1990; USNM 251429, $1 \sigma^{3}$, 1φ ovig., Long Key, Dry Tortugas, sandy mud flat of seining beach, intertidal, taken with dipnet after explosion of dynamite charge, W.L. Schmitt, 16 Aug 1930.

BAHAMAS: USNM 251202, 3 d^{*}, 1 Q (ovig.), San Salvador, Pigeon Creek, mound at mouth of *Callianassa* burrow, H.A. Curran, Jun 1985.

TURKS AND CAICOS ISLANDS: USNM 251203, 1 σ^3 , 1 Qovig., Pine Key, "Walk Cay," 1 m, yabby pump, R. Heard, 9 Apr 1988; USNM 251204, 4 σ^3 , 7 Q (3 ovig.), same, 14 Apr 1988; USNM 251205, 11 σ^3 , 11 Q (3 ovig.), same, 17 Apr 1988; USNM 251206, 1 σ^3 , 1 Q ovig., flats on S shore of Pine Cay near human shelter, 3 m, 1500, R. Heard, J.M., 15 Apr 1989 (1 σ^3 , 2 Q returned to R. Heard); USNM 251207, 8 σ^3 , 8 Q (6 ovig.), Pine Cay, south beach east Bonefish Cove, 50–100 m, 1 with bopyrid, R. Heard, 4 May 1990 (9 σ^3 , 9 Q returned to R. Heard); USNM 251208, 9 σ^3 , 10 Q (1 ovig.), Bonefish Cove, R. Heard, 13 May 1990 (10 σ^3 , 10 Q returned to R. Heard).

DOMINICAN REPUBLIC: AMNH 8771, 1 ♂,3 ♀ (2 ovig.), El Cayo, sta 201, 6 Aug 1933.

LESSER ANTILLES: St. Croix (all collected by M.L. Reaka project; in following list, excr. = experimental coral rubble sun dried and placed on reef): Teague Bay: USNM 251366, 2 juvs., excr. placed on sand-sea grass floor of lagoon behind bank barrier reef, 3-4 m, DFRF-5A, 18 Sep 1981. Boiler Bay: USNM 251367, 1 Q, naturally occurring dead coral rubble/beach rock, intertidal, BBI-1, 15 Oct 1980; USNM 251368, 1 Q, 1 cephalothorax, 2 juvs., natural dead coral rubble on fringing reef with scattered sea grass, 3 m, BBS-4, 19 Aug 1980; 4 juvs., same habitat, BBS-2, 20 Oct 1980; 4 of , 2 9, frags., same habitat, BBS-1, 11 Feb 1981; juvs., same habitat, BBS col4 wk5, 19 Jul 1981. Salt River Canyon: USNM 251369, 2 juvs., excr. base cinder block artificial reef on sandy canyon floor, 20 m, MAV-3, 12 Jan 1981; USNM 251370, 1 d, 1 Q ovig., juvs. frags., excr. base cinder block artificial reef on sand/sea grass floor, 3 m, SIV-4, 29 Jun 1981; USNM 251371, 2σ , 1 Q, 1 juv., natural dead coral rubble on back side of bank barrier reef, 3 m, SCon-9, 30 Jun 1981; 2 d, same habitat, SCon-4, 30 Jun 1981; 1 or, same habitat, SCon-4, 18 Jan 1982; 1 o², 1 Q, excr. base cinder block artificial reef on sand/sea grass bottom back of bank barrier reef, 3-4 m, SAII-6, 17 May 1982; 2 d' juvs., 1 Q ovig., same habitat, SAIV-1, 17 May 1982. Barbuda: USNM 251215, 1 Q, reefs off Martello Tower, S coast, Smithsonian-Bredin Exped., R/V Freelance sta 92-56, Nicholson, Schmitt, and Chace, 17 Apr 1956, Antigua: USNM 251724, 4 Q, Tank Bay, English Harbor, Smithsonian-Bredin Exped., R/V Freelance sta 74-56, seine hauls on mud bottom, under rocks, oyster bar and along beach, Schmitt, Chace, Nicholson, Jackson, 3 Apr 1956; USNM 251216, 1 or, 2 Q, beach N of Black's Point, Falmouth Harbor, cracked from rocks and coral, Smithsonian-Bredin Exped., R/V Freelance sta 110-59, 30 Apr 1959. Martinique: USNM 251217, 8 of ,4 Q, 20 juvs., 14°25.2'N, 60°53.8'W, rocky shore, 0-2 m, R/V Pillsbury sta P-896, Pronoxfish, 8 Jul 1969. Barbados: USNM 57951, 1 \bigcirc ovig., Pelican, Is., Univ. Iowa Barbados-Antigua Exped., shallows, 14 May 1918; USNM 68950, 1 \bigcirc , same. *Tobago:* USNM 251218, 2 σ , E of Pigeon Point, plankton tow and sponge in *Thalassia* beds near mangrove swamp, Smithsonian-Bredin Exped., R/V Freelance sta 30-59, W.L. Schmitt, 10 Apr 1959; USNM 251219, 2 σ , Charlottesville, Pirate's Bay, E side Man of War Bay, sheltered cove, 1.5-3 m (5-10 ft), hand net in poison sta, Blum, Nizinski, Williams, Howe, Munro, and Schotte, 5 Sep 1990; USNM 251434, 1 \heartsuit , Petit Trou, lagoon, sand-gravel bottom, patches of turtle grass, with *Callianassa*, 1-1.5 m, yabby pump, R.W. Heard, sta 9, 2 Apr 1992; USNM 251438, 1 σ , 1 \heartsuit , 2 juvs., Milford Bay near Pigeon Point, 11°09'N, 60°50'W, sand beach behind reef, dead coral rock washings, 1 m, R.W. Heard, sta 5, 7 Apr 1992.

