The Shrimp Genus *Atya* (Decapoda: Atyidae)

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and
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ABSTRACT

Hobbs, Horton H., Jr., and C.W. Hart, Jr. The Shrimp Genus *Atya* (Decapoda: Atyidae). *Smithsonian Contributions to Zoology*, number 364, 143 pages, 53 figures, 1 table, 1982.—The genus *Atya*, as characterized in this study, comprises an assemblage of 11 tropical freshwater species ranging through the Antilles and along the Atlantic and Pacific versants of Middle and South America and in western Africa. The literature related to these shrimps is reviewed, and the taxonomic characters are discussed. Correlations of carapace length and total length are presented, and ecological and life history data reviewed. A discussion of relationships and dispersal is followed by a definition of the genus, its range, and a key to the species. For each of the latter, a complete synonomy, a review of the literature, a summary of available illustrations, a diagnosis, an illustrated description, the range, a list of localities and the specimens examined, observed variations, its ecological distribution, and life history notes are provided. *Atya brachyrhinus*, known to occur in only a single cave on Barbados, West Indies, is the only new taxon introduced. Four species are largely restricted to the Pacific slope of the Americas: *Atya crassa*, *A. dressleri*, *A. margaritacea*, and *A. ortmannioides*; two are confined to the Antilles: *A. brachyrhinus* and *A. lanipes*; two to Africa: *A. africana* and *A. intermedia*. Two species occur in the Atlantic versant of both continents: *A. gabonensis* and *A. scabra*; and only one, *A. innocous*, is widespread on both slopes of Middle America, although *A. crassa* and *A. scabra* are known to occur in a few localities on the Atlantic and Pacific slopes, respectively.

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Contents

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Introduction

The present study was prompted by the receipt of a collection of shrimps from Brazil containing specimens of *Atya gabonensis* Giebel, 1875, that lent credence to the report of Koelbel, 1884, that his *Evatya sculptilis* (a subjective junior synonym of *A. gabonensis*) indeed had been collected in the Orinoco River. In preparing an announcement of the rediscovery of this shrimp on the South American continent, one of us (Hobbs) reviewed the most readily available information concerning the American members of the genus *Atya* and in so doing became aware of the need for both bringing together what is known about these shrimps and for a critical study of the species that have been assigned to the genus.

This summary of the present state of our knowledge of the larger tropical African and American atyids includes as exhaustive a bibliography as we have been able to assemble. Previous work is reviewed, an analysis of taxonomic characters employed in recognizing the several species is offered, and a discussion of relationships and distribution prefaces a synonomy and definition of the genus. This is followed by a key to the 11 recognized species. Diagnoses and descriptions of each precede a statement of the range, list of localities, and enumeration of specimens examined. A discussion of variations, what is known of the ecological distribution and life history, occasional remarks, and illustrations conclude the sections devoted to each. The common names and economic importance of certain members of the genus are pointed our under the treatments of *Atya innocous* (Herbst, 1764) and *Atya scabra* (Leach, 1815).

ACKNOWLEDGMENTS.—Many persons have assisted us in this study that has elicited the greater part of our attention over a period of some two years. We are most grateful to those individuals who have lent specimens to us, many collections representing previously unpublished locality records: Lawrence G. Abele of Florida State University; Jorge A. Cabrera J. of the Instituto de Biología, Universidad Nacional Autónoma de México; Jacques Forest of the Muséum National d'Histoire Naturelle, Paris; Willard D. Hartman of the Peabody Museum, Yale University; Lipke B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden; Raymond W. Ingle of the British Museum (Natural History); Catharine Kessler and Herbert W. Levi of the Museum of Comparative Zoology, Harvard University; C. Bruce Powell of the University of Port Harcourt, Nigeria; and Alejandro Villalobos F. of the Universidad Autónoma Metropolitana Iztapalapa, Mexico. The courtesies extended to one of us (Hart) by Drs. Forest, Holthuis, and Ingle during

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visits to their respective museums are also appreciated. For lending us the atyid section of his manuscript treating the shrimps of the Philippines and Indonesia, we are grateful to Fenner A. Chace, Jr., of the Smithsonian Institution, as we are for his criticisms of the penultimate draft of this paper. For information concerning types, we acknowledge with gratitude the assistance of H.-E. Gruner of the Zoologisches Museum, Berlin; Charlotte Holmquist of the Naturhistoriska Rijksmuseet, Stockholm; and Gerhard Pretzmann of the Naturhistorisches Museum, Vienna. We also extend our thanks to Bruce E. Felgenhauer of Florida State University for lending us color photographs of *Atya margaritacea* and *A. innocous* from Panama, for observations he had made on the color of these two shrimps, and for forwarding to us a copy of his unpublished manuscript, coauthored with Dr. Abele, reporting observations on the mating behavior of the latter shrimp.

For their advice and assistance in statistical analyses, we thank J.W. Craig and Lee-Ann Hayek of the Smithsonian and J.L. Russo of the National Marine Fisheries Service. The help of Janice Clark in obtaining measurements and assisting in the preparation of the maps and of Carolyn B. Gast, who inked the illustrations in Figures 2, 3, and 5, is gratefully acknowledged.

We are deeply indebted to Lipke B. Holthuis not only for criticisms of the manuscript but also for his having contributed many of the bibliographic references of which we were unaware and for providing us with the citation of Gerstaecker and Ortmann (1891–1901), collating the various sections therein with dates of publication. We acknowledge his invaluable assistance with genuine appreciation. For their suggestions and criticisms of the manuscript, we also thank Lawrence G. Abele, C. Bruce Powell (who assisted us with much of the literature pertaining to the African *Atya*), and the following Smithsonian colleagues: Margaret A. Daniel, Raymond B. Manning, and Isabel Pérez Farfante. Ms. Daniel deserves special thanks for her varied assistance throughout the course of this study. We acknowledge with appreciation the indispensable assistance of Carolyn S. Hahn and Jack F. Marquardt of the Smithsonian Library in obtaining a number of references that are included in the "Literature Cited" herein. For her help in ferreting errors in references throughout the text, we are grateful to Georgia B. Hobbs.

Finally, we extend our thanks to S. Dillon Ripley, Secretary of the Smithsonian Institution, who provided financial aid that made possible visits to the museums noted above.

COLLECTIONS STUDIED.—Most of the materials mentioned or that were examined during this study are in the collections of the following museums or persons.

BM	British Museum (Natural History), London, England
IBM	Instituto de Biología de la Universidad Nacional Autónoma de México, México, D.F., Mexico
LGA	collection of Lawrence G. Abele, Florida State University, Tallahassee, Florida, USA (recently donated to USNM)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MHNP	Muséum National d'Histoire Naturelle, Paris, France
NMW	Naturhistorisches Museum Wien, Vienna, Austria
PM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
SMNH	Naturhistoriska Riksmuseet, Stockholm, Sweden
USNM	former United States National Museum collections deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZBM	Zoologisches Museum der Humboldt-Universität, Berlin, East Germany

A Brief History of the Genus *Atya*

Although the literature dealing with the individual species is discussed for each, a brief account of the attention that has been accorded the members of the genus seems appropriate here. The earliest report of the existence of a species belonging to the genus *Atya* that we have encountered is that of Marcgrave (1648), who presented an illustration and a brief description of "Guaricuru" in Brazil, a common name that was identified with *Atya scabra* by Lemos de Castro (1962). Marcgrave's description (p. 187) was as follows.

Guaricuru Brasiliensibus, Gammarus vulgo Camaraon; quatuor digitos longus: crura habet sex, tribus internodiis constantia, cum unguiculo in extremitate: anterius par crurum quasi suras habet, crassius relinquis & vicem brachiorum fungens; paulo plus duobus digitis longum: medium parses quidigitum longum, ultimum paulo plus uno, omnia aculeata seu spinosa. Cirrhos prope os prodeuntes habet sex; duos longissimos, nimirum tres digitos singulos, versus posteriora reflexos; duos unum digitum, & duos unum digitum, & duos femidigitum: sub ore parva tenacula quatuor crassiuscula, & quatuor tenuiora, quibus cibum tenet. Oculi fimiles reliquis. Color totius fuscus. Cocti eduntur.

The notice of a second shrimp that is currently assigned to the genus *Atya* was that of Gronovius (1764), who described and illustrated "Astacus 988" from "Oceano Americano ad Martinicam." This shrimp was later designated "Astacus Nasoscopus" by Meuschen (1778) and "Cancer (Astacus) Innocous" by Herbst (1792)—descriptions based on the specimen described by Gronovius (Meuschen's publication was declared invalid in Opinion 260 of the International Commission on Zoological Nomenclature (1954:267)).

Leach (1815) introduced the name *Atys scaber* for a shrimp from an unknown locality, emending it to *Atya scabra* the following year. The name *Atya mexicana* was proposed for a shrimp from Mexico by Wiegmann (1836), and Newport (1847) described *Atya sulcatipes* from the Cape Verde Islands and *Atya occidentalis* from Jamaica. Some 17 years later, A. Milne-Edwards (1864) applied the names *Atya margaritacea* and *A. robusta* to specimens that were thought to have been collected on New Caledonia. Shrimps that had been obtained from streams on the Pacific slope in Guatemala provided the material on which Smith (1871) named *Evatya crassa*, *Atya rivalis*, and *Atya tenella*. A shrimp from Gabon was designated *Atya gabonensis* by Giebel (1875), and three years later Kingsley (1878a) described *Atya punctata* from Haiti. An ornate member of the genus from "the Orinoco" was made known by Koelbel (1884), who designated it *Euatya sculptilis*. Ortmann (1890) applied the name *Atya sculptata* to a shrimp from western Africa, and two specimens from Cameroon were designated a variety of A. Milne-Edwards' species, *Atya margaritacea* var. *claviger*, by Aurivillius (1898). Thus by 1900, 13 species and one varietal name had been applied to the shrimps herein recognized as belonging to the genus *Atya*.

Bouvier's (1904) study of shrimps belonging to the genus included the descriptions of two new members from Africa: *Atya africana* from the Ogooué River, Gabon, and *A. intermedia* from São Tomé. Most of the above were reviewed in Bouvier's monograph (1925); the synonyms, excluding misidentifications, recognized by him are included in the following list. Not until *Atya ortmannioides* was described from the Pacific versant of Mexico by Villalobos (1956) was additional information added to our knowledge of the composition of the genus, and about seven years later the presence of *Atya lanipes* on Saint Thomas, Virgin Islands, was made known by Holthuis (1963). The latter (1966) presented a noteworthy analysis of the taxonomy of several of the species, comparing *A. scabra* with *A. sulcatipes* and *A. rivalis*. He declared "*Atya margaritaria clavipes*" a synonym of *A. sulcatipes*, restricted the name *A. scabra* to "the East American species," and recognized *A. mexicana*, *A. margaritacea*, and *A. punctata* as synonyms of *Atya scabra*. *Atya intermedia* was contrasted with *A. sulcatipes*, and he noted the close affinity of the former with *A. innocous* Herbst. The validation of this name and Holthuis' clarification of its synonomy constituted a particularly valuable contribution. Although in 1966 he did not mention *A. lanipes*, *A. crassa*, and *A. gabonensis* or present formal synonymical lists, his concept of the existing species of larger atyids seems to have been as noted in the following list. The only species described since the publication of Holthuis' just-mentioned contribution is *Atya dressleri* from Panama by Abele (1975). The species and synonyms recognized herein are noted in the list below.

Other important contributions to our knowledge of members of the genus are the morphological study of *Atya scabra* by Villalobos (1943), the observations and illustrations of Chace and Hobbs (1969), the studies on the larval stages of *A. lanipes* and *A. innocous* by Hunte (1975, 1977, 1979b), and the work on functional morphology and ecology of *A. innocous* and *A. scabra* by Fryer (1977).

COMPOSITION OF THE GENUS *Atya* AS DEFINED HEREIN

(Shrimp names enclosed in parentheses signify synonyms of the species under which they are listed)

BOUVIER (1925)	HOLTHUIS (1966)	PROPOSED HEREIN
Atya africana Bouvier, 1904	*Atya africana*	*Atya africana*
Atya intermedia Bouvier, 1904	*Atya intermedia*	*Atya intermedia*
	Atya innocous (Herbst, 1792)	*Atya innocous*
Atya robusta A. Milne-Edwards, 1864	(*Atya robusta*)	(*Atya robusta*)
Atya occidentalis Newport, 1847	(*Atya occidentalis*)	(*Atya occidentalis*)
(*Atya tenella* Smith, 1871)	*Atya tenella*	(*Atya tenella*)
Atya scabra (Leach, 1815)	*Atya scabra*	*Atya scabra*
(*Atya mexicana* Wiegmann, 1836)	(*Atya mexicana*)	(*Atya mexicana*)
(*Atya punctata* Kingsley, 1878a)	(*Atya punctata*)	(*Atya punctata*)
		(*Atya sulcatipes*)
		(*Atya margaritacea claviger*)
(*Atya margaritacea* A. Milne-Edwards, 1864)	(*Atya margaritacea*)	*Atya margaritacea*
(*Atya sulcatipes* Newport, 1847)	*Atya sulcatipes*	
(*Atya margaritacea* var. *claviger* Aurivillius, 1898)	(*Atya margaritaria clavipes*)	
(*Atya rivalis* Smith, 871)	*Atya rivalis*	(*Atya rivalis*)
Atya gabonensis Giebel, 1875	not mentioned	*Atya gabonensis*
(*Euatya sculptilis* Koelbel, 1884)	not mentioned	(*Euatya sculptilis*)
(*Atya sculptata* Ortmann, 1890)	not mentioned	(*Atya sculptata*)
Evatya crassa Smith, 1871	not mentioned	*Atya crassa*
	not mentioned	*Atya ortmannioides* Villalobos, 1956
	not mentioned	*Atya lanipes* Holthuis, 1963
		Atya dressleri Abele, 1975
		Atya brachyrhinus, new species

Taxonomic Characters

Those features that have been found to be of use in distinguishing between, or may be consistent among, the several species of the genus *Atya* are briefly discussed in the following paragraphs. Except in secondary sexual characters there are only slight differences in the males and females of all members of the genus, and we have noted few apparent differences in these features between species.

CARAPACE.—Among the surface structures of the carapace that have been found to serve as useful taxonomic features are the sculpture and gross texture. Only two of the recognized species exhibit conspicuously sculptured features: in *Atya crassa* there are ridges studded with spines over much of the cephalic region, and the corresponding areas in *A. gabonensis* exhibit strong ridges that lack spines. Larger individuals of *A. scabra* and *A. margaritacea* bear rugose, somewhat weaker sculptured cephalolateral regions, but there is little irregularity in the carapace of smaller individuals.

In *A. scabra* and *A. margaritacea* the carapace, especially the lateral regions, is studded with a comparatively dense pile of short stiff brown setae

that may become abraded in later intermolt stages, and is lacking or represented by very small fine setae in the glabrous *A. innocous* and *A. lanipes*. In collecting living specimens of *A. scabra* and *A. innocous* on Dominica, it was discovered that one need not look at the shrimp to recognize its identity, for if it could be held in one's hand for more than a few seconds it was indeed *A. scabra*. The glabrous carapace of *A. innocous* makes members of this species almost impossible to grasp for any length of time.

The size and sometimes at least the number of punctations on the carapace are highly variable. Such is particularly noticeable in available specimens of *A. scabra*. Even in specimens from a single locality, the size and density of punctations differ markedly. Never, however, are they so conspicuous in *A. innocous* or in *A. lanipes* and their allies as they frequently are in *A. scabra*.

The principal features of the rostrum that have proven to be useful in distinguishing between certain species are the presence or absence of a dorsomedian row of spines, the elevation of the median carina, and the contour of the lateral margins. The latter may taper rather gently from the base to the apex, may be contracted abruptly in an angular or subangular bend, or may even be notched. As pointed out by Holthuis (1966:235), however, in juveniles this character is not always reliable, for angles that are well marked or even subacute in the adult may be broadly rounded or almost imperceptible in young individuals. The size and ornamentation of the dorsal and ventral keels are subject to considerable intraspecific variation as are the span of the anterior extension, the subapical spines, and the depth of the sulci between the median and lateral carinae. The long acumen (apical part of the rostrum) of *Atya ortmannioides* furnishes perhaps the most ready character for recognizing members of this species.

In all representatives of the genus except *Atya dressleri* and some members of *A. ortmannioides* and *A. gabonensis*, the pterygostomian angle is rather strongly produced, often in a distinct spine. In the latter it is not so strongly developed as in most individuals of other species, and in *A. dressleri* the spine, if present, is usually much reduced in size although in the holotype it is moderately strong.

Abdomen.—The presence or absence of cornified denticles on the ventral margins of the second through the fifth abdominal pleura aids in the recognition of certain species. Their occurrence on the second is characteristic of most members of *Atya scabra*, but occasional specimens from the western Atlantic versant and all of those in the eastern Atlantic watershed lack such spinules on that pleuron. Similar denticles are sometimes present on only the fifth pleuron in *A. africana*, but some specimens exhibit none. In *A. innocous*, the denticles are more delicate, and there is tremendous variation in the presence (number and conspicuousness) or absence on one or all of the third through fifth pleura. (See "Variations" under *Atya innocous*.) Such denticles have not been observed in *A. crassa*, *A. dressleri*, *A. gabonensis*, *A. intermedia*, *A. lanipes*, and *A. ortmannioides*.

Sternum of Fifth Abdominal Segment.—In all members of the genus except *Atya crassa* and *A. gabonensis*, the narrow sternal bar between the fifth pleopods bears a comparatively small, often laterally compressed, ventrally directed tubercle. In *A. crassa*, however, the tubercle is moderately to strongly developed, and in *A. gabonensis* it is comparatively enormous, resembling a curved horn, the apical end of which presses against the sternum of the sixth abdominal segment when the "tail fan" is flexed. This prominence actually prohibits complete flexion of the abdomen in this shrimp.

