Caño Rey, 12 juv (about 6.0), 18 Aug 1972, LGA. *Provincia de Darién*—(20) †USNM, trib to Río Chucunaque, Yaviza, 4♂ (13.5-21.5), 3♀ (11.1-18.1), 16 Feb 1924, J.L. Baer. *Golfo de Chiriquí*—(21) †LGA, Isla Secas, 9 juv (less than 5.0), Feb 1974, P. Glynn. *Provincia de Panamá*—(22) †USNM, Cerro Azul area, 30♂ (9.6-26.4), 17♀ (7.1-19.4), 2 ovig ♀ (19.0, 19.4), 29 Jan 1971, LGA. (23) †LGA, first stream on Cartí Rd, 11 km, 2♂ (13.3, 13.9), 15 Jan 1975, Kramer. *Archipiélago de las Perlas*—(24) *LGA, Isla Pedro González (Abele and Blum, 1977:240), 2♀ (13.3, 13.4), 13 Jun 1973, LGA; LGA, 3♂ (14.2, 15.9, 17.7), 26 Mar 1976, Kramer. (25) Isla San José (Abele and Blum, 1977:240), 2♂ (5.7, 9.5), 1♀ (4.9), 4 juv, 20 May 1973, LGA. *Provincia de San Blas*—(26) †MCZ, San Blas, 1♂ (15.6), 6 Jun 1929. (27) †LGA, 20.4 km N of El Llano on Cartí Rd, 2♂ (7.2, 12.3), 10 Mar 1973, R.L. Dressler, McPhail. *Provincia de Veraguas*—(28) †USNM, creek 8.5 km W of Soná on Remedios Rd, 3♂ (10.3-17.5), 29 Oct 1961, HL. (29) †USNM, Río Martín Grande 6.8 km S of Santiago, 3♀ (11.8-16.0), 14 Jun 1962, HL. (30) †USNM, trib to Río Tabasará 3.4 km W of El María Creek on Soná-Remedios Rd, 1♂ (25.0), 3♀ (9.4-16.0), 1 ovig ♀ (15.5), 29 Oct 1961, HL. (31) †USNM, Río Veraguas, 11.9 km W of El María, 1♂ (22.6), 11 Nov 1961, HL. (32) †LGA, Río Las Guías at Rd from Calobre, 1♂ (about 6.0), 21 Feb 1973, LGA, MHR. *Province unknown*—(33) †LGA, Cerro Jefe, 1♂ (22.8), 1969, RLD. (34) †LGA, Cerro Jefe at 635 m, 2 ovig ♀ (18.0, 19.2), 29 Apr 1973, LGA, RLD.

ERRONEOUS RECORDS.—(1) New Caledonia (A. Milne-Edwards, 1864:148) for *A. robusta.* (2) Oceania (Oliveira, 1945:179) for *A. occidentalis.*

VARIATIONS.—Among the most conspicuous variations in *Atya innocous* is the form assumed by the rostrum (Figure 29). In individuals with carapace lengths of five to seven mm, the margins are strongly tapering, sometimes with hardly a trace of the anlagen of the paired subangular bends that mark the base of the acumen in larger individuals and that become more prominent following subsequent molts. In most individuals with carapace lengths of 20 mm or more, the base of the acumen is marked by angles (with rounded apices) of 75 to almost 90 degrees. One to three small preapical spines may or may not be present on the ventral keel. There is some variation in the height of the dorsal keel, but it is never so concave along the median part of its length as to dip below the level of the lateral carinae. The length of the acumen is also variable, and although there is no consistent correlation between its length and that of the carapace, generally the smaller individuals have relatively longer ones, and the shortest are found in the larger specimens.

The pterygostomian angle, although always acute, may or may not be somewhat produced. The pile of setae on the carapace is best developed in animals that have recently molted. Even in them some magnification is essential to render them visible, and the exoskeleton is so smooth that one has difficulty in holding a living specimen. The difficulty no doubt increases with time following a molt, for in many of the shrimp much of the carapace and abdomen appear to be devoid of setae.

The height of the body, particularly in the area

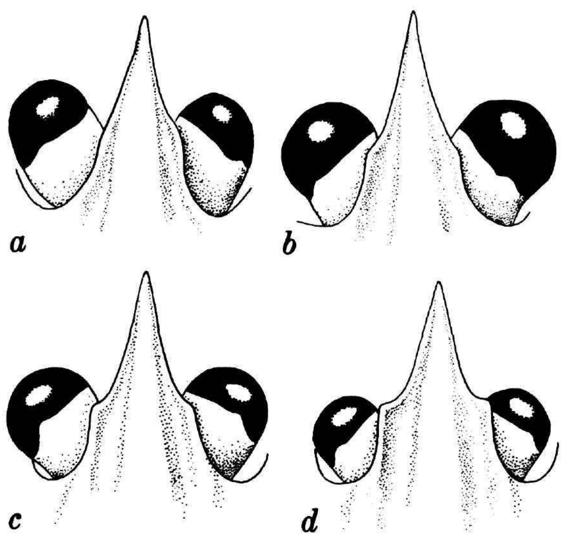

FIGURE 29.—*Atya innocous*, variations in rostrum and eyes with increase in size of animal (scaled to approx. same size; numbers in parentheses = carapace length in mm): *a*, male (7.8); *b*, male (9.9); *c*, female (15.1); *d*, male (24.7).

of the first and second abdominal segments, is quite variable, and in most of the material from the Pacific watershed it is proportionately higher than it is in specimens from the streams draining into the Gulf of Mexico and Caribbean, but among specimens from the latter drainage basins there are those that cannot be distinguished from forms frequenting the Pacific versant. The absence of denticles on the ventral margin of the third through fifth abdominal pleura will often serve to distinguish specimens from the latter basin, but frequently individuals from streams flowing into the Gulf or Caribbean lack such denticles. In a series of specimens from Mannet's Gutter, a tributary of the Layou River on Dominica, denticles are present on the ventral margin of the pleura of the third through fifth abdominal segments in most. In others, they are asymmetrically present on the fourth only, present on the fourth and fifth, a single one on each of the fifth, and occasionally absent from all of them.

The proportions of the distal four podomeres of the third pereiopod are highly variable, and except for the observation that generally the propodus in larger males is broader than in most other individuals, no generalizations relative to their structure seem possible to us. Most differences appear to be individual ones that oftentimes are not symmetrical. We have given special consideration to the ornamentation of the flexor surface of the propodus and dactyl, and some of the variations noted are depicted in Figures 22*i*, 23*g*, 30. To be sure, the development of the setae flanking (sometimes almost surrounding) the spines are best developed in individuals that have recently molted, and in some specimens that were preserved in late intermolt stages the setae are indeed few, presumably lost through abrasion. The degree of sclerotization of the spines increases, within limits, following a molt, but the size and shape of the spines seem not to be correlated with either growth or stages of the molt cycle, and certainly not with different parts of the range of the species.

The dactyl of the fifth pereiopod in some populations is provided with a pectinate comb (Figure 23*f*), but in other individuals from the same locality the denticles may be aligned in two series, or they may be more irregularly dispersed (Figure 23*k*).

Many other variations have been noted, but none of them has enabled us to distinguish all members of any population from at least some individuals of populations occurring elsewhere. A comparison of the illustrations presented herein will provide an appreciation of some of the differences and the many similarities existing in populations from several parts of the range of this shrimp.

As pointed out above, populations of this shrimp occurring in streams emptying into the Pacific usually have bodies that are, or seem to be, more highly vaulted than those in the Caribbean-Gulf Basin. They also possess more spindly legs than we thought at first to be typical of the more eastern members of the species. Later we found that these were the only two traits on which we were relying to distinguish *A. tenella* (Pacific) from *A. innocous* (Caribbean–Gulf–western Atlantic), and as more specimens were compared we discovered spindly legged individuals with highly vaulted carapaces among those insular populations in the Antilles, thus indistinguishable from specimens from the Pacific versant. To be sure, we have encountered none from the latter area that have as robust pereiopods as exist in many, if not most Antillean representatives of the species, but to recognize *A. tenella* as a distinct taxon under these circumstances seems to us to be indefensible.

ECOLOGICAL NOTES.—The most complete accounts of the habitat and habits of this shrimp are those of Chace and Hobbs (1969) and Fryer (1977). The former began their discussion of its ecological distribution (p. 60) with the statement that

> *Atya innocous* is probably the least ecologically and geographically restricted shrimp on the Island of Dominica.... It seems to be equally at home in the cascading reaches of mountain rivulets [at altitudes of approximately 800 meters], in quiet upland pools, and in low-lying sluggish brooks. In an upland pool ... some 20 or 30 individuals were

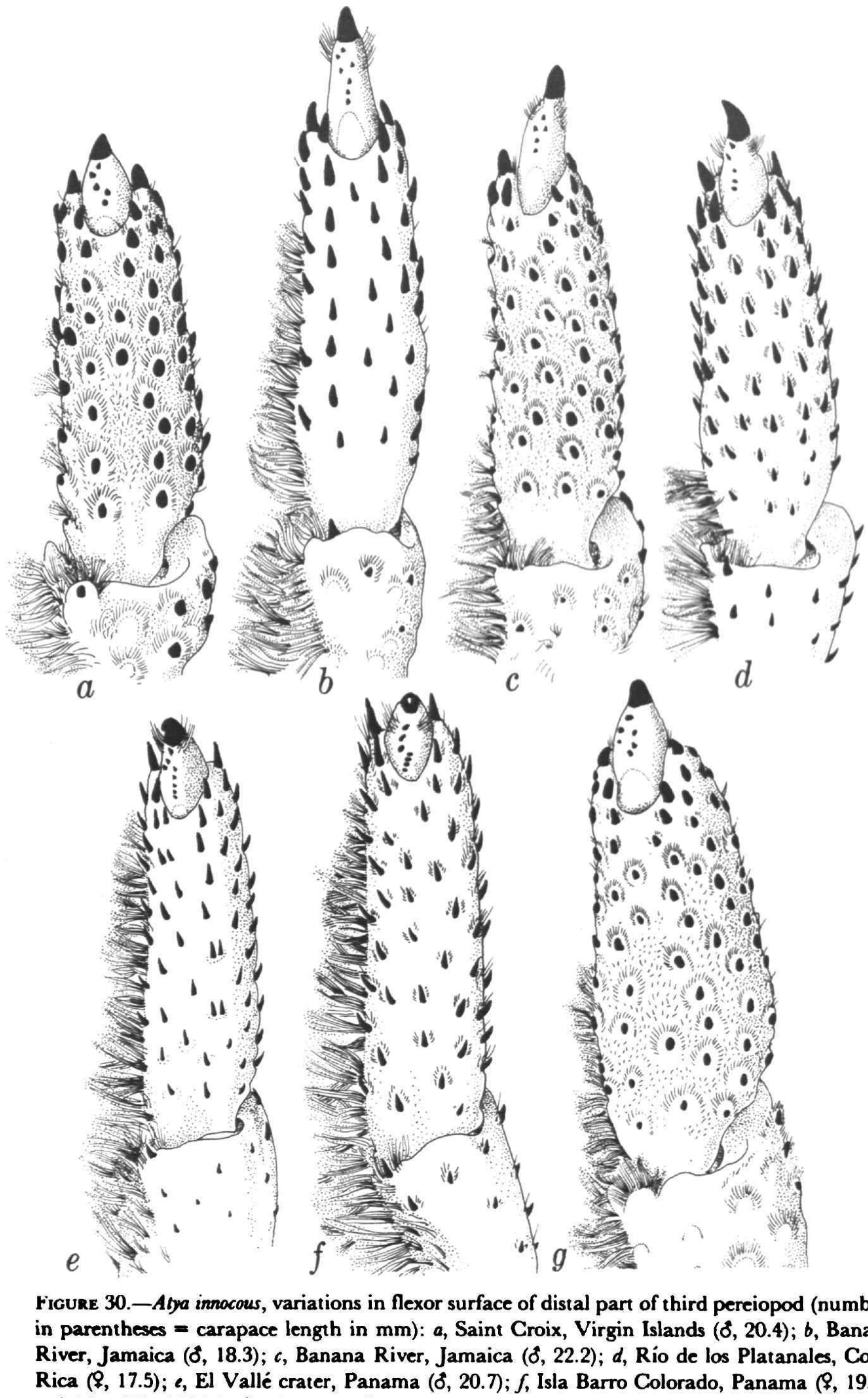

FIGURE 30.—*Atya innocous*, variations in flexor surface of distal part of third pereiopod (numbers in parentheses = carapace length in mm): *a*, Saint Croix, Virgin Islands (♂, 20.4); *b*, Banana River, Jamaica (♂, 18.3); *c*, Banana River, Jamaica (♂, 22.2); *d*, Río de los Platanales, Costa Rica (♀, 17.5); *e*, El Vallé crater, Panama (♂, 20.7); *f*, Isla Barro Colorado, Panama (♀, 19.4); *g*, 3.4 km W of El María, Panama (♂, 25.0).

observed actively crawling over the bottom at about 10:00 A.M.

