# Novitates

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A Review of the Genus *Clastotoechus* Haig, with Descriptions of a New Genus and Two New Species (Decapoda: Anomura: Porcellanidae)

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#### **ABSTRACT**

Two new species of the porcelain crab genus Clastotoechus Haig are described from the tropical eastern Pacific Ocean: C. hickmani, from the Galápagos Islands and Malpelo Island, and C. lasios, from Jalisco, Mexico. Both species have been confounded with C. diffractus Haig in the literature. C. lasios is in fact closely related to C.

diffractus, but C. hickmani is most closely related to the Atlantic C. nodosus (Streets). In addition, the Atlantic C. vanderhorsti (Schmitt) is placed in a new genus, Madarateuchus. M. vanderhorsti and all five species of Clastotoechus s.s. are described (or redescribed) and illustrated, and a key is provided to differentiate among these taxa.

#### INTRODUCTION

Clastotoechus Haig, 1960, is a small genus of unusual porcelain crabs restricted to shallow tropical and subtropical regions of the Americas. Although originally placed in the genus Petrolisthes Stimpson, 1858, these species possess several unique morphological features that led Haig (1960) to exclude them from that genus. These features include a carapace with fragmented lateral walls (from which the generic name is derived), a front that is markedly trilobate, antennules

with several strongly produced anterior projections, and a telson with only five plates.

Currently, two species, Clastotoechus diffractus (Haig, 1957) and C. gorgonensis Werding and Haig, 1983, are known from the Pacific, and two, C. nodosus (Streets, 1872), and C. vanderhorsti (Schmitt, 1924), from the Atlantic. These species are almost exclusively intertidal. One Pacific and one Atlantic species each exhibits a commensal relationship with an echinoid: C. gorgonensis with

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Echinometra vanbrunti Agassiz and C. vanderhorsti with E. lucunter (Linnaeus) (Werding, 1983). Although this unique, shared behavior hints at the possibility that C. gorgonensis and C. vanderhorsti are trans-Panamic geminate species (Werding, 1983), Werding and Haig (1983) suggested that C. gorgonensis may be instead most closely related to C. diffractus, which is not known to associate with echinoids.

In recent examinations of Pacific porcellanid specimens, I determined that specimens referred to in the literature as Clastotoechus diffractus in fact represent at least four species, two of which are new and described herein. The confusion surrounding C. diffractus suggests that all of the Pacific species need to be more thoroughly described. Because the descriptions of the two Atlantic species are incomplete as well, I provide descriptions and illustrations of all species in this genus. This comprehensive morphological information indicates that C. vanderhorsti is sufficiently distinct from the other five species to merit the creation of a new genus, Madarateuchus, described herein.

Carapace length (CL) is provided as an indicator of specimen size. I captured specimen images for illustrations on a Macintosh computer with a digital camera connected to a Wild M8 dissecting microscope. These images were then prepared for publication using the programs Adobe Photoshop and Adobe Illustrator. The position, type, and size of setae are illustrated in these drawings, except for the tight rows of long marginal setae of the third maxillipeds and telson, which I did not draw. Material used for this study remains deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), Natural History Museum of Los Angeles County (LACM), the Academy of Natural Sciences, Philadelphia (ANSP), the Museum of Comparative Zoology, Harvard University (MCZ), the Harbor Branch Oceanographic Museum (HBOM), and the Charles Darwin Research Station, Santa Cruz Island, Galápagos (CDRS).

#### ACKNOWLEDGMENTS

I thank Cleveland Hickman for initially piquing my interest in Clastotoechus. I also

thank Rafael Lemaitre (USNM), George E. Davis (LACM), Gary Rosenberg (ANSP), Ardis Johnston (MCZ), Debra Krumm (HBOM), and Cleveland Hickman for providing access to specimens. Marie Lawrence provided valuable laboratory assistance, Marilyn Lawrence provided translations of Spanish language references, and Portia Rolling assisted with the illustrations. The manuscript greatly benefitted from careful review by Roy Kropp, Jody Martin, and Rafael Lemaitre.

# SPECIAL MORPHOLOGICAL FEATURES

During the course of this study, I encountered several important diagnostic morphological characters that had not been described previously for these species, or in some cases for porcelain crabs in general. For example, the third maxilliped receives little attention in porcellanid descriptions, but this structure exhibits morphological features that can prove useful in systematics studies of porcelain crabs. The merus has a produced medial lobe on the mesial margin; the shape of this lobe is often species specific. A potentially more conservative character is the presence of small teeth on the anterior margin. These teeth, lacking in *Clastotoechus* s.s., are sometimes barely apparent in Madarateuchus, but never approach the development seen, for example, in Pachycheles velerae Haig, 1960 (Harvey, 1998) or Petrolisthes galathinus (Bosc, 1802) (fig. 1).

The laterodistal angle of the ischium of the third maxillipeds is often at least somewhat produced in porcellanids, sometimes becoming a slender, elongate lobe that can exceed the length of the ischium. This trait seems to exhibit little intraspecific variability but can vary considerably among species (see fig. 34 vs. fig. 46). In Clastotoechus s.s. and Madarateuchus, the basis and ischium of the third maxillipeds are partially fused, an unusual feature not previously reported in porcellanids (contrast with Petrolisthes galathinus, fig. 1). Finally, the coxa of the third maxilliped is produced forward at the anteromesial angle in some porcellanid genera (e.g., Pachycheles), but not in others, including Clastotoechus s.s. and Madarateuchus,

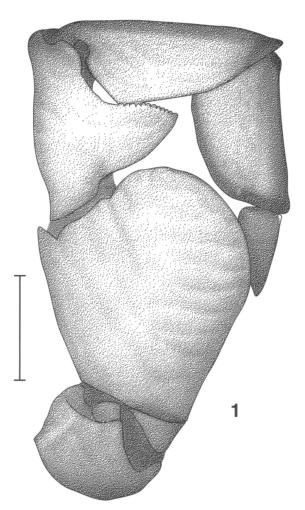


Fig. 1. *Petrolisthes galathinus* (Bosc). Right third maxilliped. Scale bar = 2.0 mm.

whereas the anterolateral angle is apparently articulated in *Clastotoechus* s.s. *Madarateuchus*, *Petrolisthes*, and *Allopetrolisthes*, but not in *Pachycheles* Stimpson, 1858, or *Neopisosoma* Haig, 1960.

In both Clastotoechus s.s. and Madarateuchus, the second through fourth pereopods have a nearly transparent, presumably decalcified "window" on the mesial surface of the merus. This window has not previously been reported for any porcelain crab species. I have observed this character in Allopetrolisthes spinifrons (H. Milne-Edwards, 1837) [but not A. angulosus (Guérin-Méneville, 1835)], and Petrolisthes lewisi Glassell,

1936, and *P. tuberculatus* (Guérin-Méneville, 1835). Roy Kropp (in litt.) observed a meral window in *P. violaceus* (Guérin-Méneville, 1831), but it appears to be absent in the great majority of species in the genus *Petrolisthes* Stimpson, 1858, and is completely absent in *Pachycheles* and *Neopisosoma* (Harvey, 1998 and unpubl. data).

Other porcellanid genera remain to be checked for this character, whose function, if any, is unknown. Similar, but clearly not homologous, "windows" occur on the *lateral* surface of the merus in several genera in the anomuran family Albuneidae (C. Boyko, personal commun.), and on the mesial surface of the coxa of the first pereopods in the hippid genus *Emerita* Scopoli, 1777, but are lacking in *Hippa* Fabricius, 1787, and *Mastigocheirus* Stimpson, 1858, the other genera in the family Hippidae (Harvey, unpubl. data). Otherwise, nothing is known of the distribution of decalcified pereopod windows among the Anomura.

# IDENTIFICATION KEY TO THE SPECIES OF CLASTOTOECHUS and MADARATEUCHUS

- Carapace, chelipeds, walking legs, and antennae smooth, slightly rugose, or finely granular, glabrous to sparsely setose; carpus of cheliped with well-spaced, pointed teeth on anterior margin; propodus of cheliped with thick, dense brush of short plumose setae extending from posterior margin onto at least posterior quarter of dorsal surface; ventral margin of propodus of walking legs with 1 medial spine.
  - ..... Madarateuchus, n. gen. [one species, M. vanderhorsti (Schmitt)] (Atlantic)
- Carapace slightly wider than long, covered with strong transverse ridges; lateral margin of cheliped propodus lacking thick brush of plumose setae; carpus and propodus of chelipeds lacking longitudinal ridge or swelling; ventral margin of propodus of walking legs

with 4 medial spines. ..... C. gorgonensis Werding and Haig (Pacific) - Carapace as long as or longer than wide, granular or tuberculate; lateral margin of cheliped propodus with thick brush of plumose setae (sometimes reduced or lacking in large males); carpus and propodus of chelipeds with longitudinal ridge or swelling; ventral margin of propodus of walking legs with 2 medial spines. .....(3) 3. Carapace granules rounded; front with lateral lobes triangular; orbits deeply rounded; ischium of third maxilliped with laterodistal projection greatly elongated (see fig. 46); carpus of chelipeds less than 1.5 times as - Carapace granules elongate, flattened; orbits angular, with margins straight, strongly oblique, separated by notch from lateral frontal lobe; ischium of third maxilliped with laterodistal projection small (see fig. 22); carpus of chelipeds 1.5 times or more as long as broad. . . . . . . . . . . . . . . . . . (5) 4. Granules on carapace and chelipeds large, irregular, crowded; "sheathed" setae (see, figs. 2 and 3), not expanded distally; carpus of walking legs with anterodistal angle lacking spines; cheliped carpus with one raised ridge that connects proximal tooth on anterior margin to median ridge, and another raised ridge that connects second and third teeth basally. ..... ..... C. nodosus (Streets) (Atlantic) — Granules on carapace and chelipeds small, rounded, loosely spaced; sheathed setae expanded distally; anterodistal angle of carpus of walking legs with 1-2 spines; anterior marginal teeth on cheliped carpus flattened, not connected to each other or median ridge. ..... C. hickmani n. sp. (Pacific) 5. Carapace lacking scattered, long, plumose setae; front with lateral lobes truncate; orbits separated from lateral lobes by acute notch; outer orbital angle acute, produced at tip; anterior lobe on second antennal segment wider than long; anterodistal angle of carpus of second walking leg with 0-1 small spines. ..... C. diffractus (Haig) (Pacific) — Carapace with scattered, long, plumose setae; front with lateral lobes rounded; orbits separated from lateral lobes by obtuse notch; outer orbital angle obtuse, not produced at tip; anterior lobe on second antennal segment longer than wide; anterodistal angle of carpus of second walking leg with 2 spines. ..... C. lasios n. sp. (Pacific)

Clastotoechus Haig, 1960, sensu stricto

Clastotoechus Haig, 1960: 175 (in part) (type species: Petrolisthes diffractus Haig, 1957, by original designation; gender masculine).

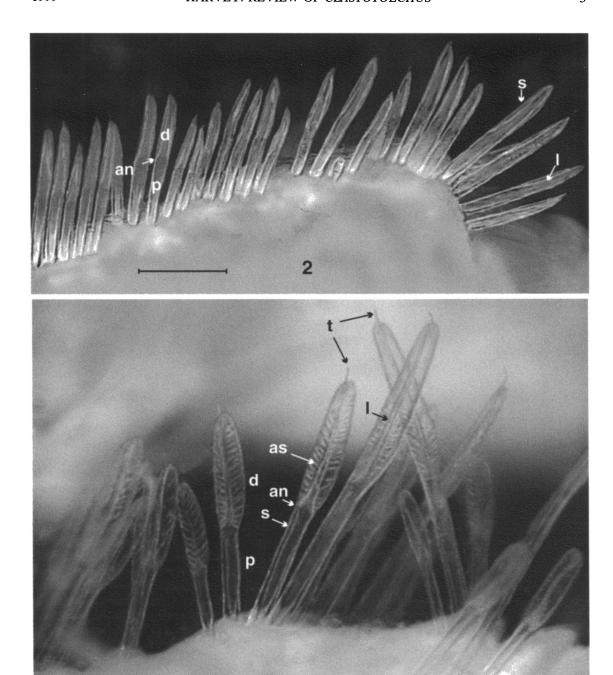
DIAGNOSIS: Sheathed setae present on carapace and pereopods (figs. 2 and 3). Carapace as long as or slightly longer than broad; dorsal surface covered with conspicuous granules, tubercles, or transverse rugae. Dorsolateral ridges pronounced, with row of setae. Rugae and granules of carapace setose anteriorly, setae visible under high magnification. Carapace spines absent. Front trilobate, lobes strongly projecting, extending beyond eyes; length of lateral lobes one-fourth or less width of front. Median lobe triangular, with thickened margin, and long, acute, strongly deflexed extension in frontal view. Lateral walls of carapace consisting of one large anterior piece and numerous small posterior fragments narrowly separated from each other by membrane.