Sternum of Sixth Abdominal Segment.—The sternal element of this segment consists of a plate that covers almost the entire ventral surface of the segment; thus it spans the distance between the pleura and extends from the posterior membranous part of the fifth sternal area to the ventral base of the telson, bearing a posteromedian notch that receives the base of the preanal carina. The relative dimensions of this plate are useful in distinguishing between certain species (see Figure 1). The longer plates occur in *A. lanipes* and *A. ortmannioides*, and the shorter ones are typical of *A. crassa* and *A. gabonensis*; in the remaining spe-

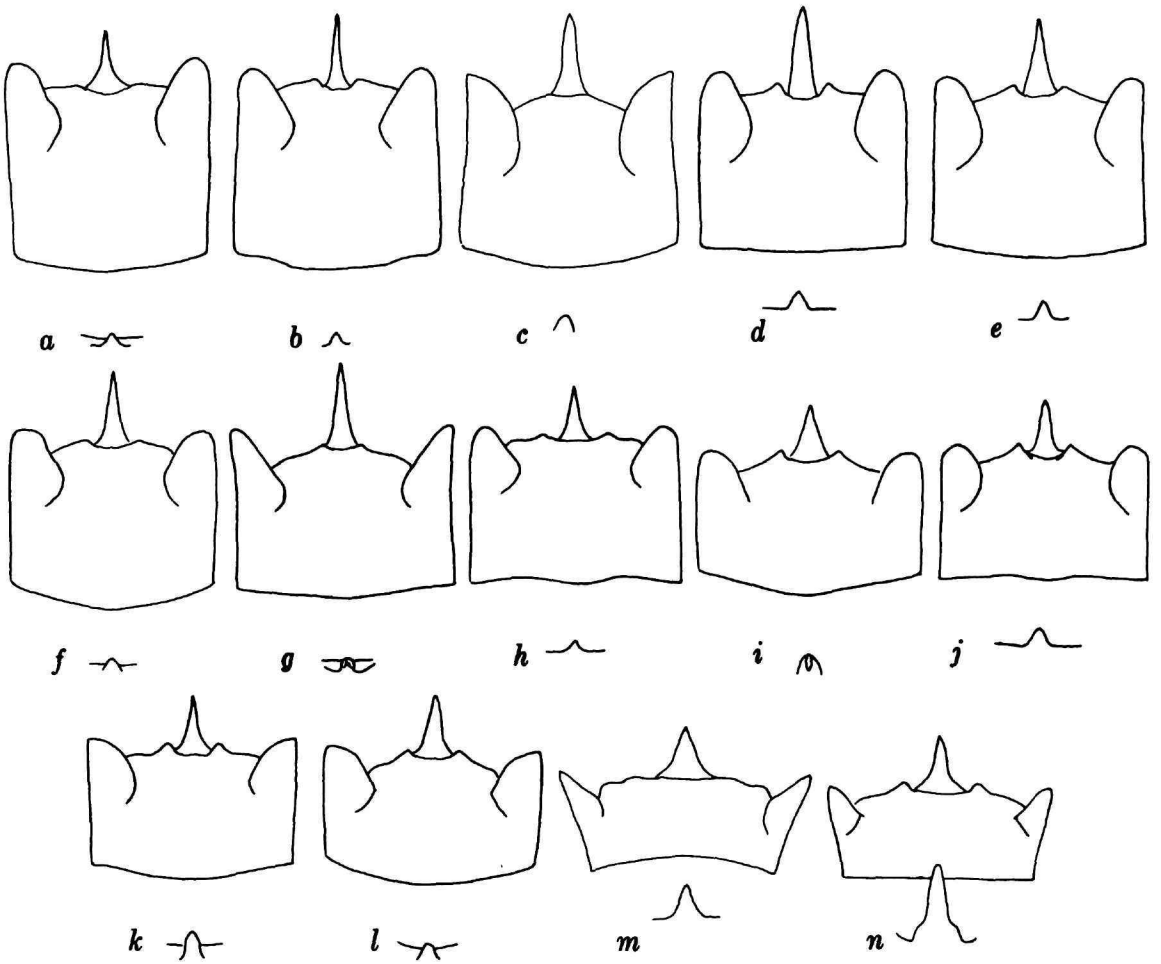

FIGURE 1.—Ventral view of preanal carina, sternum of sixth abdominal segment, and median tubercle (or projection) on fifth abdominal segment in: *a*, *Atya lanipes*; *b*, *A. ortmannioides*; *c*, *A. brachyrhinus*; *d*, *A. innocous*; *e*, *A. tenella* (= *A. innocous*); *f*, *A. intermedia*; *g*, *A. dressleri*; *h*, *A. africana*; *i*, *A. margaritacea*; *j*, *A. rivalis* (= *A. margaritacea*); *k*, *A. scabra*; *l*, *A. sulcatipes* (= *A. scabra*); *m*, *A. crassa*; *n*, *A. gabonensis*.

cies the length of the plate is intermediate between these extremes.

TELSON.—The ratio of the length to the width of the telson is useful in separating certain species from others. Among the specimens measured belonging to several species, the ratios range from 1.2 to 3.0 and are dispersed as follows: *Atya africana* 1.8 to 1.9, *A. crassa* 1.2 to 1.4, *A. dressleri* 1.9 to 3.0, *A. gabonensis* 1.2 to 1.5, *A. innocous* 1.9 to 2.2, *A. lanipes* 2.1 to 2.6, *A. margaritacea* 1.6 to 1.8, *A. ortmannioides* 2.0 to 2.7, and *A. scabra* 1.6 to 1.9. The numbers of spines on each side of the dorsal surface range from 7 to 9 in *A. dressleri* to no more than 5 in *A. africana*, *A. crassa*, and *A. gabonensis*. In the remaining species there are 5 or 6 in *A. lanipes* and *A. margaritacea*, 5 to 7 in *A. scabra*, and 5 to 8 in *A. innocous*, *A. ortmannioides*, and probably also in *A. brachyrhinus*, of which only two specimens are known.

Except in injured specimens the caudal margin

of the telson is uniformly provided with two pairs of posterolateral spines situated mesial to the posterolateral angles; the more mesial pair is longer. Between these spines is a row of strong plumose setae flanked dorsally by a row of much finer ones, and there is a dorsomedian tubercle that may or may not reach or overreach the caudal margin of the telson.

PREANAL CARINA.—Details of the form of the preanal carina are highly variable, but despite the variability its form is diagnostic for at least three species. The more distinctive ones are those of *Atya lanipes* (in which the spine is sometimes absent or vestigial), *A. gabonensis* (in which it is subconical and directed almost ventrally), and *A. intermedia* (in which there exist two posteriorly directed spines). In the other species the carina is less distinctive, although it is subconical in *A. crassa*.

OCELLAR BEAK.—This is a median prominence situated between the eyes that in the alpheids was designated the "bec ocellaire" by Coutière (1899:108); it was referred to as the "carène antennulaire" by Bouvier (1925:23). In all of the members of the genus *Atya* except *A. gabonensis*, it is comparatively inconspicuous (concealed by the rostrum above, the eyes to the sides, and the antennules below). In *A. gabonensis*, however, it is produced in a dorsally arched blade that ends in an acute apex reaching almost as far anteriorly as the tip of the stylocerite.

ANTENNULE.—The size and the intensity of cornification of the spinules, or denticles, on the dorsal surface of the three articles of the antennular peduncle are in part reflections of both the size of the individual and the stage in the molting cycle, the dark coloration intensifying during intermolt stages. Except in small individuals their distribution or absence (especially on the dorsal surface of the basal segment proximal to the distal marginal row) in combination with other features aids in recognizing certain species. For example, premarginal spinules occur typically on the dorsal surface of the proximal segment in *Atya africana*, *A. gabonensis*, *A. scabra*, and sometimes in *A. margaritacea*. The combination of this feature with tapering rostral margins is unique to the former species, and the occurrence of such spinules, angular rostral margins, and a row of contiguous scales on the flexor surface of the propodus of the third pereiopod are peculiar to *A. scabra*. Spinules unaccompanied by tapering rostral margins or a linear series of scales on the flexor surface of the comparatively short propodus of the third pereiopod are characteristic of *A. gabonensis*. The sublinear arrangement of the spinules on the lateral part of the dorsal surface of the penultimate podomere of the antennule in *A. margaritacea* usually serves as an accessory characteristic that may be used in distinguishing this shrimp from the closely allied *Atya scabra*. Useful also are the numbers of spinules on the dorsal surface of the distal two podomeres of the peduncle as are those in the distal rows of all three podomeres.

To some degree, the ratio of length to width of the three podomeres of the antennule, especially the penultimate, provides an additional feature that aids in the recognition of certain species, but the range of intra- and interpopulational variation is rather broad. The attenuation of all of the pereiopods in *A. lanipes* is conspicuous, and this is decidedly apparent in both the peduncle and flagella of the antennule. As compared with *A. scabra*, for example, the proximal thickened part of the lateral flagellum is longer and is less markedly set off from the distal more slender section.

ANTENNA.—We have found no feature of the antenna except possibly the lateral spine on the scaphocerite that might be useful in distinguishing between the various species of the genus. We have not attempted to quantify the relative degree of development in the several species, but it seems to be much more prominent in some than in others.

GNATHAL APPENDAGES.—To provide an appreciation of the structure of the gnathal appendages, we have chosen to illustrate those of *Atya innocous* (Figure 2; see also Fryer, 1977), which seem as generalized as any. Minor differences, chiefly in the development of setae, seem to exist between some of the species, although none that we have noted are any more striking than that exhibited by the shape of the flagellar lobe of the first maxilliped in *A. innocous* and *A. gabonensis* (cf.

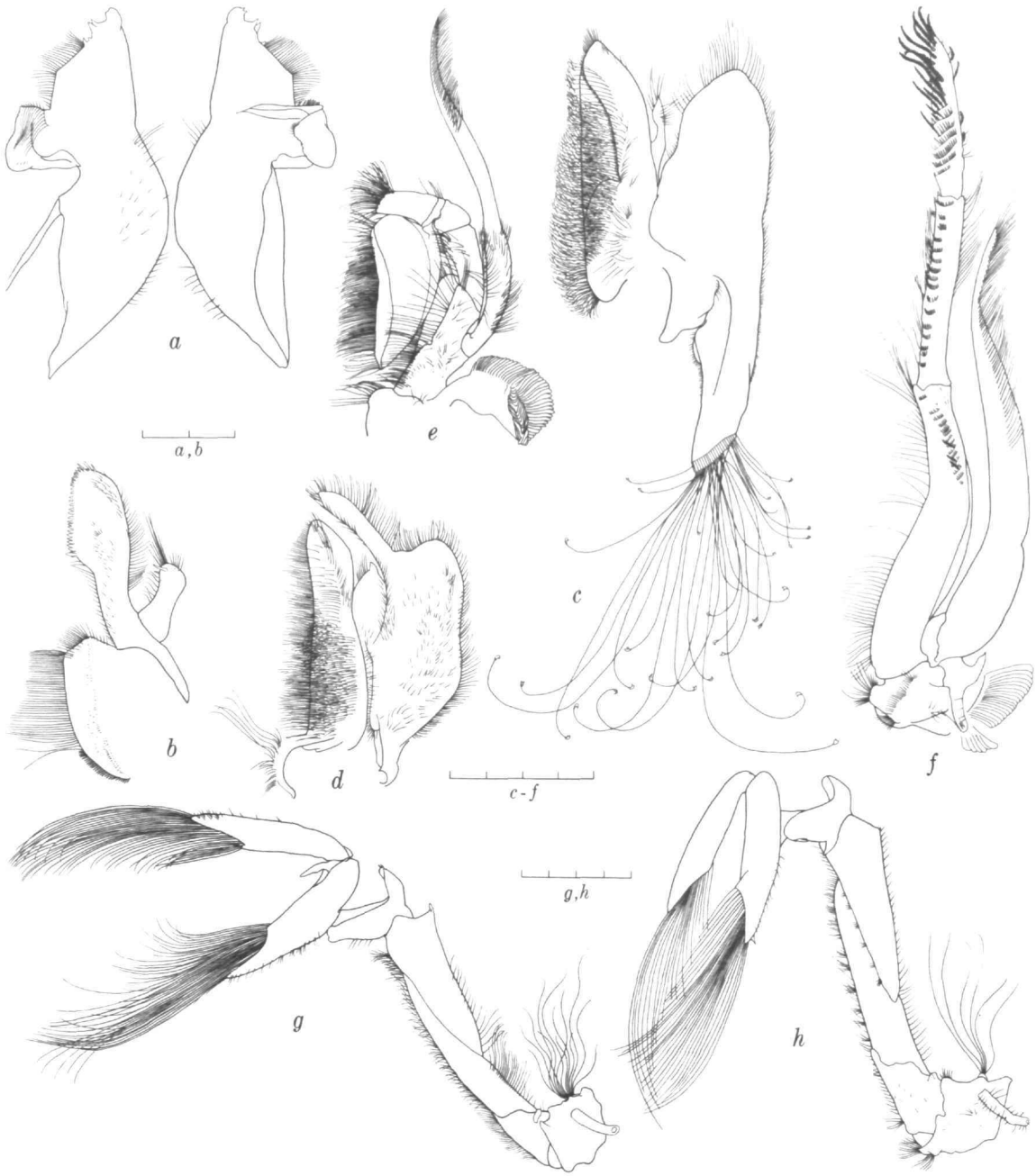

FIGURE 2.—Appendages of *Atya innocous* (all from male, Mannet's Gutter, Dominica): *a*, lateral and submesial views of mandible; *b*, first maxilla; *c*, second maxilla; *d*, first maxilliped; *e*, second maxilliped; *f*, third maxilliped, *g*, first pereiopod; *h*, second pereiopod. (Scales marked in 1 mm increments.)

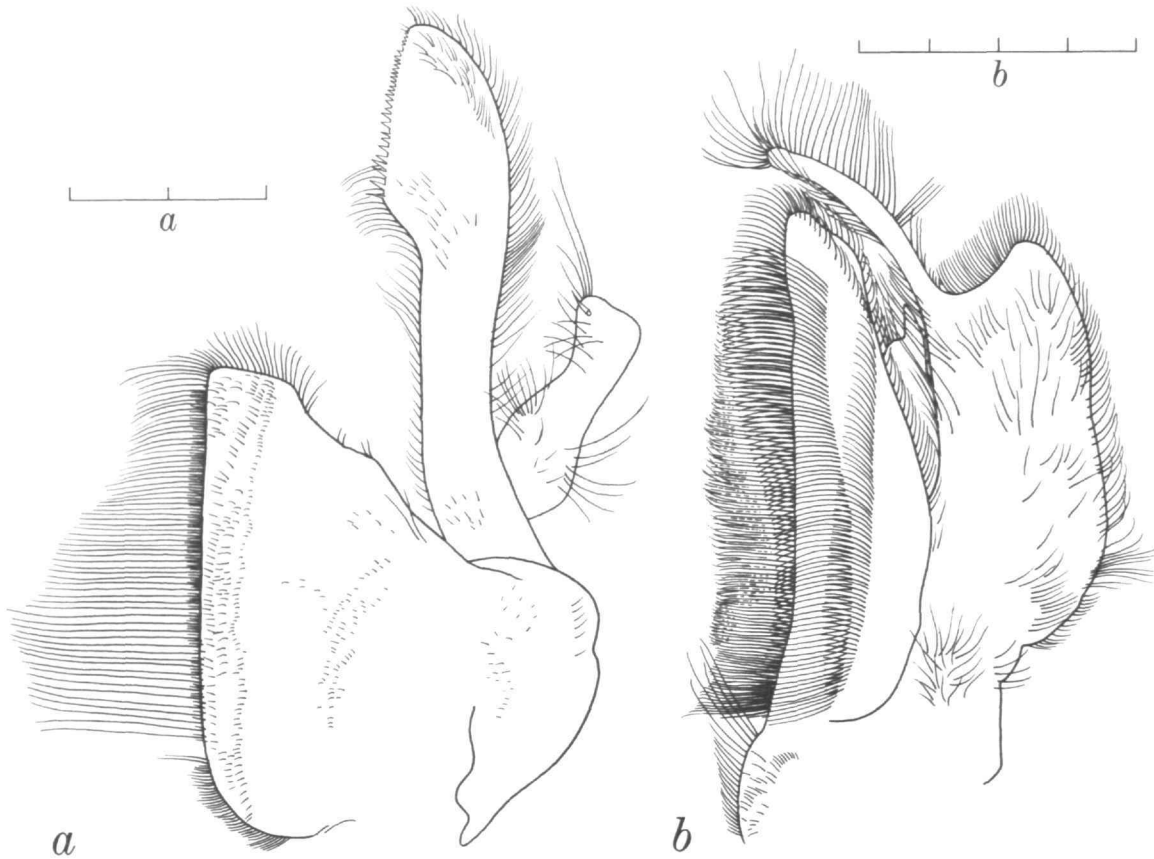

FIGURE 3.—Gnathal appendages of male of *Atya gabonensis* from Volta River, Ghana: *a*, first maxilla; *b*, first maxilliped. (Scales marked in 1 mm increments.)

Figures 2*d* and 3*b*). The relative length of the exopod of the third maxilliped in comparison to that of the endopod seems to be consistent, as does the range of numbers of bands of setae on the distal two podomeres; however, we have not examined a sufficiently large series to be assured that our preliminary observations are valid.

FIRST AND SECOND PEREIOPODS.—There is remarkable uniformity in the structure of the first and second pereiopods in all members of the genus. Minor variations have been noted in the form, length, and perhaps density of the setal tufts capping the distal extremities of the fingers, but to what extent these differences are governed by the stage of the molting cycle is not clear to us, and we are puzzled by the absence of setae that bear scraping denticles in some specimens of those species that often, if not usually, exhibit them.

In his study of functional morphology in the atyids of Dominica, Fryer (1977:58) pointed out that some of the terminal "bristles [of the chelipeds] of *A. innocous* are armed distally with minute denticles . . . that facilitate scraping and sweeping: no such are present in *A. scabra*. The difference is related to the relative importance of scraping in the two species: *A. innocous* scrapes frequently, *A. scabra* seldom." The setae of the chelae of the remaining species recognized herein have been examined, and the denticulate setal type has

been found only in *A. innocous* and *A. lanipes*. Villalobos (1956:466) also found them in *A. ortmannioides*. On the basis of our limited examinations, such setae cannot be said to be typical of all individuals of any of the three species, for we failed to find them in a number of specimens of *A. innocous* from several localities on Dominica, and they were not evident in our preparations of samples from *A. ortmannioides*. When they are present, however, there is reason to believe that the shape of the denticles may well serve as diagnostic features, as they seem to be for *A. innocous* and *A. lanipes* (cf. Figure 4*a*,*b*),

THIRD PEREIOPOD.—Among the most useful characters for distinguishing between the several species are those associated with the third pereiopod. The coxa of *Atya crassa* is unique in two respects: the ventrodistal margin is distinctly scalloped, and the anterolateral angle of this podomere on both the third and fourth pereiopods each bears a heavy spine. Another useful feature of the coxa is the degree of development or absence of a posteromedian prominence bearing setal tufts. Whereas it is strongly developed in *A. crassa* and *A. gabonensis*, moderately so in *A. margaritacea* and *A. scabra*, it is absent in *A. dressleri*, *A. lanipes*, and *A. ortmannioides*. Equally as useful are features of one or more of the distal four podomeres. For example, the ratios of their length to width serve readily to distinguish *Atya lanipes* (merus) and *A. crassa* (propodus) from other species. The absence of tubercles (sometimes few very weak ones present) or spines on the lateral surface of the merus is characteristic of *A. lanipes*, and the presence or absence of strongly sclerotized extremities of spines or scalelike tubercles aids in

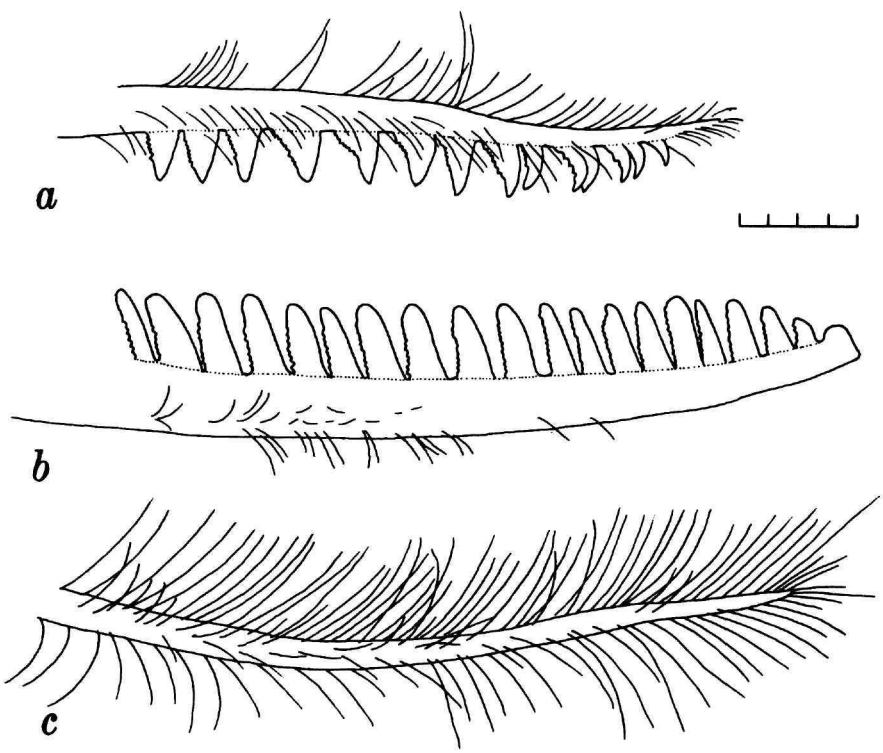

FIGURE 4.—Bristles from distal tufts of first pereiopod: *a*, distal part of bristle bearing scraping denticles in *Atya innocous*; *b*, same in *A. lanipes*; *c*, distal part of bristle that serves as a brush seta in *A. lanipes*. (Scales marked in 1 mm increments.)

separating certain species from others. The row of contiguous or subcontiguous, strongly cornified "scales" or spines on the mesioflexor surface of the propodus distinguishes *A. africana* and *A. scabra* from the remaining members of the genus. The arrangement of denticles and/or spines on the flexor surface of the dactyl is also helpful: as pointed out above, the denticles (sometimes only one, or none) are limited to a small cluster at the base of the corneous tip of the dactyl in *A. crassa* and *A. gabonensis*; in three species they are arranged in a single row (*A. africana*, *A. margaritacea*, and *A. scabra*); in the remaining ones they are dispersed in two, sometimes irregular, rows.

