

A monograph on the isopod genus *Colopisthus* (Crustacea: Isopoda: Cirolanidae) with the description of a new genus

WENDY MOORE† and RICHARD C. BRUSCA‡

†Department of Entomology, University of Arizona, Tucson, AZ 85721, USA

‡Arizona-Sonora Desert Museum, Tucson, AZ 85743, USA

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Colopisthus Richardson, 1902 is a rarely collected genus restricted in distribution to the tropical Atlantic Ocean with most species being known from the Caribbean region. *Colopisthus* species are highly endemic, none being known from more than a single island or a restricted mainland site. This monograph contains a redescription of the type species *Colopisthus parvus* Richardson, 1902, descriptions of four new species (*Colopisthus canna*, *Colopisthus cavalier*, *Colopisthus ronrico*, *Colopisthus tresesquinas*), a dichotomous key to the species, and a morphology-based phylogenetic analysis of the genus. *Colopisthus parvus* of Menzies and Glynn (1968) is shown to be a new species (*C. ronrico*), and *C. parvus* of Müller (1993) is also shown to be a new species (*C. tresesquinas*). As a result of the phylogenetic analysis, three species of *Metacirolana* Kussakin, 1979 (*M. costaricensis*, *M. moortgati*, *M. sphaeromiformis*) are assigned to a new genus, *Aphantolana*. Phylogenetic analysis indicates that *Aphantolana* and *Colopisthus* are sister groups. Within *Colopisthus*, *C. cavalier* and *C. ronrico* are a sister group to *C. tresesquinas*, *C. parvus* and *C. canna*. Biogeographic analysis suggests that *Colopisthus* and *Aphantolana* had their origins in the western Caribbean or pre-Pleistocene middle American seaway.

KEYWORDS: Crustacea, Isopoda, Cirolanidae, phylogeny, biogeography, systematics, Caribbean Sea.

Introduction

The family Cirolanidae comprises 412 species classified into 56 genera. We are currently undertaking a revision of this entire family by way of a morphology-based phylogenetic and biogeographic analysis. When inferring phylogeny it is theoretically essential that all terminal taxa of the tree represent monophyletic groups. Since some genera of Cirolanidae are suspected of being non-monophyletic, several genera are being revised as the data set for the family is being compiled (e.g. *Politolana*: Riseman and Brusca, 2002).

The genus *Colopisthus* was erected by Richardson in 1902 to contain the single species *Colopisthus parvus* from Bermuda. Since its original description, *C. parvus*

has been reported from a wide variety of locations in the Atlantic Ocean and therefore has been thought of as a widespread species. We initially thought that *Colopisthus* might not be a valid genus due to its superficial resemblance to some species in the genus *Metacirolana* Kussakin, 1979 and we anticipated a potential synonymy. However, in the course of our study we found that not only is *Colopisthus* a valid genus but it is supported by an unusually high number of previously unrecognized synapomorphies. After examining all previously reported *Colopisthus* specimens (with the exception of a specimen described by Monod (1952) from Senegal, which we have been unable to locate in any major European or North American museum), and new collection material, we recognize five distinct species. Our study further reveals that distinct species occur on each island group from which this genus has been collected. We describe new species for the material reported by Menzies and Glynn (1968) and Müller (1993), erroneously, as *C. parvus*. Based on Monod's description and the geographic location, we believe the specimen he reported from west Africa represents another species of *Colopisthus*, and we predict it is most closely related to *C. canna* n. sp. The restricted distribution of each species of *Colopisthus* attests to the poor dispersal capabilities exhibited by most Cirolanidae, as with most other isopods.

In the course of coding the species of *Metacirolana* for the phylogenetic analysis of *Colopisthus*, we discovered a new genus hidden within *Metacirolana*. Members of this new genus, herein named *Aphantolana* n. gen., superficially resemble species of *Colopisthus* and were the impetus for our initial thoughts of synonymy. The genus *Metacirolana* contains 30 described species. To date we have not identified any unique synapomorphies of this genus. It appears to be a catch-all taxon for species that share a subset of plesiomorphic characters. The present study removes three species from *Metacirolana* (*M. costaricensis*, *M. moortgati*, *M. sphaeromiformis*) and assigns them to the new genus *Aphantolana*. Our phylogenetic analysis reveals *Aphantolana* to be a well-defined genus and the sister genus to *Colopisthus*. There is, as yet, no evidence that the genus *Metacirolana* represents a monophyletic group, even after the removal of these three species. *Metacirolana* is in need of revision, but that work is beyond the scope of the present study. We anticipate that our broader study of the family Cirolanidae will reveal the status of the other taxa currently assigned to the genus *Metacirolana*.

Phylogeny

Materials and methods

Characters. We compiled a data set of 115 characters (Appendix 1). We chose characters for the analysis by comparing the external morphology of structures we deem to be homologous among the species. Characters and character states were defined in such a way that taxa were never coded as 'non-applicable' for a character.

Taxa. We include 29 taxa in our analysis: five species of *Colopisthus*, 23 species of *Metacirolana* and the monotypic genus *Hansenolana* (table 1). We chose to root phylogeny of *Colopisthus* by including the species within *Metacirolana* and *Hansenolana* since they have often been recognized as being similar to the genus *Colopisthus* (e.g. Menzies and Glynn, 1968; Muller and Salvat, 1993). The genus *Hansenolana* shares some derived characters with *Colopisthus* which has led several authors to suspect that it may have affinities with *Metacirolana sphaeromiformis* (Stebbing, 1900; Stebbing, 1905; Monod, 1971).

Table 1. Complete list of species in *Colopisthus*, *Metacirolana*, *Hansenolana*. In cases where a species has been transferred to a new genus the original generic assignment is indicated.

Taxa used in phylogenetic analysis

Colopisthus Richardson, 1902

1. *Colopisthus parva* Richardson, 1902
2. *Colopisthus canna* sp. nov.
3. *Colopisthus cavalier* sp. nov.
4. *Colopisthus ronrico* sp. nov.
5. *Colopisthus tresesquinas* sp. nov.

Hansenolana Stebbing, 1900

1. *Hansenolana anisopous* Stebbing, 1900

Metacirolana Kussakin, 1979

1. *Metacirolana agujae* Müller, 1991
2. *Metacirolana anatola* Bruce, 1986
3. *Metacirolana anocula* (Kensley, 1984) *Cirolana*
4. *Metacirolana arnaudi* Kensley, 1989
5. *Metacirolana basteni* (Bruce, 1980) *Cirolana*
6. *Metacirolana bicornis* (Kensley, 1978) *Cirolana*
7. *Metacirolana calypso* Brusca, Wetzer and France, 1995
8. *Metacirolana convexissima* (Kensley, 1984) *Cirolana*
9. *Metacirolana costaricensis* Brusca and Iverson, 1985
10. *Metacirolana fishelsoni* (Bruce and Jones, 1978) *Cirolana*
11. *Metacirolana japonica* (Hansen, 1890) *Cirolana*
12. *Metacirolana mbudya* Bruce, 1981
13. *Metacirolana monodi* (Jones, 1976) *Cirolana*
14. *Metacirolana moortgati* Müller and Salvat, 1993
15. *Metacirolana nana* (Bruce, 1980) *Cirolana*
16. *Metacirolana neocaledonica* Bruce, 1996
17. *Metacirolana pigmentata* Müller and Salvat, 1993
18. *Metacirolana ponsi* Jaume and Garcia, 1992
19. *Metacirolana rotunda* (Bruce and Jones, 1978) *Cirolana*
20. *Metacirolana rugosa* (Bruce, 1980) *Cirolana*
21. *Metacirolana serrata* (Bruce, 1980) *Cirolana*
22. *Metacirolana spinosa* (Bruce, 1980) *Cirolana*
23. *Metacirolana sphaeromiformis* (Hansen, 1890) *Cirolana*

Taxa not included in the phylogenetic analysis

Metacirolana Kussakin, 1979

1. *Metacirolana agaricicola* Kensley, 1984
 2. *Metacirolana halia* Kensley, 1984
 3. *Metacirolana hanseni* (Bonnier, 1896) *Cirolana*
 4. *Metacirolana joannae* (Schultz, 1966) *Cirolana*
 5. *Metacirolana menziesi* Kensley, 1984
 6. *Metacirolana riobaldoi* (Lemos de Castro and Lima, 1976) *Cirolana*
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All taxa were coded for 115 characters (Appendix 2). All character state assignments for the species of *Colopisthus* were made by direct examination of the specimens. *Hansenolana* and *Metacirolana* species were coded either by examination of specimens or from the literature. Some of the characters that we chose to include in the analysis are not consistently reported or illustrated in the literature, particularly those involving setation patterns of the pereopods. This resulted missing data for these characters in the data matrix (note question marks in data file, Appendix 2).

Phylogenetic inference. We searched for most parsimonious trees by using a beta version of PAUP 4.0 (version 4.0b8, Swofford, 2001) on a Macintosh PowerBook

G3 computer. A heuristic search was performed by using the following options: all characters and character-state changes were equally weighted, starting trees were made by stepwise addition, branch-swapping was done by tree bisection-reconnection (TBR), and MAXTREES was not limited. One thousand random addition sequence replicates were performed to increase the chances of finding all islands of most parsimonious trees (Maddison, 1991).

Only unambiguous character changes were reported as defining tree branches (unambiguous character changes are changes that occur along a branch under all character optimizations). Decay indices, also known as Bremer support (Bremer, 1994; Donoghue *et al.*, 1992), and bootstrap values were found for branches of particular interest. Decay indices were calculated by building a decay index PAUP file in MacClade 4.0 (Maddison and Maddison, 2000) and then using the same options listed above for the parsimony searches (heuristic search, nreps = 100). Five hundred bootstrap replicates were performed using the same options as above (heuristic search, nreps = 100).

Results and discussion

Our phylogenetic analysis found three most parsimonious trees (MPT) distributed on three different islands of trees. Each of the MPTs was found in over 12% of the total number of searches (121, 143, 186). Each MPT has a tree length of 448 and a consistency index (CI) of 0.36. The strict consensus tree of the three MPTs reveals *Colopisthus* to be monophyletic (figure 1). This tree also shows that three species currently assigned to *Metacirolana* (*M. costaricensis*, *M. moortgati*, *M. sphaeromiformis*) form a clade distinct from all other species of *Metacirolana*, including the type species *Metacirolana japonica*. We hereby recognize this monophyletic group as a distinct genus and give it the name *Aphantolana*.

We chose to present a network, or unrooted tree, rather than artificially root this tree on any particular branch. We make no claims as to where the root of this tree lies, other than that it lies outside of the *Colopisthus/Aphantolana* sister grouping since some of the synapomorphies defining the *Colopisthus/Aphantolana* sister group represent unique characters within the family Cirolanidae, as indicated below. Our analysis provides no evidence that the genus *Metacirolana* represents a monophyletic group. Of the characters that define this genus in our phylogeny, we know of none which are unique within the rest of the family Cirolanidae, i.e. they are all symplesiomorphies (they occur in many other cirolanid genera). It is thus possible that the root of this tree lies within *Metacirolana*.

The *Colopisthus*, *Aphantolana* and *Colopisthus/Aphantolana* sister group clades are supported by high bootstrap values and decay indices (figure 2). Nine synapomorphies support the *Colopisthus/Aphantolana* sister group relationship (table 2), three of which are non-homoplasious: the presence of a connate spine on the inferior-distal angle of pereopod 1 carpus (character 47), pleotelson apex with two stout setae (character 114) and pleotelson apex narrowly rounded (character 115).

The genus *Colopisthus* is defined by 16 synapomorphies, seven of which are non-homoplasious: pereonites with setae on the dorsal surface (character 4), mandibular incisors with flask-like inclusion (character 29), pereopod 1 merus superior distal angle with acute robust seta (character 40), pereopod 1 carpus inferior margin with connate spines (character 45), pereopod 3 ischium inferior distal angle with molariform setae (character 68), pereopod 7 basis length = two times width (character 70), pleopod 1 peduncle length equal or greater than width (character 84). In

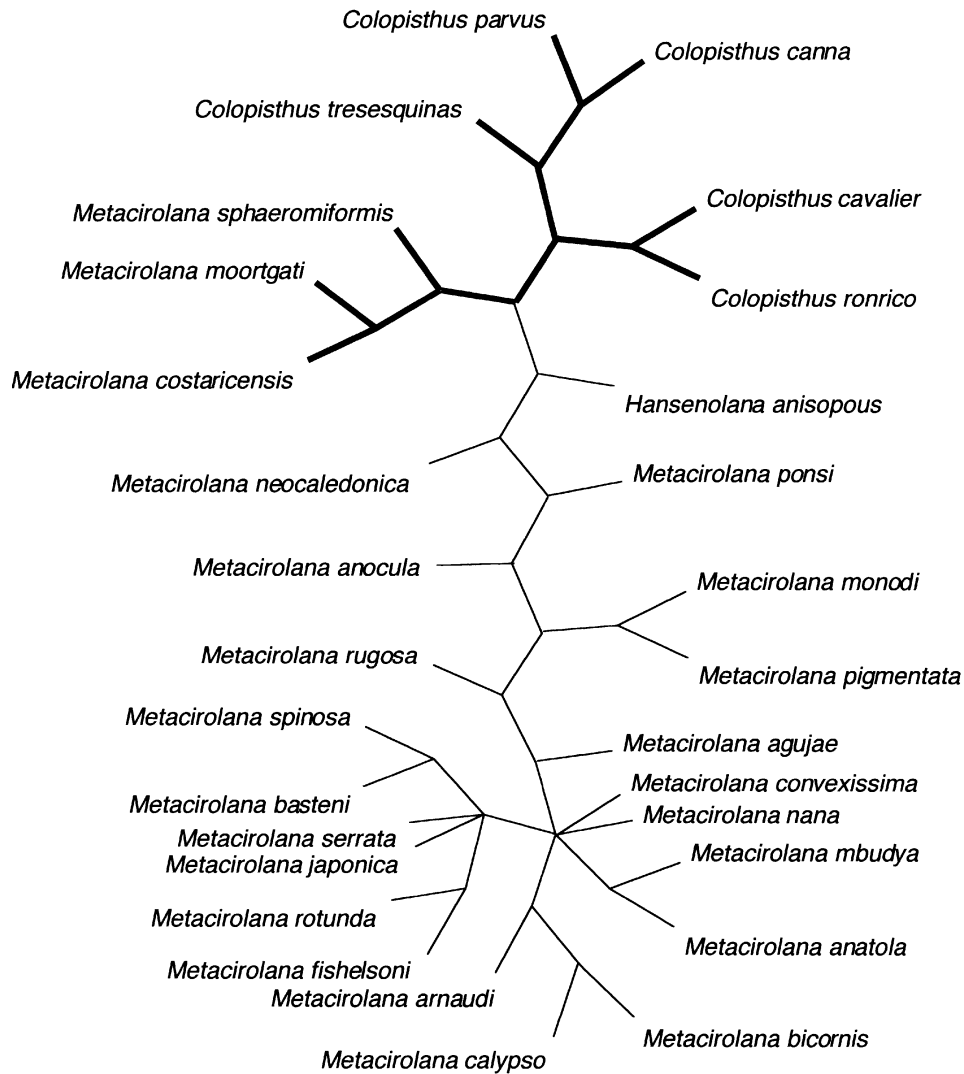


FIG. 1. Strict consensus tree of three shortest unrooted trees (tree length = 448). *Colopisthus* species and a clade of three *Metacirolana* species are highlighted in bold.

addition, *Colopisthus* is defined by having three or fewer free pleonites (see character 83). The new genus *Aphantolana* is distinguished by 12 synapomorphies, two of which are non-homoplasious: the presence of a complex seta on the inferior distal angle of the carpus of pereopod 1 (character 49) and the pereopod 2 carpus inferior distal angle forms a notched lobe (character 62).

Within the genus *Colopisthus*, *C. cavalier* + *C. ronrico* is the sister group to *C. tresesquinas* + (*C. parvus* + *C. canna*). *Colopisthus cavalier* and *C. ronrico* both have crenulate rather than smooth lateral margins on the cephalon and pereonite 1 (character 3). *Colopisthus canna* + *C. parvus* is supported by three synapomorphies: maxillipedal endite with five plumose setae (character 25), pereopod 2 merus without robust setae (character 60) and pereopod 7 carpus antero-distal margin with 10–11

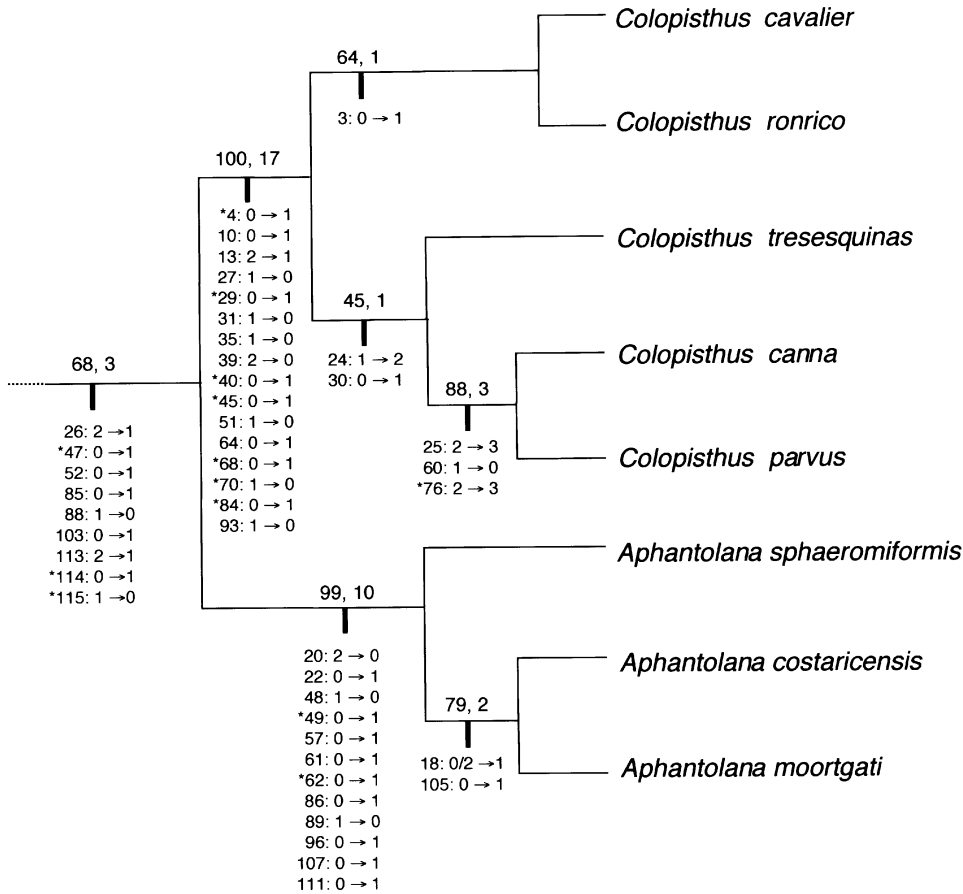


FIG. 2. Portion of the strict consensus tree showing *Colopisthus* and *Aphantolana*. Synapomorphies are provided below each branch, non-homoplasious synapomorphies preceded by an asterisk. Bootstrap values over 40, and decay indices, are shown above branches.

biplumose setae (character 76). *Colopisthus tresesquinas* shares two apomorphies with its sister group (*C. canna* + *C. parvus*): maxillipedal endite with two coupling setae (character 24) and mandibular spine row with 13 or more spines (character 30).

There are some additional characters which are diagnostic of particular clades, but which were not revealed as synapomorphies in our phylogenetic analysis due to the topology of the most parsimonious trees and the distribution of states in the taxa included in this analysis. For example, in some of the most parsimonious reconstructions of characters 53 and 63, character states change on the branch leading to the *Colopisthus/Aphantolana* sister group, and in other equally parsimonious reconstructions the character states change on the *Colopisthus* branch and also on the *Aphantolana* branch (a position of transition which would indicate a synapomorphy for both clades).

Other characters are not revealed as synapomorphies of particular clades in our analysis because they are also present in the genus *Hansenolana*. However, after a consideration of the characters in our phylogenetic analysis we believe that the genus *Hansenolana* may be only distantly related to the *Colopisthus/Aphantolana* clade,

Table 2. Complete list of synapomorphic character states for clades of interest. Non-homoplasious synapomorphies are in bold face.

<i>Colopisthus</i> + <i>Aphantolana</i>	
26: 2→1	Maxillipedal palp article 3 subquadrate
47: 0→1	Pereopod 1 carpus inferior-distal angle with connate spine
52: 0→1	Pereopod 1 propodus inferior margin with connate spines
85: 0→1	Exopod and endopod of pleopods 1 and 2 elongate (length more than twice width)
88: 1→0	Appendix masculina flask-like
103: 0→1	Uropodal exopod medial margin: with robust setae
113: 2→1	Pleotelson shape of postero-lateral margins slightly concave
114: 0→1	Pleotelson apex with two stout setae
115: 1→0	Pleotelson apex narrowly round
<i>Colopisthus</i>	
4: 0→1	Pereonites with setae on dorsal surface
10: 0→1	Antenna 1 peduncular article 2 subequal to article 3
13: 2→1	Antenna 1 peduncular article 1 subequal to article 3
27: 1→0	Left mandibular incisor quadridentate
29: 0→1	Mandibular incisor with flask-like inclusion
31: 1→0	Mandibular spine row on small lobe
35: 1→0	Pereopod 1 ischium superior distal angle without short simple setae
39: 2→0	Pereopod 1 merus superior distal angle without long simple setae
40: 0→1	Pereopod 1 merus superior distal angle with acute robust setae
45: 0→1	Pereopod 1 carpus inferior margin (not including distal angle) with connate spines
51: 1→0	Pereopod 1 propodus inferior margin without robust setae
64: 0→1	Pereopod 2 propodus inferior margin with connate spine(s)
68: 0→1	Pereopod 3 ischium inferior distal angle with molariform seta
70: 1→0	Pereopod 7 basis length subequal to twice width
84: 0→1	Pleopod 1 peduncle length subequal to or greater than width
93: 1→0	Uropodal exopod length reaches pleotelson apex
<i>Aphantolana</i>	
20: 2→0	Frontal lamina anterior margin rounded
22: 0→1	Clypeus, anterior margin projecting anterio-ventrally
48: 1→0	Pereopod 1 carpus inferior distal angle without robust setae
49: 0→1	Pereopod 1 carpus inferior distal angle with complex setae
57: 0→1	Pereopod 2 ischium superior distal angle with a few short simple setae
61: 0→1	Pereopod 2 carpus inferior margin with connate spines
62: 0→1	Pereopod 2 carpus inferior distal angle forms a notched lobe
86: 0→1	Pleopod 1 exopod less than twice endopod width
89: 1→0	Appendix masculina reaches exopod apex
96: 0→1	Uropodal endopod medial margin with plumose setae
107: 0→1	Uropodal exopod lateral margin with robust setae
111: 0→1	Pleotelson with lateral carinae

and if this is so, then the presence of these characters in the genus *Hansenolana* is a result of homoplasy (parallelism). We predict that the phylogenetic analysis of all genera of Cirolanidae will provide the broader context necessary to reveal these characters as additional synapomorphies for the clades indicated below. Three of these characters would define the genus *Colopisthus*: anterior margin of the frontal lamina concave (character 20), anterior margin of the clypeus not projecting (character 22), and pereopod 2 merus superior distal angle slightly produced, less than one-third length of propodus (character 59). One additional character would define the new genus *Aphantolana*: pereopod 1 carpus inferior distal angle slightly produced

as a blunt, connate spine (character 46). Three additional characters would define the *Colopisthus/Aphantolana* sister group relationship: pereopod 1 merus inferior margin with molariform setae (character 43), pleonite lateral margins covered by the seventh coxal plate (character 80) and the presence of a very large seventh coxal plate (character 82).

Taxonomic treatment

Materials and methods

Specimens of *Colopisthus* are uncommon and do not occur in abundance. We contacted over 90 curators of marine invertebrate collections around the world in order to borrow as many specimens of *Colopisthus* as possible. The taxonomy presented here is based upon 60 specimens of *Colopisthus* borrowed from the museum collections listed below. These institutions are designated in the text by the following abbreviations. USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; YPM, Peabody Museum of Natural History, Yale University, CT, USA; ZMB, Museum of Natural History, Berlin, Germany; ZMUC, Zoological Museum, University of Copenhagen, Denmark.

We used standard methods of visually comparing external structural features to distinguish species. Specimens for each species were thoroughly dissected and appendages were temporarily mounted in glycerine on glass slides. When multiple specimens were available, we examined individuals from throughout the species range to determine the boundaries of intraspecific variation. Structures were examined and illustrated using a Nikon Labophot compound microscope. Measurements were made with an ocular micrometer. In the text, 'longer than' means more than 1.1 times the length, and 'shorter than' means less than 0.9 times the length; comparisons of length that fall between 1.1 and 0.9 are referred to as being 'subequal' to one another. Scanning electron micrographs (SEMs) were taken with a Cambridge scanning electron microscope.

We have kept setal terminology as simple as possible to avoid confusion. We have named most setae by a combination of adjectives to describe length, robustness and complexity. Unusual setae are figured in detail separately (figure 3). In the past, confusion has arisen over the terminology used for pereopod orientation. We follow Brusca *et al.* (1995)—using standard anatomical terminology and the natural curvature of the pereopod, we refer to the margin encompassed by the concave carpus-propodus-dactyl as the inferior margin, and the opposite (convex) margin as the superior margin. The pereopods also have an anterior surface and a posterior surface; the anterior surface is the surface of the pereopod that faces toward the front of the animal, and the posterior surface faces toward the rear of the animal. Distal margins/angles of leg articles are those furthest from the body, and proximal margins/angles of articles are nearest the body. These distinctions are necessary to describe the complex setation of the pereopods. In most cases only a single side (anterior or posterior) of the pereopod is figured and described, generally the more complex or setose side. The following abbreviations are used: P-1 to P-7, pereopods 1–7; Pl-1 to Pl-5, pleopods 1–5; PMS, plumose marginal setae. Setules on PMS of pleopods are not figured. In descriptions of maxilla 2 we refer to the lateral lobe, medial lobe and gnathal (=inner) lobe. When describing the first three pereopods of *Colopisthus* we use the term haptorial in the sense of Bruce and Humphries (1993).

We include a diagnosis and description for each taxon. The description is comprehensive and includes all characters analysed for the taxon. The diagnosis is a subset of the characters in the description which are diagnostic of the taxon; this section includes synapomorphies as well as other characters that serve to clearly distinguish the taxa from their conspecifics or congeners.

Order ISOPODA Latreille, 1817

Suborder FLABELLIFERA Sars, 1882

Family CIROLANIDAE Dana, 1853

Colopisthus Richardson, 1902

Synonymy. *Colopisthus* Richardson, 1902: 289–290, pl. 38, figures 33–36; Richardson, 1905: 137, figure 119; Monod, 1952: 813–816; Menzies and Glynn, 1968; Kensley and Schotte, 1989: 146–147, figure 66a; Müller, 1993: 212–218, figures 72–96.

Type species. *Colopisthus parvus* Richardson, 1902, by monotypy. Type material deposited at USNM (Acc. No. 37555, Lot No. 24867).