MEXICO: Quintana Roo: USNM 251250, 1 Q ovig., Puerto Morelos, in old battery case S of old pier, 3 m, J.C. Markham, 520.4939010, 13 Sep 1986; USNM 251179, 1 σ , 2 Q, N of Ascension Bay, 200-300 yds SW of Suliman Pt. sand shallows, 0.6-1.5 m (2-5 ft), Smithsonian-Bredin Caribbean Exped. IV, R/V *Freelance*, sta 87-60, Bousfield, Daiber, Rehder, 17 Apr 1960.

PANAMA: USNM 251209, 4 or, Canal Zone, Galeta Island, 09°24.4'N, 79°52.35'W, ocean-side reef flat with tide pools, rock, and lithified algae, poison, 15 cm, hand, NMNH-STRI Panama Survey sta 2-3, R.B. Manning, J. Rosewater, C.A. Child, 17 Apr 1971; USNM 251210, 1 or ,1 Q, 1 cephalothorax, Galeta Island, reef and shore near STRI lab, assoc. with Thalassia, sand, marl, mangrove, algae, Panama Survey sta 60-4, D.L. Pawson, J. Del Rosario, R. Brown, J. Rosewater, 9 Nov 1971; USNM 251239, 1 J., Colon, Galeta Island, reef flat across surge channel from STRI Lab., shore, Thalassia, algae, flood tide, 24.3°C, 33 ppt, 0-1 m, sta 1546, ichthyocide, Dawson et al., 29 Apr 1972; USNM 251211, 7 of ,4 Q (1 ovig.), San Blas, Isla Pico Feo, 09°33'07"N, 78°58'33"W, N shore, mud, sand, some rocks, algae, low flood tide, 0-0.8 m, 38°C, 35 ppt, C.E. Dawson and party, sta 1610, 7 Apr 1973; USNM 251725, 124 J, 27 Q (8 ovig.; 1 J, 4 Q with bopyrids), San Blas, Isla Pico Feo, N shore, 09°33'07"N, 78°58'33"W, mud, sand, some rock, algae, etc., flood tide, 0-0.75 m, 30.5°C, 29.7 ppt, C.E. Dawson and party, sta 1592, ichthyocide, 8 Nov 1972; USNM 251726, 58 or, 28 Q (5 ovig.), San Blas, Isla Mira, 09°32'58"N, 78°54'14"W, Thalassia, mangrove, sand, some rock, low flood tide, 0-1 m, C.E. Dawson and party, sta 1593, ichthyocide, 9 Nov 1972.

COLUMBIA: USNM 138900, 2 σ , 2 φ , Caribbean Sea, A.J. Provenzano, received 8 Apr 1964.

