

A new genus and species of leptostracan (Crustacea: Malacostraca: Phyllocarida) from Guana Island, British Virgin Islands, and a review of leptostracan genera

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Saronebalia guanensis, a new genus and species of leptostracan, is described from material discovered in shallow subtidal waters of Guana Island, British Virgin Islands. The specimens were collected from light traps placed on sediment and by hand from the green alga *Halimeda*. *Saronebalia* differs from other leptostracans most notably in the morphology of the antennule and the eighth thoracic limb; the articles of the antennular flagellum are fused and bear dense clusters of setae, and the eighth thoracic limb is elongate. While its eyes, like those of *Nebalia*, are non-tuberculate, it shares the rostral spine, dentate process of antennular article 4, and serrate pleopodal protopods of *Levinebalia* and *Paranebalia*. Specimens of the new genus lack the setal row of the exopod of pleopod 1, a complex feature characteristic of *Dahlella*, *Levinebalia*, *Nebalia* and *Paranebalia*. A cladistic analysis of the 10 leptostracan genera, using 30 morphological characters from these features and others, also supports the status of *Saronebalia* as a new genus. *Saronebalia* represents the third leptostracan genus to be recorded from the Caribbean Sea.

KEYWORDS: Phyllocarida, Leptostraca, Nebaliacea, systematics, Caribbean.

Introduction

Leptostracans are marine crustaceans defined by a hinged rostrum, a folded carapace that forms two valves and encloses the thoracic segments, and the presence of eight leaf-like thoracic limbs. Little is known of the life history of these animals. The earliest works on the group were reports of specimens from relatively shallow waters (<45 m) off European coasts (e.g. Fabricius, 1780; Leach, 1814; Risso, 1826; Milne-Edwards, 1828). They are now known to occur throughout the world's oceans and in a wide variety of habitats, from hydrothermal vents and marine caves to the intertidal zone.

The Leptostraca are predominantly benthic, and many species are recovered from surficial marine sediments associated with algal mats or subtidal organic detritus (e.g. Vetter, 1994; Martin *et al.*, 1996; Haney and Martin, 2000). Other leptostracans are known from relatively oligotrophic habitats (Vetter, 1996). Many

Leptostraca from the Caribbean Sea, for instance, have been collected from the green alga *Halimeda*, reef sands, black corals and sponges (Modlin, 1991; Paulo Young, personal communication; T. Haney, unpublished). Although such habitats might appear 'clean' to the human observer, they might be rich in detrital material at a scale relevant to the leptostracans. Modlin (1996: 532), for example, recognized beds of the macroalga *Halimeda* as effective traps of organic particles, and the same could be true of the sponges and branching antipatharian corals from which leptostracans have been collected. Certainly, most leptostracan Crustacea appear to be associated with environments of high organic matter and low dissolved oxygen (e.g. Menzies and Mohr, 1952; Johnson, 1970; Gamô and Takizawa, 1986; Rainer and Unsworth, 1991; Martin *et al.*, 1996; Modlin, 1996; Vetter, 1996; Haney and Martin, 2000). Two leptostracan species have been collected only from the water column (see Sars, 1887; Petryashov, 1996). These pelagic forms of the family Nebaliopsidae may attain lengths of 50 mm (Brahm and Geiger, 1966), but adult individuals of most species of leptostracans typically reach lengths between 5 and 15 mm. Given their broad distribution and the diversity of macrohabitats that they occupy, the life history of the Leptostraca is of interest.

The few investigations into the ecology of the Leptostraca have been focused on the mechanism of leptostracan feeding (Cannon, 1927; Rowett, 1943; Kerambrun and Guerin, 1993) or biotic characteristics of the habitat and the contribution of Leptostraca to the biomass of a given site (Rainer and Unsworth, 1991; Vetter, 1994, 1995; Gerken, 1995). Leptostracan abundance can be enormous at a given site; the sex ratio in those populations for which it has been observed is typically female-biased; the reproductive cycle of some populations appears to be seasonal. Manton (1934) and, more recently, Olesen and Walossek (2000) have conducted informative studies of leptostracan development. Still, quite little is known about the biology of the Leptostraca or the role of the leptostracan fauna in any region.

The majority of all work on the group to date has been taxonomic and has consisted almost exclusively of comparative morphology. This bias toward taxonomic work is not surprising. In some cases, particularly for deep-water material, the method of sampling leaves the author with little more than the specimens, and the research by default is focused solely upon the details of leptostracan anatomy (e.g. Kikuchi and Gamô, 1992). Collection efforts and systematic work for the group have also been uneven over space and time, so new collections and the study of older material often bring new species to light. In fact, although the first of these animals was discovered in 1780, six of the 10 leptostracan genera have been described in the last 18 years (see table 1). The need for knowledge of the natural history of the Leptostraca goes hand-in-hand with inadequate knowledge of their diversity, distribution and interrelationships.

As currently understood, the crustacean order Leptostraca includes 10 genera and 33 species. Nine genera of Leptostraca had been recognized previous to this report (table 1). Herein, we describe the 10th leptostracan genus for material collected from shallow waters of Guana Island, British Virgin Islands.

Methods

An aquatic light trap from BioQuip Products, Inc., was submerged to a depth of 3 m and illuminated using a green Cyalume lightstick. Following 60 min of exposure, the contents of the trap were collected. The organisms captured were sorted while in seawater and still living using a Wild M5 stereomicroscope. In the

Table 1. List of leptostracan genera and the number of nominal species in each.

Taxon	Author	No. of nominal spp.
Family Nebaliidae	Samouelle, 1819	26
<i>Nebalia</i>	Leach, 1814	18
<i>Nebaliella</i>	Thiele, 1904	5
<i>Dahlella</i>	Hessler, 1984	1
<i>Sarsinebalia</i>	Dahl, 1985	1
<i>Speonebalia</i>	Bowman <i>et al.</i> , 1985	1
Family Paranebaliidae	Walker-Smith, 2000	5
<i>Paranebalia</i>	Claus, 1880	2
<i>Levinebalia</i>	Walker-Smith, 2000	2
<i>Saronebalia</i>	Present paper	1
Family Nebaliopsidae	Hessler, 1984	2
<i>Nebaliopsis</i>	Sars, 1887	1
<i>Pseudonebaliopsis</i>	Petryashov, 1996	1

field season of 2000, light-trap samples yielded three specimens of the new genus. Twenty-two additional specimens were found within hand-collected colonies of the green alga *Halimeda* sorted in the same fashion; three and 19 specimens were collected from *Halimeda* in the years 2000 and 2001, respectively. Selected specimens, including the holotype, were photographed while alive, after which all specimens were preserved in a solution of 95% ethanol.

At the Natural History Museum of Los Angeles County (LACM), the specimens were examined using Wild M5 and M5A stereomicroscopes and a Nikon Labophot-2 compound microscope. Dissected appendages were studied using temporary glycerol slide mounts. The dissected eyes, antennules and antennae of one specimen were stained with rose bengal. Illustrations of these and other appendages were made using a camera lucida. Three of the specimens deposited in the LACM collection were examined using scanning electron microscopy (see Martin *et al.*, 1996, for method of preparation).

Additionally, a data matrix was constructed from observations of 30 morphological characters for the 10 genera and was used for phylogenetic inference. Characters were selected only if the states of the male could be readily assigned from the literature and/or firsthand observations of specimens. These data were analysed with the software package PAUP*4.0b8 (Swofford, 2000) using the exhaustive search option, with characters left unordered and weighted equally. Multistate characters were treated as polymorphic. The in-group included the eight genera of the families Nebaliidae Samouelle, 1819, and Paranebaliidae Walker-Smith and Poore, 2001. Character polarity was established with the use of *Nebaliopsis* and *Pseudonebaliopsis* as out-groups, the two genera of the leptostracan family Nebaliopsidae. In a second analysis, the in-group was composed of all extant Leptostraca, with mysids scored and used as an out-group.

Systematics

Order LEPTOSTRACA Claus, 1880

Family PARANEBALIIDAE Walker-Smith and Poore, 2001

Genus *Saronebalia*, new genus

Diagnosis (of male). Rostrum bearing single, apical seta; eyes unornamented, non-tuberculate; antennular article 4 bearing triangular, denticulate process at apex;

antennular flagellum posteriorly directed and highly setose, forming callynophore; thoracopods stenopodous; thoracopod 8 elongate, nearly twice as long as thoracopods 1–7; pleopod 1 exopod bearing simple and palmate setae, exopod lacking spine row; flexion of abdomen after abdominal somite 5 approximately 90°.

Etymology

Saronebalia is derived from the Greek *saron*, meaning broom or sweep, for the plumose nature of the male's antennular flagellum, plus *Nebalia*.

