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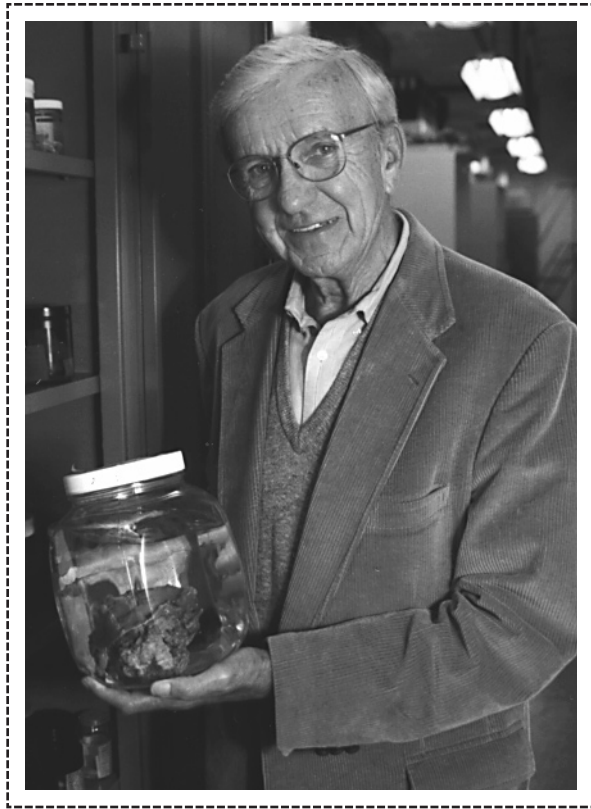
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of the
Peabody Museum of Natural History
Yale University

A Revision of
Parhyalella Kunkel
(Crustacea: Amphipoda:
Gammaridea)

Eric A. Lazo-Wasem
Michael F. Gable

Bulletin No. 46
September 2001
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Parhyalella Kunkel
(Crustacea: Amphipoda:
Gammaridea)



This paper is dedicated to Willard D. Hartman, who retired in 1992 after serving nearly 40 years as a professor in the Department of Biology, Yale University, and as curator of invertebrate zoology at the Yale Peabody Museum of Natural History, where he was director from 1997 to 1990, and where he is presently curator emeritus. Both his tireless dedication to the Museum's collections and the quality of his research have been an inspiration to us and many other scientists.

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ON THE COVER: *Parahyaella kunkeli*, new species, from Taiwan, named for Yale graduate B. W. Kunkel; YPM 8236, male paratype (above), and YPM 8237, female paratype (below). Copyright © 2001 Peabody Museum of Natural History, Yale University. All rights reserved. Photograph by William K. Sacco.

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ABSTRACT

The genus *Parhyalella* Kunkel, sensu lato, is revised, based on a review of type material for all previously described species, and on new material. *Parhyalella*, sensu stricto, is limited to four previously described species, *P. batesoni* Kunkel 1910, *P. whelpleyi* Shoemaker 1933, *P. pietschmanni* Schellenberg 1938, and *P. congoensis* Ruffo 1953; and to the new species *P. barnardi*, *P. kunkeli*, *P. nisbetae*, *P. ruffoi* and *P. steelei*. The genus *Exhyalella* Stebbing is re-established as a valid taxon that includes *E. natalensis* Stebbing 1917, *E. indica* K. H. Barnard 1935, and *Exhyalella hartmani*, new species. *Marinohyalella*, new genus, is a monotypic genus erected for *M. richardi* (Chevreux 1902). The systematic position of the three genera within the traditional concept of the Hyalidae is discussed. Keys to marine hyalid genera of the world and to species within *Parhyalella* and *Exhyalella* are provided. Lectotypes for *P. pietschmanni*, *E. natalensis* and *E. indica* are also designated.

RESUMEN

Se hace una revisión del género *Parhyalella*, sensu lato con base en el estudio de material tipo de todas las especies previamente descritas y de material recientemente recolectado. El género *Parhyalella*, sensu stricto queda restringido para cuatro especies anteriormente descritas *P. batesoni* Kunkel 1910, *P. whelpleyi* Shoemaker 1933, *P. pietschmanni* Schellenberg 1938, y *P. congoensis* Ruffo 1953, y para cinco especies nuevas, *P. barnardi*, *P. kunkeli*, *P. nisbetae*, *P. ruffoi* y *P. steelei*. Se reestablece, como un taxón válido el género *Exhyalella* Stebbing que incluye *E. natalensis* Stebbing 1917, *E. indica* K. H. Barnard 1935, y *Exhyalella hartmani*, especie nueva. El género *Marinohyalella*, género nuevo, constituye un género monotípico que se ha establecido para *M. richardi* (Chevreux 1902). Se discute la posición sistemática de los tres géneros dentro del concepto tradicional de la familia Hyalidae. Se presentan claves para los géneros marinos de Hyalidae en el mundo y para las especies de los géneros *Parhyalella* y *Exhyalella*. Además se designaron lectotipos para las especies *P. pietschmanni*, *E. natalensis* y *E. indica*.

KEYWORDS

New species, new genus, talitroidean phylogeny, *Insula*, taxonomic keys, ecology, distribution, *Parhyalella*, *Exhyalella*, *Marinohyalella*, status amendments, Hyalidae.

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From the onset of our study we hoped to examine specimens of all known species of *Parhyalella* sensu lato rather than rely on published accounts, as these contained too many inconsistencies. We were fortunate to receive cooperation from many individuals. C. Carpine, Musée de Monaco, provided us with type specimens from the Mediterranean and also outlined historical and geographical details not available in published accounts. Type specimens and copies of the original catalog data for specimens from South Africa were lent by M. G. van der Merwe, South African Museum, and final disposition of the specimens was handled by L. Hoensen. C. D. Quickelberge, Durban National History Museum, helped determine the depository for the type specimens. W. D. Hartman, Yale University, kindly arranged the loan, through S. C. Ray of the Indian Museum, for specimens from India. H. S. Feinberg, formerly of the American Museum of Natural History, lent the type specimens of *Parhyalella whelpleyi*. Specimens of *P. whelpleyi* were lent by the late J. L. Barnard, United States National Museum, and additional specimens of this species were donated by Y. Wakabara, Universidade de São Paulo, Brazil. C. O. Coleman, Zoologisches Museum, Berlin, allowed Gable to examine specimens of *P. whelpleyi* in that museum, and later re-examined these and provided further observations. V. Stagl, Naturhistorisches Museum Wien, lent type and nontype specimens of *P. pietschmanni*; questions were subsequently addressed by P. C. Dworschak of that institution. Additional specimens of *P. pietschmanni* were also lent by J. L. Barnard, United States National Museum. Type specimens of *P. congoensis* and helpful correspondence were provided by R. Jocque, Koninlijk Museum Voor Midden-Africa, Tervuren, Belgium.

In addition to specimens of previously described species, several scientists generously provided specimens that we have used in our descriptions of new species. The late J. L. Barnard, United States National Museum, provided specimens from the west coast of Mexico, and from Peru. D. H. Steele, Memorial University, Newfoundland, Canada, provided specimens from Madagascar (previously identified by him as *P. pietschmanni* in his population studies). Finally, C. F. Dai, Taipei University, generously donated a small collection of amphipods from Taiwan; these specimens prompted us to undertake the revision of *Parhyalella*. J. D. Thomas, Nova University, Florida, provided valuable insight into *Parhyalella* ecology that, along with information provided by D. H. Steele, led to the discovery of a new Caribbean species.

E. Harrison-Nelson, United States National Museum, provided invaluable assistance in processing our many loan transactions and requests for specimen information. C. B. Kim generously provided both a copy of his dissertation and useful notes concerning *Parhyalella* in Korea. C. B. Robbins allowed us to use illustrations of *P. batesoni* from Lazo-Wasem and Gable (1987). A. Patnode III, formerly of Eastern Connecticut State University, helped translate papers written in French. O. Breedy, University of Costa Rica, kindly translated the abstract into Spanish. L. F. Gall and R. D. White, Peabody Museum of Natural History, Yale University, answered questions of type terminology. This paper benefited greatly from reviews by A. J. Baldinger, Museum of Comparative Zoology, Harvard University, A. A. Myers, University College, Cork, Ireland, and W. Vader, University of Tromsø, Norway; all errors are the sole responsibility of the authors. This research has been supported in part by several Connecticut State University grants to Gable.

A Revision of
Parhyalella Kunkel
(Crustacea: Amphipoda:
Gammaridea)

Introduction

The genus *Parhyalella* Kunkel 1910 was erected for *P. batesoni* Kunkel, a species represented by a single male specimen collected by A. E. Verrill in Bermuda (Lazo-Wasem and Gable 1987). Since Kunkel's monograph (1910), six other species have been assigned to the genus either through transfer or original descriptions. These are *P. richardi* (Chevreux) 1902, *P. natalensis* (Stebbing) 1917, *P. whelpleyi* (Shoemaker) 1933, *P. indica* (K. H. Barnard) 1935, *P. pietschmanni* Schellenberg 1938 and *P. congoensis* Ruffo 1953. Only three of these species, *P. pietschmanni* Schellenberg (Barnard 1970), *P. batesoni* (Lazo-Wasem and Gable 1987) and *P. richardi* (Krapp-Schickel 1993), have received any review beyond their original descriptions.

The generic diagnosis of *Parhyalella* is based principally on the lack of a palp on maxilla 1. We examined the single specimen of *P. batesoni* deposited in Yale University's Peabody Museum of Natural History. The mouthpart appears to have a slight indentation where a palp would originate. This indentation seems natural but could be a site of microdamage or the site of origination of a broken-off palp on maxilla 1. The latter condition, if true, would be contradictory to the original diagnosis of the genus.

To corroborate the existence of *Parhyalella* as a valid genus, we obtained type specimens of all named species. Through correspondence with colleagues we learned of unattributed specimens of *Parhyalella* and *Parhyalella*-like hyalids, and we included these in our examination. A thorough study of all the specimens available indicated that *Parhyalella* as described in the literature is actually a complex of three distinct genera: *Parhyalella* sensu stricto; *Exhyalella* Stebbing 1917, previously synonymized with *Parhyalella* and herein re-established as a valid genus (revised status); and *Marinohyalella* new genus. In addition, six new species were discovered and assigned to the corresponding genera.

A diagnosis is presented for each genus, followed by diagnoses or redescrptions of component species and a section on morphological differences among congeneric species. We give geographic distributions and, when possible, ecological information for species in all three genera. Keys are provided for all species in *Parhyalella* and *Exhyalella*. We compare the three genera morphologically and address historical problems centered on synonymies. We also comment on phylogenetic affinities among the three genera and offer suggestions concerning their proper family assignment. A new key to the Hyalidae sensu lato, based on that of Barnard and Karaman (1991), incorporates the new and re-established genera. All body lengths are given in millimeters, measured from the tip of the rostrum to the base of the telson, with the amphipod in straightened (unflexed) position. The gnathopods are considered equivalent to pereopods 1 and 2. Article 7 of the gnathopods and pereopods is referred to only as the dactyl.

Institutional abbreviations used here are as follows: AMNH, American Museum of Natural History, New York, New York, U.S.A.; MBC, Museum of the Belgian Congo, Tervuren, Belgium; MOM, Musée Oceanographique, Monaco; NHMW, Naturhistorisches Museum, Vienna, Austria; SAM, South African Museum, Durban, Republic of South Africa; USNM, United States National Museum, Washington, D.C., U.S.A.; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.; ZMB, Zoologisches Museum, Berlin, Germany; ZSI, Zoological Survey of India, Calcutta, India.

Systematic Account of *Parhyalella* Kunkel 1910

Description of Genus

PARHYALELLA KUNKEL 1910

Parhyalella Kunkel; 1910:74–76.

Parhyalella Barnard and Karaman; 1991:372, fig. 70D, H.

Parhyalella Krapp-Schickel; 1993:758.

Parhyalella Gonzalez and Watling; 1998:140–141.

Diagnosis: Male antenna 2 inflated, much larger than antenna 1, first article of flagellum conjoined. Female antenna 2, flagellum with aesthetascs. Right mandible molar with plumose accessory seta. Maxilla 1 lacking a palp, with distinct shelf on outer margin of outer lobe, distal margin of outer lobe bearing nine teeth. Maxilliped palp 4-articulate, article 4 unguiform, lacking whip-like seta. Male gnathopod 1 much smaller than gnathopod 2, palm of article 6 varying from transverse to oblique; gnathopod 2, article 6 broad, palm moderately oblique. Female gnathopod 1, palm of article 6 transverse; gnathopod 2 much larger than gnathopod 1, palm moderately oblique, of distinctly different morphology than gnathopod 1. Female gnathopod 2 of similar morphology to that of male, but smaller. Uropods 1 and 2 (both sexes), outer rami spinose along margin. Telson entire.

Type species: *Parhyalella batesoni* Kunkel 1910.

Distribution: Subtropical and tropical Atlantic, Pacific and Indian Oceans.

Included species: *P. batesoni* Kunkel, *P. whelpleyi* (Shoemaker), *P. pietschmanni* Schellenberg, *P. congoensis* Ruffo, *P. barnardi* new species, *P. kunkeli* new species, *P. nisbetae* new species, *P. ruffoi* new species, *P. steelei* new species.

Species Descriptions

PARHYALELLA BATESONI KUNKEL 1910

Figures 1, 2

Parhyalella batesoni Kunkel; 1910:74–76, fig. 28.

Parhyalella batesoni Lazo-Wasem and Gable; 1987:328–331, figs. 5, 6.

Parhyalella batesoni Barnard and Karaman; 1991:368, 372, fig. 70.

Material examined: YPM 8188: male holotype, 6.8 mm, and microscope slides of appendages; Bermuda; collector and date unknown.

Diagnosis: *Male.* Eye large, oval. Antenna 1 longer than peduncle of antenna 2. Antenna 2 strongly inflated, peduncular article 4 distinctly thicker than peduncular article 1 of an-

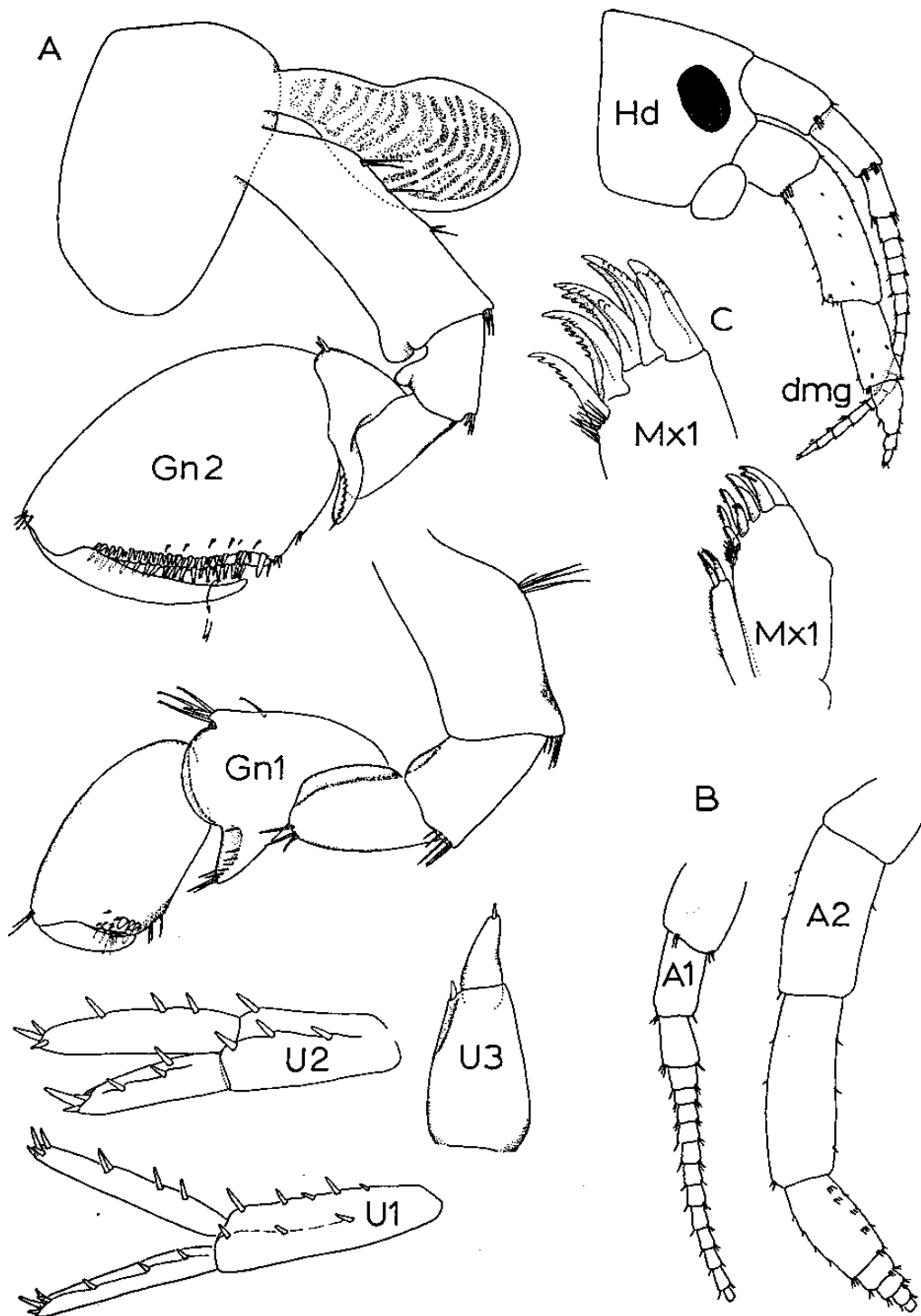


Figure 1.

Parhyalella batesoni Kunkel, YPM 8188, male holotype, 6.8 mm. A. Damaged head (from Lazo-Wasem and Gable 1987). B. Left antenna 1 and 2 with normal proportions. C. Maxilla 1, outer plate, showing correct number of distal teeth. *Abbreviations:* A, antenna; Gn, gnathopod; Hd, head; Mx, maxilla; U, uropod; dmg, damaged.

tenna 1, article 5 longer than article 4; article 1 of flagellum 5-conjointed, longer than remainder of flagellum. Gnathopod 1, article 5 anterior margin with single medial seta, article 6, palm transverse, dactyl simple. Gnathopod 2, width of article 6 is 66% length, palm longer than hind margin, hind margin with single medial setal cluster. Uropod 3, peduncle with single distal spine, ramus less than 50% length of peduncle.

Type locality: Bermuda (but note remarks).

Description: *Male.* Eye large, oval, black in alcohol-preserved specimen. Antenna 1 shorter than antenna 2, flagellum composed of 14 articles. Antenna 2, peduncle very stout, broadly inflated, article 4 distinctly longer than article 5, articles 4 and 5 with small marginal and facial spinules, first article of flagellum consisting of five conjointed segments, flagellum shorter than conjointed article. Maxilla 1, inner plate shorter than outer plate, with two distal plumose setae, outer plate lacking palp. Gnathopod 1, article 4 with three distal setae, article 5 subequal in length to article 6, with single marginal seta and cluster of four distal setae, article 6, palm transverse, nearly straight, lightly setose, posterior corner rounded, defined by stout submarginal spines, dactyl stout, simple. Gnathopod 2, article 5 very short, anterodistal corner with two small spines, article 6 very wide, palm longer than hind margin, heavily spinose, posterior corner defined by large spine and shallow excavation, hind margin with a medial setal cluster. Uropods 1 and 2, normal, spinose, uropod 2, inner ramus with one group of two spines. Uropod 3, peduncle with single, small, distal spine, ramus slightly less than 50% length of peduncle, distally with one small seta. Telson entire.

Female. Unknown.

Remarks: Since the redescription of this species by Lazo-Wasem and Gable (1987), two microscope slides bearing appendages dissected by B. W. Kunkel were found among miscellaneous unsorted material at the Yale Peabody Museum in a slide box labeled "returned by Dr. Kunkel, 1910." The slides were labeled as "*Hyalopsis batesoni*," which we believe to be a provisional name for *Parhyalella batesoni*. Mounted on one slide are one each of antennae 1 and 2, and gnathopods 1 and 2, the latter precisely matching those figured by Kunkel. Kunkel described *P. batesoni* from a single specimen, and therefore there is no doubt that the appendages on the slide belong to the holotype. The flagellum of antenna 2 seems to have lost at least one article but is otherwise intact. The newly found antenna 2 clearly shows that the antenna 2 used for our redescription of this species (Lazo-Wasem and Gable 1987) was significantly damaged, and led us to believe, erroneously, that antenna 1 is longer than antenna 2. In our former illustration (reprinted, Figure 1) article 4 of the peduncle appeared shorter than article 5, whereas the opposite is true. Furthermore, the illustration showed only eight distal teeth on the outer plate of maxilla 1. The correct number of teeth is nine, which shows clearly on the mounted maxilla on Kunkel's slide (see Figure 1C). Finally, the number of conjointed segments of article 1 of the flagellum was reported as three, but the correct number is five. This feature now clearly distinguishes the only known specimen of *P. batesoni* from *P. whelpleyi* of the Caribbean; the latter antenna 2 flagellar article 1 comprises three conjointed segments.

On the other slide are the maxilliped, maxilla 1, and lower lip, but unfortunately the mandibles are lacking, so features of the lacinia and the mandibular molar accessory seta cannot be determined. Although partially dried out, the three teeth on the outer plate of the maxilliped are distinct.

In five expeditions to Bermuda between 1985 and 1993, we failed to discover any additional specimens of *Parhyalella*, even though approximately 20,000 amphipod specimens were collected from many habitats (including those accessible only by SCUBA) at

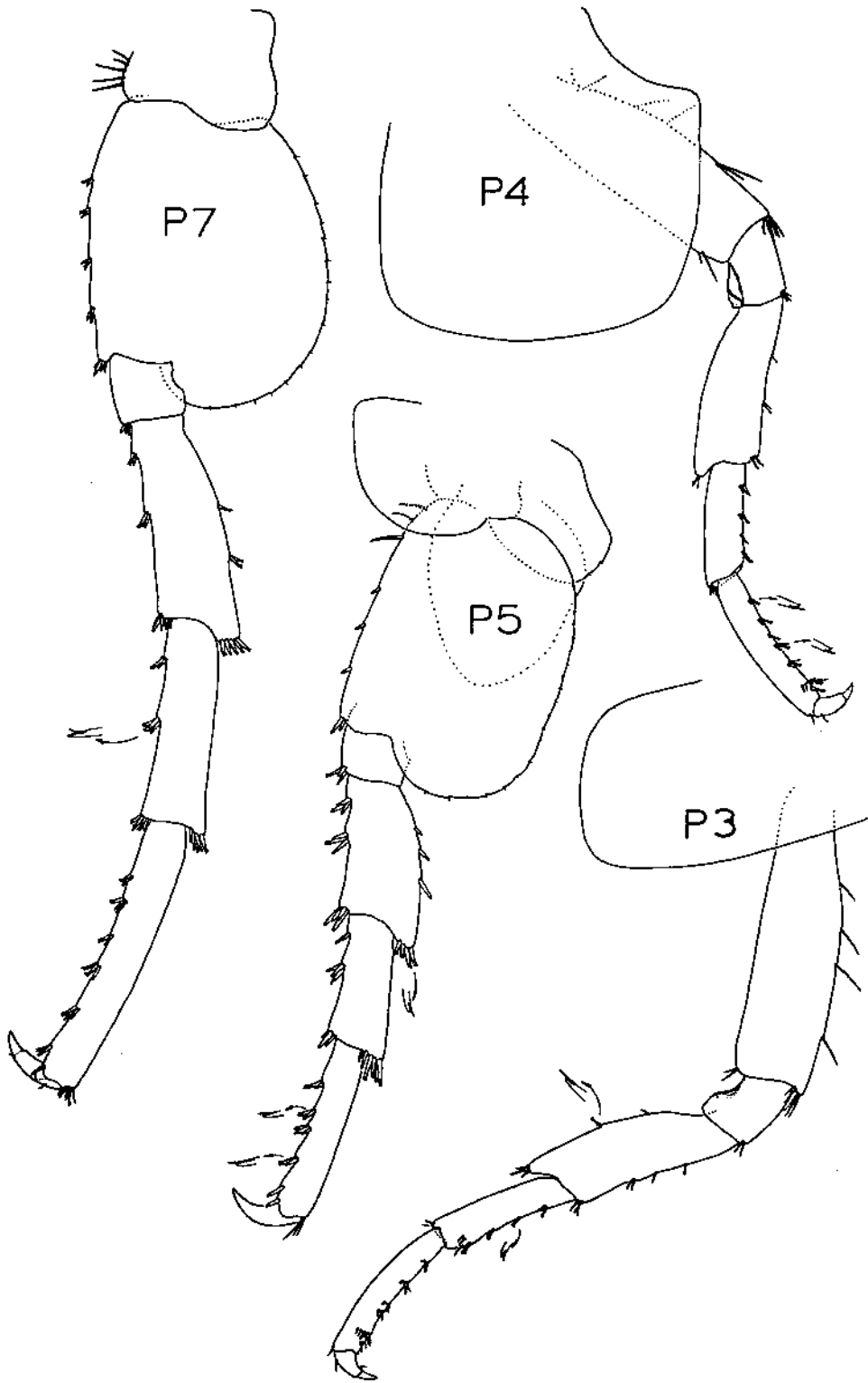


Figure 2.

Parhyalella batesoni Kunkel, YPM 8188, male holotype, 6.8 mm. Abbreviation: P, pereopod.

dozens of localities encompassing the entire island, from shallow waters to depths greater than 20 m.

At this point we must speculate on the apparent absence of this species from the Bermuda isles. The possibility exists that the specimen of *Parhyalella batesoni* described by Kunkel was not from Bermuda. In 1906, A. E. Verrill's son, A. H. Verrill, made a large collection of crustaceans from Dominica, and from New Providence Island, Bahamas. A. E. Verrill's intent was to publish an account of the Dominican crustacean fauna; although figures of many of the decapods were produced, the manuscript was never completed. Instead, some of the Dominican and Bahamian species were described in three major papers that A. E. Verrill (1908, 1922, 1923) wrote on the Bermuda crustacean fauna, primarily concerning the Decapoda.

Lazo-Wasem has encountered many labeling inconsistencies for the Bermuda specimens—not only among amphipods and other crustaceans, but also for other phyla, such as the annelids—catalogued at the Yale Peabody Museum. In some instances, pre-printed labels from the 1901 Verrill expedition were used for specimens collected in 1898, and vice versa, and do not always agree with the published data. In some cases, it is clear the labels were added to the collection vials well after the expeditions took place (based on our knowledge of the handwriting of those persons participating in the expeditions and those cataloguing the material at the Peabody Museum at that time). Furthermore, the general collection data were apparently entered in large series in the Peabody catalogs before the specimens were identified. Usually the first entry was filled in at the top of a page and then ditto marks (signifying a run of records bearing the same basic data) carried through to the end of the series. Interspersed throughout the Bermuda catalog data (noted by amendments to the records) were specimens from other localities such as Florida, the Bahamas and Dominica.

When first discovered in 1986, none of the type specimens of Kunkel had ever been catalogued, and many lacked original labels beyond the one bearing Kunkel's identification. Thus, it is conceivable that the specimen of *P. batesoni* was collected from a locality other than Bermuda. Nevertheless, we believe *P. batesoni* to be a valid species; no other specimens from the genus can be assigned to this species.

PARHYALELLA WHELPLEYI (SHOEMAKER 1933)

Figures 3, 4

Hyalella whelpleyi Shoemaker; 1933:22–24, figs. 12, 13.

Parhyalella whelpleyi non Shoemaker; 1948:11.

Parhyalella whelpleyi Barnard; 1970:271.

Parhyalella whelpleyi Barnard and Karaman; 1991:372.

Parhyalella whelpleyi da Cunha Lana and Guiss; 1992:57.

Parhyalella whelpleyi Wakabara and Serejo; 1998:570.

Material examined: AMNH 6693: male holotype, 6.4 mm. AMNH 6831: male paratype, 7.4 mm; female paratype, 4.2 mm; seven male paratypes, four female paratypes; Trinidad, Port of Spain; collector F. B. Whelpleyi, Jan 1910. YPM 9360: male, 4.0 mm. YPM 9361: ovigerous female, 4.7 mm. YPM 9830: male 5.2 mm. YPM 9362: male (damaged), 4.4 mm; Brazil, estuarine region of Cananea, lat 25°02'S, long 47°56' W, depth 0–3 m, *Spartina alterniflora* marsh, salinity 32.51‰, 23°C; collector Y. Wakabara, 14 Sep 1981. YPM 9398: 1 male, 5.3 mm; Brazil, estuarine region of Cananea, lat 25°02'S, long

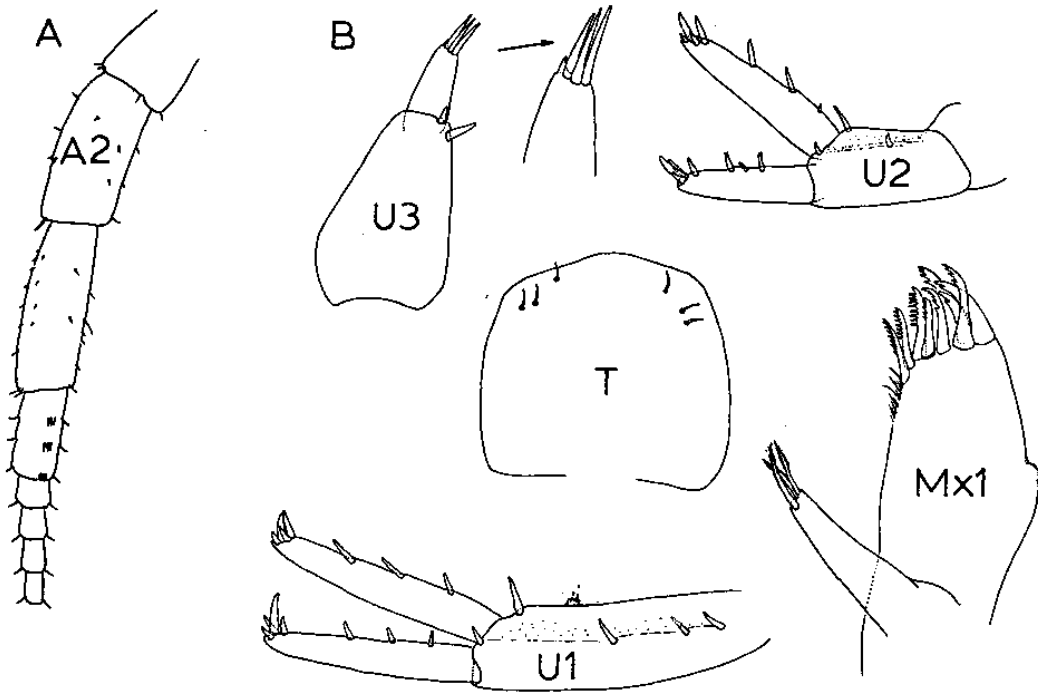


Figure 3.

Parhyalella whelpleyi (Shoemaker). A. YPM 9398, male, 5.3 mm. B. AMNH 6831, male paratype, 7.4 mm. Abbreviations: A, antenna; Mx, maxilla; T, telson; U, uropod.

47°56' W, depth 0–3 m, *Spartina alterniflora* marsh, salinity 27.71‰; collector Y. Wakabara, 21 Jun 1982. USNM 1000142: male, 5.2 mm. USNM 1000143: four males. USNM 1000144: nine females. Brazil, São Paulo, Santos; collector M. Leuderwaldt, 1922. ZMB 27193: male 6.3 mm; four females; Brazil, Ponta de Pedras, Recife, in bush-like marine algae; collector O. Schubart, 15 Sep 1936. ZMB 27194: ovigerous female; Brazil, Ponta de Pedras, Recife, on beach in small pool, low tide; collector O. Schubart, 15 Sep 1936. ZMB 27195: two males, three females; Brazil, Pina, Recife, on beach under algal wrack; collector O. Schubart, 23 Oct 1935. ZMB 27196: ovigerous female; Brazil, Pina, Recife, on beach under algal wrack; collector O. Schubart, 23 Oct 1935.

Diagnosis: Eye round, small, pale to dark in alcohol-preserved specimens (depending on length of storage time). Antenna 1 reaching slightly beyond peduncle of antenna 2. Antenna 2, peduncle stout (males), flagellum short, slightly longer than article 5 of peduncle, article 1 of flagellum 3-conjointed, 75% length of combined remaining articles. Gnathopod 1, article 5 longer than article 6, with single medial seta on anterior margin, article 6 length nearly twice width, palm transverse, convex, dactyl bifurcate. Gnathopod 2, length of article 6 is 150% width. Uropod 3, ramus less than 50% length of peduncle. Telson quadrate, distal margin slightly produced, lateral corners with two to three small spinules.

Type locality: Port of Spain, Trinidad.