Basal segment of antennule with three strong, lamellar, anterior lobes. Ventral surface with medial transverse row of small, closely set granules, with tuft of setae mesially; with short, transverse row of irregular granules extending approximately from lateral end of medial row of granules to base of anterolateral lobe.

Second segment of antenna with a strongly projecting lamellar lobe; anterior margin granular; dorsal surface with irregular longitudinal granular ridge. Third segment with one or two large, strongly projecting nodules distally and one to several large granules proximally. Fourth segment nodular on anterior margin, more or less smooth.

Third maxillipeds with sternite trilobate, median lobe greatly exceeding lateral lobes; carpus with distal ventral margin usually strongly produced (not visible in figures); merus with pronounced medial lobe with anterior margin entire; basis partly fused to ischium; coxa with anterior mesial margin not produced, apparently articulated anterolaterally.

Cheliped asymmetry varying widely within species. Merus with small pointed lobe, serrate-edged mesially, only slightly projecting, on anterior margin. Carpus and propodus covered with conspicuous granules or flattened tubercles, and short, fine pubescence



Figs. 2-3. **2.** Clastotoechus nodosus (Streets). **3.** Clastotoechus hickmani, new species. Sheathed setae along anterodistal margin of carpus of right third pereopod.  $\mathbf{s} = \mathrm{shaft}$ .  $\mathbf{l} = \mathrm{lumen}$ .  $\mathbf{p} = \mathrm{proximal}$  region of shaft.  $\mathbf{d} = \mathrm{distal}$  region of shaft.  $\mathbf{t} = \mathrm{protruding}$  distal tip of lumen.  $\mathbf{as} = \mathrm{apparent}$  lateral rows of setules. Scale bar = 1.0 mm.

not obscuring granules. Carpus, excluding marginal teeth, usually much less than twice as broad as long; anterior margin with four strongly projecting, closely spaced, granular teeth, these usually rounded, with convex, denticulate edges; proximal tooth projects at approximately right angles to carpus, others tilted progressively forward, with anterodistal tooth lying parallel to long axis of carpus; posterodistal angle produced into spine; posterior surface with oblique, rugose ridges that extend onto posterior margin of ventral surface. Dactyl with outer marginal row of small granules, submarginal row of larger granules.

Walking legs rugose, all segments with long nonplumose setae and fringed with plumose or sheathed setae on anterior margins. Mesial surface of merus with transparent, decalcified window medially. Ventral margin of propodus of walking legs with two or more medial movable spines.

Telson with five plates. Second pleopods present in males.

SPECIES: The following species are included in *Clastotoechus* as here restricted: from the Pacific, *C. diffractus* (Haig, 1957), *C. gorgonensis* Werding and Haig, 1983, *C. hickmani* n. sp., and *C. lasios* n. sp.; from the Atlantic, only a single species, *C. nodosus* (Streets, 1872).

REMARKS: Distinctive morphological features that Clastotoechus s.s. shares with Madarateuchus include the fragmented lateral walls of the carapace, trilobate front, trilobate basal segment of the antennules, partially fused basis and ischium of the third maxilliped, and five-plated telson. Compared to Madarateuchus, the front of Clastotoechus s.s. is considerably less produced anteriorly than in Madarateuchus; the carpus of the cheliped is broader, and the teeth on the anterior margin are relatively larger and more rounded. In addition, the carapace, chelipeds, walking legs and antennae of species in Clastotoechus s.s. are much more setose and "textured," although the nature of the texturing (e.g., granules, nodules, or ridges) varies widely.

All species of *Clastotoechus* s.s. possess, to one degree or another, a peculiar type of seta not previously reported in crustaceans. Hereafter referred to as "sheathed setae,"

these stout setae are transparent or slightly translucent, with a conspicuous, broad central lumen (1, figs. 2 and 3). The shaft (s, figs. 2 and 3) is divided by an annulus into distinct, subequal, proximal (p, figs. 2 and 3), and distal (d, figs. 2 and 3) halves. The proximal half is slightly constricted basally; the distal half is bluntly rounded, slightly flattened, and often somewhat opaque, at least in preserved specimens. Sheathed setae are similar in appearance to the cuspidate setae of Watling (1989: fig. 5c). However, Watling (1989) considered cuspidate setae to be synonymous with the type 1 setae of Drach and Jacques (1977), which are "large, spiniform setae, constant in number" (Jacques, 1989). In contrast, sheathed setae, though relatively conservative in location on individual crabs (see below), are no more fixed in number than other types of setae.

Sheathed setae are further modified in Clastotoechus hickmani. The distal half of the shaft is noticeably expanded relative to the proximal half, and exceptionally flattened (d, fig. 3). The lumen is relatively slender distally (1, fig. 3), and penetrates the distal margin of the shaft, which thus terminates in a short, slender, usually curved projection (t, fig. 3). The lumen appears to have two rows of fine setules arising laterally beneath the expanded distal shaft (as, fig. 3). This suggests the interesting possibility that sheathed setae are modified plumose setae. Consistent with this hypothesis, many C. diffractus and some C. gorgonensis have plumose instead of sheathed setae. However, this has not been observed in other species in the genus, nor are these putative setules visible in the sheathed setae of species other than C. hickmani. In many specimens, sheathed setae seem to grade into the more typical stout, nonplumose bristles that are found on many species of porcelain crabs. Thus the evolutionary origins of sheathed setae are currentlv unknown.

The distribution of sheathed setae on individual crabs is conservative both within and among species of *Clastotoechus* s.s. In all species, sheathed setae are normally present on the carapace along the posterior half of the dorsolateral ridge and along the largest medial linea of the lateral walls. On the chelipeds they are found along the dorsomesial margin of the merus, and anterior to the elongate rugae along the posterior margin of the carpus. Sheathed setae occur on the walking legs along the anterior margin of the merus, on the dorsal and anterior surfaces of the carpus, and on the proximal half of the propodus. In *C. nodosus* and *C. hickmani*, sheathed setae also can be found along the margin of the front of the carapace and on the antennae.

# Clastotoechus nodosus (Streets, 1872) Figures 2, 4–15

Petrolisthes nodosus Streets, 1872: 133. Benedict, 1901: 134. Schmitt, 1924: 73, pl. 8(8). Haig, 1956: 27.

Petrolisthes (Pisosoma) nodosus: Ortmann, 1897: 295.

Clastotoechus nodosus: Haig, 1960: 175, text-fig. 5(3). Rickner, 1975: 163. Werding, 1977: 178, not fig. 2 (see remarks); 1978: 215. Werding and Haig, 1983: 62.

Clastotoechus vanderhorsti: Werding, 1977: fig. 3 (see remarks). [Not Clastotoechus vanderhorsti (Schmitt, 1924).]

Not Clastotoechus nodosus: Gore and Abele, 1976: 15, fig. 2 (see remarks).

MATERIAL EXAMINED: *Holotype:* West Indies: 1 male (CL 5.30 mm), St. Martin Island (= St. Martin), ANSP 4162.

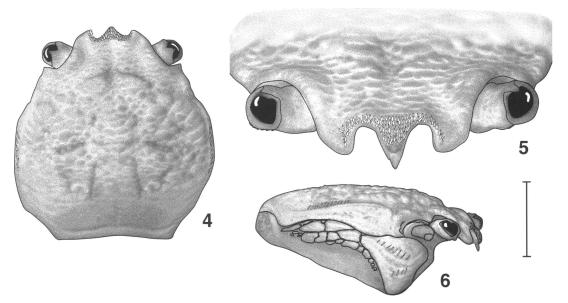
Additional Specimens: Mexico: 1 male (CL 5.90 mm), 1 ovigerous female (CL 5.52 mm), El Moro, Vera Cruz, shore, 11 Jun 1973, J. A. Rickner, LACM 73-315.1. Puerto Rico: 1 ovigerous female (CL 7.01 mm), east coast, Blake Shoal, 10 Jun 1942, B. Werding, USNM 275903. Colombia: 1 male (CL 7.48 mm), 2 ovigerous females (CL 8.44–8.48 mm), Santa Marta, intertidal, Jun 1979, LACM 79-233.1. Venezuela: 1 male (CL 2.51 mm), 1 female (CL 2.17 mm), Tortuga [= La Tortuga] Island, shore, 13 Apr 1939, LACM 39-272.1; 1 female (CL 2.80 mm), Cubagao [= Cubagua] Island, shore, 14 Apr 1939, LACM 39-271.1.

DIAGNOSIS: Sheathed setae not expanded distally. Carapace without long, scattered plumose setae. Median lobe of front with thickened, lowered margin, lateral lobes triangular; frontal margin with multiple rows of sheathed setae along margin of front between tips of lateral lobes, rarely absent. Orbits deep, rounded. Outer orbital angle obtuse, rarely acute, only slightly produced. Second

segment of antenna with strongly projecting lamellar lobe, finely granulate. Ischium of third maxilliped with laterodistal projection greatly elongated, reaching half length of merus. Carpus of chelipeds, excluding marginal teeth, approximately one-third longer than broad; covered with rough, rounded granules, with pronounced longitudinal crest, often connecting at right angles to proximal marginal tooth, granules of crest larger and more flattened; anterior margin with four acute, strongly projecting, granular teeth, denticulate on edges, second and third often connected basally by short raised ridge. Propodus very finely granular mesially, with granules becoming larger, more closely packed laterally; with low to pronounced longitudinal swelling medially; posterior margin with low rounded crest extending onto fixed finger, crest with row of small granules, with thick brush of soft, plumose setae to base of fixed finger in both sexes. Carpus of walking legs without spines; propodus with two distal, one subdistal, and one medial movable spines ventrally. Abdomen smooth, sparsely setose.

DESCRIPTION: Carapace (fig. 4) as long as or slightly longer than broad, regions moderately well defined, especially frontal; dorsal surface covered with large, imbricate nodules, which are smaller on the frontal region, cardiac region with flattened imbricate granules, intestinal region smooth or punctate, posterolateral regions smooth to plicate, dorsolateral ridges pronounced, with row of sheathed setae. Frontal region (figs. 5-6) depressed, granular, finely setose, with median groove; front with median and lateral lobes triangular, margins of median lobe usually entire, lateral lobes finely granular, median lobe with thickened, deflexed margin; margin with multiple rows of sheathed setae along margin of front between tips of lateral lobes, rarely absent; in dorsal view median lobe usually slightly more produced than lateral lobes. Orbits deep, rounded. Outer orbital angle obtuse, rarely acute, only slightly produced. Eyes large, peduncle with minute spines along ventrodistal margin.

Basal segment of antennule (fig. 7) with anterolateral lobe scoop-shaped, closely adjacent to anteromedial lobe; anteromesial lobe relatively narrow, not scoop-shaped.



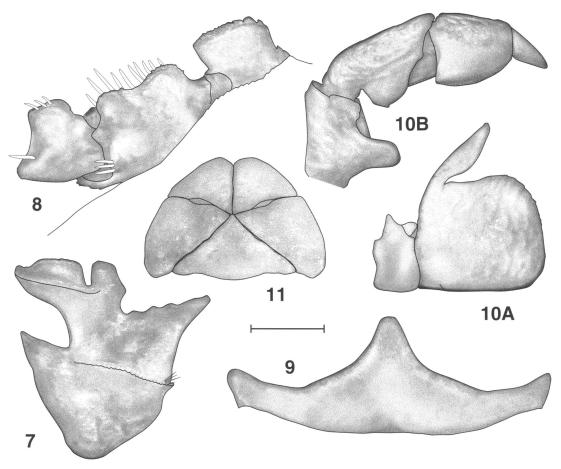
Figs. 4-6. Clastotoechus nodosus (Streets), carapace. 4. Carapace, dorsal view. 5. Frontal view. 6. Right side of carapace and lateral wall. Scale bar = 2.0 mm (figs. 4, 6) and 1.0 mm (fig. 5).