NETHERLANDS ANTILLES: RMNH 28670, 25 σ^{3} , 30 Q (5 ovig.), fragments, Curaçao Bay just NW of Piscadera Bay, in burrows made in layer of oil washed ashore on beach, oil covered with sand, inside of burrows covered with thin film of sand, L.B. Holthuis no. 1088, 2 Feb 1957; RMNH 30966, 18 σ^{3} , 17 Q (5 ovig.), Lac Bonaire, mouth at northern point of peninsula, in brown seaweed and algae, sand, L.B. Holthuis no.



FIGURE 30.—Upogebia vasquezi Ngoc-Ho $(a-d, g-j, USNM 251202, \sigma^{n}, e, f, Q)$: a, cephalic region, lateral; b, anterior carapace, dorsal; c, cheliped, right lateral, σ^{n} ; d, chela and carpus, left mesial, σ^{n} ; e, cheliped, right lateral, Q; f, chela and carpus, left mesial, Q; g-i (left), legs 2-4; j, parts of abdominal segment 6, telson, and uropods, dorsal. (Scale = 2 mm.)

1138, 6 Mar 1957; USNM 251212, 1 σ^{a} , Aruba, Klein Lagoon, R. Lemaitre, 1 m, yabby pump, 6 Jan 1987; USNM 251213, 2 σ^{a} , 2 Q, same, 10 Jan 1987, 1.5 m; USNM 251214, 5 σ^{a} , 3 Q (2 ovig.), same, west end of Commandeurs Bay, R. Lemaitre, 0.5 m, yabby pump [Jan 1987]; USNM 67423, 1 σ^{a} , Bonaire, Lac, northern lagoon, seived out of sand with *Halimeda*, ~12 m, don. P. Hummelinck, 12 Oct 1933.

BRAZIL: Natal: USNM 251241, 1 d³, 2 Q, Natal, Stanford Exped., F. Baker, 1911. Paraíba: USNM 251220, 3 Q (1 ovig.), João Pessoa, Ponta do Cabo Branco, intertidal, M.L. Christoffersen, 4 Oct 1979. Bahia: USNM 251221, 1 d³, 4 Q (3 ovig.), between Ponta Imbacuaba and Cumuruxtiba, coralline reef, intertidal, M.L. Christoffersen, J.S. Mourão, J.F. Mein, 14 Oct 1982.

DIAGNOSIS.—Projections to either side of rostrum ending in acute spine. Postocular spine present. Abdominal sternites unarmed; T subrectangular. Carpus of cheliped with 2 spines on mesiodistal margin, palm with row of spines on mesiodistal surface. Merus of P2 with proximal mesioventral spine and 1 subdistal dorsal spine; merus of P4 without ventral spines.

DESCRIPTION.—Rostrum triangular, lateral margin longer than basal width, nearly straight in lateral view, tip exceeding eyestalks; dorsal pair of strong subapical spines followed on each side by 2 well-separated spines, median dorsal area spineless; posteriorly divergent lateral ridge bearing crest of about 12–14 spines, strongest on process lateral to rostrum and decreasing almost to obsolescence posteriorly. Shoulder lateral to cervical groove usually unarmed but sometimes bearing obsolescent granule below intersection with thalassinidean line, latter continuing strongly to posterior margin. Postocular spine present.

Abdominal sternites unarmed.

T bearing moderate transverse proximal ridge confluent with low longitudinal ridge to either side.

Eyestalk stout, deepest at about midlength, concave dorsally, convex ventrally, almost horizontal in repose; prominent oval, obliquely terminal cornea narrower than diameter of stalk and longer than deep.

A1 peduncle reaching about to base of terminal article of A2 peduncle (beyond midlength of terminal article in small male), its proximal 2 articles together slightly longer than terminal article.

A2 peduncle with almost ¹/₃ its length extending beyond tip of rostrum; article 2 bearing tiny hooked subdistal ventral spine; scale moderate, oval.

Mxp3 bearing epipod.

Epistomial projection rather broad in lateral view, bearing 1 or 2 small apical projections.