Diagnosis. Sexual dimorphism not pronounced. Body length 3–4 mm. Coxae 4–7 visible dorsally. Pereon seven times pleon length. Body length 2.5–2.6 times greatest width; pereonite 1 longest with lateral margins forming an abrupt shelf-like angle. Cephalon with interocular depression. Antenna 1 short; peduncle composed of four articles, distal article minute; flagellum two-articulate or three-articulate. Antenna 2 short, peduncle five-articulate, proximal article minute (not easily dissected, but visible with SEM; see figure 4A), four to seven flagellar articles. Maxilliped with five-articulate palp, many palp setae jointed (of two parts), endite extended to third palp article, with one to three sharply curved coupling setae and four or five large circumplumose setae. Mandibular incisor middle tooth with minute flask-like inclusion. Mandibular palp with robust biserrate setae on articles two and three. P-1 propodal palm with two large complex setae and four or five connate spines. P-1 to P-7 dactylus often with thin, acute accessory seta and a secondary unguis. Coxal plates become progressively larger posteriorly; coxae of pereonite 7 largest and extended well beyond anterior margin of pleotelson. Penes simple, well-developed, rounded (not flattened), one and a half times longer than wide, separated by distance equal to one half width of one penis. Pleon with two or three free (unfused) pleonites, or one free and two partly fused pleonites; without epimeres. P1-2 appendix masculina longer than pleopodal rami, flask-like (narrows abruptly distally), grooved, and articulating sub-basally on endopod; jointed with subovate basal portion and long flask-like distal region, tapering to ridged subacute apex. Pleopods with PMS decreasing in abundance posteriorly, present on all rami except endopod of P1-5; endopods never as wide as exopods; P1-1 peduncle subquadrate. Uropodal endopod dorsal surface with two clusters (one distal and one proximo-lateral) of four or five palmate setae; peduncle with two robust setae arising from ventral surface. Pleotelson with distinct dorso-medial, longitudinal carina; apex narrowly round with fine slender setae and two stout setae.

Description

Head. Cephalon with interocular depression, without tubercles. Eyes round, well developed, partially hidden laterally by pereonite 1; ommatidia arranged in rows. Frontal margin of cephalon not medially concave, with distinct small rostral process separating first antennae. Frontal lamina not fused to rostrum, without ventral

projection, anterior end expanded, anterior margin rounded with slight medial depression, posterior end moderately stemmed and abutting clypeus. Clypeus triangular; anterior margin rounded, directed anteriorly, set at less than 25° angle to frontal lamina.

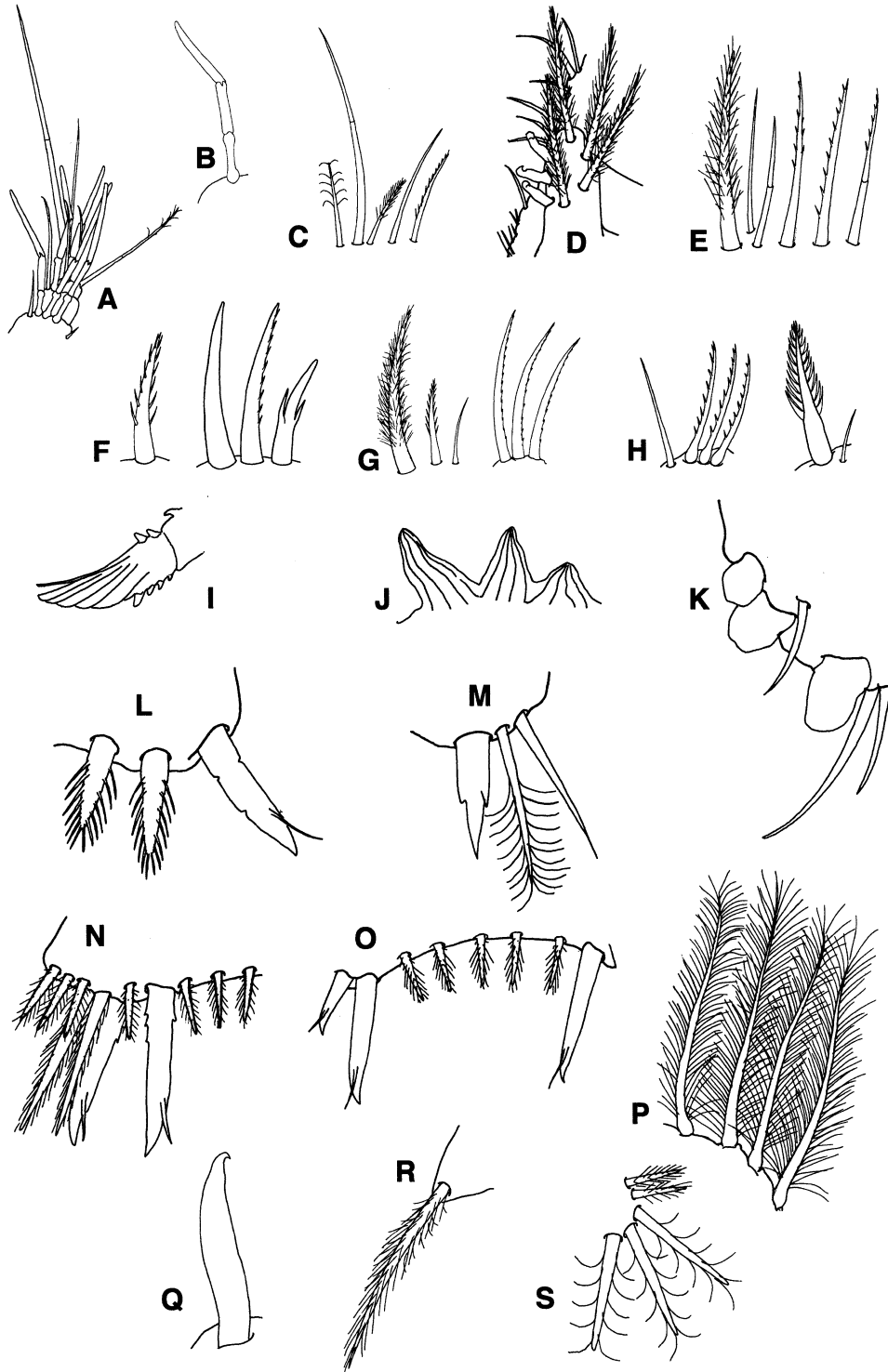
Antennae. Antennae 1 short, reaching just beyond lateral margin of cephalon; peduncle four-articulate, articles 1–3 with setae (slender and/or palmate), article 1 subquadrate, not sexually dimorphic, article 2 subquadrate, subequal or shorter than article 3; article 3 longer than wide, article 4 minute, with or without setation; flagellum two-articulate or three-articulate, the first of which is elongate (twice width), the remaining being short (width greater than or equal to length), all with jointed aesthetascs, usually with slender setae, terminal article often with one uniplumose or biplumose seta. Antennae 2 peduncular article 1 minute (generally not visible except with SEM), articles 2–3 subequal, article 5 subequal to or slightly longer than 4; four to seven flagellar articles, all with slender setae.

Maxilliped. Endite well developed and reaching third palp article; with one to three coupling setae and four or five large lateral circumplumose setae. Palp article 1 (proximal article) subquadrate; article 2 wider than long (expanded on lateral border), may be partly fused with article 3; article 3 largest; articles 3–5 subquadrate. Palp article 1 with one slender seta on medial angle, articles 2–4 with slender setae on medial margin and usually on lateral margin, most dense on distal margin; articles 4 and 5 also with uniserrate setae on distal margin. Many palp setae jointed (of two parts).

Maxillae. Maxilla 1 with medial and lateral lobes distinct, gnathal surface of lateral lobe with five to seven forked setae and three or four uniserrate setae; inner lobe with three stout biplumose setae and one or two slender or plumose setae. Maxilla 2 with apical setae on all three lobes; lateral lobe with three uniserrate setae; medial lobe with two to four uniserrate setae; gnathal lobe with one large circumplumose seta and three to five stout biplumose setae and/or slender setae.

Mandible. Incisor broad, with three large teeth and a small medial accessory tooth; with minute flask-like inclusion on large middle tooth. Molar process with 11–20 small acute spines on anterior margin, dorsal surface smooth, without setae; spine row well developed, with 9–14 large flexible spines without intermediate,

FIG. 3. Some types of setae found in *Colopisthus*. (A) Detail of antenna 1 flagellum with setae. (B) Jointed aesthetasc. (C) Setae found on antennae 2: palmate seta; slender jointed seta; biplumose seta, simple seta; uniplumose seta. (D) Detail of maxillipedal endite with setae. (E) Setae found on the maxilliped: circumplumose seta; simple seta; simple jointed seta; biserrate seta; uniserrate seta; jointed uniserrate seta. (F) Setae found on maxilla 1: stout biplumose seta; stout seta, uniserrate seta, forked seta. (G) Setae found on maxilla 2: large circumplumose seta; stout biplumose seta; slender seta; three uniserrate setae. (H) Setae found on mandible: simple seta; three unequally biserrate setae (second row of minute setules not shown); biserrate seta; simple seta. (I) Complex seta of pereopod 1 propodus. (J) Connate spines of pereopod 1 propodus. (K) Molariform setae (and simple setae) of pereopod 1 merus. (L) Biplumose setae and notched stout seta (of *C. tresesquinas* pereopods). (M) Forked seta, palmate seta and simple seta of *C. tresesquinas* pereopod, superior distal angle of propodus. (N) Setae found on pereopods 4–7 superior distal angle: biplumose setae; long biplumose setae; stout setae. (O) Setae found on pereopod 5–7 antero-distal margin: stout setae; biplumose setae. (P) Plumose marginal setae of pleopods. (Q) Coupling seta on pleopodal peduncle. (R) Circumplumose seta of uropodal peduncle. (S) Long palmate setae found on dorsal surface of the uropod.



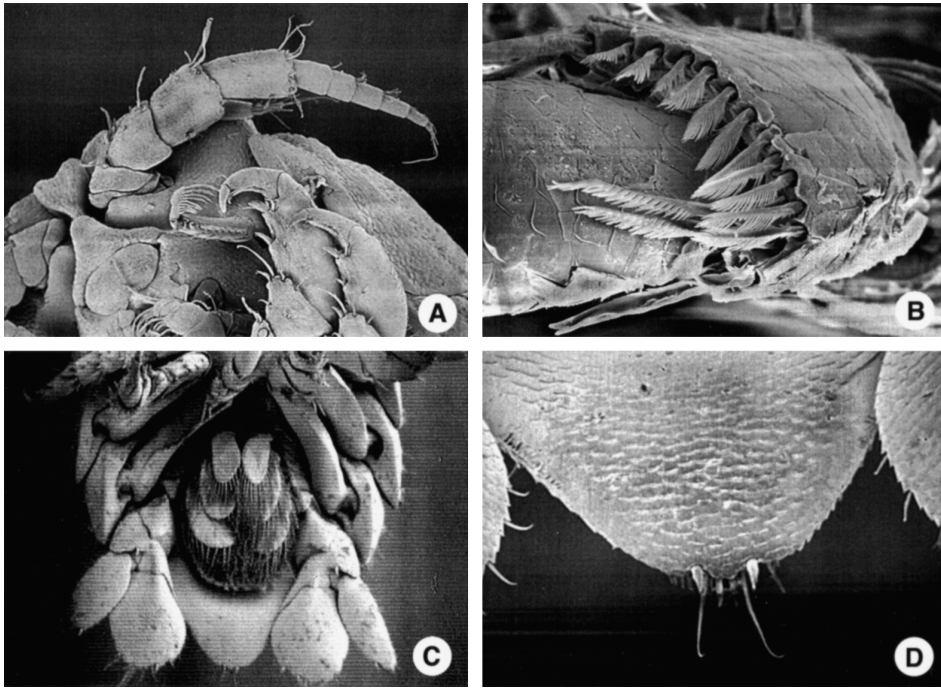


FIG. 4. Scanning electron micrographs. (A) *Colopisthus canna*. Frontal lamina-clypeus-labrum, minute first peduncular article of antenna 2. (B) *Colopisthus cavalier*. Anterior distal margin of pereopod 7 carpus showing row of biplumose setae. (C) *Colopisthus parvus*. Ventral side of the pleon showing pleopods encompassed by the coxal plates and uropods. (D) *Colopisthus parvus*. Ventral side of narrowly rounded telson showing the two stout setae at the apex.

slender setae; without a lacinia mobilis. Mandibular palp of three articles, article 2 longest with biserrate (some unequally biserrate) and slender setae; distal article well developed, two times longer than wide, with 7–10 biserrate setae on lateral margin.

Pereon. Smooth, without ornamentation; fine setae present on dorsal surface; surface of cuticle with shingle sculpturing (visible with SEM). Pereonite 1 longest (1.3–1.6 times longer than pereonite 2); with lateral margins forming an abrupt shelf-like angle; extended forward on lateral margins to partly hide eyes. Coxae 3–7 or 4–7 visible dorsally; coxae become progressively larger posteriorly; coxae 2–3 with longitudinal ridge, 4–7 with oblique ridge; posterolateral angles of coxae 7 extend beyond anterior margin of pleotelson.

Pereopods. P-1 to P-7 dactylus often with thin, acute accessory seta and a secondary unguis lying alongside primary unguis, and one to four slender setae on superior margin; basis with weak anterior ridge. P-1 to P-3 propodus expanded and ovate; P-4 to P-7 long and ambulatory.

Pereopods 1–3. Unique, complex pattern of setae and spines as follows: P-1 merus superior-distal angle not produced (superior margin of carpus is free), inferior margin with stout molariform setae, inferior distal angle with two stout setae; carpus with two to four connate spines, propodus inferior margin with four or five connate spines and two large complex setae; superior distal angle of P-1 propodus with two stout setae. P-2 merus inferior margin (and occasionally ischium) with molariform

setae; propodus (and occasionally carpus) with connate spines; propodus with two complex setae and one or two connate spines. P-3 inferior margin of ischium, merus (and occasionally carpus or propodus) with molariform setae; occasionally carpus and/or propodus with connate spines; propodus with one (occasionally two) complex setae.

Pereopods 4–7. Basis-propodus articles not greatly flattened, without connate spines or complex setae; superior distal angles of ischium, merus and carpus with one to four robust setae; merus with superior-distal angle expanded. P-5 carpus anterior-distal margin with one biplumose seta; carpus of P-6 with a row of two or three biplumose setae; carpus of P-7 with a row of five to 11 biplumose setae. P-5 to P-7 propodus with one or two robust setae on inferior margin and two or three robust setae at inferior distal angle.

Pleon. Pleon with two or three free pleonites, or with one free and two fused pleonites; without epimeres. Penes simple, well-developed, rounded (not flattened), one and a half times longer than wide, separated by distance equal to one half width of one pene.

Pleopods. Without digitate respiratory branchiae or accessory lamellae. Peduncle of Pl-1 to Pl-3 with three coupling setae on medial margin. Peduncle of Pl-4 with three or four coupling setae on medial margin. Pl-1 peduncle subquadrate; exopod and endopod elongate, not operculate. Pleopod exopods approximately 1.5 times wider than endopods; endopod and exopods subequal length on Pl-1, endopod increasingly shorter than exopod on Pl-2 to Pl-5. Endopods and exopods with PMS, decreasing in abundance posteriorly, absent on endopod of Pl-5; endopods with PMS restricted to distal margins; exopods with PMS on distal and lateral margins. Exopods of Pl-3 to Pl-5 with transverse suture. Pl-2 appendix masculina longer than pleopodal rami, flask-like (narrows abruptly distally), grooved and articulating sub-basally on endopod; jointed with subovate basal portion and long flask-like distal region, tapering to ridged subacute apex.

Uropod. Uropodal endopod and exopod extend slightly beyond pleotelson apex. Peduncle with two robust ventral setae arising from mediodistal margin; disto-lateral angle not produced, with one to three slender setae; disto-medial angle produced, subacute, with one large, apical, circumplumose seta. Endopod margins and apex with slender setae; medial margin with two large robust setae; lateral margin with one robust seta; apex broadly rounded; dorsal surface with two clusters of four or five long palmate setae, one distal and one proximo-lateral. Exopod medial margin with slender setae and two robust setae; apex round, with long slender setae; lateral margin with slender setae and occasionally one robust seta.

Pleotelson. Subtriangular, with large dorso-medial longitudinal carina; apex narrowly rounded, with fine slender setae and a pair of stout setae.

Remarks

Colopisthus is a rarely collected genus that is widely distributed in the tropical Atlantic and Caribbean, but unknown elsewhere. Specimens have been collected only from the intertidal zone, usually associated with algae. Male specimens are rare, being known from only a few individuals of three species (*C. parvus*, *C. ronrico* n. sp., *C. tresesquinas* n. sp.). Members of the genus *Colopisthus* have the most reduced pleon of all cirolanid species. The pleon is reduced from the plesiomorphic state of five free pleonal segments to two or three free segments.

World list of species

1. *Colopisthus canna* n. sp. Cape Verde Islands.
2. *Colopisthus cavalier* n. sp. Barbuda.
3. *Colopisthus parvus* Richardson, 1902. Bermuda. Type species.
4. *Colopisthus ronrico* n. sp. Puerto Rico.
5. *Colopisthus tresesquinas* n. sp. Colombia.
6. *Colopisthus* sp.? (not *C. parvus*) (Monod, 1952) Senegal.

Key to *Colopisthus* species

- 1 Lateral margins of the cephalon and pereonite 1 crenulate. Mandibular spine row with 11 or fewer spines. Pereopod 6 carpus with two setae in anterior-distal row of biplumose setae 2
 - Lateral margins of the cephalon and pereonite 1 smooth (females may have weak crenulations). Mandibular spine row with 13 or more spines. Pereopod 6 carpus with three setae in anterior-distal row of biplumose setae 3
- 2 Antennae 1 flagellum two-articulate. Antennae 2 flagellum five-articulate. Maxilliped endite with one coupling seta. Pereopod 1 merus inferior margin with two molariform setae. Pereopod 2 merus inferior margin with two molariform setae, but without tubercles *C. ronrico*
 - Antennae 1 flagellum three-articulate. Antennae 2 flagellum six-articulate. Maxilliped endite with three coupling setae. Pereopod 1 merus inferior margin with four to six molariform setae. Pereopod 2 merus inferior margin with two molariform setae and three or four tubercles *C. cavalier*
- 3 Antennae 2 flagellum seven-articulate. Maxilliped endite with four circumplumose setae. Pleon of three pleonites (plus pleotelson). Pereopod 3 merus with three molariform setae on inferior margin. Pereopod 7 with five to seven biplumose setae in anterior-distal margin *C. tresesquinas*
 - Antennae 2 flagellum six-articulate or less. Maxilliped endite with five circumplumose setae. Pleon of two or three pleonites (plus pleotelson). Pereopod 3 merus with two molariform setae on inferior margin. Pereopod 7 with 10 or 11 biplumose setae in anterior-distal margin 4
- 4 Antennae 2 flagellum four-articulate. Mandibular palp article 2 with two uniserrate setae. Pereopod 1 carpus inferior-distal angle with two connate spines. Pereopod 2 ischium inferior margin with molariform seta. Pleopod 3 exopod with complete transverse suture *C. canna*
 - Antennae 2 flagellum six-articulate. Mandibular palp article 2 with four uniserrate setae. Pereopod 1 carpus inferior-distal angle with three connate spines. Pereopod 2 ischium inferior margin without molariform seta. Pleopod 3 exopod with partial transverse suture *C. parvus*

Colopisthus canna new species
(figures 5–9)

Type material examined. HOLOTYPE, female (CRU-1969), five female paratypes in alcohol (CRU-3276) and one SEM prepared paratype mounted on stub (CRU-3277); Cape Verde Islands, St Vincent; Station No. 37, Anton Brunn, Atlantide Expedition (Cat. No. ZMUC CRU-1969).

Diagnosis. Pleon with two free pleonites (plus pleotelson). Antenna 1 flagellum three-articulate. Antennae 2 flagellum four-articulate. Maxilliped endite with five circumplumose setae and two coupling setae. P-1 to P-3 merus with two or three molariform setae on inferior margin. P-1 carpus with two connate spines on inferior

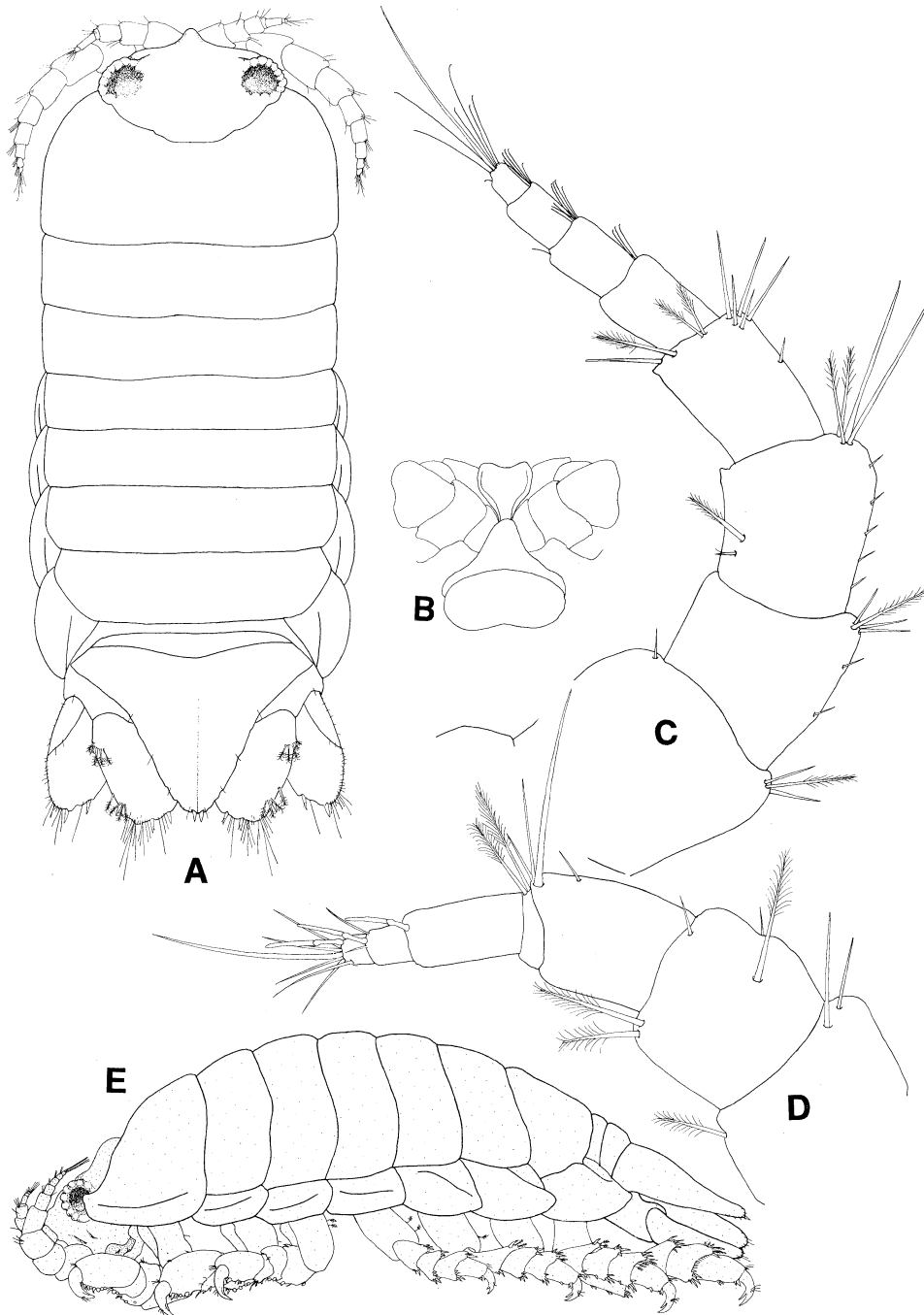


FIG. 5. *Colopisthus canna*, female holotype: (A) dorsal aspect; (B) frontal lamina, clypeus, labrum; (C) antenna 2; (D) antenna 1; (E) lateral aspect.

margin. Carpus of P-5 with one biplumose seta on anterior-distal margin; P-6 with three biplumose setae on anterior-distal margin; P-7 with 11 biplumose setae on anterior-distal margin. PI-3 exopod with complete transverse suture.

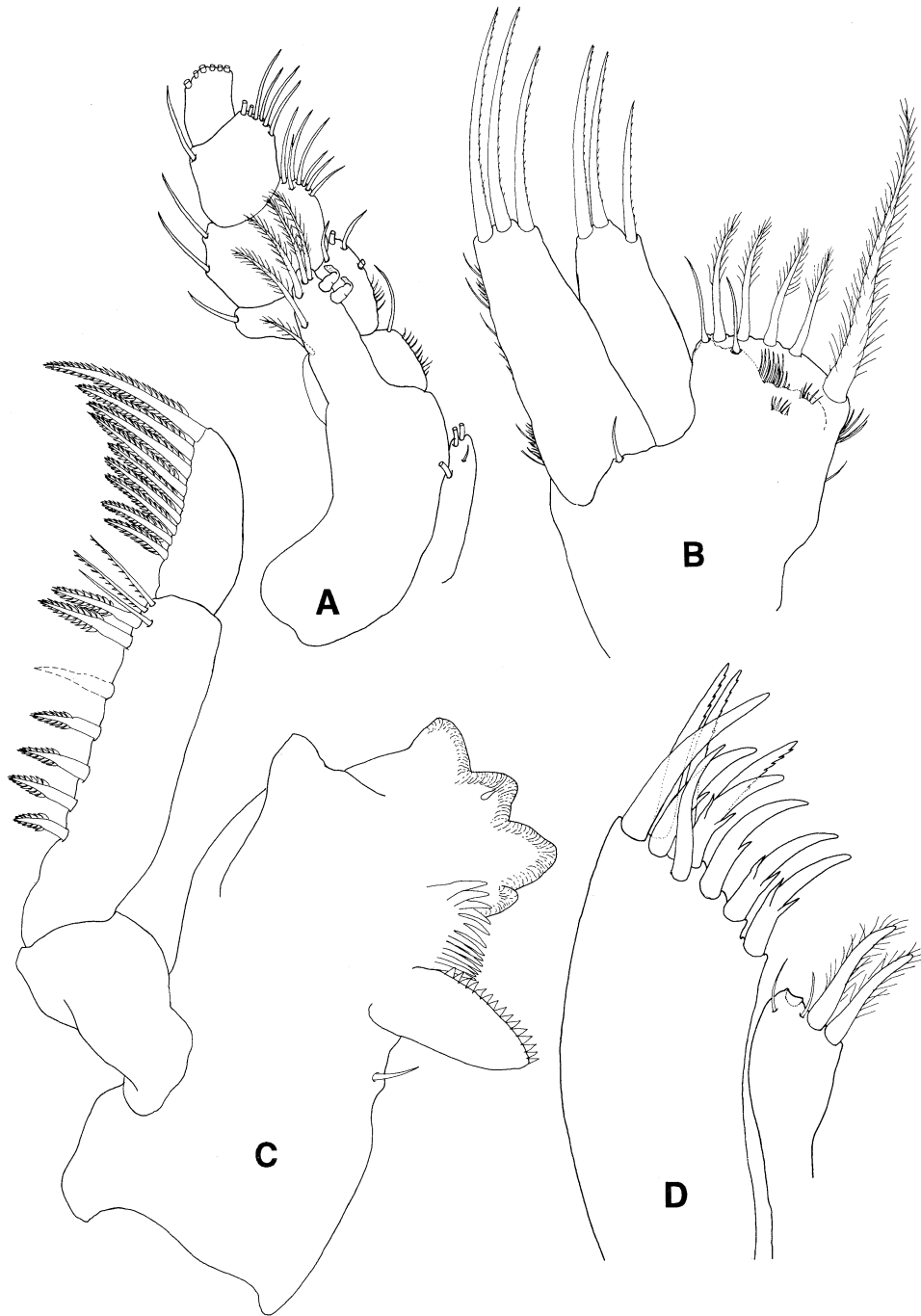


FIG. 6. *Colopisthus canna*, female holotype: (A) left maxilliped; (B) maxilla 2; (C) left mandible; (D) maxilla 1.