The shrimp ventured into full sunlight but quickly returned to the shaded area of the pool. Fryer (1977:69) wrote

that its tolerance exceeds the range of natural conditions on Dominican streams was indicated by its occurrence in a pond whose bottom was composed largely of soft ooze. When this pond, which had been constructed on a stream, was drained, hundreds of individuals were collected for human consumption.

The following quotation from Chace and Hobbs (1969:43–45) provides some insight into its niche in a small community occupying a pool on Mannet's Gutter, Clarke Hall Estate, Dominica.

A number of hours were spent in observing the decapod fauna of a small pool, approximately 4 feet wide, 10 feet long, and with a maximum depth of 2 feet.... Here, at an altitude of some 350 feet, the stream has cut a deep V-shaped valley, and boulders from the eroded walls have fallen into the stream bed, deflecting the current or obstructing the flow so that pools are interspersed between cascades and riffle areas. Except after heavy rains the water is clear, flowing over a rocky, sandy bottom overlain in the pools with a shallow layer of silt. Many of the larger trees along the 45 to 80 degree slopes have been cut and bananas have been planted between the felled trunks; as a result, during a short period in the day, the time depending upon the orientation of the adjacent slopes, full sunlight reaches the stream bed. Marginal shrubs do inhibit direct light from reaching portions of the stream. The pool referred to here received sunlight for about two hours before noon in mid-March.

The macroscopic fauna of the pool consisted of what the observer believed to be a single species of gobioid fish scarcely exceeding 40 mm in length; two atyid shrimps, *Atya innocous* and *Xiphocaris elongata*; two palaemonid shrimps, *Macrobrachium carcinus* and *M. crenulatum*; and a crab, *Guinotia dentata*. No other animals were observed. There were 1 crab, 2 *M. carcinus*, 12–15 *A. innocous*, about the same number of *M. crenulatum*, 20–25 *Xiphocaris elongata*, and approximately the same number of fish.

When the pool was first approached by observers, the fish and *X. elongata* were "resting" on the stones at the sides and bottom of the pool, only swimming occasionally for a centimeter or so to take another position on a rock. The crab was not in sight, and only the chelae of the smaller of the two *M. carcinus* could be seen protruding from beneath one of the larger rocks. In contrast, the individuals of *A. innocous* and the smaller *M. crenulatum* were scurrying back and forth across the bottom of the pool, disappearing beneath a stone and reappearing shortly thereafter. *Atya innocous* was by far the most active. Of the three or four large individuals of *M. crenulatum*, two were in view but were not moving about, and the others were concealed somewhere among the stones. Except for the almost incessant wanderings of *A. innocous* and the smaller *M. crenulatum*, there was little activity.

When an earthworm, suspended on a string, was gently lowered into the water, however, a chain reaction was initiated that set the entire population of the pool in motion. The smaller individuals of *M. crenulatum* were the first to show an awareness of the presence of the worm. Although apparently they did not see it, the rate of their random walking increased tremendously, perhaps best described as "frantic," causing them to collide with one another and with the other inhabitants; *A. innocous* joined them, the larger *M. crenulatum* began moving back and forth, and *X. elongata* left the stones on which they had been comparatively still and swam about the pool. The frenzied motion disturbed the fish and they, too, began to shift their positions on the rocks. When one of the smaller *M. crenulatum* finally located the position of the worm, the shrimp left the bottom, swam to the worm, grasped it with its chelae, and attempted to swim away with the worm. When this attempt failed, the shrimp used its abdomen to give a rapid series of strong tugs. This motion apparently attracted the attention of almost all of the shrimps in the pool. One of the larger *M. crenulatum* swam toward the worm as the smaller ones backed away, and when it had stripped the worm from the string, the shrimp sank to the bottom of the pool and scurried for the nearest cover. By this time, both individuals of *M. carcinus* had moved into the open water of the pool, and as the larger one moved about, all of the other shrimps retreated from its path, remaining beyond reach of the large chelipeds. While the commotion was going on, the crab slowly crawled from under the largest rock at the side of the pool, and all of the occupants, including the previously dominant *M. carcinus* gave wide clearance to the newcomer. A short time after the shrimp with the worm had found cover and presumably had devoured it, the crab crawled back into its lair, the large *M. carcinus* moved into crevices, and the remainder of the population returned to its original state. A second worm introduced into the pool resulted in a similar turmoil, but this worm was successfully acquired by one of the young *M. crenulatum*, which quickly swam to the shallow down-stream end of the pool and crawled beneath a stone.

According to Fryer (1977:69), *Atya innocous* is basically an "ambulatory species," rarely swimming unless disturbed, and its ability to exploit the wide range of habitats mentioned above "can be attributed to a considerable extent to its ability to collect food by two very different methods": (1) filtering and (2) sweeping and scraping, utilizing the first two pairs of pereiopods. It also tolerates a wide range of temperature. It has been found in water at 21°C, and "in aquaria it has remained healthy in spite of falls in temperature of 14°C . . . , individuals from running water survived for over two weeks in confined conditions in which temperatures rose to at least 32°C, withstood a trans-Atlantic air journey, and then flourished in aquaria."

Populations in pools were found by Fryer to be active both at night and during the day, but their nocturnal activity is greater. He observed: "By night many feeding animals frequented the walls of the pool which were almost deserted by day" (p. 70). Details of grooming, ambulation, feeding, and the functional morphology of the foregut are also described by Fryer (pp. 94-97, 111-118). The food appears to consist largely of "particulate detritus" derived from vegetation overhanging or adjacent to the streams, but filamentous algae firmly attached to rocks were also successfully removed and presumed to have been eaten (p. 96).

At night, populations in a stream on El Yunque, Luquillo National Forest, Puerto Rico (altitude 610 m) were observed by one of us (CWH) to arrange themselves in rows facing upstream in shallow riffle areas. It is assumed that this behavior facilitates the capture of detritus and planktonic organisms. Chemical and physical data recorded for this stream in June 1962 (Hart, 1964:332) included a pH of 7.2; total hardness, 34.2 ppm; SO_4, 0.4 ppm; Cl, 10.0 ppm; and a temperature of 24.8° C.

Life History Notes.—Ovigerous females having carapace lengths of 7.9 to 24.9 mm, collected during every month except September and November, are present among the specimens examined by us. Bonnelly de Calventi (1974b) found an ovigerous female in Cañada Madrigal, Dominican Republic, in February. Hunte (1979b), basing his study on larvae reared in the laboratory, found that they thrive best in a salinity of 30‰. The eggs hatched, most frequently at night, into larvae 1.8 to 1.9 mm in length bearing the typical series of crustacean appendages from the antennules through the third maxillipeds. These larvae did not feed and were present in his containers up to six days. The second larval stage, age three to eight days, was 1.85 to 2.05 mm in length. The third larval stage, age seven to 13 days, attained lengths of 2.0 to 2.15 mm. The fourth larval stage, age 12 to 17 days, exhibited lengths of 2.4 to 2.7 mm, and the endopod of the first pereiopod had become 5-segmented. Following the fourth stage, "morphological changes accompanying moults were less marked," but descriptions and illustrations of 12 stages are provided, the last of which was reached at an age of 76 to 119 days at lengths of 10.05 to 11.75 mm. Metamorphosis into juveniles followed.

Fryer (1977:72) reported: "In aquaria adults readily mated and produced fertile eggs from which larvae emerged, but never survived. Even experienced prawn-rearers at Conway failed to keep these for more than 10 days." Fryer suggested that unsuitable food or adequate space might have been responsible for their demise. In view of Hunte's success in rearing larvae, perhaps the failure was due to the necessity for them to undergo their larval development in saline water.

One of the specimens taken to England by Fryer (1977:72) "lived for about 6 years and 9 months in an aquarium and had not achieved its maximum size at the time of death. Several others lived for 3 or 4 years."

Abele and Blum (1977:245) reported two ovigerous females from the Perlas Archipelago with total lengths of 45.1 and 45.3 mm. They were carrying 2100 and 3650 eggs (0.6 to 0.7 mm in length).

Common Names.—We are aware of no vernacular names that apply only to this shrimp, but at least some of those listed for *Atya scabra* are not specific and are used to designate either or both species. See the common names of *A. scabra* below.

The FAO names cited by Holthuis (1980:69) for this species are Basket shrimp (English), Saltarelle panier (French), Camarón cestillo (Spanish).

Atya intermedia Bouvier

Figures 1*f*, 9, 10, 12*d*, 31, 32

Atya (sp. nov.?).—Bouvier, 1889:82.

Atya intermedia Bouvier, 1904:137, 138 [type-locality: "Afrique occidentale: île Saint-Thomas"; types: not extant]; 1905:110, 112, 119, 120, fig. 23; 1906:493; 1925:292, 308–313, 322, 323, 356, figs. 690–695.—Holthuis, 1951:24; 1966:235–237, fig. 5a–d.—Monod, 1967:110, 119, 135, pl. IX: figs. 18–24.—Lemasson, 1973:68.

REVIEW OF LITERATURE.—Bouvier (1889), in his study of the nervous system of decapod crustaceans, stated that

> j'ai eu l'occasion d'observer un certain nombre d'*Atya* (sp. nov.?) grâce à l'obligeance d'un jeune savant portugais, M. Nobre, qui avait reçu du Maroc un certain nombre de ces animaux. Ce Crustacé est une grande crevette africaine, et il ne diffère des Palémons asistiques étudiés par Milne-Edwards que par des caractères tout á fait secondaires.

As Professor Holthuis has pointed out to us, evidently Bouvier made two errors: (1) in stating that the animals had been obtained in Morocco, and (2) in using the term "Palémons" instead of Atyoidées to designate the shrimp mentioned by A. Milne-Edwards (1864:145–152). Holthuis (in letter) noted further that inasmuch as (1) the only *Atya* received by the Paris Museum from Nobre are the type specimens of *A. intermedia* (see Bouvier, 1904:137, 138), (2) these specimens were large, (3) A. Milne-Edwards did not publish information on Asiatic palaemonids but did on Asiatic atyids, and (4) neither large atyids nor large palaemonids occur in Morocco, there is good reason to believe that the "*Atya* (sp. nov.?)" were the types of *Atya intermedia*. (Unfortunately, these specimens could not be located when one of us (CWH) visited the Muséum National d'Histoire Naturelle, Paris.) The original description of this shrimp was prepared from four specimens, and Bouvier characterized the species as possessing a dorsal carina that reaches the tip of the rostrum but with a complete atrophy of the ventral rostral carina, and by the rounded prominences (very weakly squamiform and sparingly corneous) on the meropodites of the (presumably third through fifth) pereiopods. He stated further that the rostrum is large and little lengthened anterior to the lateral notches, which are strongly obtuse, and that its legs are much slenderer than those of any other large forms of the genus. Bouvier (1925) included this shrimp in his key to the then known species assigned to the genus, presented illustrations of the rostrum and antennal spine, and pointed out the same features included in his original description; he also included measurements of the legs, comparing them with those of members of *A. robusta* (= *Atya innocous*), *A. scabra*, and *A. africana*.

In 1906, Bouvier reported that among a small collection from the same island were three large and several small specimens of *A. intermedia*, the smallest of which are about the size of the "Caridenes" and have almost triangular rostra. The account of the species in Bouvier's monograph (1925) is somewhat expanded, and more information is given concerning the types, which were males ranging in carapace length from 62 to 82 mm. Especially emphasized were the variations in the presence or absence of prominent articulated spines and of the ornamentation of the dactyl on the ambulatory legs. He also added a more precise locality, the Ouro River, for the species on São Tomé and presented several new illustrations. Holthuis (1951) added no new information but in 1966 described specimens from an effluent of Crater Lake on Annobón, comparing them with *A. sulcatipes*. He referred to Bouvier's comparison of *A. intermedia* with *A. africana*, agreeing that the two species are distinct, and further noted the relationship to *A. innocous*. Illustrations of the cephalic region and observations of the color of the Annobón specimens were also included. Monod (1967) added no new data. Lemasson (1973), considering native African shrimps suitable for cultivation, referred to this insular species and stated that it attains a length of eight centimeters.