Saronebalia guanensis, new species

Type locality

North Atlantic Ocean, Caribbean Sea, British Virgin Islands, Guana Island, White Bay, station BVI00-100, beneath swimming dock off beach from beach house, 18°28.480'N, 64°34.662'W, depth of 3 m, sandy bottom, from light trap sample exposed from 19:30 to 20:30 h, and White Bay, station BVI00-118, approximately 50 m off beach, depth of 2 m, within colonies of the green alga *Halimeda* sp. on coral rubble. Collections were made from these sites on 26 July 2000 and 30 July 2000, respectively. Nineteen additional specimens were collected from: White Bay, station BVI01-089, depth of 1–2 m, from wash of *Halimeda*, on 28 July 2001.

Material examined

Male holotype (3.43 mm total length), from station 100, LACM CR 2000-011.1; 18 m paratypes (2.59–3.66 mm total length), from stations BVI00-118 and BVI01-089, LACM CR 2000-012.1; six male paratypes (2.78–3.07 mm total length), from station BVI01-089, USNM 1002619. Three of the 18 paratypes from the LACM collection were used for analysis by scanning electron microscopy and are maintained on stubs with the remainder of the type series.

Description of male

Rostrum (figures 1(a)–(d), 2(a)–(c)). Broadest proximally, tapering toward distal margin, nearly twice as long as wide (length 0.51 mm, range 0.43–0.51 mm; width 0.29 mm, range 0.24–0.29 mm); with ventral, keel-like ridge distally; bearing single, simple seta distally, arising from ventral face of rostrum and ventrally directed; rostral keel absent.

Carapace (figure 1(a)). Length in lateral aspect 1.54 mm (range 1.14–1.54 mm), posteriormost margin extending over pleonite 2; length in dorsal aspect, as measured from base of rostrum to posterior invagination, 1.00 mm (range 0.80–1.00 mm); invagination of posterior margin broad, terminating with sharp, triangular incision; carapace height 0.87 mm (range 0.77–0.87 mm); posteriormost margin of carapace extending to anterior margin of pleonite 3; carapace smooth anteriorly, bearing rows of minute setae on posterior half; ventral margin of carapace even, lacking folds.

Eye (figures 1(a)–(b), (d), 2(a)–(b), 4(c)). Eyestalk extending anteriorly beyond midpoint of rostrum; tubular in form, tapering toward unevenly rounded distal margin, with anterior margin slightly convex and posterior margin straight; eye surface relatively smooth, unornamented, with well-developed, round ommatidia occupying distal three-quarters of eyestalk; pigment colour deep red in living specimens; supraocular plate (scale) absent.

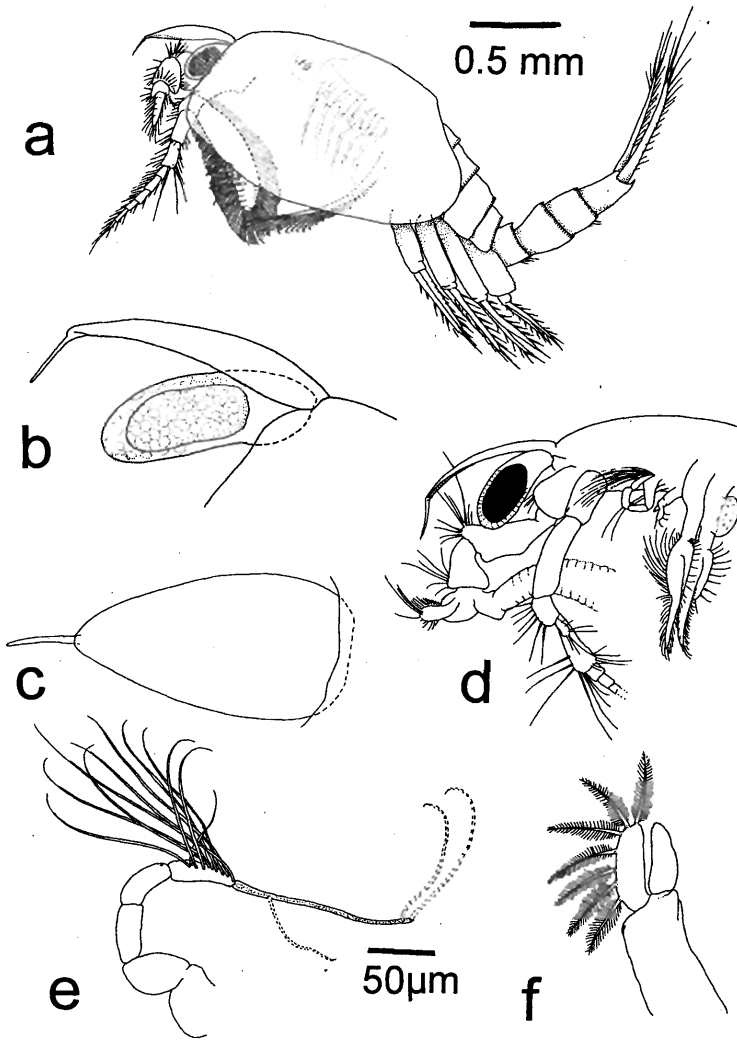


FIG. 1. *Saronebalia guanensis* n. gen., n. sp.: holotype male: (a) whole specimen; paratype male: (b) rostrum and eyestalk; (c) rostrum, dorsal view; (d) anterior, with carapace removed; (e) first maxilla (maxillule); (f) second maxilla (50 μ m scale bar refers only to (e) and (f)).

Antennule and antenna (figures 1(a), 3(a)–(c), 4(a)–(e), 5(a)–(c), 6(c)). Antennular article 2 with single stout seta and cluster of long, simple setae on antero-distal margin; article 3 with similar cluster of long, simple setae only; article 4 with subtriangular flange bearing 13–15 small teeth along apical margin, each tooth having smaller serrations along its lateral margin; article 4 giving rise to antennular scale and flagellum; antennular scale elliptical, three times longer (0.19 mm) than wide; scale bearing simple setae along anterior and distal margin, also bearing at least four pairs of setae on lateral face; articles of antennular flagellum fused, forming a callynophore-like structure with a longitudinal row of 10 well-developed aesthetascs along posterior margin; flagellum also bearing hundreds of fine setae, insertions of which form at least 21 sets of transverse rows along anterior margin of flagellum.

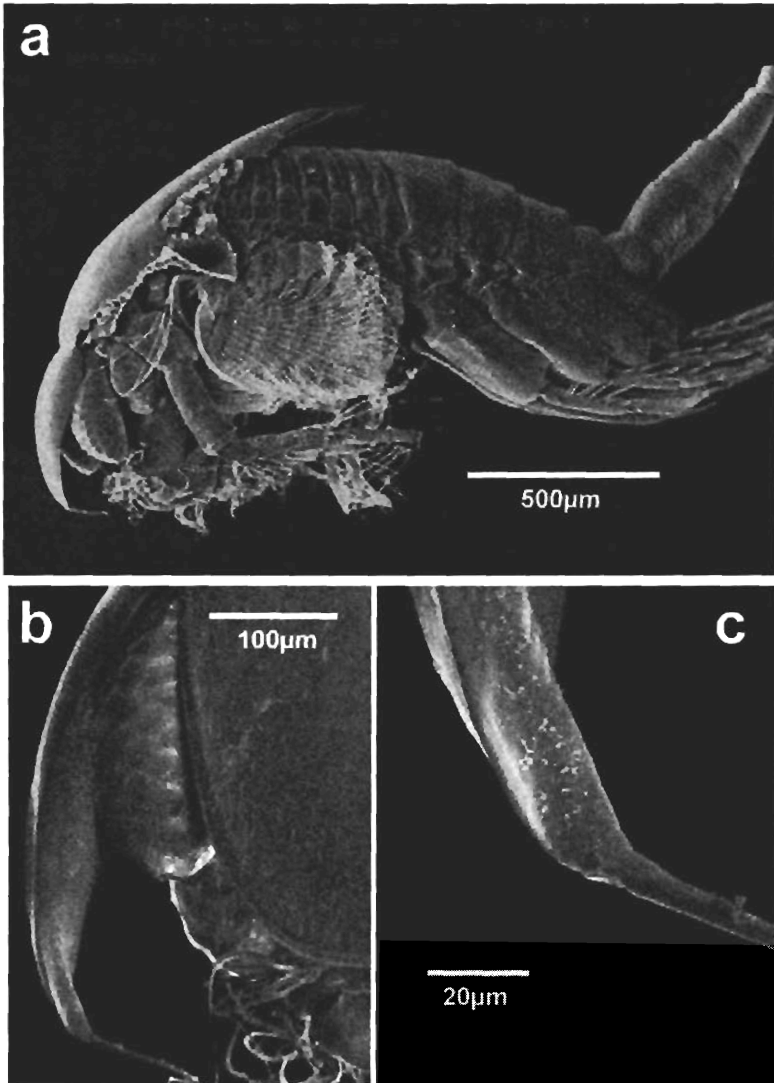


FIG. 2. *Saronebalia guanensis* n. gen., n. sp., paratype male: (a) whole specimen, left half of carapace removed; (b) surface of eye and rostrum, with antero-lateral portion of left side of carapace visible; (c) articulation between apex of rostrum and distal rostral seta.