The quantity and degree of development of pubescence on the pereiopods are variable as pointed out by Chace and Hobbs (1969:63), who noted that in none of their specimens of *Atya lanipes* from Puetro Rico are the pereiopods "clothed in hair dense enough to conceal the underlying surface" as they are in those from the type-locality. Hunte (1975:68) also observed that among his Jamaican specimens "the intensity and distribution of pubescence on the last three pereiopods is subject to much variation . . . ." The presence of a conspicuous oblique row of tufts of long plumose setae on the lateral surface of the merus has been observed in specimens of several species and are distinctly most obvious in individuals that have recently molted. Nevertheless the shaggy setal clusters on the third pereiopod of recently molted specimens of *A. crassa* seem to be unique.

The latter species is also unique in lacking a movable articulation between the propodus and dactyl of this appendage.

Fourth and Fifth Pereiopods.—Further study should be accorded the fourth and fifth pereiopods. The series of movable spines on the ventral and ventrolateral surfaces of the merus and carpus seems to be more numerous, if not proportionately better developed, in the young and tends to be lost (the more proximal ones on all podomeres disappearing first) as the animal increases in size. Because of inadequate samples in which series of stages are represented, we are uncertain as to whether or not the merus of the third and fourth pereiopods of small individuals of all species bears a row of three ventral spines and one distal ventrolateral spine. Evidence exists, however, that all have fewer with increasing size of body. Apparently there is not a direct intraspecific correlation between the number of persisting spines and the size of the shrimp.

The spinules on the flexor surface of the dactyl of the fifth pereiopod of *A. ortmannioides* (Figure 43*c*) form a pectinate row that has been observed infrequently in other species. A comparative study of this podomere in a series of specimens of each species might prove rewarding.

First and Second Pleopods.—In these appendages there is less variation between those of different species than between those of females of the same species at different stages of their adult life. There is evidence that in *Atya*, as in *Macrobrachium rosenbergii* (De Man) as pointed out by Nagamine and Knight (1980:147, 148, fig. 1), the prepartureal molt enhances the setation of the pleopods (cf. Figure 5*d* and 5*e*,*f*). This is accomplished largely by the addition of setae designated as "ovigerous" or "temporary" setae by Nagamine and Knight. In *Atya*, the molt following the ovigerous condition seems to result in a reduction of the ovigerous setae, returning the pleopods to a condition comparable to that existing prior to the prepartureal molt. Of course, many of the ovigerous setae disappear with the hatching of the eggs.

We found no conspicuous differences in these appendages in the males. There is considerable variation in the spination of the appendix masculina, but except that it is more elongate in *A. crassa* than in the other species no unique features in any of the species were apparent to us.

Branchial Complement.—The number and arrangement of the gills as reported for members of the genus *Atya* (sensu stricto) are, for the most part, consistent (Figure 6). Apparent variations have been noted, however, in elements associated with the second and third maxillipeds. Holthuis (1966:233) reported the presence of a pleurobranch on the body segment bearing the third

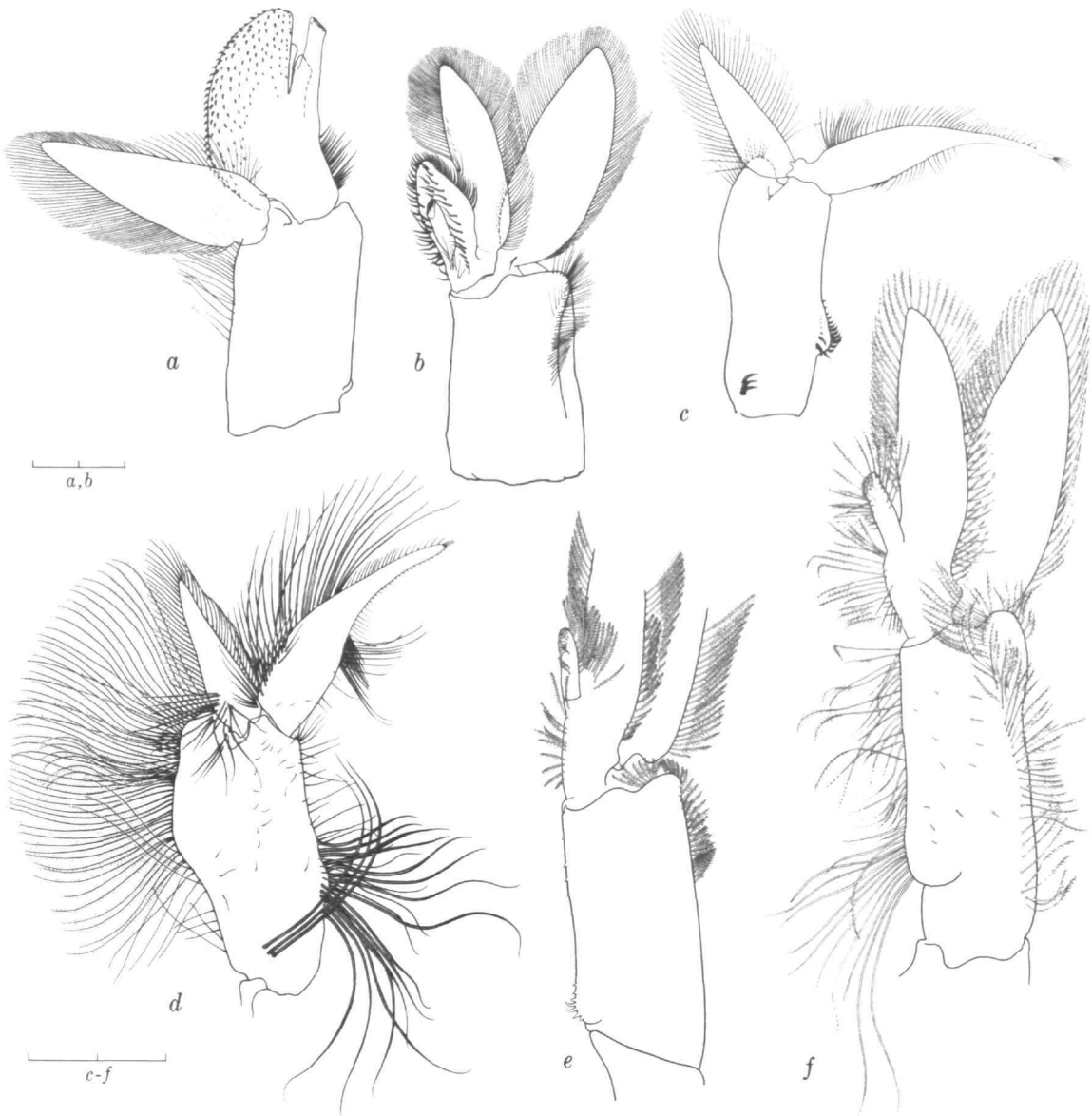

FIGURE 5.—Appendages of *Atya innocous* (all from Mannet's Gutter, Dominica); *a*, first pleopod of male; *b*, second pleopod of male; *c*, first pleopod of female; *d*, first pleopod of ovigerous female with ovigerous setae; *e*, basal part of third pleopod of nonovigerous female; *f*, third pleopod of ovigerous female. (Scales marked in 1 mm increments.)

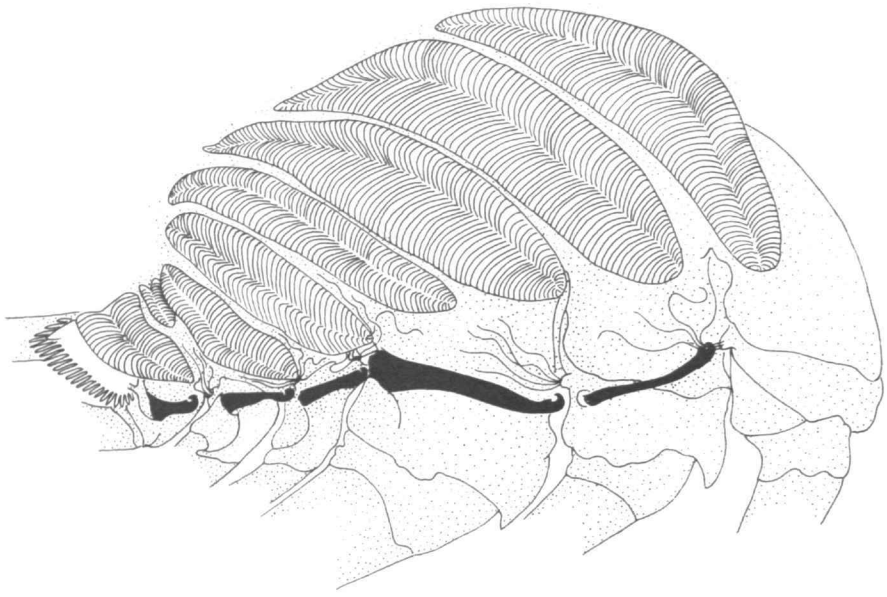

FIGURE 6.—Branchial apparatus of left side of *Atya innocous* (epipods black).

maxilliped in *Atya scabra* and *A. sulcatipes*, and Abele (1975:56) noted that one of the differences between *A. dressleri* and *A. lanipes* is in the absence in the latter of a podobranch on segment VIII. Whereas these observations may well reflect variations in the three species, all of the members of the genus that have been examined in the present study exhibit the following branchial apparatus and exopods on body segments VII through XIV shown in the accompanying tabulation.

Branchial Apparatus and Exopods

	VII	*VIII*	*IX*	*X*	*XI*	*XII*	*XIII*	*XIV*
pleurobranch				1	1	1	1	1
arthrobranch			2	1				
podobranch		1						
mastigobranch				1	1	1	1	1
epipod			1	1	1	1	1	
exopod	1	1	1					

REMARKS.—In the early stages of the present study one of the problems that we encountered was determining whether or not *Atya rivalis* differs from *A. scabra*. Some years ago, Alfred E. Smalley, of Tulane University, while on a visit to the Smithsonian Institution, told one of us (Hobbs) that large males of *Atya scabra* differ from those of *A. rivalis* in that a close-set row of "squamae" occurs on the ventral side of the third pereiopod. Chace and Hobbs (1969) pointed out and illustrated the "denticles" on the ventral surface of the second pleuron in *A. scabra* that are absent in *A. rivalis* (= *A. margaritacea*) and thus aid in separating the two. To our knowledge, however, nothing concerning the close set row of tubercles on the third pereiopod has been recorded. Having recalled Smalley's mentioning them, we found that this row, located on the flexor surface of the propodus, indeed serves not only to distinguish *A. scabra* from Smith's *A. rivalis* but also from any member of the genus except *A. africana*, and the difference in the "form" of the tubercles in the latter two is distinctive. Furthermore, this character becomes evident in juveniles of both sexes and persists in both (except perhaps in regenerated appendages) until death of the animals.

Fortunately, the syntypes of *A. margaritacea* are extant, and one of us (Hart) examined them in the Muséum National d'Histoire Naturelle (Paris). When it was discovered that the linear arrangement of the tubercles on the propodus was lacking, one of the specimens was borrowed

and subjected to further study by both of us. Comparisons of the borrowed syntypic male with specimens of Smith's *Atya rivalis* revealed no significant differences. Thus in our opinion, the types of *A. margaritacea*, which were thought to have been collected on New Caledonia, where no member of the genus (as defined here) occurs, were actually obtained from one or more streams on the Pacific slope of Central or South America. As we have noted elsewhere herein, the name *Atya rivalis* is a junior synonym of *Atya margaritacea* A. Milne-Edwards. On the basis of collections available to us, this shrimp appears to be limited to the Pacific slope of Middle and South America. Except in a few localities, *A. scabra* does not occur on the Pacific slope of the Americas but is widespread on the islands of the Gulf of Mexico-Caribbean, on the eastern slope of Mexico, and on the Atlantic versant of both South America and Africa.

Specimens of a second potential species pair, *Atya innocous* and *A. tenella*, reported to occur on the Atlantic and Pacific slopes of Middle America have been compared, and although some representatives of the two can be distinguished, the ranges of variation in the few characters in which they differ are so great and overlap to such an extent even within a local population that in our opinion the two must be considered to be conspecific.

Measurements and Size Correlations

Because several previous authors have referred to the sizes of their specimens by recording their total length (presumably the distance from the tip of the rostrum to the posterior extremity of the telson), and all of our references to size are given in terms of the carapace length (the distance from the posterior margin of the orbit to the midposterior margin of the carapace), we endeavored to determine whether there exists a close enough correlation between the two measurements to estimate one from the other. Further, we also wished to know whether or not the relationship between the two is the same for one or more species.

Measurements of the carapace length and total length were recorded for a series of 102 specimens of *Atya innocous;* these were plotted and subjected to analyses that provided us with the following equations:

total length
$$= 3.41925 + 3.03262 \text{ (carapace length)}$$
carapace length
$$= -0.77307 + 0.32241 \text{ (total length)}$$

The regression lines $y = 3.41925 + 3.03262x$ and $y = -0.77307 + 0.32241x$ are shown in Figure 7*a* and *b*, respectively. The correlation (r) value of these statistics was 0.98881 ($R^2 = 0.97775$); thus 98% of the variability in either measurement is reflected in that of the other.

Plotting the data available from all of the other species of the genus showed that the variations in them fall within the limits exhibited by *A. innocous*.

Habitat

On the basis of field experience in the West Indies and Mexico, published ecological notes, the few habitat data accompanying collections, and the apparent absence of populations in certain areas within the range of the genus, we suggest the possibility that perhaps oxygen concentration is the most important physical aspect of the environment that determines the presence or absence of *Atya*. Most collections of these shrimps have been obtained in rapidly flowing streams, and the presence of rocks on the substrate seems to be associated with the larger populations (Figure 8). In the absence of rocks, debris and macrophytes provide adequate cover to support the presence of representatives of at least some species. Streams within the range of the genus in which riffles or segments of rapid flow are absent or situated some distance inland (that is, flowing across an extended course of low gradient) seem to lack populations of *Atya*. The absence of records in streams traversing the low-lying coastal areas within the range of the genus tends to support the conclusion that these shrimps are largely re-

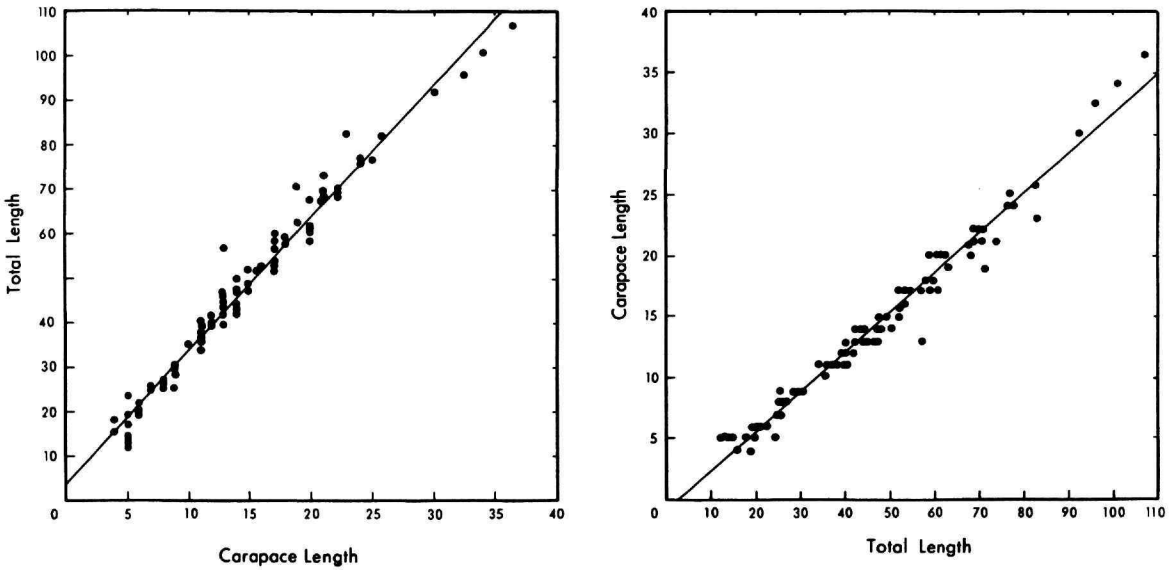

FIGURE 7.—Correlations of carapace length and total length in *Atya innocous*. (See "Measurements and Size Correlations" for explanation.)

stricted in their distribution to rapidly flowing or swift segments of streams. Such areas must lie not too distant from estuarine or marine habitats to and from which the young must travel to spend at least a part of their early larval life in water with higher salinities. What distance is "too far" has not been determined. That flowing water is not essential to these shrimps becomes evident in view of the records for *Atya intermedia* in Crater Lake on Annobón and the pond on Dominica mentioned by Fryer (see accounts below on *A. intermedia* and *A. innocous*). Although presumably there was no current in the lake or pond, water indeed flowed through them.

Possible exceptions to these generalizations exist in the Nun and Osse rivers in Nigeria where C.B. Powell (pers. comm.) found *A. gabonensis* in the faster flowing sections of the rivers that are deep, lack rocks, and, during the dry season, are sluggish.