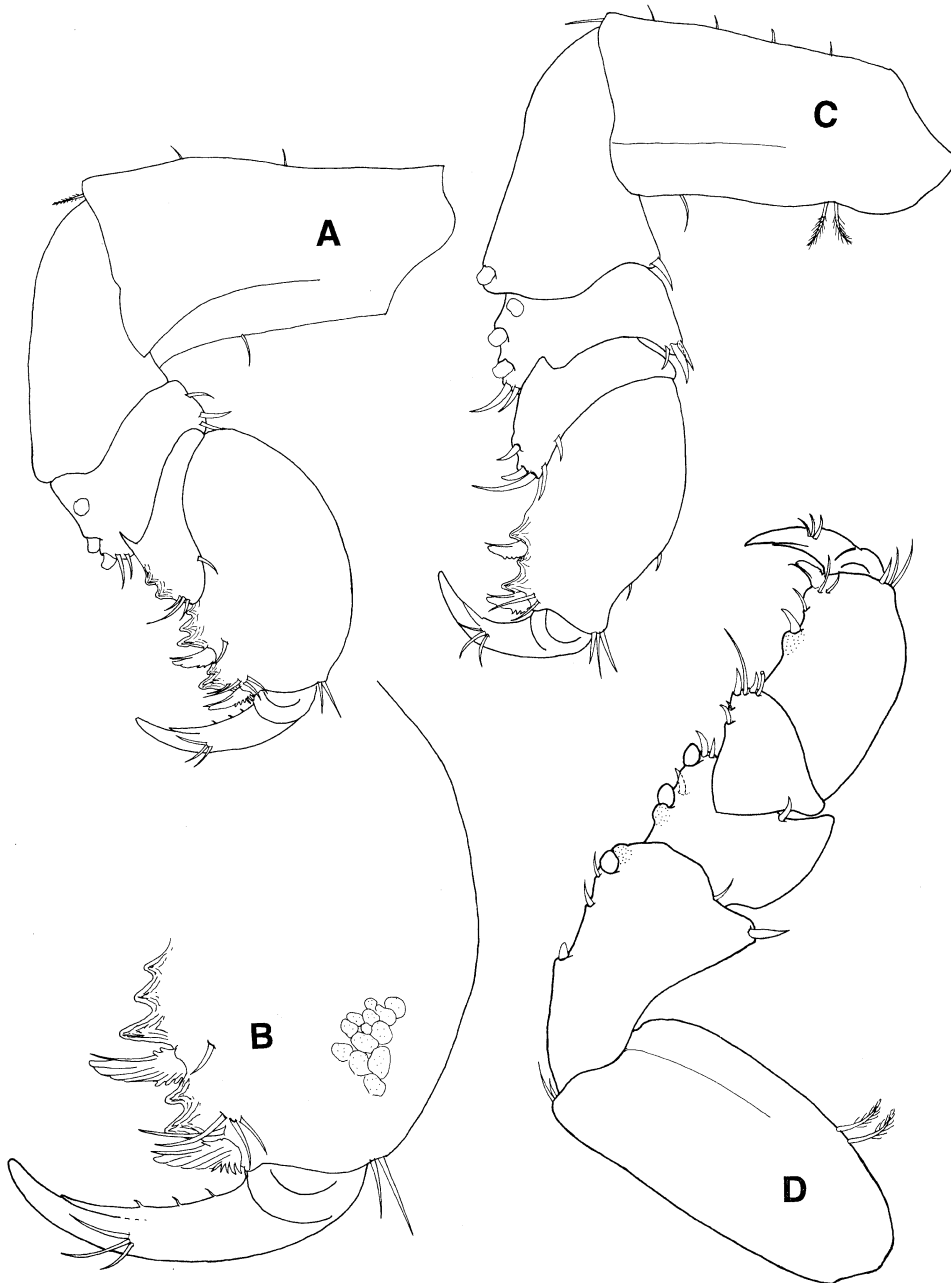


FIG. 7. *Colopisthus canna*, female holotype: (A, B) right pereopod 1; (C) right pereopod 2; (D) left pereopod 3.

Description of female

Antennae. Antenna 1 peduncular articles 1 and 2 with slender and palmate setae, article 3 with slender setae; articles 2 and 3 subequal in length; article 4 with two biplumose setae. Antenna 1 flagellum three-articulate; first article much longer than distal two articles; all flagellar articles with jointed aesthetascs. Antenna 2 peduncle

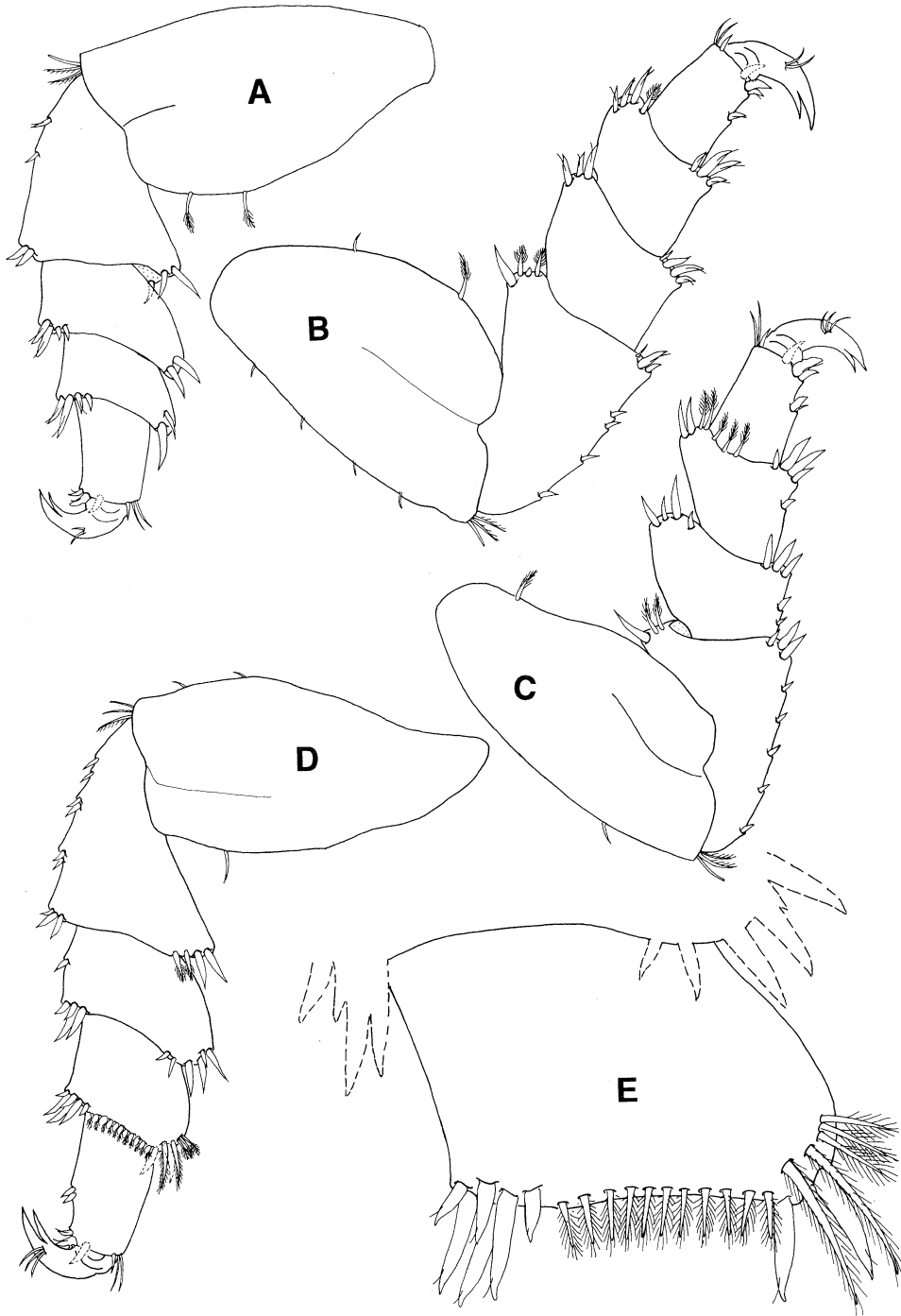


FIG. 8. *Colopisthus canna*, female holotype: (A) right pereopod 4; (B) right pereopod 5; (C) right pereopod 6; (D) right pereopod 7; (E) right pereopod 7 carpus.

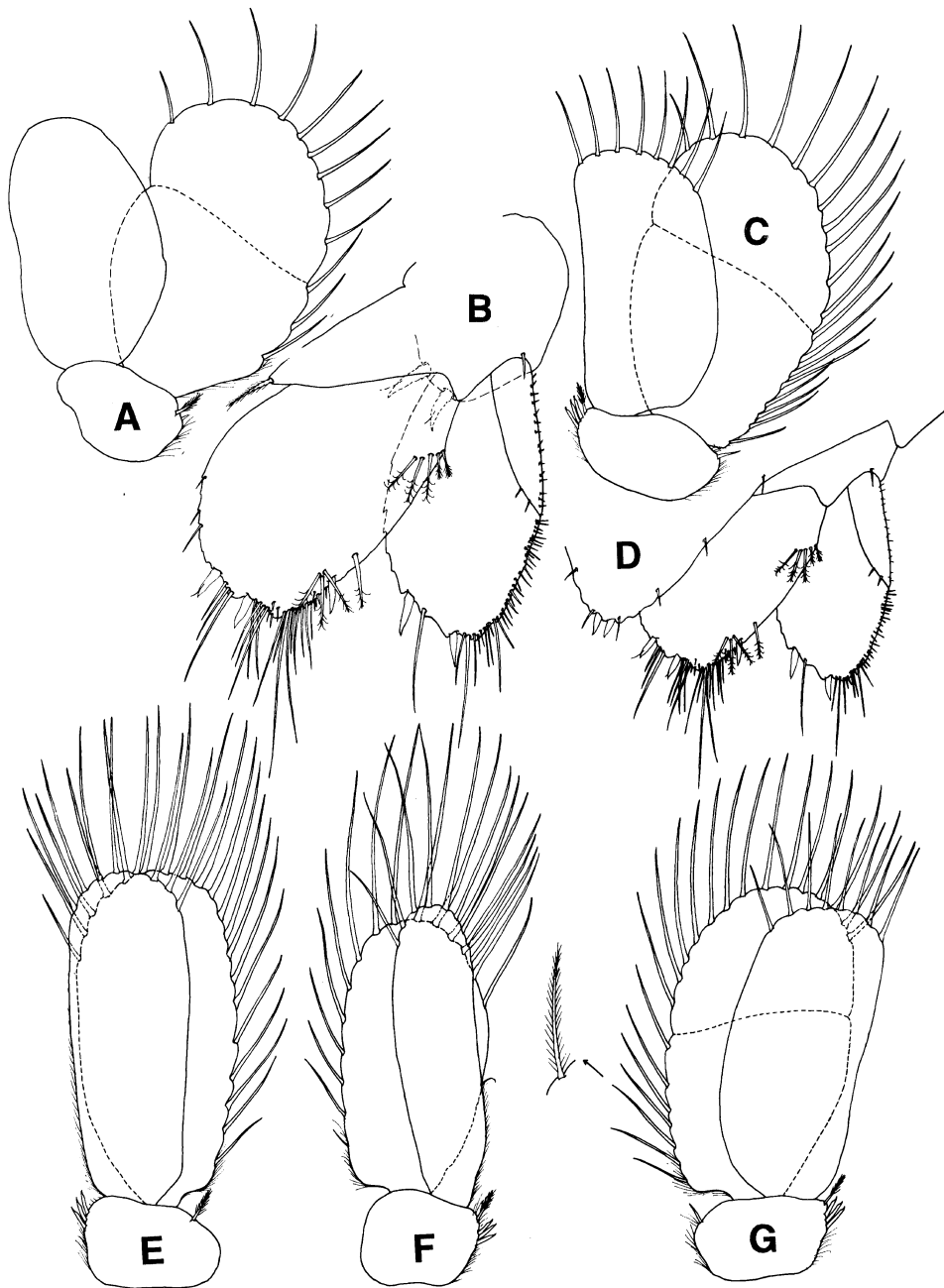


FIG. 9. *Colopisthus canna*, female: (A) left pleopod 5; (B) right uropod, holotype; (C) left pleopod 4; (D) telson-uropod, holotype; (E) left pleopod 2; (F) right pleopod 1; (G) right pleopod 3.

articles 2–5 with slender and biplumose setae; flagellum four-articulate, all with cluster of slender setae in anterior-distal region.

Maxilliped. Endite with five circumplumose setae and two coupling setae. Palp article 1 medial margin with fine and slender setae; article 2 lateral margin with one slender seta, and medial margin with fine and slender setae; article 3 with slender setae on lateral and medial margins; article 4 with one slender seta on disto-lateral angle, and slender setae on disto-medial angle; terminal article subquadrate with six apical setae (broken on holotype).

Maxillae. Maxilla 1 lateral lobe with two stout, five forked and three uniserrate setae; medial lobe with two slender and three stout biplumose setae (one biplumose seta missing from holotype). Maxilla 2 outer lobe with three uniserrate setae on distal margin and fine setae on lateral margin; medial lobe with three uniserrate setae; gnathal lobe with one slender seta at base (below outer lobe), apical margin with one large circumplumose, four stout biplumose and two slender setae.

Mandible. Spine row with 13 large spines; molar process with approximately 15 small acute marginal spines; proximal palp article without setae; middle article with one slender, seven biserrate and two unequally biserrate setae; distal article with nine biserrate setae.

Pereopods 1–3. Ischium of P-1 without setae, P-2 and P-3 with molariform seta near inferior-distal angle and stout seta on superior-distal angle, P-3 with stout setae on inferior margin. Merus with two or three molariform setae on inferior margin and a cluster of stout setae on inferior-distal angle; distal margin deeply incised (notched) on anterior surface. Carpus subtriangular, inferior margin much longer than superior margin; with cluster of stout setae on inferior distal angle; P-1 with two connate spines on inferior margin. Propodus with complex setae and connate spines on inferior margin as figured; P-1 with two complex setae and four or five connate spines; P-2 with two complex setae and two or three connate spines; P-3 with one complex seta, one robust seta and no connate spines.

Pereopods 4–7. Basis with one or two biplumose setae at inferior distal angle. Ischium with two to five clusters of stout setae on inferior margin; P-5 to P-7 with two biplumose setae at superior-distal angle. Carpus of P-5 with one biplumose seta on anterior-distal margin; P-6 with three biplumose setae on anterior-distal margin and approximately two long biplumose setae at superior-distal angle; P-7 with 11 biplumose setae on anterior-distal margin and approximately five long biplumose setae at superior-distal angle. Propodus inferior distal angle with one stout seta and one reduced complex seta; posterior-distal margin with one stout seta (drawn in dashed lines in figure 8); superior-distal angle with one stout and two slender setae. Dactyli with large secondary unguis and no accessory setae.

Pleopods. Pl-1 to Pl-4 peduncle with three coupling setae on medial margin; Pl-5 peduncle subovate, with one biplumose seta on lateral margin. Pl-2 peduncle with one biplumose seta on lateral margin. Pl-3 to Pl-5 exopod with complete transverse suture. Pl-1 endopod with approximately nine PMS; exopod with approximately 14 PMS. Pl-2 to Pl-4 endopod with approximately eight PMS; exopod with 19–21 PMS. Pl-5 endopod subovate, without setae; exopod with approximately 12 PMS.

Uropod. Endopod with slender and palmate setae; two robust setae on medial margin and one robust seta on lateral margin; apex broadly rounded, with approximately five long slender setae. Exopod with slender setae and two robust setae on medial margin; apex rounded, with approximately three or four long slender setae; lateral margin with a continuous row of short slender setae; proximal lateral margin with dorsal fold.

Distribution

This species has been collected only from St Vincent, one of the Cape Verde Islands.

Remarks

Males of this species have not yet been collected.

Etymology

This species name is taken from the Latin word, *canna*, for sugar cane, the principal ingredient of rum, a favoured libation in the tropical Atlantic region.

Colopisthus cavalier new species

(figures 10–14)

Material examined. HOLOTYPE, female (USNM 285288) and six female paratypes (USNM 285289); Barbuda, Spanish Point, intertidal beach wrack and live *Porites*; Bredin Expedition 1958, Station 112a-58, collected by Smitt and Shuster (USNM 217237).

Diagnosis. Lateral margins of cephalon and pereonite 1 with crenulations. Coxae 4–7 visible dorsally. Antenna 1 flagellum three-articulate. Antennae 2 flagellum six-articulate. Pleon with one free pleonite and two fused pleonites (suture visible only in lateral view). Maxilliped endite with four circumplumose setae and three coupling setae. P-1 to P-3 merus with four to six molariform setae on inferior margin. Carpus of P-1 with four connate spines on inferior margin; P-2 and P-3 with three to five molariform setae and cuticular tubercles on inferior margin. Propodus of P-1 and P-2 with two complex setae and four or five connate spines. P1-3 exopod with partial transverse suture. Uropodal exopod with two robust setae.

Description of female

Head. Lateral margins of cephalon and pereonite 1 with crenulations.

Antennae. Antenna 1 peduncular articles 1–3 with biplumose setae, article 3 longest and narrowest, article 4 with slender and biplumose setae; flagellum three-articulate, first article much longer than distal two articles, all flagellar articles with slender setae and jointed aesthetascs, terminal article with biplumose seta. Antennae 2 peduncular articles 2–3 wider than long with slender setae only; article 4 subquadrate with biplumose and slender setae; article 5 longer than wide with three biplumose, one palmate and approximately 11 slender setae; flagellum six-articulate, all longer than wide, all with cluster of slender setae in anterior-distal region.

Maxilliped. Endite with four circumplumose setae and three coupling setae. Palp article 1 medial margin with fine and slender setae; article 2 much wider than long, medial margin with slender setae; article 3 subquadrate with jointed slender setae on lateral and medial margins, article 4 subquadrate with one jointed slender seta on disto-lateral angle, two uniserrate and approximately four jointed slender setae on distal medial angle; terminal article length greater than width and with approximately four slender, one biplumose and two uniserrate apical setae.

Maxillae. Maxilla 1 lateral lobe with one stout, seven forked and three uniserrate setae; medial lobe with two slender and three stout biplumose setae. Maxilla 2 outer lobe with three uniserrate apical setae, fine setae on lateral margin; medial lobe with four uniserrate setae; gnathal lobe apical margin with one large circumplumose, five

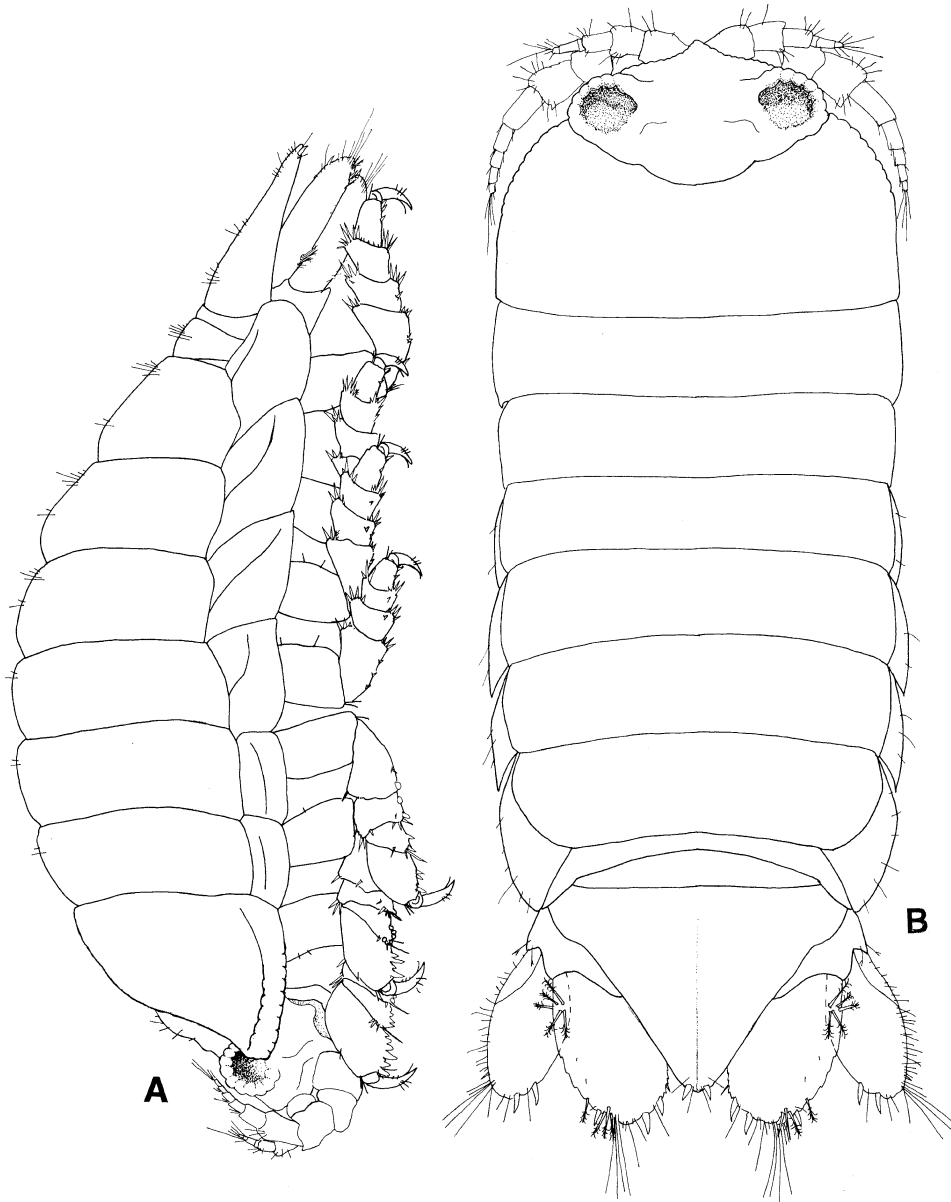


FIG. 10. *Colopisthus cavalier*, female holotype: (A) lateral aspect; (B) dorsal aspect.

stout biplumose and two slender setae; clusters of fine setae on medial and lateral margins.

Mandible. Spine row with 11 large spines; molar process with approximately 16 small acute marginal spines; proximal palp article longer than wide with one slender seta on lateral margin; middle article with three slender, seven biserrate and four unequally biserrate setae; distal article with nine biserrate setae.

Pereopods 1–3. Ischium with one or two stout setae on inferior margin and one stout seta on superior-distal angle; P-3 with molariform seta near inferior-distal

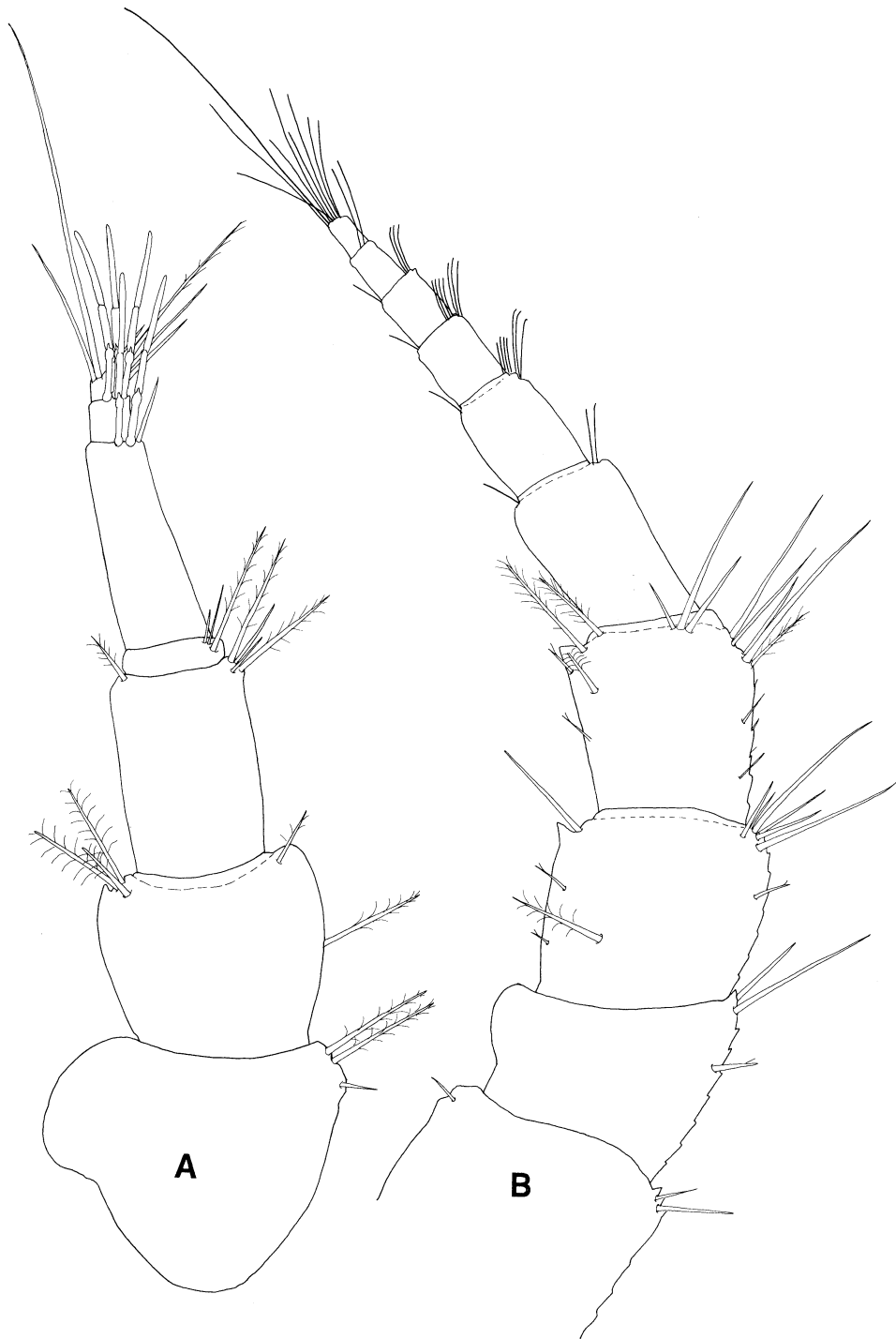


FIG. 11. *Colopisthus cavalier*, female holotype: (A) antenna 1; (B) antenna 2.