Antenna with article 2 lacking setae, and with rounded protuberance on postero-distal margin; article 3 bearing simple setae along anterior margin; article 3 also bearing one short, robust seta on antero-medial margin, a similarly robust seta subterminally, and a distal group of at least 12 elongate setae, each of which is sparsely setulate; article 3 with single elongate seta arising from postero-medial margin; antennal flagellum with six articles, most proximal two of which appear fused; each flagellar article with pair of simple, apical setae arising from anterior margin, each subequal in length to article; flagellar articles each also bearing one to two smaller, fine setae on posterior margin.

Mandible. Not observed, presumably lacking.

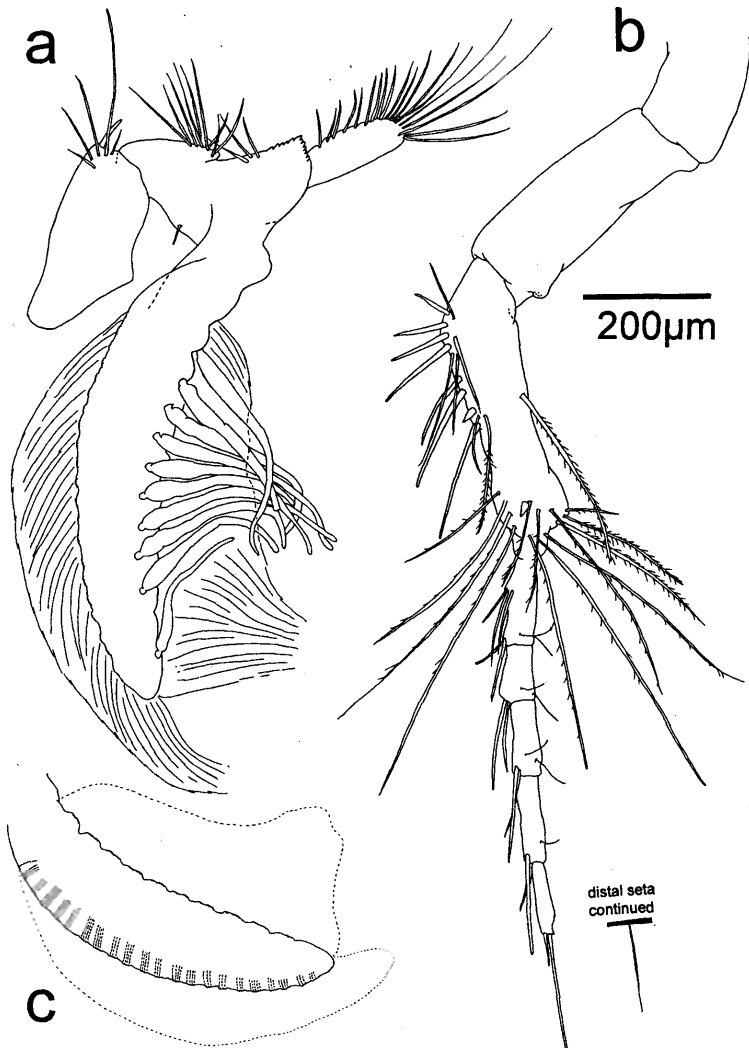


FIG. 3. *Saronebalia guanensis* n. gen., n. sp., paratype male: (a) antennule; (b) antenna; (c) antennular flagellum, drawn without setae or aesthetascs and with hashed line indicating space occupied by setae (200 μm scale bar refers only to (a) and (b)).

First maxilla (figures 1(e), 2(a)). Simple, lacking endites; maxillulary palp three-articulate, distalmost article of palp elongate, broadest proximally where it bears 12–14 long, lateral setae; palp also bearing two long terminal setae.

Second maxilla (figures 1(f), 6(a)). Simple, lacking endites; endopod uniarticulate and unornamented; exopod slightly longer than endopod, with five to six plumose setae extending from antero-distal margin.

Thoracopods (figure 7(a)–(b)). One to 6 and majority of thoracopod 7 enclosed by carapace; thoracopods 1–7 with endopods subequal, each densely setose along medial margin; endopod of thoracopods 1–7 much longer than exopod. Thoracopod 8 elongate, extending well beyond ventral margin of carapace and anteriorly directed, with exopod less than half length of endopod. Epipods of all thoracopods reduced (relative to *Nebalia*); that of thoracopod 8 minute.

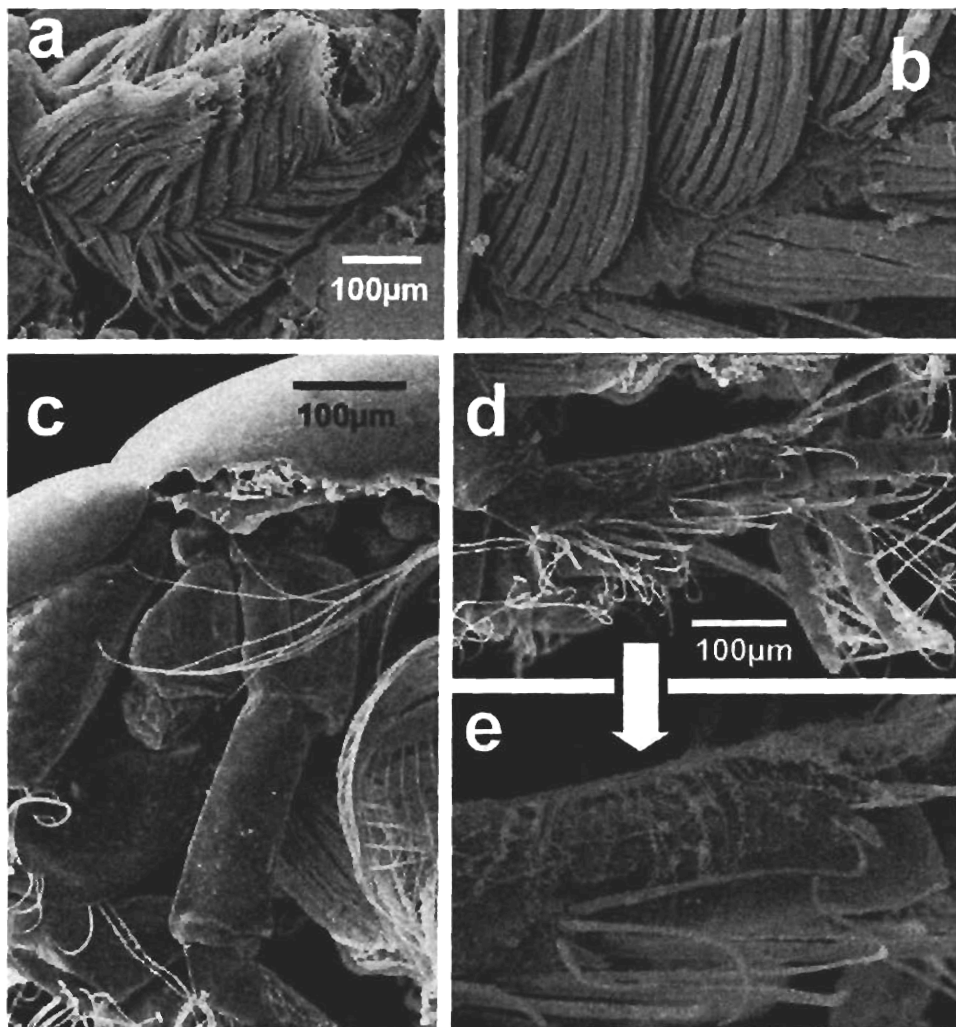


FIG. 4. *Saronebalia guanensis* n. gen., n. sp., paratype male: (a) antennular flagellum, antero-ventral surface; (b) antennular flagellum, showing clusters of setae at higher magnification; (c) anterior, left side of animal, with carapace removed, showing basal segments of antennule and antenna; (d) article three of antenna; (e) same article at higher magnification, showing one medial and one subterminal subacute process and the lack of conical setae (such as those of *Levinebalia*).

Pleonites (figures 1(a), 2(a), 8(a), 9(a)). Pleonite 4 postero-lateral corner convex, evenly rounded and lacking teeth; pleonite 5 narrower than pleonite 6; pleonites 5 and 6 with acute, triangular teeth along posterior margin, though absent ventrally.

