a junior synonym might be premature. We concur with Gómez (2000) that a thorough re-examination of *S. longicaudatus* based on a wider sampling is required before the illustrated records from Europe (Monard 1935; Petkovski 1955; Por 1959; Griga 1963; Marinov 1971, 1977) and South America (Pallares 1975) can be considered conspecific with Brady’s (1880) type material.

*Stylicletodes wellsii* **sp. nov.** can readily be assigned to the genus *Stylicletodes* by the combination of the following characters: P1 exp-3 with geniculate-like setae, P1–P4 endopods long and narrow, exopodal spines of P2–P4 with long spinules, exopod and endopodal lobe of female P5 elongate, P1 endopod as long as exopod, male P3 typically dimorphic and with inner apophysis on second segment (Lang 1948; Fiers 1996). Fiers (1996: 25) had previously hinted at the presence of several evolutionary lineages in *Stylicletodes* and it is clear that at least two well delimited groups can be recognized which may eventually receive separate generic status (Table 2). Group I combines species that have a rounded, unmodified anal operculum and fifth legs (in both sexes) that bear densely plumose armature elements. Group II accommodates species that display an anal operculum with a median linguiform extension which is bilaterally setular and backwardly directed, and fifth legs that possess either naked or sparsely pinnate setae and spines. *Stylicletodes wellsii* **sp. nov.** belongs to Group II which also includes *S. reductus* and *S. minutus*. The latter is readily distinguished from the other two members of this group by the presence of one (vs two) seta(e) on P1 enp-2 and five (vs six) setae/spines on P3 exp-3, the reduced endopodal lobe of the female P5, and the shorter extension of the anal operculum. Although morphologically similar to the European *S. reductus* in the length of the caudal rami and the linguiform extension of the anal operculum, the new species shows significant differences including the presence of (a) five instead of six setae/spines on P4 exp-3, (b) only one instead of two setae on P4 enp-3, and (c) five instead of four elements on the female P5 exopod. It should be noted that the reports of a 2-segmented exopod and the presence of only abexopodal seta in the description of the antenna of *S. reductus* (Wells 1965: Fig. 65) are conceivably based on observational errors.

### Key to species of *Stylicletodes* Lang, 1936

Both the latest dichotomous key by Bodin (1968) and the tabular key by Wells (2007) have been superseded. A new key to the seven valid species is presented below and rectifies oversights and misinterpretations contained in previous keys. Gómez (2000) pointed out the close similarity between *S. stylicaudatus* and *S. oligochaeta*; comparison between these species is necessarily based on the male of the former and the female of the latter and restricted to caudal ramus morphology.

1. Anal operculum terminating in conspicuous, median, setular extension; armature elements on P5 ♀ densely plumose . . . . . 2
- Anal operculum rounded, without median, setular extension; armature elements on P5 ♀ naked or sparsely pinnate. . . . . 4
2. P1 enp-2 with one seta; P3 exp-3 with five setae/spines . . . . . *S. minutus* Bodin, 1968
- P1 enp-2 with two setae; P3 exp-3 with six setae/spines . . . . . 3
3. P4 exp-3 with five setae/spines; P4 enp-2 with one seta . . . . . *S. wellsii* **sp. nov.**
- P4 exp-3 with six setae/spines; P4 enp-2 with two setae . . . . . *S. reductus* Wells, 1965
4. P3–P4 exp-3 with five setae/spines . . . . . 5
- P3–P4 exp-3 with six setae/spines . . . . . 6
5. Caudal ramus extremely long and narrow, about half as long as length of body somites combined, divergent; seta VII originating from middle third of ramus . . . . . *S. oligochaeta* Bodin, 1968
- Caudal ramus distinctly shorter and wider; seta VII originating from proximal third. . . . . *S. stylicaudatus* (Willey, 1935)
6. Caudal ramus maximum length:width ratio 7–11, about as long as urosome; inner margin virtually straight, with long setules in proximal half; seta II reaching to about halfway ramus length; setae I–II arising from small outer margin protuberance . . . . . *S. longicaudatus* (Brady, 1880)
- Caudal ramus maximum length:width ratio 4–5, about 60% of urosome length; inner margin convex in proximal half, without setular ornamentation; seta II reaching to posterior margin of ramus; setae I–II arising from conspicuous outer margin protuberance. . . . . *S. verisimilis* Lang, 1965

**TABLE 2.** Morphological characters of *Stylicletodes* species. An Op = anal operculum, with (+) or without (-) elongate setular extension. P5 = female fifth leg armature elements densely plumose (+) or naked/pinnate (-), ? = female condition unknown. apo = apophysis on male P3 endopod. BL = body length in  $\mu\text{m}$ .