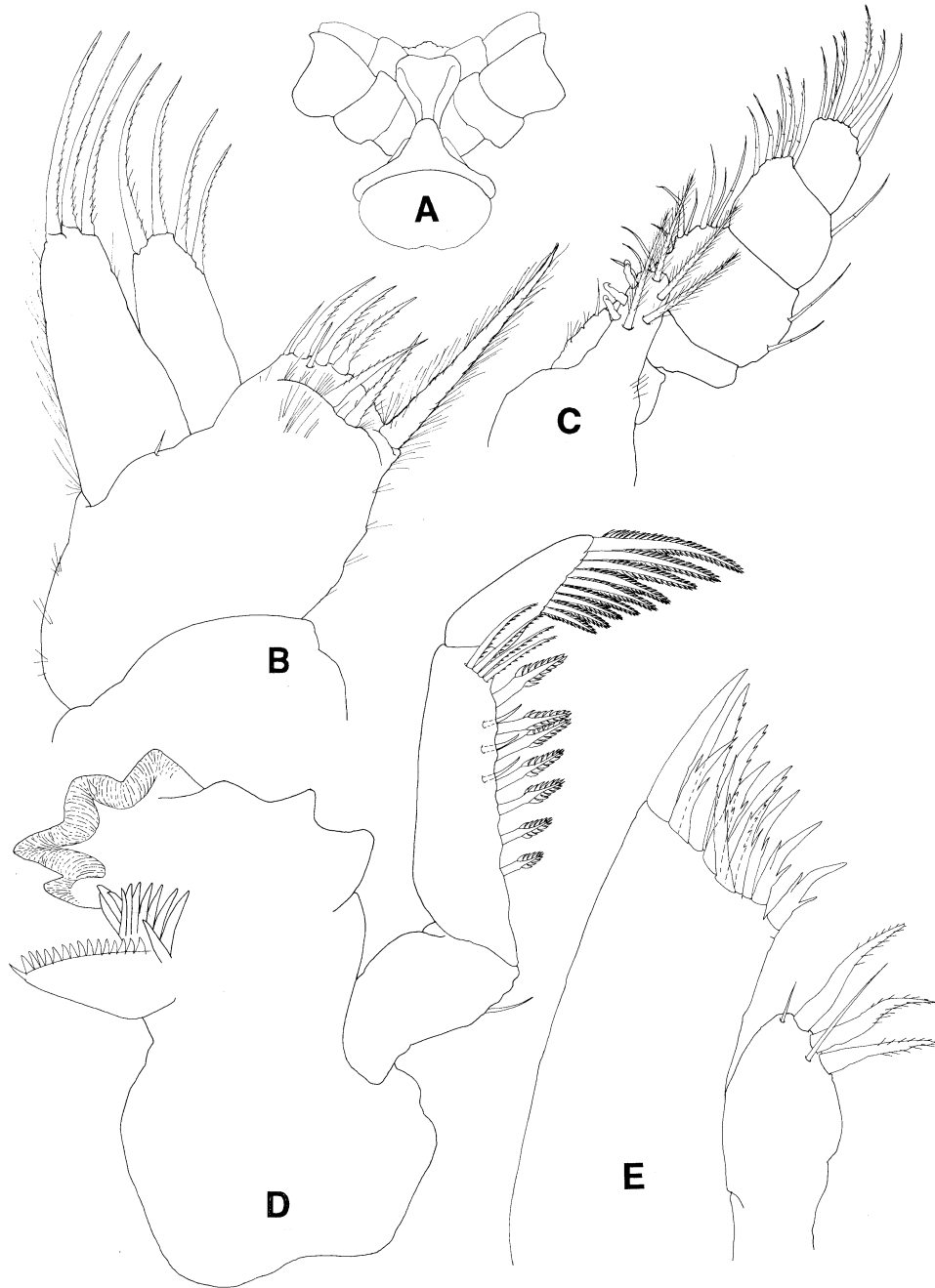


FIG. 12. *Colopisthus cavalier*, female: (A) frontal lamina, clypeus, labrum, holotype; (B) maxilla 2; (C) right maxilliped, holotype; (D) right mandible, holotype; (E) maxilla 1.

angle. Merus with cuticular tubercles on inferior margin, P-2 and P-3 with two molariform setae and a cluster of stout setae on distal angles; distal margin deeply incised (notched) on anterior surface. Carpus subtriangular, inferior margin much longer than superior margin; with cluster of stout setae on inferior distal angle; P-1

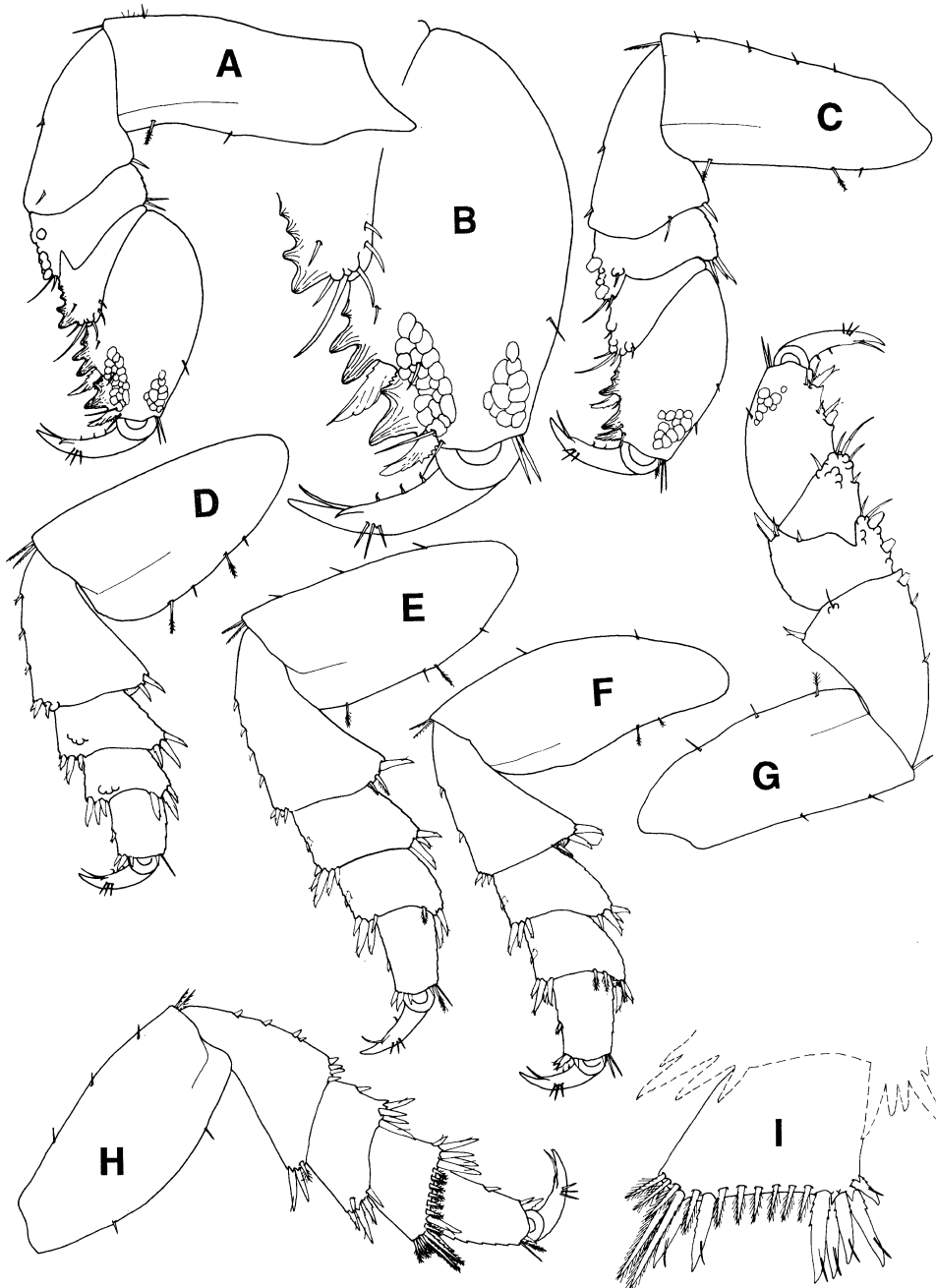


FIG. 13. *Colopisthus cavalier*, female holotype: (A, B) right pereopod 1; (C) right pereopod 2; (D) right pereopod 4; (E) right pereopod 5; (F) right pereopod 6; (G) right pereopod 3; (H) left pereopod 7; (I) left pereopod 7 carpus.

with four connate spines on inferior margin; P-2 and P-3 with three to five cuticular tubercles on inferior margin. Propodus with complex setae and connate spines on inferior margin as figured; P-1 and P-2 with two complex setae and four or five

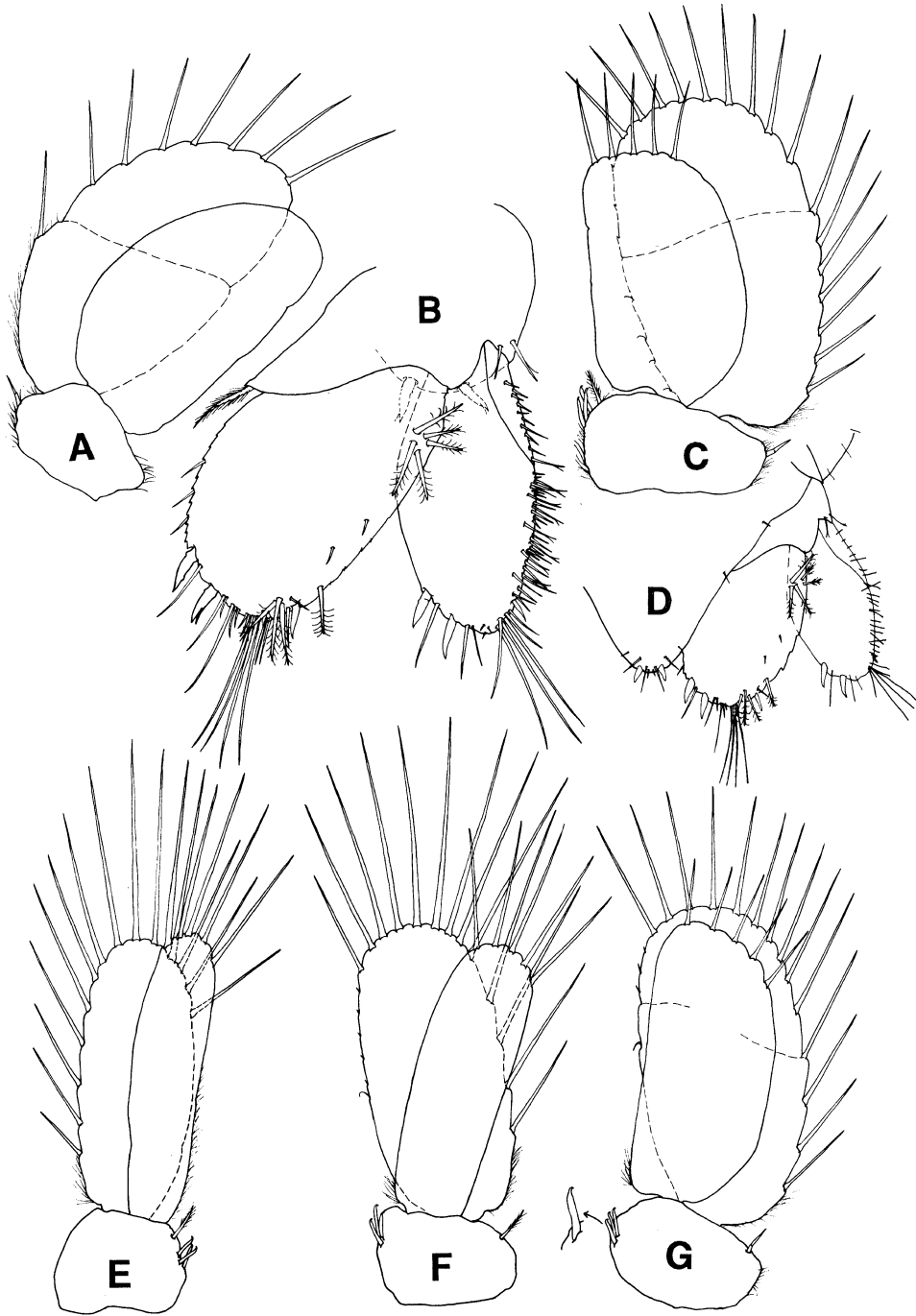


FIG. 14. *Colopisthus cavalier*, female holotype: (A) left pleopod 5; (B) right uropod; (C) left pleopod 4; (D) telson-uropod; (E) right pleopod 1; (F) right pleopod 2; (G) right pleopod 3.

connate spines; P-3 with two complex setae and no connate spines; P-1 to P-3 superior distal angle with two slender setae, P-2 also with a biplumose seta.

Pereopods 4–7. Basis with two biplumose setae at inferior distal angle. Ischium with two to four clusters of stout setae on inferior margin; P-4 with cuticular tubercles on inferior distal angle; P-5 and P-7 with two or three robust setae at superior-distal angle. Carpus of P-5 with one biplumose seta on anterior-distal margin, P-6 with two biplumose setae on anterior-distal margin and one biplumose seta on superior-distal angle, P-7 with seven biplumose setae on anterior-distal margin and approximately five long biplumose setae at superior-distal angle. Propodus superior-distal angle with stout and biplumose setae; P-4 to P-6 posterior-distal margin with one stout seta; inferior distal angle with two stout setae on P-4 and P-5 and one stout seta and one reduced complex seta on P-6 and P-7.

Pleopods. Pl-1 to Pl-4 peduncle with three coupling setae on medial margin. Pl-3 to Pl-5 lateral margin of peduncle with one stout seta. Pl-3 exopod with partial transverse suture, Pl-4 and Pl-5 exopod with complete transverse suture. Pl-1 to Pl-5 exopods with fine setae on proximo-lateral angle. Pl-1 to Pl-3 endopods with fine setae on proximo-medial angle. Pl-1 to Pl-4 endopods with approximately five PMS; exopods with approximately 13–16 PMS. Pl-5 endopod subovate, without setation; exopod with approximately eight PMS.

Uropod. Endopod with slender and palmate setae; two robust setae on medial margin and one robust seta on lateral margin; apex broadly rounded, with approximately four long slender setae. Exopod with slender setae and two robust setae on medial margin; apex rounded, with approximately three long slender setae; lateral margin with a continuous row of short slender setae; proximal lateral margin with dorsal fold.

Distribution

So far known only from Spanish Point, Barbuda, where it was collected from intertidal beach wrack and live *Porites* (a scleractinian coral).

Remarks

Known only from females.

Etymology

This species is named after Cavalier rum, a light golden rum of the islands of Barbuda and Antigua.

***Colopisthus parvus* Richardson, 1902**

(figures 15–22)

Colopisthus parvus Richardson, 1902: 289, pl. XXXVIII, figures 33–36; Richardson 1905: 137, figure 119; Kensley and Schotte, 1989: 147, figure 66A; Kensley, 1994: 319.
Not *Colopisthus parvus*. Monod, 1952; Menzies and Glynn, 1968; Müller, 1993: figures 72–96.

Type material examined. (1) Syntypes (co-types), females (USNM 24867, Acc. No. 37555): Bermuda, Bailey Bay, low water in coralline algae; Yale University Expedition 1898; collected by A. E. Verrill.

Other material examined. (2) YPM 3338; Bermuda; collected by A. E. Verrill; one female specimen. (3) YPM 3341; Bermuda, St George's Parish, Castle Harbor, Waterloo; A. E. Verrill Bermuda Expedition 1901; one male specimen. The following

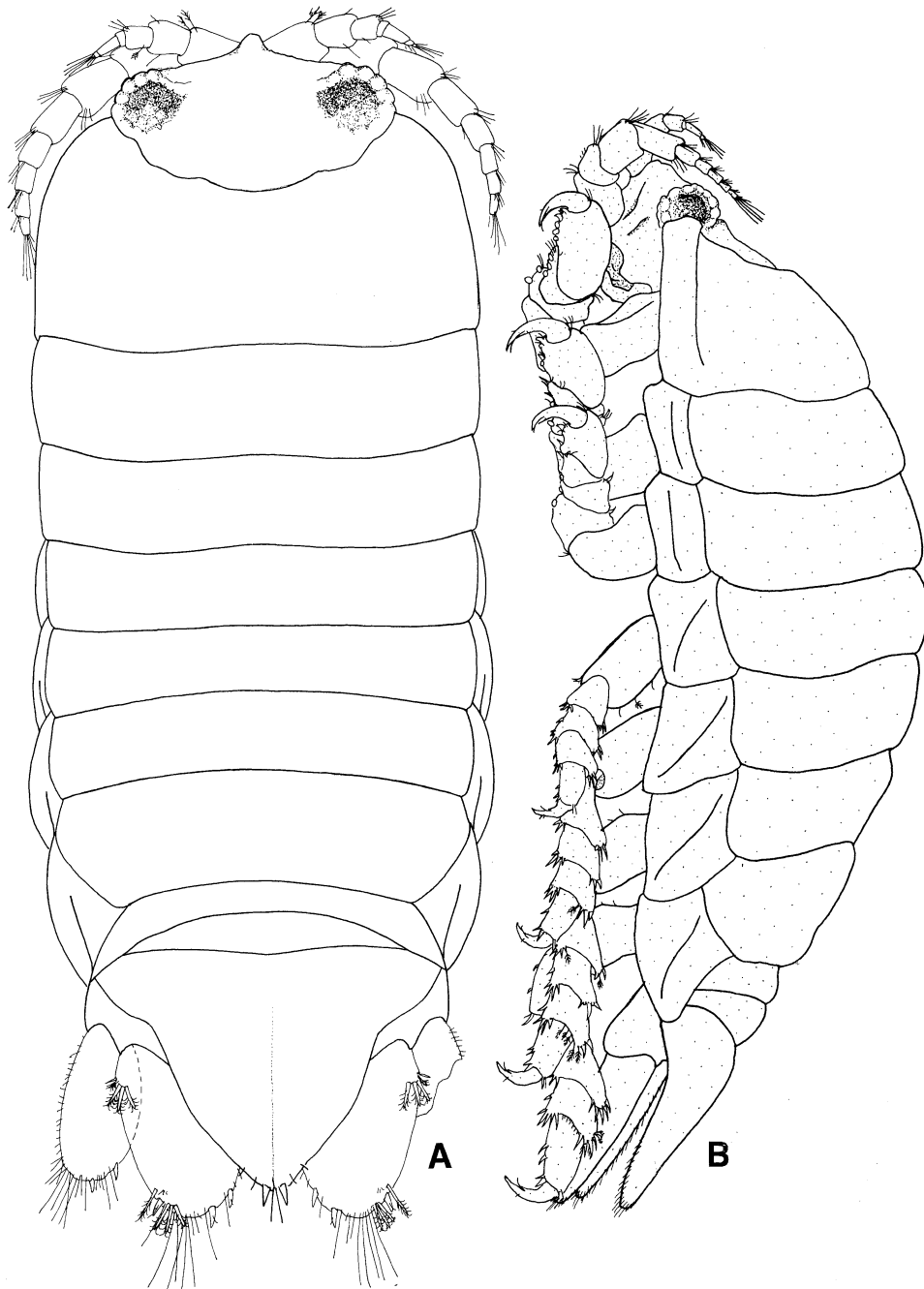


FIG. 15. *Colopisthus parvus*, female syntype: (A) dorsal aspect; (B) lateral aspect.

voucher specimens from Kensley (1994). (4) YPM 9574; Bermuda, Devonshire Bay; 1985, collected by M. F. Gable; one female and one juvenile specimen. (5) YPM 9684; Bermuda, Devonshire Bay, 0.3 m depth; 1988; collected by E. A. Lazo-Wasem; 18 female, five male and 12 juvenile specimens. (6) YPM 9685; Bermuda, St George's

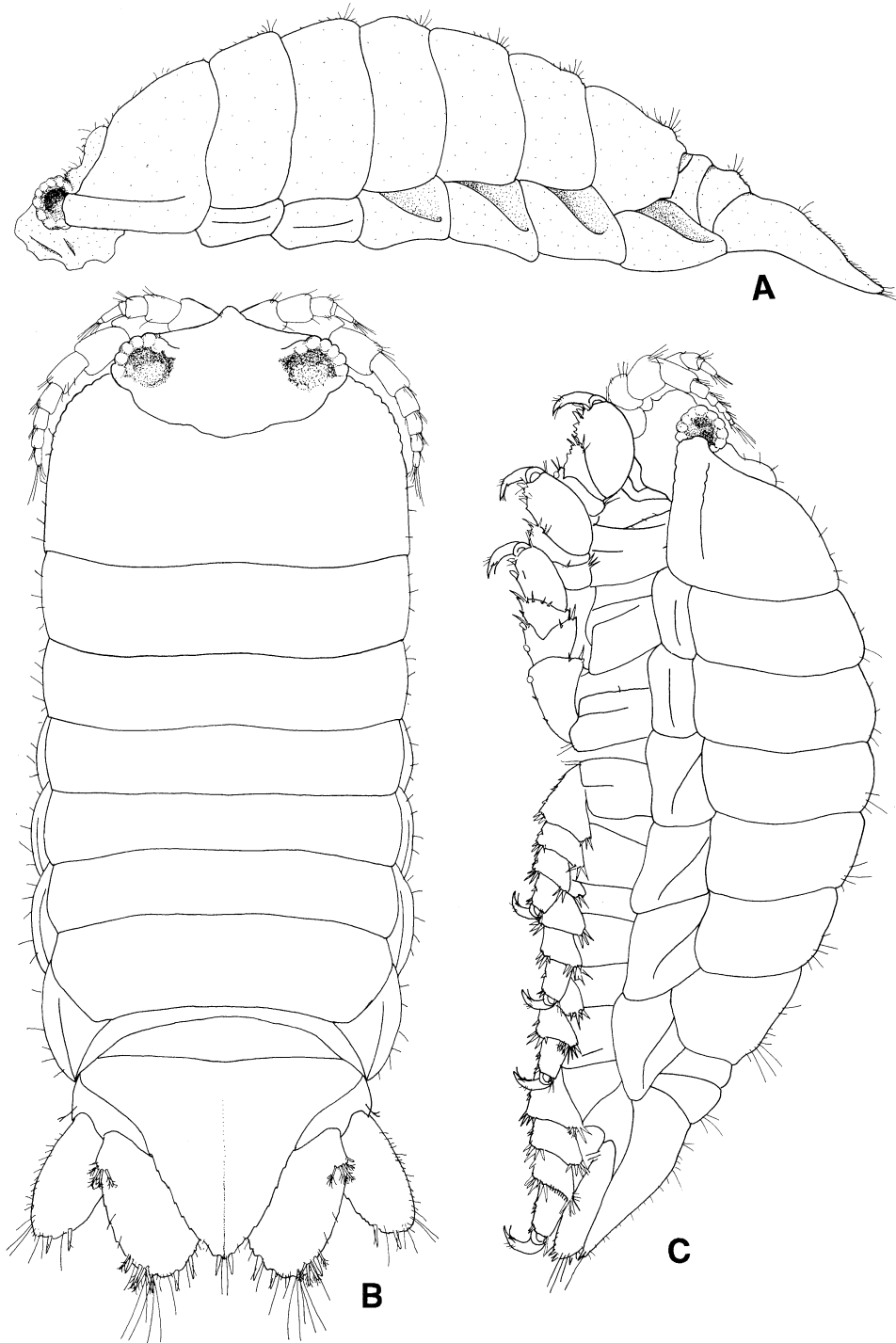


FIG. 16. *Colopisthus parvus*: (A) lateral aspect, male; (B) dorsal aspect, female; (C) lateral aspect, female.

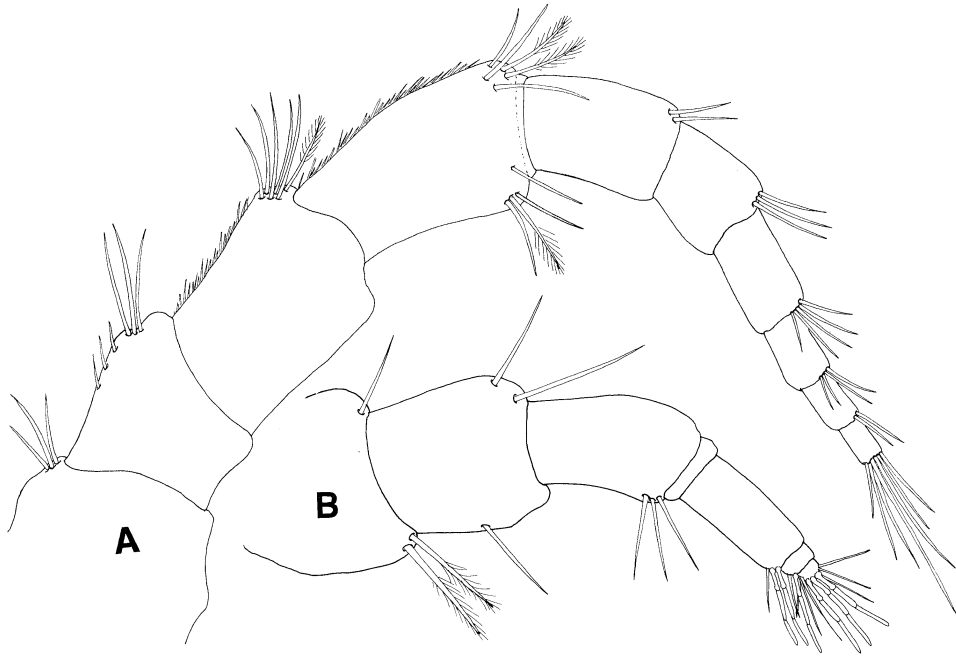


FIG. 17. *Colopisthus parvus*, female syntype: (A) antenna 2; (B) antenna 1.

Parish; 1988, collected by E. A. Lazo-Wasem and J. Hamilton; one male specimen. (7) YPM 9632; Bermuda, Hamilton Parish, Shelly Bay, 0.3 m depth; 1987, collected by M. F. Gable; three female specimens.

Diagnosis. Pleon of female with two free pleonites; males with three free pleonites. Lateral margins of pereonite 1 without crenulations or with weak crenulations. Antenna 1 flagellum three-articulate. Antennae 2 flagellum six-articulate. Maxilliped endite with five circumplumose setae and two coupling setae. Merus of P-1 to P-3 with two or three molariform setae on inferior margin. Carpus of P-5 with one biplumose seta on anterior-distal margin, P-6 with three biplumose setae on anterior-distal margin, P-7 with 10 biplumose setae on anterior-distal margin. Pl-3 exopod with partial transverse suture.

Description of female

Antennae. Antenna 1 peduncular article 1 with slender and palmate setae; articles 2–3 with slender setae only; article 3 longest and narrowest; article 4 without setae; flagellum three-articulate, first article much longer than distal two articles, all flagellar articles with slender setae and jointed aesthetascs. Antennae 2 peduncular article 1 minute, articles 2 and 3 with slender setae, articles 4 and 5 with biplumose and slender setae on distal margin; flagellum six-articulate, all with clusters of slender setae in the anterior-distal region.