Habitat: Fully marine or estuarine, often associated with *Spartina* salt marshes (da Cunha

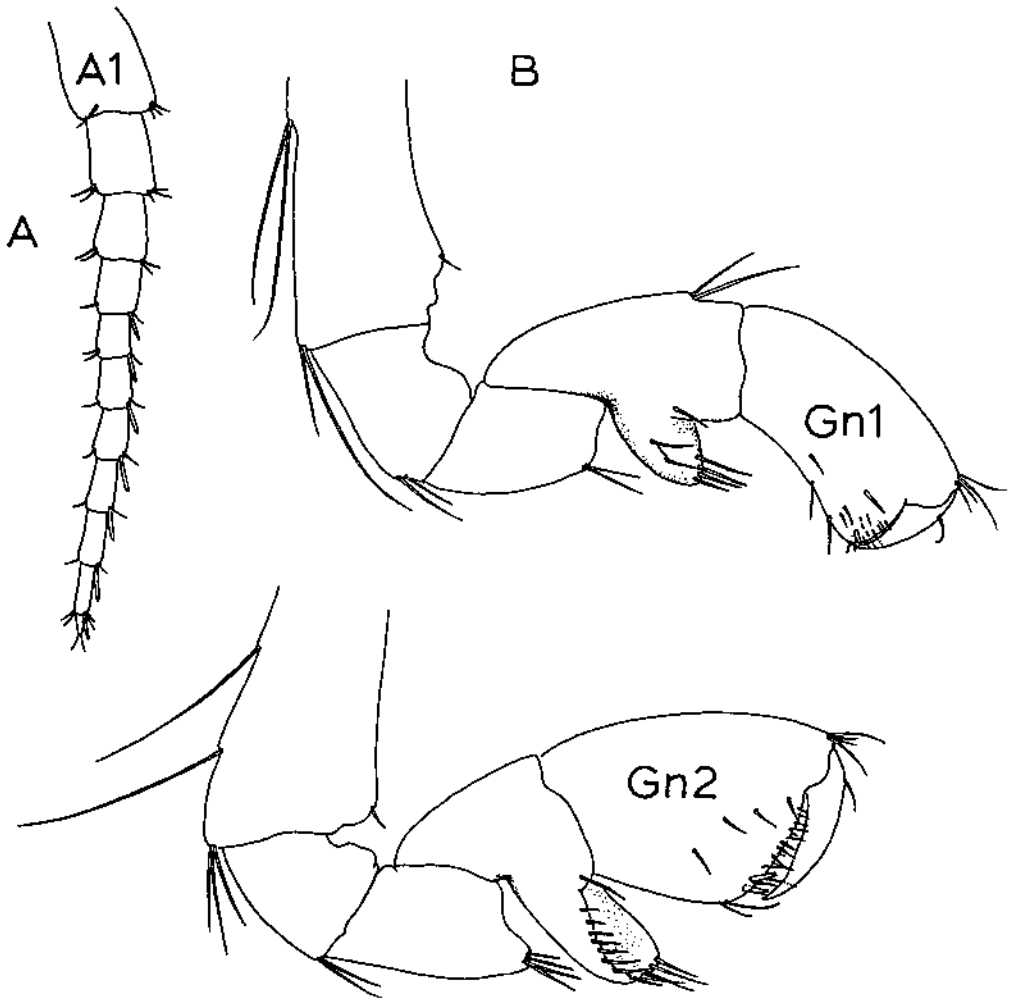


Figure 4.

Parhyalella whelpleyi (Shoemaker). A. YPM 9361, female, 4.7 mm. B. AMNH 6831, female paratype, 4.2 mm. Abbreviations: A, antenna; Gn, gnathopod.

Lana and Guiss 1992).

Remarks: This species was well illustrated by Shoemaker (1933) in his original description; therefore, only figures of female gnathopods 1 and 2, and some details of the male lacking in his description, are presented here. In most cases, the diagnostic medial seta on article 5, gnathopod 1 (male) is difficult to discern; usually we found it necessary to remove the appendage and view it under high power on a prepared slide. The seta was observed on all but one specimen (USNM 1000142, male, 5.2 mm) that we assign to this species. This specimen was damaged, however, and has only a single gnathopod 1; under high-power magnification an apparent insertion point for a medial seta is evident. One dissected individual (AMNH 6831, 7.4 mm paratype) has three distal setae on the inner plate of maxilla 1 (Figure 3), indicating that this character can vary from the usual condition (two setae).

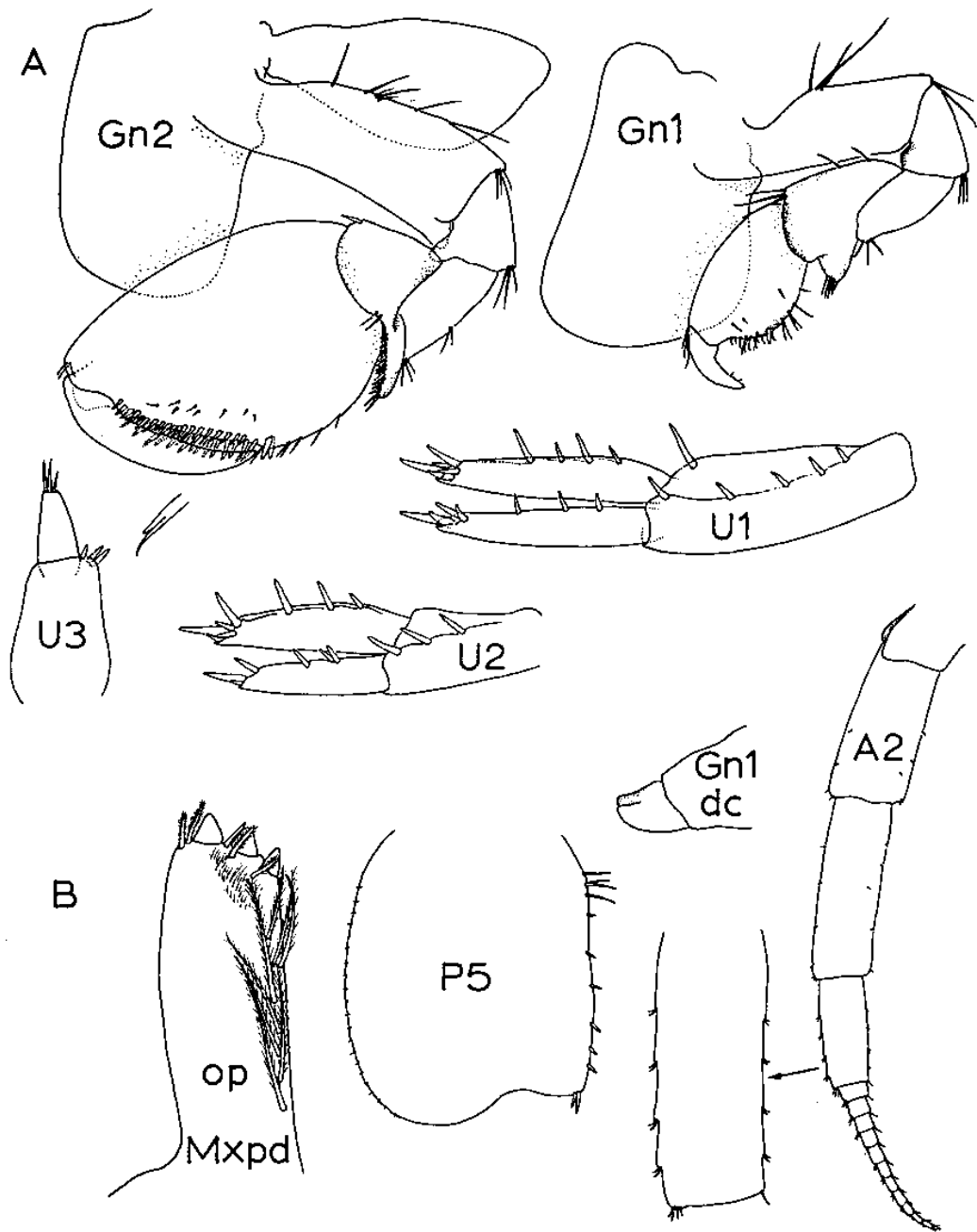


Figure 5.

Parhyaella pietschmanni Shellenberg. A. NHMW 17926, male paralectotype, 5.6 mm. B. USNM 1000145, male, 10.6 mm. Abbreviations: A, antenna; Gn, gnathopod; Mxpd, maxilliped; P, pereopod; U, uropod; dc, dactyl; op, outer plate.

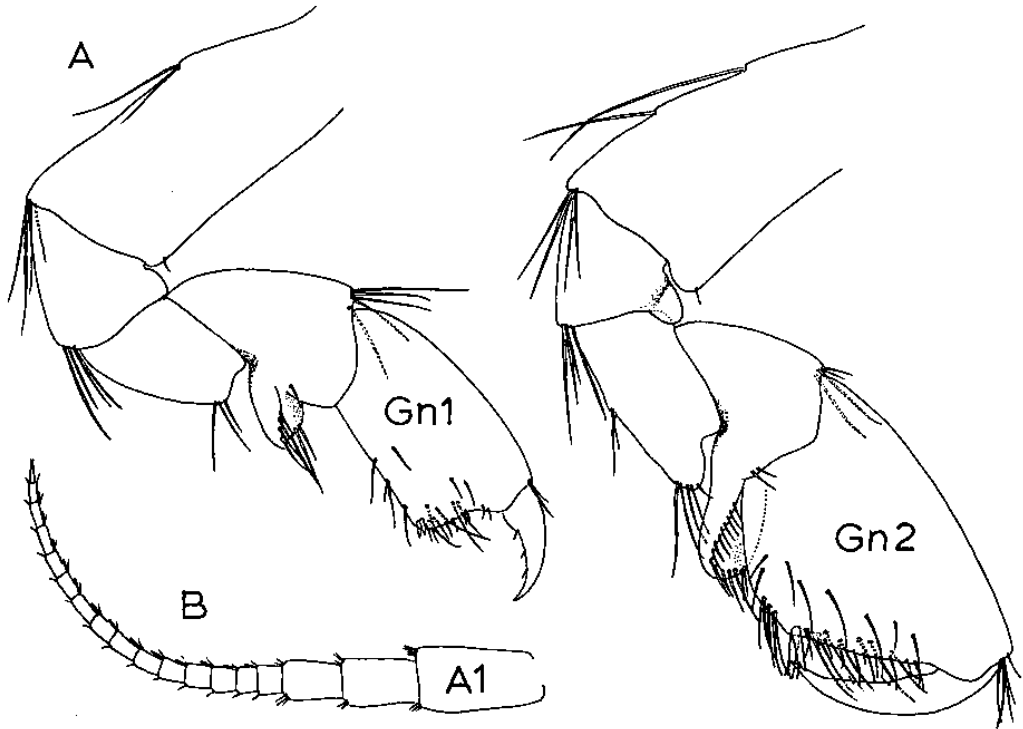


Figure 6.

Parhyalella pietschmanni Schellenberg. A. NHMW 17926, female paralectotype, 4.9 mm. B. USNM 1000150, female, 9.6 mm. Abbreviations: A, antenna; Gn, gnathopod.

PARHYALELLA PIETSCHMANNI SCHELLENBERG 1938

Figures 5, 6

Parhyalella pietschmanni Schellenberg; 1938:71–74, figs. 36, 37.

Parhyalella pietschmanni Barnard; 1970:269–271, figs. 179, 180.

non *Parhyalella pietschmanni* Steele; 1973:276–280, figs. 1–4.

Parhyalella pietschmanni Kim and Kim; 1987:17–18, fig. 15.

Parhyalella pietschmanni Kim; 1991:184.

Parhyalella pietschmanni Barnard and Karaman 1991:368, 372, fig. 70.

Material examined: NHMW 17924: male lectotype, 8.1 mm; ovigerous female paralectotype, 6.5 mm. NHMW 17926: male, 5.6 mm; female, 4.9 mm; 57 male, female and juvenile paralectotypes. Hawaii, Waikiki [Beach], Honolulu; collector Prof[essor] Pietschmann, 17 Feb 1928. NHMW 17925: female paralectotype; Hawaii, Waikiki [Beach], Honolulu; collector Professor Pietschmann, 12 Mar 1928. USNM 1000145: male, 10.6 mm. USNM 1000146: male, 11.2 mm. USNM 1000147: male, 10.8 mm. USNM 1000148: male, 9.3 mm. USNM 1000149: male, approximately 8.7 mm (slightly damaged). USNM 1000150: female, 9.6 mm. USNM 1000151: eight females. USNM 1000152: approximately 120 immatures and juveniles; Hawaii, one-half mile from town of Kailua, Oahu; collector R. Greenfield, 20 Aug 1950. ZMB 24974: 13 specimens; Hawaii, Waikiki [Beach], Honolulu; collector [Professor] Pietschmann (date unknown).

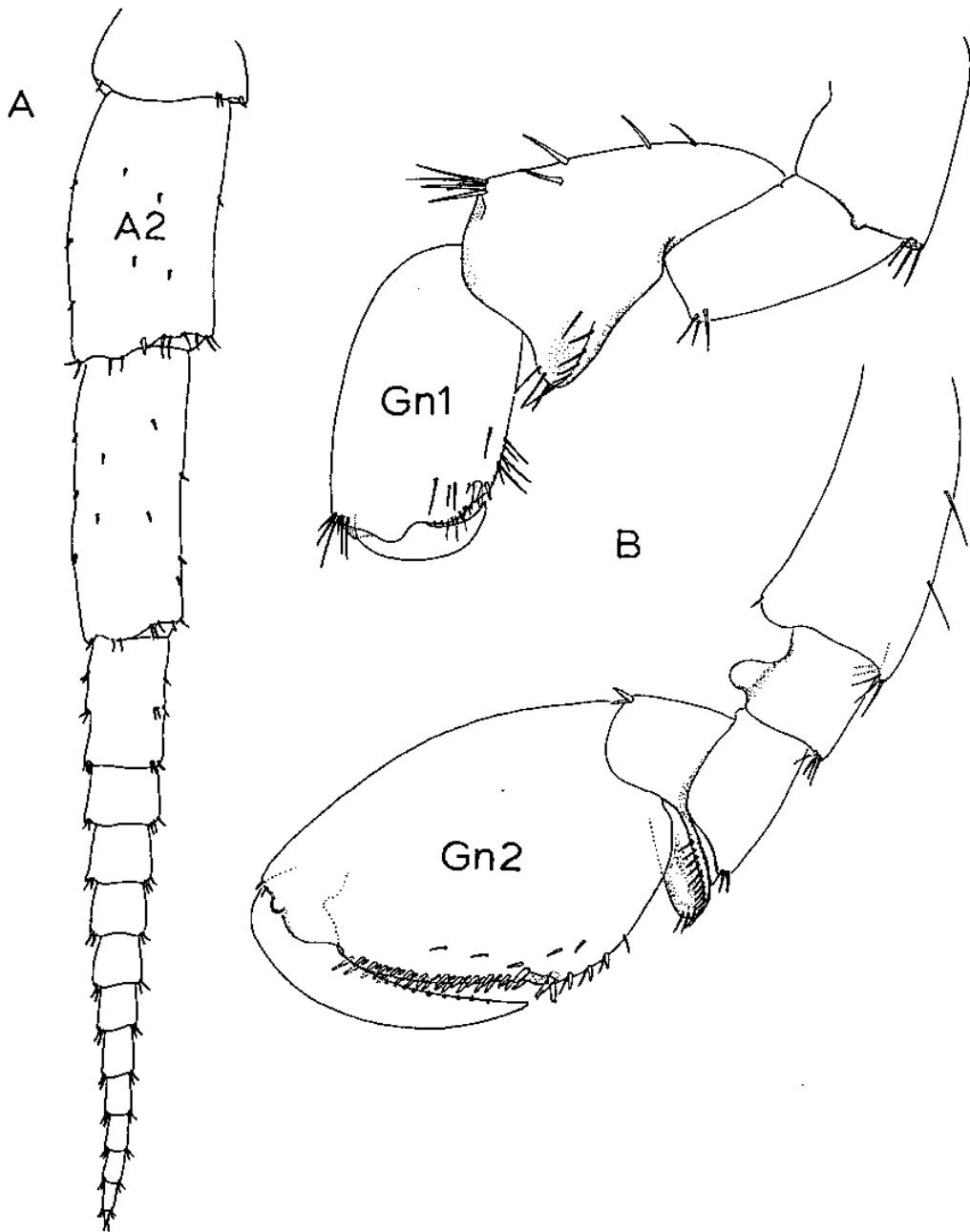


Figure 7.

Parhyaella congoensis Ruffo. A. MBC 39376, male holotype, 7.0 mm. B. MBC 39373, male holotype, 7.0 mm. Abbreviations: A, antenna; Gn, gnathopod.

Diagnosis: *Male*. Eye large, oval, dark in alcohol-preserved specimens. Antenna 2, peduncle very stout, article 1 of flagellum 5-conjointed. Gnathopod 1, article 5, anterior margin with two medial setae, article 6, palm oblique, posterior corner broadly rounded, hind margin strongly convex, dactyl bifurcate. Gnathopod 2, article 6, hind margin rounded. Uropod 2, inner ramus with one group of two spines.

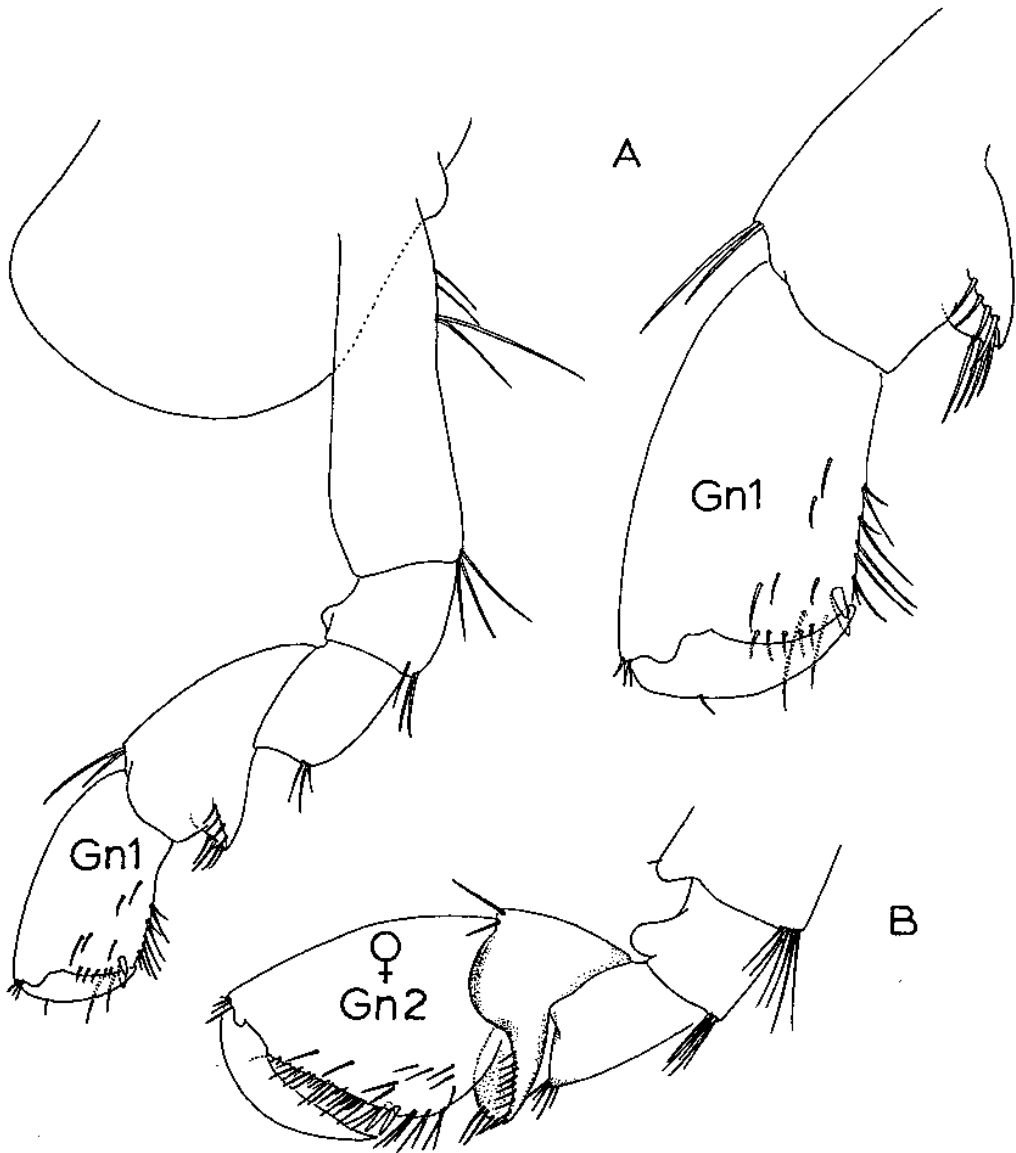


Figure 8.

Parhyalella congoensis Ruffo. A. MBC 35636–35659, female paratype, 6.1 mm. B. MBC 39374, female allotype, 5.5 mm. *Abbreviation:* Gn, gnathopod.

Type locality: Waikiki Beach, Honolulu, Hawaii, U.S.A.

Description: *Adult males.* Eye large, oval, dark in alcohol-preserved specimens. Antenna 1 reaching slightly beyond peduncle of antenna 2; antenna 2, article 4 of peduncle shorter than article 5, article 1 of flagellum 5-conjointed, total length of flagellum longer than article 5. Gnathopod 1, article 5 shorter than article 6, anterior margin with two medial setae and distal cluster of long setae, article 6 with slight distal expansion, palm oblique, posterior corner broadly rounded, hind margin strongly convex with three or four setal

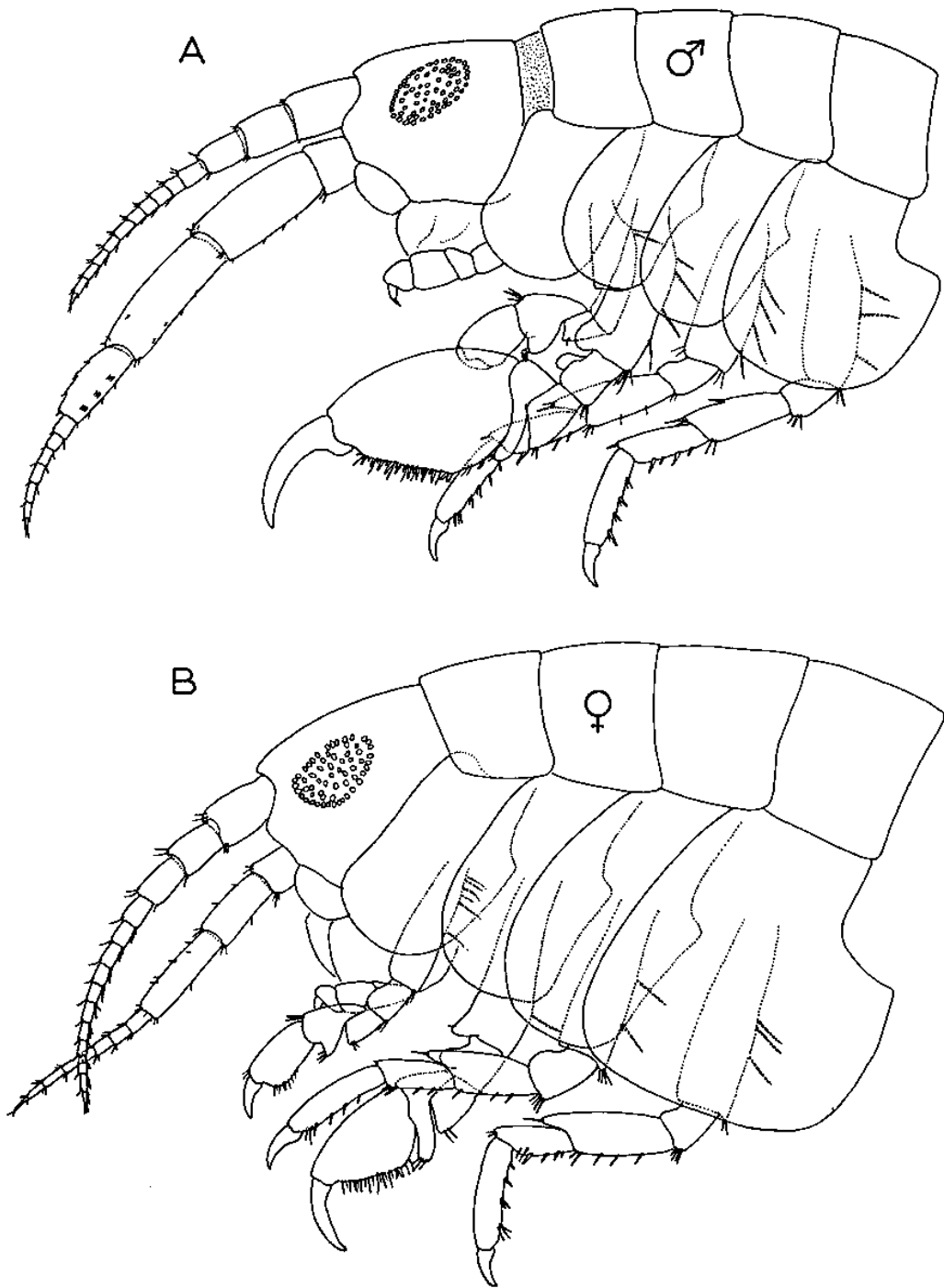


Figure 9.

Parhyaella barnardi Lazo-Wasem and Gable, new species. A. USNM 1000153, male holotype, 7.5 mm. B. USNM 1000154, female allotype, 6.4 mm.

groups, dactyl bifurcate. Gnathopod 2, article 6 width 80% of length, palm convex, oblique, hind margin with four setal clusters. Uropods 1 and 2, normal, spinose, uropod 2 inner ramus with one group of two spines. Uropod 3, width of peduncle 66% of length, with three stout distal spines, length of ramus 50% peduncle, apex with three spines. Telson slightly longer than broad, essentially pentagonal, distal margin tapering to rounded point, margin with a few small setae.

Females. Eye similar to those of male. Antenna 1 extending 66% length of antenna 2, flagellum of 14 articles; antenna 2, flagellum of approximately 15 articles. Gnathopod 1, article 6, anterior and posterior margins parallel, palm transverse, nearly straight, hind margin with three setal groups. Gnathopod 2, article 5 posterior lobe broad, extending below article 6, article 6, palm slightly sinuous, hind margin deeply convex, somewhat longer than palm, with four setal clusters.

Habitat: Beach wash associated with algae (Barnard 1970). The specimens attributed to this species by Kim and Kim (1987) were collected from a fishing net.

Remarks: Schellenberg (1938) did not designate types and refers to multiple specimens; however, he based his description and figures on an 11 mm male and 9 mm female, both measures being approximate. We did not find two specimens matching these dimensions. Two specimens (ZMB 17924), significantly smaller (8.1 mm and 6.5 mm, respectively), were found labeled "Type," but the handwriting does not match those of other labels thought to have been written by Schellenberg (Dworschak, personal communication). The male is missing its telson, but it and the female are otherwise intact. Although it is possible that Schellenberg could have figured these specimens without dissection (other than the male telson), we think this is unlikely given the considerable size discrepancies encountered.

We believe, however, that the specimens clearly represent part of a legitimate syntypic series, and so to clarify application of the name, we hereby designate the 8.1 mm male specimen, NHMW 17924, as **lectotype** for *Parhyalella pietschmanni*.

We were not able to examine the specimens from Korea cited as *P. pietschmanni* by Kim and Kim (1987) and Kim (1991), and therefore cannot confirm their identity. Doubts were expressed by C. B. Kim (personal communication) that *P. pietschmanni*, if in fact the identity is correct, should legitimately be considered part of the Korean fauna, because the specimens were from the "deck of a fishing boat" and perhaps not collected locally.

Few differences can be found between the figures of Kim and Kim (1987), the specimens we examined from the United States National Museum, and the figures of Barnard (1970). The figures of Kim and Kim (1987) lack sufficient detail to justify assigning their specimens to a new species, although such a designation may be warranted once specimens of *Parhyalella* from Korea are studied in detail. The differences we note between *P. pietschmanni* from Korea and Hawaii are as follows: in Korean specimens, article 5 of female gnathopod 1 lacking a medially placed seta on the anterior margin (present in Hawaii specimens); female gnathopod 2, palm moderately oblique (strongly oblique in Hawaii specimens); male gnathopod 1, article 5 longer than article 6 (shorter in Hawaii specimens); male gnathopod 1, marginal spines on article 5 widely separate (close together in Hawaii specimens); and pleon epimeron 3 straight (sinuous in Hawaii specimens).

With a relatively large suite of specimens from Hawaii, we were able to note some variation in two diagnostic characters. One specimen (USNM 1000146, male, 11.2 mm) had an apparent 4-conjointed flagellum article 1, as the defining setae that normally would denote the first conjointed articles were absent. That smaller individuals exhibit a

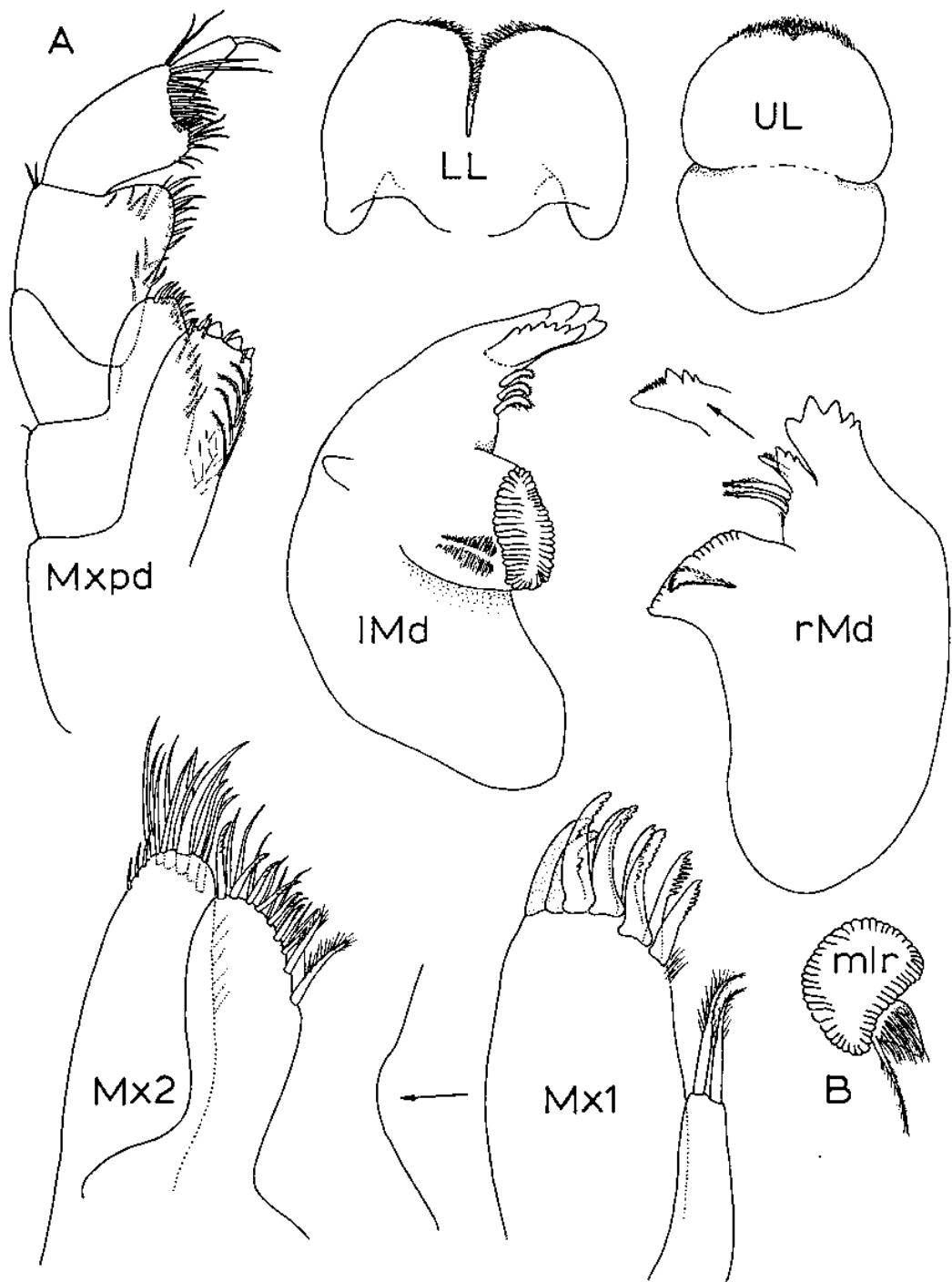


Figure 10.

Parhyaella barnardi Lazo-Wasem and Gable, new species. A. USNM 1000153, male holotype, 7.5 mm. B. USNM 1000155 male paratype, 6.4 mm; right mandibular molar showing plumose accessory seta. Abbreviations: LL, lower lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; UL, upper lip; mlr, molar; l, left; r, right.

fully 5-conjointed condition indicates that the apparent variability we noticed was not due to allometry. Another individual (USNM 1000146, male, 11.2 mm) has four strong medial setae on the anterior margin of article 5, gnathopod 1, rather than two. In all other specimens examined, the two features described above, that is, conjointed flagellum article 1 of antenna 2 and gnathopod 1 article 5 medial setae, followed the pattern diagnostic of the species.

PARHYALELLA CONGOENSIS RUFFO 1953

Figures 7, 8

Parhyalella congoensis Ruffo; 1953:132–134, fig. 5.

Parhyalella congoensis Barnard and Karaman; 1991:372.

Material examined: MBC 39372, 39373, 39375, 39376, 39385: male holotype, 7.0 mm (length from original description), dissected, on five microscope slides. MBC 39374: female allotype, 5.5 mm (length from original description), on microscope slides. MBC 35636–35659: female paratype, 6.0 mm. Democratic Republic of the Congo (formerly Zaire, and previously Belgian Congo), Moanda; collector E. Dartevelle, Sep 1947.

Diagnosis: *Male.* Antenna 2, peduncle stout, article 1 of flagellum 2-conjointed. Gnathopod 1, article 5, anterior margin with four medial setae, article 6, palm oblique, slightly convex, posterior corner rounded, dactyl simple. Gnathopod 2, article 6, palm weakly convex, hind margin with three clusters of one spine and one seta each. Uropod 2, inner ramus with row of single spines.

Type locality: Moanda, Democratic Republic of the Congo.