Life History

This account of the life history of the several species of *Atya* is based upon field observations and the studies of Fryer (1977) and Hunte (1979b). The adults frequent streams where they may occur as far as 600 and perhaps 1000 kilometers inland and at altitudes of as much as 925 meters. Almost all have been reported to live in swiftly flowing water where they tend to be concentrated on rocky substrates, although rooted vegetation and debris appear in some places to provide adequate cover for numbers of them. Many, if not most, of the females become ovigerous, bearing several hundred eggs while surprisingly small (larger females produce upward to 4000 eggs in a clutch)—the number of broods produced by a single individual is not known. The eggs are retained beneath the abdomen of the female until they hatch, and the escaping larvae, which live for some six days in the laboratory (Hunte, 1979b), do not feed but must make their way to the mouth of the river where in water of higher salinity they molt to the second instar. In *A. innocous*, a total of 12 stages (or instars) occurs over a period of 76 to 119 days (in the laboratory) before the larvae metamorphose into juveniles. Nothing is known of the habits of the larvae, but presumably the juveniles return

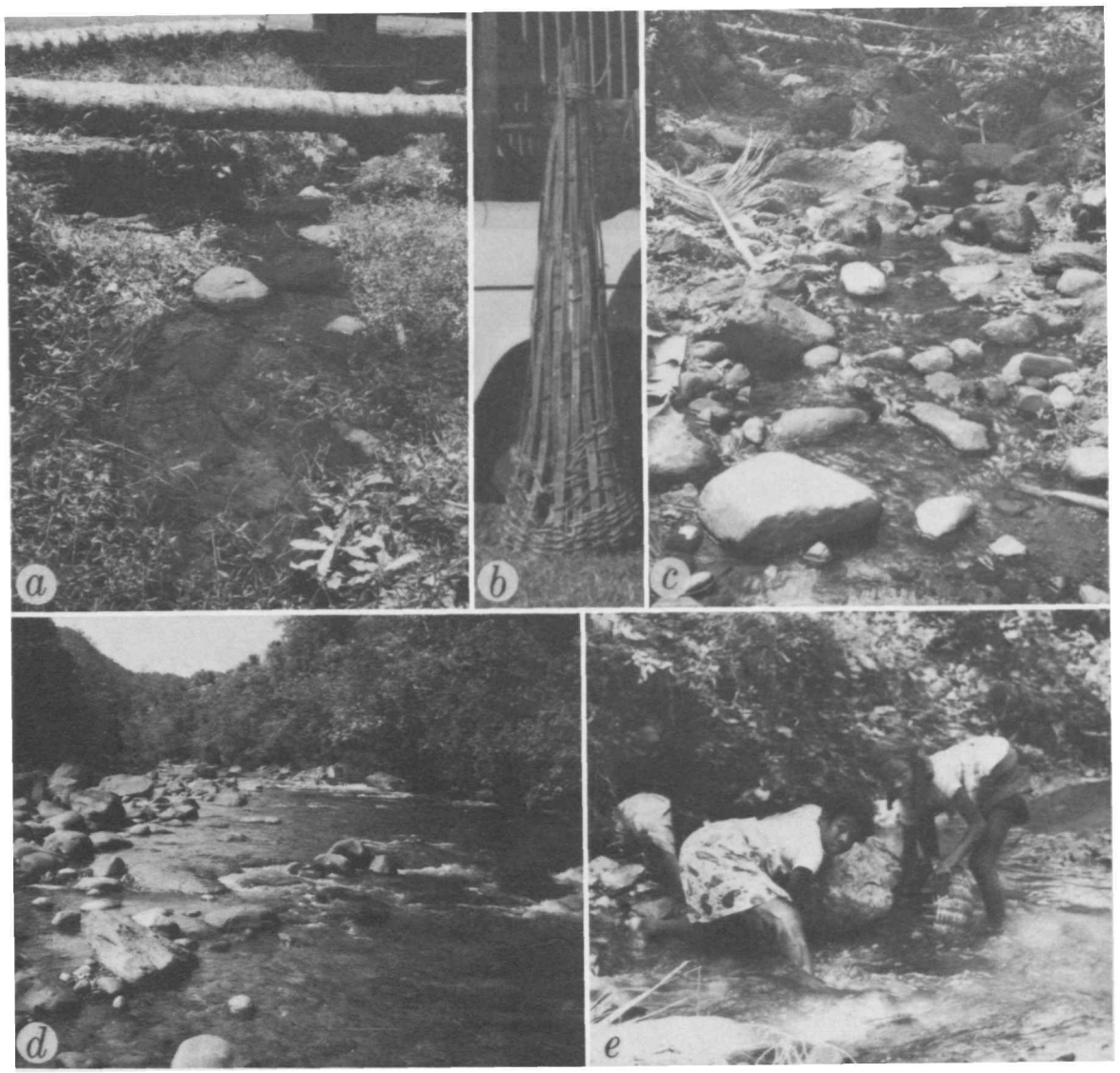

FIGURE 8.—Habitats exploited by members of the genus *Atya*, and implements used in Jamaica to catch freshwater shrimps: *a*, Mannet's Gutter, near mouth, in Dominica, frequented by *Atya innocous; b*, basket employed in Jamaica in catching both atyid and palaemonid shrimps; *c*, an upstream locality on Mannet's Gutter, Dominica, inhabited by *Atya innocous* and *A. scabra; d*, Layou River, Dominica; *e*, children using basket to catch "jongas" (freshwater shrimps) in small stream in St. Andrew Parish, Jamaica.

to the rivers, making their way upstream. As they approach maturity, they become more active at night than during the day, although they are frequently seen moving over the substrate of shaded pools during daylight hours. Both juveniles and adults dig shallow depressions under rocks or find existing crevices that satisfy their need for cover. They feed either by filtering or by

sweeping and/or scraping organic material from the substrate with the aid of the terminal tufts of setae on the first and second pereiopods. Even though the shrimp are capable of swimming, most of their locomotion is accomplished by walking and climbing. As in many decapods, fast backward propulsion is accomplished by rapid flexion of the abdomen. Not only do they occupy riffle areas of rivers, but they also make their way up small tributaries almost to the source, and inasmuch as they traverse small cascades there is every reason to believe that in their migrations upstream they leave the water for at least short distances. It is not inconceivable, therefore, that they are able to cross low divides from one headwater stream to another. There are no data as to their longevity in the wild, but Fryer (1977:72) kept a specimen of *A. innocous* in the laboratory for about six years and nine months, and Abele (1975:56) reported that a specimen of *A. dressleri* had lived in an aquarium for more than five years.

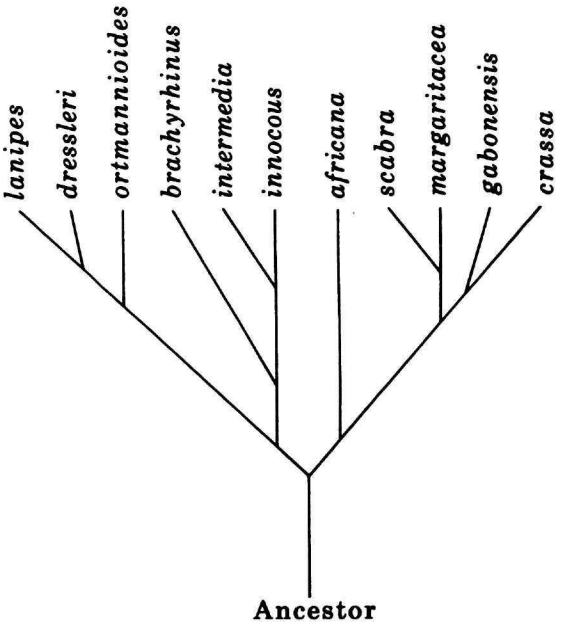

FIGURE 9.—Dendrogram depicting relationships of members of the genus *Atya*.

Relationships and Dispersal

FIGURE 9

In assessing the interrelationships of members of the genus *Atya*, we are in at least basic agreement with Bouvier (1925). The more generalized species appear to us to be those in which (1) the rostral margins tend to converge from base to apex, (2) the carapace is rather smooth, lacking prominent ridges and spines, (3) the telson is slender and elongate, (4) the ventral margin of the abdominal pleura lacks sclerotized denticles, (5) the basal segment of the antennule is devoid of premarginal sclerotized denticles, (6) the coxa of the third pereiopod has an entire, as opposed to scalloped, distal margin but lacks a lateral spine, corneous tubercles, and a caudomesial projection, (7) a comparatively slender merus on the third pereiopod, that is weakly tuberculate at most, lacks more than a vestigial distal ventromesial spine that opposes a strong tubercle on the carpus, and (8) the dactyl is hinged and freely movable, and the flexor surface is provided with two oblique (perhaps irregular) rows of tubercles. Two species, *A. lanipes* and *A. dressleri*, exhibit these features, and there seems to be little reason to choose either as having preserved the larger number of primitive characters; however, the combination of a slender, almost smooth merus of the third pereiopod and the tapered rostrum causes us to favor *A. lanipes* as perhaps having more in common with members of other genera of the family Atyidae. Were the rostral margins of *A. ortmannioides* less suddenly contracted and the merus of the third pereiopod less tuberculate, this shrimp would rival *A. lanipes* and *A. dressleri* as being one of the most primitive members of the genus. Whether a strong or weakly developed pterygostomian angle is the more generalized seems problematical, but should a weak one be the more primitive then at least in this respect *A. dressleri* merits consideration as representing the ancestral *Atya*.

Closely allied to these three species are *A. innocous*, *A. intermedia*, and *A. brachyrhinus*. In the former two the rostral margins have become subangular, and the merus of the third pereiopod is

often considerably more strongly developed and studded with tubercles, the apical parts of which are heavily cornified, and in many populations of *A. innocous* individuals have acquired sclerotized denticles on the ventral margin of the second through fifth abdominal pleura. The rostrum of *A. brachyrhinus* is very short, the acumen has become greatly reduced, and the rostral margins broadly rounded; moreover the section of the cephalic margin of the carapace between the antennal and pterygostomian spines that is excavate in this shrimp is convex in *A. innocous* and *A. intermedia*. Denticles are also present on the third through fifth abdominal pleura. Unfortunately only two females of *A. brachyrhinus* are available, and perhaps the merus in the illustration of this specimen (Figure 15*h*) should not be compared with those in the other species that depict the third pereiopods of males.

Somewhat intermediate between the latter three species and the advanced *Atya* is *A. africana*, which has a rostrum with tapered margins and abdominal pleura that lack denticles on the ventral surface. Premarginal denticles, however, are present on the dorsal surface of the proximal podomere of the antennule; some of the subspiniform tubercles on the flexor surface of the propodus of the third pereiopod are arranged in a contiguous or subcontinguous row, and the denticles on the flexor surface of the dactyl of that appendage are aligned in a single series. In all of the aforementioned species, the tubercles of the third pereiopod tend to be at least subspiniform. In those that follow, some, if not most, of the tubercles of this appendage are distally flattened and strongly cornified.

Atya margaritacea and *A. scabra* are closely allied species in which (1) the rostral margins are subparallel or concave along the basal half and form a distinct angle, often produced, at the base of the acumen, (2) the punctations of the carapace bear short stiff setae, (3) the pleura of the second or third through fifth abdominal segments bear sclerotized denticles, and (4) the denticles on the flexor surface of the dactyl of the third pereiopod are arranged in a linear series. That *A. scabra* has digressed slightly more from the supposed ancestral stock than has *A. margaritacea* is suggested by the consistent presence of sclerotized premarginal denticles on the dorsal surface of the proximal podomere of the antennule, by the contiguous or subcontiguous linear series of squamiform tubercles on the flexor surface of the propodus of the same appendage, and by the presence of denticles on the pleuron of the second abdominal segment.

The most divergent species of the genus are *Atya crassa* and *A. gabonensis*. Both display an array of unique characteristics that distinguish them from the more generalized members of *Atya*, and whereas they have several obvious advanced characteristics, both have extended certain modifications beyond that exhibited by the other. In superficial appearance, no doubt *A. crassa* seems to be the most divergent member of the genus; it possesses a rostrum with convergent margins (probably secondarily acquired), but the dorsal carina is uniquely provided with a row of spines, and most of the ridges (present also in *A. gabonensis*) adorning the carapace are studded with spines that are also unique in the genus. Whereas the ocellar beak remains rather small and the tubercle on the sternum of the fifth abdominal segment moderately prominent, the ocellar beak of *A. gabonensis* is, by comparison, very long and bladelike, and the hornlike projection (enlarged tubercle) on the sternum of the fifth abdominal segment is decidedly more prominent than in other members of the genus. Thus in different respects both *A. crassa* and *A. gabonensis* seem to be the most divergent species assigned to the genus *Atya*.

To subject our concept of the interrelationships of the members of the genus *Atya* to a more objective test, we selected 25 traits (see list of "Characters Compared") and, employing the Wagner Program of computer analysis (Farris, 1970; Farris, Kluge, and Eckardt, 1970), constructed a series of cladograms, the most parsimonious of which is depicted in Figure 10. Comparing it with the more subjective (based upon "weighted characters") dendrogram in Figure 9, the relative positions of *Atya ortmannioides* and *A. africana* with respect to their close relatives seem most in conflict. Data supporting the arrangement in Figure 10 are evident in the cladogram

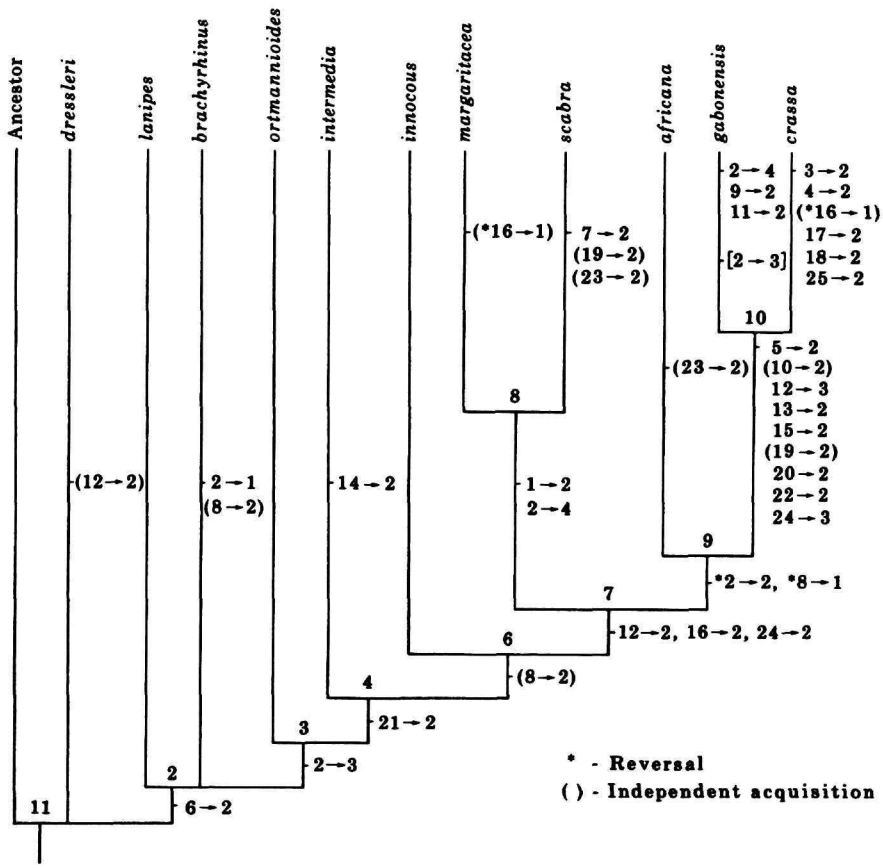

FIGURE 10.—Cladogram expressing relationships of members of the genus *Atya*.

and list of characters considered. Reasons for the groupings shown in Figure 9, however, are not so concisely summarized. Perhaps the slender body and rather spindly ambulatory pereiopods (characters that were not among those selected for computer analysis) of *A. ortmannioides* led us to group this species with the supposedly primitive *A. dressleri* and *A. lanipes*. The contrasting nature of the same features, robust body and appendages, together with others, suggested to us a recent common ancestry of *A. brachyrhinus* with *A. innocous* and *A. intermedia*.

In considering the affinities of *A. africana*, we were convinced that it shares more in common with *A. scabra* and *A. margaritacea* than with other of its congeners. Both the absence of angular margins on the rostrum and of denticles on the second through fifth abdominal pleura were considered to be primitive retentions rather than having resulted from character reversals. The arrangement of the tubercles on the flexor surface of the propodus of the third pereiopod is so much like that of *A. scabra*, yet possessing the form of those in the less specialized *A. innocous*, that we viewed those in *A. africana* as representing a transitional stage between the *A. innocous-intermedia* stock and *A. scabra*. Moreover, the general mien of *A. africana* is so much more that of *A. scabra* and *A. innocous* than that of *A. gabonensis* and *A. crassa* that one might question our having selected a sufficient number of characters to be subjected to computer analysis.

Characters Compared

(The first condition listed for each character is considered to be plesiomorphic)

1. Carapace	(1) glabrous, (2) hirsute
2. Rostrum	(2) tapering, (1) rounded, (3) subangular, (4) angular
3. Median carina	(1) spines absent, (2) spines present
4. Carapace surface	(1) no spines, (2) spines
5. Carapace surface	(1) ridges absent or weak, (2) ridges strong
6. Pterygostomian angle	(1) weak, (2) moderate to strong
7. Second pleuron	(1) denticles absent, (2) denticles present
8. Third-fifth pleuron	(1) denticles absent, (2) denticles present
9. Ocellar beak	(1) short, (2) long and bladelike
10. Sternum, fifth	(1) not hornlike, (2) hornlike
11. Sternum, fifth	(1) tubercle weak, (2) tubercle strong
12. Sternum, sixth	(1) long, (2) intermediate, (3) short
13. Preanal carina	(1) compressed, (2) conical
14. Preanal carina	(1) one spine, (2) two spines
15. Telson	(1) more than 1.5 times as long as wide, (2) less
16. Antennular peduncle I	(1) dorsal premarginal denticles absent, (2) present
17. Coxa, pereiopod III	(1) ventrodistal margin not scalloped, (2) scalloped
18. Coxa, pereiopod III	(1) anterolateral spine absent, (2) present
19. Coxa, pereiopod III	(1) caudomesial projection small or absent, (2) strong
20. Merus, pereiopod III	(1) bowed, (2) straight
21. Merus, pereiopod III	(1) lateral tubercles not strongly cornified, (2) strongly so
22. Merus, pereiopod III	(1) distoventral prominence absent or not opposed; (2) strong and opposed by tubercle on carpus
23. Propodus, pereiopod III	(1) flexor surface with tubercles scattered or not contiguous in mesial row, (2) those of mesial row contiguous
24. Dactyl, pereiopod III	(1) spinules on dactyl in two rows, (2) single row, (3) cluster
25. Propodus-dactyl III	(1) movable, (2) fixed

As noted above, the postulated interrelationships of the members of the genus *Atya* as depicted in Figure 9 are supported by morphological data involving several body regions, and there is every reason to believe that at least those species occurring on both the African and American continental masses have existed in a comparatively stable state since at least early Cenozoic times, perhaps since the middle Mesozoic. Inasmuch as the species comprising the genus are so similar in their morphology, in such elements of their life histories as are known, and in their habitat distribution as well, one must conclude that they have had a monophyletic origin, one that predated a very wide separation of the African and American continental masses. (Bouvier (1925:358) suggested the influence of plate tectonics on atyid distribution.) The progenitors of modern *Atya* with little doubt existed as recognizable members of the genus by the late Mesozoic (probably by early Jurassic times).