Maxilliped. Endite with five circumplumose setae and two coupling setae. Palp article 1 medial margin with fine and slender setae; article 2 lateral margin with slender setae and medial margin with fine and slender setae; articles 3 and 4 with slender setae on lateral and medial margins, article 4 with one uniserrate seta on

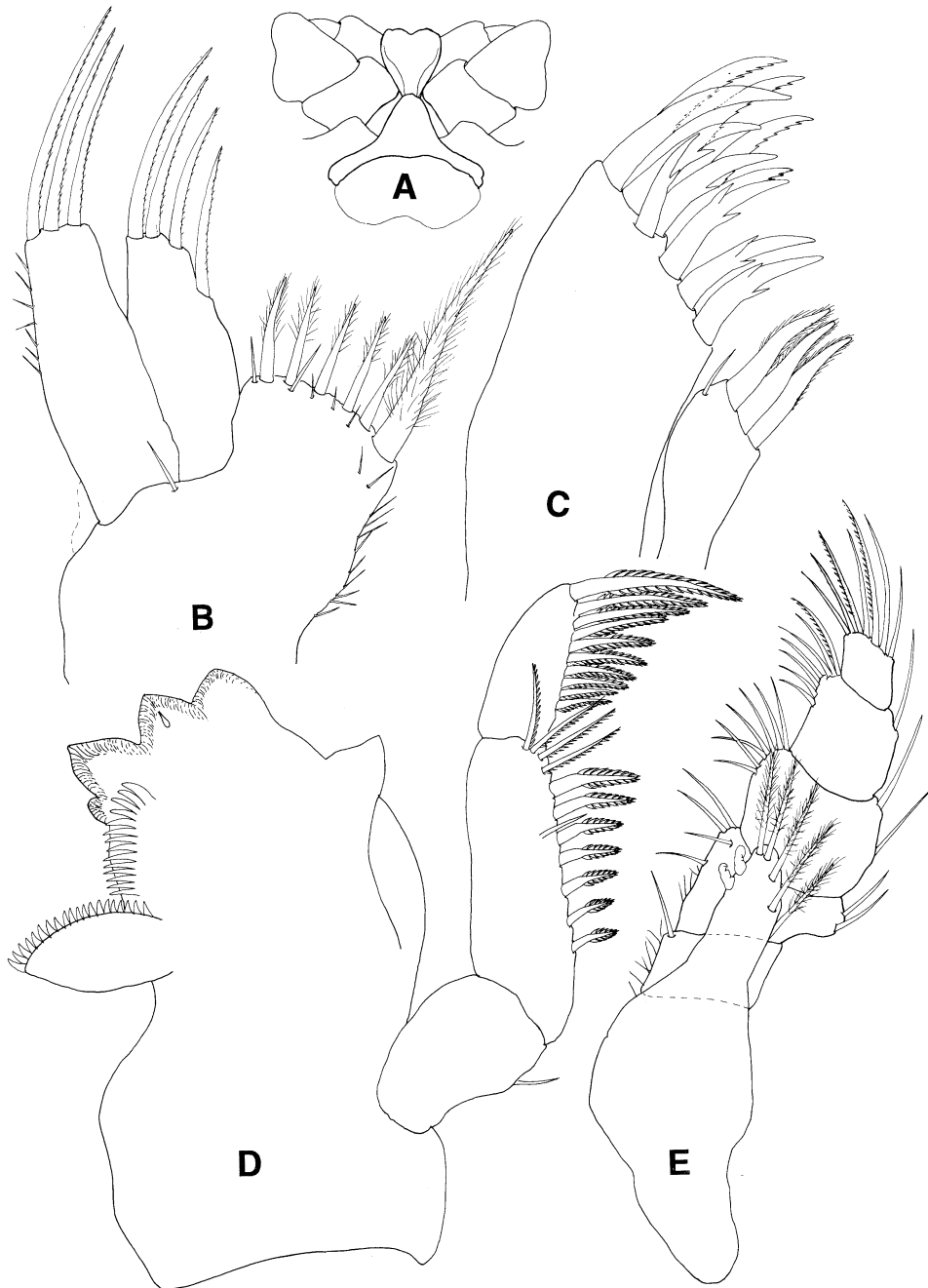


FIG. 18. *Colopisthus parvus*: (A) frontal lamina, clypeus, labrum, male; (B) maxilla 2, female syntype; (C) maxilla 1, female syntype; (D) right mandible, female syntype; (E) right maxilliped, female syntype.

distal medial angle; terminal article subquadrate, with slender and uniserrate apical setae.

Maxillae. Maxilla 1 lateral lobe with one stout, six forked and four uniserrate

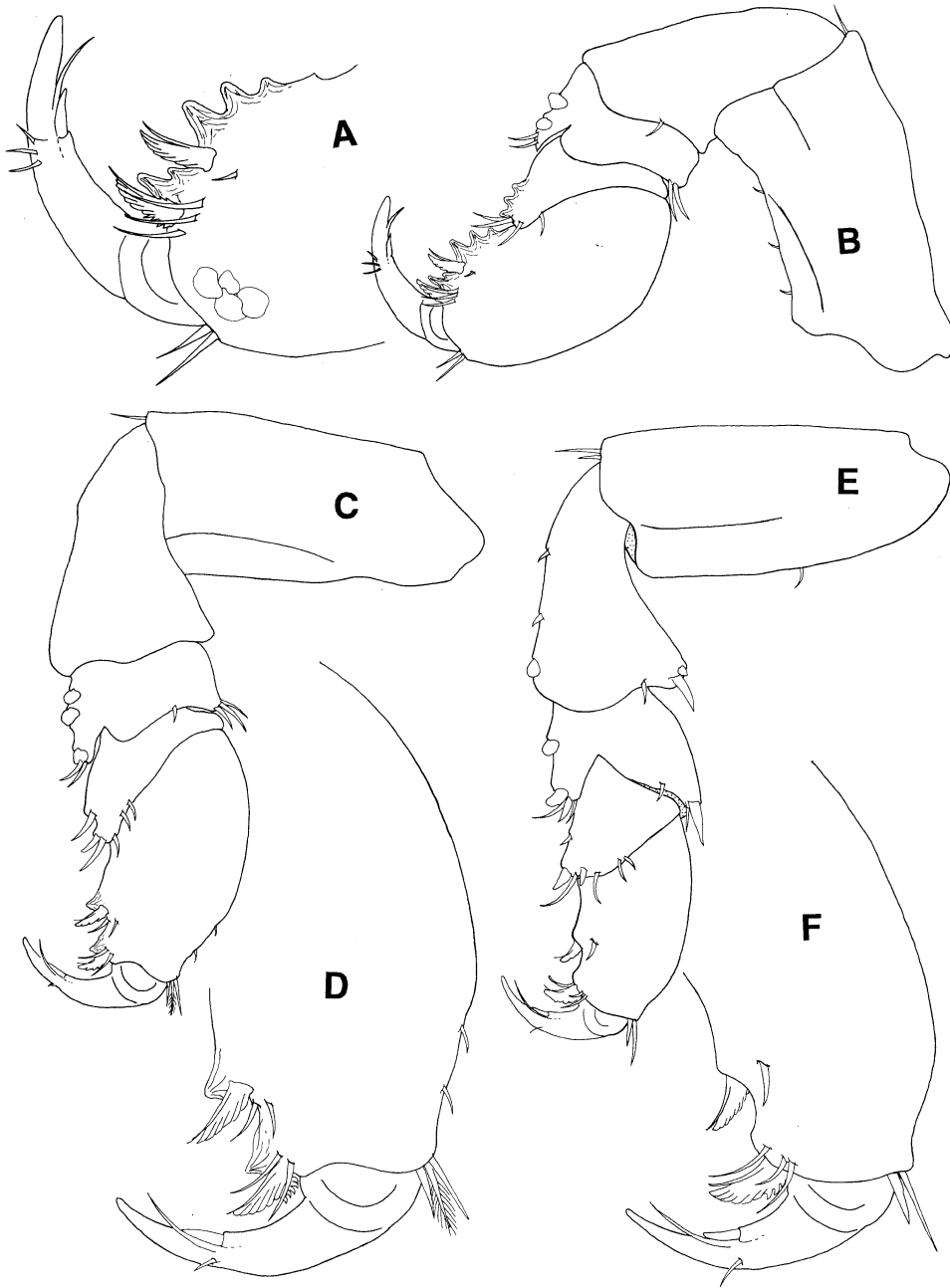


FIG. 19. *Colopisthus parvus*, female syntype: (A, B) right pereopod 1; (C, D) right pereopod 2; (E, F) right pereopod 3.

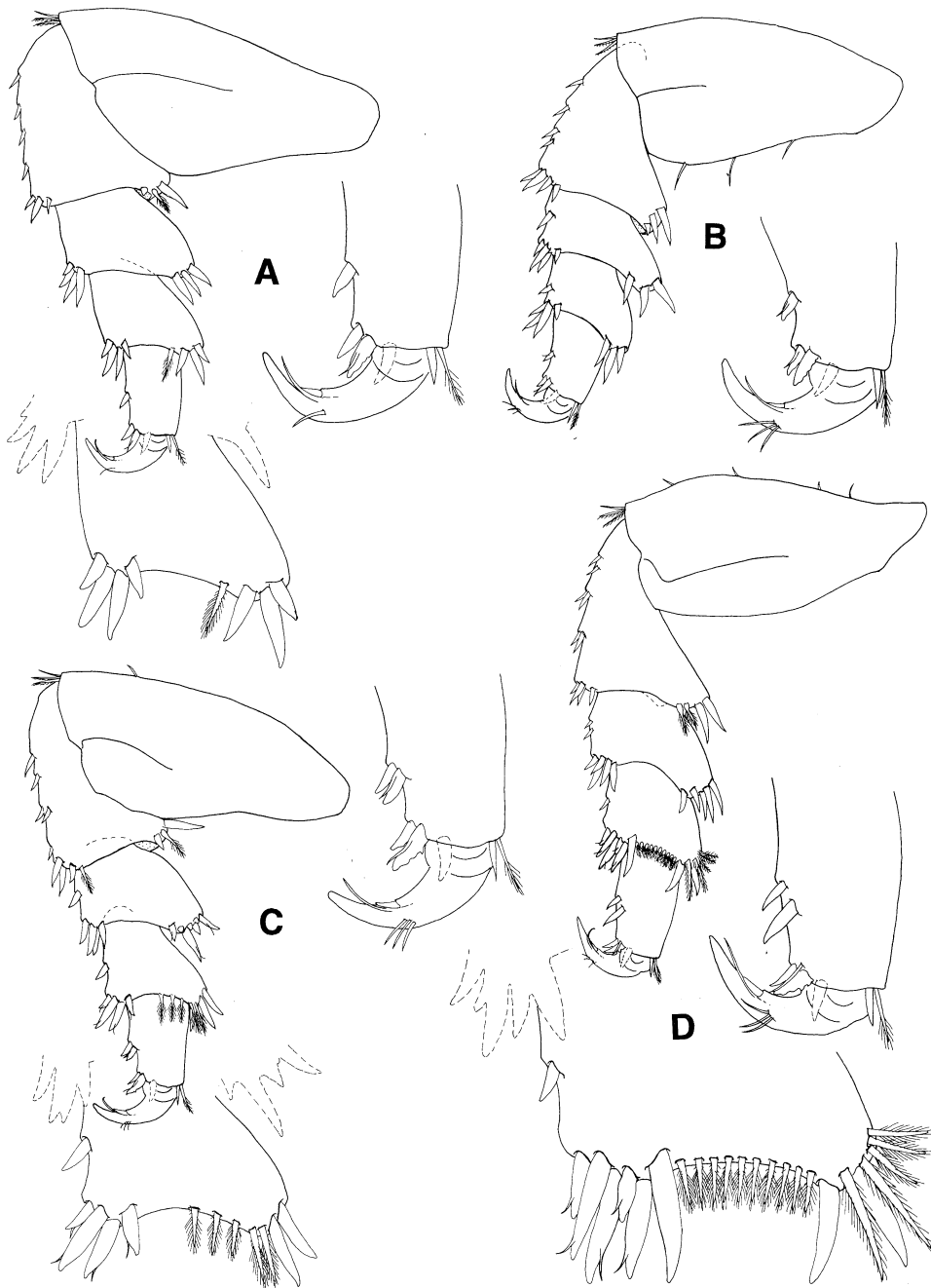


FIG. 20. *Colopisthus parvus*, female syntype: (A) right pereopod 5 with details of propodus and carpus; (B) right pereopod 4 with detail of propodus; (C) right pereopod 6 with details of propodus and carpus; (D) right pereopod 7 with details of propodus and carpus.

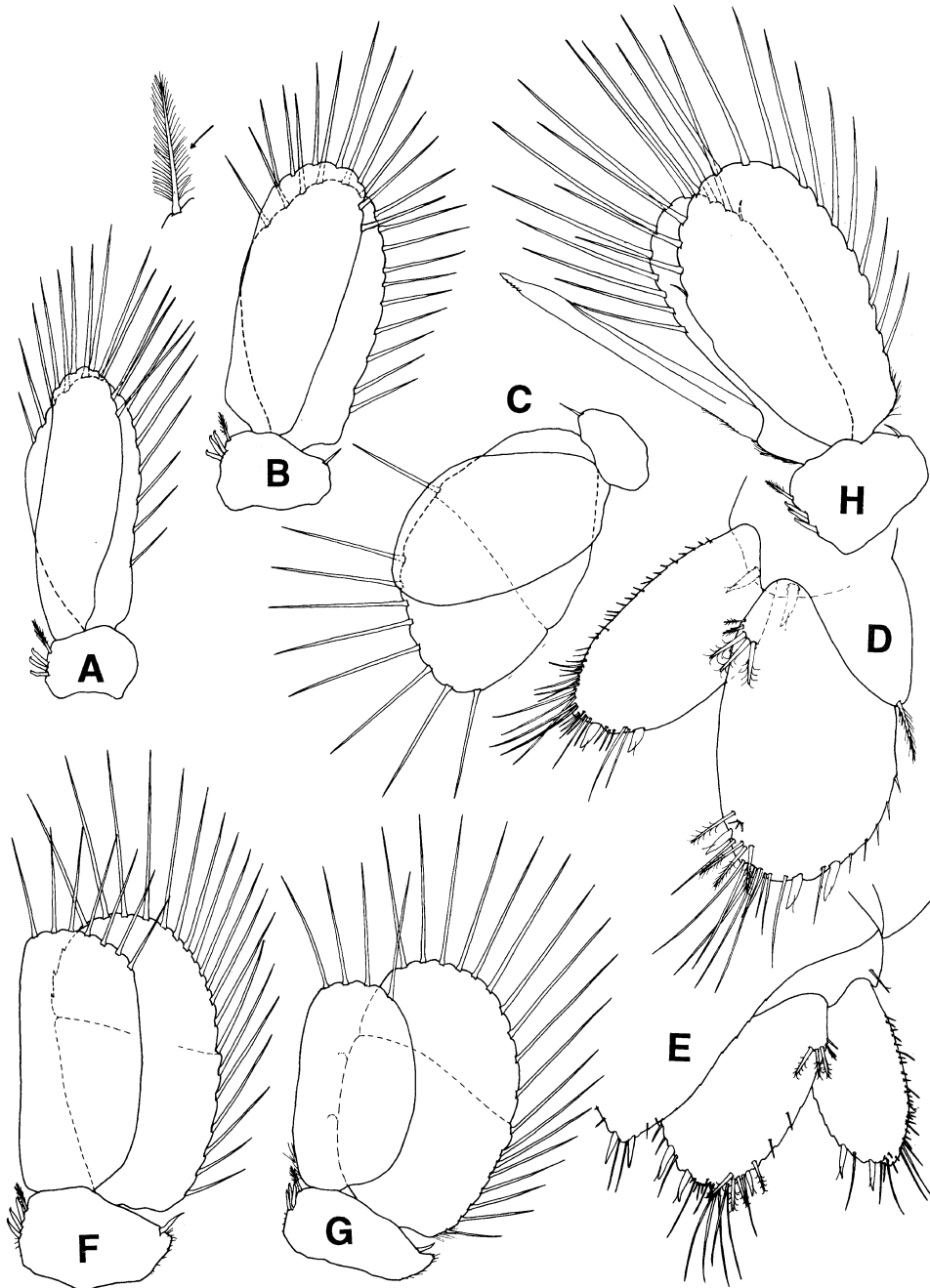


FIG. 21. *Colopisthus parvus*: (A) left pleopod 1, female syntype; (B) left pleopod 2, female syntype; (C) right pleopod 5, female syntype; (D) left uropod, female syntype; (E) telson-uropod, female; (F) left pleopod 3, male; (G) right pleopod 4, male; (H) right pleopod 2, male.

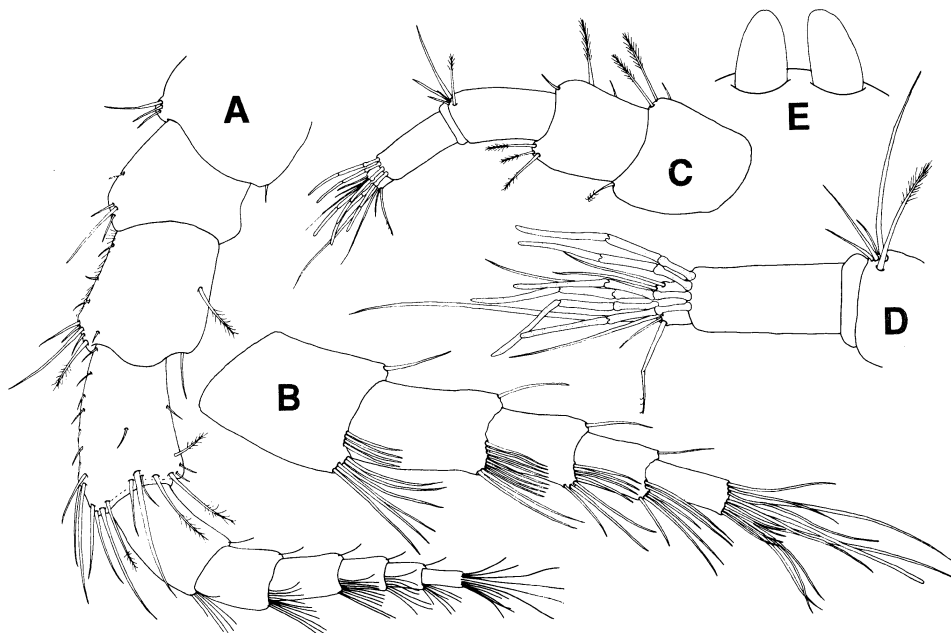


FIG. 22. *Colopisthus parvus*, male: (A) antennae 2; (B) antennae 2 flagellum; (C) antennae 1; (D) antennae 1 flagellum; (E) penes.

setae; medial lobe with one small slender and three stout biplumose setae. Maxilla 2 outer lobe with three uniserrate setae, fine setae on lateral margin; medial lobe with four uniserrate setae; gnathal lobe with one slender seta at base (below outer lobe), fine setae on medial margin; apical margin with one large circumplumose, five stout biplumose and slender setae.

Mandible. Spine row with 14 large spines; molar process with approximately 20 small acute marginal spines; proximal palp article with one slender seta on lateral margin; middle article with one slender, seven biserrate and four unequally biserrate setae; distal article with 10 biserrate setae.

Pereopods 1–3. Ischium on P-1 and P-2 without setae on inferior margin; P-3 with stout setae on inferior margin and superior-distal angle, molariform seta near inferior-distal angle. Merus with two or three molariform setae on inferior margin and clusters of stout setae on distal angles; distal margin deeply incised (notched) on anterior surface. Carpus subtriangular, inferior margin much longer than superior margin; with cluster of stout setae on inferior distal angle; P-1 with three connate spines on inferior margin. Propodus with complex setae and connate spines on inferior margin as figured; P-1 with two complex setae and four or five connate spines; P-2 with two complex setae and two connate spines, P-3 with two complex setae and no connate spines.

Pereopods 4–7. Basis with slender and biplumose setae at inferior-distal angle. Ischium with three or four clusters of stout setae on inferior margin; P-5 to P-7 with one or two biplumose setae at superior-distal angle. Carpus of P-5 with one biplumose seta on anterior-distal margin, P-6 with three biplumose setae on anterior-distal margin and approximately two long biplumose setae at superior-distal angle, P-7 with 10 biplumose setae on anterior-distal margin and approximately five long

biplumose setae at superior-distal angle. Propodus inferior distal angle with one stout and one reduced complex seta; posterior-distal margin with one stout seta; superior-distal angle with one stout and one biplumose seta.

Pleopods. Pl-1 to Pl-4 peduncle with one biplumose and three coupling setae on medial margin. Pl-2 to Pl-5 lateral margin of peduncle with one stout seta. Pl-3 exopod with partial transverse suture, Pl-4 to Pl-5 exopod with complete transverse suture. Pl-1 to Pl-3 endopods with approximately six or seven PMS; exopods with approximately 14–19 PMS. Pl-4 endopod with approximately four PMS; exopod with approximately 21 PMS. Pl-5 endopod subovate, without setation; exopod with approximately eight PMS.

Uropod. Endopod with two robust setae on medial margin and one robust seta on lateral margin; apex broadly rounded, with approximately five long slender setae. Exopod with slender setae and two robust setae on medial margin; apex rounded, with approximately five long slender setae; lateral margin with a continuous row of short slender setae.

Description of male

As described for female except for the following. Pleon with three free pleonites. Antennae 1 peduncular article 2 with palmate setae; flagellum composed of two articles, a long proximal article with four jointed aesthetascs; distal article short with two aesthetascs, one biplumose and six slender setae. Antennae 2 peduncular articles 2–5 with slender setae, articles 4 and 5 with biplumose setae; flagellum six-articulate, all articles with clusters of slender setae in the anterior-distal region. Coxae 4–7 concave.

Distribution

This species is widely distributed in the intertidal areas of Bermuda. So far it has been collected from Bailey Bay, Devonshire Bay, Castle Harbor in St George's Parish, and Shelly Bay in Hamilton Parish.

***Colopisthus ronrico* new species**

(figures 23–27)

Synonymy. *Colopisthus parvus* Menzies and Glynn, 1968: 41, figures 16, 17 (misidentification; not *C. parvus*: Richardson, 1902).

Type material examined. (1) HOLOTYPE, male (USNM 285286) and two female paratypes (USNM 285287): Puerto Rico, north coast; exact collection locality and collector unknown; donated by Ernst Williams. (2) Paratype, female (USNM 128315): Puerto Rico, Arecibo, intertidal, collected by Menzies and Glynn.

Diagnosis. Lateral margins of cephalon and pereonite 1 with crenulations. Coxae 4–7 visible dorsally. Pleon with one free pleonite and two fused pleonites. Antenna 1 flagellum two-articulate. Antennae 2 flagellum five-articulate in females, six-articulate in males. Maxilliped palp articles 2 and 3 partially fused. Maxilliped endite with four circumplumose setae and one coupling seta. Mandible spine row with eight large spines. Carpus of P-5 with one biplumose seta on anterior-distal margin; P-6 with two biplumose setae on anterior-distal margin; P-7 with four biplumose setae on anterior-distal margin. Pl-3 exopod with complete transverse suture.

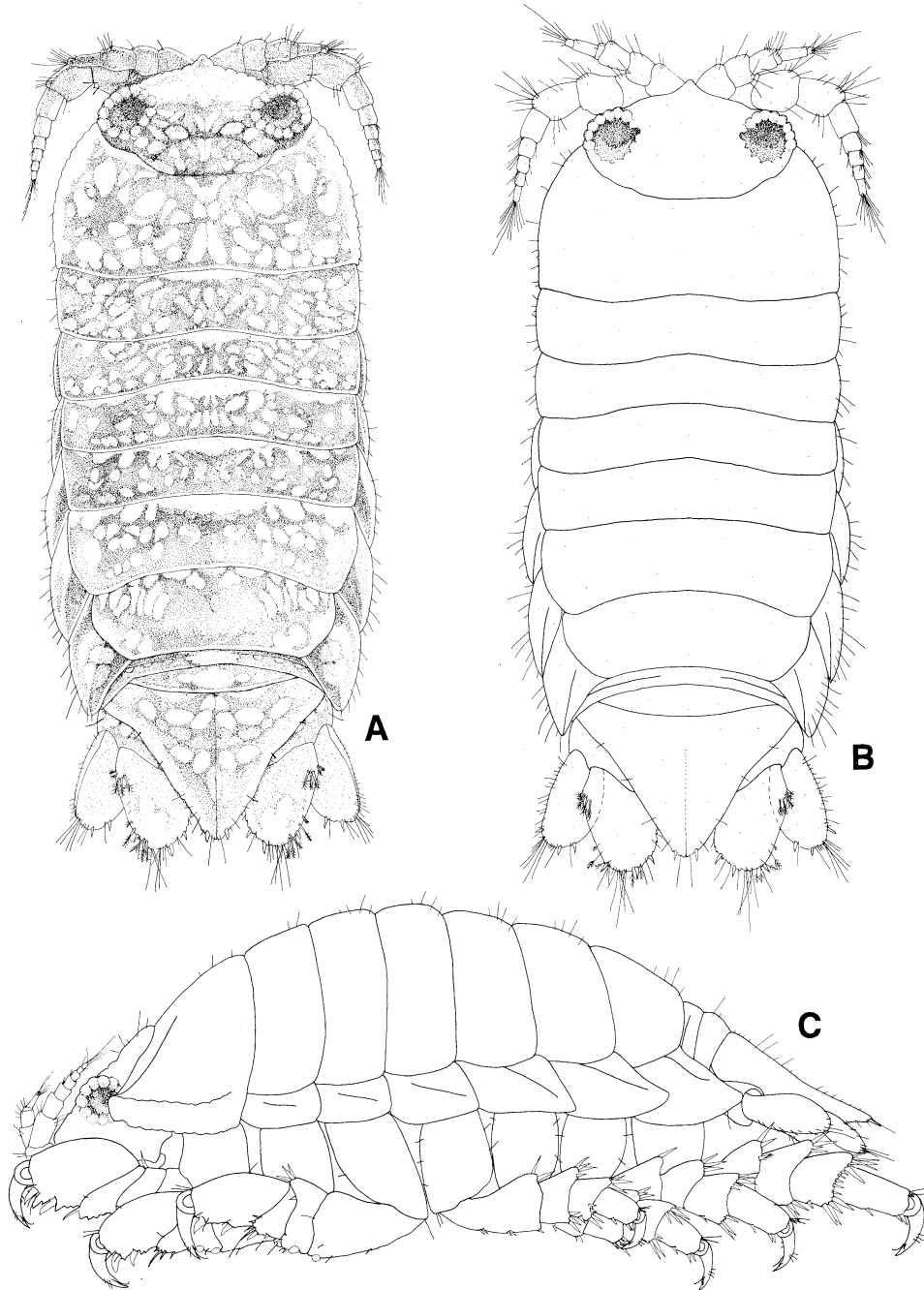


FIG. 23. *Colopisthus ronrico*: (A) dorsal aspect, male holotype; (B) dorsal aspect, female; (C) lateral aspect, female.

Description of female

Head. Lateral margins of cephalon and pereonite 1 with crenulations. Crenulations are weak on female (visible in lateral view).

