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A REVISION OF *ANATHELGES* AND *STEGOPHRYXUS*
(ISOPODA: BOPYRIDAE: ATHELGINAE) WITH DESCRIPTIONS OF
TWO NEW GENERA AND ONE NEW SPECIES

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A B S T R A C T

The paguroid-infesting bopyrid genera *Anathelges* Bonnier, 1900, and *Stegophryxus* Thompson, 1902, are found to be synonymous. Three species formerly placed in either *Anathelges* or *Stegophryxus* are not congeneric with *Bopyrus resupinatus*, the type species of *Anathelges*. A new monotypic genus *Falsanathelges* is erected for *Anathelges muelleri* Nierstrasz and Brender à Brandis, which is redescribed based on type and additional material. A second new genus, *Minimathelges*, is erected for *Stegophryxus minutus* Markham and *M. nanus* n. sp. from the Loyalty Islands. *Anathelges mossambica* Barnard is provisionally transferred to *Pseudostegias* Shiino, based on examination of the damaged lectotype. Additionally, the genus *Metathelges* Nierstrasz and Brender à Brandis is transferred from the Athelginae to the Ioninae based on examination of the holotype. A key is provided for all eight athelgine genera.

All species in the bopyrid subfamily Athelginae externally infest the abdomens of paguroid crabs, and to date, eight genera have been recognized (Kazmi and Markham, 1999). The genus *Anathelges* was erected by Bonnier (1900) to contain a single poorly known species, *Bopyrus resupinatus* Müller, 1871, from Brazil. Thompson (1902) later proposed the new genus *Stegophryxus* to contain his new taxon *Stegophryxus hyptius* (the type-species) from Massachusetts and Rhode Island, U.S.A., as well as Müller's (1871) species. It is clear that Thompson (1902) was unaware of Bonnier's (1900) work, or he would not have included the type of one genus (*A. resupinatus*) within another (*Stegophryxus*). *Anathelges* and *Stegophryxus* share many characters in common, with only the length to width ratio of the pereon, the differing elongation of the pleomeres, and the symmetry of the brood chamber appearing to differ between them (see also Markham, 1974). We suggest that the illustrations of Müller (1871) are highly stylized with regard to these supposed differing characters and that the type species of the two genera are, as first noted by Thompson (1902), actually congeneric. Accordingly, we synonymize *Stegophryxus* with *Anathelges*.

Four species have been placed in *Stegophryxus* and three in *Anathelges*, but only four of these seven can be retained in the redefined

Anathelges: *A. resupinatus*, *A. hyptius*, *A. thompsoni* (Nierstrasz and Brender à Brandis, 1931), and *A. hyphalus* (Markham, 1974). As suggested by Kazmi and Markham (1999), two taxa formerly placed in *Anathelges*, *A. muelleri* Nierstrasz and Brender à Brandis, 1931, and *A. mossambica* Barnard, 1958, are not congeneric with *A. resupinatus* and are accordingly removed from the genus. *Anathelges muelleri* is placed in its own monotypic genus and is redescribed herein based on type and additional material, while *A. mossambica* is tentatively transferred to *Pseudostegias* Shiino, 1933, based on examination of the damaged lectotype. One species formerly placed in *Stegophryxus*, *S. minutus* Markham, 1992, is also removed from the redefined *Anathelges* and placed in a second new genus along with a new species described from the Loyalty Islands.

One genus formerly placed in the Athelginae does not belong to this subfamily. We have examined the female type specimen (body length = 3.71 mm) in the Zoological Museum, Amsterdam, of *Metathelges muelleri* Nierstrasz and Brender à Brandis, 1923, the type and only species in the genus *Metathelges* Nierstrasz and Brender à Brandis, 1923. Most of the characters of this species are distinctly non-athelgine, such as the shape of the first oostegite, the non-overlapping oostegites, and the ventrally directed orientation of the last two pereopods. In

most aspects, this specimen resembles genera in the Ioninae (e.g., *Apocepon* Nierstrasz and Brender à Brandis, 1930), with which it shares a general similarity in cephalothoracic habitus, extremely thin pereopods, and first oostegite shape. The abdomen of *Metathelges muelleri* is, however, unlike any ionine or athelgine species, and we suspect that it may be malformed or juvenile in character. While the cephalothorax exhibits adult characteristics, the abdomen appears to be malformed (the specimen is also damaged with partial loss of pleopods). It is possible that *Metathelges muelleri* is congeneric or even conspecific with some other ionine taxon, but that relationship is obscured by the condition of the abdomen in *M. muelleri*. In keeping with our contention that this species is an ionine, Nierstrasz and Brender à Brandis (1923) cited the host for *M. muelleri* as "eine nicht näher bestimmbare Brachyure" (although there is a small piece of paguroid abdomen and telson in the vial with the holotype of *M. muelleri*). The vast majority of ionine bopyrids are parasites of brachyurans, while no athelgine is known from any brachyuran. Precise placement of *Metathelges* within the Ioninae is beyond the scope of this paper; however, it is clearly not an athelgine, and we formally transfer it from the Athelginae to the Ioninae. A key is provided for all the genera of the Athelginae, *sensu stricto*, based on females.

The size of the isopods is given as total length from anterior cephalon to posterior of pleotelson (exclusive of uropods); shield length (SL) is provided as an indicator of specimen size for the hosts. Specimens were studied from, or are deposited in, the following institutions: Allan Hancock Foundation (AHF, now in LACM); American Museum of Natural History, New York, New York, U.S.A. (AMNH); Los Angeles County Museum, California, U.S.A. (LACM); Museum National d'Histoire Naturelle, Paris, France (MNHN); Museum and Art Gallery of the Northern Territory, Australia (NTM); Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands (RMNH); South African Museum, Cape Town (SAM); Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida, U.S.A. (UMML); National Museum of Natural History, Washington, D.C., U.S.A. (United States National Museum, USNM); Zoological Museum, Amsterdam, The Netherlands (ZMA); and Zoological Museum, University of Copenhagen, Denmark (ZMUC). Unsuccessful attempts were made to locate the

types of Thompson (1902) in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. (MCZ), USNM, and Yale Peabody Museum, New Haven, Connecticut, U.S.A. (YPM).

Family Bopyridae
Subfamily Athelginae Codreanu
and Codreanu, 1956
Genus *Anathelges* Bonnier, 1900

Bopyrus: Müller, 1871: 57–60 (not *Bopyrus* Latreille, 1802).
Phryxus: Giard and Bonnier, 1887: 3 (part), 19, 60 (part), 62 (part).—Stebbing, 1893: 409 (not *Phryxus* Rathke, 1843 = *Hemiarthrus* Giard and Bonnier, 1887).
Anathelges Bonnier, 1900: 215.—Brasil-Lima, 1998: 640.—Kazmi and Markham, 1999: 883, 884.
Stegophryxus Thompson, 1902: 53–56, pls. 9, 10.—Richardson, 1904a: 83.—Richardson, 1905: 531.—Markham, 1974: 33.—Markham, 1978: 111 (**New Synonymy**).

Diagnosis.—Female: Body longer than broad, distorted sinistrally with right side longest; cephalon longer than wide with subparallel lateral margins, anterior margin pointed, posterior margin indented. First three oostegites extended over head, first pair forming conical projection, last two pairs forming large, enclosed marsupium; fifth oostegites largest, covering half of pereon ventrally and produced posteriorly, especially on right side. Pereomeres I–V anteriorly concave and posteriorly convex; pereomere VI largest, anterior and posterior margins concave. Pereopods I and II anterior to cephalon, III–V parallel to cephalon, VI and VII at posterior margin of pereon. Pleomeres I–V with lamellar or subovate biramous pleopods and uniramous lateral plates, all arising from common peduncle. Pleotelson with uniramous bulbous, nonpedunculate uropods.

Male: Body length approximately three times width, lateral margins of pereon almost parallel. Cephalon greater than twice as wide as long, anterior margin smoothly convex. Pereomeres separated at lateral margins, especially segments V–VII. Pleomeres fused into single segment, broadest anteriorly, tapering posteriorly to rounded or subacute distal tip; pleopods and uropods lacking (modified from Markham, 1974).

Type Species.—*Anathelges*: *Bopyrus resupinatus* Müller, 1871, by original designation; *Stegophryxus*: *Stegophryxus hyptius* Thompson, 1902, by original designation

Included Species.—Four: *A. resupinatus* (Müller, 1871); *A. hyptius* (Thompson, 1902), n.

comb.; *A. thompsoni* (Nierstrasz and Brender à Brandis, 1931), n. comb., and *A. hyphalus* (Markham, 1974), n. comb.

Remarks.—Thompson (1902) considered *Bopyrus resupinatus* to be very close to his *S. hyptius* from New England, so much so that the specific name for his species was based on its likeness to Müller's (1871) taxon. Richardson (1904a) maintained the placement of both taxa within *Stegophryxus*. We likewise believe that the two taxa are at a minimum congeneric, and suggest that Müller's (1871) illustrations were moderately to extremely stylized. Therefore, we consider *Stegophryxus* Thompson, 1902, as the junior synonym of *Anatelges* Bonnier, 1900, for reasons elaborated further below under *Anatelges resupinatus*. Richardson's (1904a) placement of *Bopyrus resupinatus* in *Stegophryxus* was doubtless the result of following Thompson (1902) and of her not having access to a copy of Bonnier (1900) until after the publication of her paper (see Richardson (1904b) for a more detailed explanation of her quest for the elusive monograph of Bonnier). Unfortunately, Richardson never treated the South American bopyrids in detail after 1904 and so never corrected this error.

Anatelges resupinatus (Müller, 1871)

Fig. 1A–D

Bopyrus resupinatus Müller in Bate and Westwood, 1868: 245 (*nomen nudum*).—Müller, 1871: 57–60, pl. 3, figs. 4–9.—Sars, 1898: 113.—Bonnier, 1900: 215.