Second segment of antenna (fig. 8) with a strongly projecting lamellar lobe, finely granulate, dorsal surface with irregular longitudinal granular ridge; third segment with one to two large, strongly projecting nodules distally and one large proximal granule, often covered with short rows of very small granules, on anterior margin, scattered smaller granules on sides and ventral surface, anteroventral surface with submarginal row of sheathed setae, posterodistal nodule with up to three sheathed setae; fourth segment nodular on anterior margin, with one to two dorsal sheathed setae posterodistally, short row of sheathed setae along anterior margin; flagellum with vestigial setae, increasing in length distally.

Third maxillipeds (figs. 9, 10) with sternite trilobate, median lobe acute, lacking anterolateral projections; carpus rugose dorsally, with distal ventral margin strongly produced; merus rugose, with elongate medial lobe subquadrate to subtriangular in shape; ischium with medioproximal angle broadly rounded, slightly acute to right-angled, laterodistal projection greatly elongated, reaching half length of merus.

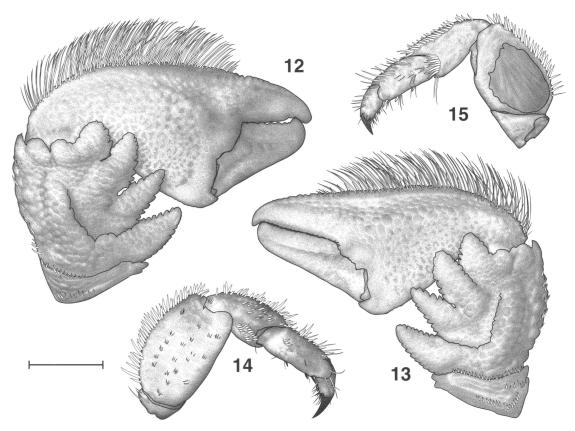
Chelipeds (figs. 12, 13) usually unequal in size, propodus noticeably wider in major than

minor, fingers dissimilar. Merus covered dorsally with flattened, imbricate tubercles; with small granular lobe, only slightly projecting, on anterior margin; dorsomesial margin with row of sheathed setae; ventromesial anterior angle with blunt, denticulate tooth, sometimes barely present; ventral surface smooth. Carpus and propodus covered with rough, rounded granules; posterodorsal granules usually with short sheathed setae. Carpus, excluding marginal teeth, approximately one-third longer than broad; dorsal surface with pronounced longitudinal crest, granules of crest larger and more flattened; posterodistal granules with sheathed setae; anterior margin with four strongly projecting, granular teeth, denticulate on edges, proximal tooth acute, sharply pointed, often connecting at right angles to longitudinal crest by short elevated ridge, distal teeth increasingly broad and rounded, second and third often connected basally by short elevated ridge; distal margin with two smaller, blunt lobes; posterodistal angle produced into blunt or curved spine; posterior surface obliquely rugose, rugae forming strong ridges and extending onto posterior margin of ventral surface, rugae with anterior rows of nonplumose setae and scattered sheathed setae; ventral surface smooth, without pubescence; ven-



Figs. 7-11. Clastotoechus nodosus (Streets). 7. Basal segment of left antennule, ventral view. 8. Left antenna, dorsal view, in situ. 9. Sternite of third maxilliped. 10A. Ischium of right third maxilliped, ventral view. 10B. Merus of right third maxilliped, ventral view. 11. Telson. Scale bar = 1.0 mm (figs. 10A, 10B, 11) and 0.5 mm (figs. 7-9).

tromesial margin with row of fine granules proximally. Propodus very finely granular mesially, with granules becoming larger, more closely packed laterally; with low to pronounced longitudinal swelling medially, large, granular tubercle near base of fixed finger sometimes present, usually as continuation of swelling; mesiodistal angle produced into forward-pointing spine or lobe; posterior margin with low rounded crest extending onto fixed finger, crest with row of small granules, with thick brush of soft, plumose setae to base of fixed finger in both sexes; ventral surface faintly granular, increasing distally, with posterior submarginal row of granules. Dactyl with closely packed transverse rows of very small granules on outer margin, submarginal row of larger granules, with medial longitudinal suture; submarginal granules with anterior tufts of short setae, little or no pubescence between fingers. Major chela with fingers usually short and blunt, but occasionally much longer; slightly gaping, crossing at tips. Dactyl with large, rounded, proximal tooth and row of smaller granules; curved in lateral view; fixed finger entire, sometimes with a few small teeth distally. Minor cheliped with fingers longer, meeting entire length of cutting edge, crossing at tips, with row of fine granules along cutting edges. Dactyl more strongly curved in lateral view; fixed finger with granular longitudinal crest adjacent to cutting edge.



Figs. 12–15. Clastotoechus nodosus (Streets), pereopods. 12. Major cheliped, dorsal view. 13. Minor cheliped, dorsal view. 14. Right third pereopod, lateral view. 15. Right second pereopod, mesial view. Scale bar = 2.0 mm.

Walking legs (figs. 14, 15) rugose to roughly granular, all segments with scattered, long nonplumose setae, and densely covered with sheathed setae on anterior margins and dorsomesial and dorsolateral surfaces. Merus with anterodistal margin entire. Carpus without spines. Propodus with two distal, one subdistal, and one medial movable spines ventrally. Dactyl with four or five corneous spines on ventral margin.

Abdomen smooth, sparsely setose.

Coloration: Live specimens purplish maroon, paler maroon in small specimens (Werding, 1977).

DISTRIBUTION: Tropical western Atlantic: Vera Cruz, Mexico; Cuba to St. Martin Island; Colombia and Venezuela; exposed rocky intertidal shores.

REMARKS: Curiously, both Haig (1956) and Gore and Abele (1976) considered this

to be an exceptionally small species while at the same time recognizing that the specimens they examined were immatures or juveniles. However, this species is one of the largest in the genus, with specimens exceeding 9 mm (Werding, 1977). Its preferred habitat (exposed, high energy rocky intertidal shores) is typically only accessible when water is unusually calm, which may make adults difficult to collect (Werding, 1978).

Werding (1977) discussed Clastotoechus nodosus and C. vanderhorsti (= Madarateuchus vanderhorsti), but his figures are mislabeled. Figure 2, labeled as C. nodosus, is clearly M. vanderhorsti, and figure 3, labeled C. vanderhosti, is clearly C. nodosus.

Gore and Abele's (1976) illustrated juvenile specimen (CL 2.1 mm) of *Clastotoechus nodosus* is also problematic. The specimen itself (LACM 72-379.1) differs in many

ways from the holotype and other specimens of C. nodosus, including similarly sized juveniles from other locations. For example, it has conspicuous spines on the anterolateral margins of the carpus of the walking legs (apparent in Gore and Abele's figure) and distally expanded sheathed setae (not apparent in Gore and Abele's figure). In these and other respects, this specimen is much more similar to the eastern Pacific C. hickmani n. sp. than to C. nodosus. There are at least three possible explanations for this. First, C. hickmani might occur on both Pacific and Atlantic coasts. Second, Gore and Abele's specimen might represent a new Atlantic species, geminate with and virtually indistinguishable, at least at juvenile sizes, from C. hickmani. Third, the locality might be incorrect, although this appears to be unlikely. Gore and Abele (1976) reported the specimen from Galeta Island, Panama, on the Atlantic coast, from Laurencia. The original label with the specimen reads, "Laurencia 16-A; March 8, 1972; 1-1NO," which according to L. Abele (in litt.) refers to a long-term collection site on Galeta Island. Additional material from Galeta Island will be required to resolve this question.

The nodular carapace of Clastotoechus nodosus is apparently size-related, because juveniles and immatures can have completely smooth carapaces. Other diagnostic features, however, such as the shape of the front and orbits, the proportions of the cheliped carpus and anterior carpus teeth, and the complete lack of spines or teeth on the anterior margin of the carpus of the walking legs, are apparent in the smallest specimens examined.

# Clastotoechus diffractus (Haig, 1957) Figures 16–27

Petrolisthes diffractus Haig, 1957: 36, pl. 9, fig. 1-6.

Clastotoechus diffractus: Haig, 1960: 175, pl. 30, text-fig. 5(1). Werding and Haig, 1983 (in part): 62.

Not Clastotoechus diffractus: Birkeland et al., 1975: 67. Werding and Haig, 1983 (in part): 62. (= Clastotoechus hickmani n. sp.) (see remarks).

Not Clastotoechus diffractus: Gore and Abele, 1976: 15 (= Clastotoechus gorgonensis Werding and Haig, 1983) (see remarks).

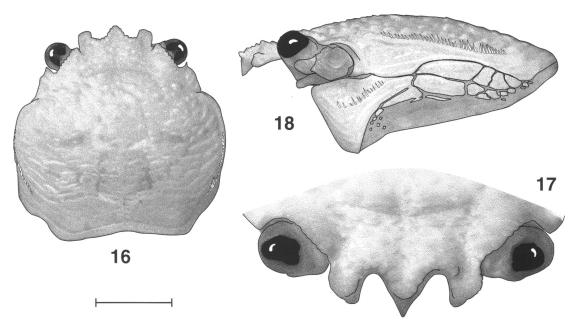
Not Clastotoechus diffractus: Gore, 1982: 4 (= Clastotoechus lasios n. sp.) (see remarks).

MATERIAL EXAMINED: *Holotype:* Mexico: 1 male (CL 5.44 mm), San Lorenzo Rocks, Acapulco, Guerrero, shore, 30 Jan 1954, Velero IV Station 2591-54, J. S. Garth, coll., LACM 54-139.1 (formerly AHF 542, in part).

Paratypes: Mexico: 3 males (CL 2.92–6.52 mm), 1 female (CL 5.41 mm), 3 ovigerous females (CL 5.36–7.85 mm), San Lorenzo Rocks, Acapulco, Guerrero, shore, 30 Jan 1954, Velero IV Station 2591-54, J. S. Garth, coll., LACM 54-139.2 (formerly AHF 542, in part).

Additional Specimens: Mexico: 8 males (CL 2.32–8.22 mm) 1 ovigerous female (CL 4.94 mm), Cabo San Lucas, Baja California Sur, 1859–1861, J. Xanthus, coll., MCZ 8019.

DIAGNOSIS: Sheathed setae not expanded distally. Carapace without long, scattered plumose setae. Front with median and lateral lobes with thickened margins, lateral lobes truncate; frontal margins lacking setae. Orbits angular, with margins straight, strongly oblique, separated by acute notch from lateral frontal lobe. Outer orbital angle acute, produced, pointed at tip. Second segment of antenna with a strongly projecting lamellar lobe, with one or two blunt spines proximally and often several smaller granules distally. Ischium of third maxilliped with laterodistal projection small, well short of posterior margin of mesial merus lobe. Carpus of chelipeds, excluding marginal teeth, 1.5-1.75 times as long as broad; dorsal surface covered with rough, rounded granules more projecting than those of carapace, with longitudinal crest, granules of crest larger and more flattened; anterior margin with four strongly projecting, granular teeth, denticulate on edges. Chelae covered dorsally with granules as in carpus. Propodus with low to pronounced longitudinal swelling medially; posterior margin with low, rounded crest extending onto fixed finger, crest with row of small granules, sometimes produced into spinules, with thick brush of soft, plumose setae to base of fixed finger, vestigial to absent in larger males. Carpus of walking legs with one moderately large spine at anterodistal an-



Figs. 16–18. Clastotoechus diffractus (Haig), carapace. 16. Carapace, dorsal view. 17. Frontal view. 18. Left side of carapace and lateral wall. Scale bar = 2.0 mm (figs. 16, 18) and 1.0 mm (fig. 17).

gle of second pereopod, usually one small spine at anterodistal angle of third pereopod; propodus with two distal, one subdistal, and one medial movable spines ventrally. Abdomen smooth.