Species	AO		P1		P2		P3		P4		P5♀		BL	
	exp	enp	exp	enp	exp	enp	exp	enp	exp	enp	exp	enp		
<b>Group I</b>														
<i>S. longicaudatus</i> (Brady, 1880)	-	0.0.022	0.110	0.0.022	0.0.022	0.020	0.1.222	0.021	0.1.222	0.021	0.1.222	0.021	+	450–840 (♀) <sup>1</sup> 500–600 (♂) <sup>1</sup>
<i>S. stylicaudatus</i> (Willey, 1935)	-	0.0.022	0.110	0.0.022	0.0.022	0.020	0.0.122	0.apo.020	0.1.122	0.021	0.1.122	0.021	?	unknown
<i>S. verisimilis</i> Lang, 1965	-	0.0.022	0.110	0.0.022	0.0.022	0.020	0.1.222	0.021	0.1.222	0.021	0.1.222	0.021	+	690 (♀)
<i>S. oligochaeta</i> Bodin, 1968	-	0.0.022	0.110	0.0.022	0.0.022	0.020	0.0.122	0.021	0.0.122	0.021	0.0.122	0.021	+	360 (♀)
<b>Group II</b>														
<i>S. reductus</i> Wells, 1965	+	0.0.022	0.110	0.0.022	0.0.022	0.020	0.1.222	0.020	0.1.222	0.110 <sup>2</sup>	0.1.222	0.110 <sup>2</sup>	-	400 (♀)
<i>S. minutus</i> Bodin, 1968 <sup>3</sup>	+	0.0.022	0.010	0.0.022	0.0.022	0.020	0.1.222	0.020	0.1.222	0.010	0.1.222	0.010	-	420 (♀)
<i>S. wellsi</i> <b>sp. nov.</b>	+	0.0.022	0.110	0.0.022	0.0.022	0.020	0.1.222	0.020	0.1.222	0.010	0.1.222	0.010	-	365–392 (♀) 360–380 (♂)

<sup>1</sup> Range based on the following sources (note that the specimens these measurements were based on are not necessarily and most likely not conspecific; cf. Gómez 2000). Brady (1880): 790  $\mu\text{m}$  (♀). Scott (1902): 840  $\mu\text{m}$  (♀). Sars (1920): 550  $\mu\text{m}$  (♀). Monard (1935): 700  $\mu\text{m}$  (♀). Lang (1948): 620–730  $\mu\text{m}$  (♀), 580  $\mu\text{m}$  (♂). Por (1959): 500–600  $\mu\text{m}$  (♂). Griga (1963): 450  $\mu\text{m}$  (♀). Lang (1965): 470–840  $\mu\text{m}$  (♀). Pallares (1975): 753  $\mu\text{m}$  (♀). Gómez (2000): 569–571  $\mu\text{m}$  (♀). Kornev & Chertoprud (2008): 560  $\mu\text{m}$  (♂).

<sup>2</sup> Wells (1965) did not illustrate P4 but stated that the endopods were similar in all legs (“... always with one apical and one inner seta”); the endopodal setal formula of P4 should probably be reinterpreted as 0.020.

<sup>3</sup> Bodin (1968) correctly listed the armature formula of P1–P4 but inadvertently mislabelled P2 and P4 in his Plate LVII; this is probably the reason why Wells (2007) incorrectly scored the number of setae on the P4 endopod as two (his KG2, p. 345).