Chelipeds with coxa bearing slender spine on mesiodistal margin. Ventral margin of ischium bearing l spine. Merus with row of 2-7 moderate to strong spines on ventral margin, decreasing in size distally; single subdistal dorsal spine reaching level of postocular spine. Carpus trigonal, shallow longitudinal groove laterally, moderate spine at anterior ventrolateral corner preceded by 1-5 or more spines in adult, but spines at this site variable and sometimes obsolete; mesiodorsal crest of almost uniform small spines behind prominent spine on anterior margin, partly obscured by setae in proximal part of row, and 2-4 variable spines often obscured by setae on anterodorsal margin mesial to articulation with propodus; strong spine near middle of distomesial margin, slightly smaller spine dorsal to it, and very strong spine behind distoventral corner. Chl about 2.5-2.7 times chh; spineless dorsal ridge terminating anteriorly near stout subdistal spine mesial to it; mesiodorsal row of forward trending spines, usually about 12-15 and well developed, fewer in juveniles, but occasionally increased in number by intercalation of small supernumerary spines between "normal-size" spines, entire series becoming reduced in size but increased in number to as many as 25 in some individuals, spines becoming obsolescent near anterior margin, occasionally with few scattered spiniform granules or small spines near proximal end; below this another row of smaller spines on upper mesial surface; diagonal longitudinal row or tract of spines on mesioventral surface, strongest distally; variable spine and row of small rounded teeth or marginal tubercles on margin below mesial dactylar condyle; sinuous transverse granular ridge on mesial surface near proximal margin arising on rather sharp and occasionally granular ventral keel. Fixed finger shorter than dactyl and more slender, continuing curve of lower margin of palm or slightly more downcurved, and tapering to usually slender tip (sometimes worn and rounded), 3-4 irregular strong teeth on proximal prehensile edge. Dactyl with corneous tip in mature male preceded on prehensile edge by subdistal tooth, an interval, then row of ill-defined closely crowded small teeth increasing somewhat proximally to larger tooth near base, and toothless section basally; mesial more or less concave surface bearing 2 rows of closely crowded perliform tubercles, upper row running nearly length of finger, lower row only 1/2 as long; comeous tip in female preceded by more or less straight prehensile edge, sometimes strong tooth at ²/₃ length opposing tip of fixed finger, section proximal to this bearing obscure small teeth, then large tooth near base and toothless section basally; curved and slightly twisted extensor surface bearing 2 rows of small crowded tubercles diminishing to obsolescence distally, and, between these rows in mature individuals, 1 or 2 additional short proximal rows of granules.

P2 reaching about to midlength of palm; carpus with small acute distodorsal spine and smaller acute subdistal ventral spine; merus with subdistal dorsal spine and proximal mesioventral spine, sometimes obscure or worn; coxa with strong acute proximal and smaller mesial spine, both occasionally worn. Merus of P3 with row of ventral spines and scattered ventrolateral spines or spiniform granules on proximal ¹/₂; coxa with mesial spine, broad and lateral to gonopore in female. P4 with spineless merus.

U with acute slender spine on protopod above base of mesial



FIGURE 31.—View of exposed tidal flat at low tide in Pigeon Creek, San Salvador, Bahamas, showing mounds cast up around mouths of callianassid burrows. Mounds are secondarily burrowed by *Upogebia vasquezi*. (Photo by H.H. Curran and E. Kotler, 1956.)

ramus; mesial rib of lateral ramus bearing tubercle proximally, distal margin of both rami bearing row of granules well-spaced apart.

MEASUREMENTS (in mm).— σ^{3} , acl 6.4, cl 8.8, chl 7.0, chh 2.8; σ^{3} , same, 6.0, 8.3, 4.6, 1.5; σ^{3} , same, 5.1, 7.4, 5.3, 2.3.

COLOR .- Ovigerous female (found dead after dynamite blast on tidal flat): Suffused with poppy red throughout. Anterior part of body, dorsum of carapace, and, to much lesser degree, branchial regions tinged with maize yellow, first abdominal segment same; alimentary tract maize yellow, giving abdomen a faint trace of this color, posterior 1/2 of abdominal segments II-V and all of epimeral regions red spotted; almost all of last abdominal segment same except 2 translucent white semicircular areas and 2 posterior spots with red dots; anterior central $\frac{1}{2}$ of telson more or less red spotted, posterior and more lateral parts clear, quite transparent. Uropods clear transparent, except anterior margin and midriff red spotted, but ribs translucent white, and accessory rib of outer ramus between midrib and outer margin without red spots. Chelipeds with 2 double lines of small red dots on either margin of narrow flat upper surface of propodus, outer face of carpus, about base of white upper anterior carpal spine, on upper margin of merus, and on flat dorsal triangular area at junction with carpus. Other legs semiopaque translucent white (from field notes of W.L. Schmitt, 16 Aug 1930).