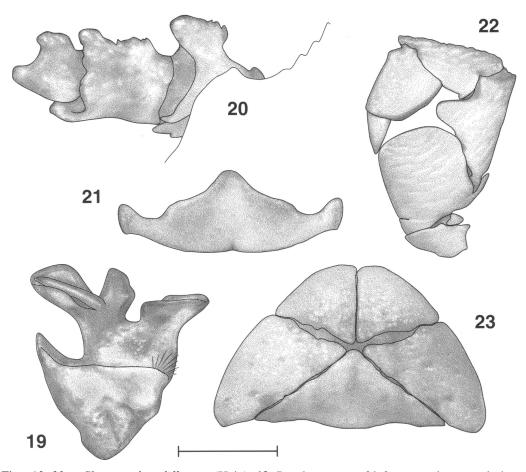
DESCRIPTION: Carapace (fig. 16) as long as broad, regions faintly defined; dorsal surface covered with large, flattened imbricate granules, which are smaller on the frontal region, posterolateral regions plicate, intestinal region smooth or punctate, cardiac region with short rugae or flattened imbricate granules, dorsolateral ridges pronounced, with row of plumose or sheathed setae, anterior epibranchial region pronounced. Frontal region (figs. 17, 18) slightly depressed, granular, finely setose, with faint median groove; front with median lobe triangular, lateral lobes truncate, margins granular, granules largest on median lobe, lobes with thickened margins; in dorsal view three lobes appear about equal in length. Orbits angular, with margins straight, strongly oblique, separated by acute notch from lateral frontal lobe. Outer orbital angle acute, produced, pointed at tip. Eyes large, peduncle with minute spines along ventrodistal margin.

Basal segment of antennule (fig. 19) with

anterolateral lobe scoop-shaped, well separated from anteromedial lobe, anteromesial lobe scoop-shaped. Second segment of antenna (fig. 20) with a strongly projecting lamellar lobe, with one or two blunt spines proximally and often several smaller granules distally, dorsal surface with irregular longitudinal granular ridge; third segment with two large, strongly projecting nodules distally and several large proximal granules, scattered smaller granules on sides and ventral surface, anteroventral surface sometimes with one minute simple seta; fourth segment nodular on anterior margin, more or less smooth, lacking setae; flagellum with vestigial setae, increasing in length distally.

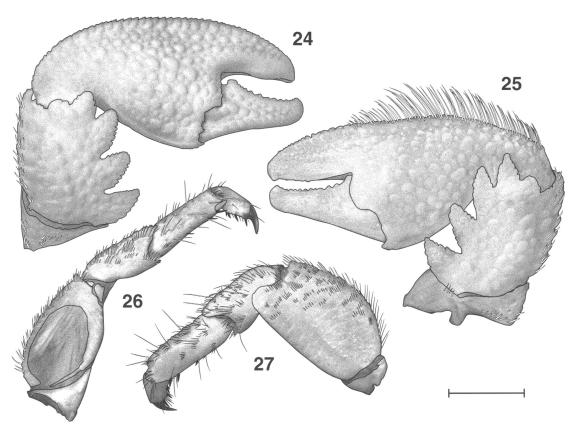
Third maxillipeds (figs. 21, 22) with sternite trilobate, median lobe broad, with anterolateral projections; carpus rugose dorsally, with distal ventral margin strongly produced; merus rugose, with pronounced medial lobe subtriangular to rounded in shape; ischium with medioproximal angle broadly rounded, right-angled or obtuse, laterodistal projection small, well short of posterior margin of mesial merus lobe.

Chelipeds (figs. 24, 25) unequal in size, noticeably wider in major than minor, fingers



Figs. 19-23. Clastotoechus diffractus (Haig). 19. Basal segment of left antennule, ventral view. 20. Left antenna, dorsal view, in situ. 21. Sternite of third maxilliped. 22. Left third maxilliped, ventral view. 23. Telson. Scale bar = 2.0 mm (fig. 22), 1.0 mm (figs. 21, 23), and 0.5 mm (figs. 19, 20).

dissimilar. Merus covered dorsally with setose granules; with small pointed lobe, serrate-edged mesially, only slightly projecting, on anterior margin; dorsomesial margin with row of plumose or sheathed setae; ventromesial anterior angle with blunt, denticulate tooth; ventral surface smooth or punctate. Carpus and propodus covered with rough, rounded granules more projecting than those of carapace; posterodorsal granules usually with plumose or sheathed setae. Carpus, excluding marginal teeth, 1.5-1.75 times as long as broad; dorsal surface with longitudinal crest, granules of crest larger and more flattened; anterior margin with four strongly projecting, granular teeth, lacking elevated ridges, denticulate on edges, proximal tooth acute, distal teeth usually increasingly broad and rounded; distal margin with one smaller, blunt lobe; posterodistal angle produced into curved spine; posterior surface obliquely rugose, rugae forming strong ridges and extending onto posterior margin of ventral surface; ventral surface smooth or punctate, without pubescence; ventromesial margin with row of fine granules proximally. Chelae covered dorsally with granules as in carpus. Propodus with low to pronounced longitudinal swelling medially; no enlarged tubercle near base of fixed finger; ventral surface faintly granular, increasing distally, with posterior submarginal row of granules; mesiodistal angle sometimes produced into forward-pointing spine; posterior margin with low, rounded crest extending onto fixed finger, crest with row of small granules, some-



Figs. 24–27. Clastotoechus diffractus (Haig), pereopods. 24. Major cheliped, dorsal view. 25. Minor cheliped, dorsal view. 26. Left second pereopod, mesial view. 27. Left third pereopod, lateral view. Scale bar = 2.0 mm.

times produced into spinules, with thick brush of soft, plumose setae to base of fixed finger, vestigial to absent in larger males. Dactyl with outer marginal row of small granules, submarginal row of larger granules, medial longitudinal suture; only a slight trace of pubescence between fingers. Major chela with short, blunt fingers, gaping, crossing at tips. Dactyl with large, rounded, proximal tooth and row of smaller granules; curved in lateral view; fixed finger with a few small teeth distally. Minor cheliped with fingers longer, meeting entire length of cutting edge, crossing at tips, with row of fine granules along cutting edges. Dactyl more strongly curved in lateral view.

Walking legs (figs. 26, 27) rugose, all segments with long nonplumose setae, and fringed with plumose or sheathed setae on anterior margins. Merus with anterodistal

margin entire. Carpus with one spine, sometimes large, at anterodistal angle of second pereopod, usually one small spine at anterodistal angle of third pereopod. Propodus with two distal, one subdistal, and one medial movable spines ventrally. Dactyl with four corneous spines on ventral margin.

Abdomen smooth, not setose.

Coloration: In alcohol, pale reddish orange, slightly darker on the granules and fingertips (Haig, 1960). After over 40 years, preserved specimens are a uniform straw color.

DISTRIBUTION: Eastern Pacific, from Cabo San Lucas, Baja California, to Acapulco, Mexico; apparently absent from the Gulf of California; intertidal.

REMARKS: Haig (1960) and Gore and Abele (1976) commented on the relative rarity of this species. The present study supports this observation, because most published re-

ports of *C. diffractus* are in fact referable to other species. Specimens identified by Birkeland et al. (1975) and referred to by Werding and Haig (1983) as *C. diffractus* from Malpelo Island, Colombia, are actually *C. hickmani* n. sp. The specimens discussed by Gore and Abele (1976) from Punta Paitilla, Panama, are actually *C. gorgonensis*, whereas the specimens discussed by Gore (1982) from Jalisco, Mexico, have been found to represent a closely related species, *C. lasios* n. sp.

Specimens of Clastotoechus diffractus from Cabo San Lucas differ from the Acapulco series in that the teeth on the carpus of the cheliped are acute rather than broad, and the lamellar lobe on the second antennal segment is distally entire rather than finely granular. These differences probably represent local variation, and by themselves do not warrant the creation of a new species.

Haig (1957, 1960) reported that males of Clastotoechus diffractus lack the thick brush of plumose setae on the posterior margin of the chela. Although Gore (1982) disagreed, his observations were based on C. lasios n. sp., not C. diffractus. However, the smaller male paratypes of C. diffractus do in fact have a brush of setae. Thus, in this species, as in the related C. hickmani, the brush appears to be a trait that is reduced or lost in larger males.

The largest known specimen of Clastotoechus diffractus, a male (CL 8.2 mm) from Cabo San Lucas, was infested with a single large rhizocephalan barnacle, Lernaeodiscus porcellanae Müller, 1862. This represents the first record of a parasite on any species of Clastotoechus s.s.

# Clastotoechus gorgonensis Werding and Haig, 1983 Figures 28–39

Clastotoechus gorgonensis Werding and Haig, 1983: 60, fig. 2-5.

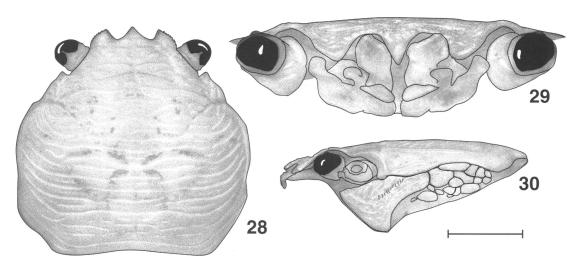
Clastotoechus diffractus: Gore and Abele, 1976: 15. [Not Clastotoechus diffractus (Haig, 1957) (see remarks).]

MATERIAL EXAMINED: **Panama:** 2 males (CL 4.60–6.06 mm) 1 female (CL 3.15 mm), 1 ovigerous female (CL 5.67 mm), Paitilla Beach, Pacific, 29 Oct 1970, HBOM 89: 37225; 1 ovigerous female (CL 4.24 mm), 1

juvenile (CL 2.63 mm), Bella Vista, shore, 2 Feb 1935, USNM 275899; 1 male (CL 3.36 mm), 1 female (CL 2.45 mm), 1 ovigerous female (CL 2.99 mm), Bella Vista, shore, 2 Apr 1935, USNM 275900; 4 males (CL 3.47–6.74 mm), 6 ovigerous females (CL 4.56–5.52 mm), Bella Vista, shore, 2 Feb 1935, USNM 275898; 1 female (CL 2.65 mm), Secas Isle, shore, 4 Feb 1935, USNM 275902; 2 males (CL 4.10–6.69 mm), 1 ovigerous female (CL 4.99 mm), shore, 2 Feb 1935, USNM 275901.

DIAGNOSIS: Sheathed setae not expanded distally. Carapace without long, scattered plumose setae, covered with strong, transverse rugae. Front with median and lateral lobes with thickened margins, lateral lobes triangular. Orbits angular, with margins straight, strongly oblique. Outer orbital angle acute, produced, pointed at tip. Second segment of antenna with a strongly projecting lamellar lobe, with two to five granules proximally. Ischium of third maxilliped with laterodistal projection small, well short of posterior margin of mesial merus lobe. Carpus of chelipeds, excluding marginal teeth, approximately 1.5 times as broad as long; with longitudinal rows of large flattened imbricate tubercles, without longitudinal crest; anterior margin with four broad, strongly projecting, granular teeth, denticulate on edges. Chelae covered dorsally with flattened tubercles, sometimes more rounded than in carpus. Propodus without longitudinal swelling medially; posterior margin with low rounded crest extending onto fixed finger, crest with row of small granules, sometimes becoming forward-pointed spines that may reach end of fixed finger, brush of setae lacking in both sexes. Carpus of walking legs with one or two large spines at anterodistal angle of second pereopod, one-two smaller spines at anterodistal angle of third pereopod, sometimes one small spine or a few granules at anterodistal angle of fourth pereopod; lateral surfaces with broken subdorsal longitudinal ridge; propodus with two distal, four medial movable spines ventrally. Abdomen smooth.