PUBLISHED ILLUSTRATIONS.—The earliest illustrations of the species are those of Bouvier (1905) consisting of a dorsal view of the rostrum and a lateral view of the rostrum and antennal spine. The most complete series is that included in his monograph (1925): a dorsal view of the rostrum, a lateral view of the cephalic region, a dorsal view of the telson, either cephalic or caudal views of the first and second pleopods of the male, and illustrations of the dactyls of the third pereiopods of two specimens. The figures presented by Holthuis (1966) are dorsal and lateral views of the cephalic region of an adult and of a juvenile. Monod's (1967) illustrations were taken from Bouvier (1925).

Diagnosis.—Cephalic region of carapace not conspicuously sculptured; spines limited to antennal, pterygostomian, and occasional small ventral rostral. Rostrum with margins rather suddenly contracted forming angle anterior to orbit, angle never produced; dorsal surface without median row of strong spines. Ventral margin of second through fifth abdominal pleura without rows of corneous spinules, and caudoventral angle of fourth and fifth pleura acute to subacute but not produced in spines. Sternum of fifth abdominal segment with small median tubercle, sternum of sixth about 1.2 times as broad as long. Preanal carina with caudoventrally directed spine and smaller spine (or at least bulge) between spine and base of carina, major spine overreaching basal part of sclerite bearing it. Telson about 1.6 times as long as wide with approximately 6 spines in each of 2 dorsal rows. Antennular peduncle with dorsal surface of proximal article devoid of sclerotized spinules proximal to transverse distal row; penultimate article 1.3 to 1.5 times as long as wide, and dorsal surface with many small scattered corneous spinules. Coxae of third and fourth pereiopods lacking anterolateral spines. Third pereiopod with merus rounded ventrally, 3.7 to 4.0 times as long as high, ventromesial surface bowed, never parallel to that of corresponding podomere of other member of pair, and lateral surface bearing corneous tubercles, most of those on merus and carpus with scalelike extremities, and most arranged in linear series; propodus almost 3 times as long as wide, flexor surface with corneous spiniform tubercles distributed in sublinear series, spines not contiguous; dactyl not fused with propodus and bearing 2 linear or sublinear series of denticles on flexor surface.

Male (Annobón Island).—Rostrum (Figure 31*a,d*) with margins weakly concave and slightly tapering to subangular bend at base of acumen, latter almost reaching articulation between proximal and penultimate podomeres of antennule; dorsal median carina, lying dorsal to lateral carinae except anteriorly, rather gently curved (not concave) almost to apex of rostrum where suddenly bent ventrally, disappearing just before reaching apex of acumen; ventral carina with 2 subapical minute teeth; ocellar beak with anterior margin directed anterodorsally, forming acute angle with dorsal margin and reaching level of distal margin of eyes, thus falling far short of tip of stylocerite; dorsal margin abutting longitudinal ventral groove posterior to ventral carina of rostrum. Antennal spine well developed; pterygostomian angle rather weakly produced, not spiniform; no spines present between antennal and pterygostomian spines. Surface of carapace with many small setiferous punctations, but devoid of ridges and spines other than those just mentioned; all setae on carapace small and inconspicuous.

Pleura of first 2 abdominal segments (Figure 31*f*) rounded posteroventrally; third subangular, and fourth and fifth distinctly angular, latter 2 although acute not produced. All pleura lacking corneous spinules and conspicuous fringe of setae on ventral margins. Fourth abdominal tergum about 1.2 times as long as fifth which subequal in length to sixth and to telson. Sternum of fifth abdominal segment bearing very small compressed tubercle at midlength (Figure 1*f*). Sternum of sixth segment about 0.8 as long as wide. Free part of preanal carina (Figure 31*e*) projecting far beyond basal part of sclerite, underlying smaller accessory spine. Telson (Figure 31*j*) about 1.6 times as long as wide, its dorsal surface bearing paired concave rows of 6 corneous denticles; posteromedian tubercle not overhanging caudal margin of telson.

Proximal podomere of antennule (Figure 31*b*) with stylocerite reaching base of distal fifth of segment; dorsal surface with linear cluster of setae but lacking corneous spinules; distal margin bearing row of 11 corneous spinules; penultimate segment of peduncle about 1.4 times as long as wide and bearing 13 (right) or 14 (left) spinules on dorsal surface and 16 on distal margin; ultimate podomere with row of 11 spinules at base of

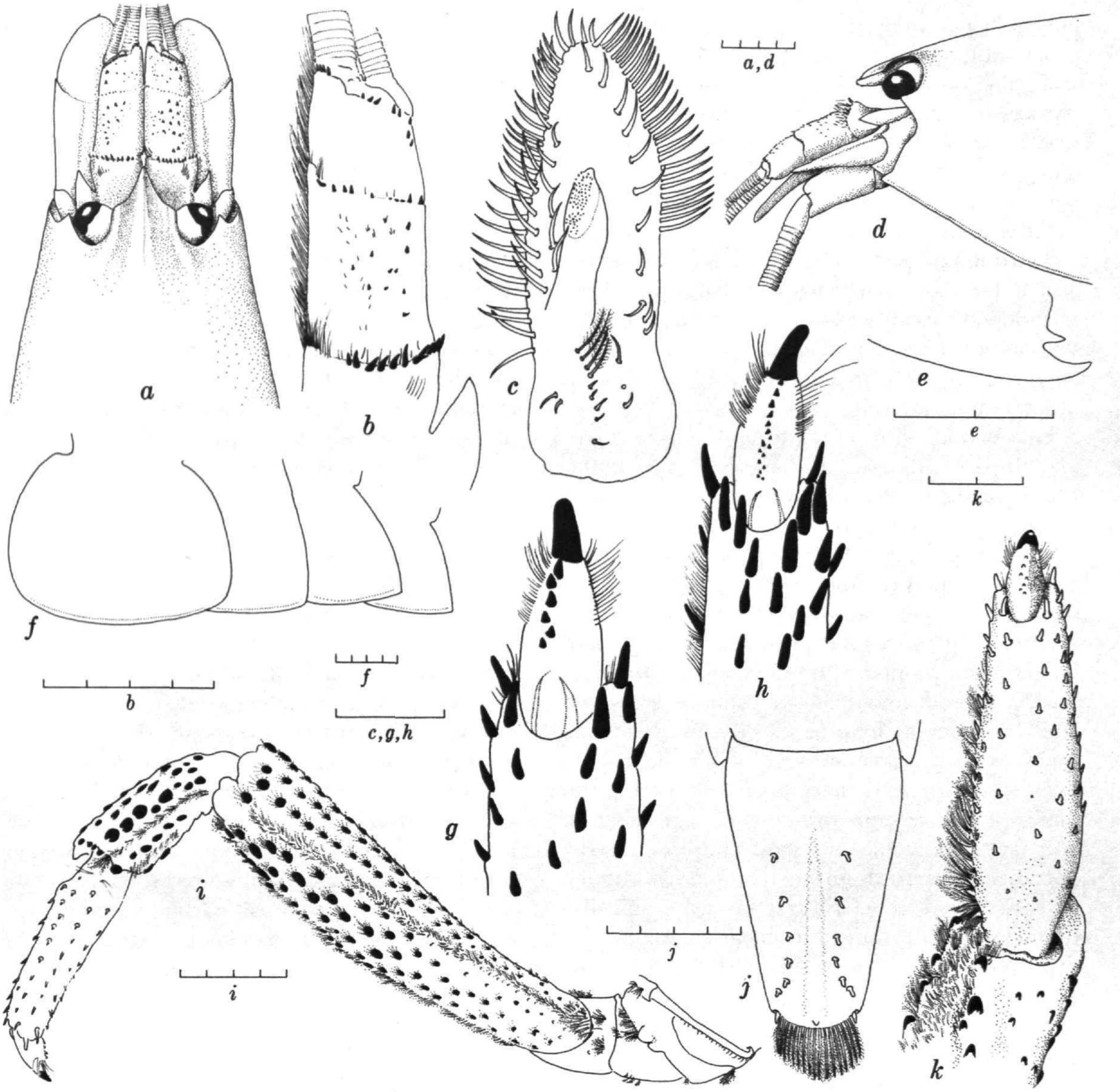

FIGURE 31.—*Atya intermedia* (all from male from Annobón): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view of cephalic region; *e*, lateral view of preanal carina; *f*, lateral view of second through fifth abdominal pleura; *g,h*, flexor surface of distal part of fourth and fifth pereiopods, respectively; *i*, lateral view of third pereipod; *j*, dorsal view of telson; *k*, flexor surface of distal part of third pereiopod. (Scales marked in 1 mm increments.)

lateral flagellum, 4 at base of mesial one, and 2 proximal to lateral row. Antenna with ventrolateral spine on basis falling a little short of tip of stylocerite; lateral spine on scaphocerite strong, reaching end of proximal third of ultimate podomere of antennular peduncle; lamella far overreaching latter; flagellum extending to end of anterior fourth of telson.

Third maxilliped overreaching antennular peduncle by about half length of distal podomere of endopod; tip of exopod reaching base of distal sixth of penultimate podomere of endopod; latter only slightly (less than 1.1) times as long as ultimate podomere.

First pereiopod reaching level of end of proximal third of ultimate podomere of antennular peduncle, second reaching base of distal third of fingers of first pereiopod; terminal brush of setae of both appendages lacking scraping denticles. Third pereiopod (Figure 31*i,k*) without spines on merus and carpus, and when extended anteriorly, overreaching antennular peduncle by dactyl and four-fifths of propodus; merus with ventromesial margin bowed, about 3.7 times as long as high and 2.4 times as long as carpus; propodus 3.5 times as long as wide, subequal in length to carpus; distoventral margin of coxa entire and mesial caudoventral prominence rudimentary and lacking conspicuous setal clusters. Lateral, dorsal, and ventral surfaces of merus studded with many small sclerotized (at least apically) tubercles, most arranged in linear series; clusters of plumose setae flanking tubercles, most conspicuous tufts forming oblique row on lateral surface; mesial extremity of podomere very weakly produced at level of mesial articular condyle of carpus. Carpus strongly tuberculate except on flexor surface where tubercles absent; tufts of long plumose setae present on flexor surface of podomere. Propodus with tubercles on extensor, mesial, and lateral surfaces arranged mostly in linear series, rows less well defined on flexor surface. Dactyl movable, its flexor surface with 2 rows of denticles, proximal one of 4 more mesially situated than lateral one of 3.

Fourth pereiopod with dactyl reaching base of distal third of carpus of third pereiopod; length of merus 1.9 times length of carpus, and latter almost as long as propodus. Fifth pereiopod reaching end of proximal fifth of propodus of fourth pereiopod; merus 1.4 times as long as carpus, latter about 0.7 as long as propodus.

Ornamentation of merus, carpus, and propodus of fourth pereiopod similar to that of third except for addition of ventrolateral spine on merus at base of distal fourth and ventral one at midlength, and 1 ventrolateral and 2 distolateral ones on carpus. Ornamentation of fifth pereiopod like that of fourth but with 2 ventral spines on merus proximal to ventrolateral spine, and 3 distolateral spines on carpus.

Diaresis of lateral ramus of uropod flanked proximally by row of 21 (right) or 22 (left) articulated, corneous denticles and slightly larger fixed spine at lateral end of row.

COLOR NOTES.—The only observations on color are those of Holthuis (1966:237): "The whole body is of a more even dark greenish grey color; it is not marbled as in *A. sulcatipes*. There is a light median spot on the fourth and sixth abdominal somites. The latter does not show the dark transverse band so conspicuous in *A. sulcatipes*."

SIZE.—The largest specimen reported was that recorded by Holthuis (1966:235); it had a total length of 83 mm, and presumably its carapace length was the maximum he recorded, 32.0 mm. The largest female measured by us had a carapace length of 19.1 mm. The smallest and largest ovigerous females had corresponding lengths of 7.9 and 15.4 mm.

DISTRIBUTION AND SPECIMENS EXAMINED.—The range of *Atya intermedia* is not known to extend beyond two islands in Gulf of Guinea: Annobón (= Pagalu) and São Tomé (Figure 32).

Records for the known localities are listed below. Collections that we have examined are marked with an asterisk. Numbers following the specimens listed are measurements, in mm, of the carapace length or, if followed by "t.l.," total length. Some listings lack dates and/or collectors; if so, these could not be determined.