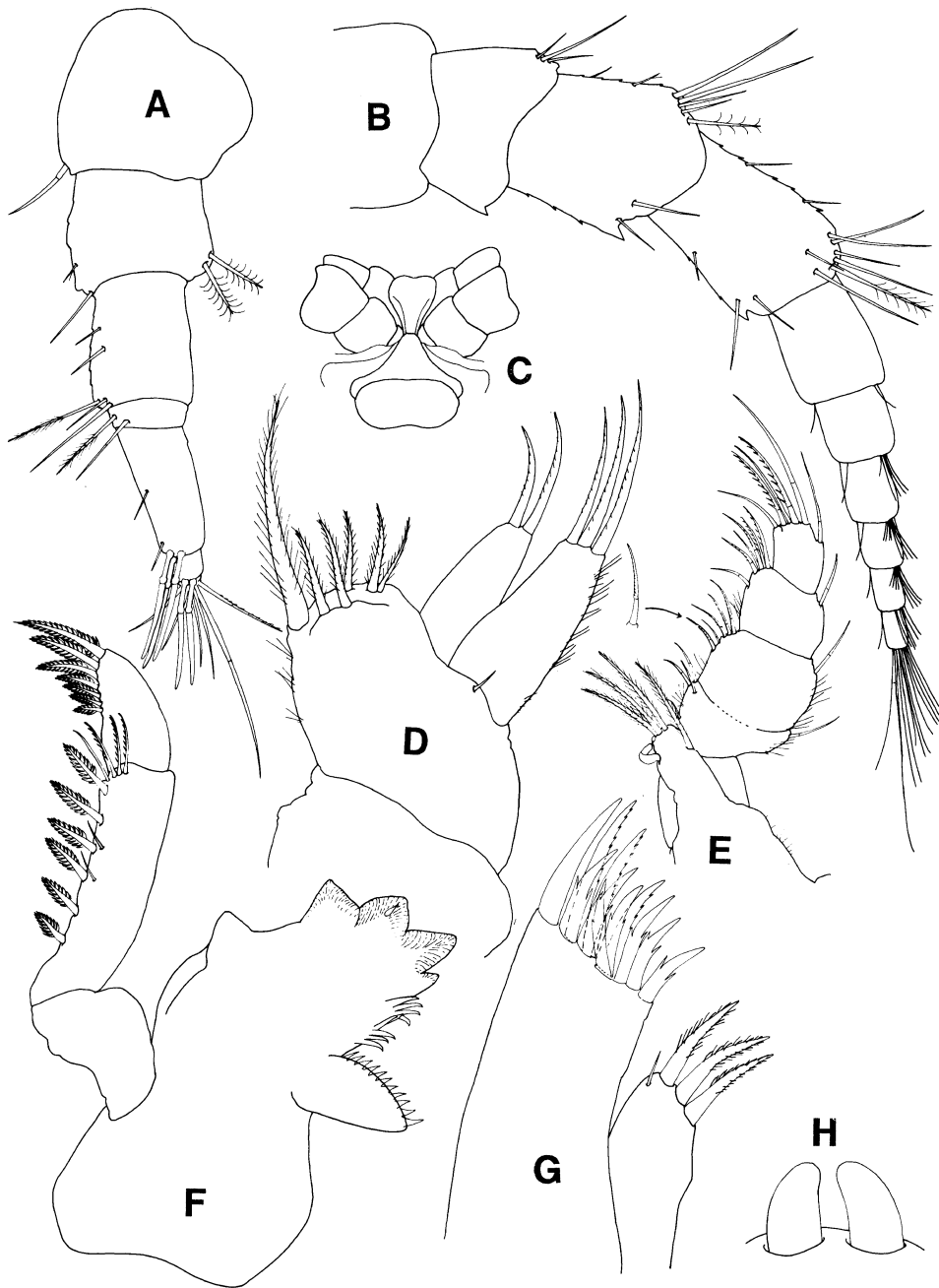


FIG. 24. *Colopisthus ronrico*, male holotype: (A) antenna 1; (B) antenna 2; (C) frontal lamina, clypeus, labrum; (D) maxilla 2; (E) right maxilliped; (F) right mandible; (G) maxilla 1; (H) penes.

Antennae. Both antennae with visible shingle sculpturing under light microscope. Antenna 1 peduncular articles 1–4 with slender and biplumose setae; flagellum two-articulate, first article much longer than distal article; both articles with slender

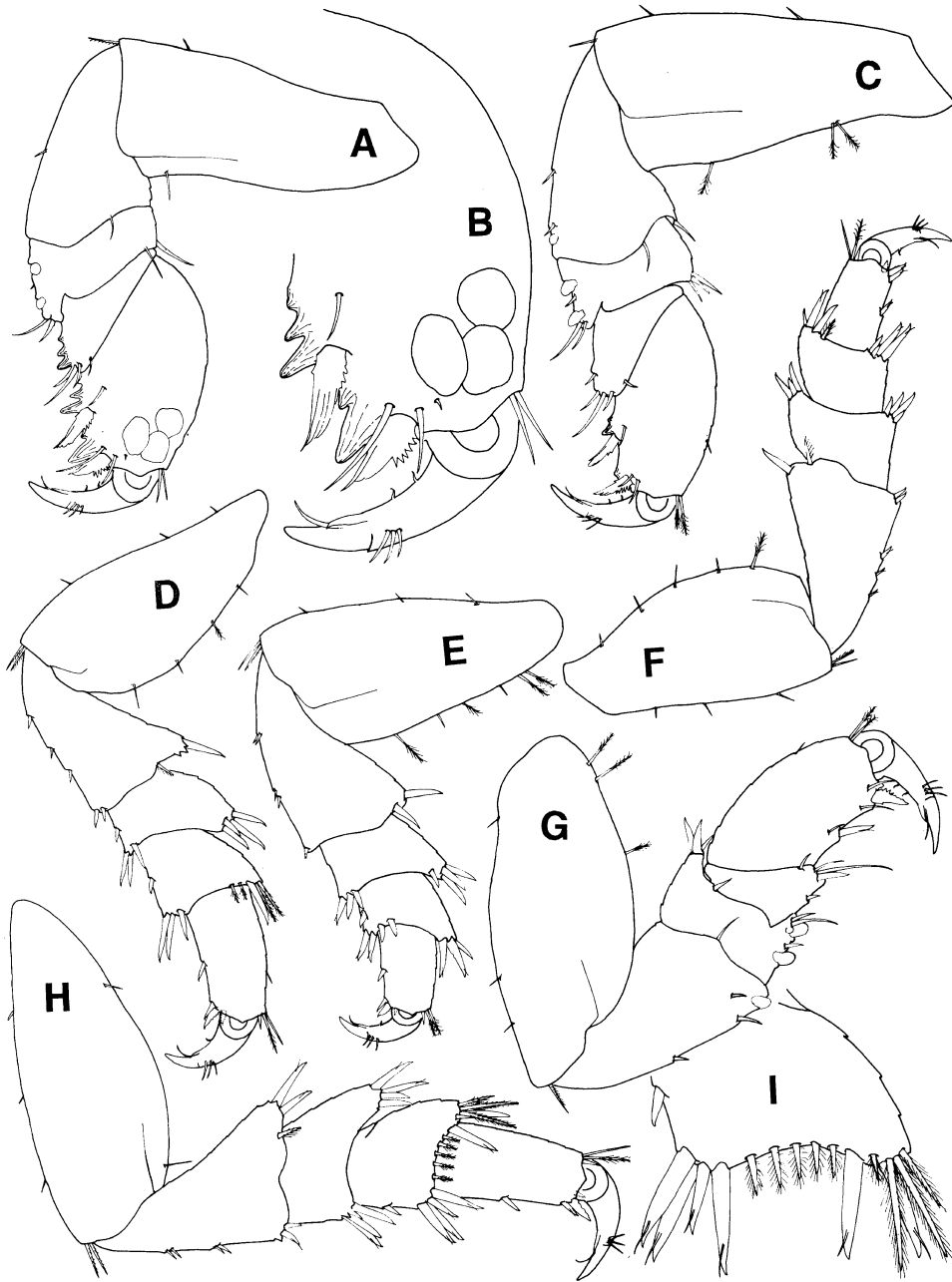


FIG. 25. *Colopisthus ronrico*, male holotype: (A, B) right pereopod 1; (C) right pereopod 2; (D) right pereopod 6; (E) right pereopod 4; (F) right pereopod 5; (G) right pereopod 3; (H) right pereopod 7; (I) right pereopod 7 carpus.

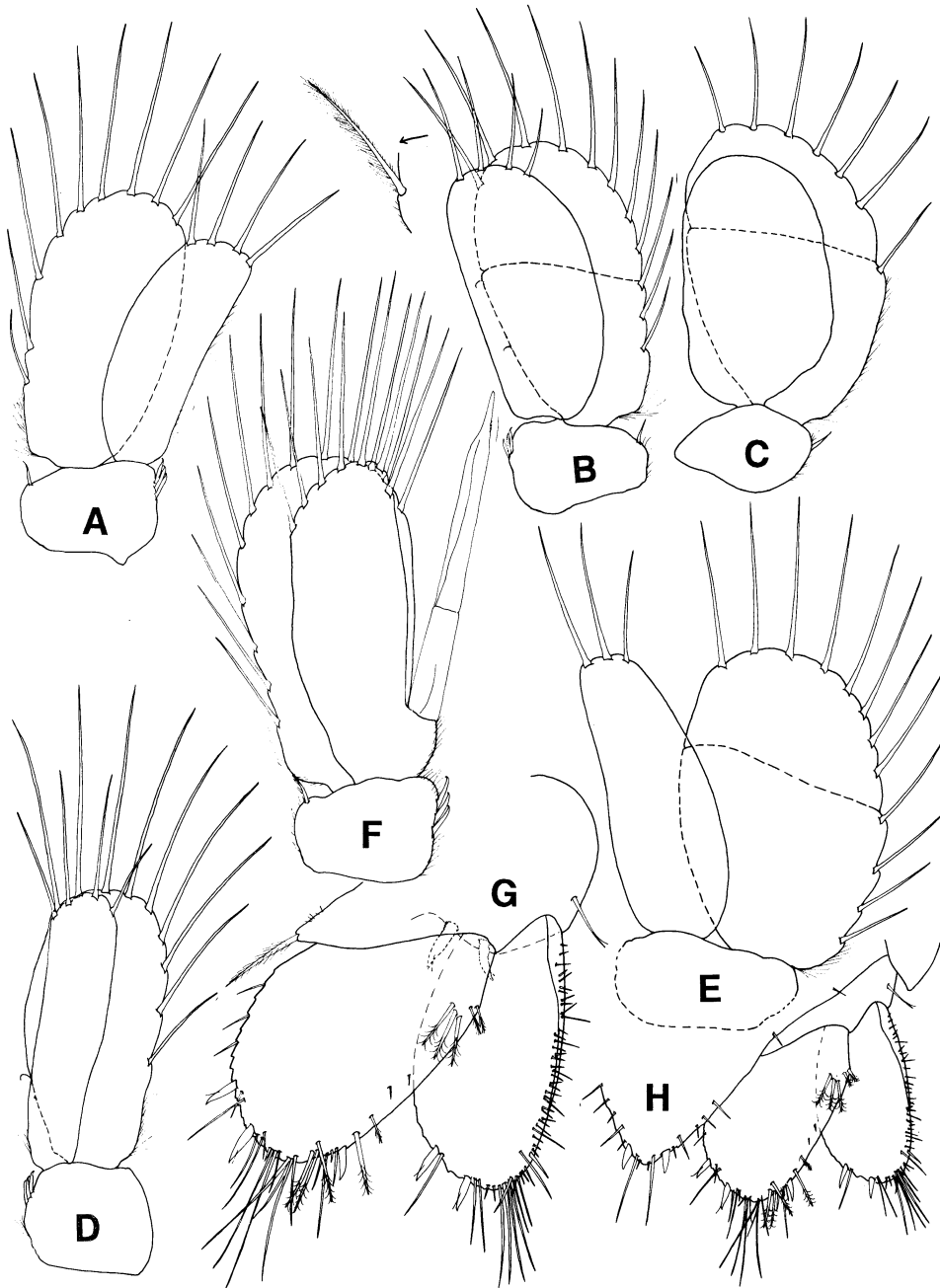


FIG. 26. *Colopisthus ronrico*: (A) right pleopod 2, female; (B) right pleopod 3, female; (C) right pleopod 5, female; (D) right pleopod 1, female; (E) right pleopod 4, female; (F) left pleopod 2, male holotype; (G) right uropod, male holotype; (H) telson-uropod, male holotype.

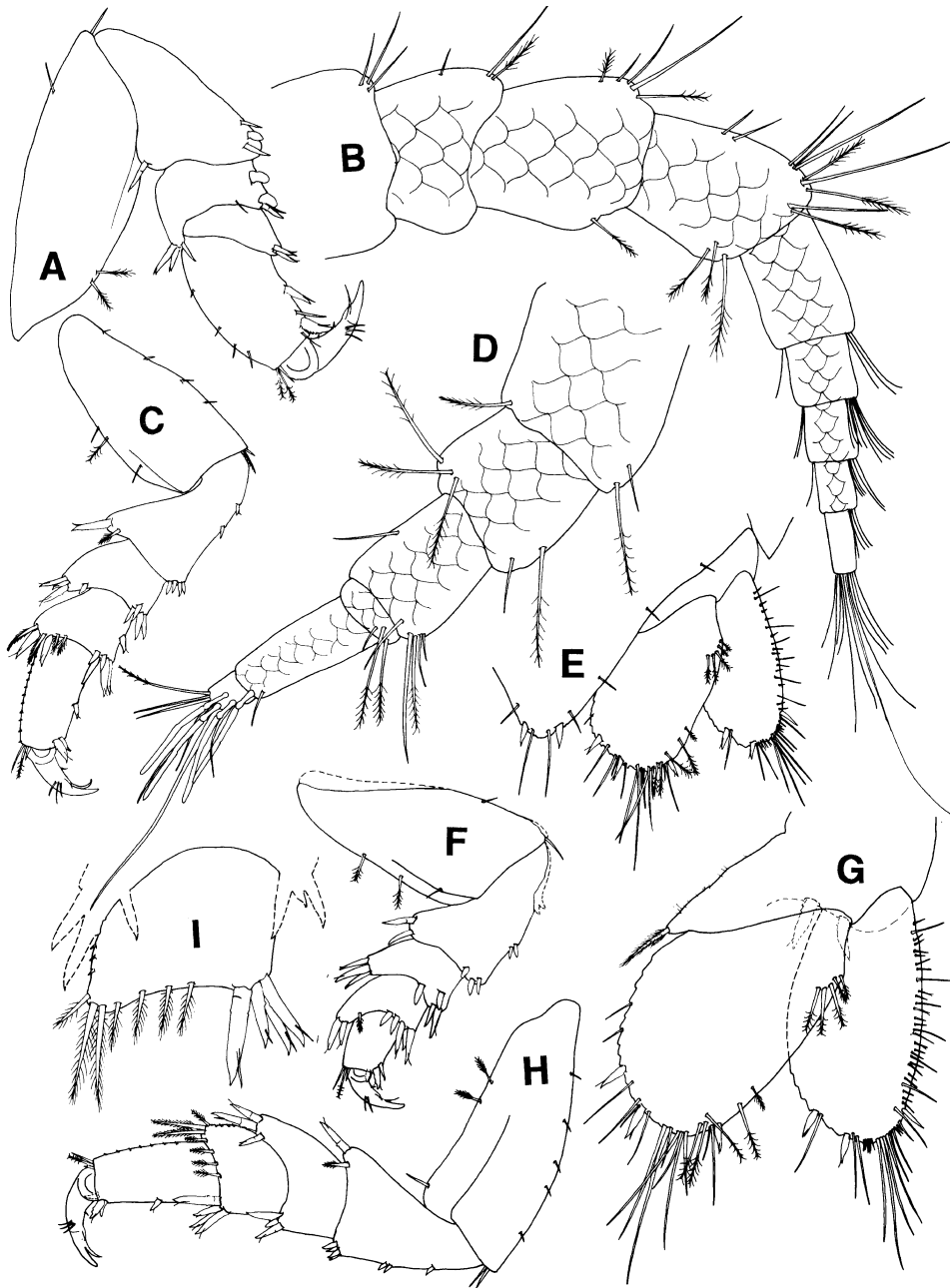


FIG. 27. *Colopisthus ronrico*, female: (A) right pereopod 3; (B) antenna 2; (C) left pereopod 6; (D) antenna 1; (E) telson-uropod; (F) right pereopod 4; (G) right uropod; (H) right pereopod 7; (I) right pereopod 7 carpus.

setae and jointed aesthetascs. Antennae 2 peduncular articles 2–5 with slender and biplumose setae; flagellum five-articulate, all with cluster of slender setae in the anterior-distal region.

Mouthparts missing; previously dissected, presumably by Menzies and Glynn (1968).

Pereopods 1–3. Ischium with one or two stout setae on inferior margin and one stout seta near inferior-distal angle; P-3 with one molariform seta near inferior-distal angle. Merus with one or two molariform setae on inferior margin and a cluster of stout setae on inferior-distal and superior-distal angles. P-3 carpus subtriangular, inferior margin much longer than superior margin; with cluster of stout setae on inferior distal angle; propodus with two complex setae and no connate spines; superior distal angle with one slender seta and two biplumose setae. Pereopod 4 missing.

Pereopods 5–7. Ischium with two clusters of stout setae on inferior margin; P-6 and P-7 with biplumose seta at superior-distal angle. Carpus of P-5 with one biplumose seta on anterior-distal margin, P-6 with two biplumose setae on anterior-distal margin and approximately two long biplumose setae at superior-distal angle; P-7 with four biplumose setae on anterior-distal margin and approximately three long biplumose setae at superior-distal angle. Propodus inferior-distal angle with one stout and one reduced complex seta; posterior-distal margin with one stout seta; superior-distal angle with one stout, one slender and one biplumose seta.

Pleopods. Pl-1 to Pl-3 peduncle with three coupling setae on medial margin. Pl-2 to Pl-5 lateral margin of peduncle with one stout seta. Pl-3 to Pl-5 exopod with complete transverse suture. Pl-1 to Pl-4 endopod with approximately three to five PMS; exopod with approximately 9–12 PMS. Pl-5 endopod subovate, without setae; exopod with approximately seven PMS.

Uropod. Endopod with slender and palmate setae, two robust setae on medial margin and one robust seta on lateral margin; apex broadly rounded with approximately four long slender setae. Exopod with slender setae and two robust setae on medial margin and one robust seta on lateral margin; apex rounded, with approximately four long slender setae; lateral margin with a continuous row of short slender setae; proximal-lateral margin with dorsal fold.

Description of male

As described for female except as follows.

Coxae 3–7 visible dorsally. Crenulations on lateral margin of cephalon and pereonite 1 more pronounced than in female.

Antennae. Antenna 1 peduncular article 1 with one slender, jointed seta, peduncular articles 2–4 with slender and biplumose setae; flagellum three-articulate. Antennae 2 peduncular article 3 with slender setae only, articles 4 and 5 with biplumose and slender setae; flagellum six-articulate.

Maxilliped. Endite with four circumplumose setae and one coupling seta. Palp article 1 without setation; articles 2 and 3 partially fused, lateral and medial margins with fine and jointed, slender setae; article 4 with one jointed, slender seta on disto-lateral angle and four uniserrate and approximately two slender setae on distal medial angle; terminal article width and length subequal and with approximately five jointed slender and two uniserrate apical setae.

Maxillae. Maxilla 1 lateral lobe with one stout, seven forked and three uniserrate setae; medial lobe with one small plumose and three stout biplumose setae. Maxilla 2 outer lobe with three uniserrate and fine setae on lateral margin; medial lobe with two uniserrate setae; gnathal lobe with one slender seta at base (below outer lobe),

apical margin with one large circumplumose and five stout biplumose setae, fine setae on lateral margin.

Mandible. Spine row with eight large spines; molar process with approximately 11 small acute marginal spines; proximal palp article without setation; middle article with three slender, six biserrate and three unequally biserrate setae; distal article with seven biserrate setae.

Pereopods 1–3. P-2 ischium with molariform seta near inferior-distal angle. Merus with distal margin deeply incised (notched) on anterior surface. P-1 carpus with three connate spines on inferior margin. Propodus with complex setae and connate spines on inferior margin as figured; P-1 with two complex setae and four connate spines; P-2 with two complex setae and two or three connate spines, P-3 with one complex seta one stout seta and no connate spines; superior distal angle with two slender setae or two biplumose setae.

Pereopods 4–7. Ischium with two or three clusters of stout setae on inferior margin; P-5 with biplumose seta at superior-distal angle. Carpus of P-7 with five biplumose setae on anterior-distal margin. Propodus of P-4 superior-distal angle with one stout, one slender and one biplumose seta; P-5 to P-7 superior-distal angle with one stout and two biplumose setae.

Pleon. Pl-2 endopod with approximately seven PMS; exopod with approximately 13 PMS. Penes curved slightly inward distally.

Uropod. Endopod apex with approximately five long slender setae; exopod apex with approximately five long slender setae.

Distribution

This species is known only from the intertidal shores of Puerto Rico.

Etymology

This species is named after Ronrico rum, one of the smoother rums produced in the type region (Puerto Rico).

Colopisthus tresesquinas new species

(figures 28–34)

Synonymy. *Colopisthus parvus* Müller, 1993: 212–218, figures 72–96 (misidentification; not *C. parvus*: Richardson, 1902).

Type material examined. HOLOTYPE, female (ZMB Cat. No. 26973); one male, three female and two juvenile paratypes; Colombia, Santa Marta, intertidal from *Sargassum*; collected by H. G. Müller.

Diagnosis. Pleon with three free pleonites. Antenna 1 flagellum three-articulate. Antennae 2 flagellum seven-articulate. Maxilliped endite with four circumplumose setae and two coupling setae; palp articles 2 and 3 partly fused. P-1 to P-3 merus with two or three molariform setae on inferior margin. Carpus of P-5 with one biplumose seta on anterior-distal margin; P-6 with three biplumose setae on anterior-distal margin; P-7 with seven biplumose setae on anterior-distal margin. Pl-3 exopod with complete transverse suture.

Description of female

Dorsal surface of pereon and pleon with fine setae.

Antennae. Antenna 1 peduncular articles 1–3 with slender and palmate setae,

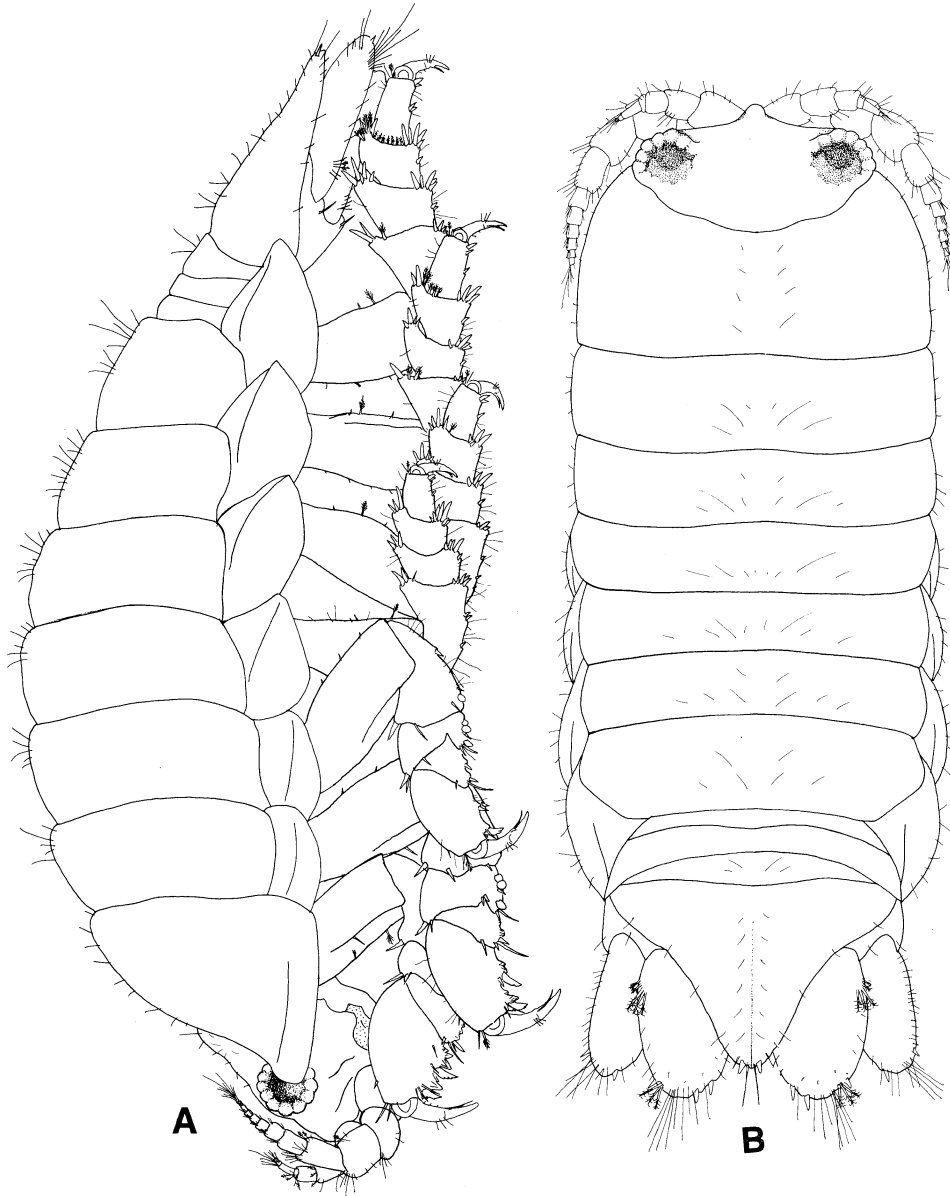


FIG. 28. *Colopisthus tresesquinas*, female holotype: (A) lateral aspect; (B) dorsal aspect.

article 4 with palmate setae; flagellum three-articulate, first article much longer than distal two articles; all flagellar articles with slender setae and jointed aesthetascs. Antennae 2 peduncular articles 2 and 3 with slender setae on anterior margin, articles 4 and 5 with biplumose and slender setae as figured; flagellum seven-articulate, all with cluster of slender setae in anterior-distal region and one or two slender setae in posterior-distal region.