Description: *Male.* Antenna 1 extending well beyond peduncle of antenna 2, flagellum of 12 articles; antenna 2, article 4 of peduncle shorter than article 5, flagellum of 12 articles, article 1 of flagellum 2-conjointed. Gnathopod 1, article 5 distinctly longer than article 6, with four medial setae along anterior margin and with distal setal cluster, article 6, width 66% of length, palm oblique, slightly convex, posterior corner rounded, defined by stout spines, dactyl simple. Gnathopod 2, article 6 depth 75% of length, palm weakly convex, hind margin with three clusters of one spine and one seta each, followed proximally by a single seta. Uropods 1 and 2, normal, spinose, uropod 2 inner ramus with one row of single spines. Uropod 3, width of peduncle little more than half length, with two distal spines, ramus less than 50% length of peduncle. Telson as wide as long, distal margin bracket-shaped, point at apex broadly rounded.

Female. Gnathopod 1, article 5 slightly longer than article 6, article 6 rectangular, anterior and posterior margins parallel, palm convex and transverse, posterior corner defined by two stout spines, hind margin with setal clusters extending one-half length of margin from the palm, dactyl bifurcate. Gnathopod 2, posterior lobe of article 5 very broad, extending below article 6, article 6 depth 80% length, palm nearly straight, oblique, posterior margin broadly rounded with three clusters of two to three setae each.

Habitat: Unknown.

Remarks: The type material consists of a series of microscope slides and the single female paratype. We were not able to obtain the paratype material deposited in the Museo Civico di Storia Naturale in Verona, Italy, as listed in the original description by Ruffo (1953). Some of the type microscope slides (in the Museum of the Belgian Congo) were also labeled "*Parhyalella angolensis*," but this name apparently was provisional and abandoned by Ruffo in favor of *P. congoensis*. Without entire specimens of the males to examine, we

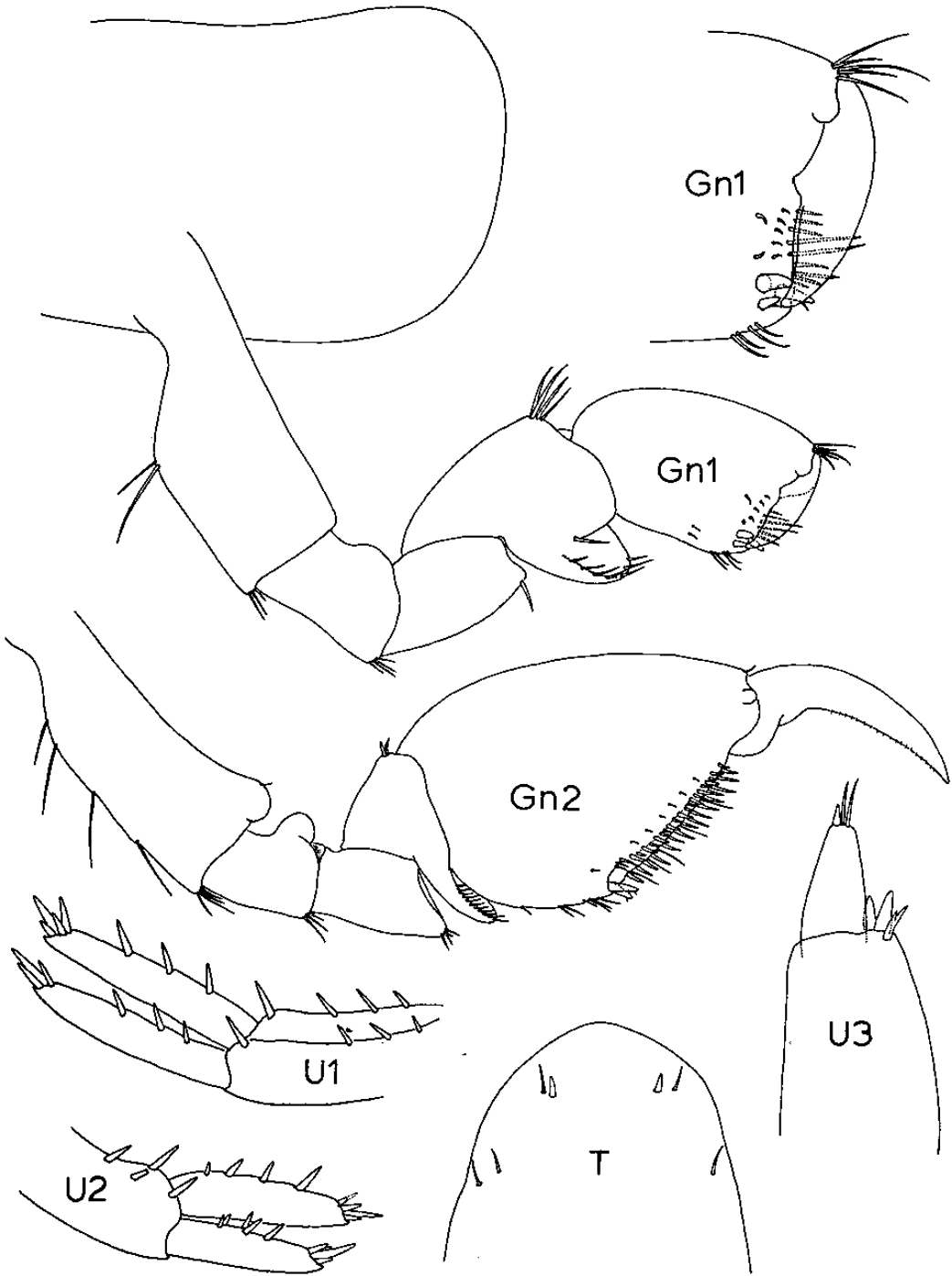


Figure 11.

Parhyaella barnardi Lazo-Wasem and Gable, new species, USNM 1000153, male holotype, 7.5 mm. Abbreviations: Gn, gnathopod; T, telson; U, uropod.

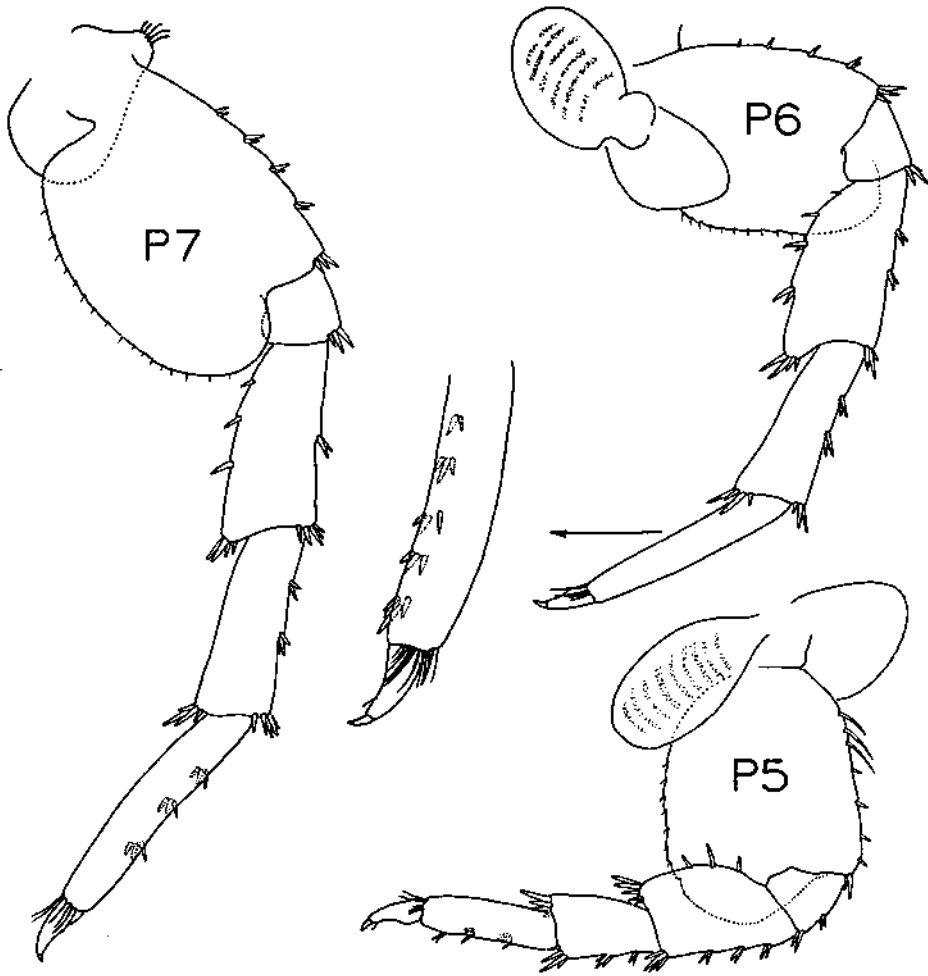


Figure 12.

Parhyalella barnardi Lazo-Wasem and Gable, new species, USNM 1000153, male holotype, 7.5 mm. Abbreviation: P, pereopod.

were only able to estimate the relative extension of antenna 1 against antenna 2 based on the dissected appendages. Because we were not able to figure an entire head with antennae, gnathopods, and pereon segments 1 to 4, we cannot accurately judge the inflation of antennae or the features of the eye. Ruffo (1953), however, distinguishes this species from *P. batesoni* and *P. pietschmanni* based on the inflation of the antennae (that is, the antennae are much less inflated in *P. congoensis* than in either *P. batesoni* or *P. pietschmanni*).

PARHYALELLA BARNARDI LAZO-WASEM AND GABLE NEW SPECIES

Figures 9–13

Material examined: USNM 1000153: male holotype, 7.5 mm. USNM 1000154: female allotype, 6.4 mm. USNM 1000155: male paratype, 6.4 mm. USNM 1000156: four male

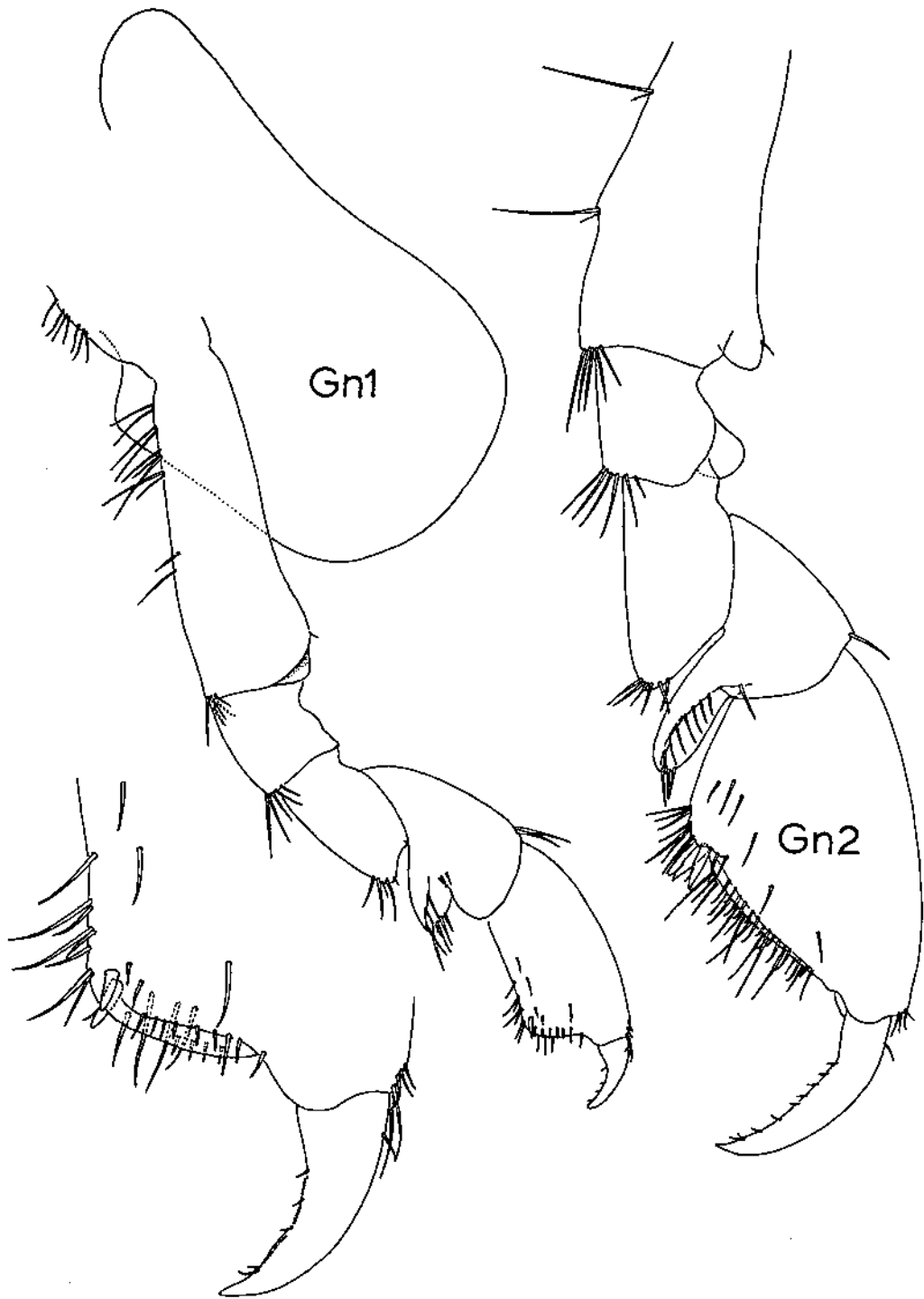


Figure 13.

Parhyalella barnardi Lazo-Wasem and Gable, new species. USNM 1000154, female allotype, 6.4 mm. *Abbreviation:* Gn, gnathopod.

paratypes. USNM 1000157: female paratype. Mexico, Ensenada, Baja California, lat 23°59'N, long 109°50'W; collector S. A. Glassell, 28 Nov 1936.

Diagnosis: *Male*. Eye large, ocelli widely spaced. Antenna 2 peduncle stout, article 1 of flagellum 4-conjointed. Gnathopod 1, anterior margin of article 5 with distal setae only, article 6 palm concave, dactyl simple. Gnathopod 2, article 6, hind margin rounded. Uropod 2, inner ramus with two groups of two spines.

Type locality: Ensenada, Baja California, Mexico.

Description: *Male*. Eye large, oval, ocelli widely spaced and pale golden in alcohol-preserved specimens. Antenna 1 extending to end of antenna 2 peduncle, flagellum with 11 articles. Antenna 2 peduncle moderately inflated, entire flagellum longer than fifth peduncular segment, article 1 of flagellum 4-conjointed. Upper lip, distal margin broadly convex, finely setose. Lower lip, outer lobes broad, finely setose. Left mandible, molar strong, triturtative, inner margin with three plumose setae, lacinia mobilis 6-dentate, incisor 5-dentate. Right mandible, similar to left, inner margin with two plumose setae, accessory plate with stout proximal teeth, distally serrate, molar with plumose accessory seta. Maxilla 1, inner plate with two stout plumose setae; outer plate with nine serrate teeth, inner margin lightly setose near base of teeth. Maxilla 2, inner plate subequal in width and slightly shorter than outer plate, with row of plumose and simple setae along inner and distal margin, proximal plumose setae stout; outer plate with a few small setae at outer distal corner, distal margin with subapical and apical rows of setae, subapical setae very stout. Maxilliped, inner plate, distally with three stout teeth, inner margin lined with plumose setae and a few fine facial setae; outer plate setose along distal and inner margin, apical setae stout; palp, article 2 with broad, setose, inner lobe, article 3, inner margin with distal lobe, distal margin setose; article 4 with long distal nail. Gnathopod 1, article 5 shorter than article 6, anterior margin with distal setae only, article 6 palm transverse, weakly concave, posterior corner acutely rounded, defined by three stout spines, hind margin with two setal groups, dactyl simple. Gnathopod 2, article 6 width less than 70% length, palm weakly convex, hind margin rounded, with two distal setal clusters and a single medial marginal seta. Pereopod 3 and 4 similar, article 2 posterior margin with a few setae, articles 5 and 6, posterior margin spinose. Pereopods 5 to 7 sequentially longer. Pereopod 5, articles 2 and 4 with distinct posterior lobe, article 4 anterior margin with three medial spine clusters, article 5 shorter than articles 4 and 7. Pereopods 6 and 7 similar, articles 2 and 4 with distinct posterior lobe, posterior margin of article 5 and 6 lacking spines. Uropods 1 and 2, normal, spinose, uropod 2 inner ramus with two groups of two spines. Uropod 3, peduncle with three stout distal spines, smallest bifid, ramus 40% length of peduncle, distally with one spine and a few setae. Telson longer than broad, roundly tapered.

Female. Eye similar to that of male. Antenna 1 nearly as long as antenna 2, flagellum with 11 articles; antenna 2, flagellum shorter than peduncle, with about eight articles. Gnathopod 1, posterior margin of article 2 with four proximal setal groups, article 5 shorter than 6, width of article 6 is 50% of length, palm transverse, broadly convex, posterior corner defined by two stout spines, hind margin with four groups of one to two setae each. Gnathopod 2, anterior distal lobe of article 2 strong, tapered to a weak point, palm of article 6 densely setose and spinose, weakly convex, hind margin shorter than palm, distally with three clusters of long setae.

Habitat: Unknown, but presumably marine, shallow water.

Etymology: This species is named in honor of the late J. Laurens Barnard.

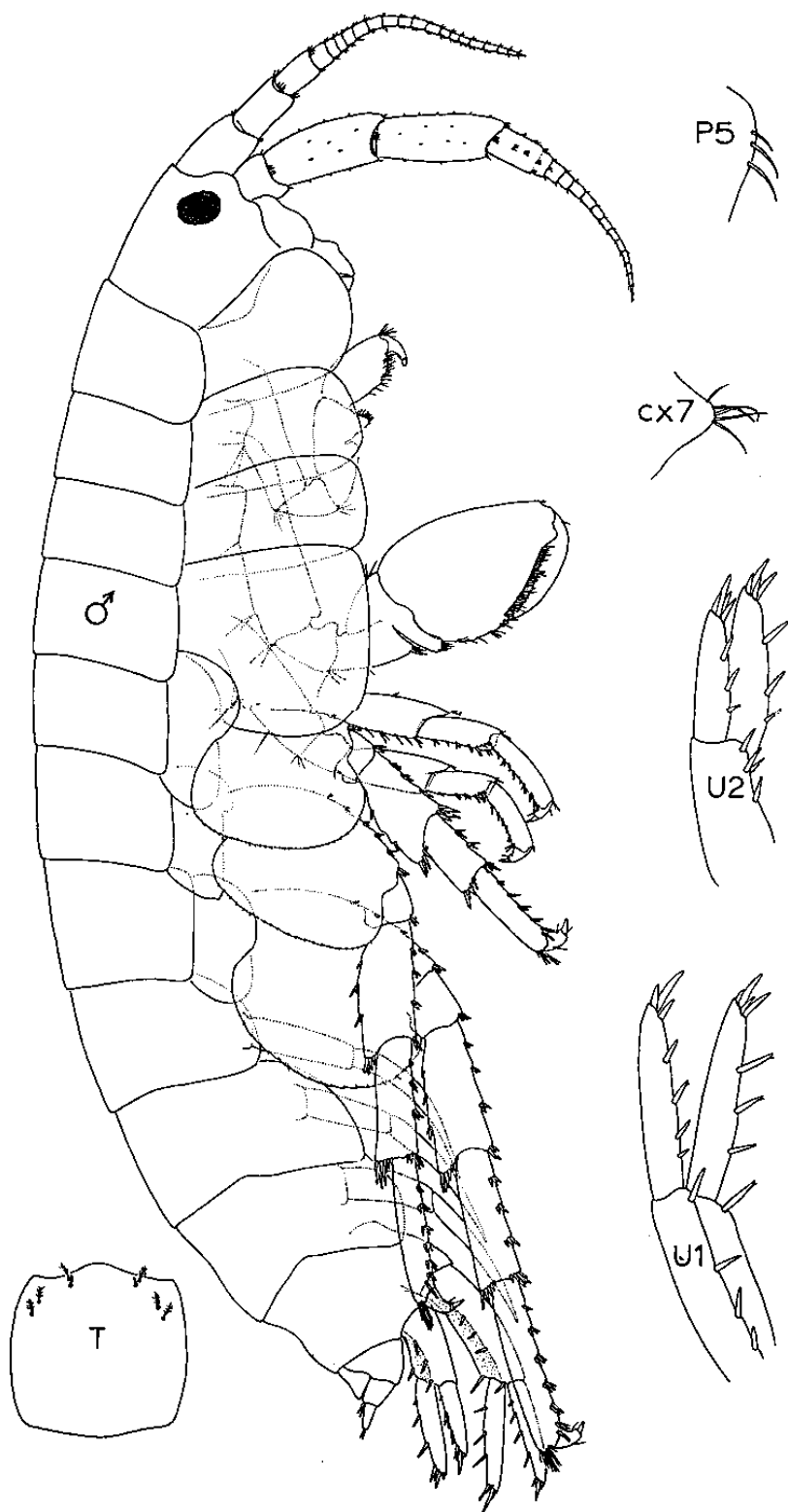


Figure 14.

Parhyaella kunkeli Lazo-Wasem and Gable, new species, YPM 8235, male holotype, 9.0 mm. Abbreviations: P, pereopod; T, telson; U, uropod; cx, coxa.

PARHYALELLA KUNKELI LAZO-WASEM AND GABLE NEW SPECIES
Figures 14–17

Material examined: YPM 8235: male holotype, 9.0 mm. YPM 8239: female allotype, 7.2 mm. YPM 8236: male paratype. YPM 8237: male paratype, 9.9 mm. YPM 8238: female paratype. Taiwan, Yenliao Bay, depth 20 m, by dredge from sand sediments; collector Ming-Shiou Jeng, 13 Feb 1986.

Diagnosis: *Male.* Eye medium-sized, oval. Antenna 2 peduncle very stout, article 1 of flagellum 4-conjointed. Gnathopod 1, article 5 anterior margin with distal setae only, article 6 palm oblique, convex, dactyl bifurcate. Gnathopod 2, article 6, hind margin rounded. Uropod 2, inner ramus, margin with row of single spines.

Type locality: Yenliao Bay, northern Taiwan.

Description: *Male.* Eye medium, oval, black in alcohol-preserved specimens. Coxal plates deep and broad, coxa 4 width subequal to length. Antenna 1 extending beyond peduncle of antenna 2, flagellum slightly longer than peduncle, and with 17 articles. Antenna 2, peduncle strongly inflated, article 4 subequal in length to article 5, flagellum twice as long as article 5, article 1 of flagellum 4-conjointed, remainder of flagellum with 12 articles. Upper lip, distal margin broadly convex, finely setose. Lower lip, outer lobes broad, widely separated, distal and inner margins finely setose. Left mandible, molar strong, triturative, inner margin with three large and two small plumose setae, lacinia mobilis 6 dentate (proximal tooth small), incisor 5 dentate. Right mandible, similar to left, molar with plumose accessory seta, inner margin with two plumose setae, accessory plate with stout proximal teeth, distally serrate. Maxilla 1, inner plate with two stout plumose setae; outer plate with nine serrate teeth, inner margin lightly setose near base of teeth, lower half of outer margin lightly setose. Maxilla 2, inner plate subequal in width and slightly shorter than outer plate, with row of plumose and simple setae along inner and distal margin, proximal plumose setae stout; outer plate with a few small setae at outer distal corner, distal margin with subapical and apical rows of setae, subapical setae very stout. Maxilliped, inner plate, distally with three stout teeth, inner margin lined with plumose setae; outer plate setose along distal and inner margin, some apical setae plumose; palp, article 2 with broad, setose, inner lobe, article 3, inner margin with distal lobe, distal margin setose; article 4 with long distal nail. Gnathopod 1, article 5 length subequal to article 6, anterior margin with distal setae only, width article 6 is 66% of length, palm oblique, convex, with slight indentation adjacent to posterior corner, posterior corner broadly rounded, hind margin straight or slightly concave, with several setal clusters along two-thirds length of distal margin; dactyl bifurcate. Gnathopod 2, width of article 6 is 75% of length, palm convex, spinose, posterior margin with two clusters of two to three setae each near posterior corner of palm. Pereopod 3 and 4 similar, article 2 posterior margin with a few setae, articles 5 and 6, posterior margin spinose. Pereopods 5 to 7 sequentially longer. Pereopod 5, articles 2 and 4 with distinct posterior lobe, article 4 anterior margin with two medial spine clusters, article 5 shorter than articles 4 and 7. Pereopods 6 and 7 similar, articles 2 and 4 with distinct posterior lobe, posterior margin of article 5 and 6 lacking spines. Uropod 3 peduncle, width nearly 75% of length, distally with three to four simple spines, ramus 66% length of peduncle, distally with one very stout spine and several long setae. Telson quadrate, width equal to length, distal margin sinuous, apical point broadly rounded, distal third of telson with plumose setae and a few spinules.

Female. Eye large (larger than that of male), oval, dark in preserved specimens. Antenna 1

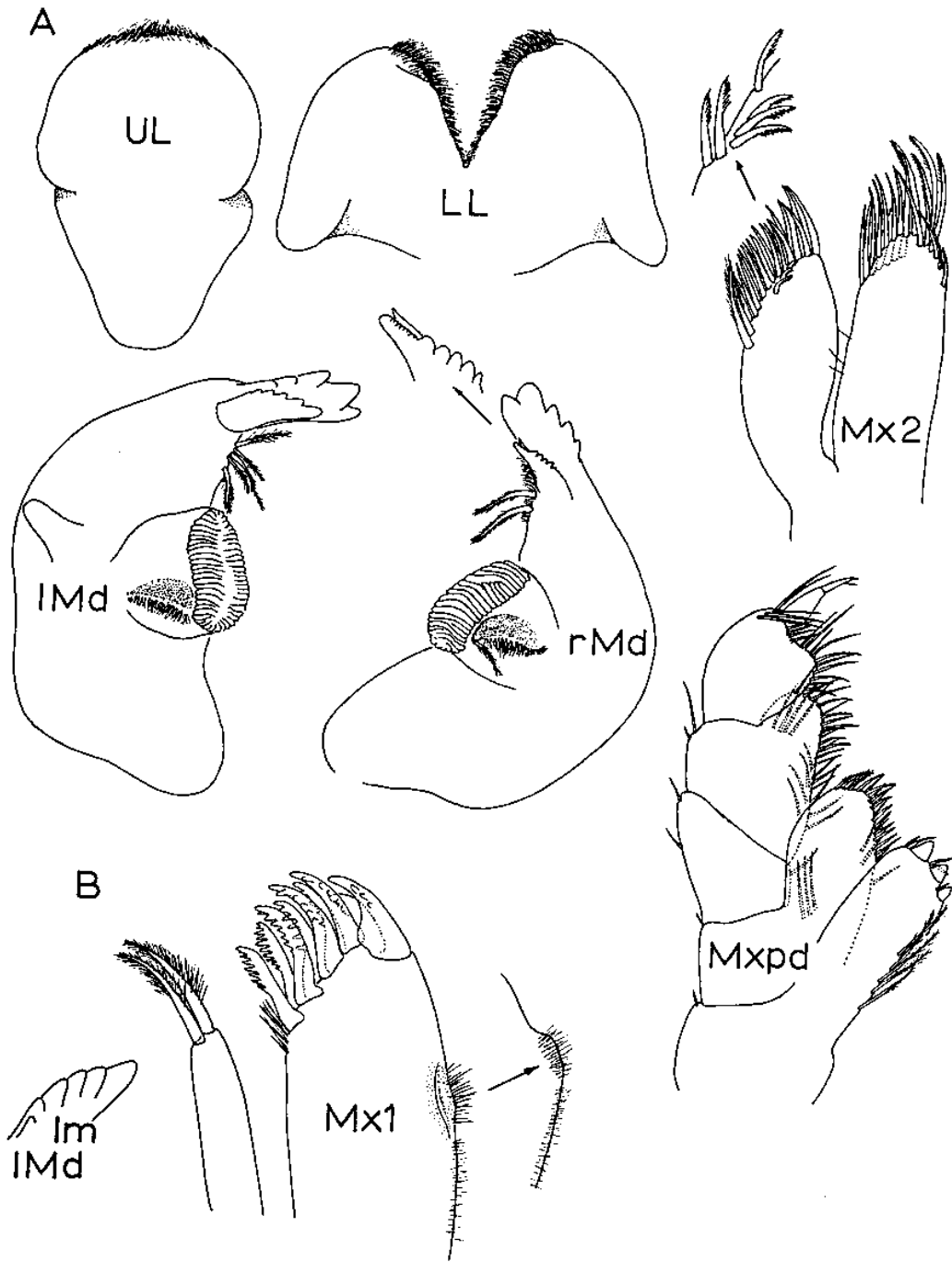


Figure 15.

Parhyaella kunkeli Lazo-Wasem and Gable, new species. A. YPM 8235, male holotype, 9.0 mm. B. YPM 8236, male paratype, 9.9 mm. Abbreviations: LL, lower lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; UL, upper lip; lm, lacinia mobilis; l, left; r, right.

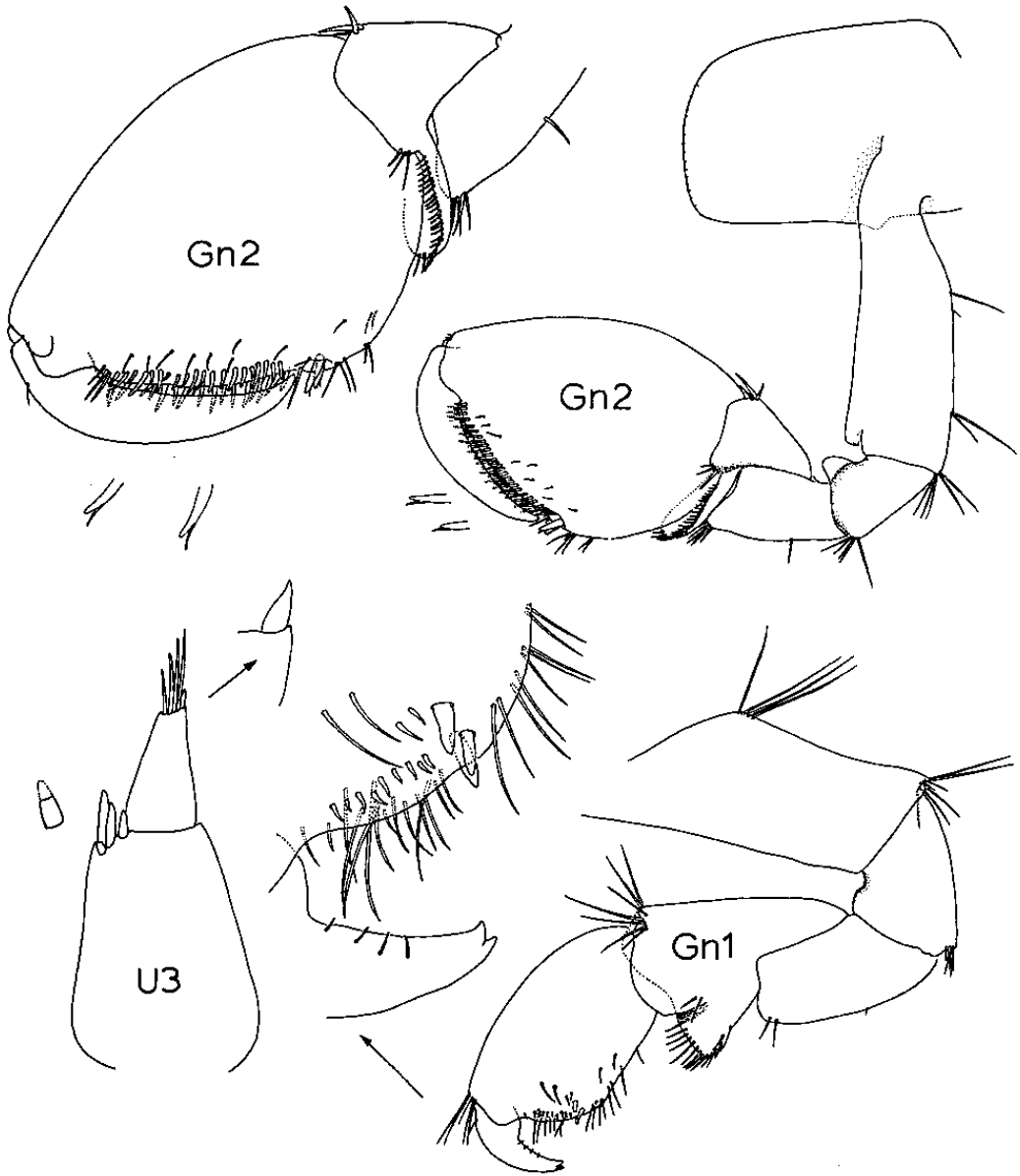


Figure 16.

Parhyaella kunkeli Lazo-Wasem and Gable, new species, YPM 8235, male holotype, 9.0 mm. Abbreviations: Gn, gnathopod; U, uropod.

extending well beyond peduncle of antenna 2, flagellum long, with 15 articles; antenna 2, flagellum much longer than peduncle, with 17 articles. Gnathopod 1, article 4 with a cluster of distal setae; article 5 posterior lobe very deep, expanded, margin densely setose; article 6 with slight distal expansion, depth slightly more than 50% length, palm transverse, nearly straight, densely setose, hind margin weakly concave, lightly setose along distal half of margin. Gnathopod 2, article 4 posterior margin densely setose at produced distal end; article 5 very broad, produced below article 6; article 6 triangular, depth 60% length, palm oblique, very weakly concave, hind margin with a few clusters of two setae each.

Habitat: Subtidal waters adjacent to coral reefs, dredged from sandy bottom, 20 m (original collection data and personal communication from C. F. Dai, donor of the specimens).

Etymology: This species is named in honor of Beverly W. Kunkel for his pioneering work on the amphipods of Bermuda and as discoverer of the genus *Parhyalella*.

PARHYALELLA NISBETAE LAZO-WASEM AND GABLE NEW SPECIES

Figures 18–22

Parhyalella whelpleyi (Shoemaker); 1948:11.