Phryxus resupinatus: Giard and Bonnier, 1887: 19.—Stebbing, 1893: 409.

Anatelges resupinatus: Bonnier, 1900: 169, 380 (list).—Brasil-Lima, 1998: 640 (list).

Stegophryxus resupinatus: Thompson, 1902: 56.—Richardson, 1904a: 83 (list).

Material Examined.—None.

Distribution.—“Desterro” (Müller, 1871) (= Florianópolis, Santa Catarina, Brazil (Young, 1993)).

Hosts.—“*Pagurus*” sp(p). (Müller, 1871).

Type Specimens.—Extensive searching by Boyko and Harvey (2000) for Müller's rhizocephalan specimens failed to turn up any material, type or otherwise, and we strongly suspect that the types of *Bopyrus resupinatus* are likewise lost.

Description.—Female: Head approximately 1/3 longer than wide, first oostegite unknown,

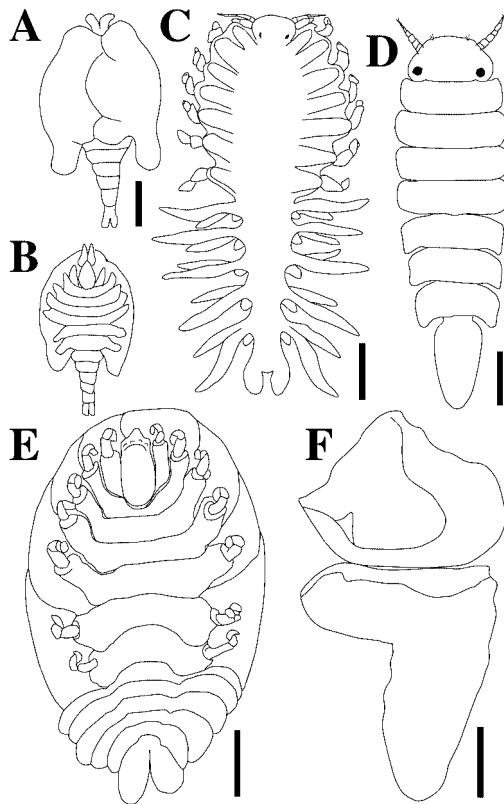


Fig. 1. *Anatelges resupinatus* (Müller, 1871) (A–D); *Pseudostegias mossambica* (Barnard, 1958) n. comb. (E, F). A, female, ventral view (without pleopods) (after Müller, 1871: pl. 3, fig. 7). B, female, dorsal view (without pleopods) (after Müller, 1871: pl. 3, fig. 8). C, immature female (after Müller, 1871: pl. 3, fig. 6). D, male, dorsal view (after Müller, 1871: pl. 3, fig. 9). E, female lectotype (SAM A10386), dorsal view (intact specimen after Kensley, 1978; possibly stylized). F, right oostegite 1, internal view. Scale bars = 2.0 mm (A, B, E), 0.4 mm (C), 0.2 mm (D), and 0.5 mm (F).

apparently symmetrical brood pouch (but see comments on possible hypersymmetry below), pleon approximately half total body length and bearing very narrow lateral plates and pleopods, uropods large.

Male: Pleon markedly narrower than pereomere VII, roughly triangular and terminally rounded (see also Müller (1871)).

Remarks.—This taxon has never been reported since its original description, despite Müller's (1871) statement that he had found 40 specimens. As noted by Nierstrasz and Brender à Brandis (1931): “Die Form ist von Müller ... unvollständig beschrieben worden, und seine Abbildungen lassen viel zu wünschen übrig.” We concur with this statement, and, as noted above,

are convinced that the stylized rendering of Müller's (1871) illustrations for females of this species exhibit nearly perfect symmetry which obscures the true appearance of the animal in life. We are unaware of any mature female bopyrid that shows such near perfect symmetry between its right and left sides, especially in regards to the placement of the pleopods and lateral plates, when those structures are well developed (juveniles do exhibit such symmetry). We have found several other cases of this illustrative "hyper-symmetry" (e.g., *Anathelges mossambica* Barnard, 1958, and *Parathelges aniculi* (Whitelegge, 1897)), where examination of the type shows that under no circumstances could the original drawing have accurately represented that specimen. The illustrations of several species of "Athelgue" (a vernacular name, now *Athelges* Gerstaecker, 1862) by Hesse (1861, 1877) are perhaps the most extreme examples of "hyper-symmetry" in the Athelginae and, as they are contemporary to the illustrations of Müller (1871), show the prevalence of this style in the bopyrid literature during the latter part of the nineteenth century. It should be noted, however, that the errors introduced by this style of illustration were noticed as early as the end of the nineteenth century, notably by Sars (1898) who correctly, if rather harshly, accused Hesse of a "deplorable want of correctness."

If a typical "*Stegophryxus*" posterior deflection for the female is introduced into Müller's (1871: pl. 3, figs. 7, 8; Fig. 1A, B herein) drawings, his taxon would be extremely close to, and perhaps conspecific with, Thompson's (1902) *S. hyptius*. Characters that females of the two species share in common, other than the obvious ones of pleopod count and morphology, are the shape and degree of the anterior prolongation of the first oostegites and the shape and relative size of the uropods. Only the degree of posterior development of the oostegites and the spacing and forward curvature of the pereomeres distinguish the two taxa and, as both of these would be greatly influenced by any introduction of "hypersymmetry" into the illustrations, it is impossible to know how accurate the depictions of these structures are in Müller's (1871) paper. Certainly, Müller's (1871: pl. 3, fig. 5) illustration of the cryptoniscid larva of *B. resupinatus* as having only four pereopods is clearly an error. The male *B. resupinatus*, as illustrated by Müller (1871: pl. 3, fig. 9; Fig. 1D herein) and that of *S. hyptius*, as illustrated by Thompson

(1902: pl. 10, fig. 1) and especially Markham (1974: fig. 2), are certainly congeneric and appear close enough to each other to give additional weight to the idea that they all represent one species. There is also a very strong resemblance between a juvenile female *S. hyptius* from Georgia (USNM 143660) and Müller's (1871) illustration of the female of *A. resupinatus* (Fig. 1C herein). Additionally, the distribution range of *A. hyptius* is considerable, and it is not difficult to envision an extension of the southernmost point from Curaçao to Brazil.

Given all of the above evidence, we think the case is strong to consider *B. resupinatus* and *S. hyptius* as synonymous taxa. However, as no material from Brazil has been discovered in the years subsequent to Müller's (1871) description, we prefer to adopt a conservative view and treat them as two distinct but congeneric taxa until Brazilian material can be collected and studied.

***Anathelges hyptius* (Thompson, 1902),
new combination
Figs. 2, 3**

Stegophryxus hyptius Thompson, 1902: 53–56, pls. 9, 10.—Richardson, 1904a: 50 (list).—Richardson, 1905: 532–535, figs. 578, 579.—Markham, 1974: 33–35, figs. 1–3 (full synonymy).—Adkison and Heard, 1978: 408.—Markham, 1978: 111.—Markham, 1988: 45, 46.—McDermott, 1998: 1042–1044.—McDermott, 2001: 629, 634, 635.

Material Examined.—1 mature female (6.56 mm), 1 male (2.68 mm), on female *Pagurus longicarpus* Say (3.25 mm), 20 Sep 1986 (AMNH 18037); 1 near mature female (3.91 mm), 1 male (1.51 mm), on female *P. longicarpus* (3.3 mm), 14 Sep 1985 (AMNH 18038); 1 mature female (6.32 mm), 1 male (2.05 mm) on male *P. longicarpus* (3.6 mm), 10 Jul 1987 (AMNH 18039); all intertidal, Hereford Inlet, New Jersey, U.S.A., J. J. McDermott leg.—1 juvenile female (6.00) mm, on *P. longicarpus* (sex and size unknown), tidepool, Sapelo Island, Georgia, U.S.A., unknown leg., Aug. 1969 (USNM 143660).

Distribution.—Massachusetts, Rhode Island (Thompson, 1902; Richardson, 1904a), New Jersey (McDermott, 1998), North Carolina (Adkison and Heard, 1978), Georgia, Florida, and Mississippi, U.S.A. (Markham, 1988); Curaçao (Markham, 1978).

Hosts.—*Pagurus longicarpus* Say (Thompson, 1902; McDermott, 1998; 2001); *P. annulipes*

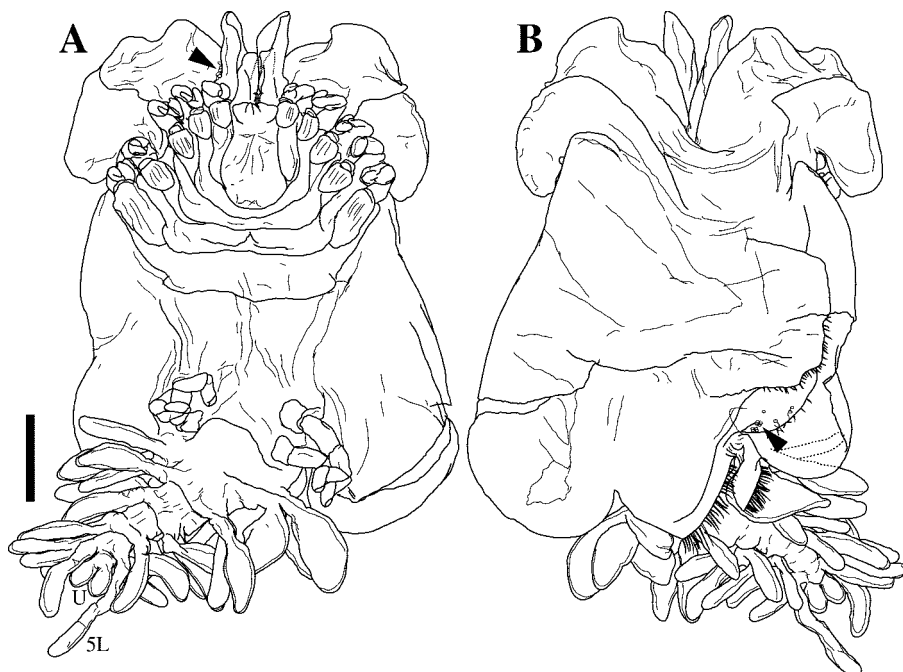


Fig. 2. *Anathelges hyptius* (Thompson, 1902), n. comb., female (AMNH 18037). A, dorsal view. B, ventral view. 5L = lateral plate V; U = uropods. Arrowheads indicate attached peritrichous ciliates. Scale bar = 1 mm.