Pleopods (figures 2(a), 7(c), 8(a)–(c), 9(a)–(b)). Pleopod 1 protopod with four or more minute serrations along posterior margin; protopod bearing appendix interna with three coupling hooks on distomedial margin; exopod bearing row of five robust setae along posterior margin and four robust setae apically, the distalmost of which is longest; lacking ‘spine row’ consisting of multiple, bipectinate setae (characteristic of *Dahlella*, *Nebalia*, *Paranebalia* and *Levinebalia*), anterior margin

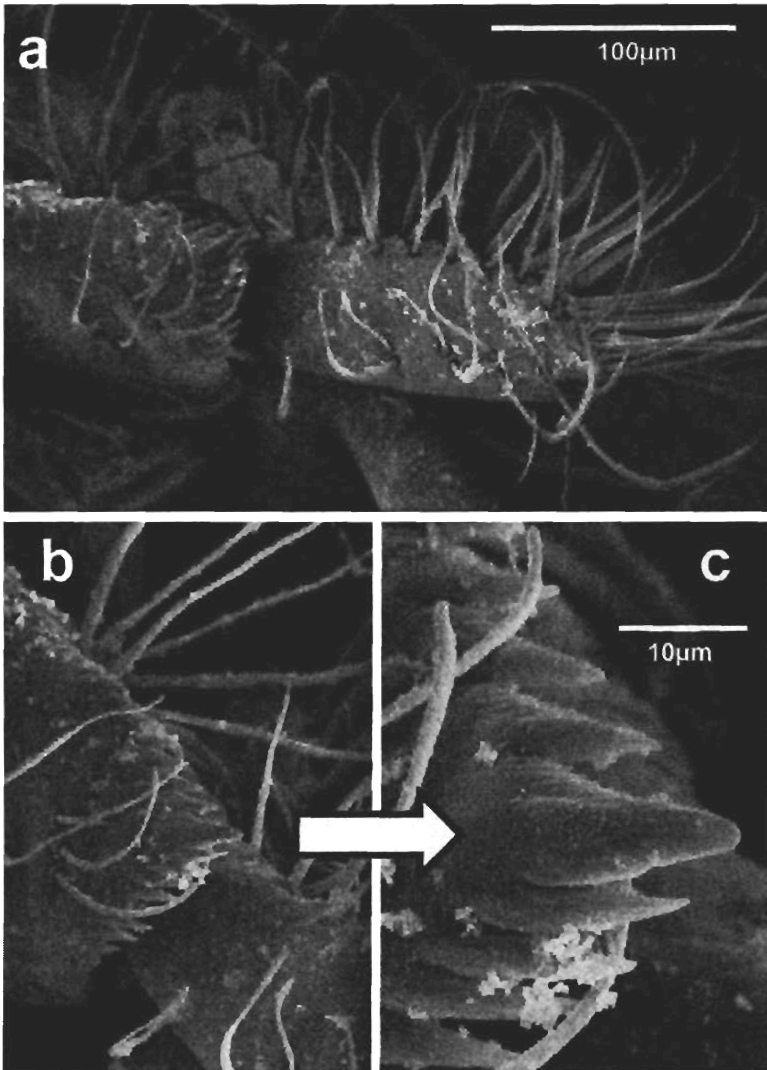


FIG. 5. *Saronebalia guanensis* n. gen., n. sp., paratype male: (a) antennular article 4 (on left side of image) and antennular scale (centre, with its setae extending to right margin of image); (b) subtriangular, denticulate process of antennular article 4; (c) apex of denticulate process of antennular article 4 at higher magnification.

with dense row of long, plumose setae; pleopods 2–4 possessing protopod with eight or nine marked serrations along posterior margin, each much larger than those of pleopod 1; bearing appendix interna similar in structure and position to that of pleopod 1; endopod slightly longer than exopod; exopod with four pairs of stout setae along posterior margin and three robust apical setae, with distalmost seta largest; pleopod 5 two-articulate, distal article much longer, lacking medial triangular process; pleopod 6 uni-articulate.

Telson and caudal furca (figures 7(d), 9(a), (c)). Telson short (range 0.16–0.27 mm), with even posterior margin, lacking dentition; bearing subtriangular

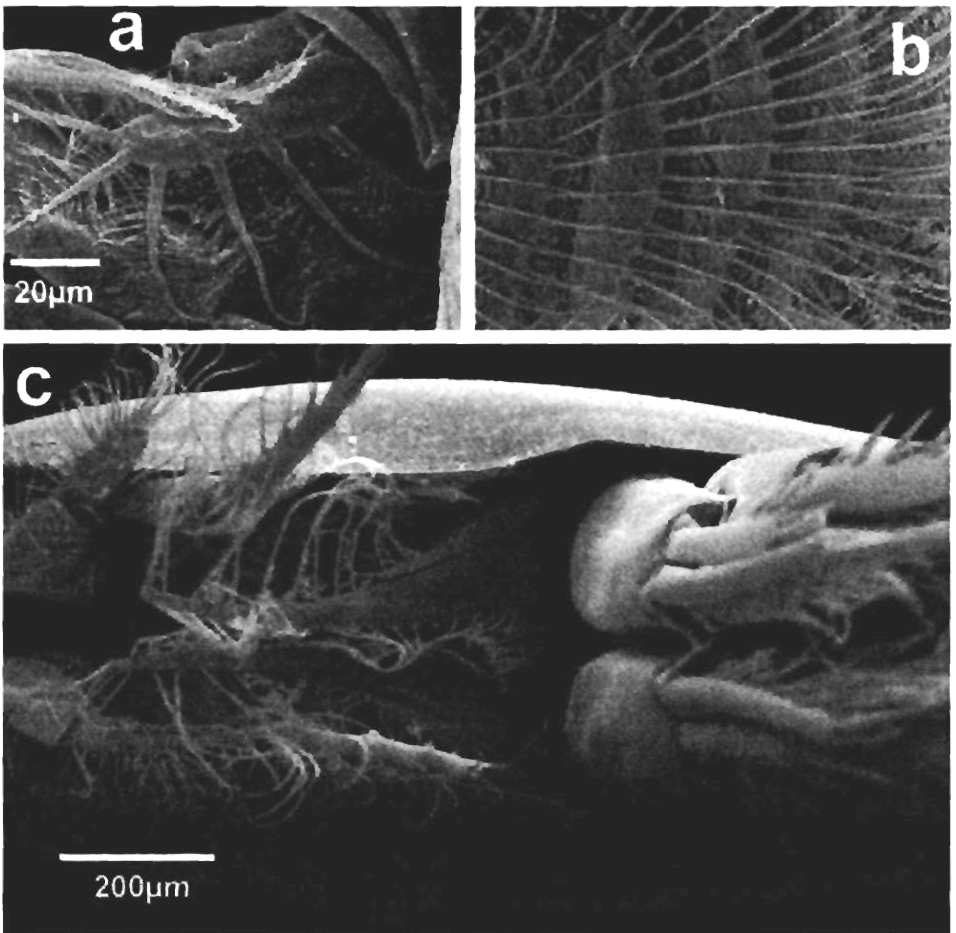


FIG. 6. *Saronebalia guanensis* n. gen., n. sp., paratype male: (a) maxilla; (b) exopods of thoracopods 3–6, showing structure of setae; (c) ventral aspect of thoracic region, showing portions of the antennules, antennae, eighth thoracopod and first pleopod.

anal plates, together producing V-shaped medial invagination; caudal furca 2.0–2.5 times as long as telson) (range 0.42–0.54 mm).

Etymology

The specific name *guanensis* is given for the type locality, Guana Island, British Virgin Islands.

Nomenclatural history of leptostracan genera

The genus *Nebalia* was erected by Leach (1814) for specimens collected along the coasts of England that had originally been referred to by Herbst (1804) and Montagu (1813) as *Cancer bipes* and *Monoculus rostratus*, respectively. According to Leach (1814), Herbst and Montagu had been unaware of the exact number of legs possessed by the specimens, and thereby Leach implied that these authors had not undertaken detailed examinations of the material. Leach recognized the animals as unique and stated 'In a systematic work, this genus [*Nebalia*] would hold a very conspicuous and important place, as it is not referable to any family hitherto

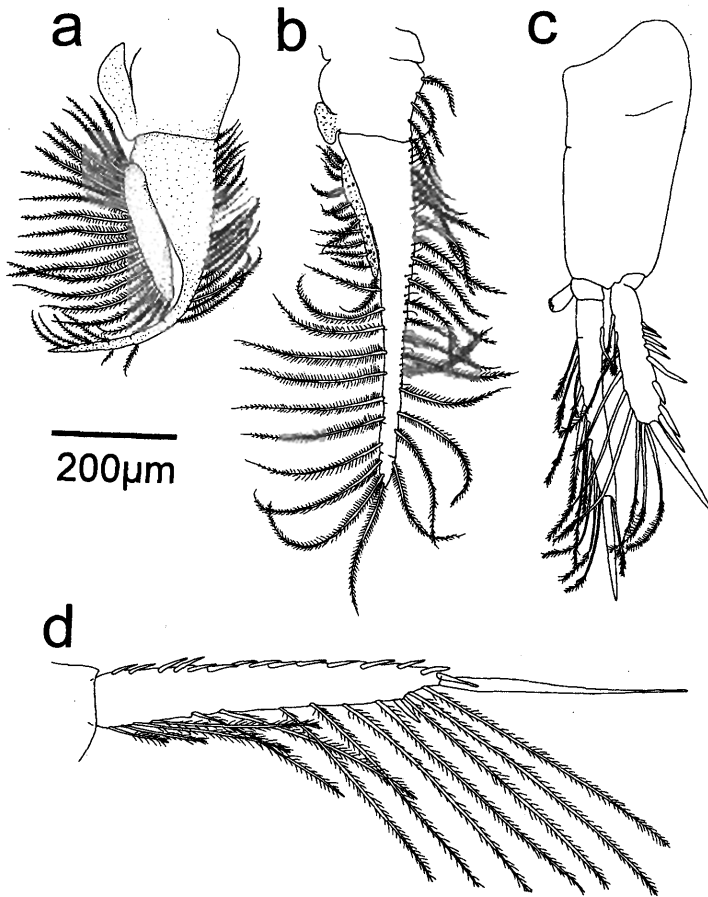


FIG. 7. *Saronebalia guanensis* n. gen., n. sp., paratype male: (a) thoracopod 4, right side, anterior face; (b) thoracopod 8, right side, anterior face; (c) pleopod 1, right side, posterior face, fine posterior margin serrations present, not visible in this aspect, see figure 8(a); (d) caudal furca, right side, dorsal view.

established. Its breathing organs are the same as in the other Crustacea Malacostraca, to which subclass it belongs'. By the end of the 19th century, a dozen species of *Nebalia* had been described.