Material examined: YPM 9392: male holotype, 6.6 mm. YPM 9390: male paratype, 5.4 mm. YPM 9391: male paratype. YPM 9384: male paratype. YPM 9395: male paratype. British West Indies, Nevis, beach at Nisbet Plantation Beach Club, lat 17°11'N, long 62°35'W, picked from floating algae washing up on shore; collector E. A. Lazo-Wasem, 23 Jun 1992. YPM 9393: female allotype, 4.9 mm; British West Indies, Nevis, beach at Nisbet Plantation Beach Club, picked from floating algae washing up on shore; collector E. A. Lazo-Wasem, 21 Jun 1992. USNM 298343: male, 6.0mm; Cuba, Bahía Corrientes, Corrientes submarine anchorage, at electric light. Smithsonian–Roebling Expedition, Station 78; collector unknown, 9 April 1937.

Diagnosis: *Male.* Eye medium-sized, oval. Antenna 2, peduncle stout, article 1 of flagellum 5-conjointed. Gnathopod 1, article 5, anterior margin with subdistal spine cluster only, dactyl bifurcate. Gnathopod 2, article 6 (largest adults), posterior margin with larger distal protuberance. Uropod 2, inner ramus, margin with row of single spines.

Type locality: Nevis, British West Indies.

Description: *Male.* Eye medium-sized, oval, dark in fresh alcohol-preserved specimens. Coxal plates medium-sized, coxa 1 anterior margin weakly produced, coxa 4 width less than length. Antenna 1 extending to end of peduncle of antenna 2, flagellum much longer than peduncle, composed of 14 articles. Antenna 2 peduncle strongly inflated, weakly spinose, article 4 with two small distal cusps on anterior margin; article 5 longer than article 4; flagellum subequal in length to article 5 of peduncle, article 1 of flagellum 5-conjointed, combined length of remaining articles subequal to length of first (not shown in Figure 18, illustration of holotype male). Upper lip, distal margin broadly convex, finely setose. Lower lip, outer lobes broad, distal and inner margins finely setose. Left mandible, molar strong, triturative, inner margin with three plumose setae, lacinia mobilis 6 dentate, incisor 5 dentate. Right mandible, similar to left, molar with plumose accessory seta, inner margin with two plumose setae, accessory plate with stout proximal teeth, distally serrate. Maxilla 1, inner plate with two stout plumose setae; outer plate with nine serrate teeth, inner margin lightly setose near base of teeth. Maxilla 2, inner plate subequal in width and slightly shorter than outer plate, with row of plumose and simple setae along inner and distal margin, proximal plumose setae stout; outer plate with a few small setae at outer distal corner, distal margin with subapical and apical rows of setae, subapical setae very stout. Maxilliped, inner plate, distally with three stout teeth, inner margin lined with plumose setae and fine facial setae; outer plate setose along distal and inner margin, apical setae stout; palp, article 2 with broad, setose, inner lobe, article 3, inner margin with distal lobe, distal margin setose; article 4 with long distal nail. Gnathopod 1, article 5 subequal to or slightly longer than article 6, with only distal spine cluster on anterior margin; article 6 depth 66% of length, palm transverse, weakly con-

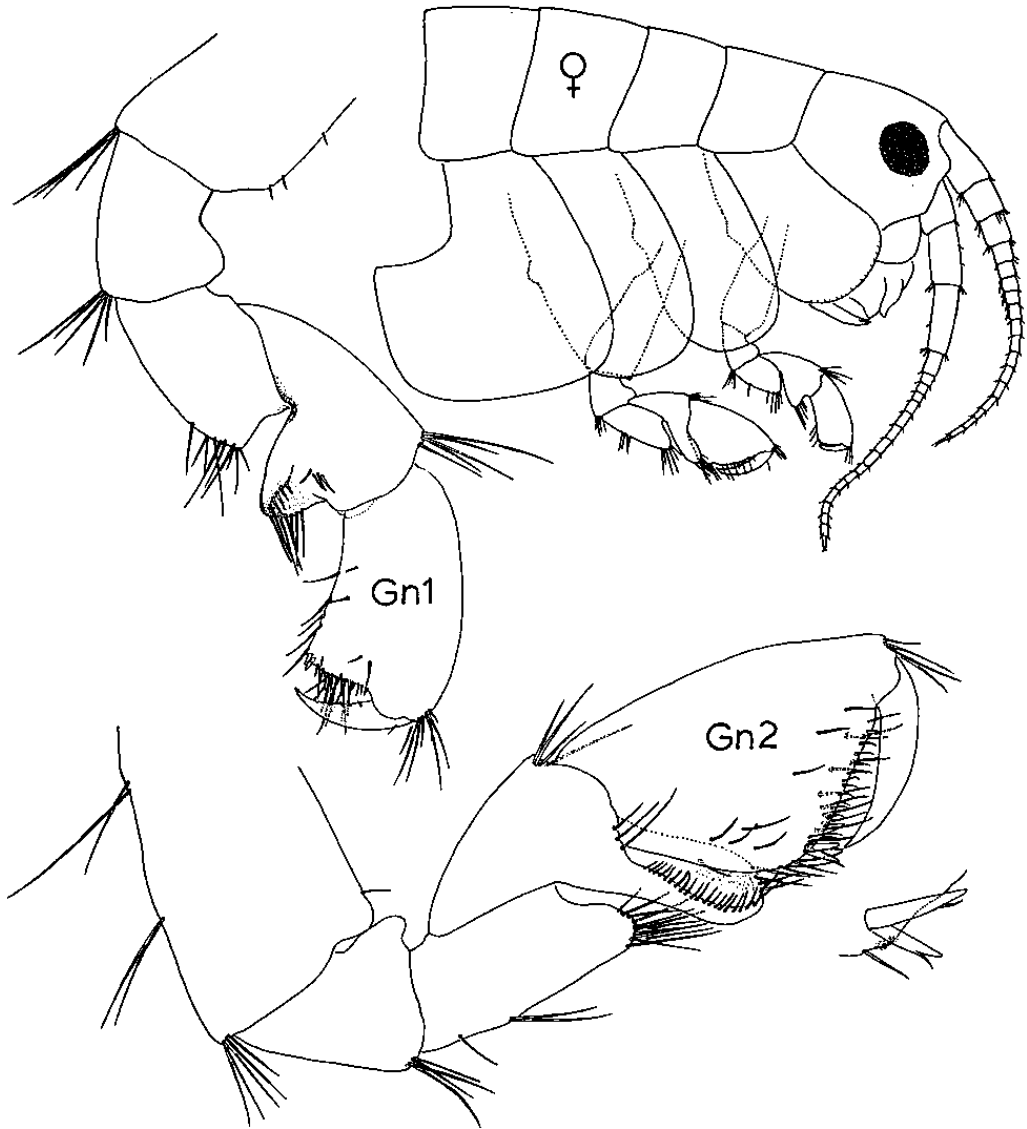


Figure 17.

Parhyaella kunkeli Lazo-Wasem and Gable, new species, YPM 8239, female allotype, 7.2 mm. *Abbreviation:* Gn, gnathopod.

cave, hind corner broadly rounded, defined by two stout spines, one each on inner and outer facial margin near corner; dactyl simple. Gnathopod 2 (full adults), article 6 depth 66% of length, palm oblique, convex, spinose, hind margin with distinct distal protuberance bearing three large spines. Pereopod 3 and 4 similar, article 2 posterior margin with a few setae, articles 5 and 6, posterior margin spinose. Pereopods 5 to 7 sequentially longer. Pereopod 5, articles 2 and 4 with distinct posterior lobe, article 4 anterior margin with two medial spine clusters, article 5 shorter than articles 4 and 7. Pereopods 6 and 7 similar, articles 2 and 4 with distinct posterior lobe, posterior margin of articles 5 and 6 lacking spines. Uropod 3 peduncle, width 50% length, ramus 50% length of peduncle, distally with one stout spine and a few setae. Telson slightly longer than broad, distal

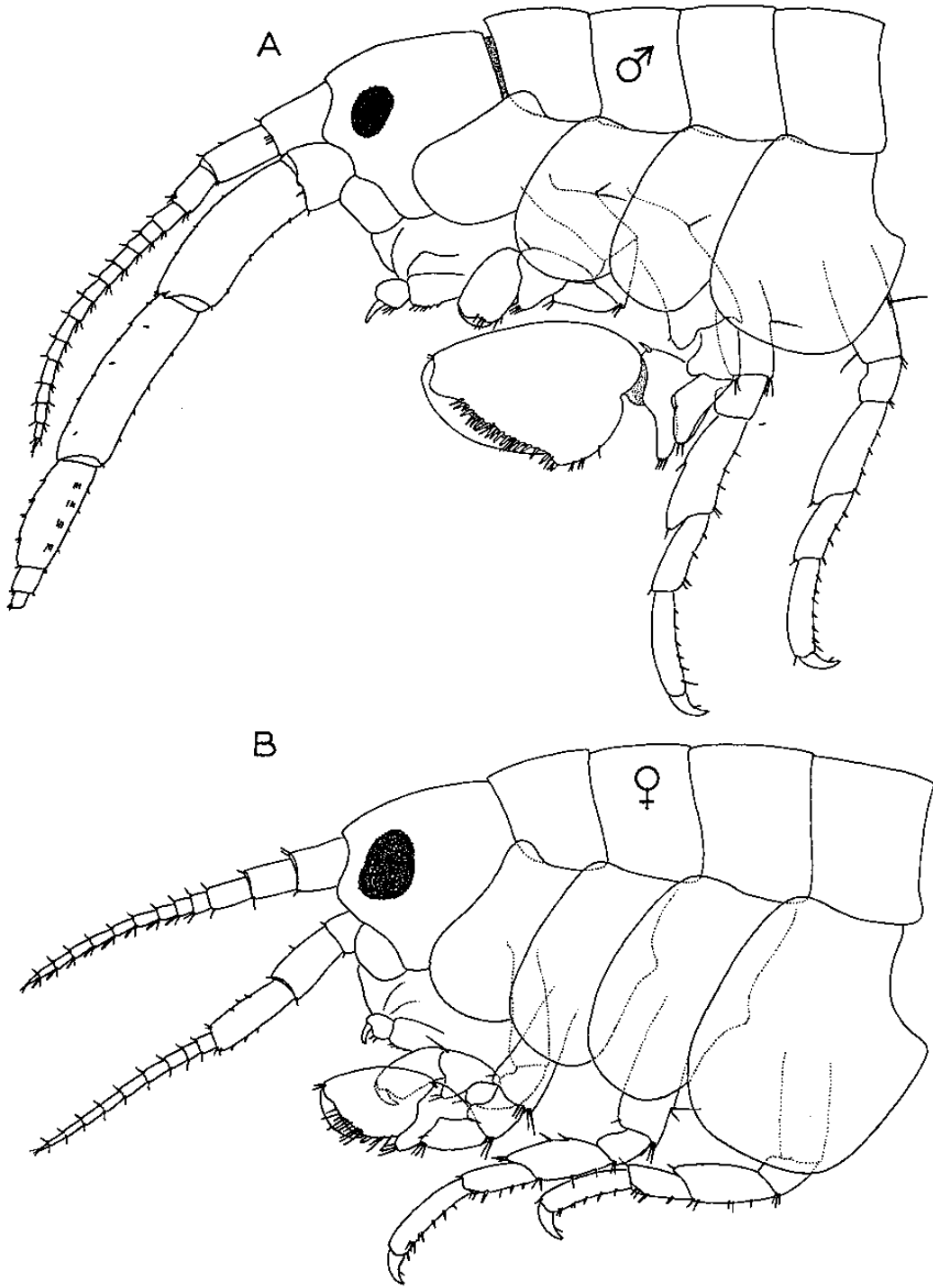


Figure 18.
Parhyaella nisbetiae Lazo-Wasem and Gable, new species. A. YPM 9392, male holotype, 6.6 mm. B. YPM 9393, female allotype, 4.9 mm.

margin tapered, rounded, with two pairs of subdistal setae, and a single distal seta.

Adult female. Eye large, oval, dark in (fresh) alcohol-preserved specimens. Antenna 1 extending well beyond peduncle of antenna 2, flagellum long, with 11 articles, aesthetascs on posterior margin; antenna 2, flagellum distinctly longer than peduncle, of about 10 articles. Gnathopod 1, article 5 length subequal to article 6; article 6, anterior and posterior margins essentially parallel, palm transverse, moderately convex, weakly spinose and setose, hind corner defined by two very stout spines. Gnathopod 2, article 5 short, produced below articles 4 and 6, article 6 width 66% of length, palm nearly straight, weakly spinose and setose, posterior corner defined by two large spines, hind margin broadly convex.

Habitat: In Nevis, all specimens were nestled among floating algae at less than 1 m depth, washing ashore on a windswept, sandy beach. This beach has a 25 m man-made rock jetty. Less than 50 m offshore is a large bed of turtle grass in water less than 4 m deep. Strong onshore winds continuously drive algae and debris onto the exposed beachfront.

Etymology: This species is named for Frances “Fanny” H. Nisbet, who married Admiral Horatio Nelson (then captain) on the tiny island of Nevis (type locality) in 1787, while on Caribbean station.

Remarks: The produced hind corner of gnathopod 2 is apparent only on the largest males. In smaller males the hind corner is only weakly produced and not distinguishable from other species in the genus. The specimen examined from the Smithsonian–Roebling Expedition, originally identified by C. R. Shoemaker as *P. whelpleyi*, has only a weakly produced proximoposterior corner of gnathopod 2. However, we refer this specimen to *P. nisbetae* based on the lack of a seta on the anterior margin of article 5, gnathopod 1 (present in *P. whelpleyi*), and the straight palm of gnathopod 1 article 6 (weakly convex in *P. whelpleyi*).

PARHYALELLA RUFFOI LAZO-WASEM AND GABLE NEW SPECIES

Figures 23–27

Parhyalella sp. Andres; 1975.

Parhyalella sp. Gonzalez; 1990:56.

Parhyalella sp. Gonzalez; 1991:102–103, fig. 7.

Material examined: USNM 1000158: male holotype, 7.8 mm. USNM 1000159: female allotype, 4.8 mm. USNM 1000160: male paratype, 8.0 mm. USNM 1000161: male paratype, 8.6 mm. USNM 1000162: female paratype (damaged), 7.1 mm. USNM 1000163: four male paratypes. USNM 1000164: nine female paratypes. Peru, Paita, lat 5°11'S, long 81°09' W; collector W. L. Schmitt, 7 Oct 1926.

Diagnosis: *Male.* Eye small- to medium-sized, oval. Antenna 2, peduncle stout, article 1 of flagellum 5-conjointed. Gnathopod 1, anterior margin of article 5 with distal spines only, article 6, palm concave, dactyl simple. Gnathopod 2, article 6, hind margin slightly rounded, two setal groups. Uropod 2, inner ramus, margin with row of single spines.

Type locality: Paita, Peru.

Description: *Male.* Eye small- to medium-sized, oval, ocelli faint red (in alcohol-preserved specimens) and separated. Antenna 1 extending nearly to end of peduncle of antenna 2, flagellum with nine articles. Antenna 2 long, peduncle strongly inflated, article 5 distinctly longer than article 4; flagellum shorter than peduncle article 5, article 1 of flagellum 5-conjointed, combined length of remaining flagellar articles shorter than con-

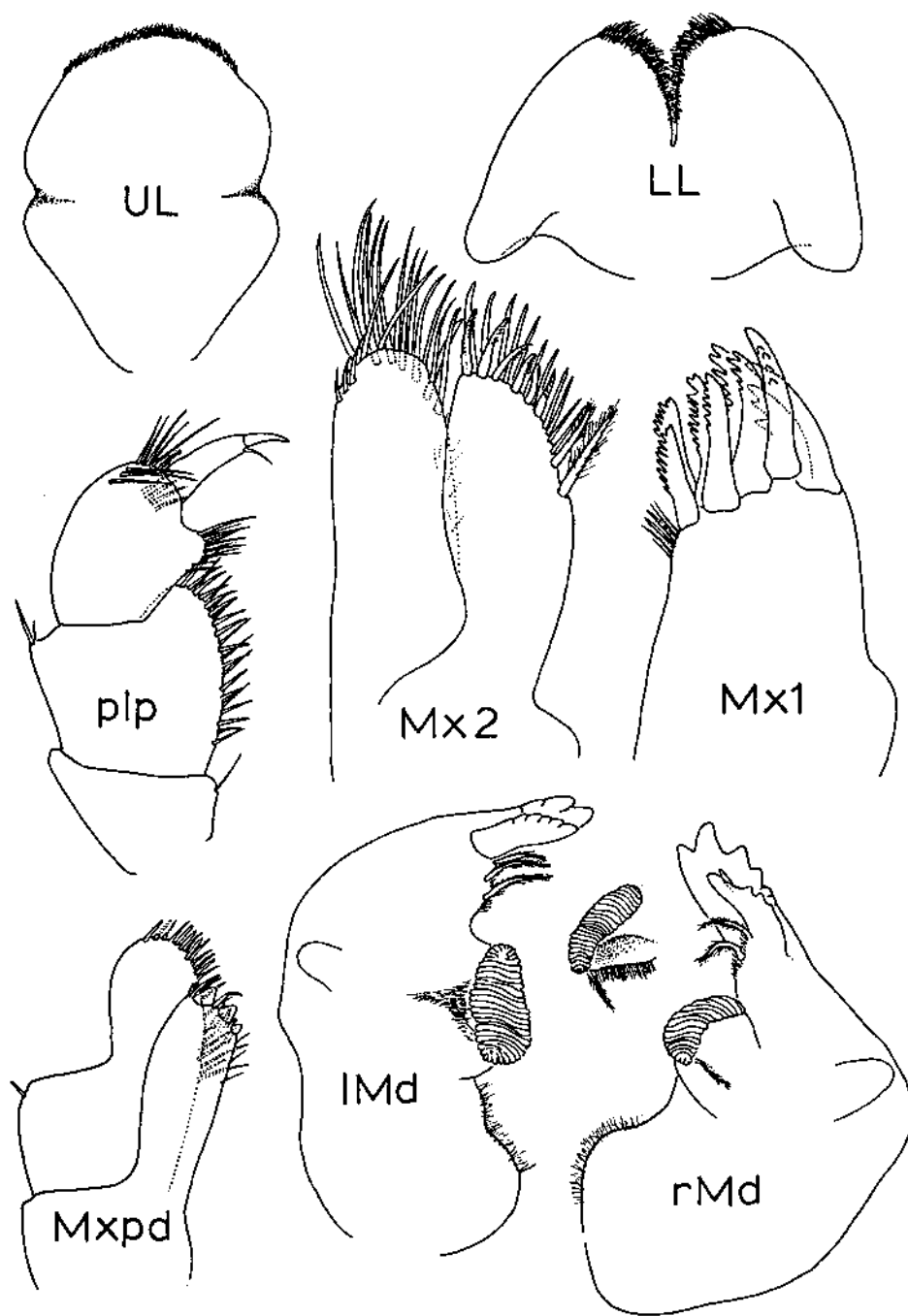


Figure 19.

Parhyaella nisbetae Lazo-Wasem and Gable, new species, YPM 9392, male holotype, 6.6 mm. Abbreviations: LL, lower lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; UL, upper lip; plp, palp; l, left; r, right.

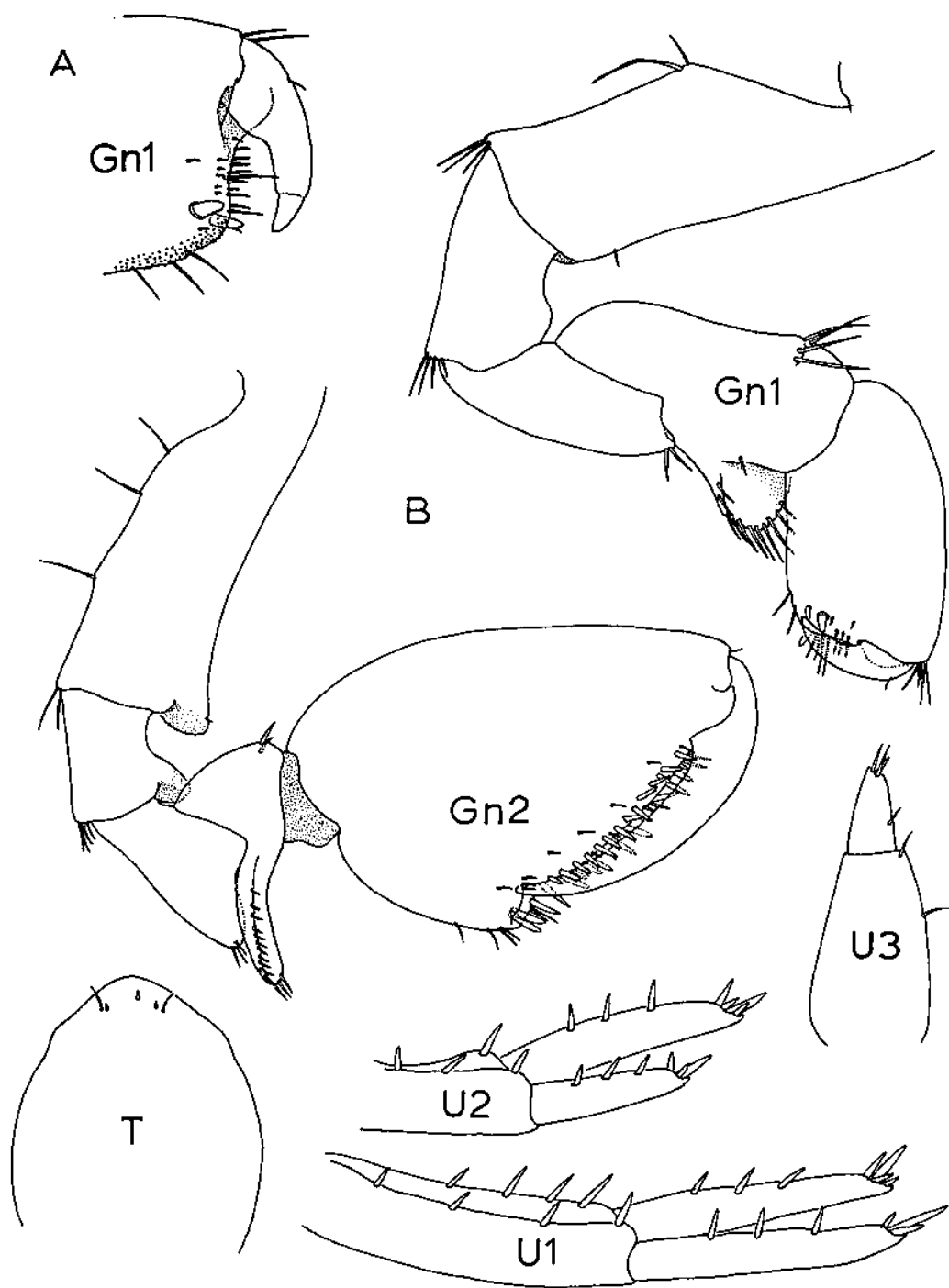


Figure 20.

Parhyaella nisbetiae Lazo-Wasem and Gable, new species. A. YPM 9390, male paratype, 5.4 mm. B. YPM 9392, male holotype, 6.6 mm. Abbreviations: Gn, gnathopod; T, telson; U, uropod.

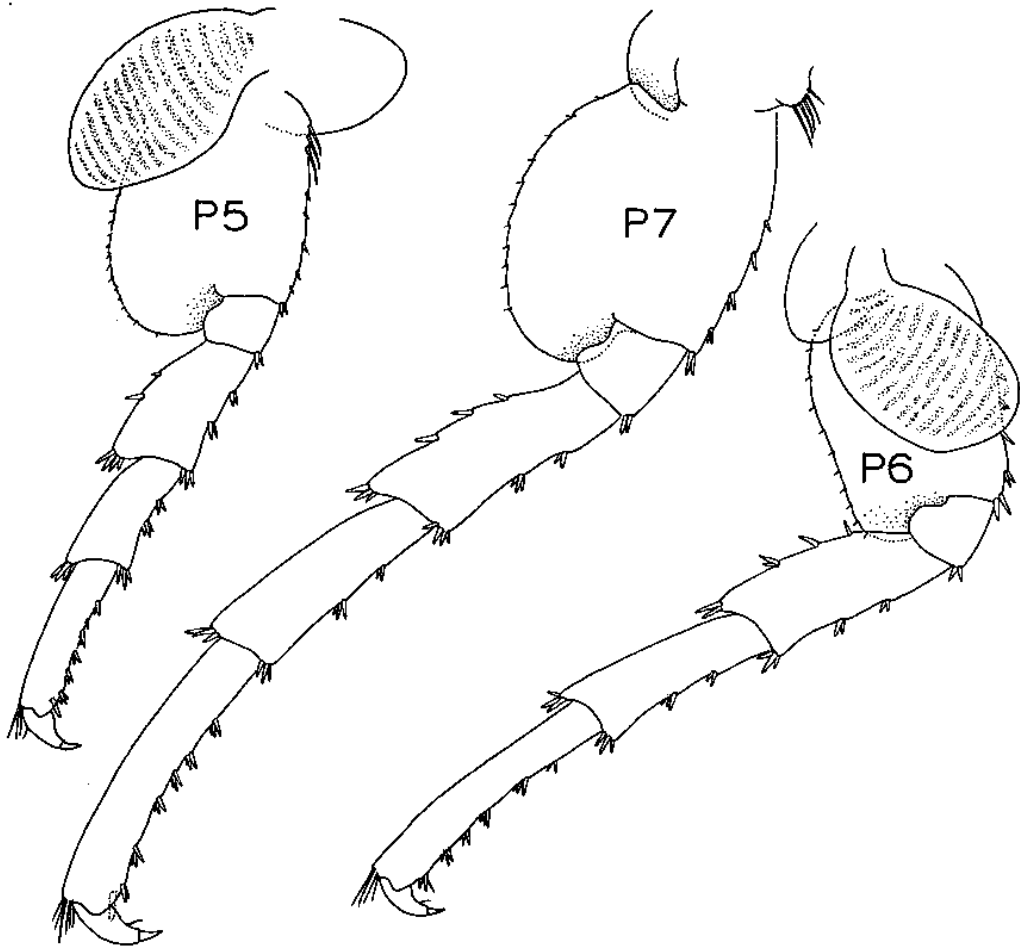


Figure 21.

Parhyaella nisbetiae Lazo-Wasem and Gable, new species, YPM 9392, male holotype, 6.6 mm. Abbreviation: P, pereopod.

jointed article. Upper lip, distal margin broadly convex, finely setose. Lower lip, outer lobes broad, distal and inner margins finely setose. Left mandible, molar strong, triturtative, inner margin with three plumose setae, lacinia mobilis 6-dentate, incisor 5-dentate. Right mandible, similar to left, molar with plumose accessory seta, inner margin with two plumose setae, accessory plate with stout proximal teeth, distally serrate. Maxilla 1, inner plate with two stout plumose setae; outer plate with nine serrate teeth, inner margin lightly setose near base of teeth. Maxilla 2, inner plate subequal in width and slightly shorter than outer plate, with row of plumose and simple setae along inner and distal margin, proximal plumose setae stout; outer plate with a few small setae at outer distal corner, distal margin with subapical and apical rows of setae, subapical setae stout, few apical setae plumose. Maxilliped, inner plate, distally with three stout teeth, inner margin lined with plumose setae and fine facial setae; outer plate setose along distal and inner margin, apical setae stout; palp, article 2 with broad, setose inner lobe, article 3, inner margin with distal lobe, distal margin setose; article 4 with long distal nail. Coxal plate 1

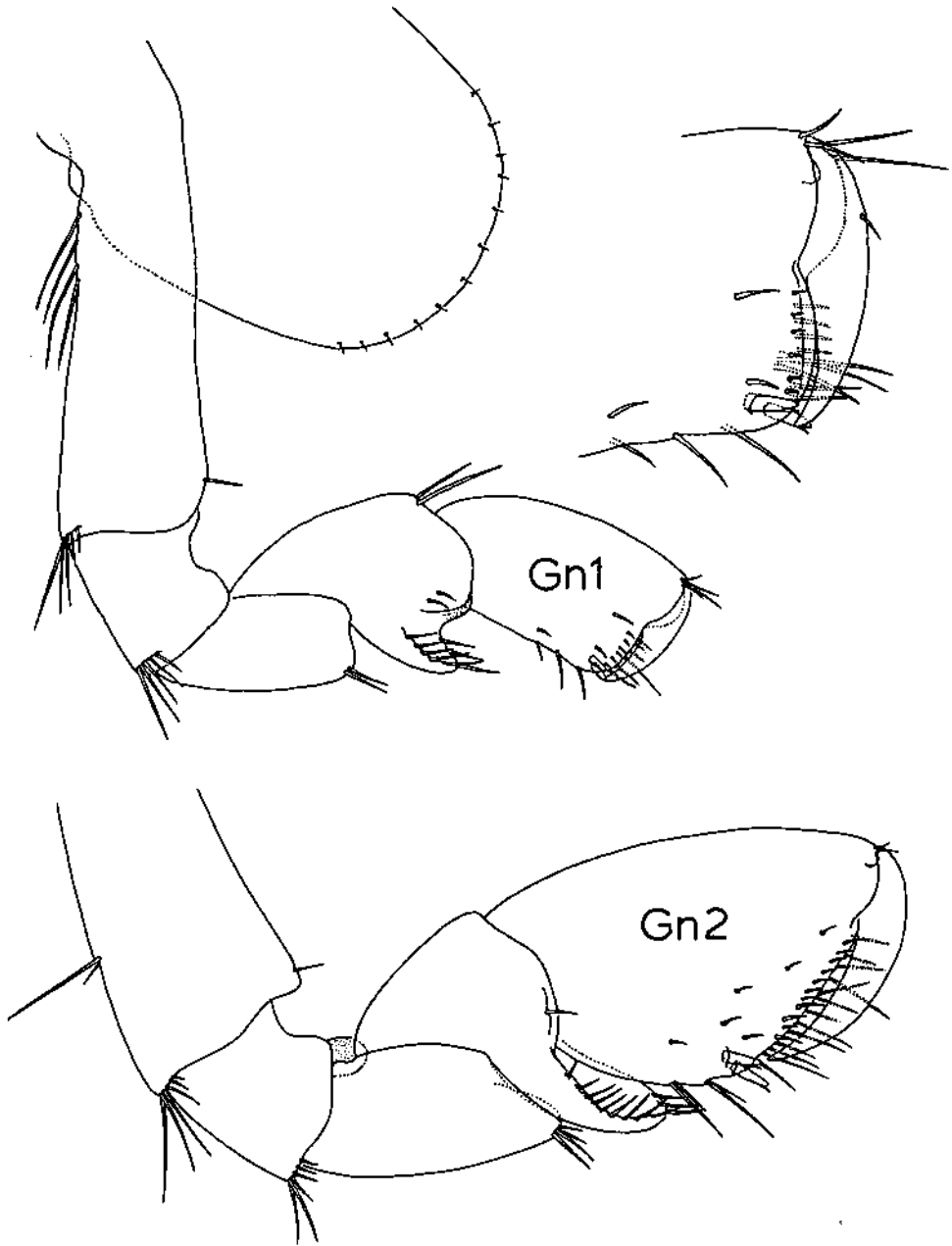


Figure 22.

Parhyalella nisbetiae Lazo-Wasem and Gable, new species, YPM 9393, female allotype, 4.9 mm. Abbreviation: Gn, gnathopod.

anteriorly produced, coxal plate 4 slightly longer than wide. Gnathopod 1, article 5 subequal to 6 in length, anterior margin with distal setae only; article 6, palm transverse, concave, posterior corner broadly rounded, defined by one small and two large spines, hind margin near palm with a few single setae and minute tubercles; dactyl simple. Gnathopod 2, article 6 very wide, width 90% of length, palm nearly straight, hind margin with two setal groups. Pereopods 3 and 4 similar, article 2 posterior margin with a few setae,

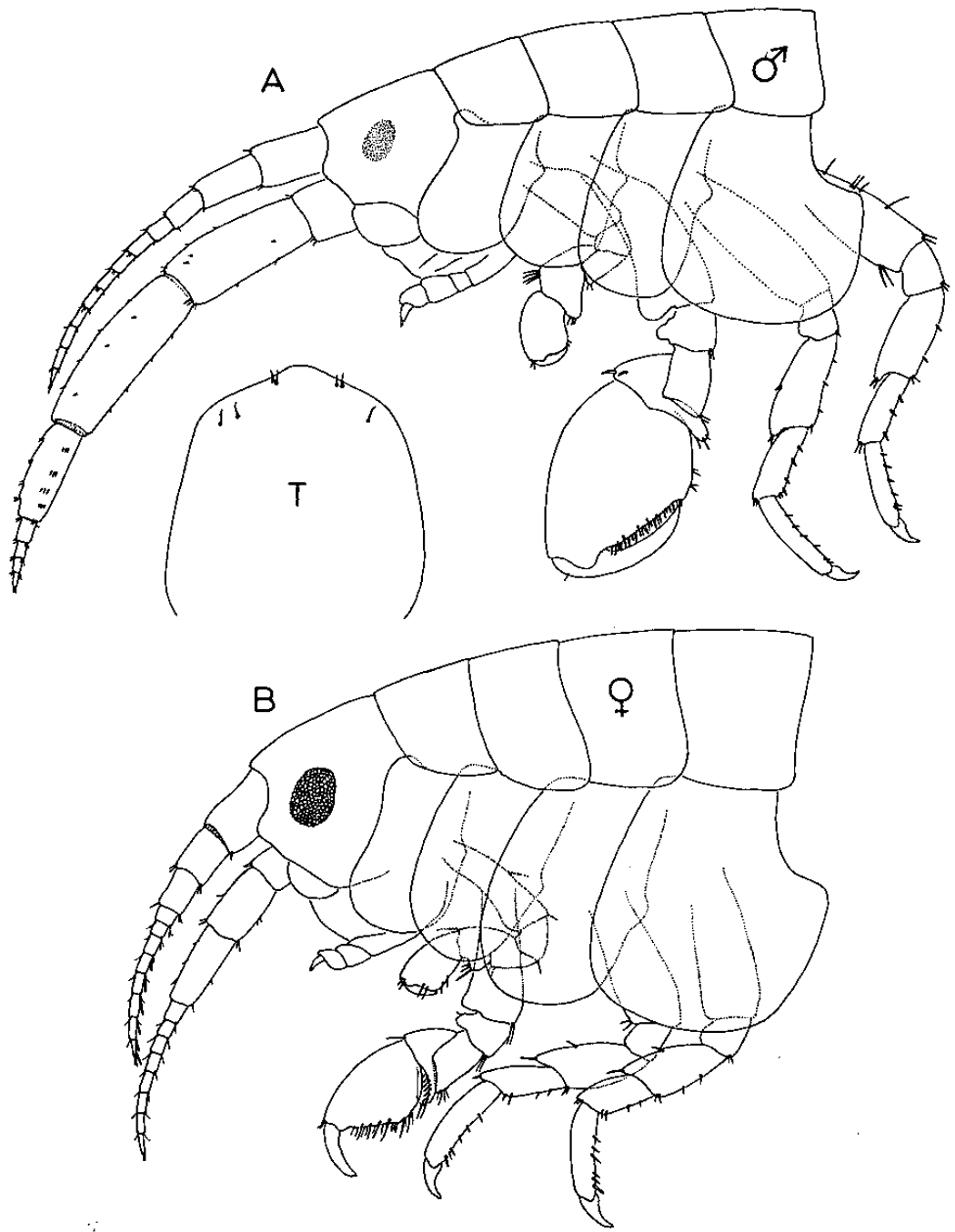


Figure 23.