Living Male: Carapace anterior to cervical groove cinereous; abdominal segments with poppy red spots in all but clear areas, but underlaid in some places by china blue, tints of this blue also on carapace; right cheliped and left chela without red spots seen on female described above; second legs with anterior part of meri red spotted; cornea of eyes black to clove brown (from field notes of W.L. Schmitt, 16 Aug 1930).

KNOWN RANGE.—Southeastern Florida and the Bahamas through the West Indies and Panama to northeastern Brazil.

REMARKS.—Upogebia vasquezi sometimes has been mistaken for U. affinis sensu lato, from which it differs in several respects. Chief among these is lack of spines on the ventral side of the rostrum and on the ventral keel of the chelae. Among the most distinguishing characters is the number of spines in the dorsal row on the chelae, which varies from 12-14 strong and forward trending to as many as 25 more or less erect small spines. Some individuals have both large and small spines in this row arrayed in varying numbers, in which cases the small spines are intercalated between the large ones. Strength of the spines does not appear to be associated with size, sex, or geography, small numerous spines being found on some large males and few coarse spines on still immature individuals. Another distinguishing character is a diagonally longitudinal row or tract of spines on the mesioventral surface of the palm. These spines vary from strong and acuminate to obsolescent, apparently bearing little or no relationship to sex or geography, and from as few as 2 in juveniles to as many as 7 in adults, grading in strength from small proximally to large distally. The 72

well-developed spine on the ventrolateral margin preceded by 1-5 or more smaller spines, but in some small individuals these spines may not be present at all.

Upogebia vasquezi first came to my attention in a collection of specimens taken from firm areas in coalesced sediment (pelloidal Ca_2CO_3 sand) cast up by a callianassid sp. around burrows in the intertidal flat of hypersaline Pigeon Creek, San Salvador (normally 42–44 ppt, tidal range about 70 cm) (Figure 30) that were sent to me for identification (H.A. Curran, Dept. Geology, Smith College, Northampton, Mass., pers. com. 15 Aug 1986). There the burrows of *U. vasquezi* almost always are inhabited by male : female pairs (examined examples of the latter often being ovigerous) and are basically Y-shape, as characteristic for *Upogebia* (see Dworschak, 1983), although the pattern is variously compounded by side branches or duplicate branches.

The disproportionate number of males and females in two large lots of specimens from Panama (USNM 251725, 124 σ^{a} : 27 Q, and 251726, 58 σ^{a} : 28 Q), among which almost all of the small individuals lack pleopods on the first abdominal segment (the male form), suggests protandry in this species.

The species appears to be widely distributed in nearshore habitats of the Caribbean region.

Upogebia incertae sedis

MATERIAL EXAMINED.—MEXICO: USNM 251409, Arrowsmith Bank E of Yucatan, 21°05'N, 86°23'W, burrows from burrow system of unknown species of *Upogebia* in coral rock (dry), 146–265 m, R/V *Pillsbury* sta 581, 10-ft otter trawl, 22 May 1967, labeled "puis va *Upogebia petalura*."

Phylogenetic Considerations

Two regions of the body provide primary bases for differentiating subgroups within the family Upogebiidae and for comparing it to other families within the Thalassinidea. These are the conformation of the anterior carapace and the posterior abdomen, which are variously modified to a burrowing mode of life. The dorsally flattened, spiny, setose surface of the anterior carapace, so characteristic of the upogebiids in a multitude of variations, seems to be adapted for anchoring the animal within its burrow and perhaps serves as a means of filtration or channelization of respiratory water currents, especially among species that burrow within sediment. The caudal complex of abdominal segment VI, telson, and uropods takes the general form of a tail fan characteristic of many long-tailed decapod crustaceans that used it for retrograde swimming by cupped contraction of the flexible abdomen; but the tail fan would seem rarely to function this way in burrowers, and it shows specializations in species that are known to be borers in stony coral or that live in the canals of sponges.