## References

- Apostolov, A. & Marinov, T.M. (1988) Copepoda Harpacticoida (morski kharpaktikoidi). [Copepoda, Harpacticoida (marine harpacticoids)]. *Fauna Bulgarii [Fauna Bulgarica]*, 18, 1–384. [in Bulgarian]
- Baguley, J.G. (2004) *Meiofauna community structure and function in the northern Gulf of Mexico deep sea*. Ph.D. dissertation, The University of Texas, Austin, Texas, xxi + 200 pp.
- Bodin, P. (1968) Copépodes Harpacticoides des stages bathyal et abyssal du Golfe de Gascogne. *Mémoires du Muséum national d'Histoire naturelle*, 55A, 1–107.
- Bodin, P. (1972) Copépodes Harpacticoides marins des environs de la Rochelle. 3. Espèces de la zone intertidale de Fouras-Nord. *Téthys*, 3, 841–864.
- Bodin, P. (1973) Copépodes Harpacticoides marins des environs de la Rochelle. IV. Espèces de la zone intertidale des Nauteries. *Téthys*, 4, 651–682.
- Bodin, P. (1977) Les peuplements de Copépodes Harpacticoides (Crustacea) des sédiments meubles de la zone intertidale des côtes Charentaises (Atlantique). *Mémoires du Muséum national d'Histoire naturelle, Paris, Nouvelle Série, (A)*, 104, 1–120 + 31 pp., appendix containing tables 2, 12, 15–16, 18–21, 23, 25, 28, 30–31, 33, 35–37, 41, 45–46, 48, 51, 54–55, 59 and faunistic index.
- Bodiou, J.-Y. (1976) Copépodes Harpacticoides (Crustacea) des sables fins infralittoraux de Banyuls-sur-Mer. I. Description de la communauté. *Vie et Milieu, (B)*, 25, 313–330.
- Bodiou, J.-Y. (1982) Copépodes Harpacticoides (Crustacea) des sables fins infralittoraux de Banyuls-sur-Mer. II. Variations saisonnières qualitatives du peuplement. *Vie et Milieu*, 30, 269–274.
- Boeck, A. (1873) Nye Slægter og Arter af Saltvands-Copepoder. *Forhandlinger I videnskabselskabet I Kristiania*, 1872, 35–60.
- Boxshall, G.A. & Halsey, S.H. (2004) *An Introduction to Copepod Diversity*. The Ray Society, London, xv + 966 pp.
- Brady, G.S. (1872) Contributions to the study of the Entomostraca. No. VII. A list of the non-parasitic marine Copepoda of the north-east coast of England. *Annals and Magazine of natural History, Series 4*, 10, 1–17, pls. II–VI. [also in *Natural History Transactions of Northumberland and Durham*, 4, 423–445, pls. XVII–XXI] <https://doi.org/10.1080/00222937208696629>
- Brady, G.S. (1880) *A Monograph of the Free and Semi-parasitic Copepoda of the British Islands. Vol. II*. The Ray Society, London, 182 pp., pls. XXXIV–LXXXII.
- Brady, G.S. (1896) On Entomostraca collected in the Solway district and the Seaton sluice, Northumberland, during the summer of 1894. *Natural History Transactions of Northumberland, Durham and Newcastle-upon-Tyne*, 13, 19–33, pls. I–III.