At least two distantly related species, *Atya scabra* and *A. gabonensis*, had become differentiated and entrenched on the disjoined drifting African and American land masses by the advent of the Cenozoic Era. Also, there is good reason to believe that the progenitors of *A. innocous* and *A. intermedia* (two species that differ in only minor respects) had likewise acquired the major features shared by them, and segments of this common stock had also become established on the two continental blocks during or shortly after their juxtaposition. The few differences that distinguish them could well have developed at any time during the Cenozoic Era. The progenitors of *Atya innocous* are likely also to have been ancestral to *A. dressleri* and *A. ortmannioides* on the Pacific side of the Middle American land mass and to *A. lanipes* and *A. brachyrhinus* in the islands bordering the eastern part of the Gulf of Mexico and Caribbean.

As may be noted on the maps (Figures 19, 25, 28, 44) devoted to the distribution of *Atya innocous*, *A. dressleri*, and *A. ortmannioides* on the Pacific slope, *A. innocous* ranges from Nicaragua southward to Panama; *A. ortmannioides* ranges from

Baja California Sur southward to Acapulco, in the state of Guerrero; and *A. dressleri* is known from only five localities in Panama. The distribution of such closely allied species on the Pacific versant suggests that a part of the late Mesozoic wide-ranging pro-*innocous* stock reached the Pacific slope and became isolated from that stock present on land masses in or abutting the Gulf-Caribbean with the emergence of a complete Middle American isthmus during the Eocene. That part of the stock moving northward ultimately reached at least as far north as Baja California and gave rise to *A. ortmannioides*, whereas that occurring in the more southern area became the immediate forerunner of *A. dressleri*. What might have served later to separate these two stocks was the submergence of part of the isthmus allowing the merger of waters from the Gulf-Caribbean and that of the Pacific—perhaps across the Isthmus of Tehuantepec (note that this area lies between the ranges of *A. ortmannioides* on the north and *A. innocous* and *A. dressleri* on the south). This event also allowed the *innocous* stock from the Caribbean to gain access once again to the Pacific watershed. With the last complete emergence of the Middle American isthmus, the *innocous* stock on the Pacific became isolated from that on the Caribbean, and at the present time it seems to be less variable than populations occurring in the West Indies. (This Pacific stock is that designated *Atya tenella* by Smith, 1871.) On the basis of our limited knowledge of the populations of this species on the Pacific slope, it seems to have been more aggressive, or perhaps to have broader ecological tolerance, than does *A. dressleri*. It is much more common and widespread in Panama where it may have largely displaced the latter from much of its presumed former continuous range along the Pacific side of the Panamanian isthmus.

There is little reason to choose one island or island group over another as representing the area in which divergence in the original widespread pro-*innocous* stock led to the isolation of ancestors of *A. lanipes* and *A. brachyrhinus*. The latter, known only from a single cave on Barbados, may be a relict of a much more widely dispersed species (at least on that island), for except for the limitation of dark pigment to the eyes we have found no feature that suggests adaptations to a spelean existence. (The reported white body could well be due to contracted chromatophores, a common response in pigmented crustaceans to darkness.) Inasmuch as *A. lanipes* has a broader range but is known to occur only in the Greater Antilles and Virgin Islands, it seems reasonable to assume that the preservation of this remnant of the parent stock occurred in the northeastern part of the Antillean region.

Supporting the suggested migrations of the ancestors of modern *A. innocous*, *A. dressleri*, and *A. ortmannioides* are the possible parallelisms that could well have occurred in the continental American origins and distributions of *A. scabra* and *A. margaritacea* and of *A. gabonensis* and *A. crassa*. We suggest that accompanying the ancestral *innocous* stock (believed to be forebears of *A. dressleri* and *A. ortmannioides*) into the Pacific watershed were members of both the ancestral *scabra* and *gabonensis* stocks that were the precursors of *A. margaritacea* and *A. crassa*, respectively. With the emergence of the isthmus in the early Cenozoic, these more advanced forms shared the streams flowing into the Pacific with the ancestral *dressleri* and *ortmannioides*, all four acquiring their distinctive features prior to the Eocene inundation of parts of the isthmus. The *crassa* and *margaritacea* stocks ultimately ranged more widely than did the other three (*ortmannioides*, *dressleri*, and *innocous*), moving northward at least to the Tropic of Cancer, perhaps at times to much higher latitudes, and in their southward migrations almost reaching, or crossing the equator. Unlike many freshwater inhabitants, some, if not all, members of the genus undergo their early postembryonic development in saline waters and are thus probably able to gain access to river basins adjacent to those in which they hatched.

We are puzzled by the apparent absence of *Atya innocous* and its relatives from the South

American continent, particularly in view of the fact that it, the commonest species in the West Indies and presumed by us to be the least ecologically restricted of the American *Atya*, occurs along both slopes of Panama and on Trinidad and Curaçao. In contrast, the supposedly more ecologically limited *A. scabra* spans the range of the genus in the islands and continental slopes of the Caribbean and Gulf and ranges as far south as the state of Santa Catarina in Brazil.

In this attempt to correlate the distribution of the Middle American members of the genus *Atya* with events in the history of the isthmus joining the Middle and South American land masses we have neglected the occurrence of *Atya scabra* in a few localities on the Pacific slope. Perhaps members of the species were introduced; if not, it is not inconceivable that they were able to cross the continental divide, moving from a small headwater stream on the Caribbean slope to others emptying into the Pacific.

As implied above, considerable stability must have been reached in the ancestors of *Atya gabonensis*, *A. scabra*, and *A. intermedia* prior to the time the American and African continents had become greatly disjoined. The fact that we are unable to distinguish members of a Brazilian population of *A. gabonensis* from African representatives of the species, in combination with the improbability of intercontinental migrations or introductions, supports such a conclusion. Virtually the same can be said of *A. scabra*, for whereas the absence of denticles from the second abdominal pleuron will serve to distinguish the African representatives of the species from many, if not most, members of American populations, more than a few of the latter also lack such denticles. As is discussed below, *A. intermedia* is so closely allied to *A. innocous* that we recognize its specific status with some reluctance. Thus these three shrimps have identical or such close counterparts in the Americas that they must be considered little, if any, changed since the Africa-American continental masses were still approximate.

An understanding of the affinities of *A. africana* is clouded by a seemingly strange combination of characters: a rostrum with tapering margins (believed by us to be plesiomorphic (tying *A. africana* to the generalized *A. lanipes* and *A. dressleri*), along with three features (denticles on the dorsal surface of the proximal podomeres of the antennule, a row of contiguous spines on the flexor surface of the propodus of the third pereiopod, and a single row of denticles on the flexor surface of the dactyl of the same appendage) that link it with the more advanced and sympatric *A. scabra*. In this instance, we are inclined to interpret the rostral character as a secondary acquisition and to believe *A. africana* to have had its most recent common ancestry with the forebears of *A. scabra*. Because the known ranges of the two in Africa are almost identical and also that almost nothing is known of their ecological distribution, little speculation concerning their past history on the continent seems warranted.

Genus *Atya* (sensu stricto)

FIGURES 11, 12

Atys Leach, 1815:345 [type-species by monotypy: *Atys scaber* Leach, 1815:345; gender masculine; junior homonym of *Atys* De Montfort, 1810:342 (Mollusca)].

Atya Leach, 1816:421 [substitute name for *Atys* Leach, 1815:345; type-species by monotypy: *Atys scaber* Leach, 1815:345; gender feminine].

Atia.—Latreille, 1817:37 [erroneous spelling].

Athys.—H. Milne Edwrds, 1838:352 [erroneous spelling].

Evatya Smith, 1871:95 [type-species by monotypy: *Evatya crassa* Smith, 1871:95; gender feminine].

Euatya.—Koelbel, 1884:317 [invalid emendation of *Evatya* Smith, 1871].

Atyia J. Roux, 1932:564 [erroneous spelling].

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

Our concept of the genus *Atya*, similar to that of Chace (in prep.), is that it comprises the larger members of the family Atyidae occurring in the tropics of West Africa and the Americas. Those species of the Indo-Pacific that formerly have been assigned to this genus are excluded from it by the restricted definition presented herein. Inasmuch as Chace has proposed their being assigned to other genera prior to the inception of our study, we refer the reader to his prospective

publication for the generic dispositions of these Indo-Pacific shrimps.

DIAGNOSIS.—Body pigmented, eyes well developed. Rostrum not strongly compressed laterally, median dorsal carina with or without spines, and ventral keel with or without 1 to several teeth. Anterior margin of carapace armed with antennal and pterygostomian spines, latter sometimes reduced to angle; orbital spine lacking. Ventral margin of second through fifth abdominal pleura with or without sclerotized spinules. Telson with paired arched rows of 5 to 9 spines in adults; subacute to acute posterolateral angles exceeded by 2 pairs of mesially contiguous spines, more mesial pair longer. Basal segment of antennule with or without dorsal corneous spinules proximal to series bordering distal margin. Flagellar lobule of first maxilliped well developed. Third maxilliped never ending in spine, distal 2 podomeres with number of oblique rows of simple setae and with fewer strongly sclerotized, biserrate ones. Pereiopods without exopods. First and second pereiopods with chelae completely divided, lacking palm; fingers not gaping, subequal in length and tipped with brushes of long setae; carpus of both appendages excavate distally, much shorter than broad, and shorter than fingers. Branchial complement consisting of 5 pleurobranchs, 3 arthrobranchs, 1 podobranch, 5 epipods, and 5 mastigobranchs. First pleopod of male with endopod broadly ovate, it preaxial surface armed with many curved spines; appendix interna arising from mesial surface of endopod; first pleopod of female with endopod tapering and lacking appendix interna. Second pleopod of male with appendix masculina compressed, slipper-shaped, flattened mesially, spines confined to margins and mesial face.

RANGE.—The members of the genus *Atya* are confined to the American and African continents. On the former it ranges on the Pacific versant from 28°N to about 8°S, whereas in the Atlantic watershed it occurs from the Tropic of Cancer to about 27°S. In Africa, the range is confined to the Atlantic slope and is situated between 15°N and 9°S.

The distribution of the species is summarized in the accompanying tabulation.

	Americas		*Africa*
	Pacific	*Atlantic*	*Atlantic*
Atya africana			x
Atya brachyrhinus		x	
Atya crassa	x	x	
Atya dressleri	x		
Atya gabonensis		x	x
Atya innocous	x	x	
Atya intermedia			x
Atya lanipes		x	
Atya margaritacea	x		
Atya ortmannioides	x		
Atya scabra	x	x	x

Conspicuously absent from this list of African and American shrimps assigned to the genus *Atya* is *Atya serrata* Bate (1888:699), which was described from São Antonio Valley, São Thiago, Cape Verde Islands. We have examined Bate's syntypes and find that their affinities are with members of one of the Indo-Pacific genera recognized by Chace (in prep.). Only two reports of the occurrence of *A. serrata* within the range of *Atya* (as defined herein) are known to us: the type-locality and Muhlenburg Mission, Liberia (Bouvier, 1925:295). Subsequent collections made in the Cape Verde Islands have not contained representatives of this species, and the specimen upon which Bouvier reported its occurrence in Liberia has been examined by us and found to be a small male (carapace length 7.1 mm) that clearly belongs to the African-American genus *Atya* and is almost certainly a member of *Atya africana.* In view of these observations, and because of the apparent affinities of the types with Indo-Pacific atyids, there is good reason to believe that Bate's specimens were not collected in the Cape Verde Islands or elsewhere in the Atlantic versant of either Africa or the Americas. Holthuis (1951:26) expressed a similar opinion in stating: "It is doubtful whether this species, which is widely distributed throughout the Indo-west pacific area, also occurs in West Africa."

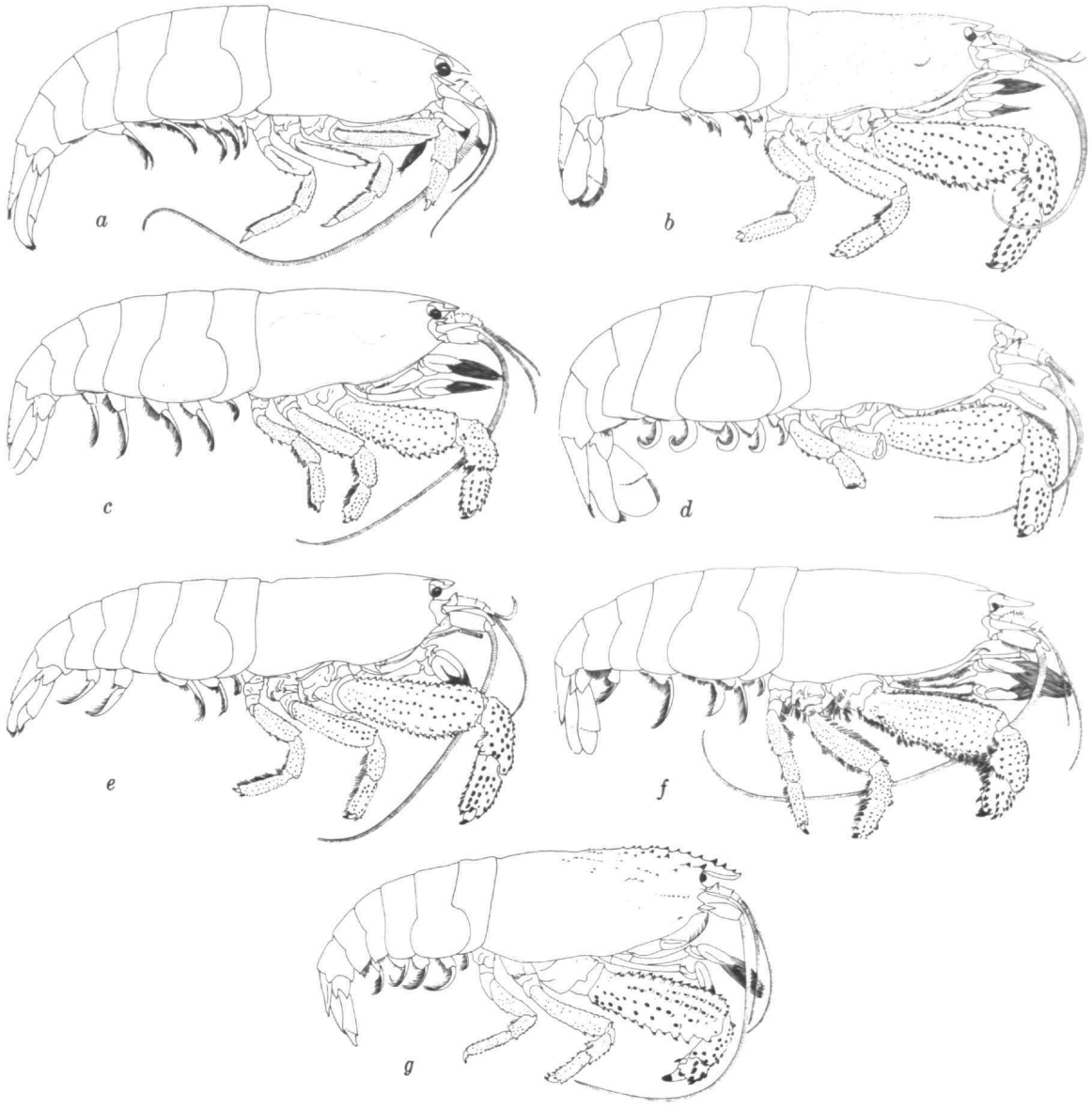

FIGURE 11.—Lateral views of members of genus *Atya* (numbers in parentheses = carapace length in mm): *a*, *A. africana*, Mount Coffee, Liberia (♂, 22.6); *b*, neotype of *A. scabra*, Misantla, Mexico (♂, 29.8); *c*, *A. scabra*, São Tiago, Cape Verde Islands (♂, 24.5); *d*, syntype of *A. margaritacea* (♂, 24.5); *e*, *A. margaritacea*, Mt. Chiriquí, Panama (♂, 25.8); *f*, *A. gabonensis*, Volta River, Ghana (♂, 28.2); *g*, *A. crassa*, Río Dagua, Colombia (♂, 37.8).

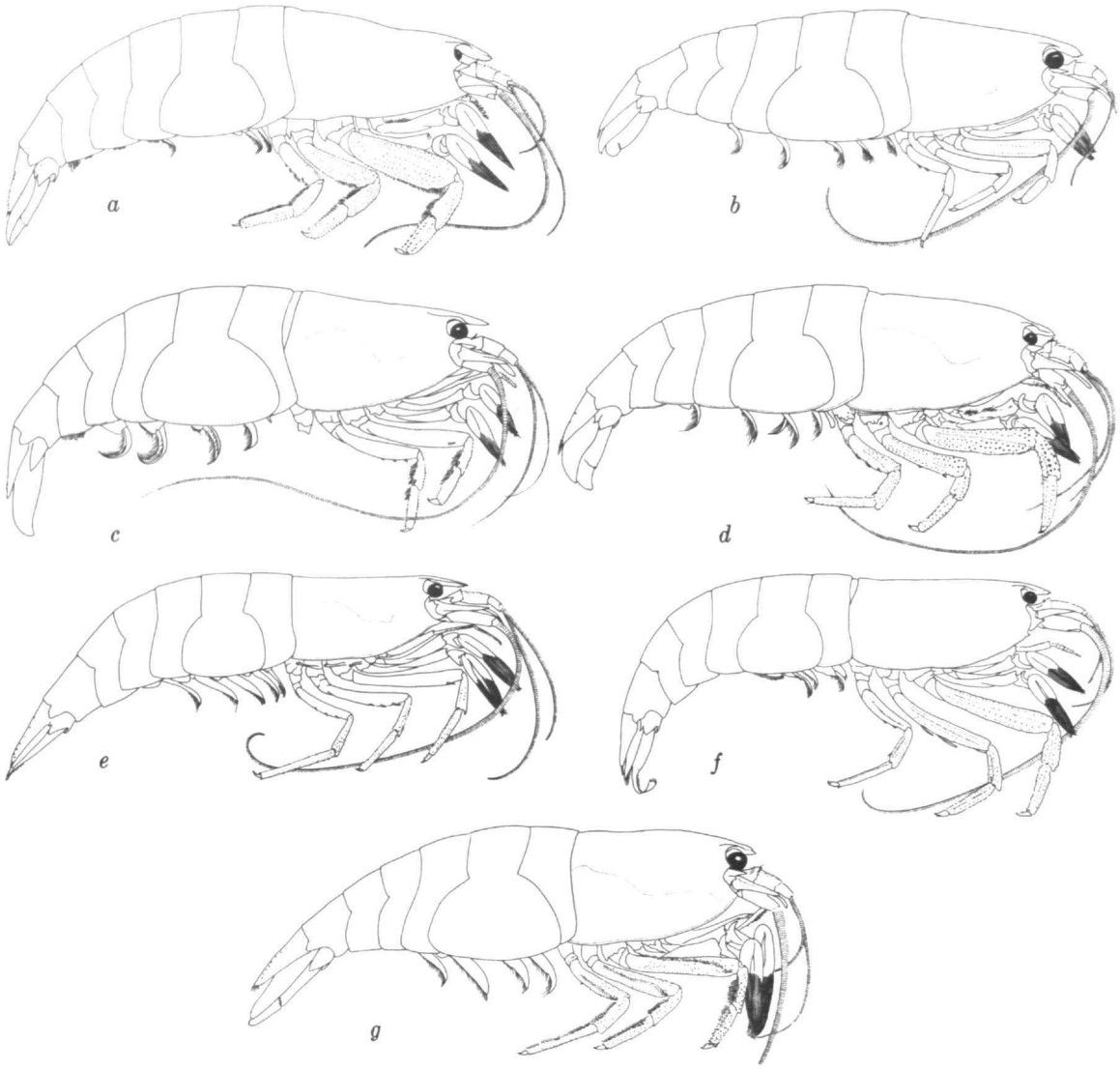

FIGURE 12.—Lateral views of members of genus *Atya* (numbers in parentheses = carapace length in mm): *a*, *A. innocous*, Mannet's Gutter, Dominica (♂, 24.4); *b*, syntype of *A. tenella* (= *A. innocous*) (♂, 16.2); *c*, holotype of *A. ortmannioides* (♀, 15.9); *d*, *A. intermedia*, effluent of Crater Lake, Annobón (♂, 25.4); *e*, *A. lanipes*, Río Maricoa, Puerto Rico (♂, 21.0); *f*, holotype of *A. dressleri* (♂, 20.4); *g*, holotype of *A. brachyrhinus* (♀, 15.7).