DESCRIPTION: Carapace (fig. 28) slightly broader than long, regions faintly defined; dorsal surface covered with strong transverse rugae, which are broken up on the frontal region, cardiac region covered with strong



Figs. 28–30. Clastotoechus gorgonensis Werding and Haig, carapace. 28. Carapace, dorsal view. 29. Frontal view. 30. Left side of carapace and lateral wall. Scale bar = 2.0 mm (figs. 28, 30) and 1.0 mm (fig. 29).

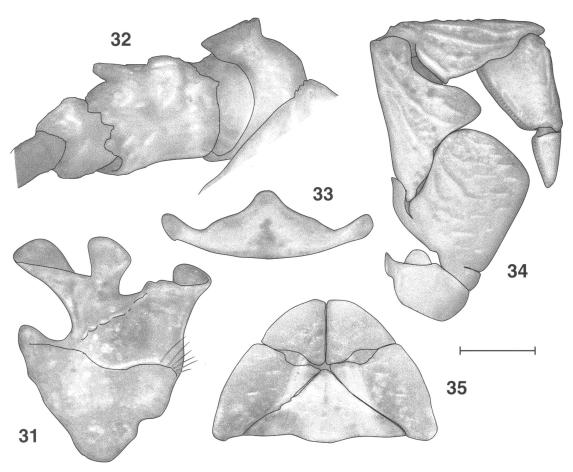
transverse rugae, intestinal region plicate, posterolateral regions plicate, dorsolateral ridges pronounced, sometimes with row of minute setae visible only under high magnification. Rugae of carapace setose and beaded anteriorly, not visible except under high magnification. Frontal region (figs. 29, 30) slightly depressed, with short transverse rugae, finely setose, with median groove; front with median and lateral lobes triangular, margins with small, close-set granules, lobes with thickened margins; in dorsal view three lobes appear about equal in length. Orbits angular, with margins straight, strongly oblique. Outer orbital angle acute, produced, pointed at tip. Eyes large, peduncle apparently unarmed.

Basal segment of antennule (fig. 31) with anterolateral lobe scoop-shaped, well separated from anteromedial lobe, anteromesial lobe scoop-shaped. Second segment of antenna (fig. 32) with a strongly projecting lamellar lobe, with two to five granules proximally, dorsal surface with irregular longitudinal granular ridge; anterior margin of third segment with two large, strongly projecting granules distally and one large proximal granule covered with short rows of very small granules, scattered smaller granules on sides and ventral surface, lacking setae; fourth segment nodular on anterior margin, smooth to slightly rugose, lacking setae; fla-

gellum with vestigial setae, usually decreasing in length distally.

Third maxillipeds (figs. 33, 34) with sternite trilobate, median lobe broad, sometimes with anterolateral projections; carpus rugose dorsally, with distal ventral margin produced; merus rugose, with pronounced medial lobe subtriangular to rounded; ischium with medioproximal angle broadly rounded, right-angled to obtuse, laterodistal projection small, well short of posterior margin of mesial merus lobe.

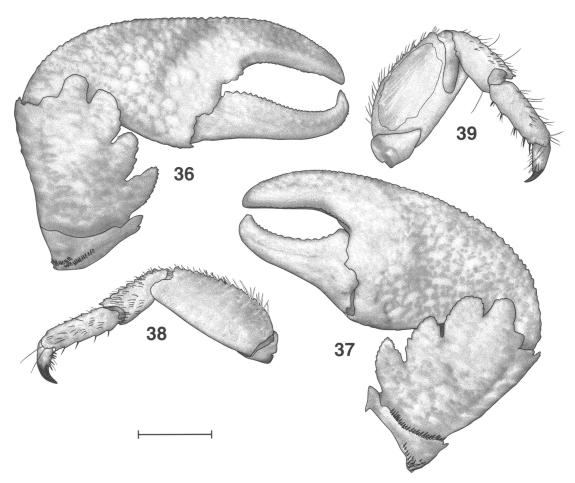
Chelipeds (figs. 36, 37) subequal in size or noticeably wider in major than minor; fingers dissimilar. Merus covered dorsally with flattened, imbricate tubercles; with small serrateedged lobe, only slightly projecting, on anterior margin; dorsomesial margin with row of plumose or sheathed setae; ventromesial anterior angle with blunt, denticulate tooth, sometimes with second acute tooth; ventral surface smooth, with low rugae on anteroventral margin. Carpus and propodus with longitudinal rows of large flattened imbricate tubercles; posterodorsal granules lacking setae. Carpus, excluding marginal teeth, approximately 1.5 times as broad as long, dorsal surface without longitudinal crest; anterior margin with four broad, strongly projecting, granular teeth, lacking elevated ridges, denticulate on edges, teeth rounded; in small specimens, proximal tooth some-



Figs. 31–35. Clastotoechus gorgonensis Werding and Haig. 31. Basal segment of left antennule, ventral view. 32. Left antenna, dorsal view, in situ. 33. Sternite of third maxilliped. 34. Right third maxilliped, ventral view. 35. Telson. Scale bar = 1.0 mm (figs. 33–35) and 0.5 mm (figs. 31, 32).

times acute, sharply pointed, with distal teeth increasingly broad and rounded; distal margin with two smaller, blunt lobes; posterodistal angle produced into blunt or curved spine; posterior surface obliquely rugose, rugae forming strong ridges and extending onto posterior margin of ventral surface; ventral surface smooth or punctate, without pubescence; ventromesial margin with row of low granules proximally. Chelae covered dorsally with flattened tubercles, sometimes more rounded than in carpus; without longitudinal swelling medially, no enlarged tubercle near base of fixed finger; mesiodistal angle not produced; posterior margin with low rounded crest extending onto fixed finger, crest with row of small granules, sometimes becoming forward-pointed spines that may reach end of

fixed finger; lacking thick brush of setae; ventral surface faintly granular, increasing distally, with one to four posterior submarginal rows of granules. Dactyl with outer marginal row of small, beaded, granules, sometimes arranged in transverse rows, submarginal row larger, beaded granules, medial longitudinal suture; little or no pubescence between fingers. Major chela with short, blunt fingers, gaping, crossing at tips. Dactyl with large, rounded, proximal tooth and row of smaller granules; curved in lateral view; fixed finger with distinct row of small teeth, fused medially. Minor cheliped normally with fingers longer, meeting entire length of cutting edge (fig. 37 illustrates an unusual specimen in which the minor chelae has a pronounced gape), crossing at tips, with row



Figs. 36–39. Clastotoechus gorgonensis Werding and Haig, pereopods. 36. Minor cheliped, dorsal view. 37. Major cheliped, dorsal view. 38. Left second pereopod, lateral view. 39. Left third pereopod, mesial view. Scale bar = 2.0 mm.

of fine granules along cutting edges. Dactyl more strongly curved in lateral view.

Walking legs (figs. 38, 39) rugose; dorsal margin of merus, carpus, and proximal half of propodus with open row of granules; all segments with long nonplumose setae, and fringed with sheathed setae on anterior margins. Merus with anterodistal margin entire, granular, or with one or two small blunt spines. Carpus with one or two large, basally constricted spines at anterodistal angle of second pereopod, one or two smaller spines at anterodistal angle of third pereopod, sometimes one small spine or a few granules at anterodistal angle of fourth pereopod; lateral surfaces with broken subdorsal longitudinal ridge. Propodus with two distal, four medial

movable spines ventrally. Dactyl with five corneous spines on ventral margin.

Abdomen smooth, not setose.

Coloration: A transverse brownish band across the cheliped propodus and a fainter band that crosses the base of the fixed finger and dactyl are detectable in specimens preserved for more than 60 years. Although preserved specimens of all species of Clastotoechus s.s. show at least some hints of iridescence ventrally, specimens of C. gorgonensis are unusual in that they exhibit considerable red-green iridescence both dorsally and ventrally.

DISTRIBUTION: Eastern Pacific; known from Isla Gorgona, Colombia, and the coast of Panama; intertidal to 9 m.

REMARKS: Often found in commensal association with the echinoid *Echinometra* vanbrunti. However, the association may not be obligatory as in *Madarateuchus vanderhorsti*, as specimens from Panama were not collected with *E. vanbrunti*.

# Clastotoechus hickmani, new species Figures 3, 40-51

Clastotoechus diffractus: Birkeland et al., 1975: 67. Werding and Haig, 1983 (in part): 62. [Not Clastotoechus diffractus (Haig, 1957) (see remarks).]

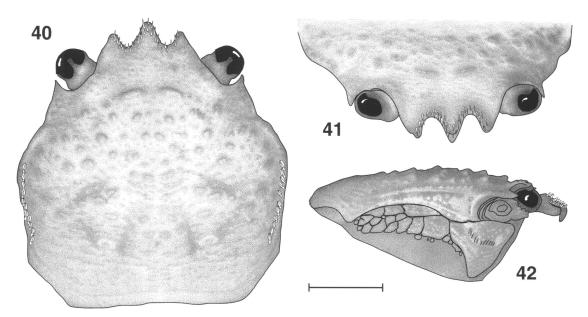
MATERIAL EXAMINED: *Holotype*: **Galápagos:** female (CL 4.33 mm), Charles [= Santa María] Island, dredged from low tide to 11.3 m, 17 Jan 1934, Taylor, coll., USNM 110552.

Paratypes: Colombia: 56 males (CL 2.07–7.69 mm), 28 females (CL 2.45–5.79 mm), 20 ovigerous females (CL 3.25–5.80 mm), 18 juveniles (CL 1.61–2.31 mm), Malpelo Island, 29 Feb–3 Mar 1972, Smithsonian Tropical Research Institute, LACM 72-378.1 Galápagos: 1 female (CL 5.48 mm), Isla Gardner at Floreana, 18 m, 9 Mar 1997, C. Hickman, coll., CDRS 97-196; 1 female (CL 9.56 mm), Caleta Iguana, Isabela, under algae, shore, 3 Feb 98, C. Hickman, CDRS 98-101; 1 male (CL 10.59 mm), Caleta Iguana, Isabela, under algae, shore, 3 Feb 98, C. Hickman, CDRS 98-100.

DIAGNOSIS: Sheathed setae expanded distally. Carapace without long, scattered plumose setae. Median lobe of front with thickened margin, lateral lobes triangular; frontal margin with double row of sheathed setae along margin of front between tips of lateral lobes. Orbits deep, rounded. Outer orbital angle acute, produced, pointed at tip. Second segment of antenna with a strongly projecting lamellar lobe, with two to five granules proximally and several smaller granules distally, distal granule enlarged. Ischium of third maxilliped with laterodistal projection greatly elongated, reaching two-thirds length of merus. Carpus of chelipeds, excluding marginal teeth, less than one-third longer than broad; covered, usually loosely, with rounded granules larger and more projecting than those of carapace; with longitudinal crest, usually pronounced, granules of crest larger; anterior margin with four acute, strongly projecting, granular teeth, denticulate on edges. Chelae covered dorsally with granules as in carpus. Propodus with low to pronounced longitudinal swelling medially; posterior margin with low rounded crest extending onto fixed finger, crest with row of small, forward-pointed spines to end of fixed finger, sometimes becoming granular on fixed finger of large males, with thick brush of soft, plumose setae to base of fixed finger; setae shorter, brush stopping well short of fixed finger in large males. Carpus of walking legs with two large spines at anterodistal angle of second pereopod, one or two smaller spines at anterodistal angle of third pereopods, one small spine or few granules at anterodistal angle of fourth pereopods, lateral surfaces with broken subdorsal longitudinal ridge; propodus with two distal, one subdistal, and one medial movable spines ventrally. Abdomen smooth, setose, usually sparsely.

DESCRIPTION: Carapace (fig. 40) as long as broad, regions faintly defined; dorsal surface with scattered small round granules on gastric region, cardiac region punctate or with short rugae, intestinal region punctate to plicate, posterolateral regions plicate, dorsolateral ridges pronounced, sometimes granular, with row of sheathed setae. Frontal region (figs. 41, 42) slightly depressed, granular, finely setose, with median groove; front with median lobe triangular, lateral lobes triangular, margins entire, lateral margin of lateral lobes sometimes finely serrate, median lobe with thickened, deflexed margin; margin with double row of sheathed setae along margin of front between tips of lateral lobes; in dorsal view median lobe usually slightly more produced than lateral lobes. Orbits deep, rounded. Outer orbital angle acute, produced, pointed at tip. Eyes large, peduncle with minute spines along ventrodistal margin.