(Stimpson) (Adkison and Heard, 1978); *P. provenzano* Forest and de Saint Laurent, *Iridopagurus margaritensis* García-Gómez (Markham, 1978); *P. stimpsoni* (A. Milne-Edwards and Bouvier), *P. brevidactylus* (Stimpson), *P. macclaghlinae* García-Gómez (Markham, 1988).

Type Specimens.—The repository of the syntypes is unknown; they are not in MCZ (Johnston, personal communication), USNM (Schotte, personal communication), or YPM (Lazo-Wasem, personal communication) and are likely lost.

Description.—Female: Head twice as long as wide, first oostegite bluntly pointed, highly asymmetrical brood pouch extending far back on right side, pleon less than half total body length and bearing very narrow lateral plates and pleopods, uropods large and elongate.

Male: Pleon markedly narrower than pereomere VII, roughly triangular and terminally rounded (see also Thompson (1902) and Markham (1974)).

Remarks.—This species was well described by Markham (1974), but additional material from McDermott's (1998) collections is illustrated herein (Figs. 2, 3) to facilitate comparison with

A. resupinatus. The mature adult female specimens from New Jersey match closely the description by Markham (1974); peritrichous ciliates were found attached to the anterior and posterior oostegites of one specimen (Fig. 2). The female specimen illustrated in Fig. 3A was classified as near mature (with partially developed oostegites) by McDermott (1998: table 1). From over 9000 specimens of *Pagurus longicarpus* examined in New Jersey, McDermott (1998) found approximately 15% harbored *A. hyptius*; all were found on the left side of the abdomens of hosts and exhibited sinistral distortion. Females of the species can produce over 3400 eggs in one brood (McDermott, 1998).

Anathelges hyptius is similar to both *A. resupinatus* and *A. hyphalus* in the shape of the female's uropods and male's pleotelson; it may prove to be synonymous with *A. resupinatus* if Brazilian material can be obtained for comparison. Even if this species does not occur as far south as Brazil, its range of latitude is extremely great for a bopyrid and certainly the greatest for any species in the western Atlantic (Markham, 1978). Most wide-ranging bopyrids exhibit broad longitudinal distributions (e.g., *Bopyroides hippolytes* (Krøyer, 1838), see Bourdon, 1968), rather than latitudinal ones. Although it

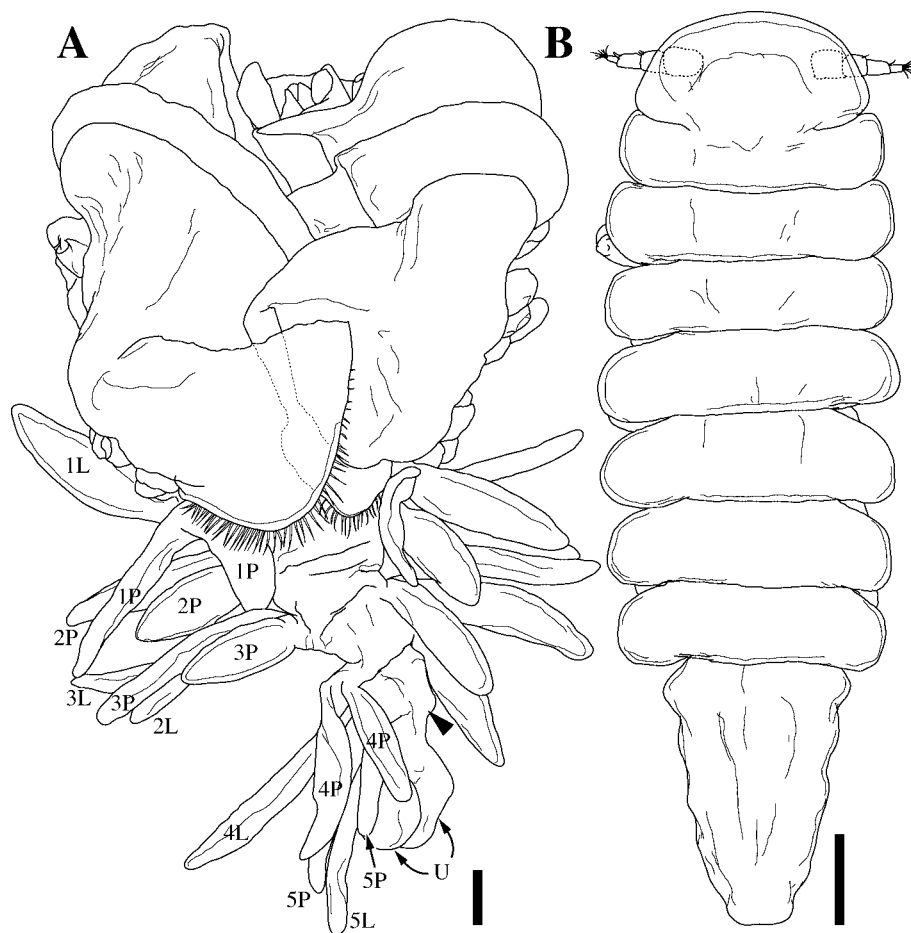


Fig. 3. *Anathelges hyptius* (Thompson, 1902), n. comb. A, near mature female, dorsal view (AMNH 18038). B, male, dorsal view (AMNH 18037). L = lateral plate; P = pleopods; U = uropods; numbers indicate pleon segment. Arrowhead indicates damaged fifth pleomere on right side. Scale bars = 0.25 mm.

appears to occur only in shallow waters, *Anathelges hyptius* is known to infest more hosts than any other species in the genus, a fact which may explain its large geographic range.

Anathelges thompsoni

(Nierstrasz and Brender à Brandis, 1931),
new combination

Stegophryxus thompsoni Nierstrasz and Brender à Brandis, 1931: 196–198, figs. 87–89.—Markham, 1974: 35, 36, figs. 4, 5.

Material Examined.—1 female lectotype (8.86 mm), on “*Pagurus*” sp. (sex and size unknown), Valparaíso, Chile, Krøyer leg. (ZMUC CRU-8383).—1 male paralectotype (2.71 mm), same data as lectotype (ZMUC CRU-8383).

Distribution.—Known only from Valparaíso, Chile (Nierstrasz and Brender à Brandis, 1931).

Hosts.—“*Pagurus*” sp. (Nierstrasz and Brender à Brandis, 1931). Because of loss of host, neither the genus nor family can be known with certainty.

Type Specimens.—Female lectotype and male paralectotype (ZMUC CRU-8383).

Description.—Female: Head twice as long as wide, first oostegite narrowly tapered, pleon nearly as long as pereon and bearing broad lateral plates and pleopods, uropods large and bulbous.

Male: Pleon about as broad as pereomere VII, ovate and terminally rounded (see also Nierstrasz and Brender à Brandis (1931) and Markham (1974)).

Remarks.—This species was well described and illustrated by Markham (1974). Markham

(1974) cited the female "holotype," but Nierstrasz and Brender à Brandis (1931) did not select a holotype. In order to avoid future confusion, and in keeping with bopyrid taxonomic tradition, we herein select the female as the lectotype. This species has not been reported since its initial description, and, as the host of the types is apparently lost, it is unknown what species of hermit crab(s) bear(s) this parasite. *Anathelges thompsoni* appears to be the sister taxon to all other *Anathelges* species; it differs from all of them in the shape and size of the uropods of the female as well as the ovate pleotelson of the male.

Anathelges hyphalus (Markham, 1974),
new combination

Stegophryxus hyphalus Markham, 1974: 36–38, figs. 6–8.—
Trilles, 1999: 287, 292, figs. 8.6B, 8.11.

Material Examined.—None.

Distribution.—Numerous locations off Southern California, U.S.A., and Baja California Norte, Mexico (Markham, 1974).

Hosts.—*Parapagurodes laurentae* McLaughlin and Haig, *P. makarovi* McLaughlin and Haig (Markham, 1974).

Type Specimens.—The holotype and allotype were AHF 3928 and 3928a, respectively (now in LACM); additional paratypes are in AHF (LACM), RMNH, UMML, and USNM (Markham, 1974).

Description.—Female: Head 1.5 times as long as wide, first oostegite tapered, brood pouch symmetrical and extending backwards subequally on both sides, pleon about three-fifths as long as pereon and bearing long, flat lateral plates and pleopods, uropods small and bulbous.

Male: Pleon/pereomere VII ratio variable, pleon roughly triangular with undulating margins and terminally tapering but rounded (see also Markham (1974)).

Remarks.—This species was well described and illustrated by Markham (1974). If *A. resupinatus* and *A. hyptius* are found to be synonymous, then *A. hyphalus* would be considered the Pacific analogue to *A. resupinatus*. If they are found to be distinct, it remains to be seen which taxon is most closely related to *A. hyphalus*, because of the poor quality of Müller's (1871) description and illustrations. Unlike *A. hyptius*, *A. hyphalus* has only been found in deeper

water (69–391 m) and within a relatively narrow latitudinal range (Markham, 1974).