Maxilliped. Endite with four circumplumose setae and two coupling setae. Palp article 1 with a jointed slender seta on medial margin; articles 2 and 3 partly fused,

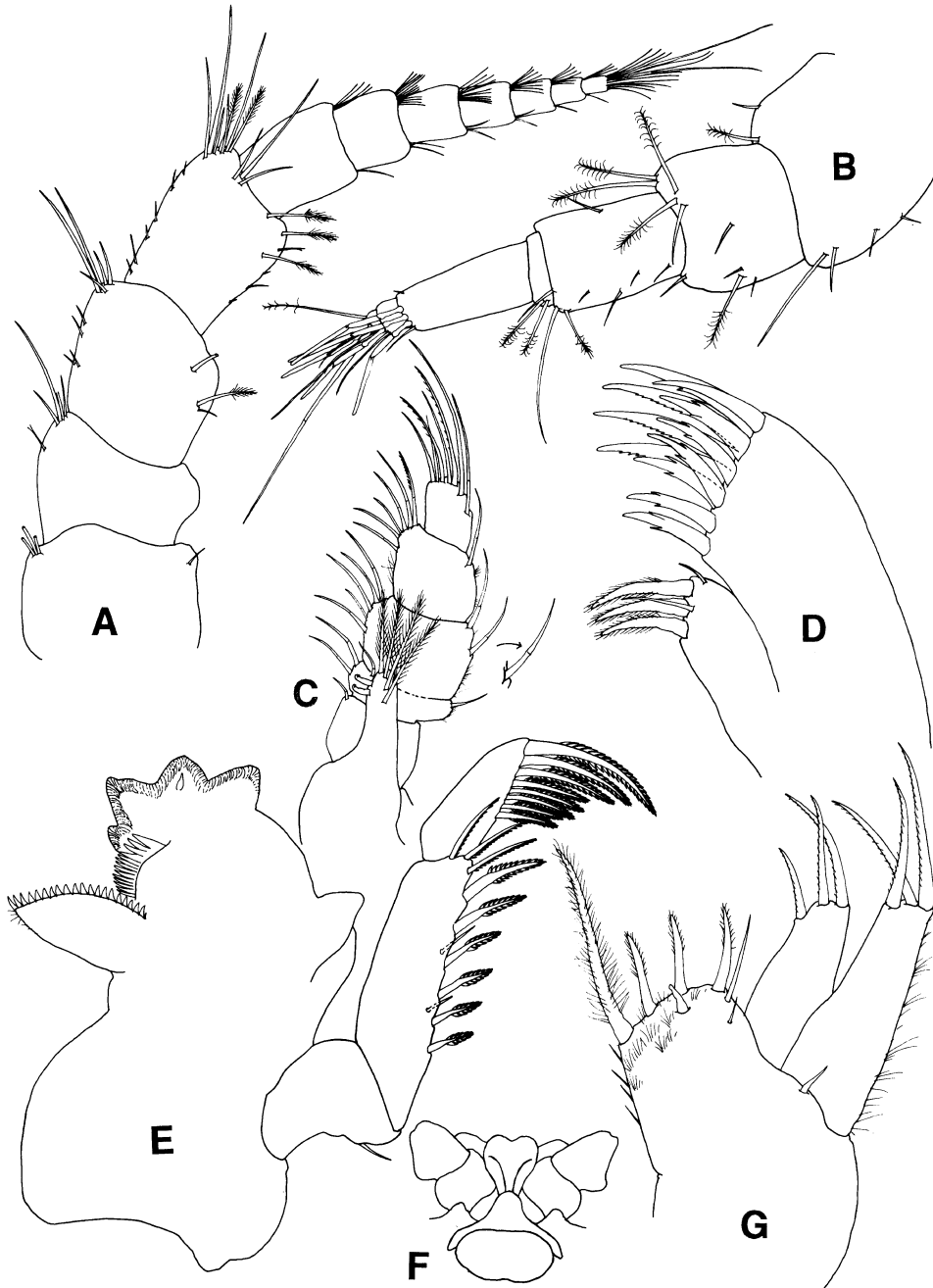


FIG. 29. *Colopisthus tresesquinas*, female holotype: (A) antenna 2; (B) antenna 1; (C) right maxilliped; (D) maxilla 1; (E) right mandible; (F) frontal lamina, clypeus, labrum; (G) maxilla 2.

lateral margins with fine setae, lateral and medial margins with jointed slender setae; article 4 with one jointed seta on disto-lateral angle, one uniserrate and approximately five jointed slender setae on disto-medial angle; terminal article length greater

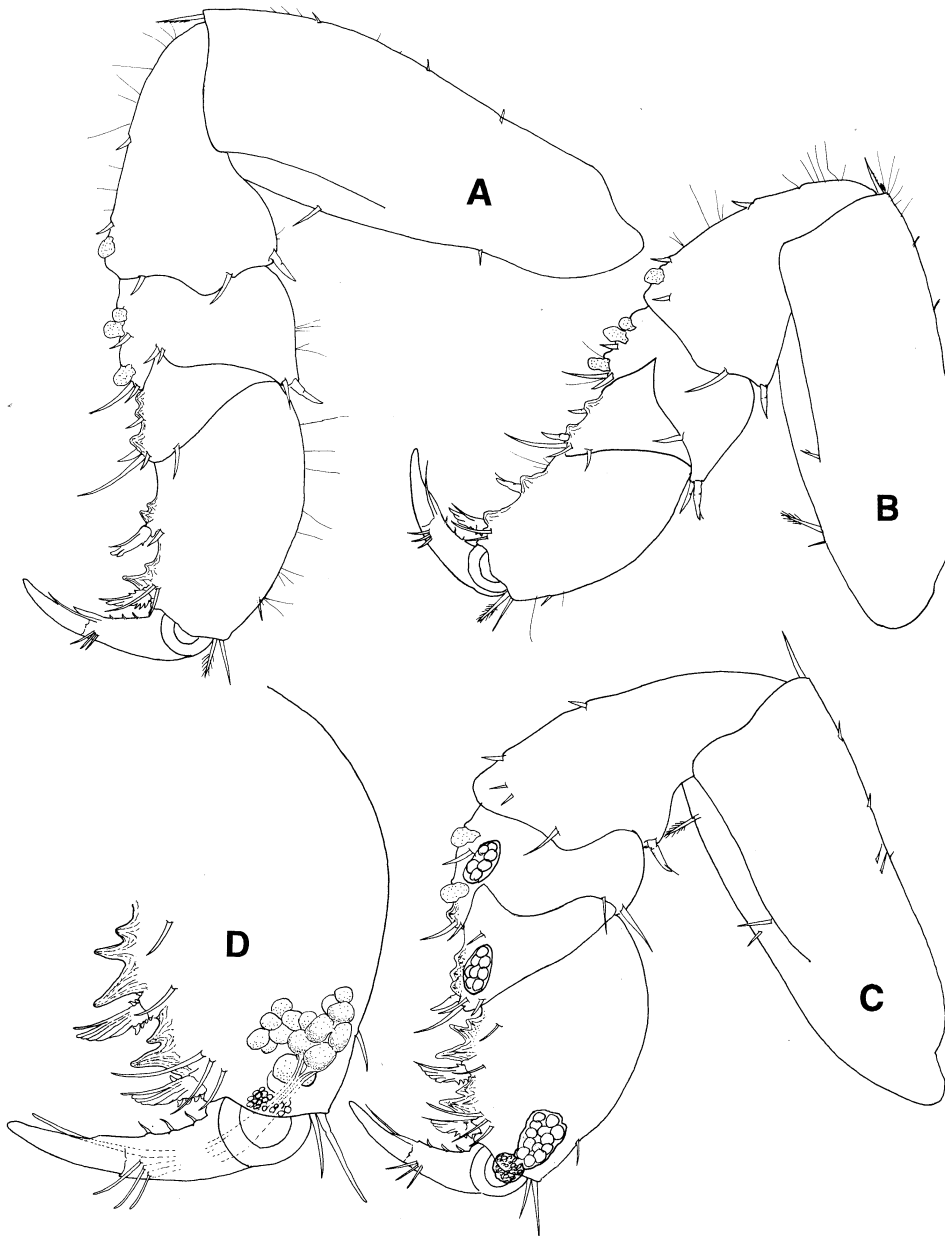


FIG. 30. *Colopisthus tresesquinas*, female holotype: (A) right pereopod 2; (B) right pereopod 3; (C) right pereopod 1; (D) right pereopod 1, detail of propodus. Internal gland-like structures of pereopod 1 shown.

than width, with approximately six slender (some jointed) and two uniserrate apical setae.

Maxillae. Maxilla 1 lateral lobe with one stout, seven forked and three uniserrate setae; medial lobe with one small biplumose, one slender and three stout biplumose setae. Maxilla 2 outer and medial lobes with three uniserrate apical setae; outer lobe

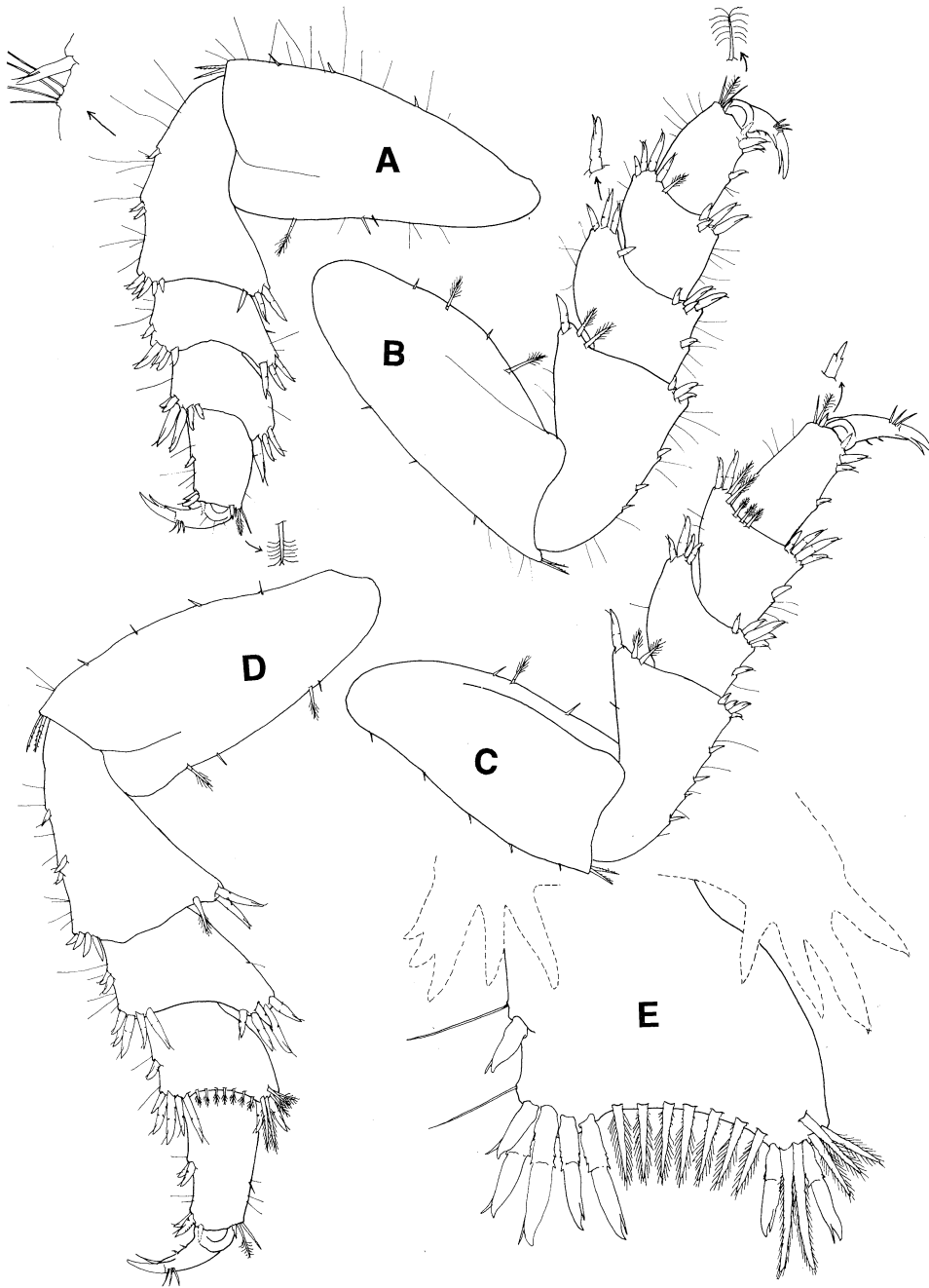


FIG. 31. *Colopisthus tresesquinas*, female holotype: (A) right pereopod 4; (B) right pereopod 5; (C) right pereopod 6; (D) right pereopod 7; (E) right pereopod 7 detail of carpus.

with fine setae on lateral margin; gnathal lobe with one slender seta at base (below outer lobe), apical margin with one large circumplumose, one stout, one slender and three stout biplumose setae.

Mandible. Spine row with 14 large spines; molar process with approximately 21

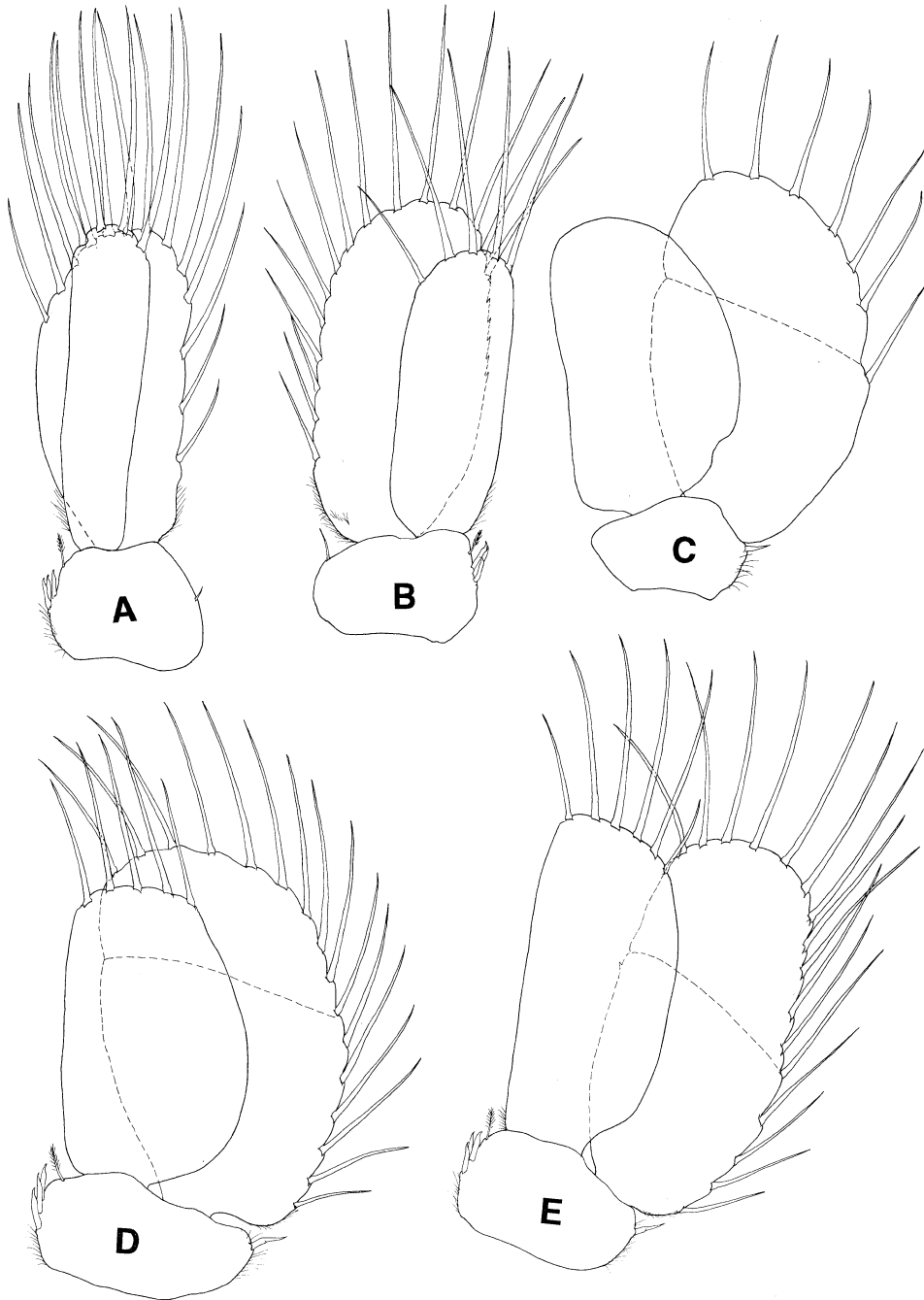


FIG. 32. *Colopisthus tresesquinas*, female holotype: (A) left pleopod 1; (B) right pleopod 2; (C) left pleopod 5; (D) left pleopod 4; (E) left pleopod 3.

small acute marginal spines; proximal palp article with one slender seta on lateral margin; middle article with two slender, six biserrate and three unequally biserrate setae; distal article with eight biserrate setae.

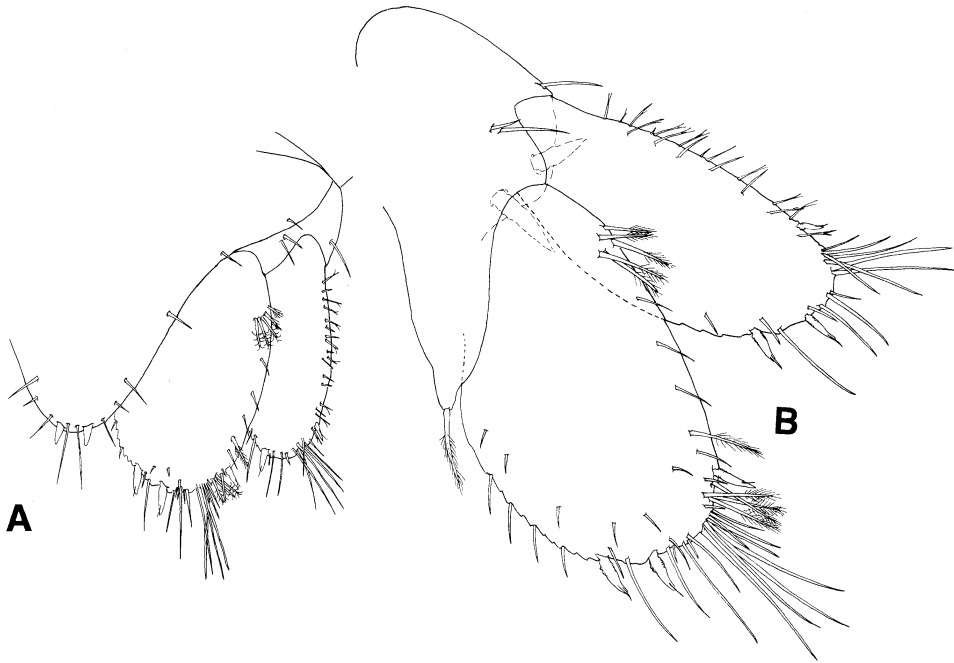


FIG. 33. *Colopisthus tresesquinas*, female holotype: (A) telson-uropod; (B) right uropod.

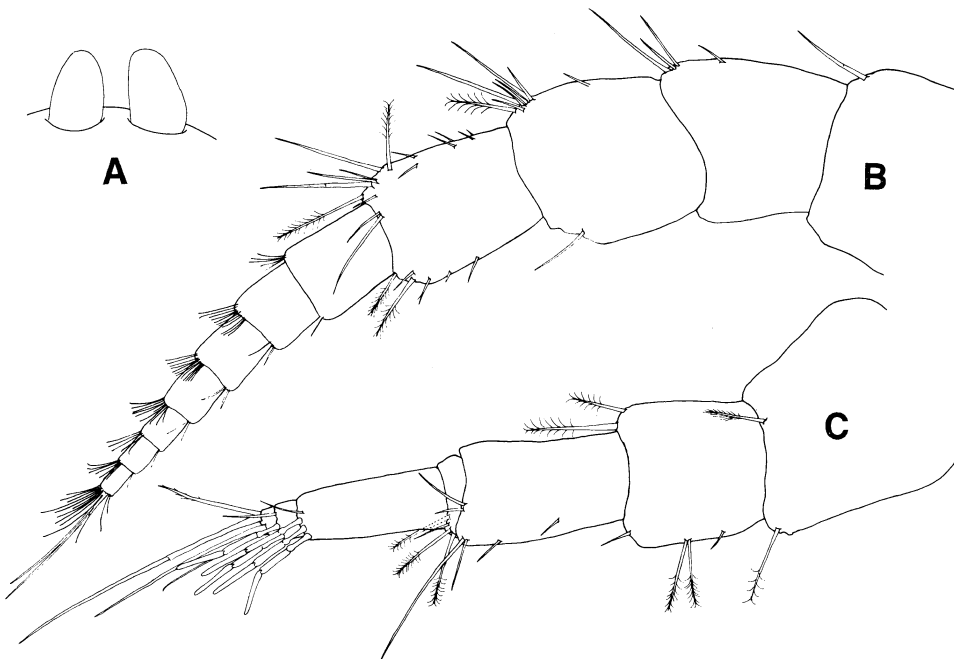


FIG. 34. *Colopisthus tresesquinas*, male: (A) penes; (B) antenna 2; (C) antenna 1.

Pereopods 1–3. Ischium with two stout setae on inferior margin and one stout seta on superior-distal angle and anterior-distal margin; P-2 and P-3 with a molariform seta near inferior-distal angle. Merus with two or three molariform setae on inferior margin and one or two stout setae on superior-distal angle; distal margin deeply incised (notched) on anterior surface; P-1 with a connate spine on inferior-distal angle. Carpus subtriangular, inferior margin much longer than superior margin; with cluster of stout setae on inferior distal angle and two or three connate spines on inferior margin. Propodus with complex setae and connate spines on inferior margin as figured; P-1 and P-2 with two complex setae and four or five connate spines; P-3 with two complex setae and two connate spines.

Pereopods 4–7. Ischium with two or three clusters of stout setae on inferior margin; P-5 to P-7 with one or two biplumose setae at superior-distal angle. Carpus of P-5 with one biplumose seta on anterior-distal margin, P-6 with three biplumose setae on anterior-distal margin, two long biplumose setae at superior-distal angle; P-7 with seven biplumose setae on anterior-distal margin and approximately five long biplumose setae at superior-distal angle. Propodus inferior distal angle with two stout setae; posterior-distal margin with one stout seta; superior-distal angle with one stout, one or two slender and one biplumose seta.

Pleopods. Pl-1 to Pl-4 peduncle with one biplumose and three coupling setae on medial margin. Pl-2 to Pl-5 lateral margin of peduncle with one stout seta. Pl-3 to Pl-5 exopod with complete transverse suture. Pl-1 to P-4 endopod with approximately five or six PMS; exopod with approximately 13–16 PMS. Pl-5 endopod subovate, without setation; exopod with approximately seven PMS.

Uropod. Endopod with slender and palmate setae, two robust setae on medial margin and one robust seta on lateral margin; apex broadly rounded. Exopod with slender and two robust setae on medial margin; apex rounded, with five long slender setae; lateral margin with a continuous row of short slender setae; without lateral fold.

Description of male

As described for female. Appendix masculina missing from specimen; figured by Müller (1993). Secondary sexual characters typical of genus.

Distribution

This species is so far known only from the intertidal shores of Santa Marta, Colombia, where it was collected from the brown alga *Sargassum*.

Etymology

This species is named after Tresesquinas rum, one of the gentle rums of Colombia.

Aphantolana new genus

(figures 35, 36)

Type species. *Metacirolana costaricensis* Brusca and Iverson, 1985: 36–37, figure 11D; Bruce, 1986: 222; Brusca, Wetzer and France, 1995: 72–74, figures 60, 63, 64; Espinosa-Perez and Hendrickx, 1997: 175–185; type material deposited at USNM.

Diagnosis. Small, body length 3–4 mm. Pereon four to five times pleon length. Body length 2.0–2.2 times greatest width; pereonite 1 longest. Cephalon without

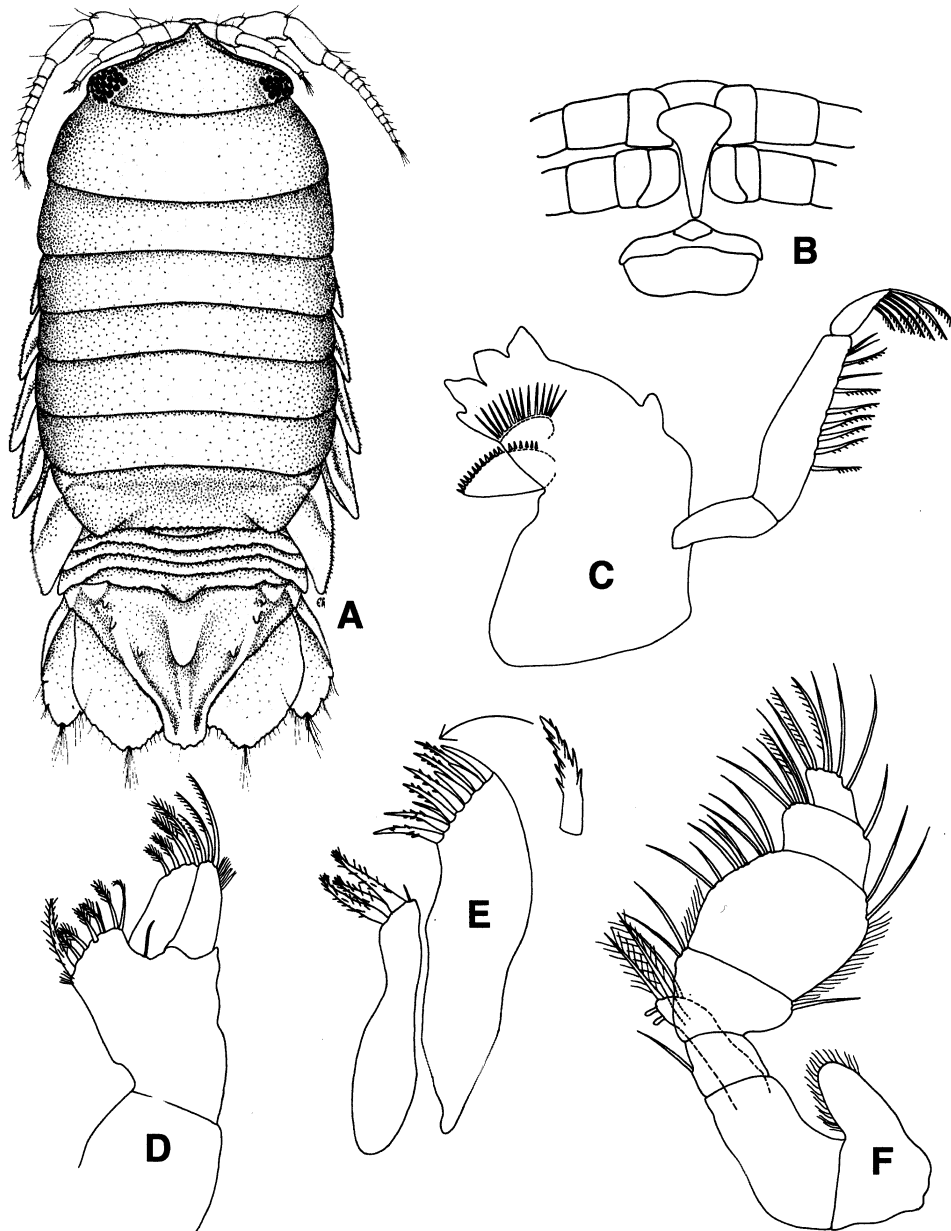


FIG. 35. *Aphantolana costaricensis*, male holotype: (A) dorsal aspect; (B) frontal lamina, clypeus, labrum; (C) right mandible; (D) maxilla 1; (E) maxilla 2; (F) left maxilliped.

interocular depression. Antenna 1 short; peduncle four-articulate, distal article minute; flagellum three-articulate or four-articulate. Antennae 2 short, extended to posterior margin of pereonite 1; peduncle five-articulate, proximal article minute (not easily dissected, visible with SEM); 8–12 flagellar articles. Maxilliped with five-articulate palp, endite extended barely to palp article 3, with one or two coupling setae and three large circumplumose setae. Clypeus triangular, anterior margin

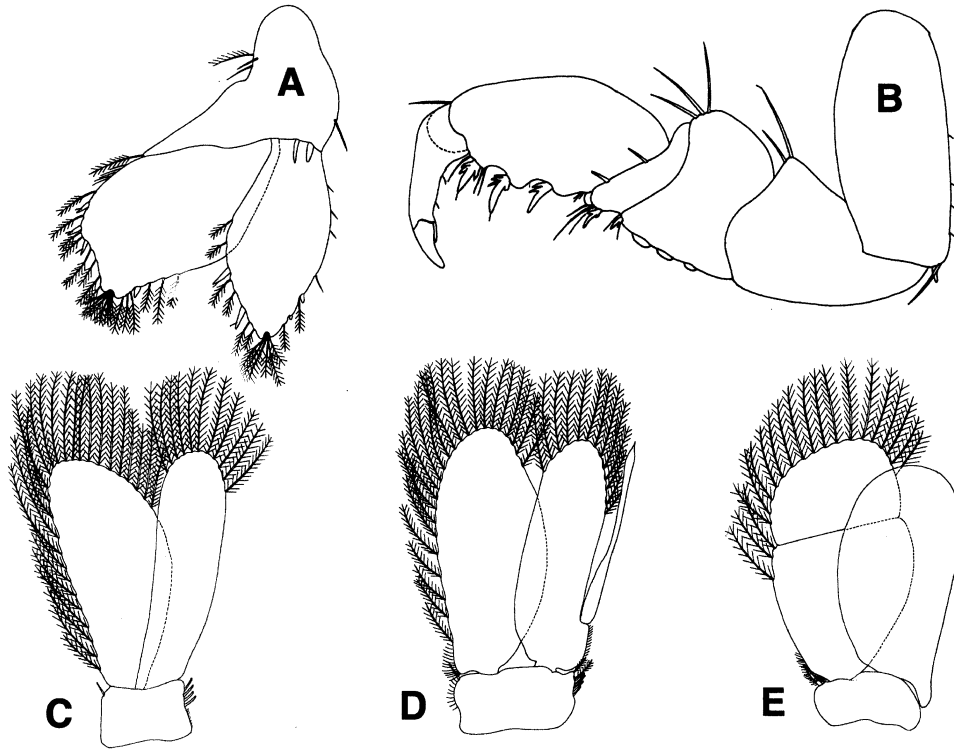


FIG. 36. *Aphantolana costaricensis*, male holotype: (A) left uropod (ventral view); (B) left pereopod 1; (C) pleopod 1; (D) pleopod 2; (E) pleopod 5.

broadly rounded, projecting antero-ventrally; set at an approximate 45° angle to frontal lamina. P-1 propodal palm with three large complex setae and two or three connate spines. P-1 to P-7 dactylus with thin, acute accessory seta and a secondary unguis. Coxal plates become progressively larger posteriorly; coxae of pereonite 7 largest and extended well beyond pleonite 3 and often beyond anterior margin of pleotelson. Pleon with five distinct pleonites; without epimeres. Appendix masculina extended to, but not beyond, distal margin of pleopodal exopod, flask-like (narrows abruptly distally), articulating sub-basally on endopod. Pleopods with PMS present on all rami except the endopod of P1-5; exopods of P1-3 to P1-5 with transverse suture; endopods never as wide as exopods. Uropodal peduncle with two robust ventral setae arising from mediobasal margin; endopod dorsal surface with two clusters of long palmate setae, one distal and one proximo-lateral; exopod not reaching pleotelson apex. Pleotelson tapering abruptly posteriorly, with three dorsal longitudinal carinae; apex narrowly rounded with fine slender setae and two stout setae.