Parhyaella ruffoi Lazo-Wasem and Gable, new species. A. USNM 1000158, male holotype, 7.8 mm. B. USNM 1000159, female allotype, 4.8 mm. Abbreviation: T, telson.

articles 5 and 6, posterior margin spinose. Pereopods 5 to 7 sequentially longer. Pereopod 5, articles 2 and 4 with distinct posterior lobe, article 4 anterior margin with two medial spine clusters, article 5 shorter than articles 4 and 7. Pereopods 6 and 7 similar, articles 2 and 4 with distinct posterior lobe, posterior margin of articles 5 and 6 lacking spines. Uropod 2, inner ramus, margin with row of single spines. Uropod 3, peduncle two to three times as long as ramus, with one stout distal spine and several small facial setae; ramus with one short distal spine and two short setae. Telson slightly longer than broad, distal margin forming a blunt point.

Female. Eyes oval, relatively larger than those of male. Coxal plate 4 longer than wide. Antennae 1 and 2 short, flagellum of each with eight articles; antenna 1 extending well beyond peduncle of antenna 2, flagellum with aesthetascs. Gnathopod 1, article 6 palm transverse, convex, lightly setose. Gnathopod 2, anterior distal projection of article 2 (and 3) strong, bluntly triangular; article 6 depth 66% of length, palm lightly setose, hind margin with two groups of two to three long setae each.

Habitat: No habitat data were associated with the specimens from the type locality. The specimens of Gonzalez (1991) were found among floating algae in shallow water.

Etymology: This species is named for Sandro Ruffo, in honor of his early work on *Parhyalella* and of his lifelong devotion to the study of amphipods.

Remarks: Gonzalez (1991) reports a *Parhyalella* sp. from northern Chile that we tentatively identify as *P. ruffoi*. Some minor differences can be found between our figures of *P. ruffoi* and those given by Gonzalez for *Parhyalella* sp. Unfortunately, Gonzalez does not figure antenna 2 of the male, a key character in the diagnosis of *Parhyalella*; therefore, it is difficult to evaluate fully the distinctiveness of the Chilean *Parhyalella*, compared to *P. ruffoi* from Peru.

PARHYALELLA STEELEI LAZO-WASEM AND GABLE NEW SPECIES

Figures 28–31

Parhyalella pietschmanni Steele; 1973:276–280, figs. 1–4.

Material examined: YPM 9381: male holotype, 7.3 mm. YPM 9382: female allotype, 5.4 mm. YPM 9380: male paratype, 6.9 mm. YPM 9383: seven female paratypes. YPM 9384: nine male paratypes. YPM 9835: 170 males, females and juveniles. Madagascar, Ambatoloaka, Nosy Bé, from shallow water among floating turtle grass (*Thalassodendron ciliatum*) washing up near shore, lat 13°15'S, long 43°15'E; collector probably A. G. Humes, 1963–1964.

Diagnosis: Male. Eye small, round, dark. Antenna 2, peduncle very stout, article 1 of flagellum 5-conjointed. Gnathopod 1, article 5 anterior margin with distal setae only; article 6 palm transverse, hind margin concave; dactyl bifurcate. Gnathopod 2, article 6, hind margin rounded. Uropod 2, inner ramus, margin with row of single spines.

Type locality: Ambatoloaka, Nosy Bé, Madagascar.

Description: Male. Eye small, round, dark in alcohol-preserved specimens. Coxal plates medium, coxa 1 anterior margin weakly produced, rounded, coxa 4 width subequal to length. Antenna 1 extending to end of peduncle of antenna 2, flagellum slightly longer than peduncle, consisting of 14 articles. Antenna 2 peduncle inflated, article 4 length subequal to article 5; flagellum longer than article 5 of peduncle, consisting of eight articles, article 1 of flagellum 5-conjointed, combined length of remaining articles equal to first. Upper lip, distal margin broadly convex, finely setose. Lower lip, outer lobes broad,

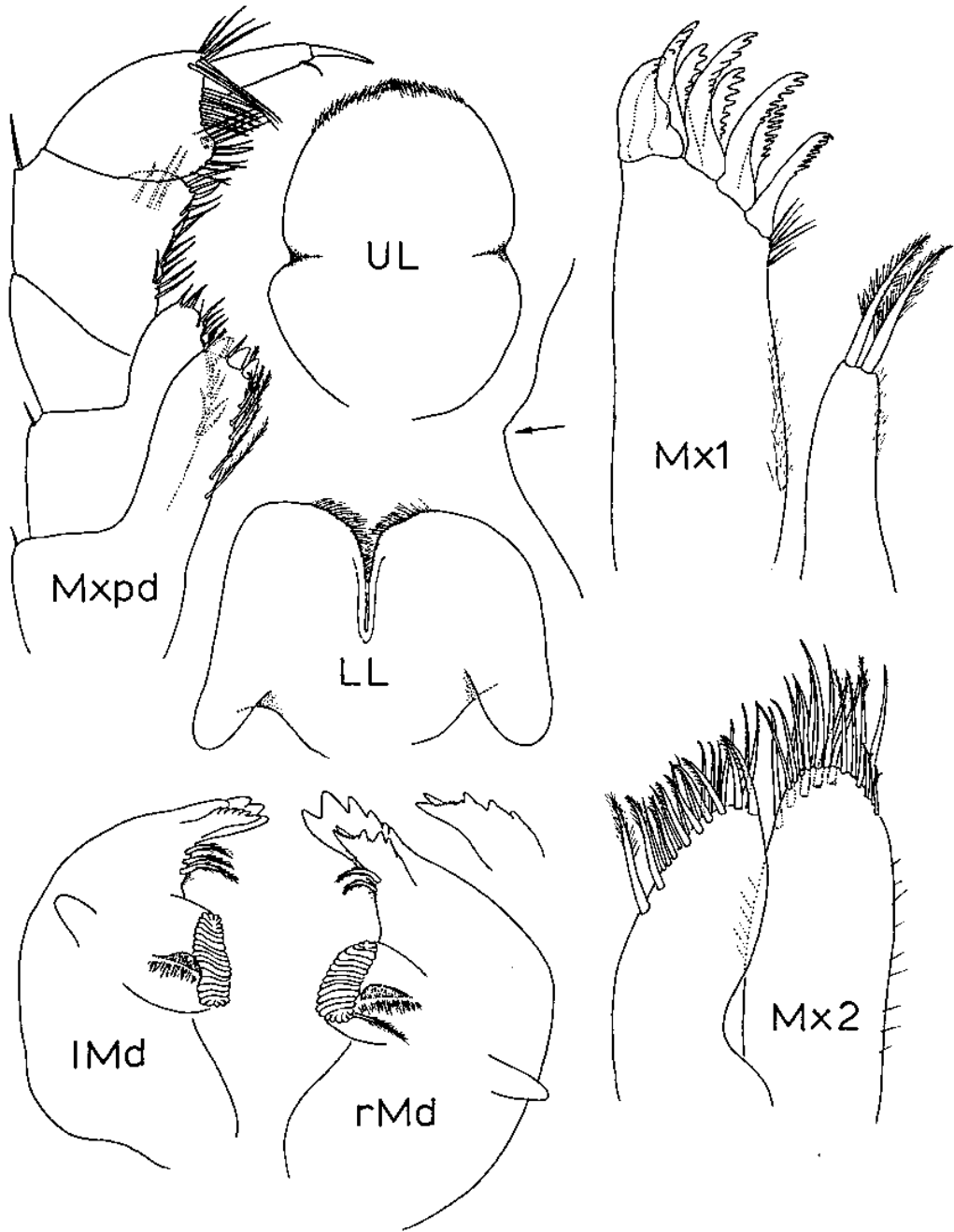


Figure 24.

Parhyaella ruffoi Lazo-Wasem and Gable, new species, USNM 1000158, male holotype, 7.8 mm. Abbreviations: LL, lower lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; UL, upper lip; l, left; r, right.

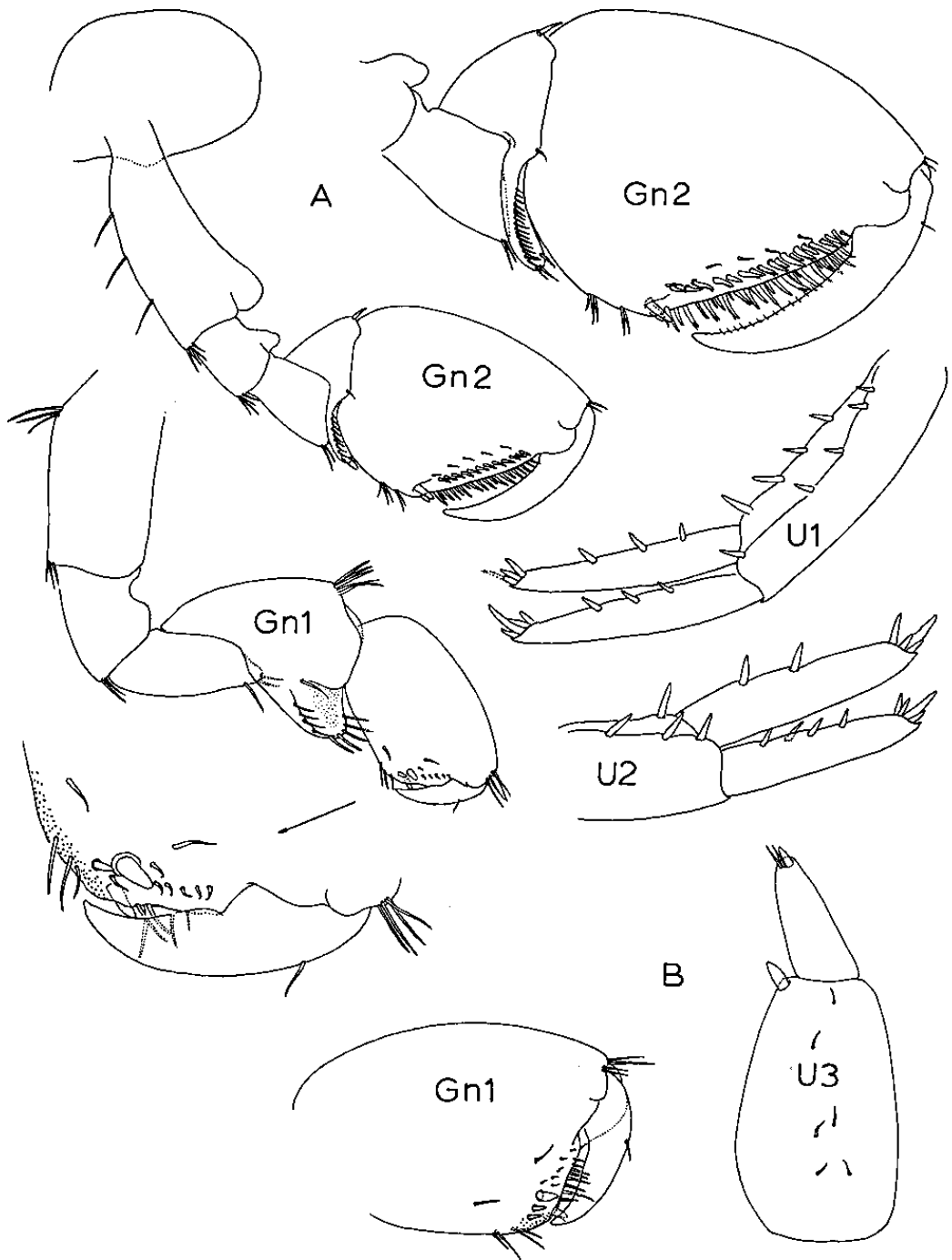


Figure 25.

Parhyaella ruffoi Lazo-Wasem and Gable, new species. A. USNM 1000158, male holotype, 7.8 mm. B. USNM 1000160, male paratype, 8.0 mm. Abbreviations: Gn, gnathopod; U, uropod.

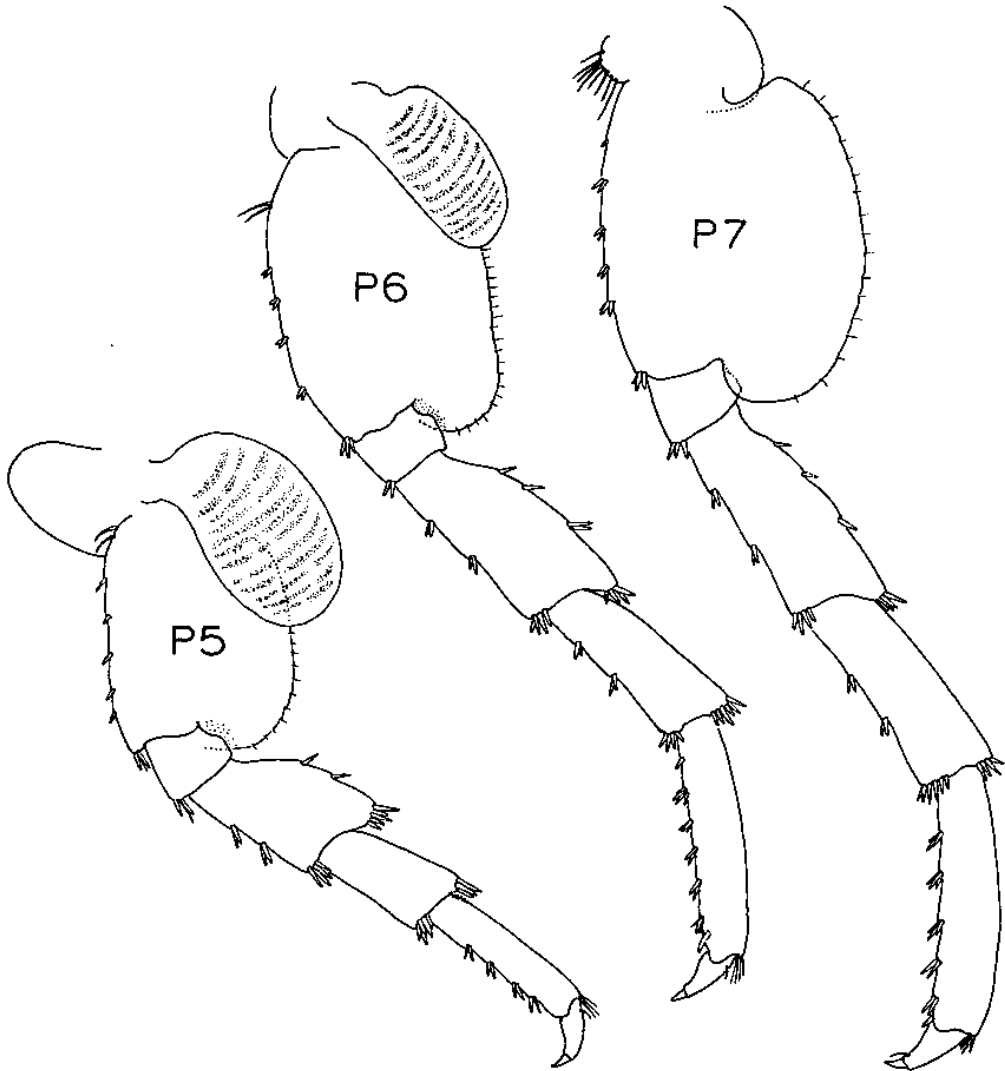


Figure 26.

Parhyaella ruffoi Lazo-Wasem and Gable, new species, USNM 1000158, male holotype, 7.8 mm. Abbreviation: P, pereopod.

distal and inner margins finely setose. Left mandible, molar strong, triturative, inner margin with three large and three small plumose setae, lacinia mobilis 6-dentate, incisor 5-dentate. Right mandible similar to left, molar with plumose accessory seta, inner margin with two large and two small plumose setae, accessory plate with stout proximal teeth, distally serrate. Maxilla 1, inner plate with two stout plumose setae; outer plate with nine serrate teeth, inner margin lightly setose near base of teeth. Maxilla 2, inner plate subequal in width and slightly shorter than outer plate, with row of plumose and simple setae along inner and distal margin, proximal plumose setae stout; outer plate with a few small setae at outer distal corner, distal margin with subapical and apical rows of setae, subapical setae very stout. Maxilliped, inner plate, distally with three stout teeth, inner margin lined with plumose setae and fine facial setae; outer plate setose along dis-

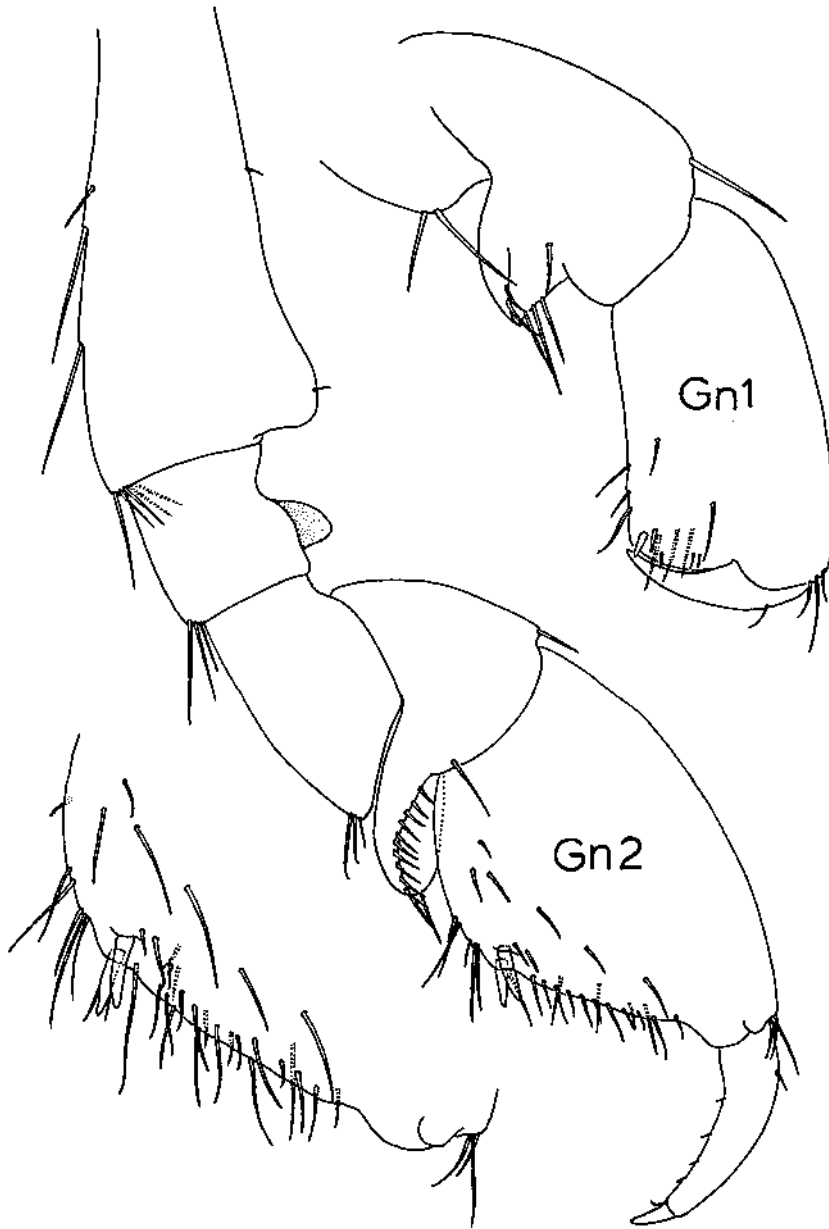


Figure 27.

Parhyaella ruffoi Lazo-Wasem and Gable, new species, USNM 1000159, female allotype, 4.8 mm. *Abbreviation:* Gn, gnathopod.

tal and inner margin, apical setae stout; palp, article 2 with broad, setose, inner lobe, article 3, inner margin with distal lobe, distal margin setose; article 4 with long distal nail. Gnathopod 1, article 5 length subequal to article 6, with only distal setae on anterior margin; article 6 width 75% of length, anterior margin broadly curved, palm transverse, weakly convex, posterior corner forming blunt right angle, defined by two stout spines near corner and one larger facial spine; dactyl bifurcate. Gnathopod 2, article 6 width 75% of length, palm oblique, slightly sinuous, spinose and setose, with two stout spines

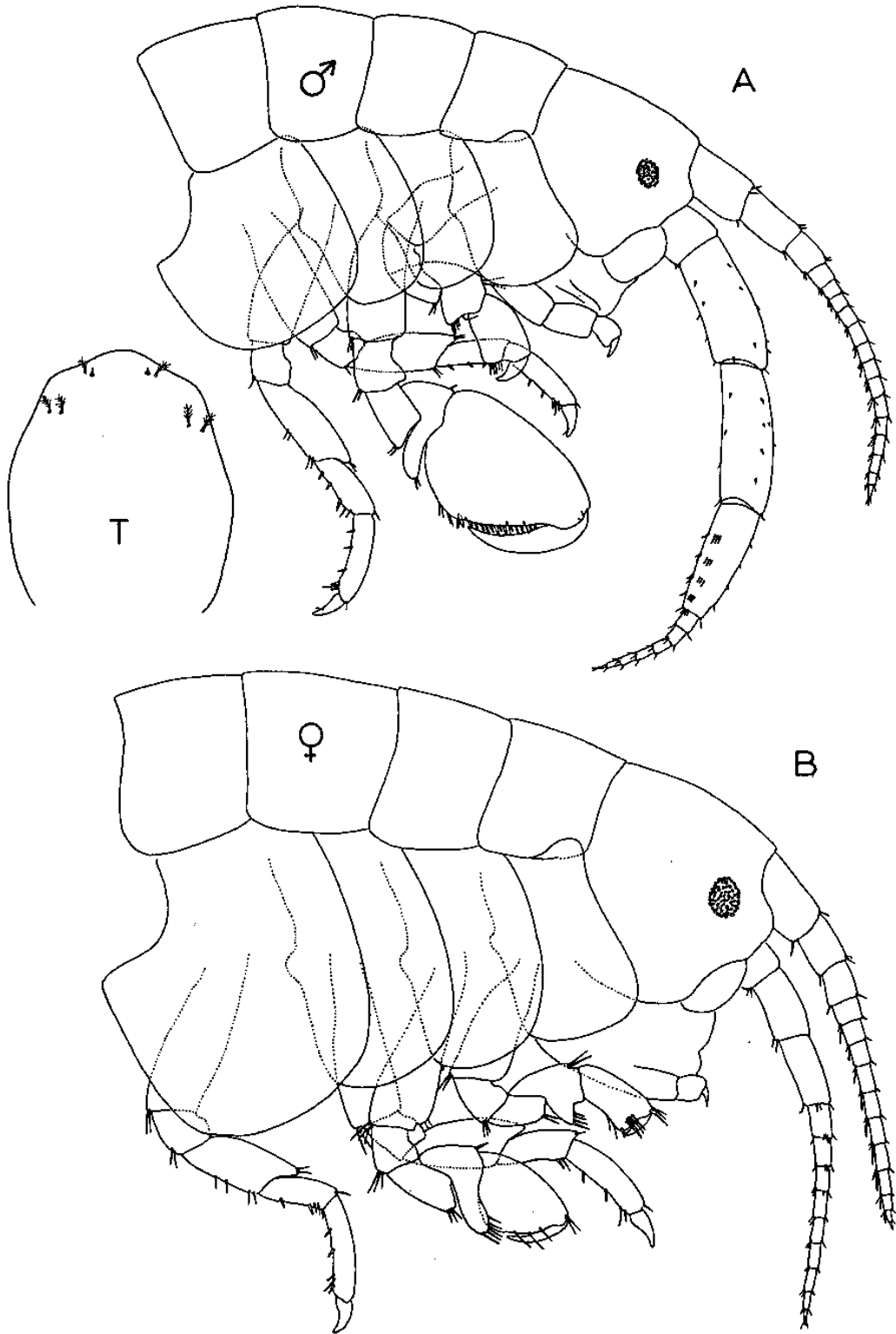


Figure 28.

Parhyaella steelei Lazo-Wasem and Gable, new species. A. YPM 9381, male holotype, 7.3 mm. B. YPM 9382, female allotype, 5.4 mm. Abbreviation: T, telson.

at posterior corner, hind margin concave with two setal groups. Pereopods 3 and 4 similar, article 2 posterior margin with a few setae, articles 5 and 6, posterior margin spinose. Pereopods 5 to 7 sequentially longer. Pereopod 5, articles 2 and 4 with distinct posterior lobe, article 4 anterior margin with two medial spine clusters, article 5 shorter than articles 4 and 7. Pereopods 6 and 7 similar, articles 2 and 4 with distinct posterior lobe, posterior margin of articles 5 and 6 lacking spines. Uropod 2, inner ramus, margin with row of single spines. Uropod 3, distal margin of peduncle with two stout spines, ramus slightly less than 50% length of peduncle, distally with one short spine and two setae. Telson longer than broad, distal margin tapered to blunt point at apex.

Female. Eye similar to that of male. Antenna 1 extending well beyond peduncle of antenna 2, flagellum long, of 11 articles; antenna 2, flagellum slightly longer than peduncle, consisting of 10 articles. Gnathopod 1, article 4 with two distal setae; article 5 shorter than article 6; article 6 distally expanded, palm essentially transverse but with slight anterior obliqueness, convex, exterior facial surface with distinct cluster of five setae at midpoint of palm, posterior corner defined by two stout spines. Gnathopod 2, anterodistal lobe of article 2 weak; article 5 posterior lobe very broad, produced below article 6; article 6 width 66% length, palm oblique, nearly straight, weakly spinose, posterior corner with very slight protuberance and two stout spines, length of hind margin equal to palm, with two groups of two setae each.

Habitat: Drifting dead turtle grass (mostly *Thalassodendron ciliatum*) washing ashore at low-water level during neap tides, driven onshore by prevailing winds (Steele 1973, and personal communication).

Etymology: Named for D. H. Steele, donor of these specimens, whose valuable information on their ecology and habitat helped lead to the discovery of the new species from Nevis, British West Indies.

PARHYALELLA SP.

Material examined: YPM 9841: female, 3.2 mm, British Virgin Islands, Anegada, bay East of Pomato Point, at Neptune's Treasure Resort, under rock at water's edge; collector A. J. Baldinger, 26 Oct 1998.

Remarks: A small female referable to this genus but otherwise unidentifiable was found among other amphipods (*Ampithoe*, *Hyale*, and others) from the island of Anegada, British Virgin Islands. Although other material from elsewhere in the area has been examined (Guana Island, Tortola, Beef Island), no additional specimens have been found.

Remarks on Species of *Parhyalella*

Several authors have commented on the difficulty of distinguishing among the species of *Parhyalella* sensu lato. Shoemaker (1933) noted that *P. whelpleyi* might prove to be a synonym of *P. batesoni* if new material were obtained from Bermuda (he apparently did not examine the type specimen of the latter). Ruffo (1953) discussed the close similarity of *P. batesoni* with *P. congoensis*, and implied that the latter cannot be distinguished from the former by their original descriptions. He further noted that *P. batesoni*, *P. pietschmanni* and *P. congoensis* constitute a group with strong morphological similarities. Steele (1973) suggested the various species of *Parhyalella* encountered in the Indian Ocean might be synonymous with what he identified as *P. pietschmanni* from Madagascar, but that the synonymy could only be confirmed by comparison with type specimens. Our studies on *Parhyalella*, sensu stricto, enable us to provide direction in distinguishing the species.

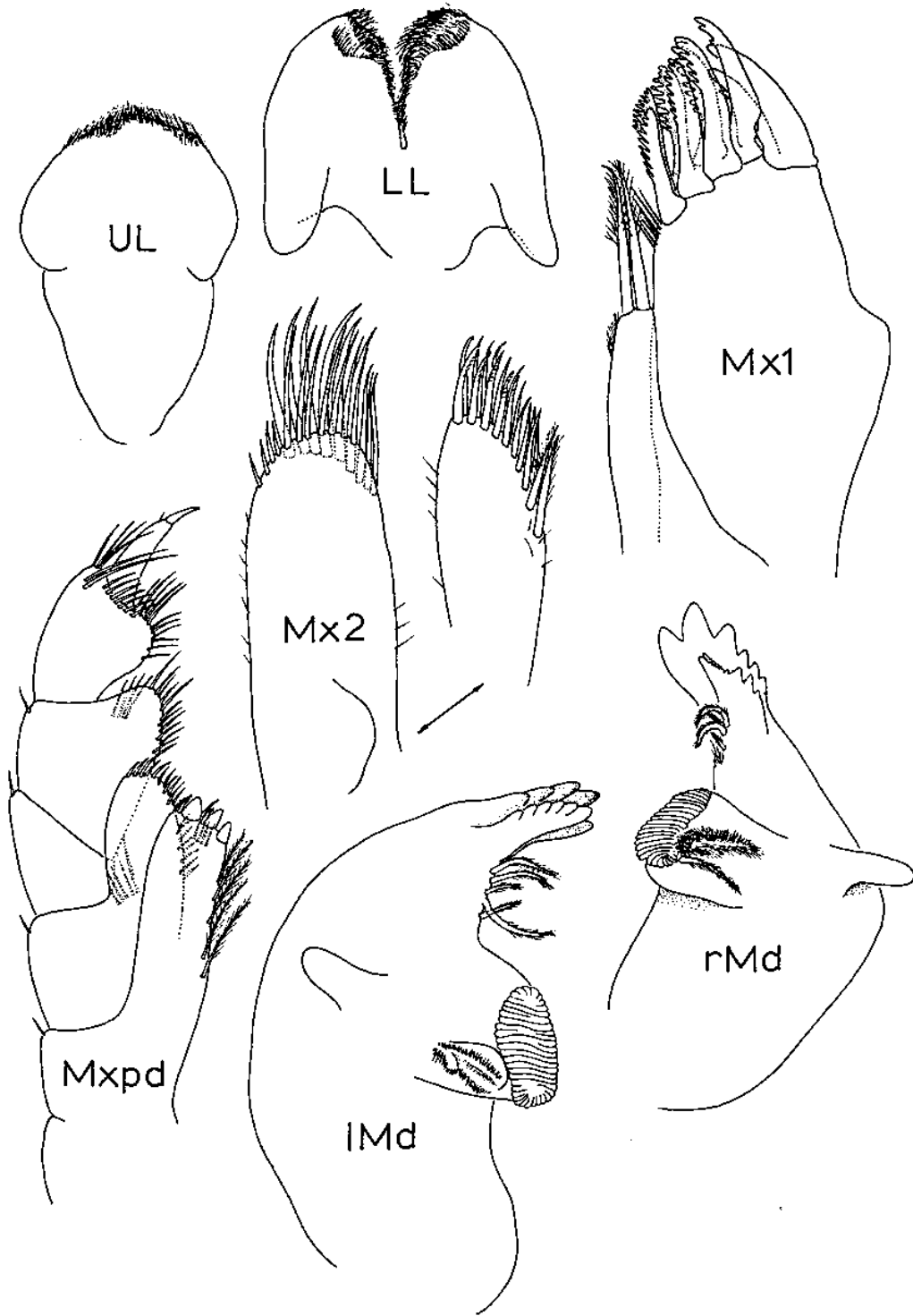


Figure 29.

Parhyaella steelei Lazo-Wasem and Gable, new species, YPM 9381, male holotype, 7.3 mm. Abbreviations: LL, lower lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; UL, upper lip; l, left; r, right.