Genus *Falsanathelges*, new genus

Anathelges: Nierstrasz and Brender à Brandis, 1931: 195
(not *Anathelges* Bonnier, 1900).

Diagnosis.—Female: Body longer than broad, not distorted, cephalon broader than long with convex lateral margins, anterior margin concave, posterior margin convex. No oostegites extended over head or produced posteriorly. Pereomeres I–III anteriorly concave and posteriorly convex, pereomere IV only slightly so, pereomere V with more or less straight margins, pereomeres VI and VII anteriorly convex and posteriorly concave; pereomeres III–V subequal in size and larger than other segments. Pereopod I anterior to cephalon, II parallel to cephalon, no large gaps between IV–VII. Pleomeres I–V with elongate-ovate biramous pleopods and uniramous lateral plates, all arising from common peduncle. Pleotelson with biramous, pedunculate, elongate-ovate uropods.

Male: Body length approximately 3.5 times width, lateral margins of pereomeres III–VII almost parallel, I, II shorter. Cephalon approximately 1.7 times as wide as long, anterior margin smoothly convex. Pereomeres widely separated. Pleomeres fused into single segment, broadest anteriorly, lateral margins showing residual segmentation, tapering posteriorly to rounded distal tip; pleopods and uropods lacking.

Type Species.—*Anathelges muelleri* Nierstrasz and Brender à Brandis, 1931.

Included Species.—One: *F. muelleri* (Nierstrasz and Brender à Brandis, 1931), n. comb.

Etymology.—The genus name is selected to emphasize the prior misidentification of the type species as a member of *Anathelges*. The gender is masculine.

Remarks.—When Nierstrasz and Brender à Brandis (1931) described *Anathelges mülleri*, they placed it in the genus with only the comment that it was clearly different from *A. resupinatus* and gave characters to separate the two species. Nowhere did they discuss the characters that purportedly united the species, and this has led to much confusion on the correct generic placement of *A. mülleri* or, more correctly, *A. muelleri* (see Kazmi and Markham, 1999). In fact, females of *A. muelleri* differ from

those of *A. resupinatus* and all other *Anathelges* species in numerous important characters: the cephalon of *A. muelleri* has the length and breadth subequal rather than longer than wide; the first oostegites are not produced anterior to the cephalon; the body shows no posterior distortion; there is no broad gap between pereopods V and VI; the pleomeres are broad and flat as in *Parathelges* Bonnier, 1900, rather than narrow and rounded; and the uropods are strongly pedunculate, elongate, and biramous rather than nonpedunculate, short and rounded, and uniramous. Only in the form of the pleopods, which are biramous with uniramous lateral plates arising from a common peduncle and occurring in five pairs, do the two genera give any indication of shared characters. Unfortunately, Nierstrasz and Brender à Brandis (1931) erroneously believed *A. muelleri* exhibited uniramous fifth pleopods (see below). The male of *Falsanathelges* is similar to *Anathelges* but differs in its proportions and, more importantly, in the shape of the lateral pleomeres which are all laterally directed and distally rounded, whereas in *Anathelges* at least some pereomeres are posterolaterally directed and distally truncated. We consider all of these characters as generic level differences, and therefore *A. muelleri* cannot be placed in *Anathelges* or into any of the other athelgine genera. Accordingly, we erect a new genus to accommodate it herein.

This new genus appears to represent the most primitive of known athelgine taxa, as it has a complete complement of five pairs of biramous pleopods, five lateral plates, and biramous uropods, as well as only minimal lateral curvature in the pereomeres towards the cephalon. All other athelgine genera show loss of at least some pleonal appendages, and a much more pronounced curvature of the pereomeres, especially in the posterior pairs.

***Falsanathelges muelleri* (Nierstrasz and Brender à Brandis, 1931), new combination**
Figs. 4–7

Anathelges mülleri Nierstrasz and Brender à Brandis, 1931: 195, 196, figs. 84–86.

Anathelges muelleri: Haig and Ball, 1988: 161.

Material Examined.—1 female holotype (18.0 mm) on “*Galathea*(?) spec.” [= *Clibanarius infraspinus* Hilgendorf, see Remarks] (sex unknown, 8.8 mm), “Poeloe Penang” [= Pulau Pinang, Malaysia], Reinhardt on “*Galathea*”

leg. (ZMUC CRU-7425).—1 female (6.0 mm), 1 male (3.1 mm) on *Calcinus lineapropodus* Morgan and Forest (sex and size unknown), Sta. 19, outside of Gunungapi, Banda Islands, Indonesia, 1–10 m, E. Ball leg., 30 Apr 1975 (LACM CR19755892).

Distribution.—Banda Islands, Indonesia.

Hosts.—*Clibanarius infraspinus* Hilgendorf; *Calcinus* undescribed sp. (Haig and Ball, 1988) [= *C. lineapropodus* Morgan and Forest *vide* Morgan and Forest, 1991; Asakura and Nomura, 2001].

Type Specimen.—Female holotype (ZMUC CRU-7425).

Description.—Female (Figs. 4, 5): Holotype body length 15.92 mm, maximal width 8.00 mm, head length 2.16 mm, head width 2.20 mm, pleon length 7.52 mm. Body longer than broad; pereon not distorted. All body regions and pereomeres distinctly segmented (Fig. 4A, B). Cephalon length and breadth subequal, with convex lateral margins, anterior margin concave, posterior margin convex. Eyes lacking. Antenna (Fig. 5A) of 4 articles, setae on distal margin of distalmost two segments and on lateral surface of middle two segments, dorsal surface of proximal two segments with area of low scales, ventral margin of second segment with smaller area of scales; antennule (Fig. 5B) of 3 articles, setae on distal margins of all segments and lateral surface of middle segment, proximal segment covered with scales. Maxilliped (Fig. 5C) with thin, short spur; palp absent. Barbula (Fig. 5C) with numerous short lobes along length. Pereon of 7 pereomeres, broadest across pereomeres III–V, tapering anteriorly and posteriorly. Pereomeres I–III anteriorly concave and posteriorly convex, pereomere IV only slightly so, pereomere V with more or less straight margins, pereomeres VI and VII anteriorly convex and posteriorly concave; pereomeres III–V subequal in size and larger than other segments. No oostegites extended over head or produced posteriorly (Fig. 4A, B). Oostegites completely enclosing brood pouch; posteriormost oostegite with fringe of setae on posterior margin, each seta approximately 0.15 mm in length (Fig. 4B). First oostegite proximal lobe subtriangular, with scalloped distal margin on exterior surface bearing area of minute low scales, distal lobe with two subtriangular lobes, proximal one narrow, internal ridge with numerous proximal

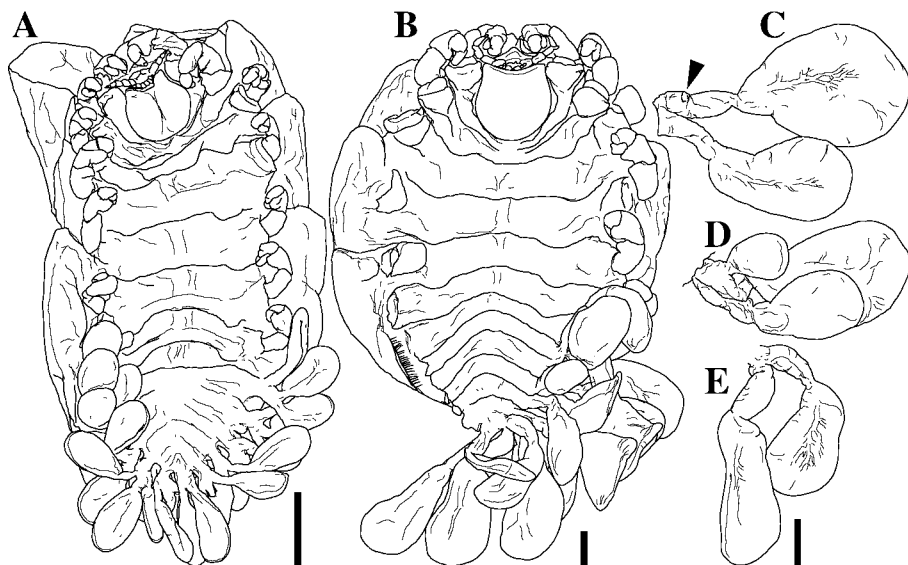


Fig. 4. *Falsanathelges muelleri* (Nierstrasz and Brender à Brandis, 1931), n. comb., female (A) (LACM CR19755892) and female holotype (B–E) (ZMUC CRU-7425). A, dorsal view. B, dorsal view. C, fifth pleopod from left side (arrowhead indicates point at which endopodite was presumably broken). D, fifth pleopod from right side with intact endopodite. E, uropods. Scale bars = 1 mm.

digitations and larger distal lobe (Fig. 5D, E). All pereopods of approximately the same size (Fig. 5F–H). Carpus, merus, and ischium of anterior pereopods with small areas of low scales and few widely scattered short setae on margins (Fig. 5F); carpi of all pereopods with distoventral tuft of setae (Fig. 5F–H); ischium of all pereopods with large lobe on median margin (Fig. 5F–H). Pereopod I anterior to cephalon, II parallel to cephalon, no large gaps between IV–VII. Pleon with 6 pleomeres, dorsal segmentation indistinct. Pleomeres I–V (Fig. 4A, B) with elongate-ovate biramous pleopods and uniramous lateral plates, all arising from common peduncle (Fig. 4C, D); pleotelson (Fig. 4A, B) with biramous, pedunculate, elongate-ovate uropods (Fig. 4E).