ANNOBÓN: *RMNH, Annobón (Holthuis, 1966:

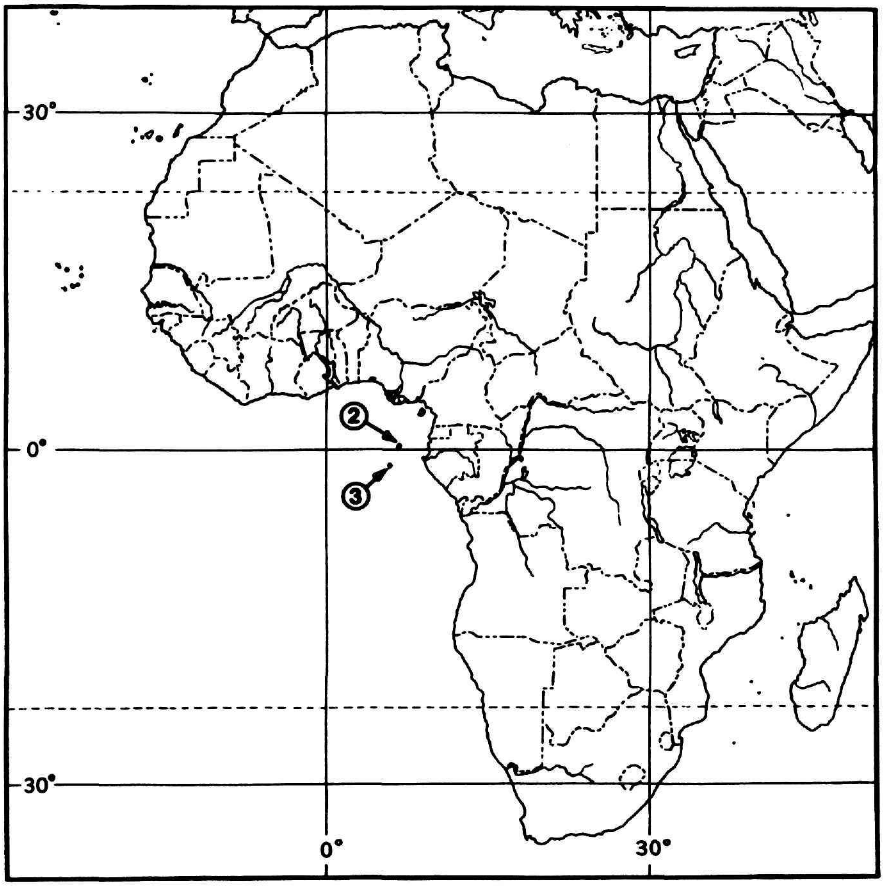

FIGURE 32.—Distribution of *Atya intermedia* (circled numerals = number of localities).

235) 1♂ (14.3) 1959, R. Zariquiey Alvarez. *BM, Annobón, 4♂ (11.2–16.0), 15♀ and juv (7.3–19.1), Jul–Aug 1959, Cambridge University President's Expedition. (1)*RMNH, Crater Lake, Annobón, Pillsbury sta 278 (Holthuis, 1966:235), 8♂ (8.5–26.7), 9♀ (8.0–9.4), 4 ovig ♀ (7.9–15.4), 87 juv (3.0–8.7); *USNM, 3♂ (8.5–25.4), 1 juv (5.6), 20 May 1969.

SÃO TOMÉ: "Saint Thomas" (Bouvier, 1904: 138), 4♂ (62–82, t.1), 1895, M. Nobre. (1) *MHNP Rio do Ouro (Bouvier, 1925:309), 2♂ (20.5, 24.5), 2♀ (8.0, 10.2) 1 sex? (19.5), M. Gravier.

ECOLOGICAL NOTES.—The only data available are the statement that some of the specimens were collected from a river (Bouvier, 1925:309) and others from an "effluent near western shore of [Crater] lake" (Holthuis, 1966:235).

LIFE HISTORY NOTES.—The only ovigerous females known are the four that were collected on 20 May 1969. No other aspects of the life history of the members of this species have been recorded.

REMARKS.—*Atya intermedia* is very closely allied to *A. innocous* and is more remotely related to *A. lanipes*. The similarities are best demonstrated in the rostrum which has margins that are angular to subangular at the base of the acumen; the basal podomere of the antennule lacks sclerotized denticles on the dorsal surface proximal to the distal transverse row; the lateral and dorsal surfaces of the merus, carpus, and propodus of the third pereiopod bear conspicuous corneous tubercles, and the tubercles on the flexor surface of the dactyl are arranged in two rows; the ventral margin of the abdominal pleura are devoid of corneous spinules, and the sternum of the fifth abdominal segment and the telson exhibit approximately the same proportions as those of *A. innocous*. Indeed the difference between the populations of *Atya* on Annobón and São Tomé and the American *A. innocous* is of such a minor nature that had these insular African populations not already received a name, we should treat them as a regionally restricted variant of the latter species.

Although Bouvier (1925:309, 310) compared his specimens of *A. intermedia* with those of *A. africana* and the type of *A. robusta*, comparing them with specimens he identified as *A. occidentalis* (= *A. innocous*) would have been more rewarding. This is especially obvious in examining the ratios cited (p. 311), among which most of those of *A. intermedia* and *A. occidentalis* overlap.

The only really distinctive feature of this shrimp that we have encountered is the occurrence of an accessory spine, or small but clearly defined, rounded prominence on the preanal carina situated just dorsal to the larger caudoventral spine.

The rostrum of small juveniles, as in all of those species in which the adult exhibits an angular rostrum, is more nearly acuminate and seems to become less so with each molt until in the adults the angles at the base of the acumen approach or surpass 80°.

Atya lanipes Holthuis

FIGURES 1*a*, 4*b*,*c*, 9, 10, 12*e*, 33–36

Atya lanipes Holthuis, 1963:61–67, figs. 1, 2 [type-locality: Saint Thomas, Virgin Islands: types: RMNH, ♂ holotype, ♂ paratype]; 1977:271, 272, 1 fig.—Chace and Hobbs, 1969:5, 14, 19, 29, 30, 33, 57, 61–63, 73, fig. 14c.—Chace, 1972:14.—Bonnelly de Calventi et al., 1973:1338.—Bonnelly de Calventi, 1974b:35, 38, 39, figs. 5, 12.—Peck, 1975:308.—Abele, 1975:56.—Hunte, 1975:66–72, figs. 1–3; 1978:135, 136, 139, 144, 145, 147, fig. 7; 1979a:153; 1979b:240; 1979c;70.—Villamil and Clements, 1976:3, 4, 20–22, 26–36, 38–40, 47, 49, 52–54, 59, figs. 6–9.—Hobbs, Hobbs, and Daniel, 1977:150.—Fryer, 1977:124.
Atya Lanipes.—Bonnelly de Calventi, 1974a:16.

REVIEW OF LITERATURE.—Holthuis (1963) named this species on the basis of two male specimens that had been obtained about 1898 by the Rijksmuseum van Natuurlijke Historie from Saint Thomas, Virgin Islands. Five years following the appearance of Holthuis' description, Chace and Hobbs (1969) included the species in their key to freshwater and terrestrial decapods of the West Indies, recorded its presence in eight localities on Puerto Rico, discussed its range and variations, and illustrated the distal part of the second pleopod of the male. Chace (1972) added no new data for the species. Bonnelly de Calventi et al. (1973) recorded this shrimp from the Río Cañada Madrigal, Dominican Republic, and Bonnelly de Calventi (1974a) reported the carapace lengths of her specimens (1♂, 18.9 mm; 7♀, 11.7–17.2 mm); the locality listed is recorded here under "Distribution and Specimens Examined." This work was expanded (1974b), including a diagnosis of the shrimp, illustrations, notes on color, size, habitat, and distribution in the Dominican Republic, where it is not very common in the southern part of the country. Peck (1975) listed *Atya lanipes* among the crustaceans frequenting caves on Jamaica. In describing *Atya dressleri*, Abele (1975) stated that *A. lanipes* is its closest relative and cited several characters in which they differ. Considerable additional information concerning this shrimp was provided by Hunte (1975) in his study of members of a population occurring in the Cane River, Saint Thomas Parish, Jamaica. He presented color notes, discussed morphological peculiarities and variations in the Jamaican specimens, and described and illustrated the first larval stage.

Villamil and Clements (1976) added many interesting data on the shrimp in the upper Río Espíritu Santo, Puerto Rico, including observations on habitat, feeding, size, and life history. Holthuis (1977) reported the presence of this shrimp in two localities in Cuba. He contrasted an ovigerous female with the types and figured the distal podomeres of the fifth pereiopod, pointing out the spine on the distal flexor extremity of the propodus that opposes the dactyl. Hobbs, Hobbs, and Daniel (1977) only reiterated the occurrence of this shrimp in spelean waters on Jamaica noted by Peck. Among the more recent references to the species is that of Fryer (1977) who pointed out that "*Atya lanipes* and *Potimirim americana* (Guérin-Méneville) are also known only from the West Indies, each being reported from three islands of which Jamaica is common to both." A discussion of the geographic and ecological distribution of *A. lanipes* on Jamaica was presented by Hunte (1978), and he (1979a) referred to his earlier description of the first larval stage. In a second paper that year (1979b), he pointed out the error in his interpretation of rudiments of the first maxillipeds. He concluded that, like *Atya innocous* and *Micratya poeyi* (Guérin-Méneville), the first larval stage of *A. lanipes* lacks periopods. This species was included by Hunte (1979c) in his list of the atyid and palaemonid shrimps of Jamaica.

PUBLISHED ILLUSTRATIONS.—The illustrations presented by Holthuis (1963) include dorsal and lateral views of the cephalic region, postaxial view of the third maxilliped, caudal view of the first pleopod of the male, caudomesial view of the second pleopod of the male, dorsal view of the telson, and illustrations of the first, third, fourth, and fifth pereiopods. Chace and Hobbs (1969) presented a posteromesial view of the second pleopod of the male. Bonnelly de Calventi (1974b) included a photograph of a specimen in lateral view and another of the cephalic region of the body in dorsal view; drawings were presented of the rostrum, appendices masculina and interna, and of the antennular peduncles. Hunte (1975) depicted dorsal and lateral views of the cephalic region, the third, fourth, and fifth pereiopods, and a dorsal view and appendages of the first larval stage. Holthuis (1977) illustrated the fifth pereiopod of an ovigerous female from Cuba in which the chela-like extremity is shown.

DIAGNOSIS.—Cephalic region of carapace not conspicuously sculptured, glabrous, lacking spines other than antennal and pterygostomian; ventral spines on rostrum usually present, pterygostomian spine strong; rostrum with margins tapering from base to apex, never bearing lateral angles. Ventral margin of all abdominal pleura without rows of sclerotized denticles and caudoventral angles of fourth and fifth pleura not produced in spines. Sternum of fifth abdominal segment with small, rather inconspicuous, median tubercle, that of sixth slightly longer than broad. Preanal carina without or with very short spine. Telson 2.1 to 2.6 times as long as wide and with 5 to 7 spines in each of 2 dorsal rows. Antennular peduncle with proximal article lacking premarginal sclerotized spinules dorsally; penultimate article about twice as long as wide and bearing very few, if any, small spinules, if present, sometimes arranged in linear series. Coxae of third and fourth pereiopods lacking prominent ventrolateral spine; that of third without mesial caudoventral prominence. Third pereiopod with merus rounded ventrally, 6 to 8 times as long as high, ventromesial surface bowed, never parallel to that of corresponding podomere of other third pereiopod, and lateral surface lacking sclerotized tubercles and spines; propodus 3 to 4 times as long as broad, extensor surface rugose but lacking heavily sclerotized tubercles and spines, flexor surface with small spines often linearly arranged, spines partly surrounded (sides and distally) by usually inconspicuous short plumose setae; dactyl freely movable and bearing 2 oblique rows of small scales or spines on flexor surface.