- Brady, G.S. (1904) Notes on Entomostraca found at the roots of Laminariæ. *Transactions of the Natural History Society of Northumberland, Durham and Newcastle-upon-Tyn*, New Series, 1, 3–9, pls. I–II.
- Brady, G.S. & Robertson, D. (1876) Report on dredgings off the coast of Durham and North-Yorkshire in 1874. *Report of the British Association for the Advancement of Science*, 45, 185–199.
- Büntzow, M. (2011) *Vergleichende gemeinschaftsanalytische und taxonomische Untersuchungen der Harpacticoidenfauna der Seeberge „Sedlo“ und „Seine“ (nördlicher Mittelatlantik)*. Ph.D. dissertation, Carl von Ossietzky Universität Oldenburg, viii + 128 pp., unpaginated tables A1–A30.
- Burgess, R. (2001) An improved protocol for separating meiofauna from sediments using colloidal silica sols. *Marine Ecology Progress Series*, 214, 161–165. <https://doi.org/10.3354/meps214161>
- Burgess, R., Sharma, J., Carr, R.S. & Montagna, P. (2005) Assessment of storm water outfalls in Corpus Christi Bay, Texas, USA using meiofauna. *Meiofauna marina*, 14, 157–169.
- Candás, M., Martínez Arbizu, P., Urgorri, V., Besteiro, C., Moreira, J., Abad, M. & Cunha, X. (2012) First results of taxonomic and ecologic studies on Copepoda Harpacticoida communities from the Ría de Ferrol (NW Iberian Peninsula). In: Borja, A. (Ed.), XVII Iberian Symposium on Marine Biology Studies (SIEBM), Donostia-San Sebastián, Spain, 11–14 September 2012. *Revista de Investigación marina*, 19, pp. 413–415.
- Chappuis, P.A. (1954) IV. Copépodes psammiques des plages du Roussillon. In: Chappuis, P.A. & Delamare Deboutteville, Cl. (Eds.), avec la collaboration de J. Balazuc & S. Ruffo. *Biospeologica LXXIV. Recherches sur les Crustacés souterrains (Première Série)*. *Archives de Zoologie expérimentale et générale*, 91, pp. 35–50.
- Chertoprud, E.S., Gómez, S. & Gheerardyn, H. (2009) Harpacticoida (Copepoda) fauna and the taxocene diversity of the South China Sea. *Oceanology*, 49, 488–498.
- Chislenko, L.L. (1977) Garpaktitsidy (Copepoda, Harpacticoida) s gubok zemli Frantsa-Iosifa. Harpacticids (Copepoda Harpacticoida) from sponges of Franz Josef Land. In: *Biotsenosy shel'fa zemli Frantsa-Iosifa I fauna sopedel'nykh akuatorii. Issledovaniya Fauny Morei*, 14 (22), 237–276. [in Russian with English summary]
- Coull, B.C. (1970) Shallow water meiobenthos of the Bermuda platform. *Oecologia*, 4, 325–357. <https://doi.org/10.1007/BF00393393>
- Coull, B.C. & Herman, S.S. (1970) Zoogeography and parallel level-bottom communities of the meiobenthic Harpacticoida (Crustacea, Copepoda) of Bermuda. *Oecologia*, 5, 392–399. <https://doi.org/10.1007/BF00815503>
- Delamare Deboutteville (1960) Biologie des eaux souterraines littorales et continentales. *Vie et Milieu*, suppl. 9, 1–740.