Description

Sexual dimorphism pronounced. Body length 2.0–2.2 times greatest width. Pereon four to five times pleon length.

Head. Cephalon without interocular depression, without tubercles. Eyes round, well developed, ommatidia arranged in rows. Frontal margin of cephalon not

medially concave, with small rostral process separating first antennae. Frontal lamina not fused to rostrum, without ventral projection, anterior end expanded, anterior margin rounded, posterior end stemmed; posterior margin abutting clypeus. Clypeus triangular, anterior margin broadly rounded, projects antero-ventrally; set at an approximate 45° angle to frontal lamina.

Antennae. Antennae 1 short, reaching just beyond lateral margin of cephalon; peduncle four-articulate; 1 and 2 subquadrate; article 3 longer than wide; article 4 minute, with setation; flagellum three-articulate or four-articulate, the first of which is elongate (length at least twice width), the remaining being short (width greater than or equal to length), all with aesthetascs, usually with slender setae, terminal article often with one uniplumose or biplumose seta. Antennae 2 peduncular article 1 minute (generally not visible except with SEM), article 4 longer than 3, article 5 longer than 4; 8–12 flagellar articles, all with slender setae.

Maxilliped. Endite well developed reaching third palp article, with one or two coupling setae and three large lateral circumplumose setae. Palp article 1 (proximal article) subquadrate; article 2 subtriangular; article 3 largest longer than wide; article 4 wider than long; article 5 subquadrate.

Maxillae. Maxilla 1 with medial and lateral lobes distinct, gnathal surface of lateral lobe with five to seven circumserrate setae and two or three stout setae; inner lobe with three stout circumplumose setae and one or two slender setae. Maxilla 2 with apical setae on all three lobes; gnathal lobe with one large circumplumose seta and three to five stout biplumose setae and/or slender setae.

Mandible. Incisor broad, with three large teeth and a small medial accessory tooth. Molar process with 16–18 small acute spines on anterior margin, dorsal surface smooth, without setae; spine row well developed, with 8–14 large flexible spines without intermediate, slender setae; without a lacinia mobilis. Mandibular palp three-articulate, article 2 longest with uniserrate, biserrate and slender setae; distal article well developed, 1.5 times longer than wide, with six or seven biserrate setae on lateral margin.

Pereon. Smooth, without ornamentation. Pereonite 1 longest.

Coxae. Coxae 2–7 or 3–7 visible dorsally; coxae become progressively larger posteriorly; coxae 2–7 with oblique ridge; posterolateral angles of coxae 7 extend beyond anterior margin of pleotelson.

Pereopods. P-1 to P-7 dactylus often with thin, acute accessory seta and a secondary unguis lying alongside primary unguis, one to four slender setae on superior margin; basis with weak anterior ridge.

Pereopods 1–3. Haptorial, propodus ovate. P-1 merus superior-distal angle not produced. P-1 broader than P-2 and P-3. P-1 to P-3 with unique, complex pattern of setae and spines as follows: merus inferior margin with three stout molariform setae, inferior distal angle with one or two stout setae; carpus with one or two connate spines, propodus inferior margin with two connate spines and three large complex setae.

Pereopods 4–7. Long, ambulatory. P-4 to P-7 without connate spines or molariform setae; distal angles of ischium, merus and carpus with one to four robust setae. P-5 to P-7 with basis-propodus articles not flattened.

Pleon. Five free pleonites; without epimeres.

Penes. Penes simple, well developed, free (not basally fused), rounded (not flattened).

Pleopods. Without digitate respiratory branchiae or accessory lamellae. Peduncles of all pleopods wider than long; Pl-1 to Pl-4 with three or four coupling setae on medial margin. Pl-1 exopod and endopod elongate, not operculate to Pl-2 to Pl-5. Exopods approximately 1.5 times wider than endopods; endopod and exopods subequal length on Pl-1, endopod increasingly shorter than exopod on Pl-2 to Pl-5. Pl-1 to Pl-4 endopods and exopods with PMS, absent on endopod of Pl-5; endopods with PMS restricted to distal margins; exopods with PMS on distal and lateral margins. Exopods of Pl-3 to Pl-5 with transverse suture.

Uropod. Uropodal endopod reaches pleotelson apex, exopods much shorter. Peduncle with two robust setae arising from ventral surface; distolateral angle not produced; disto-medial angle produced, subacute, with one large, apical, circumplumose seta. Endopod margins with biplumose setae; medial margin with three large robust setae; lateral margin with one robust seta. Exopod medial margin with biplumose setae and two robust setae; lateral margin with two robust setae.

Pleotelson. With one dorso-medial and two dorso-lateral longitudinal carinae; apex narrowly round with slender setae and two stout setae.

Remarks

Aphantolana species occur in the intertidal zone with algae and/or coral rubble. One of the species, *Aphantolana sphaeromiformis*, has been reported from the Caribbean, Indian Ocean and western Pacific. We agree with Müller and Salvat (1993) that this broad distribution is suspect and requires confirmation. Brusca *et al.* (1995) did not find this species in the Eastern Tropical Pacific, and we doubt that it has a circumtropical range, as has been suggested by some authors (Menzies and Glynn, 1968; Bruce, 1981). *Aphantolana* species are characterized by various combinations of the following features: (1) pereonite 1 longer than others; (2) antennae 2 short, extended only to the posterior margin of pereonite 1; (3) pereopods 1–3 propodal palm with complex setae and connate spines; (4) pereopods 1–7 dactyli with thin accessory setae; (5) pleonite lateral margins covered by the seventh coxal plate (at least in females); (6) pleotelson tapering abruptly, apex narrowly rounded; (7) appendix masculina flask-like and articulating sub-basally; (8) clypeus projecting antero-ventrally (rather than ventrally, as in *Metacirolana sensu stricto*); (9) antenna 1 reduced, with no more than four flagellar articles; (10) pleotelson with three longitudinal dorsal carinae; (11) carpus of P-1 inferior-distal angle with complex seta; (12) carpus of P-2 inferior-distal angle forms notched lobe. The latter two characters are synapomorphies of the genus. In addition, in *Aphantolana* and *Colopisthus* species the seventh coxal plates are the largest and they cover the lateral margins of the pleon. In comparison, *Metacirolana* have coxal plates 2–7 either subequal in size, or coxae 6 are the largest and may cover a portion of the pleon (as seen in *M. spinosa*, *M. convexissima*, *M. nana* and *M. mbudya*).

Etymology

The genus name is derived from the Greek word, *aphantos*, meaning unseen, invisible or secret, in reference to it being hidden inside the genus *Metacirolana* for over 50 years.

In 1931 Nierstrasz proposed the genus *Paracirolana* to include only *Cirolana sphaeromiformis* Hansen, 1980. In the same paper, Nierstrasz proposed the genus *Metacirolana* to include two species *Cirolana japonica* Hansen and *Cirolana hanseni* Bonnier. However, in both cases Nierstrasz did not designate a type species for the

genus, nor did he provide a description or definition that stated characters purported to differentiate the taxa. Thus both names are invalid in accordance with the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature, 2000) rules (see Articles 13.1 and 13.3). However, Kussakin (1979) designated *Cirolana japonica* as the type species of the genus *Metacirolana*, and in doing so he became the official author of the genus.

World list of species

1. *Aphantolana costaricensis* (Brusca and Iverson, 1985). Type species, herein designated. Galapagos Islands, Pacific coast of Costa Rica, north to Sinaloa, Mexico.
2. *Aphantolana moortgati* (Müller and Salvat, 1993: 211). Bora Bora and Moorea, Society Islands, French Polynesia.
3. *Aphantolana sphaeromiformis* (Hansen, 1890: 115). St Thomas, Puerto Rico, West Indies, Sri Lanka. Also see Stebbing (1905: 15–16, pl. 2B).

Biogeographic discussion

The genus *Colopisthus* is restricted in distribution to the tropical north Atlantic, with four species known from the Caribbean–Bermuda region (*C. parvus*, *C. tresesquinas*, *C. ronrico*, *C. cavalier*), one species in the Cape Verde Islands (*C. canna*), and one species reported from the coast of Senegal (Monod, 1952). All species were collected from littoral or shallow-water algae-covered rocks, and their highly restricted distributions suggest that they do not easily disperse. Because *Colopisthus* is an endemic trans-Atlantic genus, one might at first suspect the species distribution to be a remnant of the opening of the Atlantic Ocean, 175 million years ago. Were this the case, the two east Atlantic species, *C. canna* (Cape Verde Islands) and *C. sp.* (Monod's Senegal species) would be viewed as ancient remnants of the spread of North America away from north-west Africa. Such a scenario requires these two species (or their ancestors) to be derived early in the lineage of the genus, branching off at the base of the tree. The identity of the Senegal species remains unknown, but the Cape Verde Island species is embedded within the West Atlantic clade (figure 37).

By replacing the species names in the cladogram with areas of endemism, an area-cladogram is developed that reveals the following area relationships for the species of *Colopisthus* and *Aphantolana* (figure 37). The Cape Verde Island and Bermuda species are sister species, and these form a sister group to the Colombia species; and these three form a sister group to the species of the Antilles. If this area cladogram is overlain on a map, it is seen that *Colopisthus* is rooted in the west, somewhere in the Central American isthmus region, where it connects to its sister group *Aphantolana*. Thus, the origin of *Colopisthus* would seem to lie in the tropical west Atlantic, subsequent to the opening of the Atlantic Ocean. This scenario suggests that the *C. parvus* (Bermuda), *C. canna* (Cape Verde Islands) and presumably the Senegal species, are products of dispersal events.

The genus *Aphantolana*, on the other hand, like *Metacirolana*, appears to be a much older, cosmopolitan taxon with representation in both the Indo-Pacific and the Caribbean. This suggests that the closing of the Panamanian Seaway ~3.5 million years ago might have been the vicariance event that initiated the radiation of *Aphantolana* in the Pacific and *Colopisthus* in the Atlantic.

Cladistic biogeography seeks congruent patterns among area cladograms for

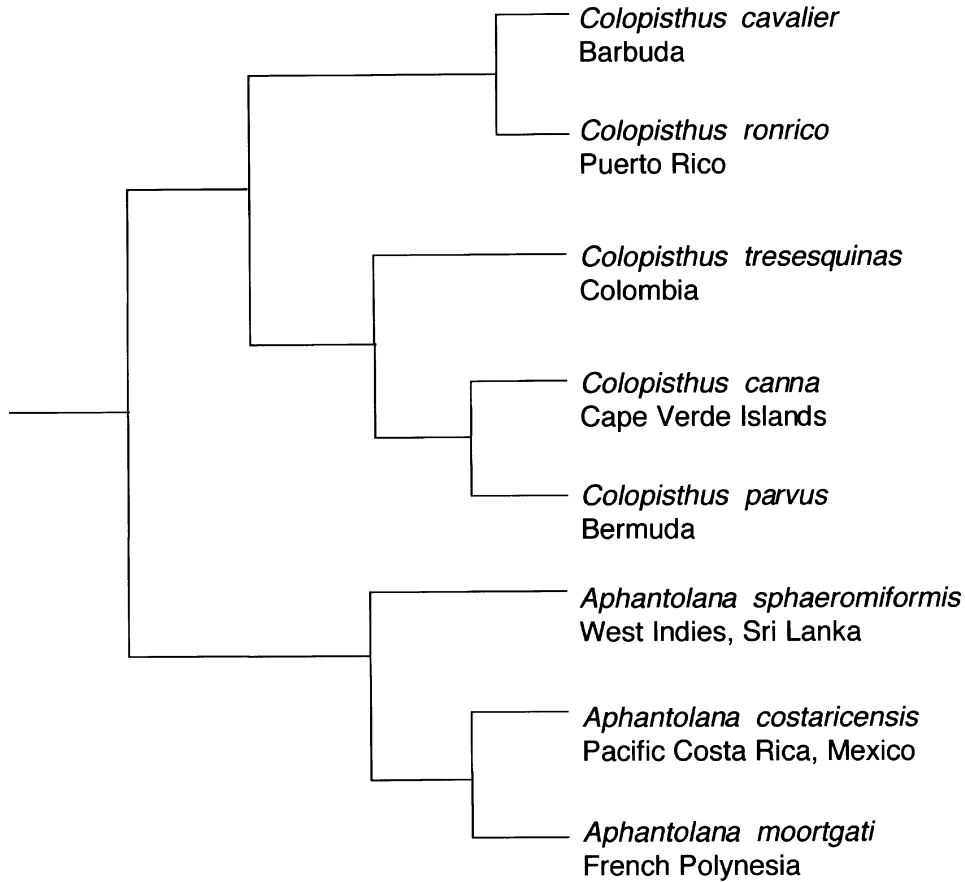


FIG. 37. Taxon-area cladogram.

different taxa, in the hope of identifying common historical explanations for biotic distributions. Unfortunately, there are virtually no other published cladograms of coastal marine taxa for the Caribbean region, so seeking this congruence is not yet possible. Hopefully, additional cladograms of coastal marine taxa will be developed that will eventually allow for a broad-scale analysis of the Caribbean marine fauna.

Acknowledgements

We wish to thank Niel Bruce, Steve Keable, Brian Kensley and Julia Kouwenberg for reviews of the taxonomic portion of this paper, and David Maddison for advice on the phylogenetic section. We are especially grateful to Niel Bruce for his critical insight on cirrolanid morphology. Chip Griffin did all of the scientific illustrations with the exception of the figures of *Aphantolana costaricensis*, which are reprinted from Brusca *et al.* (1995). We are also grateful for the assistance of the following people who helped in locating and borrowing museum specimens: Marilyn Schotte (USNM), Oliver Coleman (ZMB), Niel Bruce and Bjaime Bisballe (ZMUC) and Eric A. Lazo-Wasem (YPM). Funding for this project was provided by a NSF PEET grant (DEB-9896145) to R.C. Brusca and B. Kensley.

Appendix 1*Characters used in the phylogenetic analysis*

1. Cephalon:
 0. wider anteriorly than posteriorly
 1. not wider anteriorly than posteriorly
2. Cephalon interocular depression:
 0. absent
 1. present
3. Cephalon and pereonite 1:
 0. lateral margins smooth
 1. lateral margins crenulate
4. Pereonites:
 0. without setae on dorsal surface
 1. with setae on dorsal surface
5. Pereonite 1 length:
 0. subequal to pereonite 2
 1. longer than pereonite 2
6. Pereonite 1:
 0. not encompassing base of cephalon
 1. encompassing base of cephalon
7. Antenna 1:
 0. short, not reaching posterior margin of pereonite 1
 1. long, extended at least to posterior margin of pereonite 1
8. Antenna 1 peduncular article 1:
 0. shorter than article 2
 1. subequal to article 2 or longer
9. Antenna 1 peduncular article 2:
 0. longer than wide
 1. greatest width subequal to length
10. Antenna 1 peduncular article 2:
 0. shorter than article 3
 1. subequal to article 3
 2. longer than article 3
11. Antenna 1 peduncular article 2:
 0. without huge pappose seta
 1. with huge pappose seta
12. Antenna 1 peduncular article 3:
 0. longer than wide
 1. width subequal to length
13. Antenna 1 peduncular article 1:
 0. longer than article 3
 1. subequal to article 3
 2. shorter than article 3

14. Antenna 1 flagellum articles (other than 1):
 0. longer than wide
 1. subequal or wider than long
15. Antenna 2 peduncular article 2:
 0. subequal to article 3
 1. markedly shorter than article 3
16. Antenna 2 peduncular article 5:
 0. longer than 4
 1. subequal to 4
17. Antenna 2 proximal peduncular article:
 0. as long as wide
 1. wider than long
 2. fused to article 2
18. Antenna 2 length:
 0. reaches midpoint of pereonite 1
 1. reaches posterior margin of pereonite 1
 2. reaches well beyond posterior margin of pereonite 1
19. Rostrum:
 0. weak, not separating first antennae
 1. prominent and separating first antennae
20. Frontal lamina anterior margin:
 0. rounded
 1. angulate
 2. concave
 3. square
21. Frontal lamina posterior margin:
 0. abutting clypeus
 1. stemmed and disjunct from clypeus
 2. stemmed and abutting clypeus
22. Clypeus, anterior margin:
 0. not projecting
 1. projecting antero-ventrally
 2. projecting ventrally
23. Maxilliped endite length:
 0. reaches third palp article
 1. does not reach third palp article
24. Maxillipedal endite:
 0. without coupling setae
 1. with one coupling seta
 2. with two coupling setae
 3. with three coupling setae

25. Maxillipedal endite:
 0. with two plumose setae
 1. with three plumose setae
 2. with four plumose setae
 3. with five plumose setae
 4. with seven plumose setae
26. Maxillipedal palp article 3:
 0. longer than wide
 1. subquadrate
 2. wider than long
27. Left mandibular incisor:
 0. quadridentate
 1. tridentate
28. Mandibular setal row:
 0. without a distal sclerotized tooth (= lacinia)
 1. with a distal sclerotized tooth
29. Mandibular incisors:
 0. without flask-like inclusion
 1. with flask-like inclusion
30. Mandibular spine row:
 0. with 11 or fewer spines
 1. with 13 or more spines
31. Mandibular spine row:
 0. on small lobe
 1. on well-developed lobe
32. Mandibular palp articles 2 and 3:
 0. without biserrate setae
 1. with biserrate setae
33. Pereonite 1:
 0. without lateral carina
 1. with lateral carina
34. Pereopods 1–3 propodal palm:
 0. without complex setae
 1. with complex setae
35. Pereopod 1 ischium superior distal angle:
 0. without short simple setae
 1. with one or a few short simple setae
36. Pereopod 1 ischium superior distal angle:
 0. without acute robust setae
 1. with acute robust setae
37. Pereopod 1 ischium inferior margin:
 0. without acute robust setae
 1. with acute robust setae

38. Pereopod 1 merus superior distal angle:
 0. not produced
 1. produced to base of propodus
39. Pereopod 1 merus superior distal angle:
 0. without long simple setae
 1. with cluster of long simple setae
 2. with a few long simple setae
40. Pereopod 1 merus superior distal angle:
 0. without acute robust setae
 1. with acute robust setae
41. Pereopod 1 merus inferior margin:
 0. without simple setae
 1. with one or a few simple setae
42. Pereopod 1 merus inferior margin:
 0. without robust setae
 1. with one or a few robust setae
43. Pereopod 1 merus inferior margin:
 0. without molariform setae
 1. with molariform setae
44. Pereopod 1 carpus inferior margin:
 0. without robust setae
 1. with robust setae
45. Pereopod 1 carpus inferior margin (not including distal angle):
 0. without connate spines
 1. with connate spines
46. Pereopod 1 carpus inferior distal angle:
 0. not produced
 1. produced, and subacute
47. Pereopod 1 carpus inferior distal angle:
 0. without connate spines
 1. with connate spine
48. Pereopod 1 carpus inferior distal angle:
 0. without robust setae
 1. with robust setae
49. Pereopod 1 carpus inferior distal angle:
 0. without complex setae
 1. with complex setae
50. Pereopod 1 propodus inferior margin (not including inferior distal angle):
 0. without simple setae
 1. with simple setae

51. Pereopod 1 propodus inferior margin:
 0. without robust setae
 1. with robust setae
52. Pereopod 1 propodus inferior margin:
 0. without connate spines
 1. with connate spines
53. Pereopod 1 propodus inferior margin, distal-most robust seta:
 0. broad, fan-shaped, complex
 1. dagger/knife-shaped, broad proximally, often ctenate
 2. simple, robust seta
54. Pereopod 1 propodus inferior margin:
 0. distal-most robust seta subequal in size to other setae on the palm
 1. distal-most robust seta much larger than other robust setae on the palm
55. Pereopod 1 propodus inferior margin:
 0. distal-most robust seta same form as other setae on the palm
 1. distal-most robust seta different from others on the palm
56. Pereopod 1 dactylus secondary unguis/accessory robust seta:
 0. absent (note: slender setae may be present)
 1. present
57. Pereopod 2 ischium superior distal angle:
 0. without short simple setae
 1. with a few short simple setae
58. Pereopod 2 merus superior distal angle:
 0. without short simple setae
 1. with a few short simple setae
59. Pereopod 2 merus superior distal angle:
 0. not produced
 1. slightly produced, less than one-third length of propodus
60. Pereopod 2 merus inferior margin:
 0. without robust setae
 1. with robust setae
61. Pereopod 2 carpus inferior margin:
 0. without connate spines
 1. with connate spines
62. Pereopod 2 carpus inferior distal angle:
 0. not produced
 1. forms a notched lobe
63. Pereopod 2 propodus, ratio of length to greatest width:
 0. ~ 0.67
 1. ~ 0.50
 2. ~ 0.33

64. Pereopod 2 propodus inferior margin:
 0. without connate spines
 1. with connate spine(s)
65. Pereopod 2 propodus inferior margin:
 0. without ctenate robust setae
 1. with ctenate robust setae
66. Pereopod 2 dactylus secondary unguis/accessory robust seta:
 0. absent (note: slender setae may be present)
 1. present
67. Pereopod 3 merus inferior margin:
 0. without molariform setae
 1. with two molariform setae
 2. with three molariform setae
68. Pereopod 3 ischium inferior distal angle:
 0. without molariform seta
 1. with molariform seta
69. Pereopod 6 carpus antero-distal margin:
 0. without biplumose setae
 1. with one biplumose seta
 2. with two biplumose setae
 3. with three biplumose setae
 4. with four biplumose setae
70. Pereopod 7 basis:
 0. length subequal to two times width
 1. length greater than two times width
 2. length greater than three times width
71. Pereopod 7 basis superior margin row of simple setae:
 0. absent
 1. present
72. Pereopod 7 basis superior margin row of biplumose setae:
 0. absent
 1. present
73. Pereopod 7 ischium superior distal angle:
 0. without long simple setae
 1. with cluster of long simple setae
74. Pereopod 7 ischium inferior margin:
 0. without robust setae
 1. with robust setae
75. Pereopod 7 carpus superior distal angle:
 0. without long biplumose setae
 1. with long biplumose setae

76. Pereopod 7 carpus antero-distal margin:
 0. without biplumose setae
 1. with one biplumose seta
 2. with five to seven biplumose setae
 3. with 10 or 11 biplumose setae
77. Pereopod 7 propodus superior distal angle:
 0. without simple setae
 1. with simple setae
78. Pereopod 7 propodus superior distal angle:
 0. without robust setae
 1. with robust setae
79. Pereopod 7 propodus superior distal angle:
 0. without palmate setae
 1. with palmate setae
80. Pleonite lateral margins:
 0. free, not covered
 1. covered by 6th coxae
 2. covered by 7th coxae
81. Relative size of coxal plates:
 0. progressively larger, such that 7 is the largest and is twice as large as 2
 1. not as above
82. Size of seventh coxal plate:
 0. minute
 1. subequal to other coxal plates
 2. large
 3. very large
83. Number of free pleonites:
 0. two
 1. one free, two fused
 2. three
 3. five
84. Pleopod 1 peduncle:
 0. rectangular, much wider than long
 1. subquadrate
85. Rami of pleopods 1 and 2:
 0. exopod broad, endopod elongate (length more than two times width)
 1. exopod and endopod both elongate (length more than two times width)
86. Pleopod 1 exopod/endopod width:
 0. exopod \geq two times endopod width
 1. exopod $<$ two times endopod width
87. Appendix masculina:
 0. articulates sub-basally
 1. articulates basally

88. Appendix masculina:
 0. flask-like
 1. not flask-like
89. Appendix masculina:
 0. reaches exopod apex
 1. reaches beyond exopod apex
 2. does not reach exopod apex
90. Pleopod 5 endopod:
 0. without proximo-medial lobe
 1. with proximo-medial lobe
91. Pleopod 5 distal region of endopod:
 0. evenly rounded
 1. narrowed to obscure point
92. Uropodal exopod:
 0. not rotated
 1. rotated about 40° dorsally
93. Uropodal exopod length:
 0. reaches pleotelson apex
 1. does not reach pleotelson apex
94. Uropodal endopod medial margin:
 0. without robust setae
 1. with robust setae
95. Uropodal endopod medial margin:
 0. without simple setae
 1. with simple setae
96. Uropodal endopod medial margin:
 0. without plumose setae
 1. with plumose setae
97. Uropodal endopod apex:
 0. simple
 1. bifid
 2. placed (sub)laterally of broad oar-shaped endopod
98. Uropodal endopod apex:
 0. without simple setae
 1. with some simple setae, not in cluster
 2. with a cluster of simple setae
99. Uropodal endopod apex:
 0. without plumose setae
 1. with some plumose setae, not in cluster
 2. with a cluster of plumose setae
100. Uropodal endopod lateral margin:
 0. without robust setae
 1. with robust setae

101. Uropodal endopod lateral margin:
 0. without simple setae
 1. with simple setae
102. Uropodal endopod lateral margin:
 0. without plumose setae
 1. with plumose setae
103. Uropodal exopod medial margin:
 0. without robust setae
 1. with robust setae
104. Uropodal exopod medial margin:
 0. without simple setae
 1. with simple setae
105. Uropodal exopod medial margin:
 0. without plumose setae
 1. with plumose setae
106. Uropodal exopod apex:
 0. without simple setae
 1. with some simple setae, not in a cluster
 2. with a cluster of simple setae
107. Uropodal exopod lateral margin:
 0. without robust setae
 1. with robust setae
108. Uropodal exopod lateral margin:
 0. without plumose setae
 1. with plumose setae
109. Uropodal exopod apex shape:
 0. bifid
 1. rounded
110. Pleotelson dorsal sculpturing:
 0. smooth, without carinae
 1. with a median carina
111. Pleotelson:
 0. without lateral carinae
 1. with lateral carinae
112. Pleotelson:
 0. without plumose marginal setae
 1. with plumose marginal setae
113. Pleotelson shape of postero-lateral margins:
 0. straight
 1. slightly concave
 2. convex

114. Pleotelson apex:
0. without stout setae
 1. with two stout setae
 2. with many stout setae
115. Pleotelson apex:
0. narrowly round
 1. broadly round
 2. acute
 3. truncate

Appendix 2

Data matrix of 29 species and 115 characters used in the phylogenetic analysis. Multiple character state assignments (e.g. '0,2') represent polymorphisms rather than uncertainty.

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