MALE (Maricao River, Puerto Rico).—Rostrum (Figure 33*a,d*) with margins tapering from base, bearing only slightest angle delimiting posterior end of acumen; apex of latter slightly overreaching distal extremity of basal segment of antennular peduncle; dorsal median carina gently curved, not excavate dorsally (not dipping below level of lateral carinae posterior to acumen), and reaching apex of acumen; ventral carina with 2 preapical teeth, both well forward on acumen; ocellar beak obscured between eyes and reaching little beyond level of base of stylocerite, its cephalic border sloping posterodorsally and

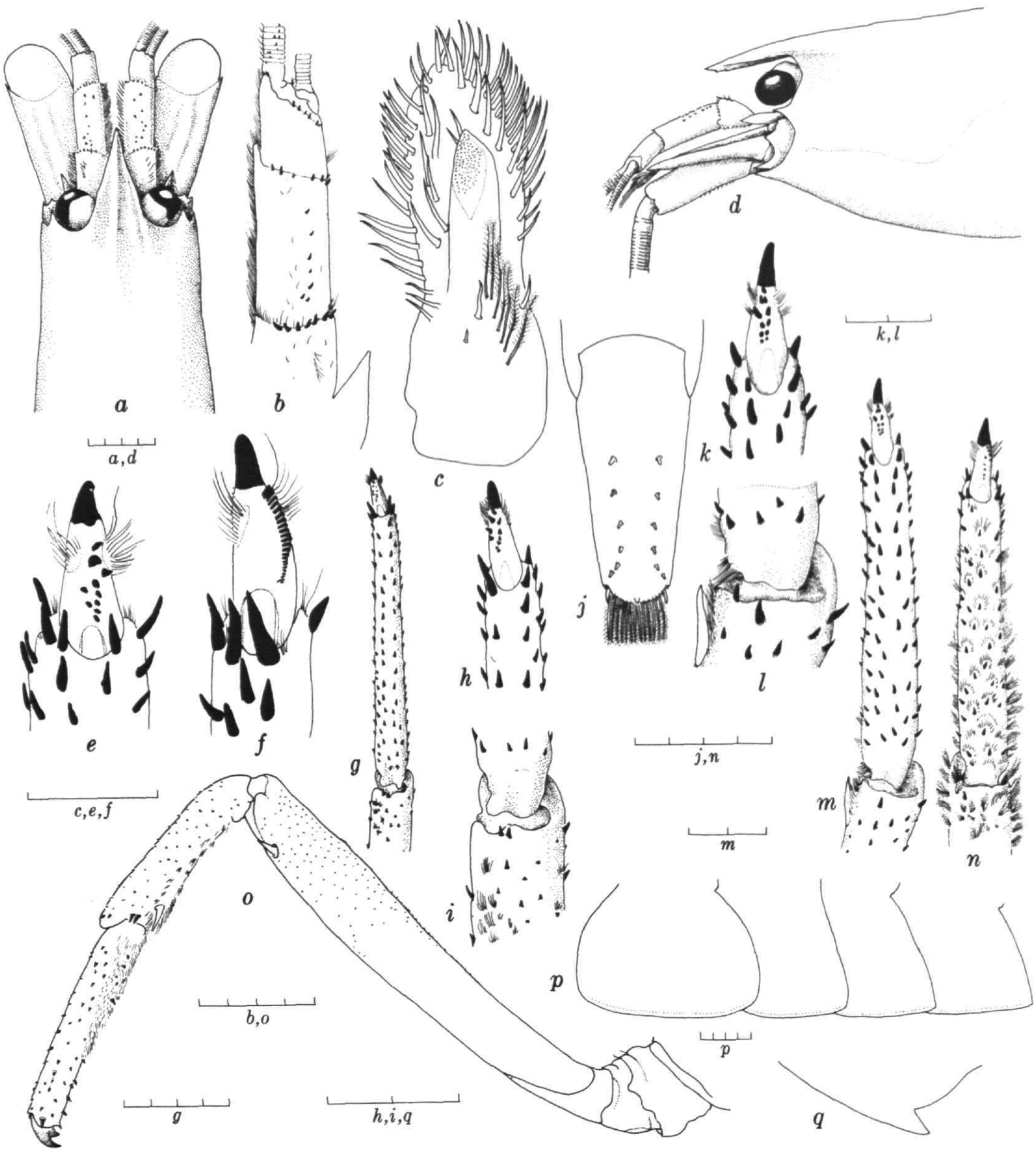

FIGURE 33.—*Atya lanipes* (all from male from Río Maricao, Puerto Rico, except *g,h,i* from Río Mameyes, Puerto Rico, and *n* from Rock Springs, Jamaica): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view of cephalic region; *e,f*, flexor surface of distal part of fourth and fifth pereiopods, respectively; *g*, flexor surface of distal part of third pereiopod; *h,i*, enlargements of distal and proximal parts of *g*; *j*, dorsal view of telson; *k,l*, enlargements of distal and proximal parts of *m*; *m,n*, flexor surface of distal part of third pereiopod; *o*, lateral view of third pereiopod; *p*, lateral view of second through fifth abdominal pleura; *q*, lateral view of preanal carina. (Scales marked in 1 mm increments.)

dorsal border embraced by sides of ventral rostral groove. Antennal and pterygostomian spines strongly acute; no spine present between them. Surface of carapace with very fine, dense punctations but devoid of ridges and spines other than those just mentioned; cephalothorax without conspicuous setae.

Pleura of first 3 abdominal segments (Figure 33*p*) with rounded posteroventral extremities; corresponding parts of fourth and fifth angular but not produced in spines. All pleura lacking corneous denticles on ventral margin, but third through fifth with moderately prominent fringe of plumose setae. Fourth abdominal tergum about 1.1 times as long as fifth, subequal in length to sixth, and almost 0.9 as long as telson. Sternum of fifth abdominal segment with very small, almost rudimentary median tubercle (Figure 1*a*). Sternum of sixth abdominal segment about 0.9 as long as broad. Free part of preanal carina (Figure 33*q*) acute and rather short, falling far short of caudal margin of basal part of sclerite. Telson (Figure 33*j*) little less than 2.4 times as long as wide, its dorsal surface bearing paired concave rows of 6 corneous denticles, and posteromedian tubercle slightly overhanging caudal margin.

Proximal podomere of antennule (Figure 33*b*) with stylocerite reaching base of distal third or fourth of segment; dorsal surface with linear cluster of setae but lacking corneous spinules; distal margin bearing row of 9 (right) or 8 (left) corneous denticles; penultimate segment of peduncle little more than twice as long as wide and bearing 10 spinules, most arranged in linear series, on dorsal surface and 10 on distal margin; ultimate podomere with row of 8 (right) or 10 (left) spinules at base of lateral flagellum and another of 6 (right) or 5 (left) at mesial base of mesial flagellum, none present proximal to rows. Antenna with ventrolateral spine on basis not reaching so far anteriorly as stylocerite; lateral spine on scaphocerite rather strong, reaching base of middle third of ultimate podomere of antennular peduncle; lamella far surpassing latter; flagellum extending almost to midlength of telson.

Third maxilliped overreaching antennular peduncle by distal fifth of ultimate podomere of endopod; tip of exopod attaining base of distal fifth of penultimate podomere.

First pereiopod reaching level of distal extremity of antennular peduncle, second extending to base of distal fifth of fingers of first pereiopod; terminal brush of both appendages containing setae with scraping denticles (Figure 4*b*). Third pereiopod (Figure 33*k,l,m,o*) with lateral distoventral spine on merus and carpus, ventral spine on right merus, carpus with 2 smaller distolateral spines, and when appendage extended anteriorly overreaching antennular peduncle by dactyl and four-fifths of propodus; merus with ventromesial margin bowed, approximately 6 times as long as high, about 2.2 times as long as carpus, and 2.2 to 2.4 times as long as propodus; latter about 9 times as long as wide and about 1.1 times as long as carpus; distoventral margin of coxa entire (evenly rounded), and mesial caudoventral prominence absent. Lateral, dorsal, and ventral surfaces of merus studded with many minute apically sclerotized tubercles, most of which arranged in sublinear series; setae inconspicuous; mesial extremity of podomere very weakly produced at level of mesial articular condyle of carpus. Carpus more strongly tuberculate, except on flexor surface, than merus, and clusters of moderately conspicuous tufts of long plumose setae present ventrolaterally, most abundant near large ventrolateral spine. Propodus with most tubercles arranged in series on dorsal, mesial, and lateral surfaces, those on flexor surface less obviously so, especially proximally; prominent tufts of setae present along proximal half of lateral surface. Dactyl movable, its flexor surface with 2 longitudinal rows of 4 to 6 denticles each flanked distally by setal clusters.

Fourth pereiopod with dactyl reaching slightly beyond distal margin of carpus; length of merus almost twice that of carpus, latter approximately 0.9 as long as propodus. Fifth pereiopod reaching anteriorly as far as fourth; merus almost 1.7 times as long as carpus, latter 0.6 as long as propodus. Ornamentation of merus, carpus, and propodus of fourth pereiopod similar to that of third except for 3, instead of 2, distolateral spines on carpus. Ornamentation of fifth pereiopod like third and fourth but with 2 ventral spines on merus proximal to distal ventrolateral spine, and row of 5 distolateral spines on carpus.

Diaresis of lateral ramus of uropod flanked proximally by row of 22 (right) or 23 (left) articulated corneous denticles, and fixed spine at lateral end of row.

COLOR NOTES.—From Hunte (1975:67).

The ground colour of the cephalothorax and abdomen is dark green, but the presence of scattered cream chromatophores laterally produces a mottled effect. The cream chromatophores tend to become white in a dorsoventral direction on the lateral surfaces, and along the ventral margins of the pleura form a distinct white line. There is a mustard-coloured strip running centrally on the dorsal surface from the tip of the rostrum to the tip of the telson where it terminates in an orange-coloured chromatophore. The strip remains narrow for the length of the carapace, but then widens to form a series of triangles, one in each abdominal segment. In the first two segments the apex of the triangle is posteriorly directed, in the last three anteriorly directed. In the last two segments the strip covers the bulk of the dorsal surface. The remainder of the dorsal surface of the abdomen, i.e. the area on either side of the strip, is dark green; as is the posterior half of the dorsal part of the carapace. The anterior half of the dorsal surface of the carapace is tan-coloured on either side of the strip.

The antennular and antennal peduncles are mottled green; the flagella are tan. The antennal scales are faintly mottled green at the base, but this quickly grades into translucency. All five pairs of pereiopods are distinctly banded with alternating strips of white and olive green. The tufts of hair borne distally on pereiopods 1 and 2 are strikingly orange in colour. All pleopods are white at their base, quickly belonging translucent distally.

Bonnelly de Calventi (1974b) found the coloration of this shrimp in the Dominican Republic to be quite variable: dark brown, or sometimes light with irregular cream spots over the entire body.

SIZE.—The largest specimen we have examined is a male from Puerto Rico having a carapace length of 29.0 mm; that of the largest female, from Saint Croix, 18.2 mm. The carapace length and total length (latter in parentheses) of the holotypic and paratypic males were reported by Holthuis (1963:61) to be 25 (73) and 23 (70) mm, respectively. Carapace lengths of specimens from Puerto Rico reported by Chace and Hobbs (1969:62) for 16 males ranged from 4.2 to 28 mm, for 6 females 4.9 to 21.8 mm, and for 9 ovigerous females, 9.4 to 17.7 mm. The carapace lengths of Hunte's (1975:66) four females from Jamaica were 9.8, 12.6, 13.7, and 14.0 mm. The specimen from the Jamaican cave recorded by Peck (1975) is a male having a carapace length of 21.5 mm. Villamil and Clements (1976:21) measured 73 specimens: the 34 males had total lengths of 50.25 to 74.55 (average (61.87) mm; the non-ovigerous females, 30.15 to 62.90 (average 44.18) mm; and the single ovigerous female, 34.25 mm.

DISTRIBUTION AND SPECIMENS EXAMINED.—This shrimp has been collected on only six islands of the West Indies: Cuba, Jamaica, Hispaniola, Puerto Rico, Saint Croix, and Saint Thomas (Figures 34, 35).

Records for the known localities are listed below. Collections that we have examined are marked with an asterisk if they have been previously reported and with a dagger if they are reported herein for the first time. Numbers following the specimens listed are measurements in mm, of the carapace length. Some listings lack the date the collection was made and/or the name of the collector; these could not be determined.

CUBA: (1) RMNH, Río Caburny near Topes de Collantes, Provincia de Las Villas (Holthuis, 1977:271), 1 ovig ♀ (12.0), "Cubano- Roumanian Biospeleological Expd to Cuba." (2) †USNM, Trinidad Mts, Provincia de Las Villas, 1 ovig ♀ (11.0), 5 Jun 1959, M. Westfall. (3) †USNM, Baracoa, Provincia de Oriente, 1♂ (6.2), 30 Jan 1902, W. Palmer. (Holthuis, 1977:272, reported a juvenile collected in Río Ceiba with a carapace length of 5.5 mm that he suspected as being a member of this species.)