Male (Figs. 6, 7): Body length 2.42 mm, maximum width 0.69 mm, head length 0.23 mm, head width 0.37 mm, pleon length 0.63 mm. Head suboval, widest posteriorly, distinct from pereomere I. Large eyes near posterolateral margin. Antenna (Fig. 7A) of 5 articles, all but proximal one distally setose, proximal two with marginal scales, extending posterolaterally from head; antennule of 3 articles (Fig. 7B), all distally setose, proximal article with marginal scales.

Pereomere IV broadest, tapering anteriorly and posteriorly. All pereomeres directed later-

ally with rounded distal margins. No detectable pigmentation pattern. First four pereopods with larger dactyli than posterior pairs (Fig. 7C, D), but otherwise of equal size, all articles distinctly separated, ventral margin of carpus, merus, and cutting edge of propodus with few stout setae, ventral margin of carpus and cutting edge of propodus with few low scales (Fig. 7D). Pleon tapering posteriorly, all pleomeres fused but with lateral indication of segmentation; posterior margin rounded. No midventral tubercles, pleopods, or uropods (Fig. 6A, B).

Remarks.—Nierstrasz and Brender à Brandis (1931: figs. 85, 86) reported that the fifth pleopod of the holotype possesses only a rudimentary endopodite, whereas the endopodites of all other pleopods were well developed. Examination of the holotype reveals that, due to an unfortunate choice, Nierstrasz and Brender à Brandis (1931) dissected and illustrated pleopods from the left side of the specimen. The endopodite of pleopod V from the left side (Fig. 4C; now contained in a separate vial) is as illustrated by Nierstrasz and Brender à Brandis (1931) but is clearly damaged (endopodite missing), as pleopod V on the right side possesses a well-developed endopodite comparable in development to all the other pleopodal endopodites (Fig. 4D).

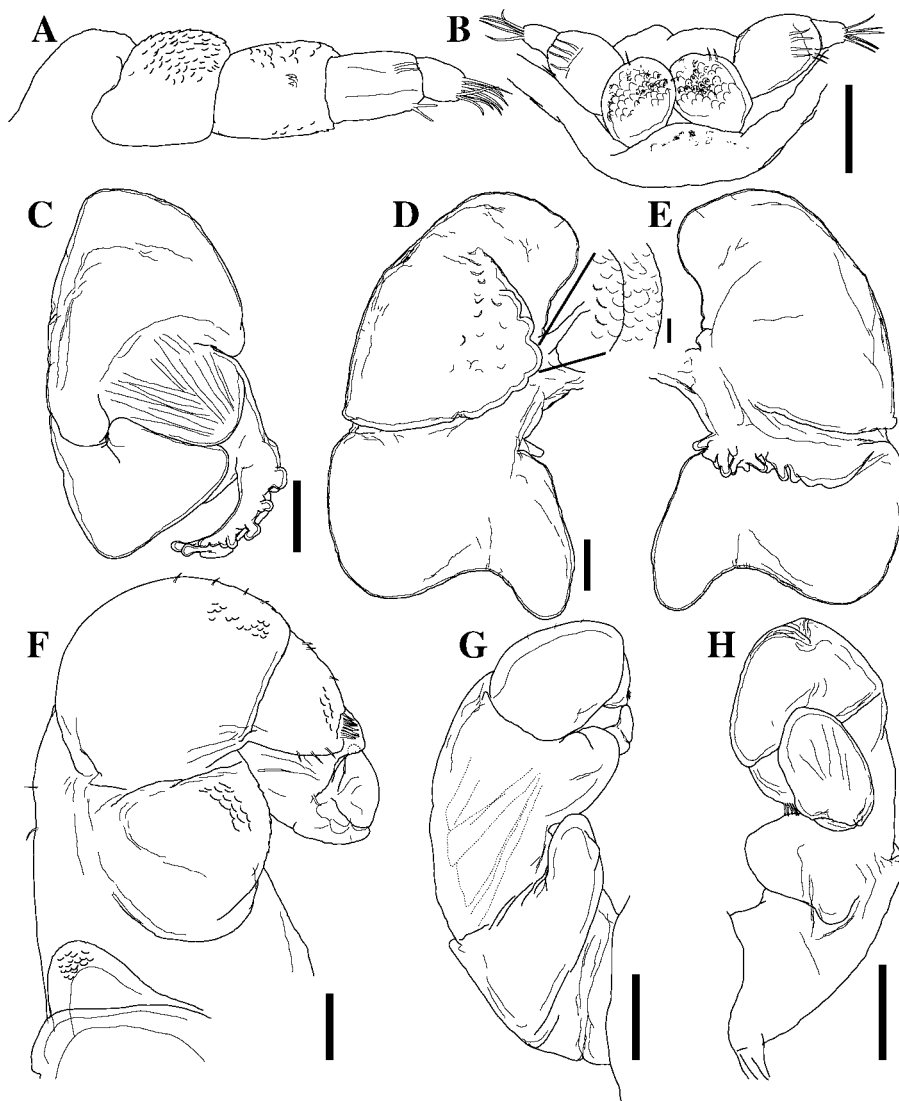


Fig. 5. *Falsanathelges muelleri* (Nierstrasz and Brender à Brandis, 1931), n. comb., female (LACM CR19755892). A, right antenna. B, antennules. C, left maxilliped, external view. D, left oostegite 1, external view (inset showing scales along scalloped edge). E, left oostegite 1, internal view. F, right pereopod I. G, right pereopod I. H, right pereopod VII. Scale bars = 0.075 mm (A, B), 0.25 mm (C–E), 0.0125 mm (inset of D), 0.025 mm (F), and 0.15 mm (G, H).

The host for the holotype was given as a “*Galathea*(?)” specimen (Anomura: Galatheiidae) by Nierstrasz and Brender à Brandis (1931), but they obviously never saw the host specimen themselves, as it is clearly a hermit crab (see Material Examined). The erroneous host data was derived from the name of the vessel that collected the type material, the “*Galathea*.”

The above redescription is based on all the examined material, with the exception of the female measurements, which are of the holo-

type. Although the LACM female is considerably smaller than the holotype (body length 6.77 mm, maximal width 2.93 mm, head length 0.81 mm, head width 0.87 mm, pleon length 2.71 mm), the characters of the two specimens are in complete agreement. Characters of the male are given for the first time herein and included in the diagnosis of the genus.

Genus *Minimathelges*, new genus

Stegophryxus: Markham, 1992: 290 (in part) (not *Stegophryxus* Thompson, 1902 = *Anathelges* Bonnier, 1900).

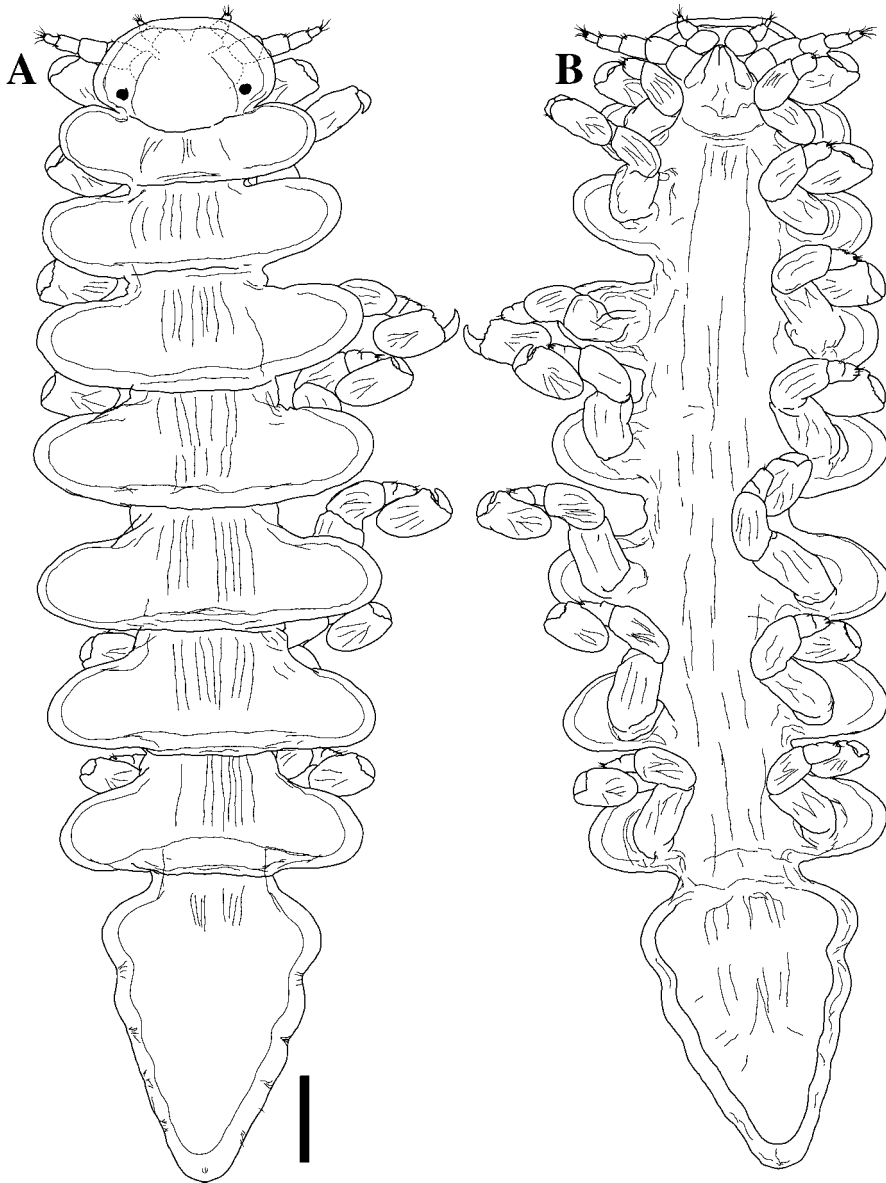


Fig. 6. *Falsanathelges muelleri* (Nierstrasz and Brender à Brandis, 1931), n. comb., male (LACM CR19755892). A, dorsal view. B, ventral view. Scale bar = 0.5 mm.