Basal segment of antennule (fig. 43) with anterolateral lobe scoop-shaped, closely adjacent to anteromedial lobe, anteromesial lobe scoop-shaped. Second segment of antenna (fig. 44) with a strongly projecting lamellar lobe, with two to five granules proximally and several smaller granules distally, distal granule enlarged, dorsal surface with irregular longitudinal granular ridge; third segment with large, strongly projecting nod-



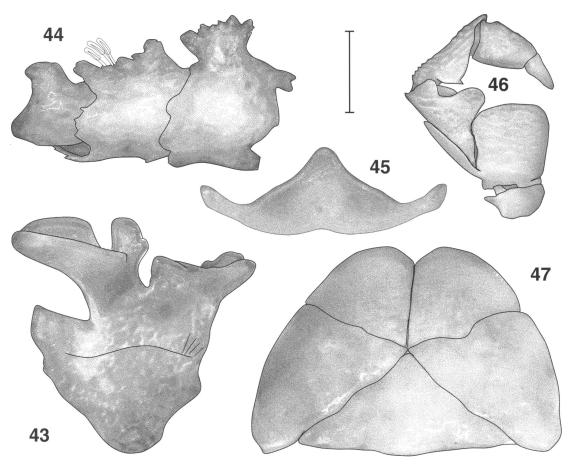
Figs. 40–42. Clastotoechus hickmani, new species, carapace. 40. Carapace, dorsal view. 41. Frontal view. 42. Right side of carapace and lateral wall. Scale bar = 2.0 mm.

ule distally and several smaller proximal granules on anterior margin, scattered smaller granules on sides and ventral surface, anteroventral surface with usually with one to several sheathed setae in submarginal row, posterodistal margin usually with one sheathed seta; fourth segment nodular on anterior margin, more or less smooth, usually with single dorsal sheathed seta posterodistally; flagellum with vestigial setae, increasing in length distally.

Third maxillipeds (figs. 45, 46) with sternite trilobate, median lobe acute, lacking anterolateral projections; carpus rugose dorsally, with distal ventral margin produced, usually strongly; merus rugose, with pronounced medial lobe subquadrate to subtriangular in shape; ischium with medioproximal angle right-angled, laterodistal projection greatly elongated, reaching two-thirds length of merus.

Chelipeds (figs. 48, 49) subequal in size, fingers usually dissimilar; cheliped asymmetry increases with size, more pronounced in males. Merus covered dorsally with setose granules or flattened, imbricate tubercles; with small pointed lobe, serrate-edged mesially, barely to only slightly projecting, on anterior margin; dorsomesial margin with row of sheathed setae; ventromesial anterior

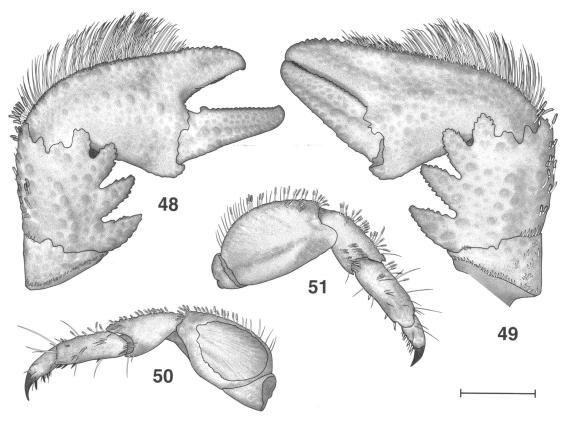
angle with blunt, denticulate tooth, sometimes barely present; ventral surface smooth to finely granular. Carpus and propodus covered, usually loosely, with rounded granules larger and more projecting than those of carapace. Carpus, excluding marginal teeth, less than one-third longer than broad; dorsal surface with longitudinal crest, usually pronounced, granules of crest larger; posterodistal granules with sheathed setae; anterior margin with four acute, strongly projecting, granular teeth, lacking elevated ridges, denticulate on edges, teeth rounded; distal margin with one or two smaller lobes, posterior lobe acute, sometimes vestigial or absent, anterior lobe bluntly rounded; posterodistal angle produced into curved spine; posterior surface rugose, rugae with anterior rows of sheathed setae; ventral surface smooth, without pubescence; ventromesial margin with row of low granules proximally, occasionally distally as well. Chelae covered dorsally with granules as in carpus. Propodus with low to pronounced longitudinal swelling medially, large, granular tubercle near base of fixed finger sometimes present, usually as continuation of swelling; mesiodistal angle produced into forward-pointing spine; posterior margin with low rounded crest extending



Figs. 43–47. *Clastotoechus hickmani* new species. **43.** Basal segment of left antennule, ventral view. **44.** Left antenna, dorsal view. **45.** Sternite of third maxilliped. **46.** Right third maxilliped, ventral view. **47.** Telson. Scale bar = 2.0 mm (fig. 46), 1.0 mm (figs. 45, 47), and 0.5 mm (figs. 43, 44).

onto fixed finger, crest with row of small, forward-pointed spines to end of fixed finger, sometimes becoming granular on fixed finger of large males, with thick brush of soft, plumose setae to base of fixed finger; setae shorter, brush stopping well short of fixed finger in large males; ventral surface faintly granular, increasing distally, with posterior submarginal row of granules. Dactyl with outer marginal row of small, sometimes beaded, granules, submarginal row larger, with granules sometimes beaded, medial longitudinal suture; sheathed setae basally, only a slight trace of pubescence between fingers. Major chela with fingers either short, blunt, and gaping (in large males only), or long, meeting entire length of cutting edge, crossing at tips. Dactyl with moderately large, rounded, proximal tooth and row of smaller granules; curved in lateral view; fixed finger with distinct row of small teeth, sometimes fused medially, sometimes restricted to distal margin. Minor cheliped with fingers longer, meeting entire length of cutting edge, crossing at tips, with row of fine granules along cutting edges. Dactyl more strongly curved in lateral view.

Walking legs (figs. 50, 51) rugose, all segments with scattered long nonplumose setae, and densely covered with sheathed setae on anterior margins and dorsomesial and dorsolateral surfaces. Merus with anterodistal margin entire or finely granular. Carpus with two large spines at anterodistal angle of second pereopod, one or two smaller spines at anterodistal angle of third pereopods, one



Figs. 48-51. Clastotoechus hickmani, new species, pereopods. 48. Major cheliped, dorsal view. 49. Minor cheliped, dorsal view. 50. Right second pereopod, mesial view. 51. Right third pereopod, lateral view. Scale bar = 2.0 mm.

small spine or few granules at anterodistal angle of fourth pereopods, lateral surfaces with broken subdorsal longitudinal ridge. Propodus with two distal, one subdistal, and one medial movable spines ventrally. Dactyl with four corneous spines on ventral margin.

Abdomen smooth, usually sparsely setose. *Coloration* (based on color slide of CDRS 97-196 taken by C. Hickman): In life, overall ground color pale brownish orange. Carapace brownish tan, with frontal lobes and delineations of carapace regions darker brown, posterior gastric pits white, dorsolateral ridges darker brown interrupted with short pale bands. Chelipeds brownish orange, ground color of propodus paler than carpus, with large dark brown patches near base of fixed finger and dactyl; distal two-thirds of dactyl dark brown, proximal third pale, with dark brown patch anteriorly and bright orange patch adjacent to cutting edge; fixed finger

dark brown; lateral brush grayish. Propodus of walking legs with broad dark brown band medially and pale distal band; dactyl with narrow whitish distal band. In preserved specimens the orange coloration initially intensifies, but eventually fades to a uniform straw color.

Variations: With more than 120 specimens ranging from 1.6 to 7.7 mm CL, the Malpelo Island sample provides an excellent opportunity to examine the effects of size and sex on morphology in members of this uncommonly encountered genus. As in the much smaller samples of the closely related Clastotoechus nodosus, the carapace granules that characterize the adults are often not obvious in juveniles, whereas other diagnostic features are apparent at all sizes: the shape of the front and orbits, the spines on the anterior margin of the carpus of the walking legs, the distally expanded sheathed setae.

As is common in decapods, cheliped asymmetry increases with size, and is more pronounced in males. In *Clastotoechus hickmani* n. sp., the lateral brush on the chela is always present in both sexes, but decreases in size, with respect to both the length of the setae and the anterior extension of the brush, in males. In this respect *C. hickmani* is intermediate between *C. nodosus*, in which the brush is well developed in males of all sizes, and *C. diffractus*, in which large males lack the brush altogether.

DISTRIBUTION: Galápagos Islands, Ecuador; Malpelo Island, Colombia; intertidal to 18 m.

ETYMOLOGY: Named after Dr. Cleveland Hickman, Washington and Lee University, who collected the specimen that led to this review.

REMARKS: Although Clastotoechus hickmani has been confused with C. diffractus, the two are easily distinguished. In C. diffractus, the granules on the carapace are larger, flattened, and more crowded; the lateral lobes of the front are truncate, with thickened margins; the orbits are angular, with straight, strongly oblique margins, separated by a notch from the lateral lobes; the carpus of the cheliped is relatively longer, and the laterodistal projection of the ischium of the third maxillipeds is very small.

Clastotoechus hickmani n. sp. is very similar to its Atlantic geminate species, C. nodosus. The latter has larger, coarser granules on the carapace and chelipeds, no spines on the walking legs, and numerous rows of somewhat simpler sheathed setae on the front. The granulations of the carapace and chelae are less developed in very small specimens of both species, but other features appear to be independent of size.

# Clastotoechus lasios, new species Figures 52–63

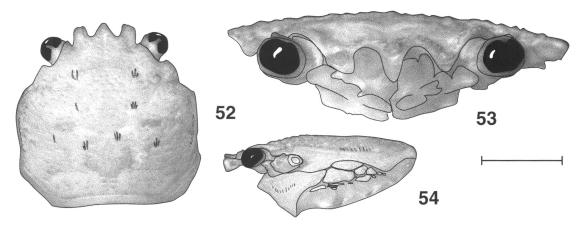
Clastotoechus diffractus: Gore, 1982: 4. [Not Clastotoechus diffractus (Haig, 1957) (see remarks).]

MATERIAL EXAMINED: *Holotype:* **Mexico:** female (CL 3.78 mm), north of Barra Navidad, Bahia Cuastecomate, Jalisco, 0–1 m, 25 Jul 1972, Dawson-Child Central American Expedition, USNM 184903.

Paratypes: Mexico: 4 males (CL 2.37–4.89 mm), north of Barra Navidad, Bahia Cuastecomate, Jalisco, 0–1 m, 25 Jul 1972, Dawson-Child Central American Expedition, USNM 184903.

DIAGNOSIS: Sheathed setae not expanded distally. Carapace with long, scattered plumose setae. Front with median and lateral lobes with thickened margins, lateral lobes rounded; frontal margin sometimes with double row of sheathed setae along margin of front between tips of lateral lobes. Orbits angular, with margins straight, strongly oblique, separated by obtuse notch from lateral frontal lobe. Outer orbital angle obtuse, only slightly produced. Second segment of antenna with a strongly projecting, truncate, lamellar lobe, with 1-2 blunt spines proximally and several smaller granules distally, distal granule enlarged. Ischium of third maxilliped with laterodistal projection small, well short of posterior margin of mesial merus lobe. Carpus of chelipeds, excluding marginal teeth, 1.5-1.7 times as long as broad, covered with rough, rounded granules larger and more projecting than those of carapace, with pronounced longitudinal crest, granules of crest larger; anterior margin with four acute, strongly projecting, granular teeth, denticulate on edges. Chelae covered dorsally with granules as in carpus. Propodus with pronounced longitudinal swelling medially; posterior margin with low rounded crest extending onto fixed finger, crest with row of small granules produced into forward-pointing spines to about base of fixed finger, with thick brush of soft, plumose setae to base of fixed finger in both sexes. Carpus of walking legs with one (second pereopod) or two (third pereopod) small spines at anterodistal angle; propodus with two distal, one subdistal, and one medial movable spines ventrally. Abdomen smooth, sparsely setose.