JAMAICA: (1) Cane River, Saint Thomas Parish (Hunte, 1975:67), 4♀. (2) †USNM, Rock Springs Cave, 0.9 km E of Pear Tree Grove, alt 400 m, Saint Mary Parish (Peck, 1975:308, locality not cited), 1♂ (21.5), Aug 1974, S.B. Peck. (3) Wagwater rivulet N of Kingston, alt 700 m, Saint

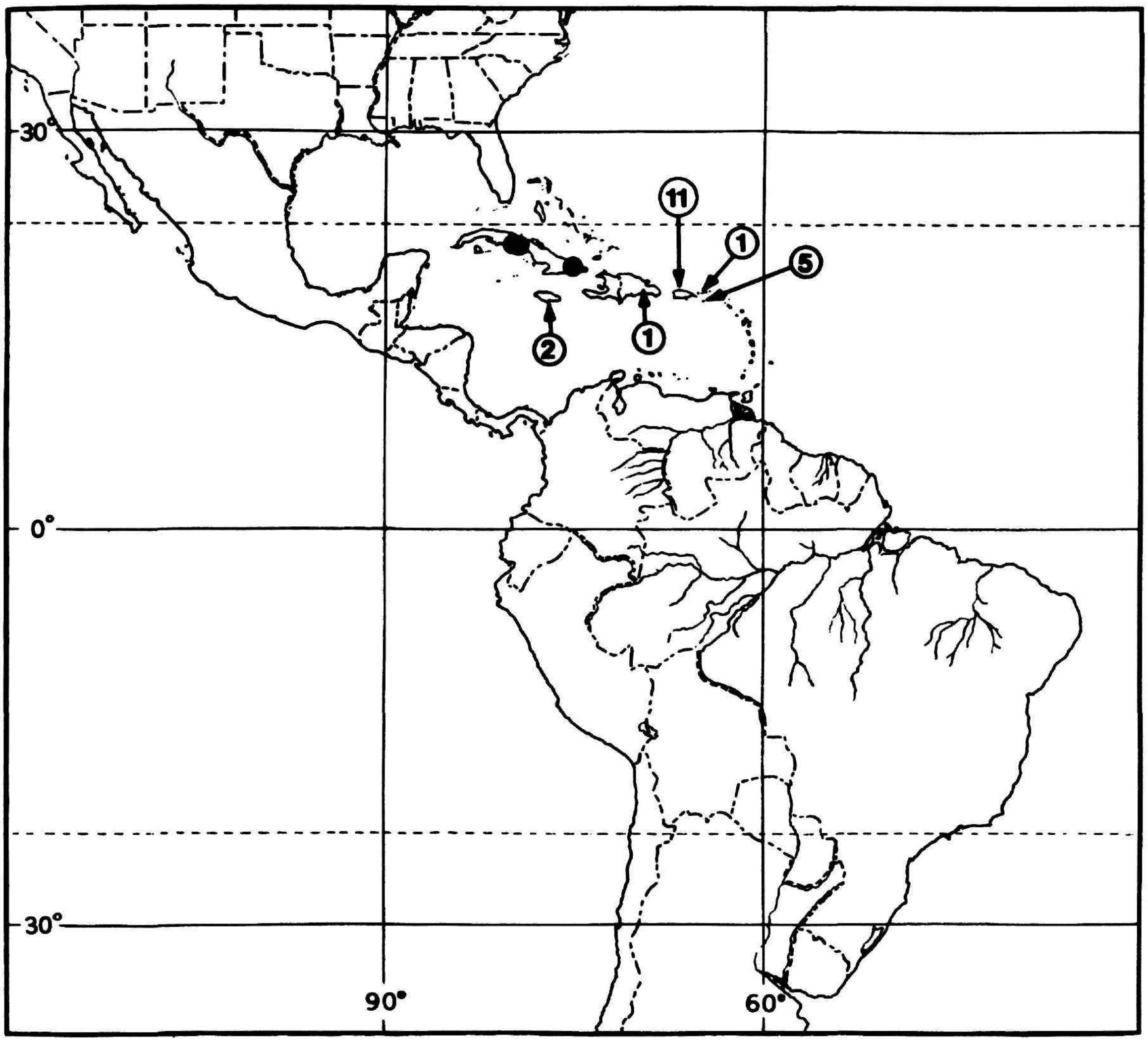

FIGURE 34.—Distribution of *Atya lanipes* (circled numerals = number of localities; see Figure 35).

Andrew Parish, 1 specimen (fide L.B. Holthuis).

PUERTO RICO: (1) *USNM, Río Culebrinas at Rte 13, 1,000 m S and 300 m E of San Sebastián (Chace and Hobbs, 1969:62), 1♂ (16.2), 2 Jun 1953, H.W. Harry. (2) *USNM, Río Maricao at Maricao (Chace and Hobbs, 1969:62), 2♂ (21.0, 22.7), 2♀ (13.2, 13.4), 1 Feb 1965, N.T. Mattox. (3) *USNM, freshwater streams at Jayuya (Chace and Hobbs, 1969:62), 1♂ (29.0), 1♀ (22.0), 1 ovig ♀ (17.5), spring 1954, L.A. Costas Grava. (4) *USNM, Río Lajas, 2800 m E and 3,000 m S of Vega Alta (Chace and Hobbs, 1969:62), 1♂ (4.6), 1♀ (9.3), 8 May 1953, HWH. (5) *USNM, Río Cibuco at Rte 20, 1,500 m S and 3,500 m W of Corozal (Chace and Hobbs, 1969:62), 5♂ (5.7–11.1), 2♀ (5.2, 5.9), 2 ovig ♀ (9.6, 11.8), 5 May 1953, HWH. (6) *USNM, Río Mantí at rd from Corozal to Orcovis (Chace and Hobbs, 1969:62),

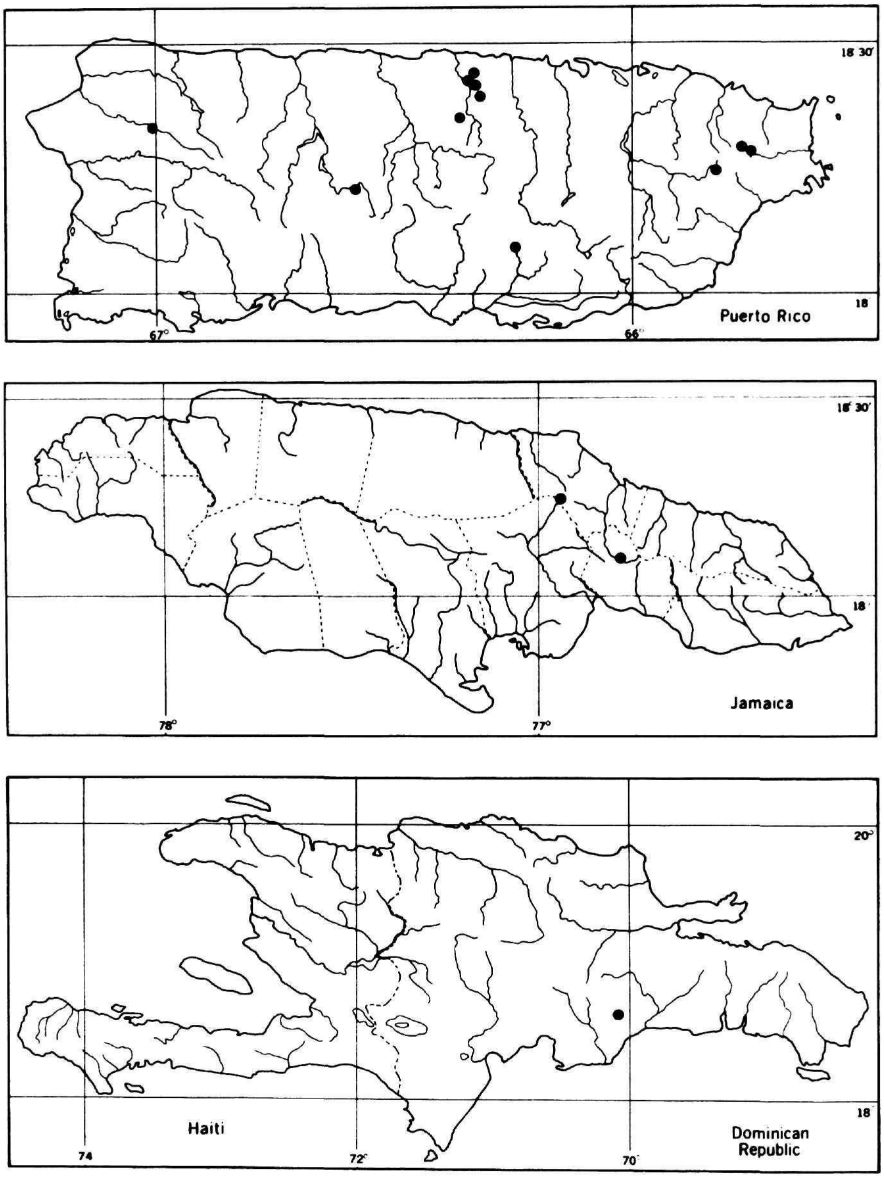

FIGURE 35.—Distribution of *Atya lanipes* in the Greater Antilles.

1♂ (23.4), 2 ovig ♀ (14.9, 18.0), 23 Nov 1954, HWH. (7) *USNM, trib to Río Mameves at Rte 112, 100 m N and 1,500 m E of El Yunque summit (Chace and Hobbs, 1969:62), 3♂ (19.6–20.5), 1♀ (15.5), 2 ovig ♀ (14.1, 14.9), 8 Jun 1953, HWH. (8) *USNM, El Yunque (Chace and Hobbs, 1969:62), 1♂ (about 6.2), 19 Feb 1899. (9) †USNM, below dam on Río Cubuy at Rte 112, 500 m S and 1,000 m W of El Yunque summit, 3♀, (5.5–12.9), 8 Jun 1953, HWH. (10) †USNM, creek below Maricao, 1♂ (5.8), 1♀ (5.3), 7 Feb 1934. (11) †USNM, falls of Río Grande de Aibonito, 1♂ (17.1), 1♀ (11.5), 26 Jan 1899, *Fish Hawk*. (12) †USNM, Luquillo Nat Forest, 3♂ (15.0–20.2), 9 Mar 1934, S.F. Hildebrand. (13) *USNM, San Juan Market, 7♂ (16.6–18.5), 1♀ (18.0), 14 Jan 1899, *Fish Hawk*. (14) almost all parts of the upper Río Espíritu Santo Basin at elevations of 550 to 820 m (Villamil and Clements, 1976:15–16, 22). (15) "at low elevations in other forested areas of the Espíritu Santo River basin . . . ." (Villamil and Clements, 1976:40).

HISPANIOLA: (1) Cañada Madrigal, Dominican Republic (Bonnelly de Calventi et al., 1973:1338; Bonnelly de Calventi, 1974a:16), 1♂ (18.9), 7♀ (11.7–17.2). (2) Cañada de los Anones, Municipio de Villa Altagracia, Dominican Republic (Bonnelly de Calventi, 1974b:39).

SAINT CROIX: (1) †USNM, Fairplain Street, 1♂ (5.4), 1 ovig ♀ (12.5), H.A. Beatty. (2) †USNM, Caledonia Street, 4♂ (16.9–18.2), 2♀ (9.1, 13.2), 4 ovig ♀, (16.9–18.2), HAB. (3) †USNM, Christiansted, 1♀ (7.3), HAB. (4) *USNM, no locality data, 4 juv (3.2–3.3), 22 Mar 1937, HAB. (5) †USNM, Cave at Juan Díaz, 2♀ (13.0, 17.1), 21 Feb 1932, Chapman Grant.

SAINT THOMAS: *RMNH, no locality data (holotype and paratype), 2♂ (18.1, 19.9).

VARIATIONS.—Chace and Hobbs (1969:63) pointed out that in none of the specimens from Puerto Rico examined by them are "the last three pereiopods clothed in hair dense enough to conceal the underlying surface." They also noted considerable variation in the pterygostomian angle; it is longer and more slender in the larger males than in the types but less prominent in smaller specimens of both sexes, "often being reduced to no more than a broadly acute angle."

Hunte (1975:67, 68) in discussing the "Peculiarities of, and variation within, Jamaican specimens" noted that the rostra attain the proximal one-fourth to one-third of the second article of the antennular peduncle, and one or two teeth are present on the ventral surface. Minor variations are pointed out in the spination of the podomeres of the third, fourth, and fifth pereiopods, and, like Chace and Hobbs, he noted considerable variation in the pubescence borne on them. The longitudinal rows of spinules on the dorsal surface of the telson range from five to eight, with differences of as many as two in the paired rows on an individual specimen.

Holthuis (1977) cited several differences between his ovigerous female and the types, including the less conspicuous pubescence on the legs, the presence of an "anteroventral spine" on the carpus of the third through fifth pereiopods and on the merus of the fourth and fifth. Spinules are distributed over the surface of the carpus and propodus, and on the fifth pereiopod the long ventrodistal spine forms a "chela-like structure" with the dactyl.

Among the specimens examined by us, the rostrum shows marked variation in shape; in some of the smaller individuals the margins are somewhat suddenly contracted some distance posterior to the apex (Figure 36), but the angles are lacking; the margins in most specimens, however, taper from the base; the apex may not reach the distal extremity of the first segment of the antennular peduncle, or it may extend as far as the end of the proximal third of the penultimate segment; the ventral keel may lack teeth or there may be as many as three. Most of the specimens exhibit paired rows of six spinules on the dorsal surface of the telson, but there may be as few as five and as many as eight in at least one of the two rows. The variations noted by the above mentioned authors have been observed by us. As for the distal part of the fifth pereiopod, there is considerable variability in the size of the distoventral spines on the propodus, and although the chela-like arrangement mentioned by Holthuis has been observed, some of our specimens have spines opposing the dactyl that are very much reduced, others have paired long ones, but in most in which the fifth leg remains intact the spines are intermediate in size; furthermore the long spines occur in males as well as in females.