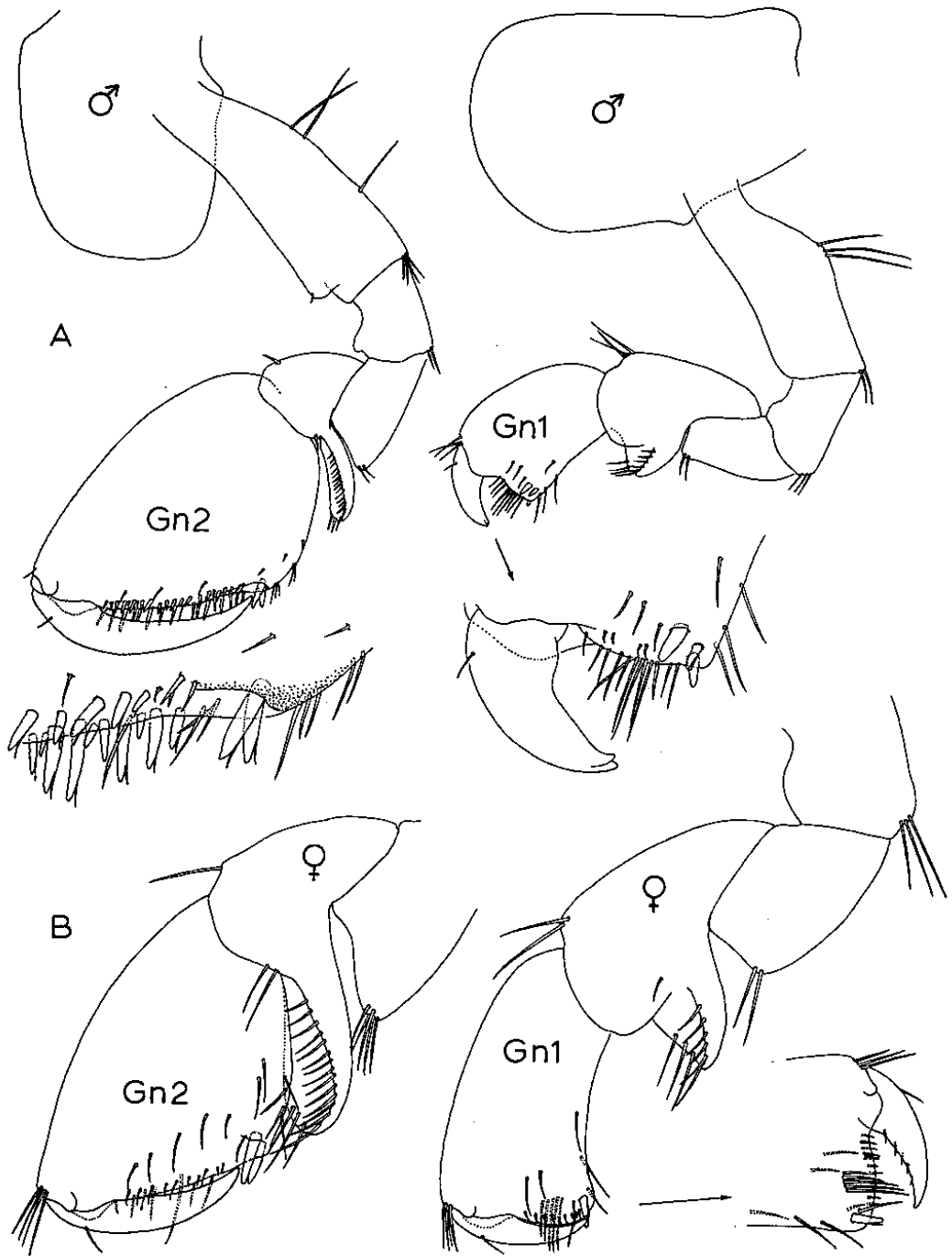


Figure 30.

Parhyaella steelei Lazo-Wasem and Gable, new species. A. YPM 9381, male holotype, 7.3 mm. B. YPM 9382, female allotype, 5.4 mm. Abbreviation: Gn, gnathopod.

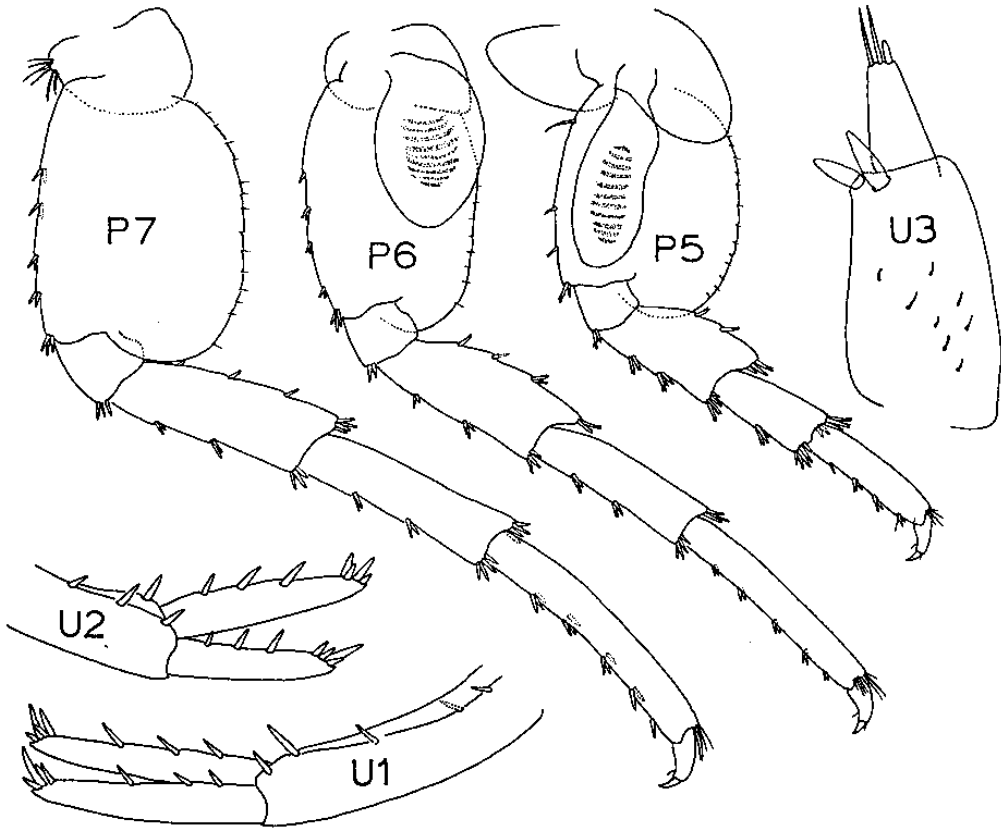


Figure 31.

Parhyaella steelei Lazo-Wasem and Gable, new species, YPM 9381, male holotype, 7.3 mm. Abbreviations: P, pereopod; U, uropod.

Our guiding statements, unfortunately, apply only to males; more study of female characters is necessary before most females in *Parhyaella* can be distinguished with certainty.

The primary diagnostic features for *Parhyaella* are: (1) the presence or absence of medial setae on article 5 of gnathopod 1, including their number when present, and (2) the number of conjointed segments of the flagellum of article 1 on antenna 2.

Other features, such as the morphology or appearance of the eyes, the shape of the palm of gnathopod 1, and the presence of a simple or bifurcate dactyl on gnathopod 1, are additional characters useful in differentiating the species.

The presence of medial setae on the anterior margin of article 5, gnathopod 1, serves to separate *P. batesoni*, *P. congoensis*, *P. pietschmanni* and *P. whelpleyi* from all the newly described species. In *P. batesoni* and *P. whelpleyi* this character is represented by a single small seta. In *P. whelpleyi*, antenna 2 flagellum article 1 is 3-conjointed, and the dactyl of gnathopod 1 is bifurcate. In contrast, antenna 2 of *P. batesoni* has a 5-conjointed flagellar article 1, and the dactyl of gnathopod 1 is simple.

Parhyaella pietschmanni and *P. congoensis* both have multiple medial setae, rather than a single seta, on the anterior margin of article 5 of gnathopod 1. These two species are clearly distinguished by the number of these setae (two in *P. pietschmanni* and four in *P. congoensis*). The number of conjointed flagellar segments of article 1 of antenna 2

Table 1.

Key diagnostic characters distinguishing species of *Parhyalella*.

	Eye shape and color	A2, relative stoutness	A2, flagellum article 1, number of conjoined segments	Gn1, article 5, medial anterior margin	Gn1, palm	Gn1, article 7	Gn2, article 6, hind margin	U2, inner ramus
<i>P. batesoni</i>	Large, oval, black	Very stout	5	1 small seta	Transverse, nearly straight	Simple	Slightly rounded	1 group, double spines
<i>P. whelpleyi</i>	Small, round, pale to dark	Stout	3	1 small seta	Transverse, convex	Bifurcate	Straight	Single spines
<i>P. pietschmanni</i>	Large, oval, dark	Very stout	5	2 thick setae	Oblique, convex	Bifurcate	Rounded	1 group, double spines
<i>P. congoensis</i>	Unknown	Stout	2	4 thick setae	Oblique, slightly convex	Simple	Rounded	Single spines
<i>P. barnardi</i>	Very large, oblong, golden, widely spaced ocelli	Stout	4	Bare	Transverse, concave	Simple	Rounded	2 groups, double spines
<i>P. kunkeli</i>	Medium, oval, black	Stout	4	Bare	Oblique, convex	Bifurcate	Rounded	Single spines
<i>P. nisbetae</i>	Medium, oval, dark	Stout	5	Bare	Transverse, weakly concave	Simple	With large protuberance	Single spines
<i>P. ruffoi</i>	Large, oval, faded red to brown	Stout	5	Bare	Transverse, concave	Simple	Slightly rounded	Single spines
<i>P. steelei</i>	Small, round, dark	Very stout	5	Bare	Transverse, weakly concave	Bifurcate	Rounded	Single spines

also distinguishes the species (five in *P. pietschmanni*, two in *P. congoensis*). The former species, in addition, has a bifurcate dactyl on gnathopod 1, whereas in the latter species the dactyl is simple.

Parhyalella nisbetae is unique and immediately recognizable in having a produced distal hind margin on article 6 of gnathopod 2. *Parhyalella ruffoi* and *P. barnardi* are both from the eastern Pacific coast and their geographic distributions may eventually be found to overlap. However, these two species are easily distinguished. *Parhyalella ruffoi* has a stout antenna 2 with a 5-conjointed flagellar article 1. *Parhyalella barnardi* has a much less stout second antenna and possesses a 4-conjointed flagellar article 1. *Parhyalella ruffoi* also has small eyes that are faded red or brown when preserved, whereas *P. barnardi* has large and oblong eyes with a distinctly golden appearance in preservative.

Parhyalella kunkeli and *P. steelei* differ in the number of conjointed flagellar segments of article 1 on antenna 2. In addition, the shape of the palm of gnathopod 1 differs between the species. *Parhyalella kunkeli* has a 4-conjointed flagellar article 1 on antenna 2 and an oblique gnathopod 1 palm, whereas *P. steelei* has five conjointed articles and the palm of gnathopod 1 is transverse. Furthermore, in both these species the palm is convex, in contrast to the concave palms of *P. ruffoi* and *P. barnardi*. Also, both species have a bifurcate dactyl on gnathopod 1, whereas in *P. ruffoi* and *P. barnardi* the dactyl is simple.

Appendages such as the uropods, although traditionally useful in distinguishing amphipod taxa, are not found to be useful in *Parhyalella* as the spination is variable and remarkably similar among the various species. Only *P. barnardi*, with two groups of two spines on the inner ramus of uropod 2, shows any consistent difference from the other species. *P. batesoni* and *P. pietschmanni* have a single group of two spines proximally on the inner ramus of uropod 2. The former, however, is known only from the holotype, and the latter is apparently variable, as the figure of Barnard (1970) does not show a double spine group for the inner ramus of uropod 2.

Several characters of the mouthparts and pereopods are of potential interest in future analyses of variation, as more adult individuals become available. The lacinia mobilis, although typically 6-dentate, appears 5-dentate in *P. kunkeli*; in this species the proximal tooth on the lacinia is minute. The specimen of *P. pietschmanni* illustrated by Barnard (1970:270, fig. 180) has a 5-dentate lacinia. Furthermore, his figure (1970:270, fig. 180) of the maxilliped shows five stout teeth on the distal margin of the inner plate. In all other species examined the inner plate has only three teeth on the distal margin. Our examination of specimens from Hawaii does not agree with Barnard's figures in this respect; all specimens examined for this feature have only three teeth. Subtle differences are also seen in the number of relatively stout setae on the proximal anterior margin of pereopod 5, article 2; these are placed together as a distinct group separate from the setae found along the same margin. The setal group varies from one or two setae (*P. congoensis*, *P. whelpleyi* and *P. steelei*), to three setae (*P. batesoni*, *P. barnardi*, *P. kunkeli* and *P. nisbetae*), to four to five setae (*P. pietschmanni*). In the latter, the pattern is of three or four primary setae, the most proximal of which is coupled with a smaller seta; observed variation may be allometric. These setation patterns may represent a useful diagnostic character if they are found to be consistent.

Many more specimens of *Parhyalella*, beyond the type series, will have to be analyzed before the morphological and geographic boundaries separating the various species can be defined more precisely. Nevertheless, we believe that the diagnostic characters we have selected represent the terminus of allometric growth and are therefore reliable (see Table 1).

Key to the Species of *Parhyalella*

(males)

1. Gnathopod 2, article 6, posterior corner produced *P. nisbetae* new species
 Gnathopod 2, article 6, posterior corner rounded, not produced 2
2. Gnathopod 1, article 5, anterior margin with medial setae 3
 Gnathopod 1, article 5, anterior margin bare 6
3. Gnathopod 1, article 5, anterior margin with one seta 4
 Gnathopod 1, article 5, anterior margin with more than one seta 5
4. Antenna 2, article 1 of flagellum 5-conjointed *P. batesoni*
 Antenna 2, article 1 of flagellum 3-conjointed *P. whelpleyi*
5. Gnathopod 1, article 5, anterior margin with two setae *P. pietschmanni*
 Gnathopod 1, article 5, anterior margin with four setae *P. congoensis*
6. Gnathopod 1, palm concave 7
 Gnathopod 1, palm straight or convex 8
7. Antenna 2, article 1 of flagellum 4-conjointed *P. barnardi* new species
 Antenna 2, article 1 of flagellum 5-conjointed *P. ruffoi* new species
8. Antenna 2, article 1 of flagellum 4-conjointed *P. kunkeli* new species
 Antenna 2, article 1 of flagellum 5-conjointed *P. steelei* new species

Systematic Account of *Exhyaella*

Description of Genus

EXHYALELLA STEBBING 1917 REVISED STATUS

Exhyaella Stebbing; 1917:435.

Exhyaella Stebbing; 1918:66.

Type species: *Exhyaella natalensis* Stebbing 1917.

Diagnosis: Mandibular molars without plumose accessory seta. Maxilla 1 lacking a palp but represented by a distinct small spine in shallow excavation. Maxilliped palp with 4-articulate palp, article 4 unguiform, lacking whip-like seta. Male antenna 2 peduncle equal in width to antenna 1 peduncle. Male gnathopod 1 much smaller than gnathopod 2, article 6 with transverse palm; gnathopod 2, article 6 palm strongly oblique. Female gnathopod 1, article 6 with transverse palm; gnathopod 2 much larger than gnathopod 1, article 6 with palm oblique, of distinctly different morphology than gnathopod 1. Female gnathopod 2 of similar morphology to that of male. Uropods 1 and 2, outer rami spinose along margin. Telson entire.

Distribution: Indian Ocean.

Included species: *Exhyaella natalensis* Stebbing, *E. indica* (K. H. Barnard), *E. hartmani* new species.

Species Descriptions

EXHYALELLA NATALENSIS STEBBING 1917

Figures 32–35

Exhyaella natalensis Stebbing; 1917:435.

Exhyaella natalensis Stebbing; 1918:66–67, pl. 11.

Parhyaella natalensis K. H. Barnard; 1925:359–360.

Parhyaella natalensis K. H. Barnard; 1935:294–295, fig. 11f.

Parhyaella natalensis Griffiths; 1974:253.

Parhyaella natalensis Barnard and Karaman; 1991:372.

Material examined: SAM A4574: male lectotype, 8.0 mm; female paralectotype, 10.6 mm; female paralectotype, 10.4 mm; male paralectotype, 7.8 mm; male paralectotype, 8.3 mm; 27 male and 19 female paralectotypes; four male and two ovigerous female paralectotypes separated out by C. L. Griffiths; South Africa, Durban; collector H. W. Bell Marley, 28 May 1917.

Diagnosis: *Male.* Gnathopod 1, palm of article 6 transverse, posterior corner demarcated

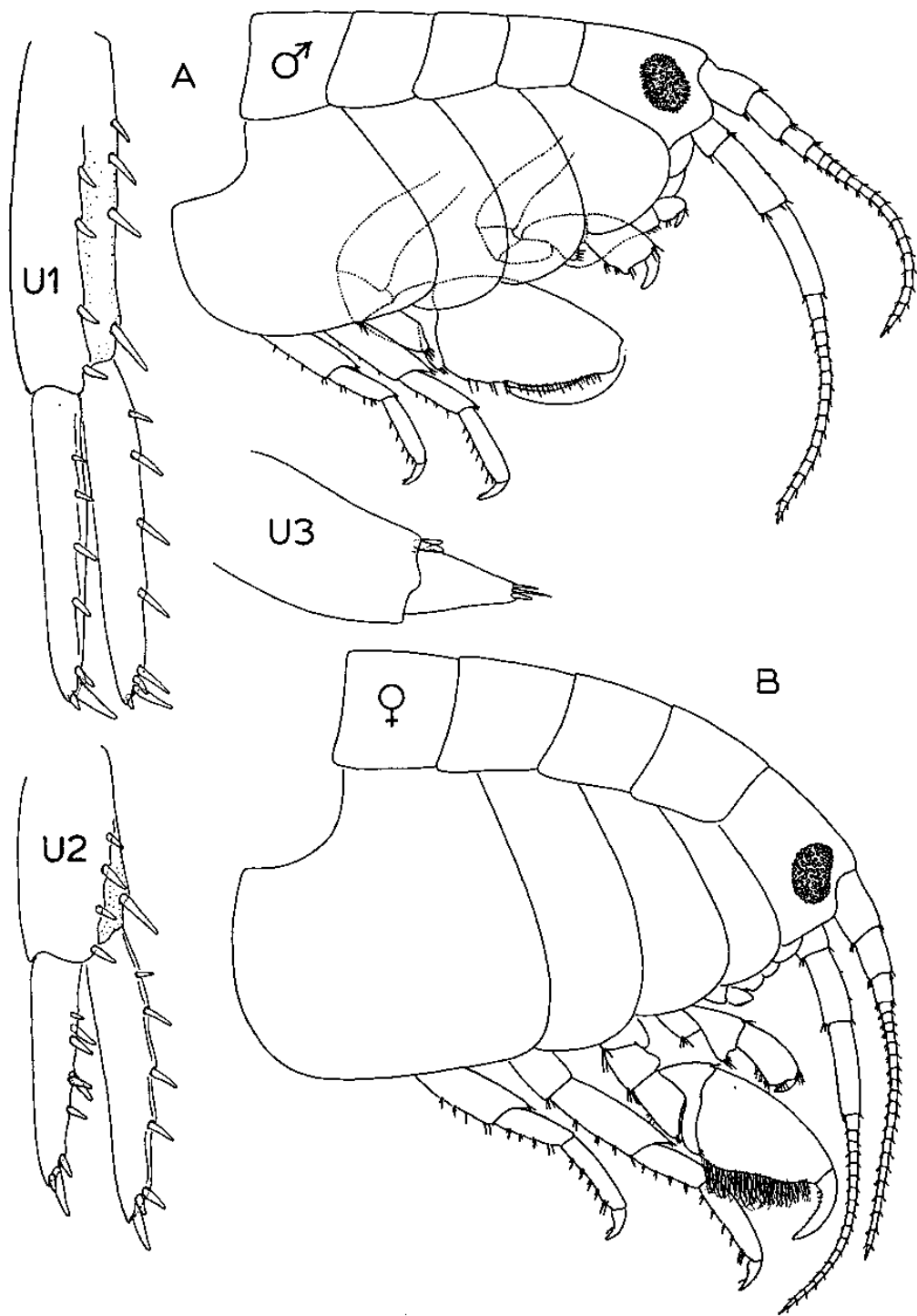


Figure 32.

Exhyalella natalensis Stebbing, SAM A4574. A. Male lectotype, 8.0 mm. B. Female parallolectotype, 10.6 mm.
Abbreviation: U, uropod.

by distinct protuberance and stout, recurved spine.

Female. Gnathopod 2, article 6, palm strongly oblique, very densely lined with long, fine, distally curved setae, posterior corner with broad excavation, marked by three large spines at point of dactyl closure.

Type locality: Durban, South Africa.

Description: *Male.* Eye large, oval, pale yellow in alcohol-preserved specimens. Coxal plates 1 to 3 deeper than broad, coxa 1 anteriorly produced, coxa 4 as broad as deep, nearly twice as broad as 3; distal margins of coxae smooth. Antenna 1 extending beyond peduncle of antenna 2, peduncle slightly thicker than that of antenna 2, less than one-half length of flagellum, flagellum of 16 articles. Antenna 2, peduncle articles 4 and 5 subequal in length, flagellum slightly longer than peduncle, with 16 articles. Left mandible, incisor with five teeth, lacinia with three to four proximal teeth, distally with bifurcate blade; right mandible, incisor process with four teeth, lacinia 5-toothed; molars of both left and right mandible strong, triturate. Maxilla 1, inner plate with two distal plumose setae, outer plate with eight distally serrate teeth, lacking palp but with single small spine on outer margin. Maxilla 2, inner and outer plates of equal width, inner plate with row of stout, plumose setae along apical margin and distal half of inner margin, outer plate with distal setae only. Maxilliped palp much larger than outer plate, 4-articulate, article 4 unguiform, with large distal nail. Gnathopod 1 much smaller than gnathopod 2, article 5 slightly longer than article 6, posterior lobe broad, spinose; article 6, broad, subquadrate, palm with strong recurved spine arising at base of bulbous protuberance of posterior corner, hind margin with three setal clusters, dactyl stout, distally bifurcate, directed inward. Gnathopod 2, article 5 short, strongly produced between articles 4 and 6, article 6 twice as long as deep, palm strongly oblique, lined with spines and setae, hind margin 30% length of palm. Pereopods 3 and 4 slender, article 2, anterior margin with distal setae, articles 4 to 6, anterior margins nearly bare; pereopod 5 stout, spinose, shorter than pereopods 6 and 7, articles 2 and 4 with posterior lobes; pereopods 6 and 7, articles 2 and 4 with posterior lobes, pereopod 7 longest. Uropods 1 and 2 slender, spinose; uropod 1, rami subequal in length, of same length as peduncle; uropod 2, rami longer than peduncle, inner ramus longer than outer, four times longer than broad. Uropod 3, peduncle with two distal spines; ramus 50% length of peduncle, distally with one spine and a few setae. Telson apically tapered to acute angle.

Female. Antennae long and thin; antenna 1 flagellum, 14 to 20 articles. Coxal plates deeper and broader than in males. Gnathopod 1, article 5 subequal in length to article 6, article 6 twice as long as wide, palm transverse, slightly convex, two spines defining posterior corner, hind margin setose along distal half. Gnathopod 2, article 5 lobe very deep, as wide as length of article; article 6, width about 60% of length, palm strongly oblique, convex, very densely lined with fine, curly tipped setae, three large spines at point of dactyl closure.

Remarks: The type material consists of approximately 50 specimens and one slide of dissected appendages from one male and one female. From the records available, no specimen was specifically designated as the holotype. The data in the original catalog at the South African Museum that correspond with this lot indicate the original manuscript name of "*Parhyalella retundata*" and make no reference to type status. One 8.3 mm male and one 10.4 mm female included in the specimen lot had been previously dissected, with the missing parts partially corresponding to those on the microscopic slide preparation. Unfortunately, the poor quality of Stebbing's figures do not allow detailed comparisons with those of the dissected specimens and microscope slide. We consider the

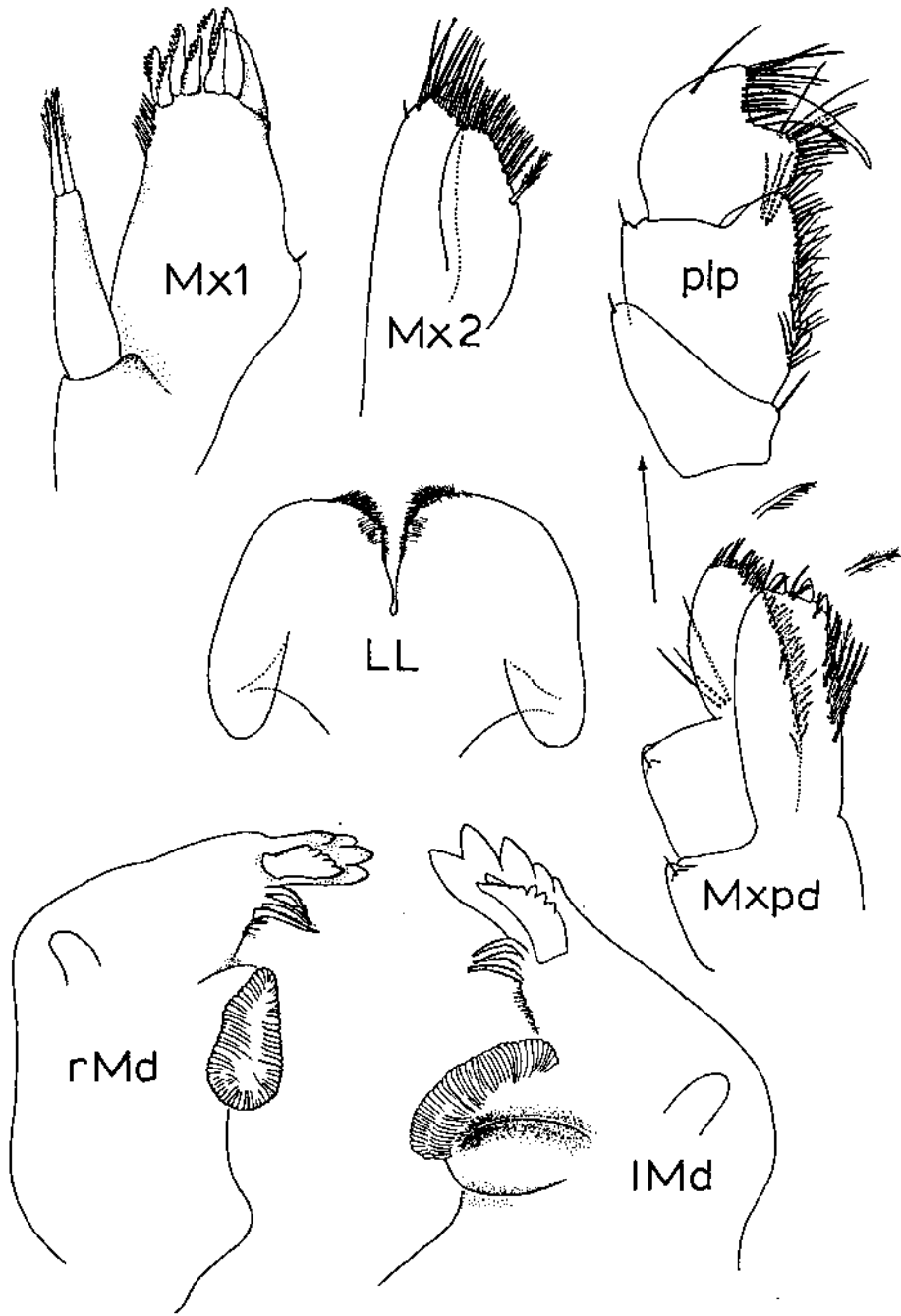


Figure 33.

Exhyalella natalensis Stebbing, SAM A4574, male lectotype, 8.0 mm. Abbreviations: LL, lower lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; plp, palp; l, left; r, right.

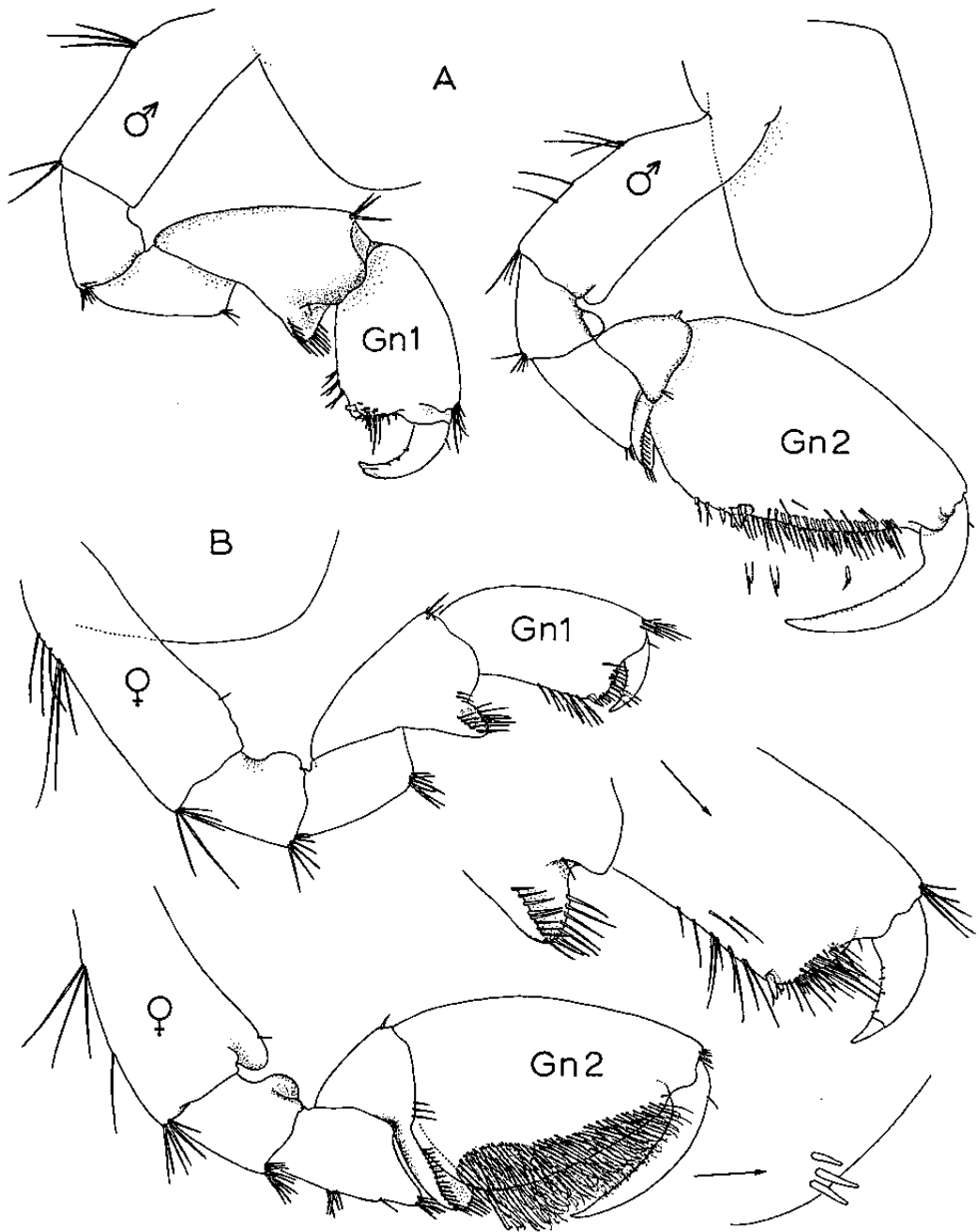


Figure 34.

Exhyalella natalensis Stebbing, SAM A4574. A. Male lectotype, 8.0 mm. B. Female parallolectotype, 10.6 mm. Abbreviation: Gn, gnathopod.

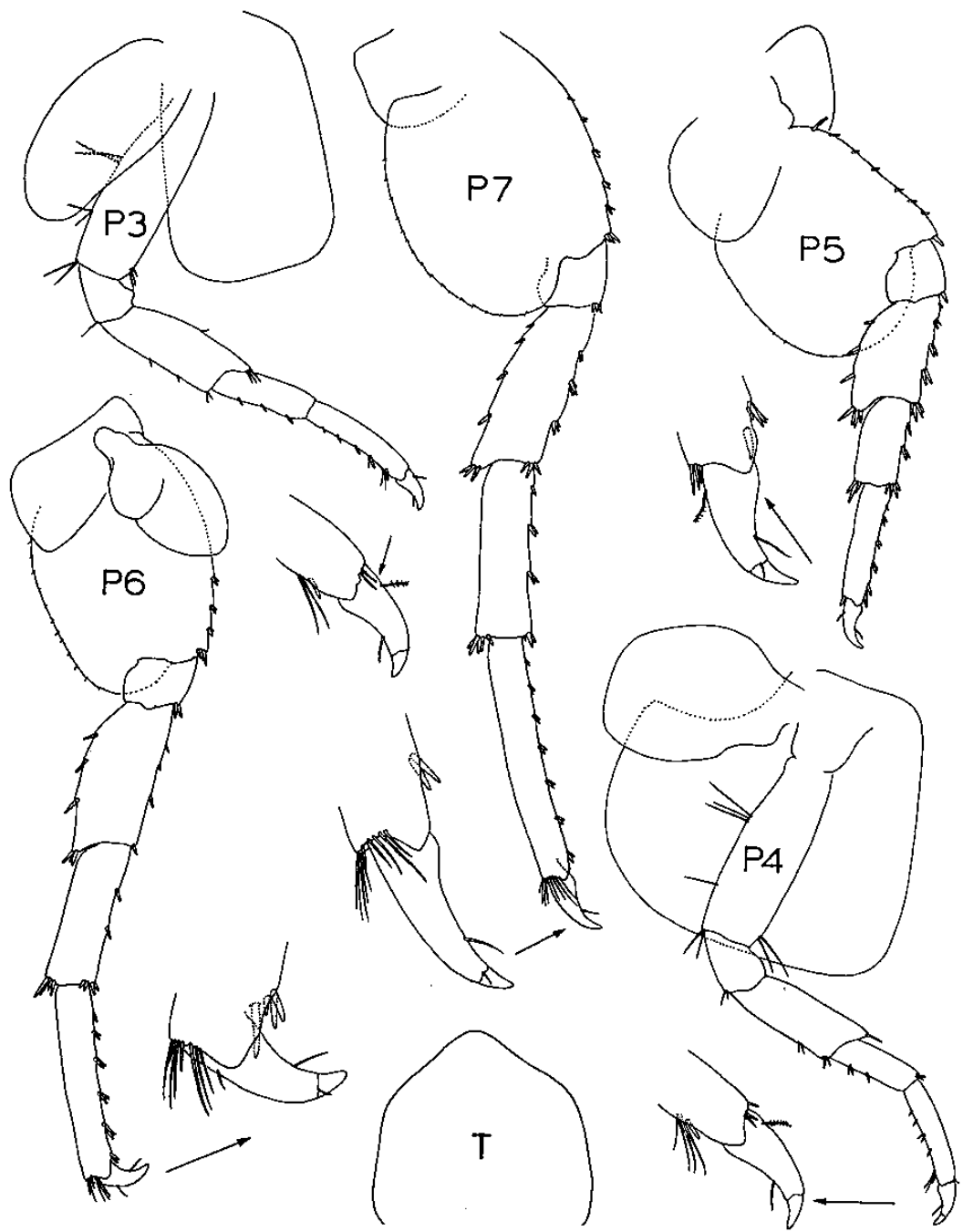


Figure 35.