Key to Species of the Genus *Atya*

1. Cephalic section of carapace with median dorsal row of spines extending onto rostrum; prominent ridges on carapace also studded with spines ..... ***A. crassa***

1′. Cephalic section of carapace and rostrum lacking median dorsal row of spines; ridges present or absent from carapace, if present never studded with spines 2

2(1′). Rostral margins with angular (acute or right angle, never obtuse) bend or lateral prominences; tubercles on flexor surface of dactyl of third pereiopod arranged in small cluster or in single row ... 3

2′. Rostral margins with or without subangular bend, if present obtuse or with extremities rounded; tubercles on flexor surface of dactyl of third pereiopod never arranged in cluster or single row except latter in *A. africana* in which rostral margins tapering from base 5

3(2). Flexor surface of propodus of third pereiopod with some of heavily cornified squamous tubercles arranged in longitudinal rows, at least part of those in mesial row quite or nearly contiguous; most American representatives with row of sclerotized denticles on ventral margin of second abdominal pleuron ..... ***A. scabra***

3′. Flexor surface of propodus of third pereiopod with few to many heavily sclerotized elevated or squamous tubercles, if some forming linear series, those in mesial row never nearly or quite contiguous; sclerotized denticles never present on second abdominal pleuron 4

4(3′). Carapace strongly sculptured; flexor surface of propodus of third pereiopod with conspicuous tufts of long plumose setae and with very few squamous tubercles; corresponding surface of dactyl of same appendage with single or cluster of tubercles just proximal to sclerotized tip; sternum of fifth abdominal segment with median curved hornlike projection ..... ***A. gabonensis***

4′. Carapace comparatively weakly sculptured; flexor surface of propodus of third pereiopod without conspicuous tufts of long plumose setae, with prominent squamous tubercles; corresponding surface of dactyl of same appendage with single row of tubercles; sternum of fifth abdominal segment with small median tubercle ..... ***A. margaritacea***

5(2′). Dorsal surface of proximal article of antennular peduncle with 1 to 3 sclerotized spinules; flexor surface of propodus of third pereiopod with tubercles arranged in 2 subparallel rows, those in mesial row subcontiguous and none between rows; corresponding surface of dactyl of same appendage with tubercles arranged in single row ..... **A. *africana***

5′. Dorsal surface of proximal article of antennular peduncle lacking sclerotized spinules; flexor surface of propodus of third pereiopod with scattered tubercles, if rows evident always with other tubercles between them; corresponding surface of dactyl of same appendage disposed in 2 rows, more proximal one almost always situated proximomesial to distal row 6

6(5′). Rostrum with margins strongly convex laterally, apex falling far short of second segment of antennular peduncle ..... ***A. brachyrhinus***

6′. Rostrum with margins subparallel to strongly convergent, apex reaching or almost reaching base of second article of antennular peduncle 7

7(6′). Rostral margins with strong subangular bend; ventral margin of third through fifth abdominal pleura with or without sclerotized spinules 8

7′. Rostral margins tapering from base; ventral margin of third through fifth abdominal pleura without sclerotized spinules 10

8(7). Lateral surface of merus of third pereiopod lacking conspicuous tubercles, all small and weakly, if at all, cornified; cephalolateral surface of carapace straight; rostrum, with acumen longer than basal part, directed anteriorly ..... ***A. ortmannioides***

8′. Lateral surface of merus of third pereiopod studded with tubercles; cephalolateral surface of carapace convex (anterior to posterior); rostrum directed anteroventrally 9

9(8′). Ventral margin of third through fifth abdominal pleura, except in specimens from Pacific Basin, usually with sclerotized spinules; median tubercle on sternum of fifth abdominal segment comparatively inconspicuous; preanal carina with single spine ..... ***A. innocous***

9′. Ventral margin of third through fifth abdominal pleura always devoid of sclerotized spinules; median tubercle on sternum of fifth abdominal segment comparatively large; preanal carina with 2 spines ..... ***A. intermedia***

10(7′). Pterygostomian angle produced in prominent spine; dorsal surface of penultimate podomere of antennular peduncle with scattered spines; merus of third pereiopod without tubercles dorsally or laterally; preanal carina with vestigial spine; dorsal surface of telson with rows of 5 to 7 spines ..... ***A. lanipes***

10′. Pterygostomian angle weak or obsolete; dorsal surface of penultimate podomere of antennular peduncle with lateral row of about 6 spines and 1 to 3 more mesially situated; merus of third pereiopod with distinct tubercles dorsally and laterally; preanal carina produced in well developed caudally directed spine; dorsal surface of telson with rows of 7 to 9 spines ..... ***A. dressleri***

Atya africana Bouvier

FIGURES 1*h*, 9–11*a*, 13, 14

Atya scabra.—Rathbun, 1900:313 [in part]; 1901:119 [in part].—De Man, 1925:28 [in part].

Atya africana Bouvier, 1904:138 [type-locality: "Samkitta dans la rivière Ogooué," Gabon; type: MHNP 593, 1♂]; (?)1905:120, fig. 24; 1925:292, 305–308, 310, 311, 322, 323, 356, 358, figs. 682–689.—De Man, 1925:26, 27, fig. 3a,b.—(?)Holthuis, 1951:20–24, fig. 3; 1963:67; 1966: 237.—Lebour, 1959:121, 134.—Vogel and Crewe, 1965:122.—Monod, 1967:110, 119, 135, pl. 9: figs. 1–10; 1980:375, 376, figs. 3, 4, 7.—Disney, 1969:292; 1971:83, 85, 87–89, 91, fig. 1; 1975:69.—Lewis, Disney, and Crosskey, 1969:229, 232, 238.—(?)Crosnier, 1971:570, 571.—Lemasson, 1973:68, 70.

Atya serrata.—Bouvier, 1925:295 [in part].—Holthuis, 1951:25, 26 [in part].

Atya gabonensis.—Holthuis, 1951:25 [in part].

REVIEW OF LITERATURE.—The first reference to this shrimp was that of Rathbun (1900) who reported the occurrence of *Atya scabra* in Liberia, a record established in part upon the misidentification of specimens of *A. africana* from Mt. Coffee and Beulah, Liberia. One of the specimens (USNM 20662) from the former was a member of *A. scabra*. Presumably the inclusion of "West Africa" in her summary of the range (1901) was based upon the same specimens. The Mt. Coffee record was repeated for *A. scabra* by De Man

(1925). A single male from the Ogooué River at Samkitta, Gabon, constituted the material on which Bouvier (1904) briefly described *Atya africana*, largely contrasting it with his concurrently described *A. intermedia*. The features pointed out were the longer, narrower rostrum on which the dorsal carina is not deflected apically, the strong, toothed ventral rostral carina, and the well-developed armature of the merus of the third pereiopod. Bouvier (1905) illustrated the cephalic region of the holotype in dorsal and lateral aspects and amplified his earlier description by adding that the third legs are enormously developed and covered with numerous irregularly dispersed corneous tubercles, and furthermore that the inferior border of the merus of this appendage possesses a movable spine. In the account of this species in his monograph of the family, Bouvier (1925) contrasted *A. africana* with *Atya moluccensis* De Haan (1850:186), describing and illustrating the former much more completely. A number of the characters chosen, however, are shared by other members of the genus, and few of those mentioned are useful in distinguishing *A. africana* from its congeners. Only three specimens of *A. africana* were reported by Bouvier, the holotype and a male and female from Booué, Gabon. A fourth specimen was available to him, for the single shrimp in the collection of the (former) United States National Museum from the "Muhlenberg Mission, W. Africa, O.J. Cook" referred to by Bouvier (1925:295) and assigned to *Atya serrata* Bate (1888), is a member of *A. africana*. (See locality 4 in Liberia below).

De Man (1925) recorded the presence of this shrimp in Mbuma, Zaire, and Holthuis (1951) tentatively assigned juveniles collected from off Liberia and Cameroon and from Boma, Zaire, to this species. Holthuis described the specimens from the latter in considerable detail and pointed out several striking differences between these juveniles collected in fresh water and those from the two marine localities. He illustrated the cephalic region, caudal part of the telson, and several appendages of the specimens from Boma and the caudal part of the telson of one of those from off Cameroon. He suggested (p. 23) that the differences noted

> may be due to the different stages of development. The specimens from Boma show more resemblances to the adult form (absence of exopods on the pereiopods, shape of the telson), than the specimens from Stations 57 [off Liberia] and 119 [off Cameroon]. The smallest specimen from Boma, 9 mm. in length, is, however, quite identical with the other material from the same lot and is different from the largest specimen from Sta. 119. The Boma specimens were collected in fresh or brackish water, while the specimens from Sta. 57 and 119 were taken in pure sea water. This might indicate that the early stages of this species are spent in the sea and that, when growing older, it returns to fresh water, just as is the case in some species of the Palaemonid genus *Macrobrachium*.

Holthuis' (1951:25, 26) reference to Bouvier's (1925) report of *A. serrata* from Muhlenberg Mission (see above) was based upon Bouvier's misidentification of *Atya africana*. Lebour (1959) cited a new Liberian record for the species.

In describing *Atya lanipes*, Holthuis (1963) stated that *A. africana* was its closest relative and that the former could be distinguished from the latter by the more slender third pereiopod of the adult male, the shape of the endopod of the first pleopod, and by the appendix masculina. Following his redescription of *Atya intermedia*, Holthuis (1966) noted its close relationship to *A. africana* and corroborated the existence of the differences between the two species pointed out by Bouvier (1925). Vogel and Crew (1965) recorded this shrimp from the Mungo River, Cameroon.

Monod (1967) reported *Atya africana* to be a large species (as long as 11 cm) occurring in Gabon and Congo; the illustrations were those of Bouvier (1925) and De Man (1925). Disney (1969) and Lewis, Disney, and Crosskey (1969) found that the young stages of certain phoretic blackflies utilize *Atya africana* as a host in the Bille, Meme, and Mungo rivers in West Cameroon. In much expanded reports, Disney (1971, 1975) presented his observations on this shrimp in tributaries of the Mungo and Meme rivers near Kumba, West Cameroon, where it is infested with the larvae and pupae of three species of blackflies (*Simulium dukei*, *S. kenyae*, and *S. damnosum*). Most

of the adult shrimp were found under stones, whereas the smaller individuals were more abundant among tangles of leaves. The composition of a population as revealed by netted specimens was roughly 57% having a total carapace length (c.l.) of 6 to 15 mm, about 23% with 16 to 20 mm c.l., 11% with 21 to 25 mm c.l., 6% with 26 to 30 mm c.l., and the remaining 3% with 31 to 45 mm c.l. He found that in 1968–1969 the ovigerous females, which possessed total carapace lengths from 11 to 25 mm, occurred in greatest numbers from October to November and from April to May (ratio of 8:5) with an apparent "breeding pause" from December to March. The *Simulium* larvae occur in the gill chamber or among the cephalothoracic appendages of the shrimp, and the pupae were found only on the ventral side of the scaphocerite.

Crosnier (1971) found juvenile specimens, which he tentatively assigned to *A. africana*, at a depth of about 10 meters in the Bay of Pointe Noire, Congo. He stated that they resemble the specimens from off Cameroon described by Holthuis (1951) and not those from the freshwater habitat in the Belgian Congo (= Zaire). Lemasson (1973) added no new information but expressed the opinion that this shrimp, which attains a total length of 11 cm, might lend itself to cultivation in Africa.

PUBLISHED ILLUSTRATIONS.—The following illustrations of Bouvier's *Atya africana* are available. Dorsal and lateral views of the cephalic extremity of the carapace were presented by Bouvier (1905) and republished by him (1925) along with others of the first pleopod of the male, the appendix masculina, the caudal angles of the fourth and fifth abdominal segments, the uropodal angle, and the caudal region of the telson; in the same year, dorsal and lateral views of the cephalic region were depicted by De Man (1925). Monod (1967) reproduced the illustrations of Bouvier (1925) along with those of De Man (1925).

Illustrations of juvenile specimens tentatively assigned to this species by Holthuis (1951) include dorsal and lateral views of the cephalic region as well as drawings of the basal antennular segment, mandible, first maxilla, distal podomeres of the first, third, and fifth pereiopods, and caudal part of the telson. These drawings were based on specimens from off Cameroon and from Boma.

DIAGNOSIS.—Cephalic region of carapace not conspicuously sculptured, lacking spines other than antennal, pterygostomian, and ventral rostral; pterygostomian spine strong. Rostrum with margins tapering from base, lacking angular bends. Ventral margin of all abdominal pleura usually lacking sclerotized spinules (occasionally present on fifth), and caudoventral angles of fourth and fifth pleura not produced in spines. Sternum of fifth abdominal segment with small median tubercle, that of sixth about 1.5 times as broad as long. Preanal carina with compressed spine not overreaching posterior extremity of basal part of carina. Telson 1.8 to 1.9 times as long as broad with 4 or 5 spines in each of 2 rows. Antennular peduncle with dorsal surface of proximal article bearing 1 to 7 sclerotized spinules proximal to distal row; penultimate article 1.1 to 1.5 times as long as wide and dorsal surface with several to many spinules, some of which sometimes arranged in sublateral row. Coxae of third and fourth pereiopods lacking prominent anterolateral spine. Third pereiopod with merus rounded ventrally, 2.9 to 4.1 times as long as high, ventromesial surface slightly to strikingly bowed, never parallel to that of corresponding podomere of other third pereiopod, and lateral surface rather strongly tuberculate, tubercles sublinearly arranged; propodus 2.1 to 3.2 times as long as wide, extensor surface studded with strongly sclerotized subspiniform tubercles, and flexor surface with similarly sclerotized scalelike to spiniform ones somewhat linearly arranged, those comprising row immediately mesial to median line contiguous to subcontiguous; dactyl freely movable and bearing single row of corneous scalelike to spiniform denticles on flexor surface.

MALE (Cavalla River, Bolobo, Liberia).—Rostrum (Figure 13*a*, *d*) with margins tapering from base, bearing only slightest angle delimiting posterior end of acumen; apex of latter reaching no more than 0.25 length of penultimate podomere

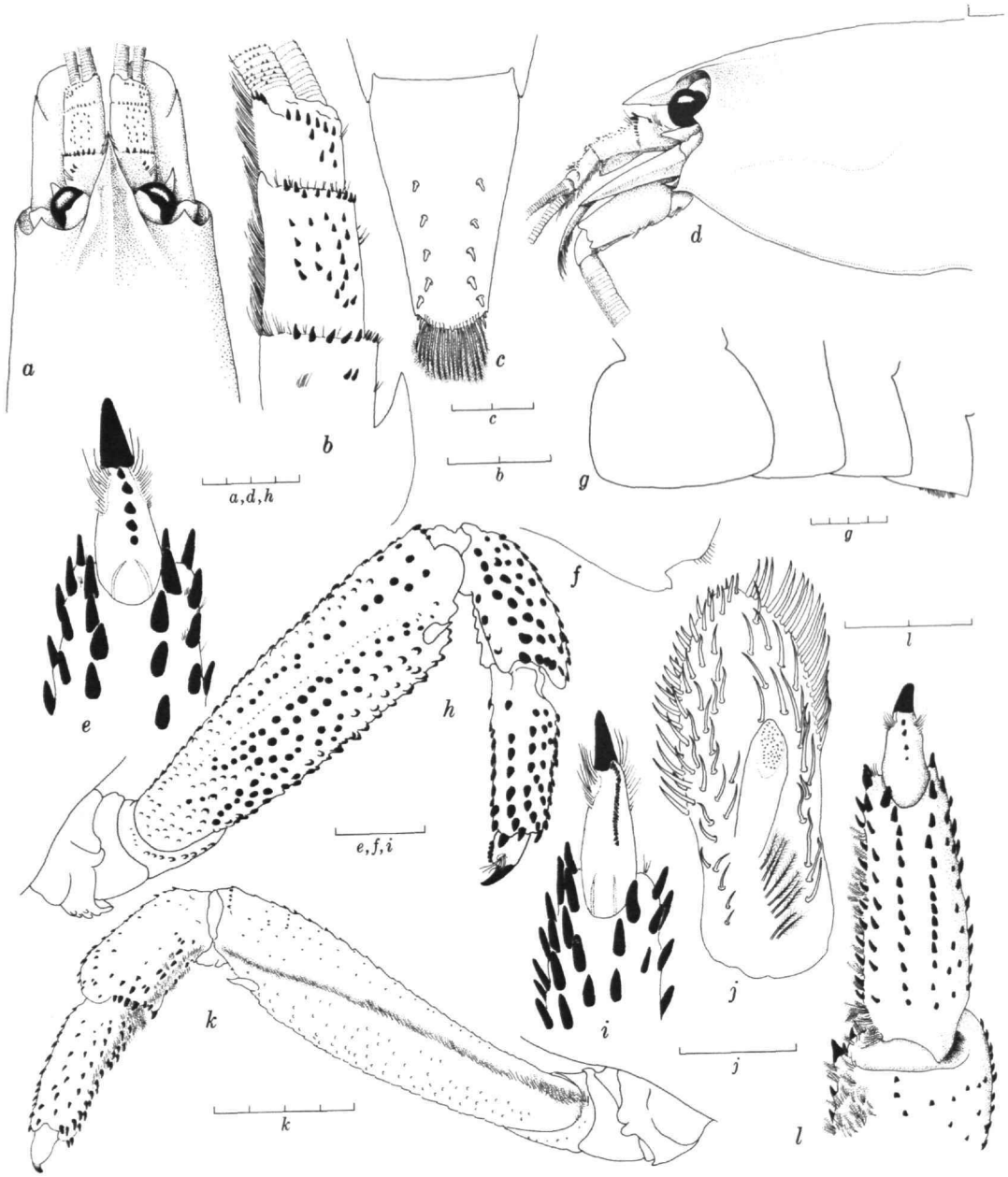

FIGURE 13.—*Atya africana* (all from male from Cavalla River, Bolobo, Liberia, except *e,h,i* from Mt. Coffee, Liberia): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, dorsal view of telson; *d*, lateral view of cephalic region; *e*, flexor surface of distal part of fourth pereiopod; *f*, lateral view of preanal carina; *g*, lateral view of second through fifth abdominal pleura; *h,k*, lateral view of third pereiopod; *i*, flexor surface of distal part of fifth pereiopod; *j*, mesial view of appendices masculina and interna, *l*, flexor surface of distal part of third pereiopod. (Scales marked in 1 mm increments.)

of antennule; 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 single weak tooth at base of apical fourth of rostrum; ocellar beak, hidden in lateral view by eyes, with dorsal margin only slightly arched and meeting vertical anterior margin at right angle, its anterior extremity not approaching level of tip of stylocerite. Antennal and pterygostomian spines moderately strong and acute; no spines present between them. Surface of carapace with many small, shallow, setiferous punctations, but devoid of ridges and spines other than those just mentioned; setae borne in ventral submarginal punctations not conspicuous.