ECOLOGICAL NOTES.—All of the habitats cited by Chace and Hobbs (1969:62) in Puerto Rico were lotic, but the data recorded by them contained no further ecological notes. Bonnelly de Calventi (1974b:38) observed that in the Domin-

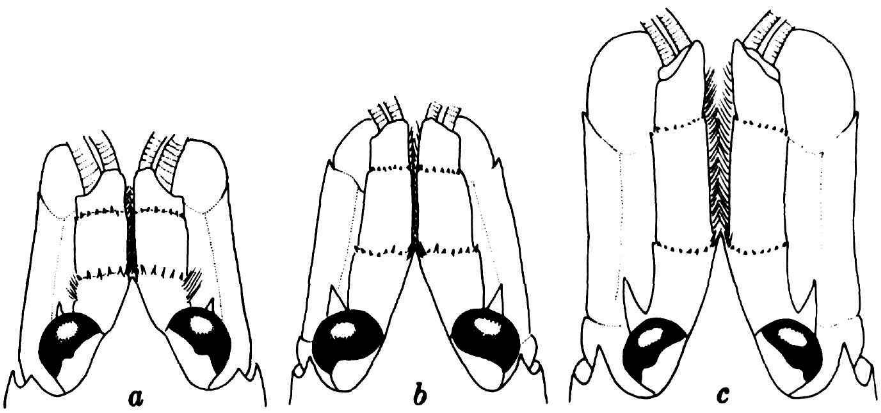

FIGURE 36.—*Atya lanipes*, variation in the rostrum of 3 specimens from Río Mantí, Puerto Rico (numbers in parentheses = carapace length in mm): *a*, ovigerous female (14.9); *b*, ovigerous female (18.0); *c*, male (23.4).

ican Republic this shrimp frequents tranquil, shaded waters beneath the "hojarascas" floating on the surface, but it also lives beneath stones. Hunte (1975:67) stated that his specimens "were collected in pure freshwater where the rate of water flow was high and bottom substrate stony." Peck (1975:308) reported the presence of *Atya lanipes* in a Jamaican cave where he collected it in company with *Atya innocous* and *Macrobrachium* species beyond the entrance pool, "deeper in the cave. The water temperature was 23.3° C .... Tubificid worms and psychodid fly larvae were abundant in guano pools" (p. 320). Villamil and Clements (1976) found this shrimp in the Espíritu Santo Basin, Puerto Rico, in every stream where shrimp were present and "where apparently *A. innocous* cannot live" (p. 4). They concluded that it was not restricted in the streams by any physical or chemical characteristic investigated (p. 26). According to them, Gifford and Cole (1970, unpublished) believed *Atya lanipes* to be

> the single most important specie[s] for the recycling of detritus and nutrients washed into the stream .... In a pool approximately 48 square feet, a minimum of 26 individuals were counted by Gifford and Cole. Through skin-diving and [sic] average of 25 individuals per square meter were counted over large boulders in riffle areas. [Villamil and Clements, 1976:28, 29]

Both filter feeding and direct grazing were observed. Villamil and Clements (1976) estimated that at one of their stations a shrimp would filter 0.00006 gm of particulate matter per hour (p. 48). They also observed that "sex exclusion in habitat preference" existed throughout the study area (p. 29). Males occupied the parts of pools where the current was strongest, and boulders were a prominent feature of the substrate. In contrast, females tended to frequent the marginal areas where the flow was weaker and where the substrate consisted of rubble and gravel.

LIFE HISTORY NOTES.—The ovigerous females reported by Chace and Hobbs (1969:62) to have carapace lengths of 9.4 to 17.7 mm were collected on 8 June 1953, 23 November 1954, and 5 May 1955. The oval eggs ranged from 0.3 × 0.6 mm to 0.4 × 0.7 mm. The latter range was reported by Holthuis (1977:271) for the ovigerous female collected in Cuba. Bonnelly de Calventi (1974b:39) recorded the occurrence of ovigerous females in February, March, April, May, and August. Hunte (1975:69–72) described and illustrated the "first stage larvae" that hatched from eggs borne by a female having a carapace length of 9.8 mm. These larvae were planktonic and swam constantly, tail first and on their backs. They were attracted to light and were not apparently harmed by a change of salinity from 0 to 20‰ over a period of three hours. They failed to accept any food offered them. The nearly transparent body, 1.73 to 1.78 mm in length and bearing red chromatophores, was slightly bent at the third abdominal segment. Illustrations of the dorsal view of the larva and its appendages were included. Neither the date of collection of the ovigerous female nor the diameters of the eggs was recorded. Villamil and Clements (1976:40) stated that the only ovigerous female they captured was obtained in November, but others were observed in the Espiritu Santo River basin from December to February. They concluded that the breeding season extends from November to March with larval release occurring in February. The new and previously recorded data summarized here indicate that egg laying occurs, somewhere within the range of the species, from November to February and in May and June.

Atya margaritacea A. Milne-Edwards

FIGURES 1*b*, 9, 10, 11*d,e*, 37–41

Atya margaritacea A. Milne-Edwards, 1864:148, 149, pl. 3, fig. 2 [type-locality: New Caledonia (as pointed out by Holthuis, 1966:234, "evidently in error"); types: MHNP, No. 601, 2♂, 1♀].—Giebel, 1875:52.—Bate, 1888:693.—Ortmann, 1890:465, 466, pl. 36: fig. 7; 1895:408, 409.—Bouvier, 1905:121, 122.—Holthuis, 1969:92.

Atya rivalis Smith, 1871:94 [type-locality: "Fresh water streams, Polvon [12°21'N, 87°05'W], Occidental Department, Nicaragua"; types: MCZ 317, 3 dismembered ♂ in one bottle, single specimen of undetermined sex in another].—Kingsley, 1878a:92; 1878b:57.—Pocock, 1889: 16.—Oliveira, 1945:179.—Holthuis, 1966:234.—Chace and Hobbs, 1969:66.—Solar, 1972:8.—Abele, 1975:56, 57.—Abele and Blum, 1977:240–242, 245, 250.—Méndez, 1981:14, 70, pl. 4: fig. 34; pl. 27: figs. 209–211.—Rodríguez, 1981:46.

Atya scabra.—(?)Kingsley, 1878b:57.—Ortmann, 1895:408–410, 415, 416; 1897:183–185.—(?)Rathbun, 1900:313; 1901:119.—Bouvier, 1904:138; 1905:112, 121, fig. 25M; 1925:293, 314–317, figs. 703, 704.—De Man, 1925:28.—J. Roux, 1926b:217.—Monod, 1933:461.—Schmitt, 1935: 136.—Coventry, 1944:534.—(?)Oliveira, 1945:177.—Holthuis, 1951:25; 1966:234, 238; 1969:92.—Parodiz, 1960:38, 39 [only specimens from Costa Rica, not figs. 1–3].—Chace and Hobbs, 1969:63. [All in part.]

Atya scabra var. *margaritacea*.—Monod, 1967:140, pl. IX: figs. 13, 14 [not 15 and 16 as noted by Monod; see comment under "Published Illustrations" below].

Ataya margaritacea.—Chace and Hobbs, 1969:63 [erroneous spelling].

REVIEW OF LITERATURE.—*Atya margaritacea* was described by A. Milne-Edwards (1864) who based his account on specimens that he believed to have been collected on New Caledonia. Smith (1871) described the same species from Nicaraguan specimens, designating them *Atya rivalis*. In describing *Atya gabonensis*, Giebel (1875) noted the previously known members of the genus and included a reference to Milne-Edwards' species. Kingsley (1878a) contrasted certain characters of *A. rivalis* with those of his *Atya punctata* and mentioned the species in a second publication that year (1878b); in the latter he also recorded *A. scabra* from freshwaters of western Mexico, a record almost certainly based upon a misidentification of *A. margaritacea* or *A. ortmannioides*. According to Pocock (1889), "the features pointed out by Mr. Kingsley to distinguish his *punctata* from ... *rivalis* ... are ... regarded as due either to individual variation or to difference of age." Bate (1888) did not add to our knowledge of the species. Two years later, however, Ortmann (1890) presented a brief diagnosis and illustrated the rostrum of *A. margaritacea* and placed it, together with *A. robusta*, *A. scabra*, and *A. sculptipes* (= *sculptata*), in his "*margaritacea*-Gruppe." In his study of the family Atyidae, Ortmann (1895:408) included *A. margaritacea* in his key to the members of the genus, but he expressed the opinion that "the locality given by Milne-Edwards for *margaritacea* and *robusta* is not correct ...." Among the several synonyms he cited for *A. scabra* was *Atya rivalis*, and the same recognition was accorded these two species by him in his study of the shrimps of South America (1897). Rathbun (1900, 1901) seems to have agreed with Ortmann that *A. rivalis* is a synonym of *A. scabra*, for she listed Nicaragua in citing the distribution of the latter, and, to our knowledge, no locality record for *A. scabra* in Nicaragua exists. Even though Rathbun did not cite *A. rivalis* among the synonyms of *A. scabra*, we suspect that her inclusion of that country in the range of *A. scabra* was based upon Smith's record for *Atya rivalis*, perhaps influenced by Ortmann.

Bouvier (1904) cited *Atya margaritacea* as a synonym of *A. scabra* and the following year (1905) added *A. rivalis*, among others, to his list of synonyms of *A. scabra*, and both *A. margaritacea* and *A. rivalis* were included among the synonyms of *A. scabra* in his monograph (1925). De Man (1925) also considered *A. rivalis* to be a synonym of *A. scabra*. *Atya margaritacea* was relegated to the synonomy of the latter by J. Roux (1926b), but he expressed doubt that his shrimp occurs on New Caledonia, for among 150 atyids collected in six localities there, no representative of the genus *Atya* (as restricted herein) was among them. Monod (1933) and Schmitt (1935) followed Bouvier in citing New Caledonia within the range of *A. scabra*. Nicaragua was included among the areas frequented by *A. scabra* by Oliveira (1945), an inclusion that almost certainly was based upon the assumed identity of *A. scabra* and *A. rivalis*. Coventry (1944) cited a new locality in Panama for a shrimp that was identified by him as *A. scabra*. In all probability this record is for *A. margaritacea*.

Although Holthuis (1951) did not list *A. rivalis* among the synonyms of *A. scabra*, he reported the species' occurrence on the west coast of America from Lower California to Costa Rica, an area inhabited by *A. margaritacea* instead of *A. scabra*. He also noted that the latter had been reported from New Caledonia, no doubt referring to Milne-Edwards' locality. Parodiz (1960) reported the presence of this shrimp (identified by him as *Atya scabra*) from Río de Colón, Costa Rica. In his study of the freshwater shrimps of Annobón, Holthuis (1966) pointed out certain differences between *A. scabra* and specimens of *Atya* from Ecuador and Peru. Those specimens from the two South American countries (which have relatively shorter and broader segments of the antennular peduncle, the second segment being much longer than the third, and in which the mesiodistal lobe of the merus of the third pereiopod forms a strong "bluntly triangular process," and the legs more robust than in the eastern American and West Indian *A. scabra*) he assigned to *A. rivalis*. In commenting on the range of *A. scabra* recorded by Bouvier (1925), he stated that records from New Caledonia are almost certainly based on specimens (= syntypes of *A. margaritacea*) bearing erroneous data. Holthuis (1969) and Chace and Hobbs (1969) included *A. margaritacea* in their synonomy of *A. scabra*, but the latter tentatively regarded *A. rivalis* as a distinct species. The latter opinion was concurred in by Abele (1975). Solar (1972) included *A. rivalis* in his catalogue of the Crustacea of Peru, citing Holthuis (1966) and Chace's identification of specimens from ríos Chicama and Jequetepeque. In their study of the freshwater decapods of the Perlas Archipelago, Panama, Abele and Blum (1977) found *A. rivalis* only on San José; their six specimens ranged in length from (3♂) 40.4 to 32.4 mm and (3♀) 6.5 to 10.4 mm. A summary of their observations on the habitat occupied by this shrimp on the island is included in "Ecological Notes" below. Méndez (1981) reported the occurrence of *A. rivalis* in six river basins in Peru between 3°47′S and 11°04′S and at altitudes of 0 to 210 m. Illustrations are also provided.