Exhylaella natalensis Stebbing, SAM A4574, male lectotype, 8.0 mm. Abbreviations: P, pereopod; T, telson.

two dissected specimens to be figured syntypes from among a large series of syntypes, and so, to clarify application of the name, we hereby designate the 8.0 mm male specimen from lot SAM A4574 as **lectotype** for *Parhyalella natalensis*.

EXHYALELLA INDICA (K. H. BARNARD 1935) NEW COMBINATION
 Figures 36, 37

Parhyalella indica K. H. Barnard; 1935:294–295, fig. 11a–e.

Parhyalella indica Sivaprakasam; 1969:299–301, fig. 2.

Parhyalella indica Barnard and Karaman; 1991:372.

Material examined: ZSI 1728: male lectotype, 7.2 mm; four male paralectotypes. India, Tuticorin Harbor, shore; collector H. S. Rao, Feb–Mar 1926.

Diagnosis: Gnathopod 1, palm convex, posterior corner of palm rounded, defined by two stout spines projecting distally; gnathopod 2, palm sinuous.

Type locality: Tuticorin Harbor, India.

Description: *Male*. Eyes medium, black in alcohol-preserved specimens. Coxal plates 1 to 3 deeper than broad, coxa 1 anteriorly produced, coxa 4 as broad as deep, and one and one-half times as broad as coxa 3. Antenna 1, peduncle article 1 slightly wider than peduncle of antenna 2, flagellum extending 50% length of antenna 2, composed of 14 articles. Antenna 2, flagellum longer than peduncle, composed of 14 articles. Gnathopod 1 much smaller than gnathopod 2, article 5 slightly longer than article 6, posterior lobe broad, with relatively few setae; article 6 subquadrate, slightly longer than broad, palm transverse, convex, lined with setae, posterior corner rounded, marked by two stout spines directed distally, inner spine one-third larger than outer, hind margin with short row of single setae, dactyl simple, annulate. Gnathopod 2, article 5 short, produced between articles 4 and 6; article 6, length nearly twice the width, palm strongly oblique, distinctly sinuous, moderately lined with spines and setae, posterior corner with excavation and four spines. Uropods 1 and 2 normal, spinose. Uropod 3, peduncle nearly three times wider than ramus, distally with two stout spines and a few setae; ramus 50% length of peduncle, distally with one stout spine and a few setae. Telson quadrate, width equal to length, posterior margin bracket-shaped.

Female. None examined. We had an opportunity to examine only male specimens and therefore must rely on the original description of K. H. Barnard (1935) and the short re-description by Sivaprakasam (1969) for female morphology. Although neither author produced greatly detailed figures of the gnathopods, both refer to a dense brush of setae on the palm of gnathopod 2. In comparing the gnathopod 2 setal brush of female *E. natalensis* and *E. indica*, K. H. Barnard (1935) noted it was more dense in the latter. His figure of the female gnathopod 2 of *E. indica* is poorly drawn (for example, the hind margin of article 6; Barnard 1935:295, fig. 11b). Gnathopod 2, as illustrated, seems produced posteriorly (ironically, he comments on the poor quality of Stebbing's [1918, pl. xi] figures of *E. natalensis*). Sivaprakasam's (1969:302, fig. 2) figure of female gnathopod 2 is substantially better and does not show a posterior projection as illustrated in K. H. Barnard's (1935) figure. We believe that Barnard's illustration is incongruent with hyalid female gnathopod 2 morphology, and that Sivaprakasam's (1969) illustration, therefore, likely represents the true state of this character.

Remarks: Barnard did not specifically assign type status in his original description. The five specimens we received from the Zoological Survey of India were labeled "types"

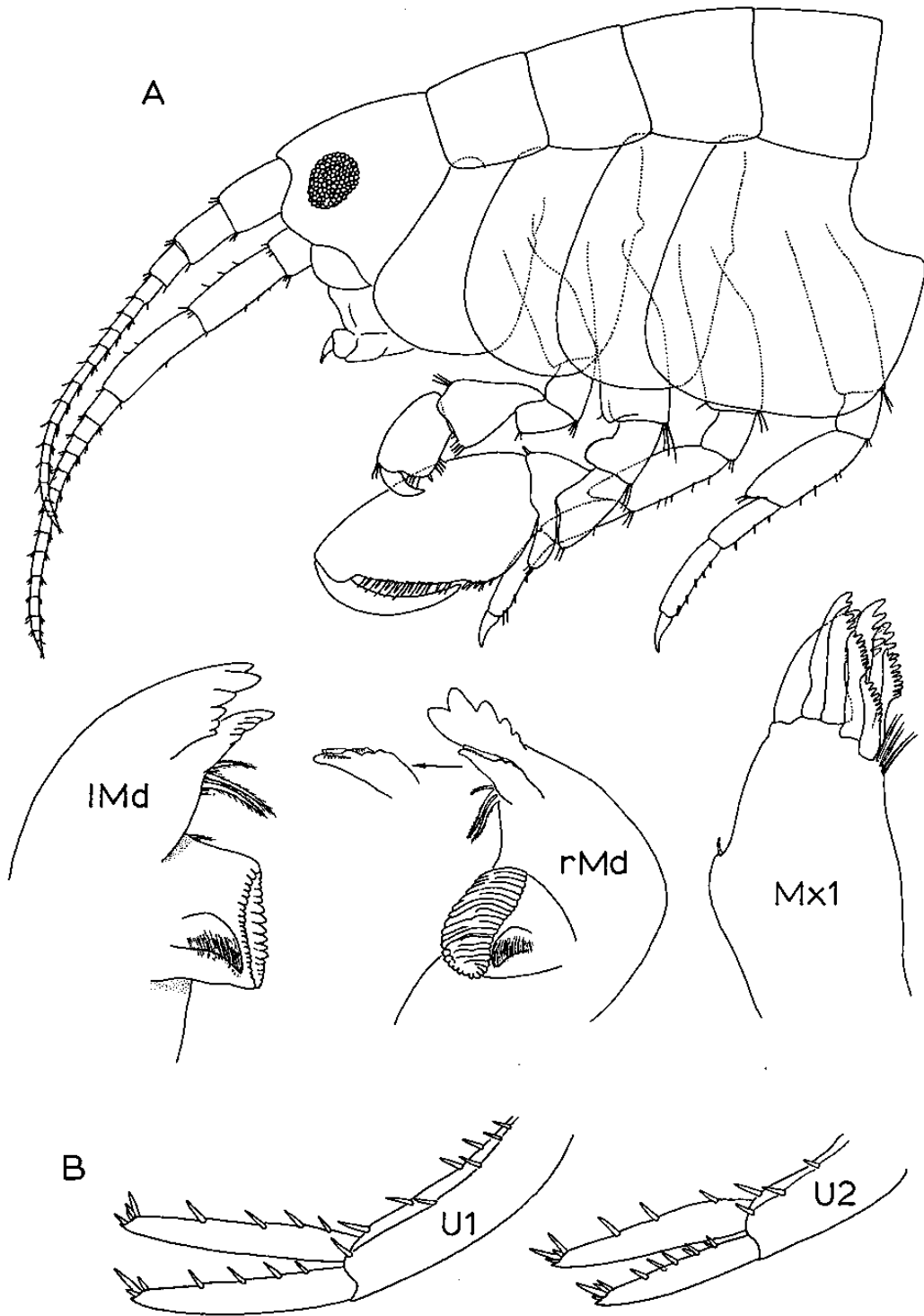


Figure 36.
Exhyalella indica K. H. Barnard. A. ZSIC 1728/1, male lectotype, 7.2 mm. B. ZSIC 1728/1, male paralectotype, 7.0 mm. Abbreviations: Md, mandible; Mx, maxilla; U, uropod; l, left; r, right.

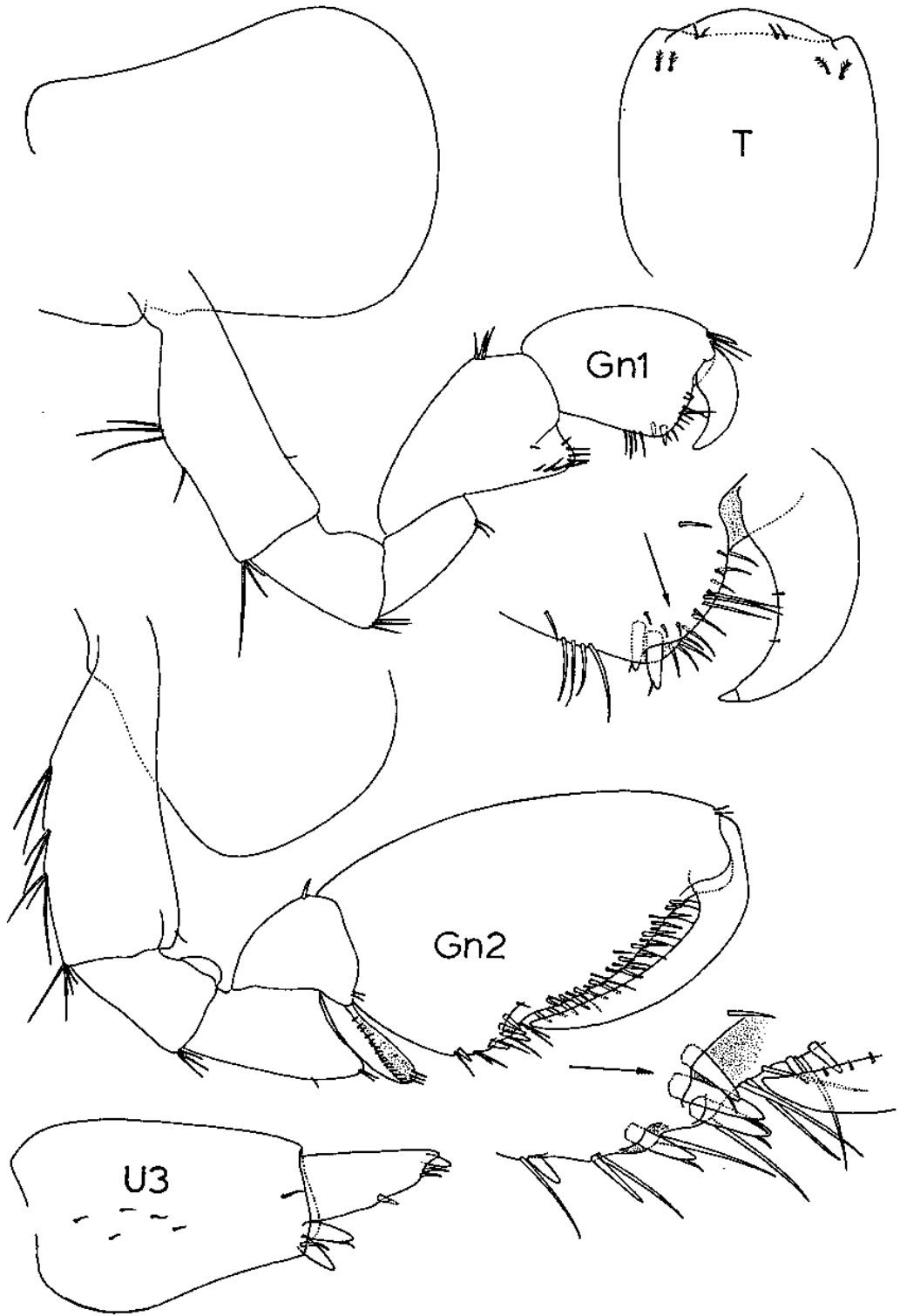


Figure 37.

Exhyaella indica K. H. Barnard, ZSIC 1728/1, male lectotype, 7.2 mm. Abbreviations: Gn, gnathopod; T, telson; U, uropod.

(=syntypes). To clarify application of the name, we hereby designate the 7.2 mm male specimen from lot ZSI 1728 as **lectotype** for *Parhyalella indica*.

EXHYALELLA HARTMANI LAZO-WASEM AND GABLE NEW SPECIES

Figures 38–41

Material examined: YPM 9280: male holotype, 6.8 mm. YPM 9284: female allotype, 6.2 mm. YPM 9282–9283: two male paratypes, each on SEM stub. YPM 9286: 11 male paratypes. YPM 9287: male paratype, 6.2 mm. YPM 9835: male paratype, 6.2 mm. YPM 9836: male paratype, 6.2 mm. YPM 9837: male paratype, 5.1 mm. YPM 9840: male paratype, 6.3 mm. YPM 9281: female paratype, 5.1 mm. YPM 9285: four female paratypes. Seychelles, Beau Vallon, Mahé Island, Yale Seychelles Expedition Station 33, lat 4°37'S, long 55°26'E; collector A. J. Kohn, 24 Jan 1958.

Diagnosis: *Male*. Gnathopod 1, article 6, proximoposterior corner of palm demarcated by a distinct protuberance and stout, curved spine; gnathopod 2, article 6, hind margin with three bifurcate spines distinctly set away from posterior corner of palm.

Female. Gnathopod 2, article 6, palm strongly oblique, weakly sinuous, densely lined with long thin setae, posterior corner with three large spines and slight excavation.

Type locality: Mahé Island, Beau Vallon, Seychelles.

Description: *Male*. Eye large, oval, black in alcohol-preserved specimens, coxa 1 anteriorly produced, coxae 2 and 3 longer than broad, coxa 4 broader than deep, nearly twice as broad as coxa 3. Antenna 1, article 1 of peduncle slightly thicker than peduncular articles 4 and 5 of antenna 2, flagellum composed of 16 articles, extending beyond peduncle of antenna 2. Antenna 2, peduncle slightly shorter than flagellum, flagellum composed of 13 articles. Upper lip broadly rounded, distally setose. Mandibular molar tritritative, incisor 6 toothed, left lacinia mobilis with five teeth, right accessory plate bifurcate, one margin unevenly toothed and serrate. Maxilla 1 palp lacking, but represented by a small spine on a distinct prominence on exterior margin. Maxilla 2, inner plate slightly narrower than outer plate, distal half of inner margin lined with row of plumose and simple setae, proximally defined by one stout plumose seta; outer plate distally setose with submarginal setae and one plumose seta. Maxilliped palp unguiform, composed of four articles, article 4 with distal nail. Gnathopod 1, article 6 nearly one-third longer than wide, palm transverse, nearly straight, and lined with setae and small facial spines, posterior corner with stout, slightly curved spine, hind margin weakly concave at distal end, dactyl bifurcate. Gnathopod 2, article 5 strongly produced between articles 4 and 6, margin very spinose, length of article 6 twice the width, palm strongly oblique, spinose, sinuous, proximally defined by four spines somewhat stouter than those lining palm; hind margin proximal to palm one-third length of palm, nearly straight, with three marginal spines set off from the posterior corner. Pereopods 3 and 4 slender, article 2, anterior margin with distal setae, posterior margin with medial and distal setae, articles 4 to 6, anterior margins nearly bare; pereopod 5 stout, spinose, shorter than pereopods 6 and 7, articles 2 and 4 with posterior lobes; pereopods 6 and 7, articles 2 and 4 with posterior lobes, pereopod 7 longest, 66% of body length in largest males, spines on anterior margin of article 6 in groups of three. Uropod 1 extending beyond uropod 2, peduncle subequal in length to rami; uropod 2,

Figure 38.

Exhyalella hartmani Lazo-Wasem and Gable, new species, YPM 9280, male holotype, 6.8 mm. *Abbreviations:* T, telson; U, uropod.

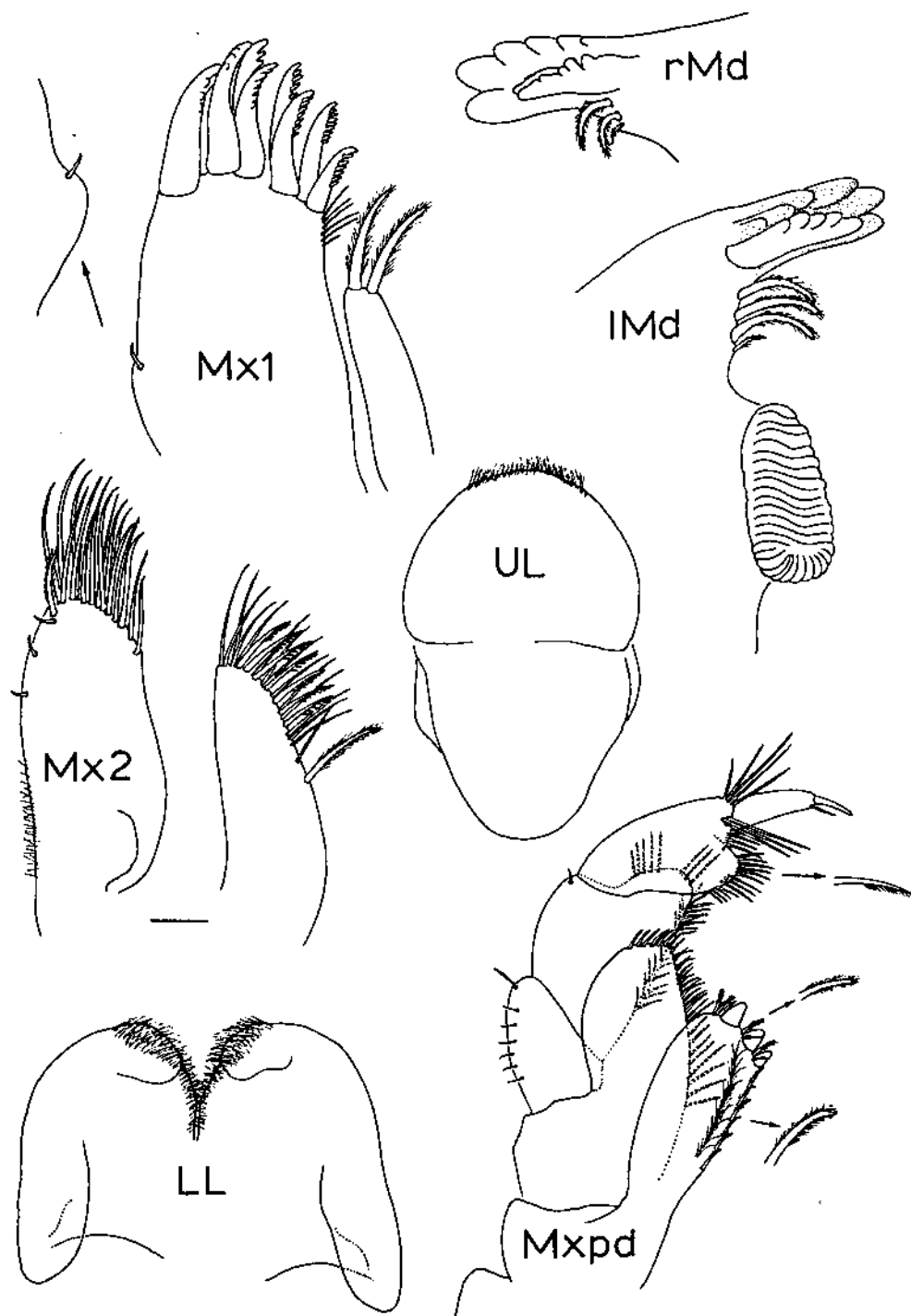
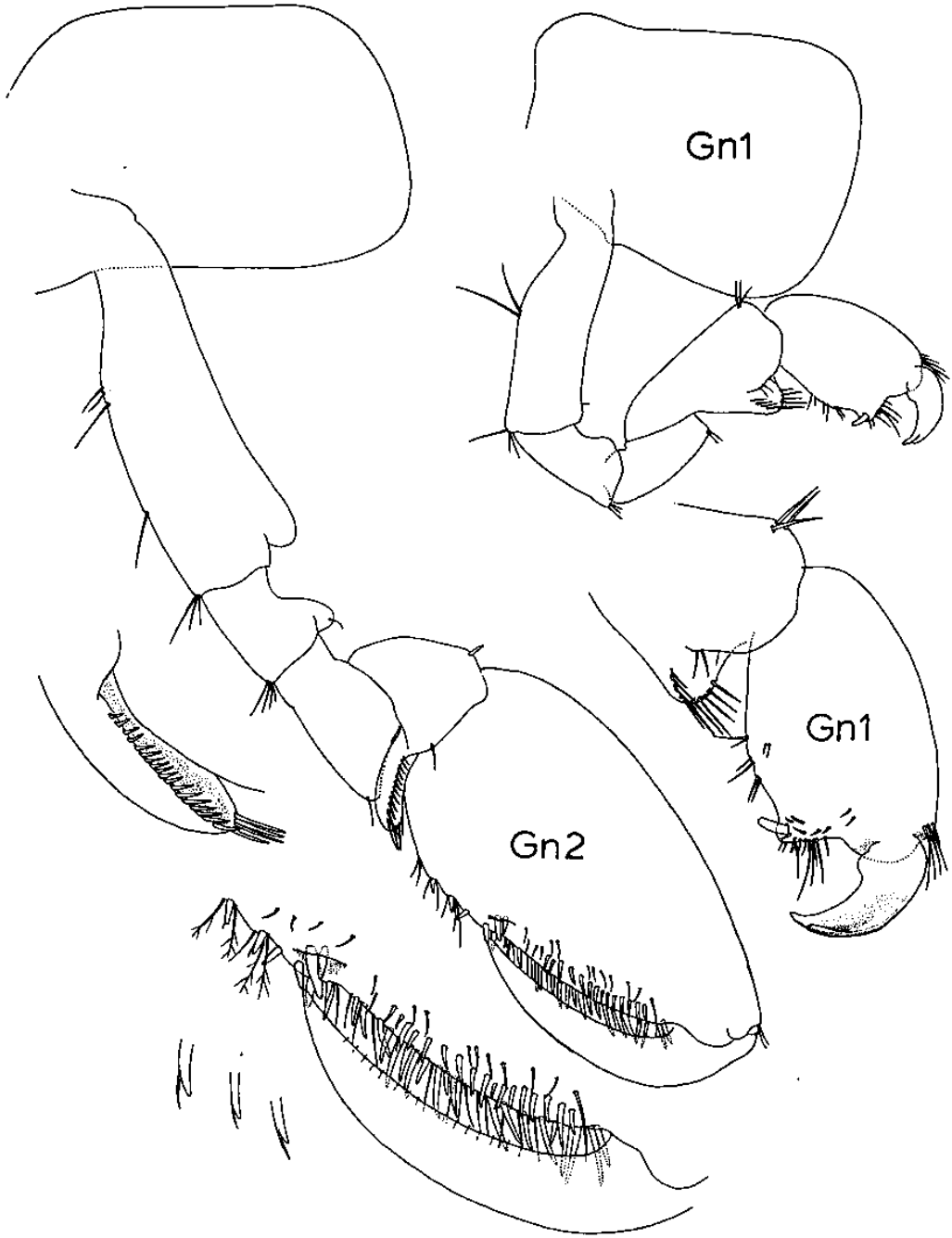


Figure 39.

Exhyalella hartmani Lazo-Wasem and Gable, new species, YPM 9280, male holotype, 6.8 mm. Abbreviations: LL, lower lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; UL, upper lip; l, left; r, right.



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Figure 40.
Exhyalella hartmani Lazo-Wasem and Gable, new species, YPM 9280, male holotype, 6.8 mm. Abbreviation:
Gn, gnathopod.

inner ramus longer than outer; uropod 3, peduncle with many small facial spines and two (rarely, three) stout distal spines; ramus nearly 75% length of peduncle. Telson longer than wide, tapering to a weak point, lateral margins with setae, and apex with two pairs of setae. *Female*. Antenna 1, flagellum with aesthetascs. Gnathopod 1, article 6 rectangular, length of article 6 twice the width, palm transverse, posterior corner rounded, defined by two stout spines, hind margin weakly setose. Gnathopod 2, posterior margin of article 4 setose, length article 6 nearly twice the width, palm weakly sinuous, densely lined with setae (some plumose), with three stout spines at point of dactyl closure.

Habitat: Shallow water, among coralline rubble.

Etymology: This species is named in honor of Willard D. Hartman of Yale University, the senior invertebrate zoologist of the Yale Seychelles Expedition (1957–1958).

Remarks on *Exhyalella*

The three species of *Exhyalella* are primarily distinguished by characters of gnathopod morphology. Unfortunately, unless both males and females are collected together and examined, specific identification can be difficult. Males of *Exhyalella indica* lack the prominent tubercle and stout recurved spine at the posterior corner of article 6, gnathopod 1, found in both *E. hartmani* and *E. natalensis*. Unfortunately, because of considerable morphologic and allometric variation, no single character definitively distinguishes the males of *E. hartmani* and *E. natalensis*. However, several characters in combination will separate these two species. The relative size of the eye is greater in *E. natalensis* than in *E. hartmani*: in similar-sized individuals the eyes of the former appear 20% to 25% larger than those of the latter. In *E. natalensis*, the length of the ramus of uropod 3 rarely exceeds one-half the length of the peduncle, and often is much shorter, especially in larger individuals. In *E. hartmani* the ramus of uropod 3 is often 75% or more of the length of the peduncle. Finally, the hind margin of article 6 of gnathopod 2 is usually much shorter relative to the palm in *E. natalensis* than in *E. hartmani*.

Aside from the characters that help to distinguish males of *E. hartmani* from males of *E. natalensis*, there are clear morphological characters that separate the females of these two species. Females of *E. natalensis* and *E. indica* have a brush-like appearance of the setae lining the palm of gnathopod 2, which is lacking in *E. hartmani*. In *E. hartmani*, although the palm of gnathopod 2 of the females is densely lined with setae, the setae are much stouter and do not present a brush-like appearance. Females of *E. natalensis* and *E. indica*, however, are virtually indistinguishable.

Key to the Species of *Exhyalella*

(males and females)

1. Female gnathopod 2, article 6 palm with dense, brush-like setae 2
 Female gnathopod 2, article 6 palm with fine spines and setae,
 not appearing brush-like *E. hartmani* new species
2. Male gnathopod 1, posterior corner of article 6 with distinct protuberance *E. natalensis*
 Male gnathopod 1, posterior corner of article 6 broadly rounded,
 lacking a protuberance *E. indica*

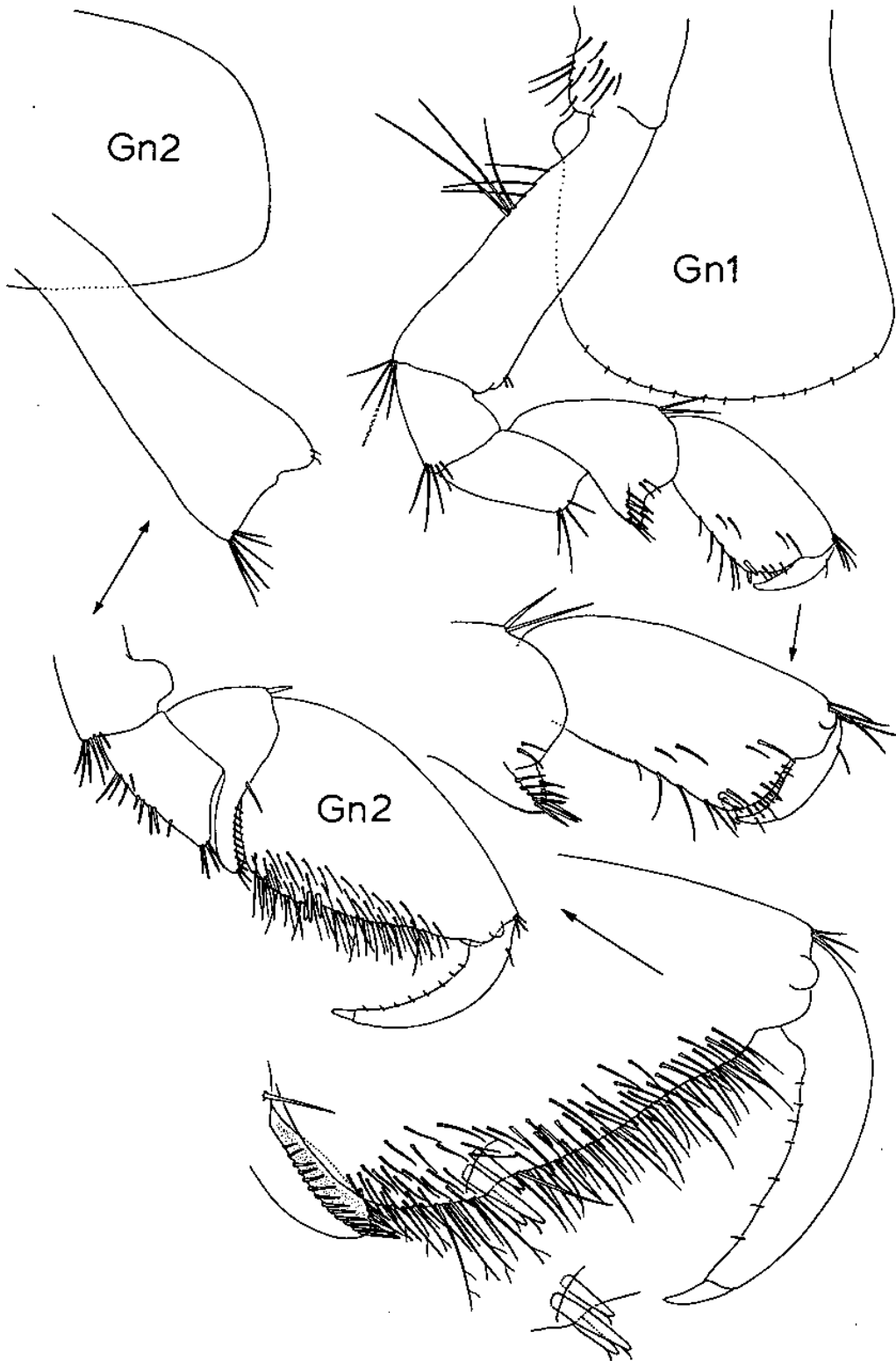


Figure 41.

Exhyalella hartmani Lazo-Wasem and Gable, new species, YPM 9284, female allotype, 6.2 mm. Abbreviation: Gn, gnathopod.

Systematic Account of *Marinohyalella*

Description of Genus

MARINOHYALELLA LAZO-WASEM AND GABLE NEW GENUS

Diagnosis: Mandibular molar (left and right) with plumose accessory seta. Maxilla 1 with minute, 1-articulate palp. Maxilliped with 4-articulate palp, article 4 unguiform and lacking whip-like seta. Male antenna 2, peduncle not greatly thicker than peduncle of antenna 1. Male gnathopod 1 much smaller than gnathopod 2, palm transverse; gnathopod 2, palm strongly oblique. Female gnathopods subequal in size, palms transverse, of similar morphology. Female gnathopod 2 of distinctly different morphology than that of male. Uropods 1 and 2, outer rami lacking marginal spines. Uropod 3 uniramous. Telson entire. Type species: *Hyalella richardi* Chevreux 1902 (by monotypy).

Distribution: Mediterranean Sea, off Isle of Alboran, Spain; Banyuls, France; and Genoa, Italy.

Included species: *Marinohyalella richardi*.

Remarks: Chevreux placed his species in the freshwater genus *Hyalella* (his fig. 1 erroneously indicates the genus as *Hyale*), undoubtedly because the characteristics of the gnathopods and maxilla match those for *Hyalella*. Possibly because it occupies a fully marine habitat, Charniaux Legrand (1951) removed this species to the genus *Parhyalella*, but gave no specific reasons for doing so.

Species Description

MARINOHYALELLA RICHARDI (CHEVREUX) 1902 NEW COMBINATION

Figures 42–45

Hyalella richardi Chevreux; 1902:223–227, figs. 1, 2.

Hyalella richardi Chevreux; 1935:121, pl. 16, figs. 1, 2.

Hyalella richardi Brian; 1940:5, figs. 1–4.

Parhyalella richardi Charniaux Legrand; 1951:377.

Parhyalella richardi Barnard and Karaman; 1991:372.

Parhyalella richardi Krapp-Schickel; 1993:758–759, fig. 519.

Material examined: MOM 37-0992: male holotype, female allotype, male paratype, 8.6 mm; female paratype, 5.5 mm; six paratypes. Mediterranean Sea, off Isle of Alboran, Spain, “Princess Alice” Station 643; collector Richard and Neuville, 1896. ZMB 25333: four males, one ovigerous female. Italy, Genoa, on beach or near shore, in sea grass; collector [L.] Brian, 7 Apr 1940.

Type locality: Mediterranean Sea, off Isle of Alboran, Spain.