Claus (1880) considered one of these species, *Nebalia longipes* Willemoes-Suhm, 1875, distinctive enough to erect a second genus, *Paranebalia*. Claus defined *Paranebalia* by the presence of a seta on the distal margin of the rostrum, the serrate posterior margins of the pleopodal protopods and the presence of tuberculate eyes. Following the recommendation made by Walker-Smith (2000) and Walker-Smith and Poore (2001), *Paranebalia* is now represented by three species, two endemic to the north-western Atlantic Ocean and an undescribed species from southern Australia.

The monotypic genus *Nebaliopsis* was the third genus established, described by Sars (1887) for deep-water (2514–4663 m) specimens originally collected during the Challenger Expedition. The collection of *Nebaliopsis* represents the greatest depth from which Leptostraca are known, although the measurement represents the amount of line used for the trawl, and therefore the specimens could have been

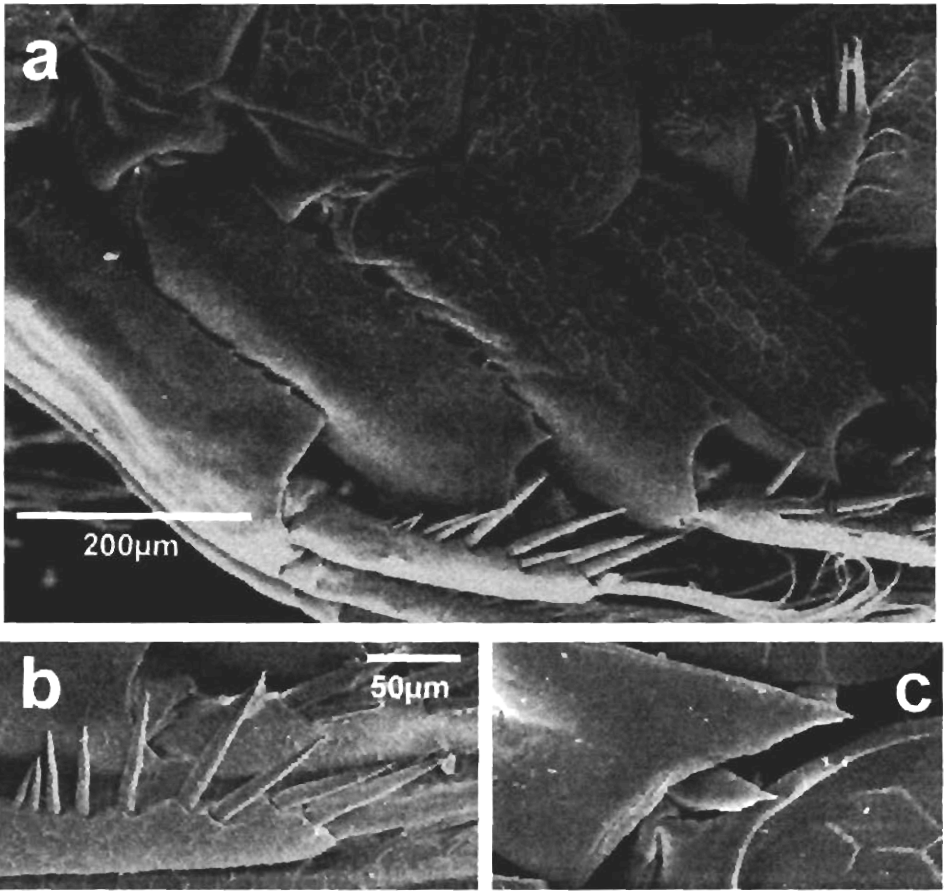


FIG. 8. *Saronebalia guanensis* n. gen., n. sp., paratype male: (a) lateral view of protopods of pleopods 1–4 (portion of pleopod 5 also visible), with full view of exopod of pleopod 1 and postero-lateral margin of pleonite 4. Note absence of dentition on margin of pleonite 4 and microstructure of surface of cuticle; (b) lateral setae of exopod of pleopod 1 at higher magnification; (c) acute process between point of limb attachment and proximal margin of protopod of pleopod 3 (also present for pleopods 1, 2 and 4).

collected at shallower depths. *Nebaliopsis* differs from other Leptostraca, reaching lengths of 50 mm and bearing a markedly sculptured cuticle, reduced abdomen and broad caudal furcae.

In 1904, Thiele added to the list of genera, describing *Nebaliella* from material collected in waters of the Southern Ocean in only 9–20 m. Thiele's specimens were most notable for the possession of elongate, cylindrical eyes that lacked visual elements and thoracic limbs that lacked epipods. Walker-Smith (1998) provided a review of the genus; *Nebaliella* is now known to include at least five species recorded primarily from deep waters (up to 2085 m) in the North Atlantic Ocean and off south-eastern Australia.

Clark (1932) erected the name *Epinebalia* for specimens that she examined from Puget Sound, Washington; however, Clark established the genus on the basis of only one character, stating 'The genus is determined by the antennae of the male; if females alone are under observation, the locality is the only guide' (p. 225).

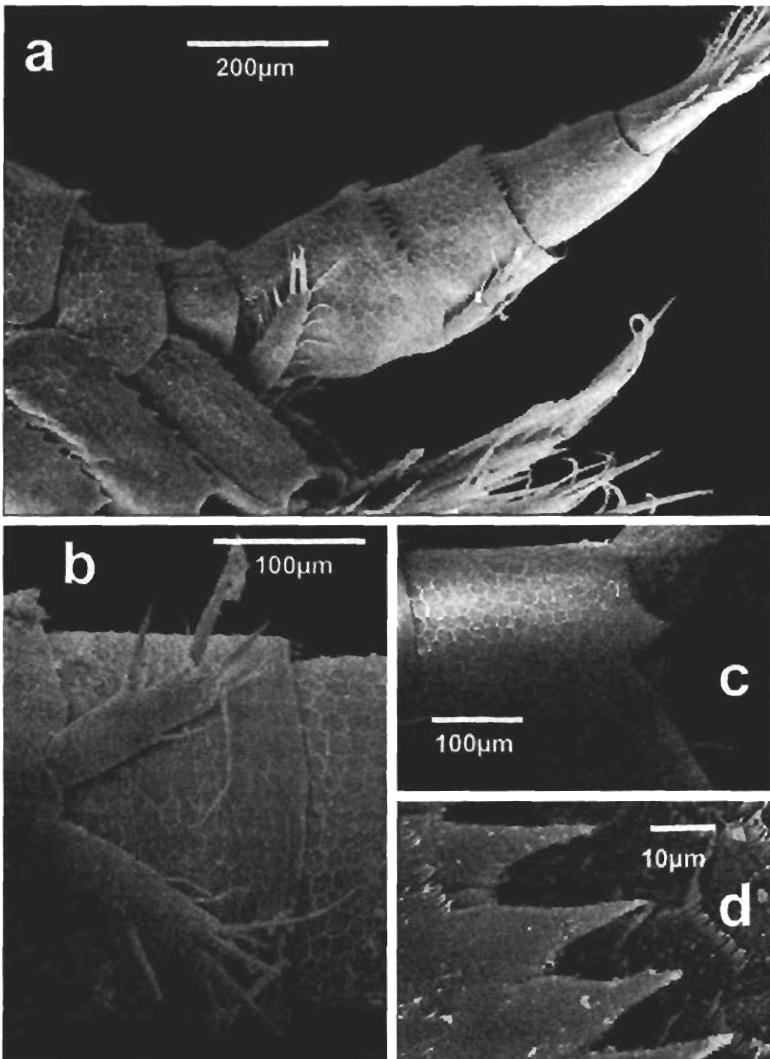


FIG. 9. *Saronebalia guanensis* n. gen., n. sp., paratype male: (a) posterior half of specimen, showing pleonites 3–7, telson and half of the caudal furca; (b) sixth pleopod, ventral view; (c) telson, showing anal plates, ventral view; (d) dentition of postero-dorsal margin of pleonite 6, showing form of teeth.