Diagnosis.—Female: Body longer than broad, distorted sinistrally with right side longest; cephalon longer than wide with subparallel margins, posterior margin convex. First two oostegites extended over head, other pairs forming large, enclosed marsupium produced posteriorly on right side. Pereomeres I–V anteriorly concave and posteriorly convex; pereomere VI largest, anterior and posterior margins subparallel. Pereopod I anterior to cephalon, III–IV parallel to cephalon, VI and

VII at posterior margin of pereon. Pleomeres I–V with lamellar uniramous pleopods and uniramous lateral plates, not arising from common peduncle. Pleotelson with uniramous lamellar uropods.

Male: Body length approximately 3.1 times width, lateral margins of pereomeres III–VI almost parallel, I, II, VII shorter. Cephalon approximately 4.3 times as wide as long, anterior margin with median indentation. Pereomeres closely approximated. Pleomeres

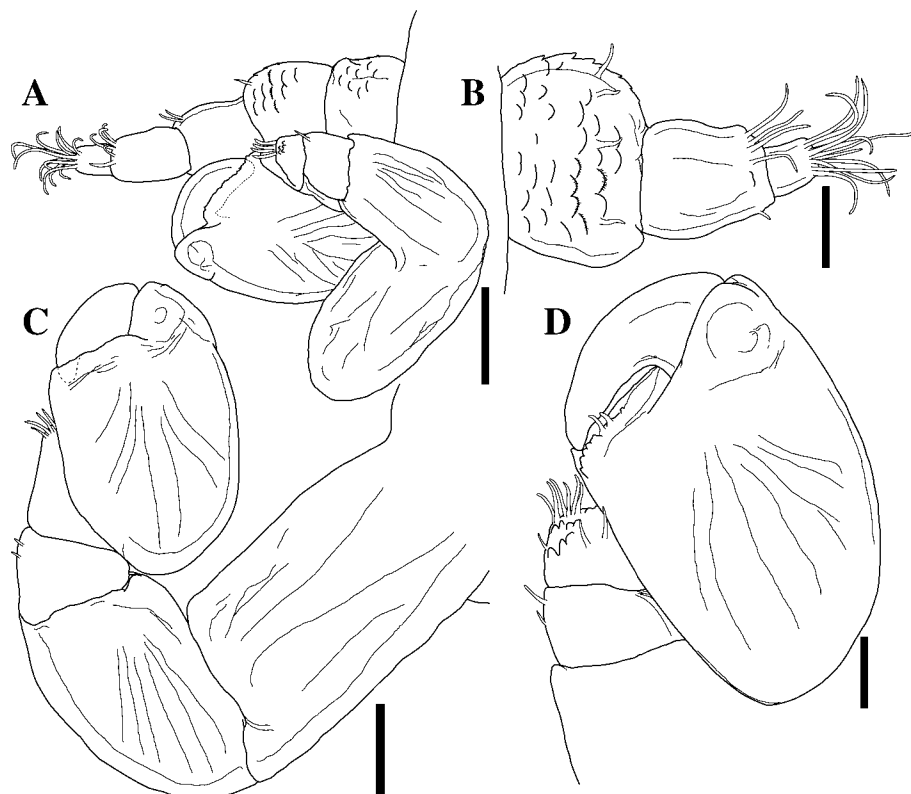


Fig. 7. *Falsanathelges muelleri* (Nierstrasz and Brender à Brandis, 1931) n. comb., male (LACM CR19755892). A, right antenna and pereopod I. B, left antennule. C, left pereopod VII. D, left pereopod I. Scale bars = 0.075 mm (A), 0.025 mm (B, D), 0.0375 mm (C).

fused into single segment with partial demarcation of at least first pleomere ventrally, broadest anteriorly, lateral margins showing residual segmentation, tapering posteriorly to rounded distal tip; pleopods and uropods lacking.

Type Species.—*Stegophryxus nanus* n. sp.

Included Species.—Two: *M. nanus* n. sp., *M. minutus* (Markham, 1992), n. comb.

Etymology.—The genus name is given to emphasize the small size of both known species. The gender is masculine.

Remarks.—Markham (1992) placed his species *minutus* in *Stegophryxus* (now *Anathelges*) based on what he suggested were several shared characters such as the forward-sweeping anterior oostegites, the placement and structure of the pereopods, and the extended pleon with prominent lateral plates, pleopods, and uropods. However, the most obvious differences between all *Anathelges* taxa and *S. minutus* are the presence of uniramous, separate, pedunculate

pleopods in *S. minutus*, not biramous and arising from a common peduncle with the lateral plates as found in *Anathelges*, as well as lamellar uropods in *S. minutus* rather than bulbous uropods as in all *Anathelges*. An ovigerous female specimen from the Loyalty Islands, described as the holotype of a new species herein, also shows these differences from all *Anathelges* spp. and is clearly congeneric with *S. minutus*. The morphology of the ovigerous female from the Loyalty Islands confirms that the nonovigerous female of *S. minutus* was likewise mature. The developmental state of the female specimens shows that the loss of one branch of the pleopods is not related to immaturity, but it may be correlated with the extremely small size of these species. The above-stated differences suggest that *S. minutus* and the new species are not derived from within *Anathelges* but should be considered the sister taxa to all *Anathelges* and, as such, require their own genus. Although it is the earliest described species, *Minimatelges minutus* is not selected as the type-species because its male is unknown.

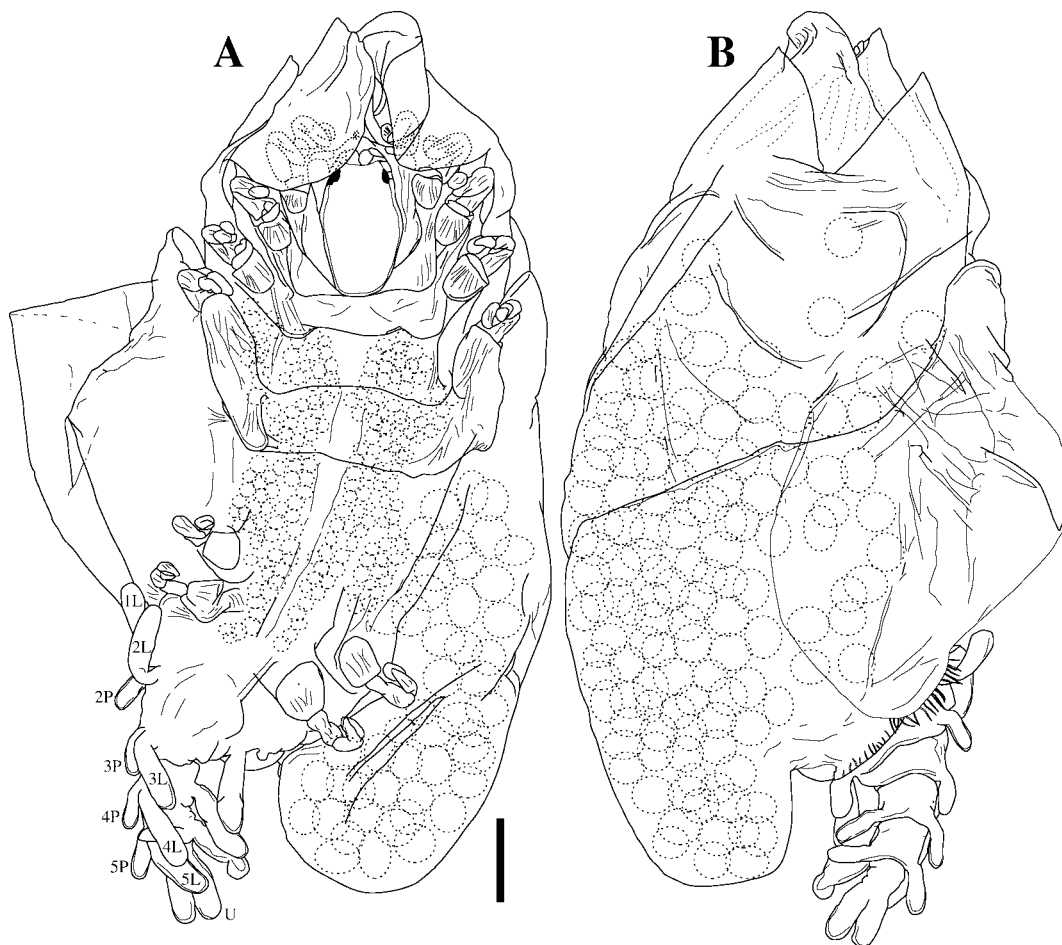


Fig. 8. *Minimathelges nanus* n. sp., female holotype (MNHN-Ep 924). A, dorsal view, developing eggs and embryos within brood pouch shown in dotted line. B, ventral view, embryos in brood pouch indicated in dotted line. L = lateral plates, P = pleopods, U = uropods; numbers indicate pleon segment. Scale bar = 0.25 mm.

It remains to be seen whether *Minimathelges* is composed entirely of dwarf species, as evidenced by the two taxa known to date, or whether larger species with these characters will eventually be found.

***Minimathelges nanus*, new species**

Figs. 8–11

Material Examined.—1 female holotype (2.81 mm), 1 male allotype (1.13 mm) on female *?Anapagrides* sp. (2.18 mm), St. 22, 20°55.6'S, 167°04.5'E, Baie de Gaatcha, Lifou, Loyalty Islands, 5 m, MUSORSTOM LIFOU 2000 leg., Nov 2000 (MNHN-Ep 924).

Distribution.—Known only from Lifou, Loyalty Islands.

Host.—*?Anapagrides* sp. (see Remarks).