- De Troch, M. (2001) *Ecologie van harpacticoïde copepoden: structurele biodiversiteit in tropische zeegrasvelden. Ecology of harpacticoïd copepods: structural biodiversity in tropical seagrass beds*. Ph.D. dissertation, Universiteit Gent, Gent, 254 pp.
- Fiers, F. (1996) Redescription of *Enhydrosoma lacunae* Jakubisiak, 1933 (Copepoda, Harpacticoida); with comments on the *Enhydrosoma* species reported from West Atlantic localities, and a discussion of cletodid development. *Sarsia*, 81, 1–27. <https://doi.org/10.1080/00364827.1996.10413608>
- George, K.H. (1999) Gemeinschaftsanalytische Untersuchungen der Harpacticoidenfauna der Magellanregion, sowie erste similaritätsanalytische Vergleiche mit Assoziationen aus der Antarktis [Community analysis of the harpacticoïd fauna of the Magellan Region, as well as first comparisons with Antarctic associations, basing on similarity analyses.]. *Berichte zur Polarforschung*, 327, 1–187.
- George, K.H. (2005) Sublittoral and bathyal Harpacticoida (Crustacea: Copepoda) of the Magellan region. Composition, distribution and species diversity of selected major taxa. In: Arntz, W.E., Lovrich, G.A. & Thatje, S. (Eds.), *The Magellan-Antarctic Connection: Links and Frontiers at High Southern Latitudes*. *Scientia marina*, 69 (Supplement 2), pp. 147–158. <https://doi.org/10.3989/scimar.2005.69s2147>
- George, K.H., Pointner, K. & Packmor, J. (2018) The benthic Copepoda (Crustacea) of Anaximenes Seamount (eastern Mediterranean Sea)—taxa diversity, community structure and distribution. *Progress in Oceanography*, 165, 299–316. <https://doi.org/10.1016/j.pocean.2018.06.006>
- Gómez, S. (2000) *Cletodes confusum* sp. nov., *C. pseudodissimilioris* sp. nov., and *Stylicletodes longicaudatus* (Copepoda: Harpacticoida: Cletodidae) from a coastal lagoon in south-eastern Gulf of California (Mexico). *Cahiers de Biologie marine*, 41, 265–280. <https://doi.org/10.21411/CBM.A.C99C1BB9>
- Grego, M., Riedel, B., Stachowitsch, M. & De Troch, M. (2014) Meiofauna winners and losers of coastal hypoxia : case study harpacticoïd copepods. *Biogeosciences*, 11, 281–192. <https://doi.org/10.5194/bg-11-281-2014>
- Griga, R.E. (1963) Harpacticoida donnykh biotsenozov yuzhnogo berega Kryma i Kavkaza. (Harpacticoida of the bottom biocoenoses of the southern shore of the Crimea and the Caucasus). *Trudy Sevastopol'skoi biologicheskoi Stantsii*, 16, 159–172. [in Russian with English summary]
- Guidi-Guilvard, L.D., Thistle, D., Khripounoff, A. & Gasparini, S. (2009) Dynamics of benthic copepods and other meiofauna in the benthic boundary layer of the deep NW Mediterranean Sea. *Marine Ecology Progress Series*, 396, 181–195. <https://doi.org/10.3354/meps08408>
- Guille, A. & Soyer, J. (1969) La faune benthique des substrats meubles de Banyuls-sur-Mer. Premières données qualitatives et quantitatives. *Vie et Milieu*, (B), 19, 323–360.
- Hicks, G.R.F. (1977a) Species composition and zoogeography of marine phytal harpacticoïd copepods from Cook Strait, and their contribution to total phytal meiofauna. *New Zealand Journal of marine and freshwater Research*, 11, 441–469. <https://doi.org/10.1080/00288330.1977.9515703>
- Hicks, G.R.F. (1977b) Species associations and seasonal population densities of marine phytal harpacticoïd copepods from Cook Strait. *New Zealand Journal of marine and freshwater Research*, 11, 621–643. <https://doi.org/10.1080/00288330.1977.9515702>
- Hicks, G.R.F. (1986) Distribution and behaviour of meiofaunal copepods inside and outside seagrass beds. *Marine Ecology Progress Series*, 31, 159–170. <https://doi.org/10.3354/meps031159>
- Huys, R. (2009) Unresolved cases of type fixation, synonymy and homonymy in harpacticoïd copepod nomenclature (Crustacea: Copepoda). *Zootaxa*, 2183 (1), 1–99. <https://doi.org/10.11646/zootaxa.2183.1.1>
- Huys, R., Gee, J.M., Moore, C.G. & Hamond, R. (1996) Marine and Brackish Water Harpacticoids, Part 1. In: Barnes, R.S.K. & Crothers, J.H. (Eds.), *Synopses of the British Fauna (New Series)*, 51, 1–352.
- Huys, R., Herman, P.M.J., Heip, C.H.R. & Soetaert, K. (1992) The meiobenthos of the North Sea: density, biomass trends and distribution of copepod communities. *ICES Journal of marine Science*, 49, 23–44. <https://doi.org/10.1093/icesjms/49.1.23>
- Janssen, A., Chevaldonné, P. & Martínez Arbizu, P. (2013) Meiobenthic copepod fauna of a marine cave (NW Mediterranean) closely resembles that of deep-sea communities. *Marine Ecology Progress Series*, 479, 99–113. <https://doi.org/10.3354/meps10207>
- Karanovic, T., Kim, K. & Lee, W. (2015) Concordance between molecular and morphology-based phylogenies of Korean *Enhydrosoma* (Copepoda: Harpacticoida: Cletodidae) highlights important synapomorphies and homoplasies in this genus globally. *Zootaxa*, 3990, 451–496. <https://doi.org/10.11646/zootaxa.3990.4.1>
- Kim, K., Trebukhova, Y., Lee, W. & Karanovic, T. (2014) A new species of *Enhydrosoma* (Copepoda: Harpacticoida: Cletodidae) from Korea, with redescription of *E. intermedia* and establishment of a new genus. *Proceedings of the biological Society of Washington*, 127, 248–283. <https://doi.org/10.2988/0006-324X-127.1.248>
- Kitahashi, T., Kawamura, K., Kojima, S. & Shimanaga, M. (2013) Assemblages gradually change from bathyal to hadal depth:



- A case study on harpacticoid copepods around the Kuril Trench (north-west Pacific Ocean). *Deep-Sea Research Part I: Oceanographic Research Papers*, 74, 39–47.  
<https://doi.org/10.1017/S0025315411001536>
- Kitahashi, T., Kawamura, K., Kojima, S. & Shimanaga, M. (2014) Bathymetric patterns of  $\alpha$  and  $\beta$  diversity of harpacticoid copepods at the genus level around the Ryukyu Trench, and turnover diversity between trenches around Japan. *Progress in Oceanography*, 123, 54–63.  
<https://doi.org/10.1016/j.pocean.2014.02.007>
- Kolesnikova, E.A. (1983) Garpaktitsidy v soobshchestvakh rykhlykh gruntov raona yuzhnogo berega Kryma. Harpacticides in communities of loose grounds within the limits of the Crimean southern coast. *Ekologiya Morya*, 15, 20–26. [in Russian with English summary]
- Kornev, P.N. & Chertoprud, E.S. (2008) *Veslonogie Rakoobraznye Otryada Harpacticoida Belogo Morya: Morfologiya, Sistematika, Ekologiya. [Copepod Crustaceans of the Order Harpacticoida of the White Sea: Morphology, Systematics, Ecology]*. Tovarischestvo Nauchnikh Izdaniy KMK, Moscow, 379 pp.
- Kotwicki, L. (2002) Benthic Harpacticoida (Crustacea, Copepoda) from the Svalbard archipelago. *Polish polar Research*, 23, 185–191.
- Lang, K. (1936) Die Familie der Cletodidae, Sars, 1909. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, 68, 445–480.
- Lang, K. (1948) *Monographie der Harpacticiden. Vols. 1 & 2*. Håkan Ohlsson, Lund, 1682 pp.
- Lang, K. (1965) Copepoda Harpacticoida from the Californian Pacific coast. *Kungliga Svenska Vetenskapsakademiens Handlingar, Serier 4*, 10 (2), 1–560.
- Marinov, T.M. (1971) Kharpaktikoidi ot b'lgarskoto kraibrezhnie na Cherno more. Harpacticoides of the Bulgarian Black Sea coast. *Izvestiya na Instituta po Okeanografiya i Ribno Stopanstvo, Varna*, 11, 43–87. [in Bulgarian with English and Russian summaries]
- Marinov, T.M. (1977) Kharpaktikoidi ot tsentralnata chast na iztochnoto kraibrezhie na Atlanticheskiya orms. Harpacticoida from the eastern Central Atlantic coast. *Izvestiya. Institut po Ribni Resursi, Varna*, 15, 83–98. [in Bulgarian with Russian and English summaries]
- Monard, A. (1935) Les Harpacticoides marins de la région de Salammbô. *Bulletin de la Station océanographique de Salammbô*, 34, 1–94.
- Montagna, P.A. & Spies, R.B. (1985) Meiofauna and chlorophyll associated with *Beggiatoa* mats of a natural submarine petroleum seep. *Marine environmental Research*, 16, 231–242.  
[https://doi.org/10.1016/0141-1136\(85\)90021-2](https://doi.org/10.1016/0141-1136(85)90021-2)
- Moore, C.G. (1979) Analysis of the associations of meiobenthic Copepoda of the Irish Sea. *Journal of the marine biological Association of the United Kingdom*, 59, 831–849.  
<https://doi.org/10.1017/S0025315400036870>
- Moore, P.G. (1973) The kelp fauna of northeast Britain. II. Multivariate classification: turbidity as an ecological factor. *Journal of experimental marine Biology and Ecology*, 13, 127–164.  
[https://doi.org/10.1016/0022-0981\(73\)90074-9](https://doi.org/10.1016/0022-0981(73)90074-9)
- Mu, F.-H., Somerfield, P.J., Warwick, R.M. & Zhang, Z.-N. (2002) Large scale spatial patterns in the community structure of benthic harpacticoid copepods in the Bohai Sea, China. *Raffles Bulletin of Zoology*, 50, 17–26.
- Norman, A.M. & Scott, T. (1906) *The Crustacea of Devon and Cornwall*. William Wesley & Son, London, xv + 232 pp., pls. I–XXIV.
- Packmor, J. & George, K.H. (2016) Littoral Harpacticoida (Crustacea: Copepoda) of Madeira and Porto Santo (Portugal). *Journal of the marine biological Association of the United Kingdom*, 98, Special Issue 1 (Special Section: European Marine Biology Symposium Papers 2016), 1–12.  
<https://doi.org/10.1017/S0025315416001168>
- Pallares, R.E. (1975) Copépodos marinos de la Ría Deseado (Santa Cruz, Argentina). Contribución sistemático ecológica. IV. Conclusión. *Physis, Buenos Aires, (A)*, 34, 213–227.
- Pallares, R.E. & Hall, M.-A. (1974) Analisis bioestadístico-ecológico de la fauna de Copépodos asociados a los bosques de *Macrocystis pyrifera*. *Physis, Buenos Aires, Série A*, 33, 275–319.
- Petkovski, T.K. (1955) Weitere Beiträge zur Kenntnis der Grundwasser-Copepoden der Adriatischen Küste. *Acta Musei macedonici Scientiarum naturalium*, 3 (8), 209–225.
- Por (Pór), F.D. (1959) Harpacticoides noi (Crustacea, Copepoda) din mîlurile Mării Negre. (Harpacticoides nouveaux (Crustacés, Copépodes) des vases de la mer Noire). *Studii și Cercetări de Biologie, Seria Biologie animal*, 4 (11), 347–368.
- Por, F.D. (1964a) Les Harpacticoides (Crustacea, Copepoda) des fonds meubles du Skagerak. *Cahiers de Biologie marine*, 5, 233–270.
- Por, F.D. (1964b) A study of Levantine and Pontic Harpacticoida (Crustacea, Copepoda). *Zoologische Verhandelingen, Leiden*, 64, 1–128.
- Rohal, M., Thistle, D. & Easton, E.E. (2018) Extraction of metazoan meiofauna from muddy deep-sea samples: Operator and taxon effects on efficiency. *Journal of experimental marine Biology and Ecology*, 502, 105–110.  
<https://doi.org/10.1016/j.jembe.2017.01.006>
- Rossel, S. & Martínez Arbizu, P. (2019) Revealing higher than expected diversity of Harpacticoida (Crustacea: Copepoda) in the