Features of these regions of the body, as enumerated in the following list, have long been used to distinguish species, subgenera, and genera, but character bases for the latter have become compromised as alleged gaps between them have been closed by the growing number of recognized species.

1. Rostrum triangular in dorsal view (primitive) or strap-like in shape (advanced). Almost all species of Upogebiidae have a rostrum that is basically triangular in dorsal outline. Rarely is the rostrum nearly parallel sided, hence strap-like in outline, perhaps being thus narrowed to provide room for the eyes. The latter condition is known in only one small species among those in the western hemisphere.

2. Dorsal spines and setae on rostrum confluent with flattened field of spines and setae on gastric region (advanced). This is a common feature of the family, but some species lack spines and/or setae on the rostrum and gastric region, and related thalassinideans lack this combination feature (primitive).

3. Lateral groove flanking armed gastric field, present in majority of upogebiids, that itself is flanked laterally by a crest armed dorsally with spines and ending in an anterior projection flanking the base of the rostrum (advanced). The lateral groove perhaps acts as a filtering channel for respiratory water currents. Some forms living commensally in sponges or corals lack this feature or exhibit it in reduced form.

4. The rostrum usually bears no ventral spines, but in some species, such as, *Upogebia affinis*, there are from 0 to 8 ventral spines, with spinelessness or few weak spines being the predominant state. However, a few species have well-developed ventral rostral spines whose shape and arrangement are almost diagnostic. This is a multistate character.

5. The cervical groove is emphasized by a shoulder that parallels it lateroventrally. This shoulder is usually spineless, although there are often tubercles just below its juncture with the thalassinidean line, and in a few species the shoulder bears a row of spines.

6. The anterolateral margin bears from 0 to 1 to several spines. The genus *Calliadne*, considered a subgenus by some authors, was characterized as having the spineless condition. One spine in a postorbital position is by far the commonest condition, and multiple spines are found in a few species. Both 5 and 6 are multistate characters that often track together.

7. The linea thalassinica is variously developed in the Thalassinidea. It seems to be universally present in the Upogebiidae and Callianassidae, which are specialized burrowing forms, but it is not present in some other families of the group. Absence of the linea thalassinica may be the primitive condition, but there is no certainty about this.

8. Appendix masculina present on the male second pleopod (primitive) or absent. Loss of this appendix seems to be universal in the Upogebiidae, but it is present in Axiidae and Callianassidae.

9. Tail fan normal (primitive) or opercular (advanced). This structure in most upogebiids consists of a telson and uropods

articulated with abdominal segment VI to form a caudal swimming fan, but in some coral boring species this complex is modified into an operculum with an eroded and rugose surface that serves as a plug that can be inserted into the burrow opening.

10. The normal tail fan is arranged around a telson that is (a) subtriangular, tapering to a broadly truncate tip, (b) roughly rectangular, having a posterior margin slightly narrower than the anterior margin and straight or barely biconvex, or (c) noticeably concave in posterior margin. The latter condition has been used as one of the defining characters of the genus *Gebiacantha*.

11. The normal tail fan has uropodal lateral rami that are equal in length to the mesial rami and the telson (primitive), but in some species the lateral rami are noticeably longer than the mesial rami or telson (advanced).

12. Abdominal segment VI is adapted in all Upogebiidae to interlock with the protopodite of the extended uropod. The

usual state of this lateral margin is sinuous (primitive), but in some species the anterolateral sinuosity is drawn into a hooked process, and in still others the margin is drawn into a lateral process (advanced).

13. There is sketchy evidence that species commensal in sponges have few or moderate numbers of large eggs, hence abbreviated larval development, whereas the usual condition among noncommensal burrowers is many small eggs (primitive), with extended larval development in plankton. Data are insufficient to categorize species in these putative groups at present.

14. *Calliadne* originally was described as having fingers of the chelipeds equal in length. They are, but many species having fingers of equal length do not fit other presumed descriptors for this genus. Rather, these equal fingers may have distinctive tooth patterns that correlate with large egg size. Data are insufficient at present to categorize species having these features.

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