PUBLISHED ILLUSTRATIONS.—In the original description of the species, A. Milne-Edwards (1864) included a lateral view of the entire animal, dorsal and lateral views of the rostrum, and a dorsal view of the telson. The only other figures available are those of Ortmann (1890), a dorsal view of the rostrum, and of Bouvier (1905), a dorsal view of the rostrum and lateral view of the cephalic region of the carapace. The last two were reprinted but mislabeled by Bouvier (1925), for figures 703 and 704 correspond to those labeled as "*A. margaritacea*" in 1905, fig. 25 M. Inasmuch as Monod's (1967) figures were taken from Bouvier (1925), those attributed to "Typical" *scabra* and to the "var. *margaritacea*" are reversed. Méndez (1981) included two drawings of *Atya rivalis* in lateral view, one of a dorsal view of the rostrum, and another of the first pereiopod.

DIAGNOSIS.—Cephalic region of carapace not conspicuously sculptured; spines limited to antennal, moderately strong pterygostomian, and occasional ventral rostral. Rostrum with margins suddenly contracted forming distinct angle anterior to orbit, angle often produced anteriorly; dorsal surface without median row of strong spines. Ventral margin of third through fifth abdominal pleura with short to moderately long rows of corneous denticles, such never present on second; caudoventral angle of fourth and fifth pleura not produced in spines. Sternum of fifth abdominal segment with comparatively large median tubercle, that of sixth about 1.6 times as broad as long. Preanal carina with short, somewhat compressed spine directed caudoventrally, spine not reaching level of caudal margin of basal part of sclerite bearing it. Telson 1.6 to 1.8 times as long as broad with 5 to 7 spines in each of 2 dorsal rows. Antennular peduncle with dorsal surface of proximal article usually devoid of sclerotized spinules proximal to distal transverse row; penultimate article 1.4 to 1.6 times as long as wide, and dorsal surface with many scattered spinules. Coxae of third and fourth pereiopods lacking prominent anterolateral spine. Third pereiopod with merus rounded ventrally, 2.1 to 2.4 times as long as high, ventromesial surface slightly to strikingly bowed, never parallel to that of corresponding podomere of other member of pair, and lateral surface bearing corneous spines and tubercles, many of latter with flattened scalelike extremities, most arranged in linear series; propodus 1.7 to 1.9 times as long as broad, studded with scalelike tubercles on extensor surface and with moderate number of similar, rather large ones scattered on flexor surface, if any of those on latter arranged in row, those comprising it never contiguous or overlapping; dactyl not fused with propodus and bearing single distinct straight to slightly curved, longitudinal row of scalelike tubercles on flexor surface.

SYNTYPIC MALE.—Eyes collapsed but obviously well developed and presumably pigmented. Rostrum (Figure 37*a,d*) with slightly concave margins produced in acute angles flanking base of acumen, latter slightly overreaching basal podomere of antennule; high, rounded dorsal carina excavate dorsally (dipping below level of lateral carinae posterior to acumen) and almost reaching tip of acumen. Ventral carina with 1 small tooth near apex of acumen; ocellar beak terminating in acute angle, dorsal margin horizontal and anterior margin oblique. Antennal spine acute; pterygostomian angle produced in short acute spine; no spines present between antennal and pterygostomian spines. Carapace (length 24.3 mm) devoid of other spines and conspicuous ridges; surface studded with short erect setae borne in rather crowded punctations.

Pleuron of second abdominal segment (Figure 37*e*) with rounded posteroventral extremity, that of third, fourth, and fifth angular although none produced in spines. Ventral margin of third, fourth, and fifth pleura with linear clusters of 15, 17, and 9 corneous denticles, respectively; that of sixth with sparse setal fringe posteriorly. Fourth abdominal tergum approximately 1.2, 1.2, and 1.1 times as long as fifth, sixth, and telson, respectively; length of sixth subequal to that of fifth, and 0.9 as long as telson. Sternum of fifth abdominal segment (Figure 1*i*, 37*g*) with rather large, compressed median tubercle; sternum of sixth 1.6 times as broad as long. Preanal carina (Figure 37*j*) with short spine, tip of which barely reaching midlength of sclerite. Telson (Figure 37*m*) about 1.8 times as long as wide, its dorsal surface bearing paired mesially concave rows of 6 denticles each and posteromedian tubercle, latter slightly overhanging midcaudal margin.

Proximal podomere of antennule (Figure 37*b*) with strong, acute, corneous-tipped stylocerite overreaching midlength of segment, dorsal surface with linear cluster of setae, and left member with 1 (right with 2) premarginal cornified spinules, distal margin studded with dorsolateral row of 7 cornified spinules; penultimate segment of peduncle subequal in length and width, its dorsal surface bearing 15 (right) or 13 (left) small, corneous spinules, more laterally situated ones forming curved row, dorsodistal margin with row of 6; ultimate podomere of peduncle, little more than half as long as penultimate segment, armed with rows of 8 similar spinules at dorsal base of each flagellum and groups of 3 or 4 proximal to row flanking base of lateral flagellum. Antenna with ventrolateral spine on basis almost reaching level of tip of stylocerite; lateral spine on scaphocerite extending to about midlength of ultimate podomere of antennular peduncle, falling short

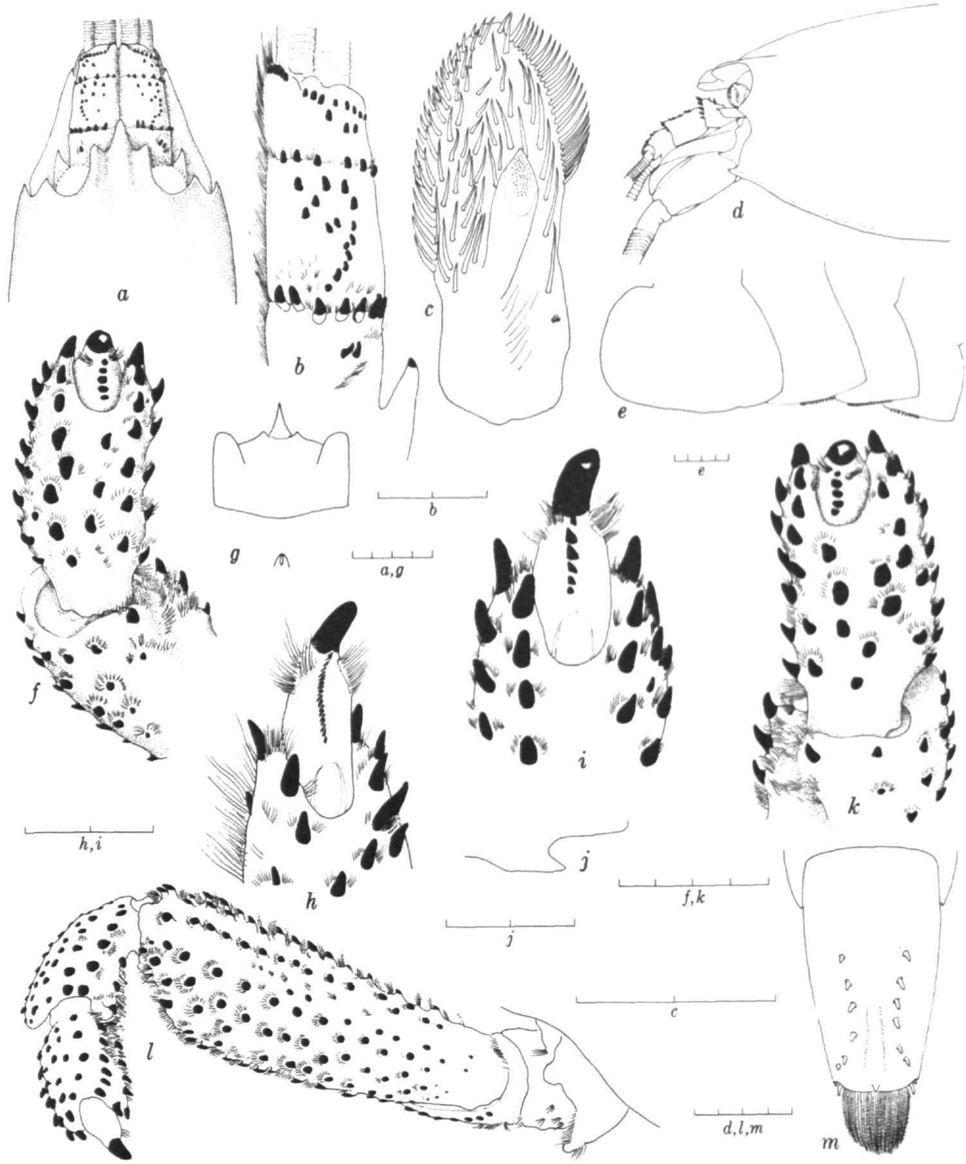

FIGURE 37.—*Atya margaritacea* (all from syntypic male): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view of cephalic region; *e*, lateral view of second through fifth abdominal pleura; *f*, flexor surface of distal part of right third pereiopod; *g*, preanal carina, sternum of sixth abdominal segment, and median tubercle of fifth; *h,i*, flexor surface of distal part of fifth and fourth pereiopods, respectively; *j*, lateral view of preanal carina; *k*, flexor surface of distal part of left third pereiopod; *l*, lateral view of third pereiopod; *m*, dorsal view of telson. (Scales marked in 1 mm increments.)

of distal end of peduncle of antenna; lamella of scaphocerite overreaching peduncles of both antennule and antenna. Flagellum of antenna broken.

Third maxilliped overreaching antennular peduncle by about 0.25 length of ultimate podomere of endopod; tip of exopod reaching base of apical third of penultimate podomere, latter about 1.6 times as long as ultimate.

First pereiopod reaching base of distal third of ultimate podomere of antennular peduncle; second pereiopod attaining distal fourth of fingers of first; terminal brush of both appendages apparently lacking scraping denticles. Third pereiopod (Figure 37*f,k,l*) lacking spines, and, when extended anteriorly, overreaching antennular peduncle by length of distal three-fourths of carpus and entire propodus and dactyl. Merus with ventromesial margin bowed, 2.6 times as long as high, twice as long as carpus, and 2.4 times as long as propodus; latter 1.8 times as long as wide and 0.9 as long as carpus; distoventral margin of coxa with prominent tubercle, otherwise gently curved (not scalloped), and mesial caudoventral prominence setiferous but very weak. Lateral, dorsal, and ventral surfaces of merus studded with linear series of large tubercles bearing cornified discs, free margins of which sharp; each tubercle flanked by semicircular cluster of conspicuous plumose setae; longitudinal row of long setae on lateral surface made inconspicuous by setae flanking subtending tubercles; mesial extremity of podomere produced in moderately strong lobe at level of mesial articular condyle of carpus. Carpus strongly tuberculate, tubercles tipped with corneous discs, latter increasingly produced toward distal end of podomere, tubercles flanked distally by setae as on merus, setae long and forming conspicuous tufts ventrolaterally. Propodus also strongly tuberculate with corneous apices ranging from scalelike proximally to clawlike distally, those on flexor surface somewhat irregularly dispersed (none arranged in contiguous or subcontiguous linear series); clusters of plumose setae on lateral surface conspicuous at least proximally. Dactyl movable, its flexor surface with single longitudinal row of 5 denticles flanked distally by paired setal clusters.

Fourth pereiopod with dactyl reaching end of proximal fourth of carpus of third; length of merus 2.3 times as long as carpus, latter slightly shorter than propodus. Fifth pereiopod (lacking propodus and dactyl) with merus about 1.4 times as long as carpus. Ornamentation of merus, carpus, and propodus of fourth pereiopod consisting of strong distoventral spine on both merus and carpus, smaller ventral spine at base of distal third on merus, and row of 3 corneous tubercles on distolateral margin of carpus; distal ventrolateral part of merus, entire ventrolateral part of carpus, and proximolateral two-thirds of propodus with conspicuous tufts of long plumose setae. Ornamentation of merus and carpus of fifth pereiopods similar to that of fourth except merus of right with 2 ventral spines and 4 instead of 3 distolateral tubercles on carpus.

Diaresis of lateral ramus of uropod flanked proximally by row of 16 articulated corneous denticles and fixed spine at lateral end of row.

COLOR NOTES.—The following remarks concerning the color of this shrimp are based on transparencies of specimens from El Vallé, Panama, lent by Bruce E. Felgenhauer and on observations he kindly communicated to us. He has observed what he terms three "fairly distinct phases": in juveniles the ground color is light brown and there are two or three transverse dark bands on the abdomen; larger individuals are dark brown, resembling adult *A. tenella* (= *A. innocous*) and the largest become uniformly blue-black.

In the transparencies of an individual with a carapace length of eight mm, the only conspicuous markings are two dark transverse bands, one spanning the posterior margin of the carapace and anterior part of the first abdominal segment, and the other extending across the anterior half of the sixth abdominal segment. A few dark patches occur dorsally, one pair situated lateral to the base of the rostrum, and another in the posterior gastric region.

The photograph of an animal with a 20 mm