Type Specimen.—The holotype and allotype are MNHN-Ep 924 and 924bis.

Etymology.—The specific name is the Latin adjective *nanus*, meaning dwarf, in recognition of the small size of the species.

Description.—Female (Figs. 8, 9): Body length 2.41 mm, maximal width 0.91 mm, head length 0.40 mm, head width 0.24 mm, pleon length 0.78 mm. Body longer than broad; pereon distorted sinistrally. Only some body regions and pereomeres distinctly segmented. Cephalon longer than broad, with convex lateral margins, anterior margin concave, posterior margin convex. Eyes present. Cephalon overlapping

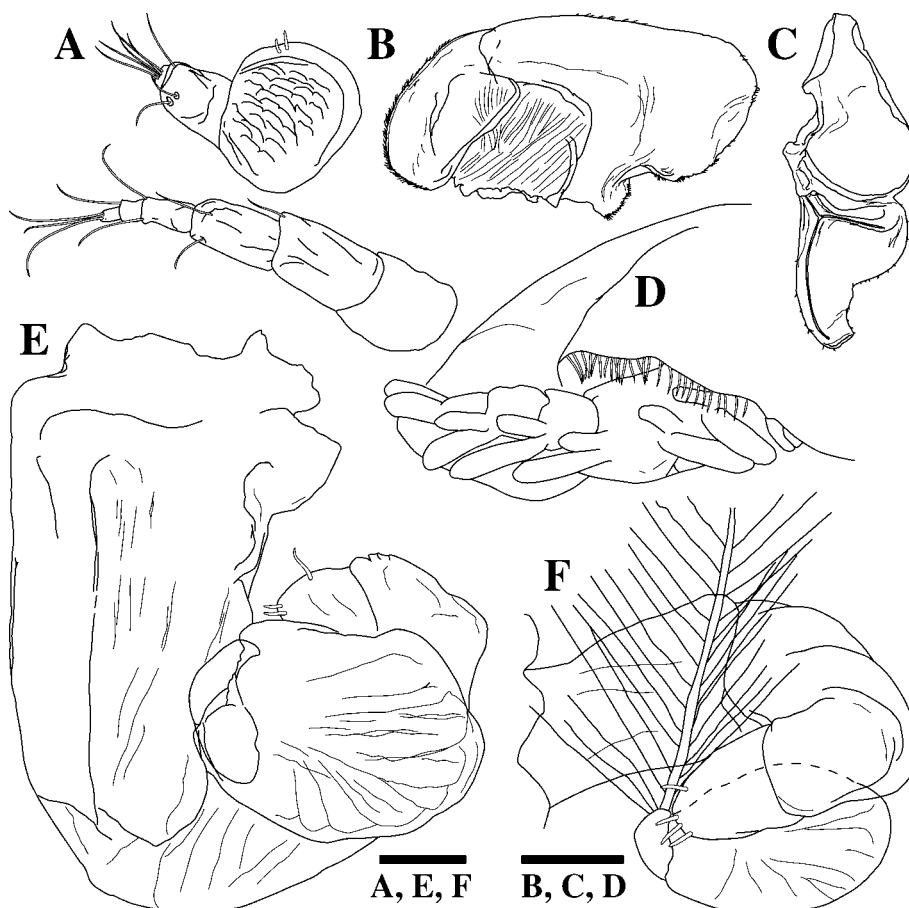


Fig. 9. *Minimatelges nanus* n. sp., female holotype (MNHN-Ep 924). A, left antennule (top) and antenna (bottom). B, left maxilliped, external view. C, left oostegite I, internal view. D, left lateral view of pleon. E, left pereopod I. F, left pereopod VII, shown attached to pleopod of host. Scale bars = 0.025 mm (A, E, F), 0.15 mm (B), 0.3 mm (C), and 0.275 mm (D).

median regions of pereomeres I and II completely. Antenna (Fig. 9A) of 6 articles; antennule (Fig. 9A) of 3 articles, distal margins of segments with setae, basal segment of antennule with scales. Maxilliped (Fig. 9B) with low rounded spur; palp absent; posterior margin densely setose. Pereon of 7 pereomeres, broadest across pereomere V, tapering anteriorly and posteriorly. Pereomeres I and II medial margins obscured by cephalon, III–V anteriorly straight to slightly convex and posteriorly straight to slightly concave, pereomeres VI and VII segmentation indistinct. First oostegite proximal lobe subtriangular, distal lobe with ovate distal lobe and narrow, bladelike proximal lobe, internal ridge smooth (Fig. 9C). First two oostegites extended over head into acute cone, posterior oostegite produced posteriorly on one side (Fig. 8A, B); lateral oostegites extended and

doubling body width. Oostegites completely enclosing brood pouch; posteriormost oostegite with fringe of setae on posterior margin. Brood pouch contains 135–150 developing embryos [mean maximal length \pm SD, 0.110 ± 0.004 mm ($n = 20$)] (Fig. 8B) and developing eggs [mean diameter \pm SD, 0.052 ± 0.003 mm ($n = 20$)] on ventral side between pereopods V–VII (Fig. 8A). Pereopod I smaller than II–VII, which are subequal (Fig. 9E, F). Pereopods I, II anterior to cephalon, II, IV parallel to cephalon, large gap between V and VI. Pleon with 6 pleomeres, dorsal segmentation of first three indistinct, deflexed dextrally giving specimen an S-shaped aspect. Pleomeres I–V (Fig. 9D) with short, slender, and pedunculate uniramous pleopods and longer, slender, pedunculate uniramous lateral plates, arising from common base but not common peduncle (Fig. 8A); pleotelson

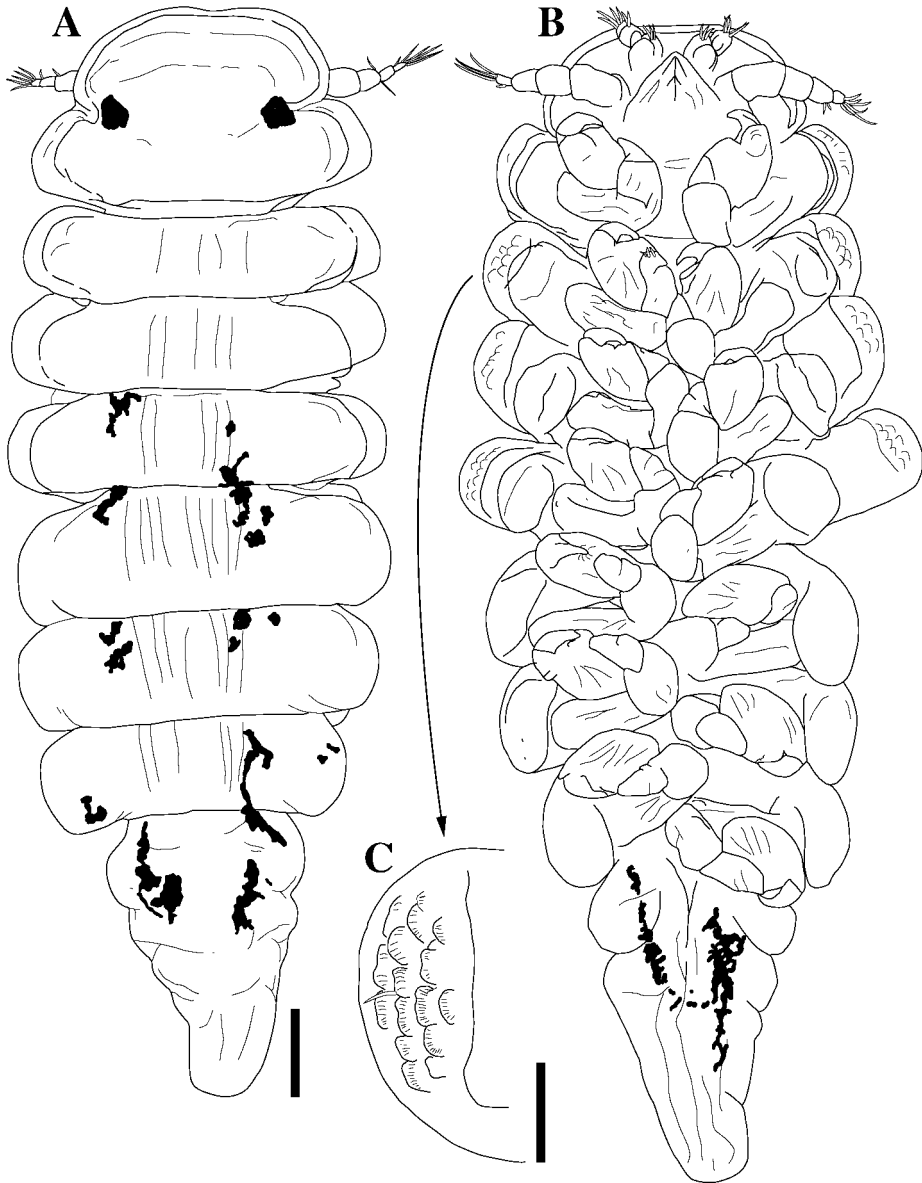


Fig. 10. *Minimatelges nanus* n. sp., male allotype (MNHN-Ep 924bis). A, dorsal view. B, ventral view. C, detail of ventral surface of second pleomere. Scale bars = 0.075 mm (A, B) and 0.025 mm (C).

(Fig. 9D) with uniramous, lamellar, distally rounded uropods.