DESCRIPTION: Carapace (fig. 52) as long as broad; regions faintly defined, dorsal surface covered with flattened imbricate granules, which are smaller on the frontal region, posterolateral regions punctate to plicate, intestinal region smooth or punctate, cardiac region with short rugae, dorsolateral ridges pronounced, with row of sheathed setae, sometimes granular. Carapace covered with long, scattered, plumose setae, often consid-



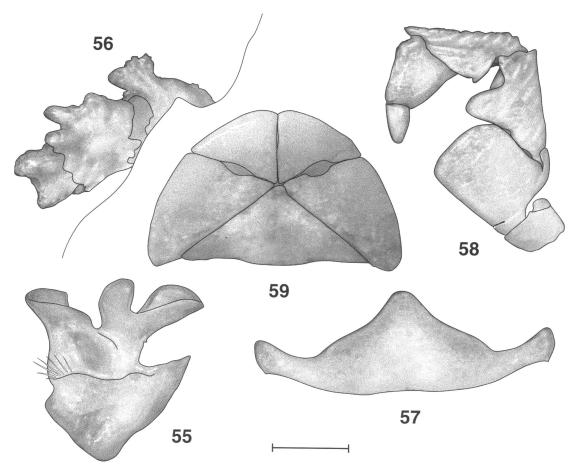
Figs. 52-54. Clastotoechus lasios, new species, carapace. 52. Carapace, dorsal view. 53. Frontal view. 54. Left side of carapace and lateral wall, lateral view. Scale bar = 2.0 mm (figs. 52, 54) and 1.0 mm (fig. 53).

erably longer than illustrated (fig. 52); in addition, rugae and granules of carapace setose anteriorly, setae not visible except under magnification. Frontal region (figs. 53, 54) slightly depressed, granular, finely setose, with faint median groove; front with median lobe triangular, lateral lobes rounded, margins granular, granules largest on median lobe, lobes with thickened margins; margin sometimes with double row of sheathed setae along margin of front between tips of lateral lobes; in dorsal view three lobes appear about equal in length. Orbits angular, with margins straight, strongly oblique, separated by obtuse notch from lateral frontal lobe. Outer orbital angle obtuse, only slightly produced. Eyes large, peduncle apparently unarmed.

Basal segment of antennule (fig. 55) with anterolateral lobe scoop-shaped, somewhat separated from anteromedial lobe, anteromesial lobe scoop-shaped. Second segment of antenna (fig. 56) with a strongly projecting, truncate, lamellar lobe, with one or two blunt spines proximally and several smaller granules distally, distal granule enlarged, dorsal surface with irregular longitudinal granular ridge; third segment with two large, strongly projecting nodules distally and several large proximal granules, scattered smaller granules on sides and ventral surface, lacking setae; fourth segment nodular on anterior margin, more or less smooth, lacking setae; flagellum with vestigial setae, increasing in length distally.

Third maxillipeds (figs. 57, 58) with sternite trilobate, median lobe broad, with anterolateral projections; carpus rugose dorsally, with distal ventral margin strongly produced; merus rugose, with pronounced medial lobe subtriangular to rounded in shape; ischium with medioproximal angle broadly rounded, right-angled, laterodistal projection small, well short of posterior margin of mesial merus lobe.

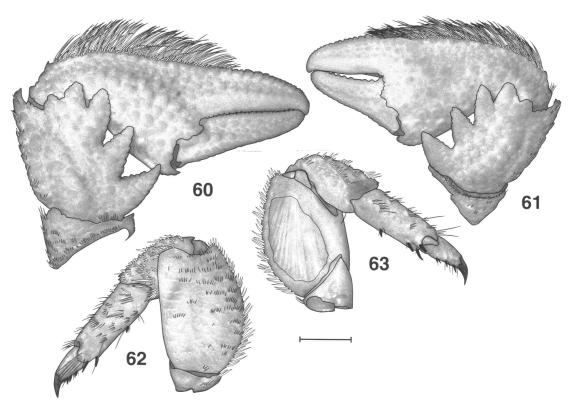
Chelipeds (figs. 60, 61) subequal in size, fingers dissimilar. Merus covered dorsally with setose granules; with small pointed lobe, serrate-edged mesially, only slightly projecting, on anterior margin; dorsomesial margin with row of sheathed setae; ventromesial anterior angle with blunt, denticulate tooth, sometimes barely present; ventral surface smooth or punctate. Carpus and propodus covered with rough, rounded granules larger and more projecting than those of carapace; posterodistal granules with sheathed setae. Carpus, excluding marginal teeth, 1.5–1.7 times as long as broad; dorsal surface with pronounced longitudinal crest, granules of crest larger; anterior margin with four acute, strongly projecting, granular teeth, lacking elevated ridges, denticulate on edges, teeth acute, sharply pointed, distal tooth slightly broader and rounder; distal margin with one smaller, blunt lobe, sometimes absent; posterodistal angle produced into curved spine; posterior surface obliquely rugose, rugae forming ridges, often strong, and extending onto pos-



Figs. 55-59. Clastotoechus lasios, new species. **55.** Basal segment of right antennule, ventral view. **56.** Left antenna, dorsal view, in situ. **57.** Sternite of third maxilliped. **58.** Left third maxilliped, ventral view. **59.** Telson. Scale bar = 1.0 mm (fig. 58), 0.75 mm (fig. 59), and 0.5 mm (figs. 55-57).

terior margin of ventral surface; ventral surface smooth or punctate, without pubescence; ventromesial margin with row of fine granules proximally. Chelae covered dorsally with granules as in carpus. Propodus with pronounced longitudinal swelling medially, no enlarged tubercle near base of fixed finger; ventral surface faintly granular, increasing distally, with posterior submarginal row of granules; mesiodistal angle produced into forward-pointing spine; posterior margin with low rounded crest extending onto fixed finger, crest with row of small granules produced into forward-pointing spines to about base of fixed finger, with thick brush of soft, plumose setae to base of fixed finger in both sexes, although reduced in large males. Dactyl with outer marginal row of small granules, submarginal row of larger granules, no median longitudinal suture; no pubescence between fingers. Major chela with short, blunt fingers, gaping, crossing at tips. Dactyl with large, rounded, proximal tooth and row of smaller granules; curved in lateral view. Fixed finger entire. Minor cheliped with fingers longer, meeting entire length of cutting edge, crossing at tips, with row of fine granules along cutting edges. Dactyl more strongly curved in lateral view.

Walking legs (figs. 62, 63) rugose, all segments with long nonplumose setae, and fringed with sheathed setae on anterior margins. Merus with anterodistal margin entire. Carpus with one (second pereopod) or two



Figs. 60-63. Clastotoechus lasios, new species, pereopods. 60. Minor cheliped, dorsal view. 61. Major cheliped, dorsal view. 62. Right third pereopod, lateral view. 63. Right second pereopod, mesial view. Scale bar = 2.0 mm.

(third pereopod) small spines at anterodistal angle. Propodus with two distal, one subdistal, and one medial movable spines ventrally. Dactyl with four corneous spines on ventral margin.

Abdomen smooth, sparsely setose.

Coloration: Preserved material uniformly straw-colored.

DISTRIBUTION: At present only known from the type locality, Bahia Cuastecomate, Jalisco, Mexico; intertidal.

ETYMOLOGY: From the Greek *lasios*, meaning "hairy," and referring to the long, plumose setae on the carapace, which are most apparent in small specimens.

REMARKS: Gore (1982) noted that his specimens of *Clastotoechus diffractus* differed from Haig's descriptions of that species in having more granulate chelae, acute rather than broad teeth on the anterior margin of the cheliped carpus (incorrectly referred to as meral teeth by Gore), and a lateral brush on

the chelae of two of the four males. In Gore's specimens, which are referable to *C. lasios* n. sp., males actually do have a lateral brush, although it is greatly reduced in the larger males. *C. lasios* n. sp. can also be distinguished from *C. diffractus* by the long, plumose setae on the carapace (which are unique in the genus), the more rounded frontal lateral lobes, the rather truncate anterior projection on the second antennal segment, and the spines on the anterodistal margin of the carpus of the walking legs.

#### Madarateuchus, new genus

DIAGNOSIS: Sheathed setae absent on carapace and pereopods. Carapace as long as broad, dorsal surface punctate to finely granular, dorsolateral ridges moderately pronounced. Carapace glabrous. Front trilobate, lobes strongly projecting, extending well beyond eyes, with length of lateral lobes more

than one-third width of front, median lobe broad, lateral and median lobes with thickened margins, in frontal view median lobe with long, acute, strongly deflexed extension. Epibranchial spine absent. Lateral walls of carapace consisting of one large anterior piece, two smaller posterior pieces, and several very small posterior fragments narrowly separated from each other by membrane.

Basal segment of antennule with three strong, lamellate, anterior lobes; ventral surface with medial transverse row of small, closely set granules, with tuft of setae mesially; transverse row of irregular granules absent. Second segment of antenna with a somewhat projecting lobe, sometimes with a few faint granules proximally; third segment faintly rugose, lacking tubercles or nodules, on anterior margin; fourth segment more or less smooth.

Third maxillipeds with sternite trilobate, median lobe exceeding lateral lobes; carpus with distal ventral margin strongly produced; merus with pronounced medial lobe, with anterior margin occasionally finely dentate; basis partly fused to ischium; coxa with anterior mesial margin not produced, apparently articulated anterolaterally.

Chelipeds subequal in size, fingers usually dissimilar. Merus with small pointed lobe, serrate-edged mesially, only slightly projecting, on anterior margin. Carpus and propodus covered with fine granules, these occasionally transversely elongated laterally; sometimes with short, fine pubescence not obscuring granules. Carpus, excluding marginal teeth, 1.5-2 times as long as broad, relatively broader in large specimens; anterior margin with four acute, projecting, widely spaced, granular teeth, sharply pointed, edges concave, weakly denticulate, the proximal tooth projecting slightly forward at right angles to carpus, others tilted progressively forward, with distal tooth, formed by a projection of the anterodistal angle, lying parallel to long axis of carpus; posterodistal angle produced into elongate, curved spine; posterior surface obliquely rugose, rugae forming strong ridges and extending onto posterior margin of ventral surface. Propodus with thick brush of short, soft, plumose setae along posterior margin and extending well onto dorsal surface. Dactyl smooth to finely granular.

Walking legs smooth to slightly granular, segments lacking setae, except for scattered nonplumose setae at distal end of propodus and ventral margin of dactyl; mesial surface of merus with transparent, decalcified window medially; ventral margin of propodus of walking legs with one medial spine.

Telson with five plates. Second pleopods present in males.

ETYMOLOGY: From the Greek madaros, meaning "bald," and ateuches, meaning "unarmed," and referring to the sparse setation and armature of this genus compared to Clastotoechus s.s.

TYPE SPECIES: Clastotoechus vanderhorsti Schmitt, 1924, by monotypy.

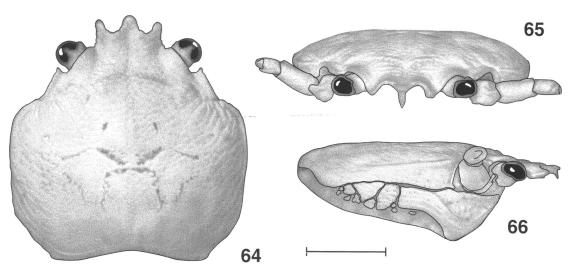
REMARKS: Although *Madarateuchus* is obviously closely related to *Clastotoechus* s.s., there are numerous differences between the two. Most conspicuous are the greatly exaggerated front, the nature of the marginal brush of plumose setae on the posterior margin of the chela, and the carapace, antenna, chelipeds, and walking legs, which lack the granules and setae characteristic of *Clastotoechus* s.s.