Recognizing that the shape of the male antenna merely represented sexual dimorphism and noting the presence of this character in species of *Nebalia*, Cannon (1960) rejected *Epinebalia*, declaring it to represent a junior synonym of *Nebalia*. Cannon's decision has been observed by other authors (Wägele, 1983; Dahl, 1985; Martin *et al.*, 1996; Vetter, 1996).

Hessler (1984) erected the fifth valid genus, *Dahlella*, for samples collected from hydrothermal vents of the Galapagos Spreading Centre and East Pacific Rise (at latitudes of 0, 9, 13, 20 and 21°). Unlike that of *Nebalia*, the rostrum of *Dahlella* lacks a keel. The eyes are elongate, sickle-shaped and bear a series of blunt denticles along their anterior margin. Additionally, the epipod of the second maxilla of

Dahlella is smaller than those of other leptostracans. To date, *Dahlella* has been recorded only from vent fields of the North Pacific Ocean.

The following year, two new genera were recognized. Bowman *et al.* (1985) described *Speonebalia* for specimens collected from marine caves in the Turks and Caicos Islands. Again, the diagnosis of the genus was based largely on the morphology of the rostrum, eye and mouthparts. As with *Dahlella*, the rostrum lacks a keel and the eyes lack visual pigments. Additionally, *Speonebalia* lacks a mandibular incisor and possesses an unusually long mandibular palp (Walker-Smith and Poore, 2001). The postero-dorsal margin of the carapace is ornamented with a series of small teeth, a feature that it shares only with *Nebaliella*. *Speonebalia* is known from sites at each end of the Bahama Island chain.

Dahl (1985) assigned a species of *Nebalia* to his new genus, *Sarsinebalia*. He observed several differences between *N. typhlops* and all other named species of *Nebalia*, including the presence of a rostral 'spine', the 'irregularly rectangular or circular' shape of the eyes, and the absence of the setal row of pleopod 1. Walker-Smith and Poore (2001) performed a phylogenetic analysis of the Leptostraca and stated 'We are unable to find any characters which support separate generic status for the monotypic *Sarsinebalia* and the genus must be synonymised with *Nebalia*...'. The dendrogram produced from their analysis placed *Sarsinebalia typhlops* with their undescribed *Nebalia* sp. B. However, the results of their analysis were not robust with respect to this particular taxonomic issue, and it might be the case that *Nebalia* sp. B of Walker-Smith and Poore (2001) could instead be referred to the genus *Sarsinebalia*. Dahl (1985) did note the existence of three undescribed leptostracan species, all of which he considered to belong to *Sarsinebalia*; two of these collections were from Australia.

Petryashov (1996) created an eighth genus, *Pseudonebaliopsis*, for new material collected from mesopelagic waters. The little-known specimens of this monotypic genus were said to differ from *Nebaliopsis* in several features, including the extent to which the carapace enclosed the body and details of the appendages. The validity of *Pseudonebaliopsis* has not been assessed, as no other authors have studied the original material. Still, if not synonymous with *Nebaliopsis*, undoubtedly it can be considered as its closest extant relative.

Recently, with the discovery of new specimens from Australian waters, Walker-Smith (2000) erected the genus *Levinebalia*. *Levinebalia* is distinguished by its unique antennular armature and the lack of a setal brush on the mandibular incisor. The genus includes one species from Australia and one from New Zealand (Walker-Smith, 2000). In the collections of the Natural History Museum of Los Angeles County, we have identified a specimen that extends the range of *Levinebalia* to Chile (Haney and Martin, unpublished data).

Saronebalia guanensis n. gen., n. sp. differs from all other extant Phyllocarida in the structure of the antennule; the antennule bears a denticulate, triangular scale on the fourth peduncular article and a highly setose, callynophore-like flagellum. The morphology of thoracopod 8 is also unique, as it is much longer than the other thoracic limbs and extends well beyond the ventral margin of the carapace. The dentition of the posterior margins of the pleonites is restricted to pleonites 6 and 7, whereas other leptostracans typically bear tooth-like processes along the posterior margins of all abdominal segments. The arrangement of minute scales seen on the cuticle of the pleonites and pleopods, appearing almost as a honeycomb-like pattern (see especially figures 8, 9), might also be a unique feature of *Saronebalia*.

However, with comparable SEM studies of most other leptostracans lacking, we cannot say how widespread this microstructure patterning might be. Live specimens of the new genus and species are rose-coloured and easy to discern from the beige coloration of specimens of other taxa.

Discussion

The use of Nebaliopsidae as an out-group in the phylogenetic analysis produced four equally parsimonious hypotheses. A consensus of these trees shows *Levinebalia* and *Paranebalia* as sister taxa to which *Saronebalia* in turn is the closest relative (see figure 10). The use of Mysidacea, rather than the Nebaliopsidae, for assigning character polarity resulted in five equally parsimonious trees. Although the relationship among *Saronebalia*, *Levinebalia* and *Paranebalia* was not altered, one of the five trees revealed a (*Speonebalia* (*Nebaliopsis* + *Pseudonebaliopsis*)) clade as the sister-group to the clade (*Saronebalia* (*Levinebalia* + *Paranebalia*)). The idea that *Speonebalia* might be more closely related to Nebaliopsidae than to nebaliids was also supported by the analysis of Olesen (1999: figure 7(b)), based mainly on the shared presence of a two-articulate sixth pleopod. However, Olesen's analysis also placed *Nebaliella* in this clade, and the resulting group (*Speonebalia* (*Nebaliella* + *Nebaliopsis*)) was the sister of a (*Sarsinebalia* (*Dahlella* + *Nebalia*)) clade. In the present study, we found greater support for a (*Nebaliella* + *Dahlella* (*Sarsinebalia* + *Nebalia*)) grouping. It is clear that these hypotheses should be considered as no more than a preliminary step toward resolution of relationships among leptostracan genera. The relationships depicted, for instance, are sensitive to out-group selection (see Walker-Smith and Poore, 2001, for a discussion of this problem as it relates to the inference of leptostracan phylogeny).

Regardless of variability in support for other (above-mentioned) clades, the analyses herein strongly corroborate the hypothesis of the close relationship of the new genus to the Paranebaliidae. *Saronebalia* shares a number of apomorphic characters with members of the genera *Levinebalia* and *Paranebalia*. Species of all three of these genera possess: (1) a seta at the apex of the rostrum; (2) males with callynophore-like antennular flagella; (3) two robust, conical setae on the third article of the antenna; (4) stenopodous thoracopods; and (5) four pairs of pleopodal protopods with serrate margins.

Despite sharing these characteristics with *Levinebalia* and *Paranebalia*, the specimens from Guana Island lack other features diagnostic of these genera. The eyes of *Saronebalia*, for instance, are more similar in form to those of *Nebalia*, being broader than those of either *Levinebalia* or *Paranebalia*. Although the ommatidia are well developed, the surface of the eyes of *Saronebalia* is also even and unornamented, differing greatly from the tuberculate eyes of *Paranebalia*. The ratio of carapace size to body size is smaller for the new specimens than in *Levinebalia* and *Paranebalia*, and the living colour of *Saronebalia* is reddish, whereas that of the others is a light tan or beige. The first seven thoracopods of *Saronebalia* are short, concealed almost entirely by the carapace. In *Levinebalia* and *Paranebalia*, in both males and females, all of the thoracopods extend well beyond the ventral margin of the carapace. The eighth thoracopod of *Saronebalia* is anteriorly directed and elongate, extending to the mouthfield. In *Saronebalia*, the first abdominal limb (i.e. pleopod one) also differs from that of *Dahlella*, *Nebalia*, *Levinebalia* and *Paranebalia* in that it lacks the comb-row of bipectinate setae on the exopod.