Pleura of first three abdominal segments (Figure 13*g*) with rounded posteroventral extremities; corresponding parts of fourth and fifth angular but not produced in spines. All pleura lacking corneous spinules on ventral margin, but fifth with conspicuous fringe of plumose setae. Fourth abdominal tergum about 1.1 times as long as fifth (sixth subequal in length to fifth) and subequal in length to telson; sixth tergum only slightly shorter than telson. Sternum of fifth abdominal segment with small laterally compressed median tubercle (Figure 1*h*). Sternum of sixth segment almost 0.7 as long as broad. Free part of preanal carina (Figure 13*f*) very short, apex not reaching level of caudal extremity of basal part of sclerite. Telson (Figure 13*c*) little more than twice as long as broad, its dorsal surface bearing paired concave rows of 5 corneous denticles and posteromedian tubercle, latter slightly overhanging caudal margin.

Proximal podomere of antennule (Figure 13*b*) with stylocerite reaching base of distal third or fourth of segment; dorsal surface with linear cluster of setae and 2 corneous spinules; distal margin bearing row of 7 (right) or 9 (left) corneous spinules; penultimate segment of peduncle about 1.2 times as long as wide and bearing 20 spinules on dorsal surface and 10 on distal margin; ultimate podomere with row of 6 spinules at base of lateral flagellum, 3 at base of mesial one, and 4 proximal to lateral row. Antenna with ventrolateral spine on basis reaching about same level as left stylocerite but not quite so far as right (latter attaining base of distal third of proximal segment of antennular peduncle); lateral spine on scaphocerite strong, extending much beyond tip of rostrum, almost to end of antennular peducle; lamella overreaching latter; flagellum extending to fifth abdominal tergum.

Third maxilliped overreaching antennular peduncle by almost half length of distal podomere of endopod; tip of exopod reaching base of distal third of penultimate podomere of endopod; latter between 1.3 and 1.4 times length of ultimate podomere.

First pereiopod reaching distal end of antennular peduncle, second reaching base of distal fifth of fingers of first pereiopod; terminal brush of setae of both appendages lacking scraping denticles. Third pereiopod (Figure 13*k*,*l*) with lateral distoventral spine on merus and carpus, and, when extended anteriorly, overreaching antennular peduncle by dactyl and four-fifths length of propodus; merus with ventromesial margin bowed, about 4 times as long as high, 2.2 times as long as carpus, and 1.8 times as long as propodus; latter 2.7 times as long as wide, 1.2 times as long as carpus; distoventral margin of coxa entire (weakly undulate), and mesial caudoventral prominence lacking conspicuous setal clusters. Lateral, dorsal, and ventral surfaces of merus studded with many small apically sclerotized tubercles, most arranged in sublinear series; clusters of plumose setae flanking tubercles, most conspicuous tufts forming oblique row on lateral surface; mesial extremity of podomere weakly produced at level of mesial articular condyle of carpus. Carpus strongly tuberculate except ventrally where fewer tubercles, but clusters of long plumose setae present, especially ventrolaterally. Propodus with most tubercles arranged in linear series, 2 parallel rows on flexor surface well defined. Dactyl movable, its flexor surface with single longtitudinal row of 4 denticles flanked distally by paired clusters of setae.

Fourth pereiopod with dactyl reaching end of

proximal third of propodus of third pereiopod; length of merus 2.5 times that of carpus, and latter 0.7 as long as propodus. Fifth pereiopod reaching articulation of carpus and propodus of fourth; merus about 1.3 times as long as carpus, latter approximately 0.8 as long as propodus. Ornamentation of merus, carpus, and propodus of fourth pereiopod similar to that of third except for additional spine on ventral surface of merus at base of distal third, 3 distolateral spines and conspicuous row of long plumose setae on lateral surface of carpus and propodus. Ornamentation of fifth pereiopod like fourth but with 2 ventral spines on merus proximal to distal ventrolateral spine, and 3 distolateral spines.

Diaresis of lateral ramus of uropod flanked proximally by row of 17 articulated corneous denticles and slightly larger fixed spine at lateral end of row.

COLOR NOTES.—According to C.B. Powell (pers. comm.), in Nigeria this shrimp is rich brown with a yellowish to tan mid-dorsal stripe, bordered with black, extending from the rostrum almost to the tip of the telson, and there is a dark band across the tail fan in young individuals.

SIZE.—The largest specimen of which we are aware is a male with a carapace length of 35.2 mm. The largest female measured by us has a carapace length of 21.0 mm. The smallest and largest ovigerous females have corresponding lengths of 11.1 and 20.4 mm, respectively.

DISTRIBUTION AND SPECIMENS EXAMINED.—*Atya africana* ranges from Liberia southward to Zaire (Figure 14). 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 or, if followed by "t.l.," total length. Some listings lack the date the collection was made and/or the name of the collector; these could not be determined.

LIBERIA: (1) †USNM, Beulah, Bassa Co, 1♀ (12.9), Feb 1896, O.F. Cook. (2) †BM, St. Paul River near Hendi, Bong Co, 1♂ (8.2), 1 ovig ♀ (13.5), 13 Jun 1969, R. Garms. (3) †USNM, Mt. Coffee, St. Paul River, 1♂ (22.9), 21 Apr 1897, R.P. Currie. (4) †USNM, Muhlenburg Mission, 1♂ (7.1), May 1892, OFC. (5) *BM, St. John River near Yila, at 190m, 1♂ (27.7), 2 Mar 1971, RG. (6) †USNM, Cavalla River at Bolobo, 5♂ (11.4–18.6), 2 ovig ♀ (10.8–13.9), Jun 1946, H.A. Beatty. (7) †BM, Cavalla River near Nyaake (4°52′N, 7°35′W), Grand Gedeh Co, 1♂ (35.2), 13 Dec 1970, RG. (8) †BM, Monot River (4°51′N, 7°39′W), Grand Gedeh Co, 1♂ (14.3), 16 Oct 1969, RG. (9) †BM, Masowa Creek at Bendaja (7°9′N, 11°15′W), Grand Cape Mount Co, 1♀ (9.1), 14 Apr 1971, RG. (10) †BM, Masowa Creek near Dambala, Grand Cape Mount Co, 4♂ (6.1–13.3), 1♀ (8.5), 14 Apr 1971, RG. (11) †BM, Koejar River near Mano River Mine (7°16′N, 11°10′W), 1♂ (19.2), 1 ovig ♀ (13.8), 18 Jun 1969, RG. (12) †BM, Mafa River near Bendouma (7°12′N, 10°59′W), Grand Cape Mount Co, 1♀ (8.6), 17 Jun 1967, RG. (13) †BM, Yah River near Zangbuck Town (6°50′N, 9°6′W) at 200 m, 1♀ (17.9), 2 Mar 1971, RG. (14) †BM, Lower Given River (6°8′N, 9°4′W), Nemba Co, 3♀ (9.1–13.0), 4 May 1971, RG. (15) †BM, Koene near Bestmantown, Kulu, Sinse Co, at 100 m, 13♂ (6.5–23.7), 12♀ (6.9–17.3), 2 ovig ♀ (12.9, 14.7), 19 Mar 1970, RG. (16) Atlantide sta 57 "off Liberia" (5°59′N, 10°27′W), bottom sample, 1 juv (9.0, t.l.) questionably assigned to this species, 8 Jan 1946 (Holthuis, 1951:20). (17) Atlantide sta 53 off Port Marshall (Lebour, 1959), "a few specimens" questionably assigned to this species, 4–7 Jan 1946.

NIGERIA: (1) †BM, Ataiyo River at Oban Hills, at 150 m, 1♀ (12.6), P.A. Talbot. (2) Affluent of Akpe-Yafe River at Aking, Cross River State (5°25′N, 8°37′E) (fide C.B. Powell). (3) near Ogoja, migrating juveniles (fide CBP). (4) Nun River at Kaiama, migrating juveniles (fide, CBP); 17 juv (3.7–5.2), 22 Jun 1977, CBP (these specimens from the Nun River are tentatively assigned to this species).

CAMEROON: (1) *BM, Blackwater River (4°22′N, 9°47′E) (Lewis, Disney, and Crosskey, 1969:232), 2♂ (10.6, 20.0), 1 juv (5.8), R.L.H. Disney; 1♂ (25.6), 7 Oct 1968, RLHD; 2♂ (14.5, 24.8), 2♀ (14.2, 20.4), 1 juv (7.0), 3 Dec 1968,

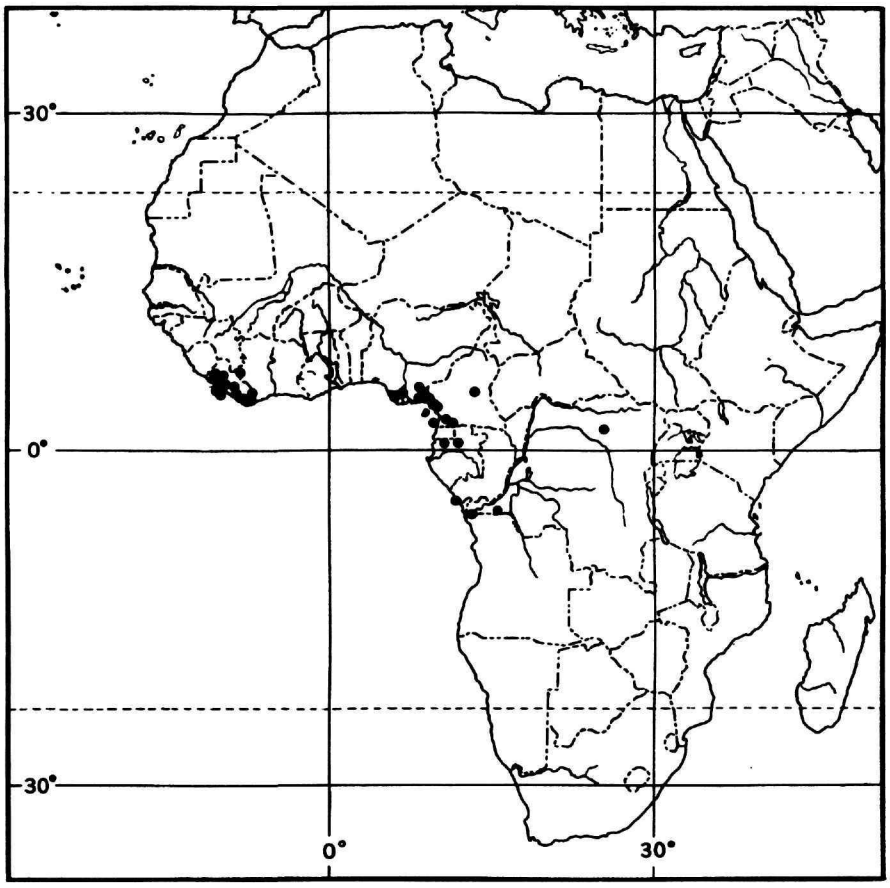

FIGURE 14.—Distribution of *Atya africana*.

RLHD; 2♂ (27.1, 28.5), 11 Dec 1968, RLHD; 2♂ (28.0, 31.8), 13 Feb 1969, RLHD; 6♂ (8.9–20.1), 6♀ (8.5–17.7), 2 ovig ♀ (13.1, 18.0), 1 juv (5.3), 17 Mar 1969, RLHD; 4♂ (9.8–16.0), 6♀ (8.8–16.9), 22 Mar 1969, RLHD; 1♂ (18.8), 1♀ (12.1), 1 ovig ♀ (19.6), 31 Mar 1969, RLHD; 5♂ (10.0–29.2), 6♀ (11.1–17.9), 1 juv (6.8), 10 Apr 1969, RLHD; 1 ovig ♀ (16.4), 23 Apr 1969, RLHD. (2) *BM, Meme River (4°19′N, 9°4′E) (Disney, 1971), 1♂ (27.3), 2 Nov 1968, RLHD; 1♂ (20.0), 5♀ (8.7–15.0), 4 ovig ♀ (12.5–16.0), 1 juv (4.6), 8 Nov 1968, RLHD; USNM, 1♀ (17.2), 2 ovig ♀ (11.7, 17.1), 8 Nov 1968, RLHD; BM, 1♀ (14.0), 3 ovig ♀ (13.9–14.0), 19 Nov 1968, RLHD; 1♂ (24.0), 1♀ (14.1), 25 Nov 1968, RLHD; 1♂ (19.6), 1♀ (12.0), RLHD. (3) †BM, Wowe River, 1♂ (25.0), 3♀ (8.1–21.0), 1 ovig ♀ (12.2), 12 Apr 1969, RLHD; 1 ovig ♀ (15.8), 28 Apr 1969, RLHD; 27 juv (4.9–6.2), 23 Oct 1970, RLHD. (4) †BM, Kobe Let, 1 juv (4.6), 11 Jun 1970, RLHD. (5) †BM, Kobe River near Etam, 1 ovig ♀ (20.0), 6 Dec 1968, RLHD; 2 juv (5.3, 5.5), 12 Mar 1969, RLHD; 2♂ (10.9, 12.1), 24 Apr 1969, RLHD. (6) *BM, Bille River (Disney, 1971), 3 ovig ♀ (11.1–18.2), 1 juv (7.0), 11 Nov 1968, RLHD; 4♂ (17.3–23.8), 1 ovig ♀ (15.3), 12 Nov 1968, RLHD; 4♂ (10.8–27.6), 1♀ (15.2), 1 juv (5.0), 5 Dec 1968, RLHD; 2♀ (9.2, 10.1), 18 Mar 1969, RLHD; 1♂ (10.9), 2♀ (7.4, 12.0), 1 ovig ♀ (14.8), 17 Apr 1969, RLHD; 3♂ (10.5–13.0), 2 ovig ♀ (13.6, 15.4), 19 May 1969, RLHD. (7) †BM, Mengo River, 1♂ (11.4), 3♀ (10.4–13.4), Mar 1969, RLHD; 1♂

(12.1), 29 Oct 1969, RLHD. (8) *BM, Mungo River near Boduma (Vogel and Crewe, 1965), 1 ovig ♀ (14.8), 8 juv (5.1–6.5), 26 Nov 1968, RLHD. (9) Atlantide sta 119 (2°55′N, 9°21′E), stramin net 100 cm, 3 juv ♂ (2.3–3.0) (questionably assigned to this species; Holthuis, 1951:20), 28 Feb 1946.

GABON: (1) Booué, 1♂, 1♀ (Bouvier, 1925:307). (2) *MHNP, Ogooué River at Samkitta (Bouvier, 1904:138), 1♂ (46.0, holotype), Mar 1877. (3) †MHNP, Ogooué, 1♂ (14.3), M. Marche.

CONGO: "baie de Pointe-Noire, 10 m env.," 54 juv (9.9–11.5, t.l.), A. Crosnier (Crosnier, 1971: 570, questionably assigned to this species).

ZAIRE: (1) MBuma dans le Mayumbe (De Man, 1925:26), 1♂ (96, t.l.), 2 ovig ♀ (65, 70, t.l.), 7 other specimens, 25–26 Oct 1920, Dr. Schouteden. (2) *BM, Atlantide sta 127, Boma, 4 juv (2.3–4.2), (questionably assigned to this species; Holthuis, 1951:20), 10 Mar 1946. (3) ? †MCZ, Zaire River near Bulu, W of Luozi (5°1′S, 14°1′E) swimming at surface in protected cove, 1 juv ♀ (7.1), 15 Jul 1973, T.R. Roberts, D.J. Stewart (see "Variations").

VARIATIONS.—Few variations worthy of mention have been noted. Most appear to be associated with the size, and presumably the age, of the individual. This is particularly true of the larger spines on the various podomeres of the ambulatory pereiopods; the smaller specimens, for the most part, have more, a full complement consisting of a series of three spines on the ventrolateral surface of both the merus and carpus of all three legs; the spines are progressively larger from proximal to distal end of each podomere, and the most persistent with age of the shrimp is the distal ventrolateral member on the merus. The fringe of setae that extends along the lateral surface of the merus distally to about midlength of the propodus of the same pereiopods is also best developed in comparatively small individuals that have recently molted, but in the more crusty, larger males, little more than a trace of the row is evident on the merus, and it is often reduced throughout its length. The rostrum is variable in length, attaining the basal one-third to almost two-thirds of the penultimate podomere of the antennular peduncle and exhibits as many as three ventral spines, but they may be lacking. The range of variation in the number and disposition of the corneous spinules on the antennular peduncle is mentioned in the "Diagnosis." None of the variations noted seems to be restricted to a limited part of the range of the species.

Like those specimens cited above that were questionably assigned to this species by Holthuis (1951) and Crosnier (1971), the juvenile female listed from the third locality in Zaire is only tentatively assigned to this species. The absence of a pterygostomian angle and only three spines in each of the two rows on the dorsal surface of the otherwise typically appearing telson are unique among the specimens we have examined. The third pereiopods are so poorly developed that they are not helpful in identifying the specimen. The long tapered rostrum is the single character that suggests its being a young member of *Atya africana*.

ECOLOGICAL NOTES.—There is little information concerning the habitats exploited by members of this species except that these shrimp frequent creeks and rivers from sea level to 200 m. A juvenile with a carapace length of 7.1 mm, believed to be a member of this species, was caught swimming at the surface of a protected cove in the Zaire River near Bulu, Zaire. If the juveniles described by Holthuis (1951:20–23) and Crosnier (1971:571) prove to be members of *A. africana*, then a part of the life cycle is probably typically spent in salt water at depths ranging from five to 62 meters; at least the young can tolerate sea water within this depth range. As pointed out by Holthuis (pp. 20, 23), juveniles that may be conspecific and that are smaller than the largest found in salt water also occur in fresh water.

Disney (1971), working in streams in the vicinity of Kumba, West Cameroon, found that most of the adult members of the *A. africana* population occurred under stones and that the smaller individuals were found more frequently among leaves and other debris, suggesting to him a difference of preference in the microhabitats of the smallest and adult members of the species. A brief account

of the population structure reported by him is presented in the "Review of Literature" above.

We were informed by C.B. Powell (pers. comm.) that his specimens taken at Aking, Nigeria, came from a wide, shallow river with a bottom made up almost entirely of rocks and boulders, and where there was a swift current. The specimens were caught among accumulations of dead leaves and other debris wedged between rocks in places where the current was fastest.

Life History Notes.—Ovigerous females have been obtained from March to June and from October to December. To our knowledge, collections have not been made during other months of the year. Reference to the juveniles in "Ecological Notes" above suggests that if those in question are members of this species, like the larval members of other species of the genus studied by Hunte (1975, 1977, 1979b), the first larva must return to salt or brackish water. At least some of these juveniles occur in such habitats when they attain a total length of 12 mm (Holthuis, 1951:20). De Man (1925) reported the eggs of ovigerous females from "MBuma," Zaire, to be 0.32 mm wide and 0.58 to 0.62 mm long. In specimens from the Blackwater River, Cameroon, we found eggs ranging from 0.3 to 0.4 mm wide by 0.6 to 0.7 mm long.

Disney (1971) has added more than any other to our knowledge of the life history of this shrimp. In the vicinity of Kumba, West Cameroon, he found that the ovigerous females, ranging in total carapace length from 11 to 25 mm (about half of them 16 to 20 mm) appeared in greatest numbers from October to November and about five-eighths as many from April to May. An apparent "breeding pause" occurs from December to March. Juveniles of small size, which were believed to be migrating, were collected by an assistant to C. B. Powell (pers. comm.) near Ogoja and Kaiama, Nigeria.