Male (Figs. 10, 11): Body length 1.00 mm, head length 0.22 mm, head width 0.94 mm, pleon length 0.28 mm. Head elongate ovate with shallow anterior median indentation, widest posteriorly, fused with pereomere I. Large eyes on posterolateral margin, pigment overlapping anterior margin of pereomere I (Fig. 10A). Antenna (Fig. 11B) of 7 articles, distally setose; extending posterolaterally from

head; antennule of 3 articles, distally setose (Fig. 11A). Pereomere IV broadest, tapering anteriorly and posteriorly. Pereomeres I–III with slight anterolateral deflection, IV–VII directed laterally. Diffuse pigmentation present on pereomeres IV–VII and pleon (Fig. 10A, B). Ventrolateral surfaces of pereomeres with overlapping, irregular scales and few short setae (Fig. 10C). All pereopods (Fig. 11C, D) of equal size, all articles distinctly separated; cutting edge of propodi with blunt teeth. Pleon tapering

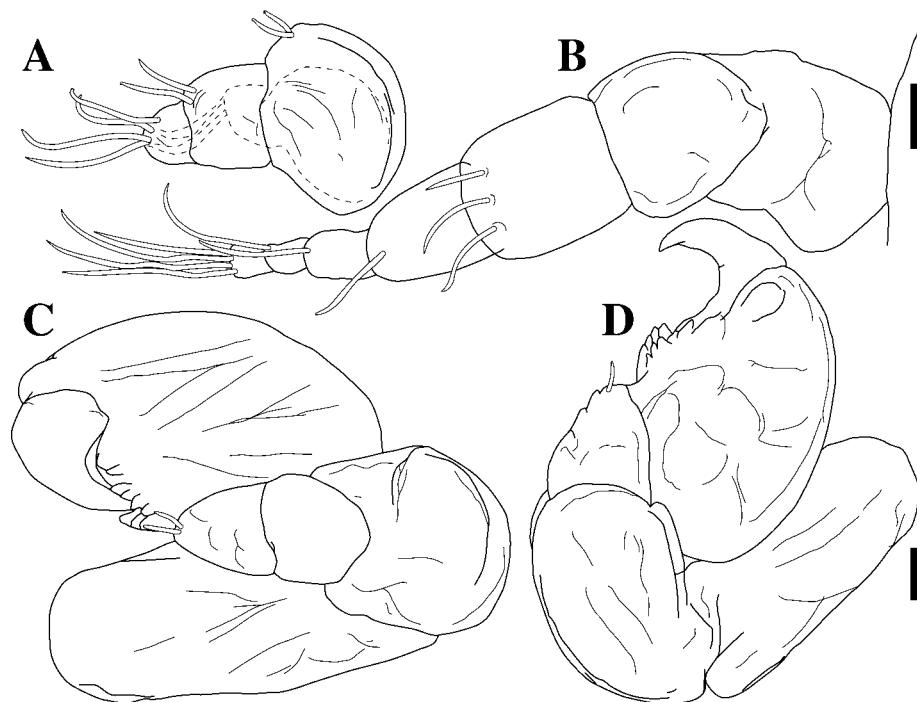


Fig. 11. *Minimathelges nanus* n. sp., male allotype (MNHN-Ep 924bis). A, right antennule. B, right antenna. C, right pereopod VII. D, left pereopod I. Scale bars = 0.0125 mm.

posteriorly, all pleomeres fused but distinct partial separation of pleomere I in ventral view and lateral indication of segmentation on one or two other pleomeres; posterior margin rounded. No midventral tubercles, pleopods, or uropods (Fig. 10B).

Remarks.—*Minimathelges nanus* can be separated from *M. minutus* by the shape and orientation of the pleomeres, lateral plates, and uropods of the female. The pleomeres of *M. minutus* are broad and gradually tapering posteriorly, whereas the posterior two pleomeres of *M. nanus* are abruptly much narrower than the preceding segments, resulting in a much more slender appearing abdomen. Additionally, the pleon of *M. nanus* is deflexed to the right, giving the female an S-shaped appearance, whereas the pleon of *M. minutus* is deflexed to the left in keeping with the dextral condition of the pereon. The lateral plates of *M. minutus* are broad, lamellar and nonpedunculate, whereas those of *M. nanus* are elongate, slender, and pedunculate. Finally, the uropods of *M. minutus* are short (less than the length of the lateral plates of pleomere V), whereas those of *M. nanus* are distinctly longer than the lateral

plates of pleomere V. The males of the two species cannot be compared, as that of *M. minutus* is unknown.

The host has been tentatively identified as a member of *Anapagrises* de Saint Laurent Dechancé by Patsy McLaughlin. There are currently three species in this genus (Komai, 1999), but because this specimen is a lone female, it cannot be identified to species.

***Minimathelges minutus* (Markham, 1992),
new combination**

Stegophryxus minutus Markham, 1992: 290, 291, figs. 12, 13.

Material Examined.—1 female holotype (1.88 mm) on unknown hermit crab (sex and size unknown), south of Fung Chau (Moon Island), Hoi Ha Wan, Hong Kong, China, 1 m, C. Erséus leg., 24 April 1989 (NTM Cr007136).

Distribution.—Known only from Hong Kong (Markham, 1992).

Host.—"... immature pagurid hermit crab unidentifiable to genus." (Markham, 1992).

Type Specimen.—The unique holotype is NTM Cr007136.

Description.—See Markham (1992). One correction to Markham's (1992) description of *M. minutus* is that pleopods are pedunculate, whereas the lateral plates and uropods are lamellar. The male remains unknown.

Remarks.—This species was well described and illustrated by Markham (1992). Of all the species in the sister taxon *Anathelges*, *M. minutus* is closest to *A. thompsoni*, especially in the shape of the first oostegite. The species can be distinguished from its sole congener by the characters given above in the Remarks for *M. nanus*.

Pseudostegias Shiino, 1933

Pseudostegias mossambica (Barnard, 1958),
new combination
Fig. 1E, F

Anathelges mossambica Barnard, 1958: 23.—Kensley, 1978: 151, fig. 67A.—Kazmi and Markham, 1999: 883, 884 (discussion).

Material Examined.—1 female lectotype (approximately 12.0 mm) on unknown hermit crab (sex and size unknown), Inhaca (so stated on specimen label), Delagoa Bay (= Lourenço Marques Bay), Moçambique (Mozambique), unknown leg. (SAM A10386).

Distribution.—Known only from Delagoa Bay, South Africa (Barnard, 1958).

Host.—"a Hermit crab" (Barnard, 1958).

Type Specimens.—The lectotype female is SAM A10386; the paralectotype male cited by Barnard (1958) is lost.

Remarks.—Of the unique male and female pair described by Barnard (1958), only the female is still present in SAM, although it is damaged and was not recognized as a type specimen prior to this study. Accordingly, we select it herein as the lectotype in order to provide some measure of nomenclatural stability to this specific name that has been the source of much confusion in the past. It appears that Kensley's (1978) figure of the female type (Fig. 1E, herein) may have been based on an unpublished illustration of Barnard, in light of the current poor condition of the specimen. The cephalon and pereomeres of the lectotype are in good condition, but the pleomeres have been roughly pulled apart, probably by Barnard in an attempt to properly count the overlapping pleopods. Ordinarily, this would not be problematic, but the posterior

pleomere and the uropods have been lost. This makes observation of the presence or absence of the globular fifth pleomere lateral plates impossible, and as the first oostegite (Fig. 1F, herein) is somewhat intermediate in shape between those of *Anathelges* and *Pseudostegias*, it also cannot be used to answer the question of generic placement. There are, however, several good reasons to consider this taxon a member of *Pseudostegias* rather than *Anathelges*: the anterior lateral plates are broad and serve to continue the shape of the brood chamber enclosed by the oostegites; the anterior lateral plates of *Anathelges* are thin and similar to the posterior lateral plates; the habitus is anteroposteriorly straight, rather than posteriorly deflected as in species of *Anathelges*; and the uropods were described and figured as large and resembling the lateral plates, whereas all species of *Anathelges* have small, bulbous uropods (see also Williams and Boyko, 1999). Therefore, in spite of the absence of the key segments of the female lectotype, it is obvious that the species cannot be retained in *Anathelges*, and we provisionally transfer it to *Pseudostegias*, pending rediscovery of this enigmatic species.

KEY TO THE GENERA OF ATHELGINAE
(BASED ON FEMALES)

- | | | |
|----|--|---|
| 1. | Lateral plates present | 2 |
| - | Lateral plates lacking | 6 |
| 2. | Lateral plates on pleomeres I-V | 3 |
| - | Lateral plates on pleomeres I-III only
<i>Stegias</i> Richardson, 1904a (3 spp.) | |
| 3. | Lateral plates on pleomere V normal | 4 |
| - | Lateral plates on pleomere V reduced, globular or
scarlike <i>Pseudostegias</i> Shiino, 1933 (7 spp.) | |
| 4. | Uropods uniramous | 5 |
| - | Uropods biramous <i>Falsanathelges</i> n. gen. (1 sp.) | |
| 5. | Pleopods uniramous <i>Minimathelges</i> n. gen. (2 spp.) | |
| - | Pleopods biramous <i>Anathelges</i> Bonnier, 1900 (4 spp.) | |
| 6. | Uropods uniramous <i>Parathelges</i> Bonnier, 1900 (12 spp.) | |
| - | Uropods lacking or extremely reduced | 7 |
| 7. | Pleopods on pleomere V present | |
| - | <i>Allathelges</i> Kazmi and Markham, 1999 (1 sp.) | |
| - | Pleopods on pleomere V lacking
<i>Athelges</i> Gerstaecker, 1862 (12 spp.) | |

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regarding the status of *A. resupinatus* in Brazil. Ardis Johnston (MCZ), Marilyn Schotte (USNM), and Eric Lazo-Wasem (YPM) kindly looked for type material of *A. hyptius* in their respective collections. Alan Harvey (Georgia Southern University) provided identifications for all hermit crab hosts, except the *Anapagrises* which was identified by Patsy McLaughlin (Shannon Point Marine Center, Washington). We appreciate the comments of two anonymous reviewers that improved the manuscript.

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