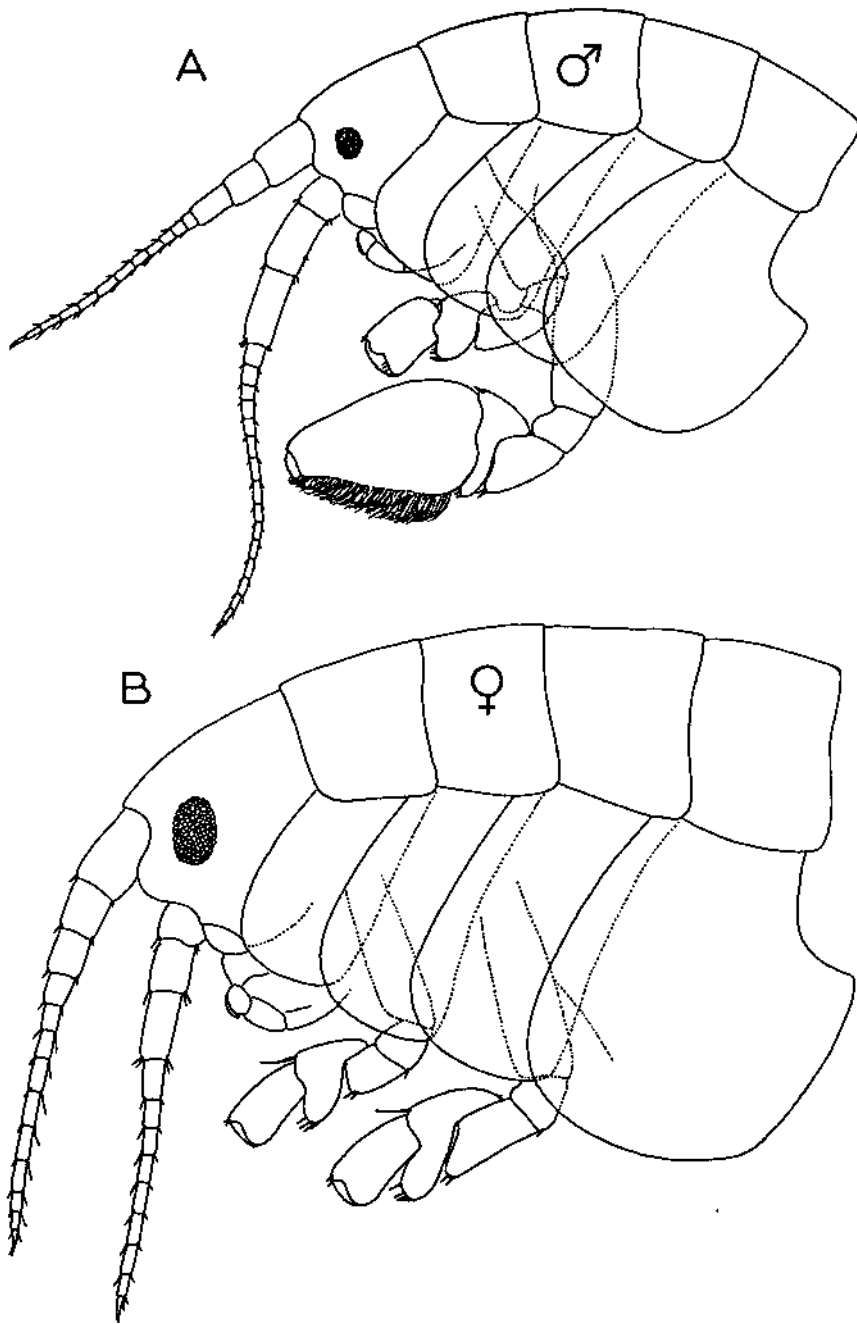


Figure 42.

Marinohyaella richardi (Chevreux), MOM 37 0992. A. Male paratype, 8.6 mm. B. Female paratype, 5.5 mm.

Diagnosis: As for the genus.

Description: *Male.* Eyes small, nearly round. Coxae 1 to 4 large, broad and deep, lower margins bare. Antenna 1 slender, extending well beyond peduncle of antenna 2, flagellum with 12 to 13 articles. Antenna 2 slender, flagellum with 13 to 16 articles. Mandibles lacking a palp, with 5-toothed incisor, left mandible with 5-toothed accessory plate (lacinia), right mandible with serrate, bifurcate accessory plate, proximally with two teeth. Maxilla 1 with minute, 1-articulate palp with distal spine, outer plate distally with eight (nine?) serrate spines, inner plate distally with two large, plumose setae. Maxilla 2, inner plate inner margin with a few small setae, distal half with row of setae and a single proximal plumose seta, outer plate with long setae distally, outer margin finely setose. Maxilliped inner plate with setose inner margin and three stout apical teeth, palp 4-articulate, article 3 with facial setal row, article 4 unguiform with distal nail. Coxal gills from gnathopod 2 through pereopod 6; pereopods 5 and 6 with accessory gills. Gnathopod 1 much smaller than gnathopod 2, posterior lobe of article 5 broad, lined with small marginal setae; article 6, palm transverse, posterior corner with stout spine on inner and outer face, dactyl stout, closing tightly against palm. Gnathopod 2, article 6, palm strongly oblique, nearly full length of article, densely lined with fine setae, inner margin lined with several rows of small spines, dactyl long and curving, closing against excavation and small spine at posterior corner of palm. Pereopods 3 and 4 similar, weakly setose, article 2 narrow; pereopods 5 and 6, article 2 broad, articles 4 to 6 strongly spinose; pereopod 7 spinose, article 2 broadly expanded, posterior margin moderately serrate. Uropods 1 and 2, inner rami slightly wider than outer, two spines along inner margin; outer rami with terminal spines only; uropod 3, peduncle and ramus with two distal spines each. Telson subquadrate, posterior margin slightly pointed.

Female. Eyes relatively larger than those of male and slightly oblong. Antennae 1 and 2 slender, with 8 to 10 flagellar articles. Gnathopod 1, article 5 broad, article 6 twice as long as wide, palm transverse; gnathopod 2 of similar size and form, article 6 relatively longer than that of gnathopod 1. Brood lamellae from gnathopod 2 to pereopod 5, thin, consecutively smaller from 2 to 5, densely lined with short setae. Uropods 1 and 2, outer rami with terminal spines only.

Remarks: Chevreaux indicated a type series that included 11 specimens; we found only 10 specimens.

Krapp-Schickel (1993) states in her generic diagnosis that *Parhyalella* lacks a palp on maxilla 1, but she clearly illustrates and describes a rudimentary palp on that mouthpart in her figures of *P. richardi* (1993:759, fig. 519). Our figures agree with hers except for a few minor differences in setation; most notably, her figure of male gnathopod 2 (1993:759, fig. 519) lacks setae on the posterior margin of article 2, which are evident in the type material examined.

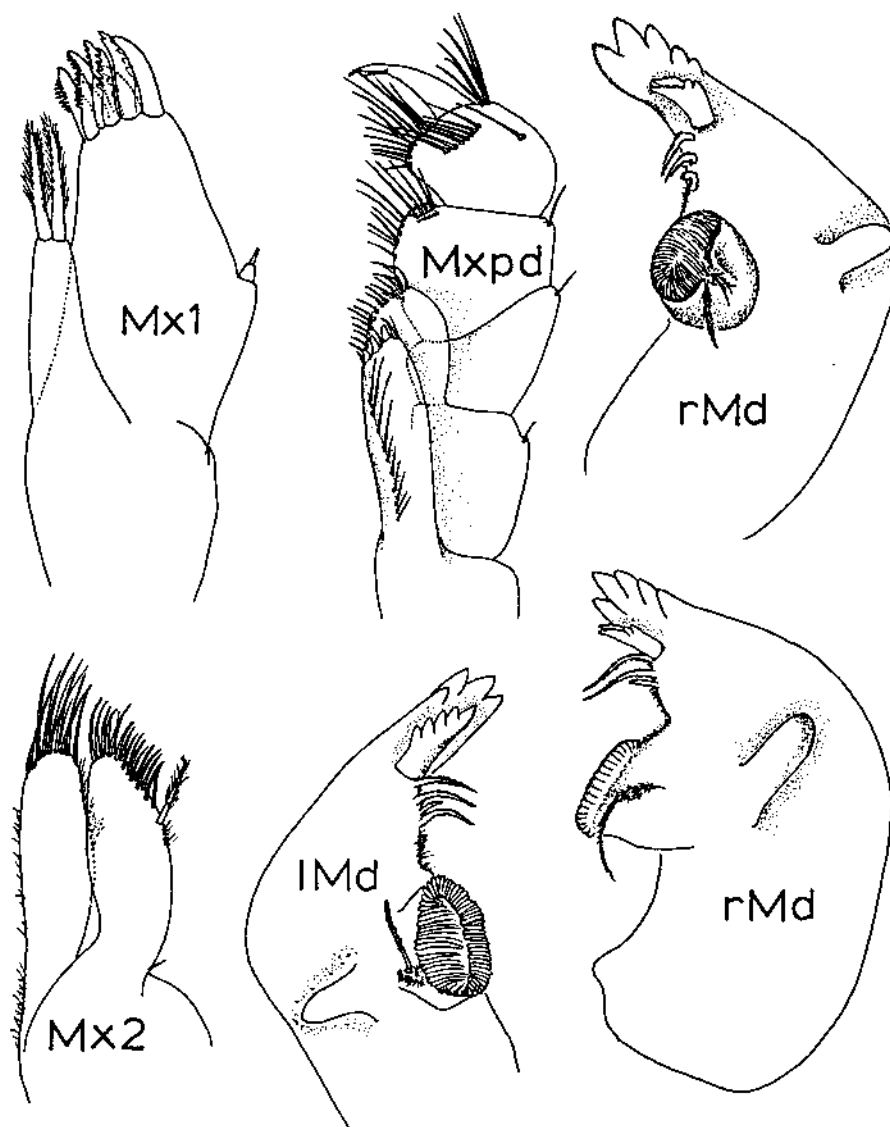


Figure 43.

Marinohyalella richardi (Chevreux), MOM 37 0992, male paratype, 10.4 mm. Abbreviations: Md, mandible; Mx, maxilla; Mxpd, maxilliped; l, left; r, right.

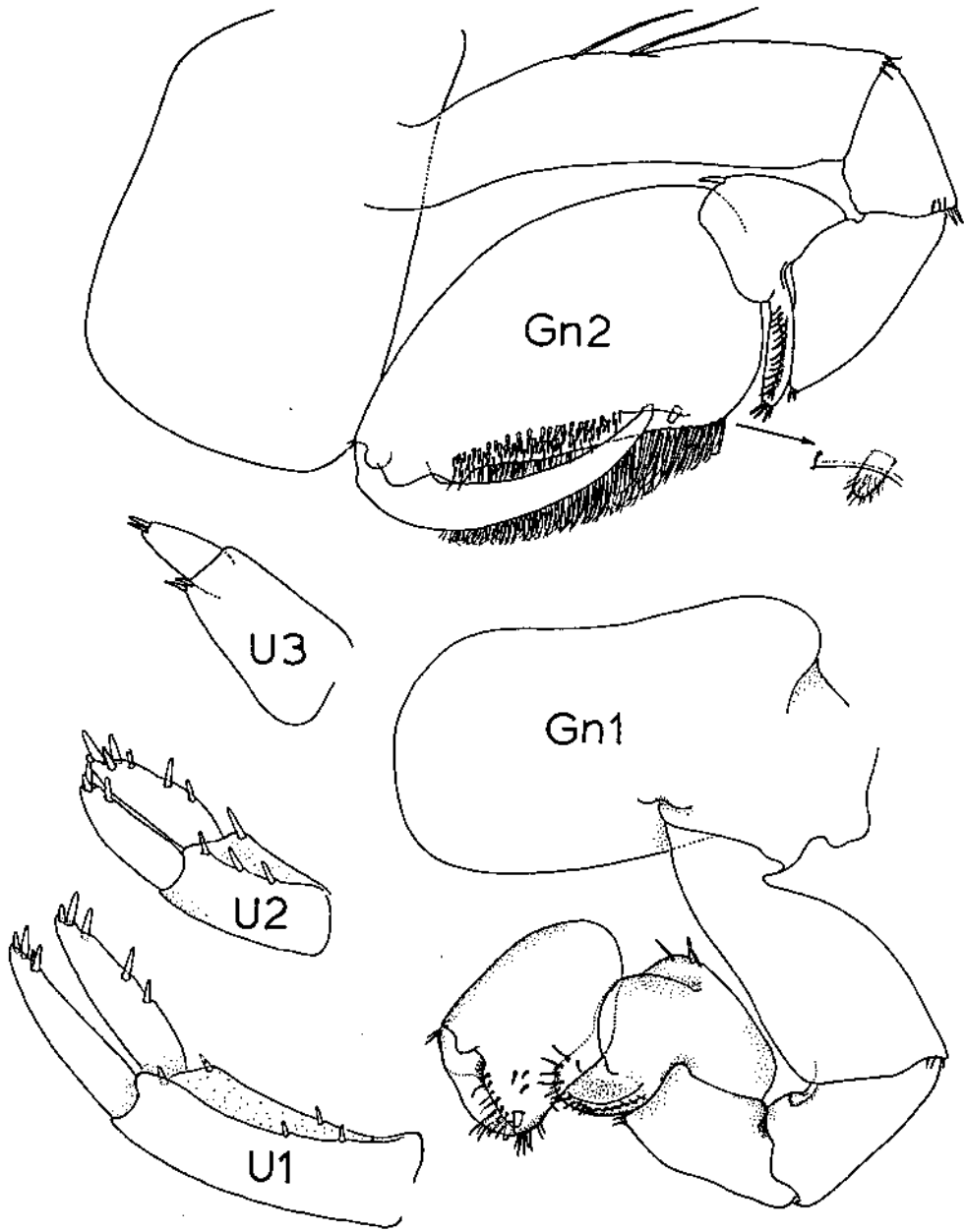


Figure 44.

Marinohyalella richardi (Chevreux), MOM 37 0992, male paratype, 10.4 mm. Abbreviations: Gn, gnathopod; U, uropod.

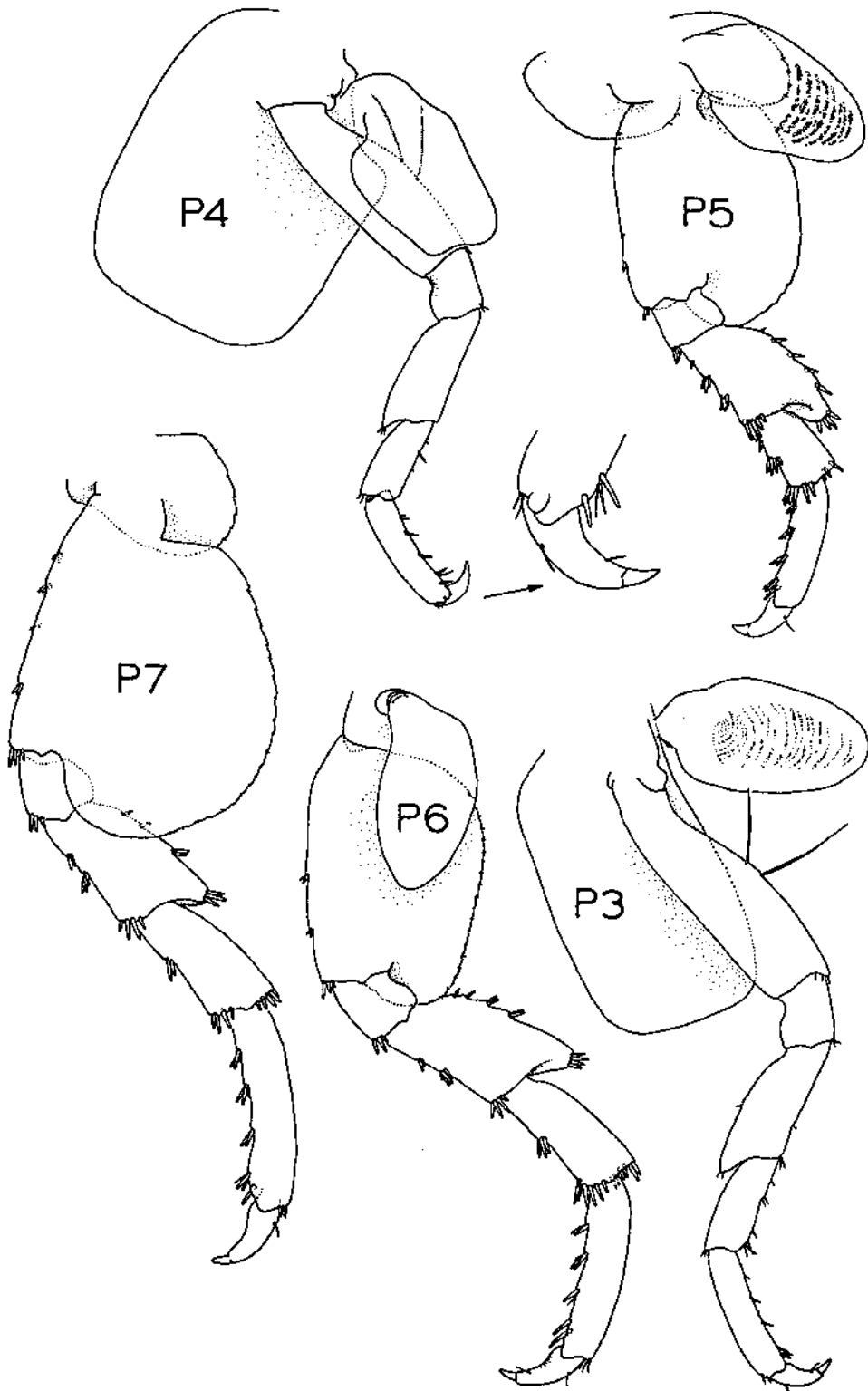


Figure 45.

Marinohyalella richardi (Chevreux), MOM 37 0992, male paratype, 10.4 mm. Abbreviation: P, pereopod.

Remarks on the Hyalidae

Historically, the generic diagnoses within the hyalid–hyaellid talitroideans have been defined as in Bulycheva (1957). The currently accepted and expanded diagnoses are those of Barnard and Barnard (1983) and Barnard and Karaman (1991). Although the core of nontalitrid genera has been realigned several times with respect to familial or subfamily placement (Hyalidae/Hyalinae or Hyaellidae/Hyaellinae), the generic composition has been generally stable. Characteristics of the telson (cleft or entire), maxilla 1 palp (lacking, 1-, 2- or 3-segmented), uropod 3 inner ramus (present or lacking), and basic gnathopod architecture have served to distinguish the various hyalid genera. It is somewhat surprising, therefore, that *Marinohyaella richardi* could have been assigned to the genus *Parhyaella*. Although Charniaux Legrand (1951) did not provide justification for doing so, the change has been virtually unquestioned for more than 50 years. Similarly, *Exhyaella natalensis* Stebbing and *E. indica* were incorrectly subsumed under *Parhyaella* without justification. In light of the clear and accepted morphological distinctions separating the genera now assigned to the Hyalidae by Barnard and Karaman (1991), the transfer of *Hyaella richardi* to the new genus *Marinohyaella* is definitely warranted. By similar reasoning, both of the previously known species of *Exhyaella* must be removed from *Parhyaella*, and *Exhyaella* re-established as a valid taxon. The principle diagnostic features distinguishing the genera are summarized in Table 2.

The genus *Parhyaella* has been placed in various families, although most often it has been aligned with the Hyalidae. Bulycheva (1957) placed *Parhyaella* in the Hyalidae after devising the concept of the superfamily Talitroidea, an arrangement accepted and followed by Barnard (1969). Bousfield (1982) removed *Parhyaella* from the Hyalidae and placed it within the Hyaellidae. Zeidler (1991) also recommended aligning *Parhyaella* and *Allorchestes* with the Hyaellidae. Barnard and Karaman (1991) repositioned *Parhyaella* again into the Hyalidae, an arrangement recently followed by Ruffo and Vader (1998) and Wakabara and Serejo (1998). Previously, Krapp-Schickel (1993) had placed *Parhyaella* and *Hyale* within the family Talitridae. Bousfield (1996) again assigned *Parhyaella* and *Allorchestes* to the Hyaellidae; in all previous classifications other than Zeidler's (1991) *Allorchestes* had been placed within the Hyalidae. Gonzalez and Watling (1998) also place *Parhyaella* within the Hyaellidae but did not address family level classification.

In most of the taxonomic assignments described above, authors have not justified their deviations from Bulycheva's (1957) original arrangement of talitroidean genera. We have adhered to the classification of Barnard and Karaman (1991) and place *Parhyaella* in the Hyalidae. Our justification for doing so is pragmatic: most authors have associated *Parhyaella* (and *Allorchestes*) with marine and estuarine hyalids, rather than with freshwater hyaellids, and generally identify taxa according to this arrangement. Clearly, rigorous cladistic and molecular analyses are needed to resolve talitroidean classification more fully. In the case of the former, variability of potentially useful characters within the

Table 2.

Key characters distinguishing *Parhyaella*, *Exhyaella* and *Marinohyaella*.

	A2, peduncle, males	A2, flagellum article 1	Mandibular molar, accessory seta(e)	Maxilla 1, palp	Gn1 and Gn2, females
<i>Parhyaella</i>	Tumescent	Conjointed	On right mandible	Absent, margin often finely setose	Dissimilar
<i>Exhyaella</i>	Normal	Normal	Absent	Absent, margin with a single spine	Dissimilar
<i>Marinohyaella</i>	Normal	Normal	On left and right mandible	Present, 1 articulate	Similar shape and size

three genera must be assessed if an analysis is to be based on stable character states.

As a taxonomic aid, we offer here a revised version of Barnard and Karaman's (1991:366) "Key to Genera of Hyalidae," but have included new couplets to account for the inclusion of *Exhyaella* and *Marinohyaella* and have arranged for the placement of the questionable genus *Insula* at the end of the key. In Barnard and Karaman's (1991:718) "Key to Families of Talitroidea," couplet 6 separates Hyalidae from the Hyaellidae by the possession of a cleft telson (Hyalidae) rather than an uncleft telson (Hyaellidae). However, Barnard and Karaman (1991:366) include *Parhyaella* (which possesses an entire telson) in their key to the hyalid genera and recognize both cleft and entire telsons in their description of the family Hyalidae.

Within the context of the talitroidean genera (Bulycheva 1957, Barnard 1969) or the current arrangement of Barnard and Karaman (1991), the distinctions among hyalid, hyaellid and talitrid genera remain clear even with the addition of *Marinohyaella* and *Exhyaella* to the talitroidean complex.

Ruffo (1953) was the first to observe that three species groups occur in *Parhyaella*, noting that *P. batesoni*, *P. pietschmanni* and *P. congoensis* are morphologically allied, and distinct from other congeners. Furthermore, he noted the close morphological relationship between *Exhyaella* (then *Parhyaella*) *natalensis* and *Exhyaella* (then *Parhyaella*) *indica* and their combined distinctiveness from *Marinohyaella* (then *Parhyaella*) *richardi*. Barnard (1972) suggested that *Parhyaella* represents a composite genus, and he discussed its morphological, ecological and evolutionary relationships with other talitroids. Although he clearly disagreed with Bulycheva's synonymy of *Parallorchestes* with *Parhyale* on the basis of mouthpart morphology, he did not extend this reasoning to the morphological incongruencies of the *Parhyaella* complex.

Parallorchestes, a marine genus with a 2-articulate maxilla 1 palp and a minutely biramous uropod 3, has been treated as one of the most primitive hyalids (Barnard 1979; Bousfield 1981; Barnard and Karaman 1991). With an adaptation to the terrestrial habitat in talitroids, originating from a *Parallorchestes*-like ancestor, there is a clear morphological trend toward reduction of the maxillary palp and the disappearance of the

biramous condition of uropod 3. *Parhyalella*, *Exhyalella* and *Marinohyalella richardi* with their reduced or absent maxilla 1 and uniramous uropod 3, occupy a position between *Parallorchestes* and the advanced, land-dwelling talitrids. However, the relationships among these three genera is unclear. If *Exhyalella* and *Marinohyalella* are excluded, the remaining genus, *Parhyalella*, apparently represents a morphological and ecological link between the fully marine hyalids and the terrestrial talitrids. Although *Parhyalella* possesses typical preadaptations to terrestriality (for example, the incrassate condition of male antenna 2), Barnard (1972) has pointed out that the entire telson of *Parhyalella* sensu lato represents an improbable reversal in the progression from marine hyalids to the terrestrial talitrids, both of which have a fully cleft telson. It is possible that *Parhyalella* represents a sister group, along with *Exhyalella* and *Marinohyalella*, to an antecedent of the terrestrial taxa. Demonstrating this would require a detailed phylogenetic analysis of all genera within the talitroidean complex.

Placement of *Insula*

The genus *Insula* was erected by Kunkel (1910) for a single species, *Insula antennullela* from Bermuda. Barnard (1969) speculated that *I. antennullela* was probably incorrectly described, in part because of the improbability of a hyalid possessing a 3-articulate (rather than 4-articulate) maxilliped palp. Barnard (1969) suggested that the single specimen used by Kunkel for his description was actually a juvenile *Hyale*. Strangely, Barnard (1979) later synonymized all three species of *Hyale* reported by Kunkel (1910) as occurring in Bermuda with *Parhyale hawaiiensis* (Dana). Recent collections, however, conclusively show that *Hyale* spp. occur in Bermuda (Baldinger and Gable 1995), and therefore ironically support Barnard's (1969) original suggestion concerning *Insula*.

Several years ago, Lazo-Wasem located the microscope slide apparently used by Kunkel for his illustration of the maxilliped of *Insula*. Unfortunately, the slide is dried out and the features of the maxilliped are obliterated. It is therefore impossible to determine the status of Kunkel's *Insula* based on original material. Furthermore, an examination of newly collected material from Bermuda over the last decade has failed to produce any specimens conforming to Kunkel's description of *Insula*. We agree, therefore, with Barnard's opinion, and believe that disregarding the genus *Insula* is warranted. It is provisionally included in our key for comparative purposes, but we have not made reference to the questionable feature of the maxilliped. We believe *Insula* should be suppressed after a careful review of all Bermudian hyalids.

Ecological and Distributional Notes on *Parhyalella*, *Exhyalella* and *Marinohyalella*

The distribution and ecology of *Marinohyalella richardi* and *Exhyalella* spp. can be summarized only in general terms, because little detailed information exists beyond the original collection data associated with type specimens and a few subsequent collection records for some species. At present, *Marinohyalella* is known only from shallow waters of the Mediterranean Sea, where it sometimes occurs in large numbers. *Exhyalella*, restricted to the Indian Ocean, is found intertidally near sandy beaches. Two species, *E. indica* and *E. natalensis*, have been found nestled among algae.

For species of *Parhyalella* more detailed distribution and habitat information is known, although again, provided only from original collection data for most species.

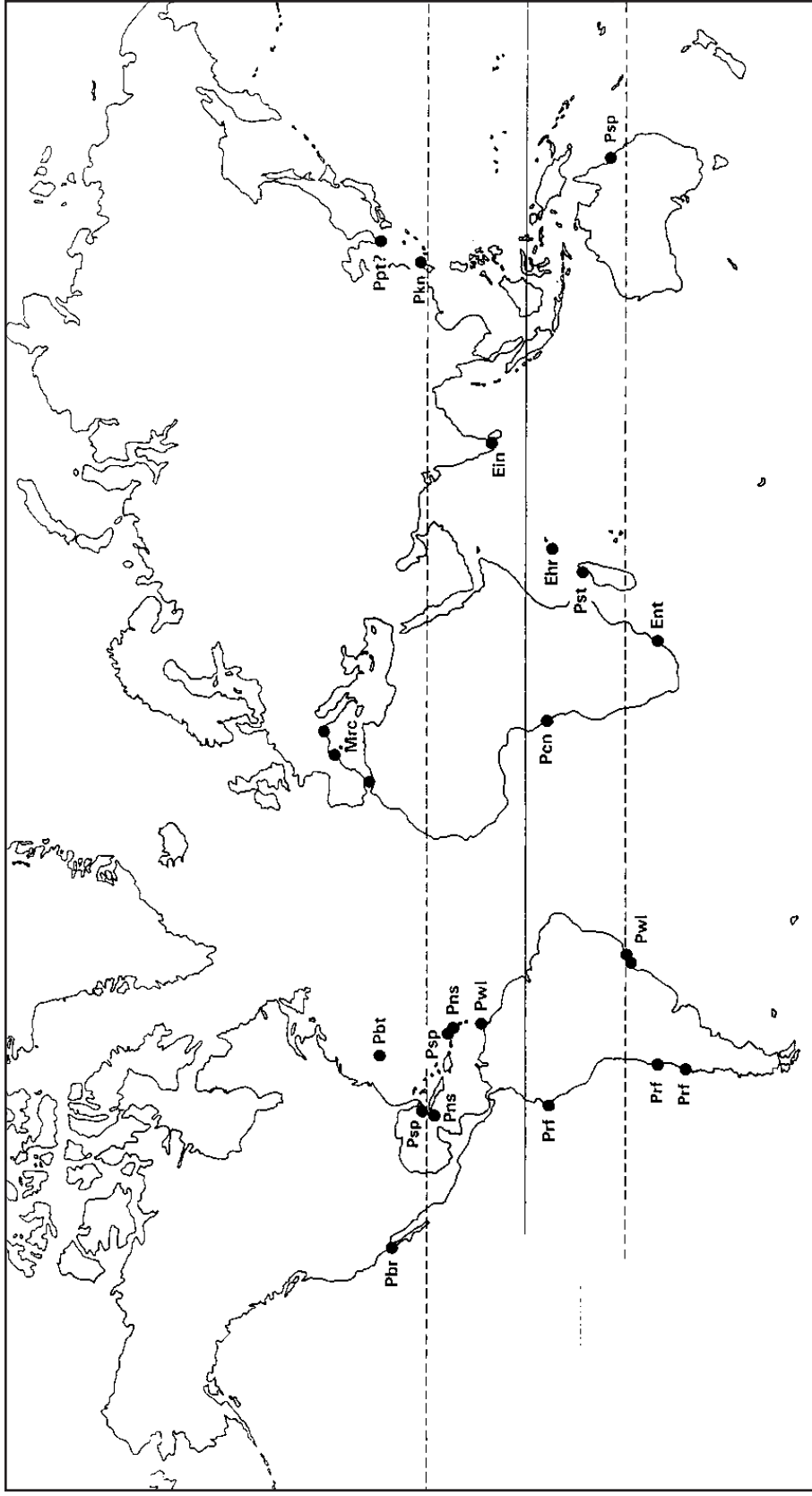


Figure 46.

Geographic distribution of *Parhyalella*, *Exhyalella* and *Marinohyalella*. Abbreviations: Mrc, *Marinohyalella richardi*; Ent, *Exhyalella natalensis*; Ein, *E. indica*; Ehr, *E. hartmani*; Pbt, *Parhyalella batesoni*; Pwt, *P. whelpleyi*; Pns, *P. pietschmanni*; Pcn, *P. congoensis*; Pbr, *P. batesoni*; Pkn, *P. barnardi*; Pkn, *P. kunkeli*; Pns, *P. nisbeti*; Prf, *P. ruffoi*; Pst, *P. ruffoi*; Pst, *P. steelei*; Psp, *Parhyalella* species.

Parhyalella has a circumglobal distribution, and is widely distributed in the Atlantic, Pacific and Indian Oceans (see Figure 46). Half of the species of *Parhyalella* have been recorded from beaches adjacent to near-shore coral reefs. *Parhyalella whelpleyi* is the only species that has been recorded from salt marshes with estuarine salinity (da Cunha Lana and Guiss 1992; Wakabara, personal communication). Although *Parhyalella* spp. are typically found intertidally, *P. kunkeli* has been recorded from an offshore locality in relatively deep water (20 m). An unidentified species of *Parhyalella* is found associated with mangroves (predominantly *Rhizophora stylosa*) in Australia (Lee 1997).

Several species (e.g., *P. nisbetiae*, *P. steelei* and *P. pietschmanni*) have been collected at the ocean–shore interface, often among algae or turtle grass washed onshore by prevailing winds. J. D. Thomas (personal communication) has reported occasionally encountering large numbers of an unidentified species of *Parhyalella* in the Florida Keys (United States) after periods of extended onshore winds; at other times in the same places he never encountered *Parhyalella*. It is possible that some species of *Parhyalella* normally inhabit subtidal algal or grass beds, and wash inshore when wind patterns are favorable. If this is true, it may explain our inability to recollect *P. batesoni* in Bermuda. In the years we collected in Bermuda, prevailing wind patterns did not carry large amounts of plant material inshore, as often happens in Bermuda (Gable, personal observation). If *P. batesoni* is associated with offshore subtidal plants and algae, then wind and storm conditions would have created unfavorable collecting conditions during our stays. In sum, the species of *Parhyalella* occupy a surprisingly diverse and perplexing array of habitats, and detailed field work is needed before even a basic understanding of their ecology can be obtained.

Key to the Genera of Hyalidae

(modified from Barnard and Karaman 1991)

1. Dactyl of maxilliped short and blunt
 or uropod 3 lacking ramus Ceinidae, especially *Hyachelia*
 Dactyl of maxilliped unguiform 2
2. Uropod 3 with minute inner ramus 3
 Uropod 3 lacking inner ramus 4
3. Maxilla 1 palp 1-articulate *Parhyale*
 Maxilla 1 palp 2-articulate *Parallorchestes*
4. Telson cleft 5
 Telson entire 8
5. Dactyl of maxilliped lacking long whip-like seta 6
 Dactyl of maxilliped bearing long whip-like seta 7
6. Male gnathopod 2, article 5 produced into a lobe
 between articles 4 and 6; palp of maxilla 1 short,
 not extending to end of outer plate *Allorchestes*
 Male gnathopod 2, article 5 not produced;
 palp of maxilla 1 long, extending to end of outer plate *Hyale*

7. Male and female gnathopods diverse, male gnathopod 2 enlarged *Lelehua*
 Gnathopods of both sexes small and female-like *Micropythia*
8. Male gnathopod 2 enlarged, different from gnathopod 1 9
 Male gnathopod 1 and 2 of medium size, similar 10
9. Male antenna 2 peduncle tumescent, palp of maxilla 1 absent *Parhyalella*
 Male antenna 2 peduncle not thickened, similar in diameter
 to antenna 1, palp of maxilla 1 a single seta *Exhyalella*
10. Maxilla 1 palp 1-articulate, vestigial, length equal to width *Marinohyalella*
 Maxilla 1 palp 1-articulate, length three times longer than width *Insula*

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