Another notable difference between *Saronebalia* and other leptostracans involves

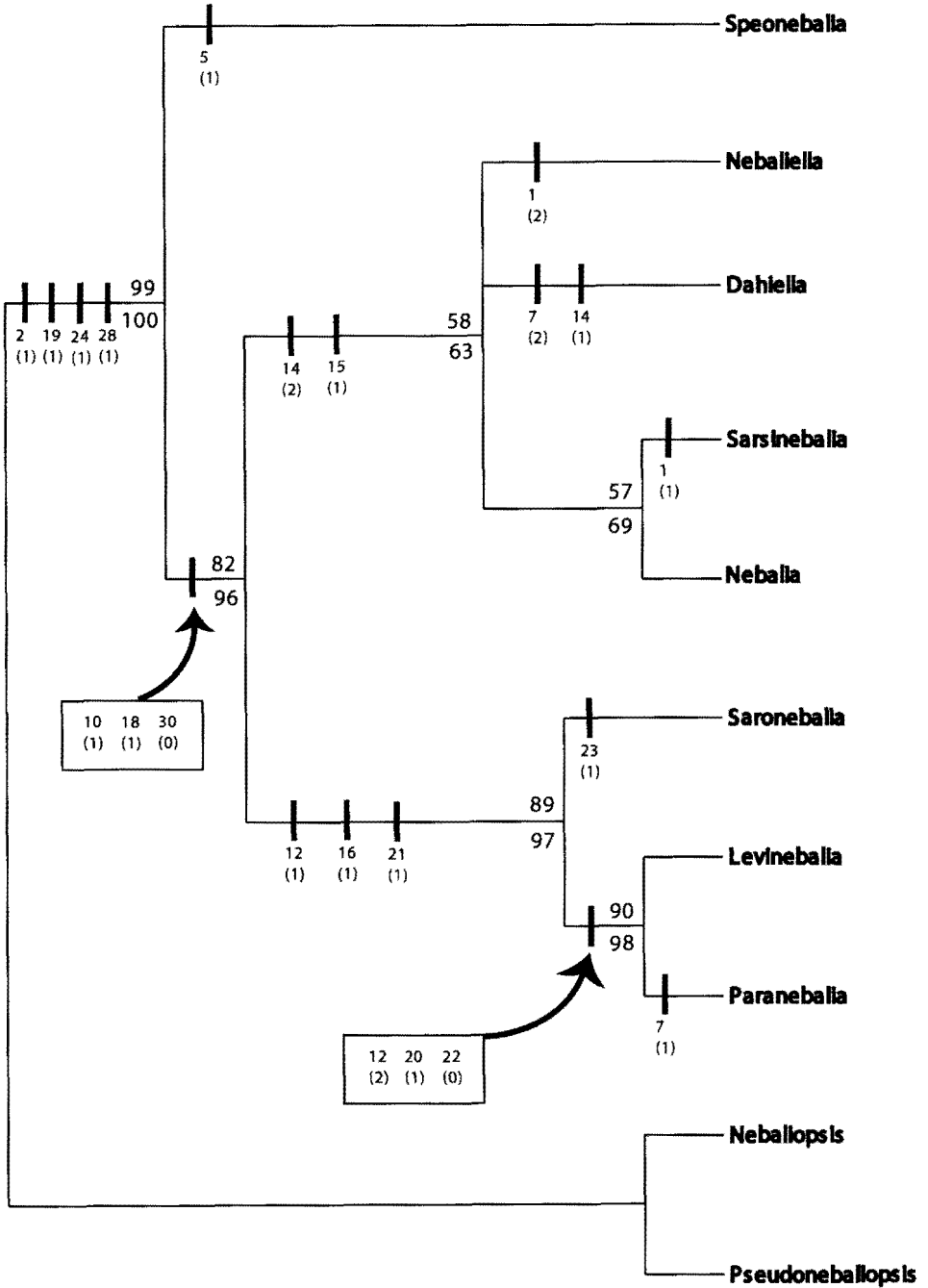


FIG. 10. Phylogenetic hypothesis of relationships among genera of the leptostracan families Nebaliidae and Paranebaliidae; strict consensus of two most parsimonious trees (consistency index, 0.784) found using 30 morphological characters and the exhaustive search option in PAUP*4.0b8. Character numbers shown beneath bars on branches, with apomorphic character state indicated in parentheses. Numbers above and below branches indicate bootstrap consensus and jackknife consensus values, respectively. See Appendices.

several features of the male's antennule. In *Levinebalia*, *Paranebalia* and the Nebaliopsidae the fourth peduncular article of the antennule bears a narrow flange with pronounced marginal teeth. *Saronebalia*, too, bears such a flange, but it is broad, subtriangular and much shorter than that of any species described to date (figures 3(a), 5(a)–(c)). The antennular flagellum of the male of *Saronebalia* forms a callynophore-like structure, with the articles mostly fused to one another and with each bearing both densely arranged setae and a large aesthetasc. Similar flagella have been noted on males of *Paranebalia* (Brattegard, 1970: figure 1(a), (b); Modlin, 1991: figure 5(a), (b)) and *Levinebalia* (Walker-Smith, 2000: figure 3); however, in *Saronebalia* the flagellum is longer, narrower, more setose and bears more aesthetascs. Modification of the antennular flagellum into a callynophore is not unique to these Leptostraca. Lowry (1986) described the callynophore in Eucarida and Peracarida as a sensory organ 'formed through fusion of the proximal flagellar articles and proliferation of transverse rows of aesthetascs on the medial or ventral face of the fused articles'. The aesthetascs of leptostracans appear to be arranged in a single longitudinal row, rather than a series of transverse rows; i.e. none of the 'articles' bears more than one aesthetasc. This is certainly the case with *Saronebalia*, in which all of the articles of the flagellum are fused and a single row of aesthetascs lines the posterior margin. As with the callynophores of other Crustacea, the morphology varies widely within the Leptostraca. We also note that aesthetascs are common among leptostracans in which the antennular flagellum is articulated and that, in some such species, the number of articles composing the flagellum is reduced (e.g. *Nebalia daytoni* Vetter, 1996; *N. marerubri* Wägele, 1983). Aesthetascs, and particularly the callynophore, are likely to serve a sensory function; Dahl (1975) and Lowry (1986: 348) both suggested that the callynophore of some amphipods might serve as a chemoreceptor for the detection of reproductively receptive females. Gardiner (1975), speaking of tanaids, stated 'their specialized first antennae are important in detecting the presence of females'. Some evidence indicates that this might also be its function (or one of its functions) in male leptostracans. First, the structure has been found thus far only in male leptostracans. Second, the general sparsity of male specimens in collections suggests that males and females sometimes might be spatially separated. It is not known whether the male specimens of *Saronebalia* caught using the light trap emerged from nearby bottom sediments in response to the light or were already free-swimming in the water column.

Lastly, the morphology of the mouthparts of *Saronebalia* is in many ways unique. The mandible appears to be altogether absent, and the maxillulary palp is highly elongate. The maxilla exists as a single lobe, with a sparsely setose exopod and unornamented endopod. These differences, however, might only pertain to male specimens and/or the particular life history stage of the specimens that were captured. Mouthpart reduction in terminal males is known, for instance, for some tanaids (see Gardiner, 1975: 176; Hansknecht, personal communication) and isopods (Wägele, 1981).

With recent field efforts targeted at the collection of leptostracans and with the study of museum collections, it is becoming clear that the order Leptostraca might be incredibly diverse. Indeed, six of the 10 genera have been described in the last 18 years (see table 1). Specimens housed in the collections of the US National Museum of Natural History appear to be sufficiently distinct to warrant the establishment of still another new leptostracan genus (personal observation). More taxonomic work is needed to assess the diversity of this group of Crustacea. The distribution of sampling efforts has been uneven, with the most intense sampling performed in the north-eastern

Atlantic Ocean, western coast of North America and Australia. Currently, six of the 10 genera are monotypic, and two of the genera include only two species.

Saronebalia is known only from Guana Island. To date, 25 male specimens have been collected, three of which were captured using a light trap and 22 of which were discovered in samples of *Halimeda* collected during the day. Neither the sorting of samples of *Halimeda* collected in 1998 and 1999 from adjacent localities on Guana Island nor the examination of other species of algae has yielded additional material of *Saronebalia*. We have found two other unidentified species of leptostracans from Guana Island, one of the genus *Nebalia* and one of *Paranebalia*; the latter species is sympatric with *Saronebalia* on a fine scale, being found in the same collections of *Halimeda*. Collections of *Nebalia* and *Paranebalia* from Guana Island included both male and female specimens. In fact, collections of Leptostraca are typically female-biased, and we consider it unusual that female specimens of *Saronebalia* have not been found. One explanation is that the males of the sympatric *Paranebalia* are dimorphic. Modlin (1996: 531), for instance, collected leptostracans from *Halimeda* in Belize and stated 'antennal flagella of mature males of *P. belizensis* were heavily covered with setae; they looked like bottle brushes'. Modlin's observation begs the question of whether those specimens represent males of *P. belizensis*, *Saronebalia* or something altogether different. The idea that the specimens herein named *Saronebalia guanensis* actually represent a second mature male morph or different ontogenetic stage of *Paranebalia* sp. seems unlikely given the dramatically different eyestalk, antennule, antenna, mouthpart and thoracopod morphology, and the difference in colour. We instead assume that the females were rare or separated from the males in space and/or time. In any case, additional information on the ecology of these Leptostraca might clarify taxonomic issues. Insights into the biology of these animals (and tests of our taxonomic hypotheses) stand to be gained from observations of the behaviour and distributions of these leptostracans *in situ*, manipulations of live specimens in the laboratory and the comparative analysis of genetic data from Caribbean populations.

Saronebalia guanensis is the fourth species of leptostracan described from the Caribbean Sea (see figure 11, which summarizes all known records). *Paranebalia longipes* (Willemöes-Suhm) was originally described from Bermuda but has been reported from islands throughout the Caribbean. The collections of the National Museum of Natural History, for instance, house a large number of specimens of this species from Dry Tortugas, Florida. *Paranebalia belizensis* Modlin, 1991, has been described only from *Halimeda* collected at Twin Cays on the barrier reef of Belize. *Nebalia lagartensis* Escobar-Briones and Villalobos-Hiriart, 1995, is known only from the Yucatán Peninsula of Mexico. A fifth species, *Speonebalia cannoni* Bowman, occurs in the region but is known only from marine caves of the Bahamas.