## Madarateuchus vanderhorsti (Schmitt, 1924) Figures 64–75

Petrolisthes vanderhorsti Schmitt, 1924: 73, pl. 8(7). Lewis, 1960: 425, fig. 16 [see remarks]. Clastotoechus vanderhorsti: Haig, 1960: 175, fig. 5(2). Markham, 1975: 257. Gore and Abele, 1976: 10. Werding, 1977: 180, fig. 1a, not fig. 3 (see remarks); 1978: 220; 1983: 3. Werding and Haig, 1983: 62. Schoppe, 1991: 373, fig. 2; 1994: 107, figs. 1–8.

Clastotoechus nodosus: Werding, 1977: fig. 2 (see remarks). [Not Clastotoechus nodosus (Streets, 1872).]

MATERIAL EXAMINED: **British Virgin Islands:** 1 juvenile (CL 1.91 mm), Treasure Point, Norman Island, Tortola, shore, 6 Apr 1958, USNM 275904. **Barbados:** 1 female (CL 4.90 mm), 6 ovigerous females (CL 4.59–5.65 mm), surf zone, 1958, J. B. Lewis, coll., USNM 102360. **Bonaire:** 2 males (CL 2.20–3.77 mm), 1 ovigerous female (CL 4.68 mm), Kralendijk, water line, 1954, J. Haig, coll., USNM 67416. **Colombia:** 2 males (CL 6.42–6.58 mm), 1 ovigerous female (CL 5.66 mm), Santa Marta, Sep 1974, LACM 74-



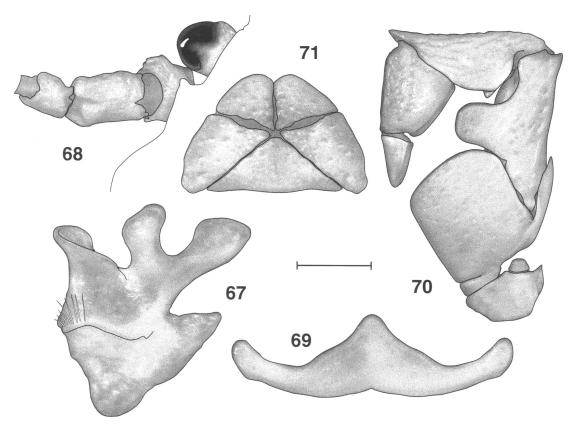
Figs. 64-66. *Madarateuchus vanderhorsti* (Schmitt), carapace. **64.** Carapace, dorsal view. **65.** Frontal view. **66.** Right side of carapace and lateral wall. Scale bar = 2.0 mm.

228.1 (formerly AHF 728-01). **Venezuela:** 1 ovigerous female (CL 5.55 mm), Cubagao [= Cubagua] Island, shore, 14 Apr. 1939, LACM 39-271.2

DIAGNOSIS: Carapace glabrous. Front with median and lateral lobes with thickened margins, lateral lobes rounded. Orbits angular, with margins straight, strongly oblique, separated by acute or obtuse notch from lateral frontal lobe. Outer orbital angle acute or obtuse, rounded or somewhat produced, pointed at tip. Second segment of antenna with a somewhat projecting lobe, sometimes with a few faint granules proximally. Ischium of third maxilliped with laterodistal projection elongate, reaching posterior margin of mesial merus lobe. Carpus of chelipeds almost twice as long as broad, somewhat broader in very large specimens; covered with low granules, these occasionally transversely elongated laterally, with longitudinal crest; anterior margin with 4 acute, strongly projecting, granular teeth, denticulate on edges. Chelae covered dorsally with fine granules. Propodus with low longitudinal swelling medially; posterior margin with sharply defined, granulate ridge, extending onto fixed finger, with thick brush of soft, plumose setae to base of fixed finger that extends well onto dorsal surface in both sexes. Carpus of walking legs with longitudinal subdorsal ridge on lateral surface; propodus with two distal and one subdistal medial movable spines ventrally. Abdomen smooth.

DESCRIPTION: Carapace (fig. 64) as long as broad; regions faintly defined, dorsal surface punctate to finely granular on gastric region, posterolateral regions plicate, intestinal region punctate, cardiac region punctate, dorsolateral ridges at least moderately pronounced, lacking setae. Carapace glabrous. Frontal region (fig. 65, 66) depressed, granular, lacking setae, with deep median groove; front with median lobe broad, lateral lobes rounded, margins usually entire, sinus between median and lateral lobes sometimes granular, lobes with thickened margins; in dorsal view median lobe usually slightly more produced than lateral lobes. Orbits angular, with margins straight, strongly oblique, separated by acute or obtuse notch from lateral frontal lobe. Outer orbital angle acute or obtuse, rounded or somewhat produced, pointed at tip. Eyes large, peduncle with minute spines along ventrodistal margin.

Basal segment of antennule (fig. 67) with anterolateral lobe scoop-shaped, well separated from anteromedial lobe, anteromesial lobe flattened dorsoventrally, not scoop-shaped. Second segment of antenna (fig. 68) with a somewhat projecting lobe, sometimes with a few faint granules proximally; third segment rugose, lacking tubercles, nodules, or setae, longitudinal seam along dorsal sur-



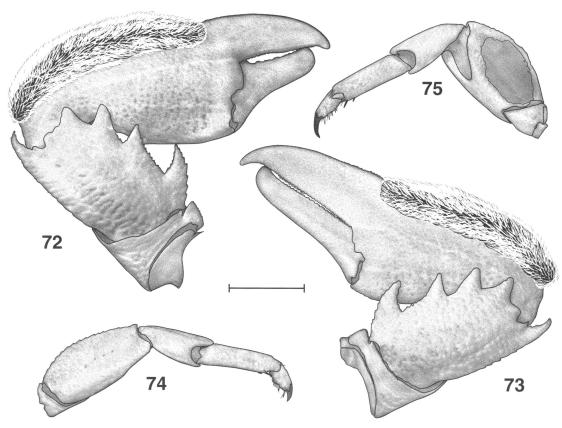
Figs. 67–71. *Madarateuchus vanderhorsti* (Schmitt). **67.** Basal segment of right antennule, ventral view. **68.** Left antenna, dorsal view, in situ. **69.** Sternite of third maxilliped. **70.** Left third maxilliped, ventral view. **71.** Telson. Scale bar = 1.0 mm (figs. 68, 70, 71), 0.75 mm (fig. 69), and 0.5 mm (fig. 67).

face, most distinct distally; fourth segment more or less smooth, lacking setae; flagellum with short setae, increasing in length distally.

Third maxillipeds (figs. 69, 70) with sternite trilobate, median lobe usually broad, lacking anterolateral projections; carpus rugose dorsally, with distal ventral margin strongly produced; merus rugose, with pronounced medial lobe subquadrate in shape; ischium with medioproximal angle obtuse, laterodistal projection elongate, reaching posterior margin of mesial merus lobe.

Chelipeds (figs. 72, 73) subequal in size, fingers usually dissimilar. Merus lightly rugose or covered dorsally with flattened, imbricate tubercles on dorsal surface; with small pointed lobe, serrate-edged mesially, barely to only slightly projecting, on anterior margin; dorsomesial margin without setae; ventromesial anterior angle with denticulate tooth, some-

times barely present, anteroventral margin with row of granules; ventral surface smooth to finely granular. Carpus and propodus covered with low granules, these occasionally transversely elongated laterally; often with short, fine pubescence not obscuring granules. Carpus 1.5-2 times as long as broad, relatively broader in very large specimens; dorsal surface with longitudinal crest; anterior margin with four acute, strongly projecting, granular teeth, lacking elevated ridges, denticulate on edges, teeth sharply pointed; distal margin with one or two smaller lobes, posterior lobe acute, sometimes vestigial or absent, anterior lobe bluntly rounded; posterodistal angle produced into elongate, curved spine; posterior surface obliquely rugose, rugae forming strong ridges and extending onto posterior margin of ventral surface; ventral surface smooth or punctate, without pubescence; ventromesial margin with



Figs. 72–75. *Madarateuchus vanderhorsti* (Schmitt), pereopods. 72. Major cheliped, dorsal view. 73. Minor cheliped, dorsal view. 74. Right second pereopod, lateral view. 75. Right third pereopod, mesial view. Scale bar = 2.0 mm.

row of fine granules proximally. Chelae covered dorsally with fine granules. Propodus with low longitudinal swelling medially; no enlarged tubercle near base of fixed finger; ventral surface punctate, with posterior submarginal row of granules; mesiodistal angle sometimes produced into blunt, forward-pointing lobe; posterior margin with sharply defined, granulate ridge, extending onto fixed finger, with thick brush of short, soft, plumose setae, extending well onto dorsal surface to base of fixed finger in both sexes. Dactyl smooth to finely granular; no pubescence between fingers. Major chela with fingers either short and blunt, or long and slender; slightly gaping, crossing at tips. Dactyl with moderately large, rounded, proximal tooth and row of smaller granules; curved in lateral view; fixed finger with distinct row of small teeth, fused medially. Minor cheliped with fingers long, meeting entire length of cutting edge or slightly gaping, crossing at tips, with row of fine granules along cutting edges. Dactyl more strongly curved in lateral view.

Walking legs (figs. 74, 75) smooth to slightly granular, segments lacking setae, except for scattered nonplumose setae at distal end of propodus and ventral margin of dactyl. Merus with anterodistal margin entire. Carpus with longitudinal subdorsal ridge on lateral surface. Propodus with two distal and one subdistal medial movable spines ventrally. Dactyl with four to seven (usually five) corneous spines on ventral margin.

Abdomen smooth, not setose.

Coloration: In life, carapace brilliant maroon, gradually darkening toward front, with phosphorescent blue spots and longitudinal lines. The chelipeds are dark maroon, becoming black distally, with two thin white

longitudinal lines on the propodus. The lateral brush of setae on the propodus is white, contrasting strongly with the chelae. The walking legs are brilliant maroon with phosphorescent blue lines (Werding, 1978). The longitudinal lines on the chela remain apparent even in long-preserved material.

DISTRIBUTION: Tropical eastern Atlantic; from Cuba (Werding, 1992 in Schoppe, 1994) to Bonaire, Venezuela, and Colombia.

REMARKS: In Werding's (1977) publication, the illustrations of *Clastotoechus nodosus* and *Madarateuchus vanderhorsti* (as *C. vanderhorsti*) were transposed, such that figure 2 is in fact *M. vanderhorsti*, and figure 3 is actually *C. nodosus*.

Lewis (1960: fig. 16) illustrated a first-stage zoeae of *Clastotoechus* (= *Madarateuchus*) vanderhorsti, and stated (p. 426) that freshly hatched zoeae are 1.6 mm in length, half of which is the length of the rostral spine. Such a size seems improbably small. Schoppe (1994) put the total length of the first-stage zoea, including spines, at around 5 mm, which is a more reasonable size for a porcellanid.

Markham (1975) reported the bopyrid isopod Astalione cruciaria Markham, 1975 from C. (= Madarateuchus) vanderhorsti.

Madarateuchus vanderhorsti is one of two species considered in this paper that lives as

a commensal on echinoids of the genus Echinometra, the other being Clastotoechus gorgonensis (Werding, 1983; Werding and Haig, 1983). Unlike C. gorgonensis, M. vanderhorsti has not been collected except in association with E. lucunter, and Schoppe (1994) asserted that in the field the megalopae colonize burrows of E. lucunter. Werding (1983) considered the commensalism in M. vanderhorsti and C. gorgonensis to have been established in a single trans-Isthmus population that was divided by the closure of the Isthmus of Panama and, presumably, subsequently speciated. This scenario would seem to suggest that M. vanderhorsti and C. gorgonensis are geminate species, but Werding and Haig (1983) considered C. gorgonensis to be most closely related to C. diffractus, which in turn Haig (1960) did not consider to be closely related to M. vanderhorsti. The present analysis, of course, does not support the idea that M. vanderhorsti and C. gorgonensis are geminate species. However, commensalism with Echinometra may represent a symplesiomorphy, lost in other species of Clastotoechus s.s., which would not require M. vanderhorsti and C. gorgonensis to be sister taxa. Phylogenetic analyses currently underway involving Clastotoechus s.s., Madarateuchus, and related porcellanid genera may shed some light on the evolution of this commensalism.

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