- North Sea using MALDI-TOF MS and molecular barcoding. *Scientific Reports*, 9, 9182.  
<https://doi.org/10.1038/s41598-019-45718-7>
- Sars, G.O. (1903) Copepoda Harpacticoida. Parts I & II, Misophriidae, Longipediidae, Cerviniidae, Ectinosomidæ (part). *An Account of the Crustacea of Norway, with short Descriptions and Figures of all the Species*, 5, 1–28, pls. I–XVI.
- Sars, G.O. (1920) Copepoda Supplement. Parts VII & VIII. Harpacticoida (continued). *An Account of the Crustacea of Norway, with short Descriptions and Figures of all the Species*, 7, 73–92, pls. XLIX–LXIV.
- Saunders, G.R. (2000) *The effects of copper on meiobenthic communities: field and laboratory studies*. Ph.D. dissertation. Heriot Watt University, Edinburgh, 306 pp.
- Schmidt, C., Lins, L. & Brandt, A. (2018) Harpacticoida (Crustacea, Copepoda) across a longitudinal transect of the Vema Fracture Zone and along a depth gradient in the Puerto Rico trench. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 148, 236–250.  
<https://doi.org/10.1016/j.dsr2.2017.12.024>
- Schmidt, C., Sattarova, V.V., Katrynskić, L. & Martínez Arbizu, P. (2019) New insights from the deep: Meiofauna in the Kuril-Kamchatka Trench and adjacent abyssal plain. *Progress in Oceanography*, 173, 192–207.  
<https://doi.org/10.1016/j.pocean.2019.02.010>
- Schriever, G. (1986) Distribution and ecology of Cletodidae (Crustacea, Copepoda) at the Iceland-Faroe ridge from 290 m to 2500 m water depth. In: Schriever, G., Schminke H.K. & Shich, C.-T. (Eds.), *Proceedings II. International Conference on Copepoda*, Ottawa, Canada, 13–17 August 1984. *Sylogosus*, 58, pp. 448–458.
- Schückel, S., Sell, A.F., Kihara, T.C., Koeppen, A., Kröncke, I. & Reiss, H. (2013) Meiofauna as food source for small-sized demersal fish in the southern North Sea. *Helgoland marine Research*, 67, 203–218.  
<https://doi.org/10.1007/s10152-012-0316-1>
- Scott, T. (1899) Report on the marine and freshwater Crustacea from Franz Josef Land, collected by Mr. William S. Bruce, of the Jackson Harmsworth Expedition. *Journal of the Linnean Society, Zoology*, 27, 60–126, pls. 3–9.  
<https://doi.org/10.1111/j.1096-3642.1899.tb01421.x>
- Scott, T. (1900) Notes on some Crustacea from Fairlie and Hunterston, Firth of Clyde. *Transactions of the natural History Society of Glasgow*, New Series, 5 (3), 346–355.
- Scott, T. (1902) Notes on gatherings of Crustacea collected by the fishery steamer “Garland”, and the steam trawlers “Star of Peace” and “Star of Hope”, of Aberdeen, during the year 1901. *Reports of the Fishery Board for Scotland, Edinburgh*, 20 (3), 447–485, pls. XXII–XXV.
- Scott, T. (1905) On some new and rare Crustacea from the Scottish seas. *Reports of the Fishery Board for Scotland, Edinburgh*, 23 (3), 141–153, pls. X–XIII.
- Scott, T. (1906) A catalogue of the land, fresh water and marine Crustacea found in the basin of the River Forth and its estuary. *Proceedings of the Royal physical Society of Edinburgh*, 16, 97–381.  