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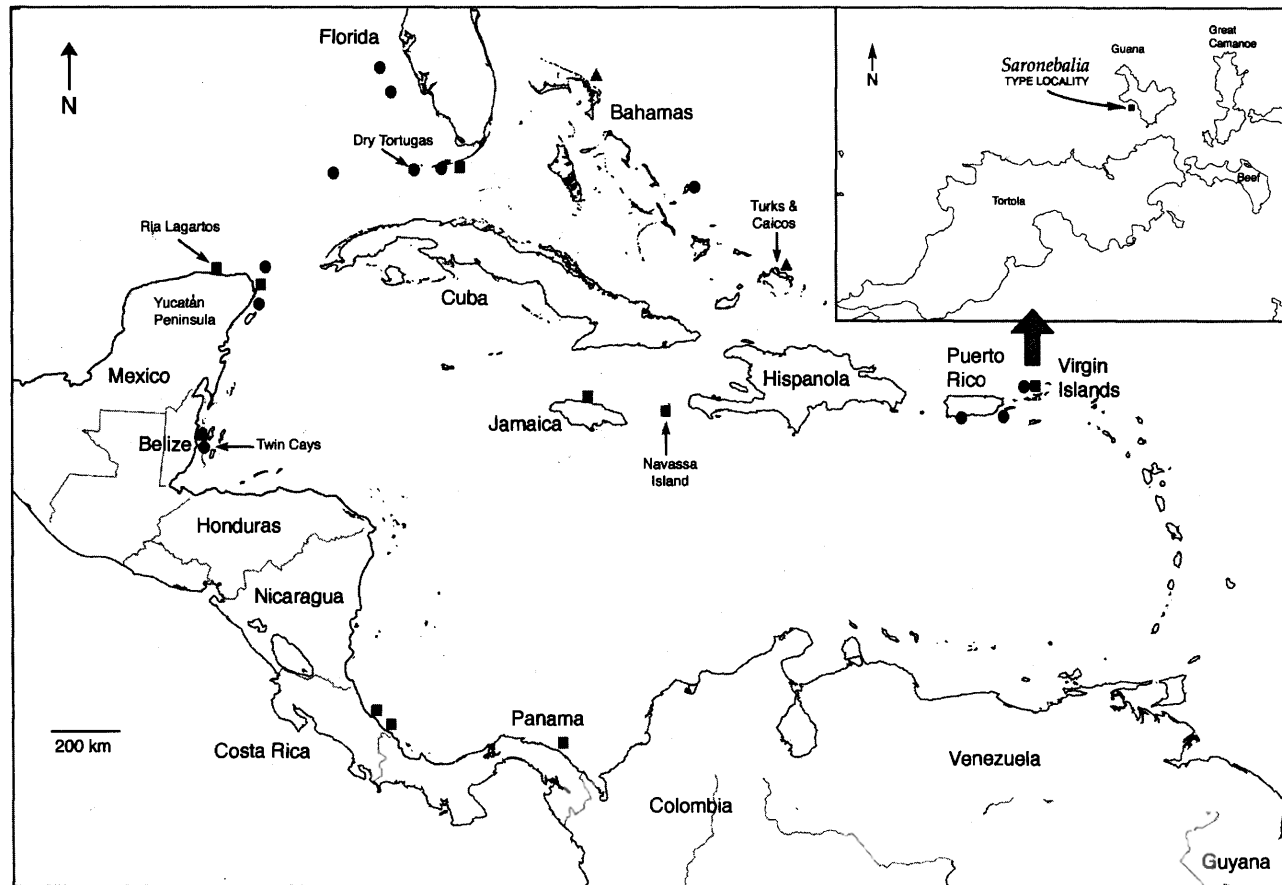


FIG. 11. Known distribution of leptostracan genera in the Caribbean Sea and adjacent waters, with inset showing type locality of *Saronebalia guanensis* n. gen., n. sp. Symbols represent areas from which leptostracans have been collected; multiple collections have been made in some of these areas. Square (■), record of *Nebalia*; circle (●), record of *Paranebalia*; triangle (▲), record of *Speonebalia*.

Appendix 1

Character data matrix

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Dahlella</i>	0	1	0	0	2	0	2	0	0	1	0	0	1	1	1	0	2	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>Nebalia</i>	0/1	1	0	0	0	0/1	0	0	1	1	0	0	1	2	1	0	1/2	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>Nebaliella</i>	2	1	0	1	2	0	0	1	0	0/1	0	0	0	2	1	0	2	1	1	0	0	1	0	1	0/1	1	0	1	0	0
<i>Sarsinebalia</i>	1	1	1	0	0	0	0	0	1	1	0	0	1	2	1	0	1	1	1	0	0	1	0	1	0	0	1	1	1	0
<i>Speonebalia</i>	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	0	1
<i>Levinebalia</i>	0	1	1	1	0	0	0	0	0	1	1	2	1	0	0	1	0	1	1	1	1	0	0	1	0	1	1	1	1	0
<i>Paranebalia</i>	0	1	1	1	0	0	1	0	0	1	1	2	1	0	0	1	0	1	1	1	1	0	0	1	1	1	1	1	1	0
<i>Saronebalia</i>	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	?	1	0	1	1	1	1	1	1	0	1	1	0
<i>Nebaliopsis</i>	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1
<i>Pseudonebaliopsis</i>	0	?	0	1	0	0	0	?	0	0	1	0	0	0	0	?	0	0	0	0	0	1	0	0	?	0	0	0	0	1
<i>Mysidacea</i>	0	?	?	0	?	?	0	0	0	?	0	0	0	0	0	0	0	1	0	1	?	0	0	0	0	0	?	0	?	?

Appendix 2*List of characters and character state descriptions*

1. Rostrum ventral surface smooth, lacking keel (0); with short, subrectangular keel (1); with pronounced keel, extending beyond distal margin of rostrum (2).
2. Rostrum with dorso-medial carina (0); with smooth dorsal surface (1).
3. Rostrum unornamented apically (0); bearing distal seta (1).
4. Eyestalk with supraocular scale (0); lacking supraocular scale (1).
5. Eyestalk shorter or subequal in length to rostrum (0); slightly longer than rostrum, tapering distally (1); highly elongate, much longer than rostrum, curving along anterior margin of carapace (2).
6. Eye dorsal papilla absent (0); present (1).
7. Eyestalk anterior margin relatively smooth, unornamented (0); with multiple subacute protuberances (1); with multiple blunt protuberances (2).
8. Carapace postero-dorsal margin smooth, even (0); bearing series of fine teeth (1).
9. Antennular article 4 robust apical seta(e) absent (0); present (1).
10. Antennular scale subcylindrical, slender and tapering distally (0); broad, blade-like (1).
11. Antennular article 4 apical margin normal, lacking flange (0); extended, producing dentate flange (1).
12. Antennular flagellum articles separate (0); fused, producing elongate callynophore-like structure (1); fused and inflated, forming globose callynophore-like structure (2).
13. Antenna with four peduncular articles (0); with three peduncular articles (1).
14. Antennal article one antero-distal margin unornamented (0); with rounded protuberance (1); with acute process (2).
15. Antennal article two antero-distal margin unornamented (0); with acute spine (1).
16. Antennal article three anterior margin bearing simple setae (0); with simple setae and robust conical sensory organs (sensu Walker-Smith, 2000) (1).
17. Antennal flagellum with eight or fewer articles (0); with 10–20 articles (1); with more than 20 articles (2).
18. Mandibular incisor absent (0); present (1).
19. Maxilla 1 grooming palp absent (0); present (1).
20. Thoracopods 1–7 concealed by carapace (0); extending notably beyond ventral margin of carapace (1).
21. Thoracopods 1–7 exopod much wider than endopod (0); slender, narrower than endopod (1).
22. Thoracopod 8 stenopodous (i.e. narrow) (0); foliaceous (1).
23. Thoracopod 8 subequal in length to thoracopods 1–7 (0); elongate, much longer than thoracopods 1–7 (1).
24. Pleonite 7 posterior margin, even, unornamented (0); crenate, with distally rounded or acute serrations (1).
25. Pleopod 1 protopod posterior margin even (0); with multiple serrations (1).
26. Pleopod 1 exopod bearing robust simple setae (0); with spine row and robust simple setae (1).
27. Pleopods 2–4 exopod with row of large, unpaired smooth seta (0); with paired smooth setae (1).

28. Pleopod 4 exopod broad, plate-like (0); narrow, of width similar to endopod (1).
29. Pleopod 6 two-articulate (0); uni-articulate (1).
30. Caudal furca narrow, tapering evenly from anterior to posterior (0); plate-like, broadest at mid-length (1).

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