<https://doi.org/10.5962/bhl.title.53706>
- Scott, T. & Scott, A. (1901) On some Entomostraca collected in the Arctic Seas in 1898 by William S. Bruce, F.R.S.G.S. *Annals and Magazine of natural History*, Series 7, 8, 337–356, pls. III–VI.  
<https://doi.org/10.1080/03745480109443332>
- Soyer, J. (1966) Copépodes Harpacticoides de Banyuls-sur-Mer. 3. Quelques formes du coralligène. *Vie et Milieu*, (B), 17, 303–344.
- Soyer, J. (1971) Bionomie benthique du plateau continental de la côte catalane française. III. Les peuplements de Copépodes Harpacticoides (Crustacea). *Vie et Milieu*, (B), 21 (2), 337–511, annexe.
- Thistle, D. & Eckman, J.E. (1990) What is the sex ratio of harpacticoid copepods in the deep sea? *Marine Biology*, 107, 443–477.  
<https://doi.org/10.1007/BF01313427>
- Thompson, I.C. (1889) Third report on the Copepoda of Liverpool Bay (the L.M.B.C. District). *Proceedings of the Liverpool biological Society*, 3, 181–191, pl. VIII. [Also in Herdman, W.A. (Ed.), *Reports upon the Fauna of Liverpool Bay and the neighbouring Seas, written by Members of the Liverpool Marine Biology Committee*, 2, 54–64, pl. VIII]
- Thompson, I.C. (1893) Revised report on the Copepoda of Liverpool Bay. *Proceedings and Transactions of the Liverpool biological Society*, 7, 175–230, pls. XV–XXXV. [also in Herdman, W.A. (Ed.) (1895) *Reports upon the Fauna of Liverpool Bay and the neighbouring Seas, written by Members of the Liverpool Marine Biology Committee*, 4, 81–136, pls. XV–XXXV]
- Vasconcelos, D.M. (2008) *Distribuição dos Copepoda Harpacticoida da meiofauna em área de talude no litoral de Sergipe, Brasil*. Ph.D. Dissertation, Universidade Federal de Pernambuco, 96 (unnumbered) pp.
- Venthham, D. (2011) *Harpacticoid Copepods from the Sussex Coast (Eastern Channel): Records 1992–1997*. The Booth Museum of Natural History, Brighton, 133 pp.
- Vijaya Bhanu, C.H., Srinivasa Rao, M., Annapurna, C., Satyanarayana, A., Ambedkar, A. & Chandra Rao, K. (2017) Checklist of harpacticoid copepods (Class: Crustacea) from Nizampatnam Bay, Bay of Bengal. *Golden Research Thoughts*, 6 (8), 1–8.
- Wells, J.B.J. (1965) Copepoda (Crustacea) from the meiobenthos of some Scottish marine sub-littoral muds. *Proceedings of the Royal Society of Edinburgh*, 69B, 1–33.  
<https://doi.org/10.1017/S0080455X00010110>



- Wells, J.B.J. (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). *Zootaxa*, 1568 (1), 1–872.  
<https://doi.org/10.11646/zootaxa.1568.1.1>
- Willen, E. (2004) Harpacticoida (Crustacea, Copepoda) from a hydrothermal active submarine volcano in the New Ireland Fore-Arc system (Papua New Guinea) with the description of a new genus and species of Pseudotachidiidae. *Meiofauna Marina*, 13, 113–135.
- Wiley, A. (1935) Harpacticoid Copepoda from Bermuda. Part II. *Annals and Magazine of natural History*, Series 10, 15 (85), 50–100.  
<https://doi.org/10.1080/00222933508654944>