Remarks.—Because of the tapering rostral margins of this shrimp, its identity is as readily recognized among the African members of the genus as is the highly sculptured *Atya gabonensis*. Its affinities, however, are not entirely clear. In most of its features it resembles *Atya dressleri*, *A. lanipes*, and, to a lesser extent, *A. innocous* and *A. intermedia*. The acuminate rostrum, the rather weakly developed tubercles on the merus of the third pereiopod, the proportions of this podomere, and the absence of corneous spinules on the ventral margin of the abdominal pleura align this shrimp with *A. dressleri* and *A. lanipes*. The moderately short sternum of the sixth abdominal segment is more like that of *A. dressleri*, *A. innocous*, and *A. intermedia* than like that of *A. lanipes*, but the preanal spine is quite short. Certainly it appears to be more closely allied to the four just mentioned species than it is to *A. scabra* and *A. margaritacea*. Nevertheless the ornamentation of the flexor surface of the propodus and ischium of this appendage is positioned as it is in *A. scabra*, that is, the spines on the mesioventral surface of the propodus are arranged in a row, and are subcontiguous, and those of the dactyl are dispersed in a single series. Individually, however, the spiniform tubercles of the entire appendage, especially those on the flexor surface of the propodus, resemble those of *A. dressleri* and *A. lanipes* more closely than they do the more heavily cornified discoid ones in *A. scabra* and *A. margaritacea*. Cornified spinules on the dorsal surface of the basal segment of the antennule are similar to those in *A. scabra*.

Atya brachyrhinus, new species

Figures 1*c*, 9, 10, 12*g*, 15

Diagnosis.—Cephalic region of carapace not conspicuously sculptured, densely covered with fine setae borne in small punctations, lacking spines other than antennal and pterygostomian; rostrum with convex margins tapering anteriorly, only slight irregularity in position corresponding to angle in some congeners; apex not nearly reaching distal extremity of proximal segment of antennule; pterygostomian angle acute but dorsal margin not excavate. Ventral margin of third, fourth, and fifth abdominal pleura with linear clusters of sclerotized spinules; caudoventral angles of fourth and fifth pleura not produced in

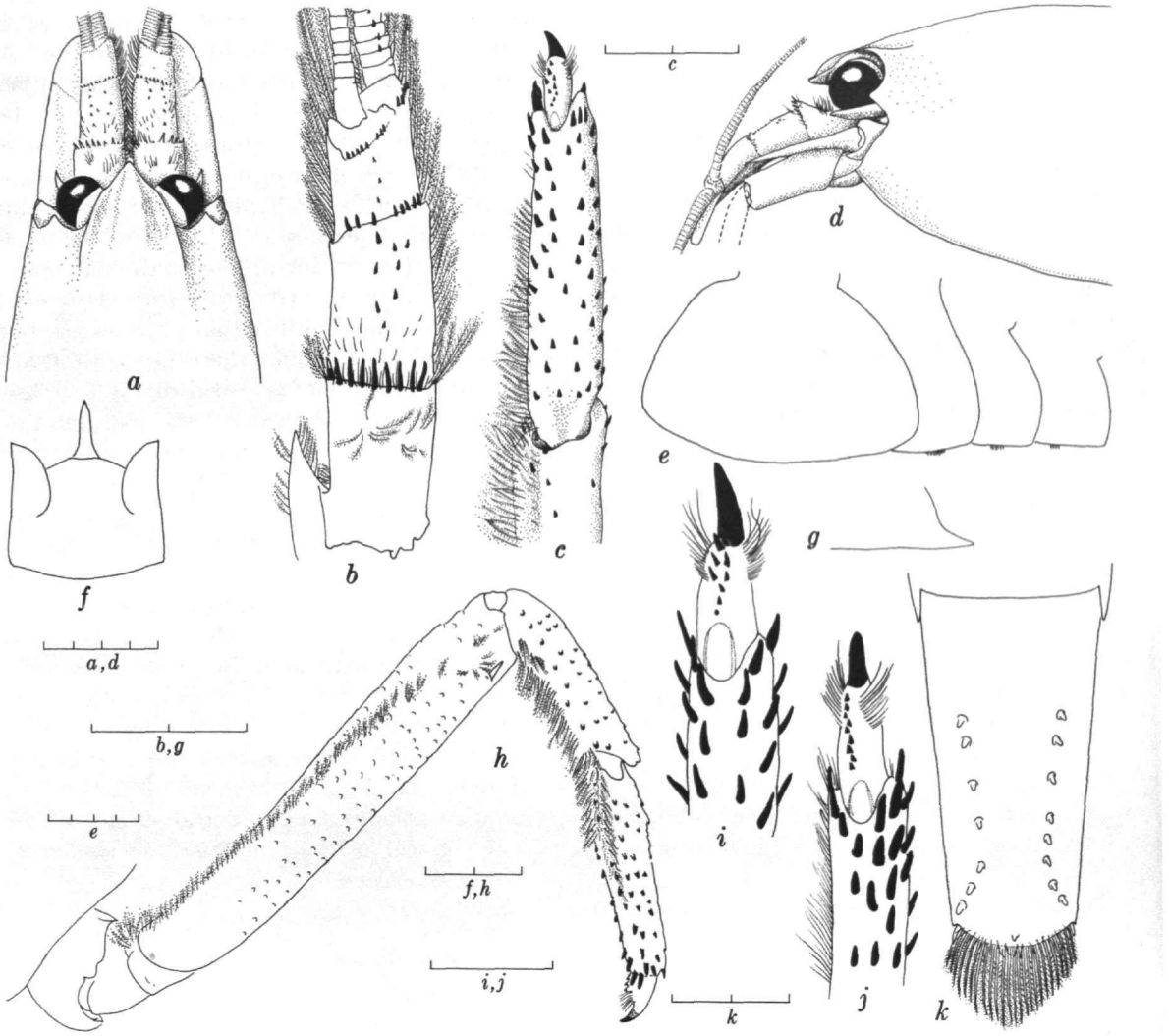

FIGURE 15.—*Atya brachyrhinus* (all from holotypic female except *b*, *i*, *j* from paratypic female): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, flexor surface of distal part of third pereiopod; *d*, lateral view of cephalic region; *e*, lateral view of second through fifth abdominal pleura; *f*, sternum of sixth abdominal segment and preanal carina; *g*, lateral view of preanal carina; *h*, lateral view of third pereiopod; *i*, flexor surface of distal part of fourth pereiopod; *j*, flexor surface of distal part of fifth pereiopod; *k*, dorsal view of telson. (Scales marked in 1 mm increments.)

spines. Sternum of fifth abdominal segment with prominent median tubercle, that of sixth about 1.3 times as broad as long. Preanal carina with well-developed spine. Telson about twice as long as wide and with 7 to 9 spines in each of 2 dorsal rows. Antennular peduncle with proximal article lacking premarginal sclerotized spinules dorsally; penultimate article approximately 1.4 times as long as wide, its dorsal surface provided with somewhat linearly arranged spinules. Coxae of third and fourth pereiopods lacking prominent ventrolateral spine. Third pereiopod with merus

rounded ventrally, about 5.5 times as long as high, ventromesial surface bowed, never parallel to that of corresponding podomere of other third pereiopod; lateral surface with small, inconspicuous, nonsclerotized tubercles; propodus about 5 times as long as broad; extensor and flexor surfaces bearing many small sclerotized spines; dactyl approximately 3 times as long as wide, freely movable, and bearing 2 oblique rows of sclerotized spines on flexor surface; rather prominent band of setae extending from dorsolateral surface of basis to beyond midlength of lateral margin of propodus.

HOLOTYPIC FEMALE.—Rostrum (Figure 15*a,d*) with convex margins bearing trace of emargination delimiting base of acumen, latter falling far short of distal margin of proximal podomere of antennule; rounded dorsal carina not excavate dorsally (not dipping below level of lateral carinae posterior to acumen) and ending preapically on acumen; ventral carina lacking teeth or serrations; ocellar beak, hidden in lateral view by eyes, with anterodorsal margin arched, its anterior extremity falling short of faceted part of eye. Antennal spine acute; pterygostomian angle acute but dorsal side not strongly concave, thus not appearing produced in prominent spine. Carapace devoid of other spines or ridges; surface punctate with fine setae, lacking pile of short stiff setae.

Pleura of second and third abdominal segments (Figure 15*e*) with rounded posteroventral extremities, although fourth and fifth subangular, none produced in spines. Ventral margin of third, fourth, and fifth pleura with linear clusters of 9, 6, and 4 fine corneous spinules, respectively, also with additional fine plumose setae. Fourth abdominal tergum approximately 0.9, 0.7, and 0.55 times as long as fifth, sixth, and telson, respectively; that of sixth about 1.3 times length of fifth and 1.4 times that of telson. Sternum of fifth abdominal segment (Figures 1*c*, 15*f*) with rather large tuberculiform prominence, that of sixth about 0.76 as long as broad. Preanal carina (Figure 15*g*) with strong spine extending caudally beyond base of carina. Telson (Figure 15*k*) almost twice (1.9) as long as wide, its dorsal surface studded with paired, mesially concave rows of corneous denticles (dextral row of 9 and sinistral of 7) and posteromedian premarginal tubercle.

Basal segment of antennule (Figure 15*b*) with well-developed stylocerite overreaching midlength of segment, dorsal surface with clusters of setae but lacking corneous spinules; distal margin bearing row of 8 (left) and 6 (right) cornified spinules; penultimate segment of peduncle about 1.4 times as long as broad, studded dorsally with 7 (left) or 5 (right) small corneous spinules and 7 (left) or 8 (right) on distal margin; ultimate segment, about 0.5 as long as penultimate, armed with 7 spinules at base of lateral flagellum and row of 4 at base of mesial flagellum. Antenna with ventrolateral spine on basis almost reaching level of tip of stylocerite; lateral spine of scaphocerite weak, extending short distance beyond base of ultimate podomere of antennular peduncle and almost attaining distal end of that of antenna, lamella of scaphocerite overreaching peduncles of both antennule and antenna. Flagellum of antenna broken, but that of paratype extending beyond caudal margin of telson.

Third maxilliped overreaching antennular peduncle by about 0.25 length of distal podomere; tip of exopod reaching base of apical third of penultimate segment of endopod; penultimate segment of endopod about 1.4 times as long as ultimate.

First pereiopod slightly overreaching distal extremity of antennular peduncle; second overreaching first by about 0.25 length of fingers; terminal brush of setae lacking scraping denticles. Third pereiopod (Figure 15*c,h*) unarmed except for rather prominent spine on distal ventrolateral surface of merus, and when extended anteriorly overreaching antennular peduncle by length of propodus and dactyl. Merus with ventromesial margin weakly bowed, about 5 times as long as high, 2.3 times as long as carpus, and 2.1 times as long as propodus; latter about 4 times as long as wide and 1.1 times as long as carpus; distoventral margin of coxa entire and both mesial caudoventral prominence and distolateral spine lacking. Lateral, dorsal, and ventral surfaces of merus studded with weak, squamous tubercles flanked

distally by plumose setae; longitudinal band of long plumose setae present on lateral surface; mesial extremity of podomere produced in prominent rounded lobe at level of mesial articular condyle of carpus. Carpus studded with small, distally directed, corneous spines, and lateral surface with prominent distoventral spine somewhat obscured by conspicuous ventrolateral tufts of plumose setae extending along length of podomere, setae increasing in length from proximal to distal end of podomere. Propodus also studded with corneous spines, those on flexor surface tending to be linearly arranged toward lateral surface which provided with conspicuous longitudinal band of plumose setae. Dactyl movable, its flexor surface bearing 9 corneous spinules arranged in 2 somewhat arched rows; clusters of setae flanking rows distally.

Fourth pereiopod with dactyl reaching end of proximal third of carpus of third; merus almost twice as long as carpus, latter about 0.7 as long as propodus. Fifth pereiopod reaching slightly beyond midlength of carpus of fourth pereiopod; merus 1.3 times as long as carpus, latter approximately 0.7 as long as propodus. Ornamentation of merus, carpus, and propodus of fourth pereiopod consisting of distal ventrolateral spine on merus, ventrolateral row of 4 spines (increasing in size distally) on carpus, and band of plumose setae extending on lateral surface of podomeres from base of merus almost to end of propodus, broadening distally on both merus and carpus. Ornamentation of fifth pereiopod like that on fourth except merus provided with 3 additional spines ventrally, and ventrolateral surface of carpus with only 2 spines.

Diaresis of lateral ramus of uropod flanked proximally by row of 22 articulated corneous denticles and fixed spine at lateral end of row.

Color Notes.—On the label accompanying the holotype was the following: "It was colorless with pink tail when seen. Two black dots only give away."

Size.—Carapace length of holotype and paratypic female 15.7 and 15.8 mm, respectively.

Types.—The holotypic female is in the British Museum (Natural History), number 1972:539, and the fragmentary paratypic female, in the National Museum of Natural History, Smithsonian Institution, number 184857.

Type-Locality.—Cole's Cave, Barbados, West Indies, 13°10'40"N, 59°34'30"W. Notes accompanying the holotype state that the specimen was collected

> high up the side of the large cavern. Water issues . . . through an apperture [sic] estimated two yards horizontally wide with 9" running sheet of water under 6" air space . . . Shrimps seen 15' downstream from tunnel and made off to the tunnel fast . . . in the dark it took up a normal "legs down" position. In the light it went on its side and even on its back and jerked about in spasms.

The identity of the collector is unknown, but the specimen was obtained on 6 October 1972. The paratypic female was found in the same cave by R.R. Allen and C.E. Ray on 28 February 1963.

Distribution and Specimens Examined.—Known only from the type-locality. The sources of the two known specimens are related under "Type-locality": 1♀ (16.0), 23 Feb 1963, R.R. Allen, C.E. Ray; 1♀ (15.7, holotype), 6 Oct 1972.

Ecological Notes.—See "Type-locality."

Life History Notes.—None.

Relationships.—*Atya brachyrhinus* has its closest affinities with the sympatric *Atya innocous*, with which it shares most of the features mentioned in the "Diagnosis" of each of the two. It differs from all members of the genus in possessing a broad, short rostrum that has strongly convex lateral margins and does not reach the distal end of the proximal podomere of the antennule. It differs from *A. innocous* most conspicuously by the shape of the rostrum; in that species the base of the acumen is clearly delimited by abrupt constrictions of the rostral margins. The pterygostomian angle of *A. brachyrhinus* is less acute, the tubercles on the third pereiopod are much less strongly developed, and the spine on the preanal carina projects much beyond the basal part. From its other sympatric relative, *A. scabra*, it differs more strikingly by the absence of an angular bend in the rostral margin marking the base of the acumen, in the absence of corneous spinules on the dorsal surface of the proximal podomere of the antennule, in the absence of short stiff setae stud-

ding the surface of the carapace, in the less spiniform pterygostomian angle, in lacking corneous denticles on the ventral margin of the pleuron of the second abdominal segment, in the proportionately narrower telson with a greater number (7 or 8) tubercles in each of the dorsal rows, in the proportionately longer sternum of the sixth abdominal segment, in the less well-developed tubercles on the lateral surface of the merus and carpus of the third pereiopod, and in the size and arrangement of the tubercles on the flexor surface of the propodus and dactyl of the third pereiopod.

Atya crassa (Smith)

FIGURES 1*m*, 9, 10, 11*g*, 16, 17

Evatya crassa Smith, 1871:95–97 [type-locality: "Fresh water streams, Polvon, and the 'Rio Fulva, two and a half miles northwest of Realejo,' Occidental Department, Nicaragua"; types: (?)USNM 84261, 1♀; (?)PM 6038, 1♂, 1♀].—Kingsley, 1878b:57.—Holthuis, 1955b:26.

Euatya crassa.—Koelbel, 1884:318, 320.

Euatya (Evatya) crassa.—Koelbel, 1884:318.

Atya (Evatya) crassa.—Ortmann, 1895:408, 410, 415.—Doflein, 1900:127.

Atya (Euatya) crassa.—Ortmann, 1897:184, 186.

Evatya crassus.—Sheldon, 1905:343 [erroneous spelling].

Atya crassa.—Bouvier, 1905:110, 113, 124; 1925:26–28, 293, 319–323, figs. 54, 68.—Pesta, 1931:173, 178.—Oliveira, 1945:178.—Holthuis, 1951:9; 1955b:26, fig. 9.—Balss, 1955, fig. 1050.—Kaestner, 1970, figs. 13–18f.—Burukovsky, 1974, fig. 85.

REVIEW OF LITERATURE.—Smith (1871) described this shrimp along with *Atya rivalis* and *A. tenella* from freshwater streams at El Polvón in the western part of Nicaragua; he also cited a second locality for *A. crassa*, "Rio Fulva, two and a half miles northwest of Realejo." Kingsley (1878b) added no new information but listed the species and cited it from the west coast of Nicaragua. Koelbel (1884), in describing *Euatya sculptilis* (= *Atya gabonensis* Giebel, 1875) and emending the spelling of *Evatya*, assigned Smith's species to the same genus and reported its occurrence in Río Presidio (perhaps near Mazatlán, Sinaloa), Mexico. Ortmann (1895) recognized two subgenera of the genus *Atya* and placed *A. crassa* in the monotypic subgenus *Evatya*; no new data relative to the species were included. Doflein (1900), who followed Ortmann in the subgeneric assignment, listed this shrimp from the Atlantic side of Panama. In the meantime, Ortmann (1897) had employed the combination *Atya* (*Evatya*) *crassa*, presented a diagnosis of the species, and included Nicaragua and Mexico in his summary of distribution. Sheldon (1905) added no new information. Bouvier (1905), not recognizing the subgeneric designations of Ortmann, provided a key to the species of the genus, and pointed out the similarity in the serrate rostra of *A. crassa* and *A.* (= *Micratya*) *poeyi* Guérin-Méneville (1855). In his monograph of the Atyidae, Bouvier (1925) emphasized the relationships of *A. crassa* with *A. gabonensis*, considering them to be the most advanced members of the genus. A key to the species was provided along with a summary of the locality records (those just cited), an illustration, in lateral aspect, of a male, and another of the telson. Pesta (1931), reporting on the Austrian expedition of 1930 to Costa Rica, added a new locality for the species: Río Nuevo that flows into Golfo Dulce. Oliveira (1945), in his study of *Atya scabra* in northeastern Brazil, mentioned *A. crassa* but added nothing to our knowledge of the species, nor did Holthuis (1951); however, the latter (1955b) cited this shrimp as the type of Smith's *Evatya* and included the illustration of the entire animal that appeared in Bouvier's monograph. Balss' (1955) figure was also taken from Bouvier, Kaestner's (1970) from Balss, and Burukovsky's (1974) from Holthuis.

PUBLISHED ILLUSTRATIONS.—The only illustrations of this shrimp are a dorsal view of the telson and a lateral one of an entire animal included in Bouvier (1925). The latter figure was reprinted by Holthuis (1955b) and Balss (1955), and indirectly by Kaestner (1970) and Burukovsky (1974).

DIAGNOSIS.—Cephalic region of carapace strongly sculptured and bearing many rows of corneous-tipped spines and tubercles. Rostrum with margins tapering from base and studded with median dorsal row of corneous-tipped spines. Pterygostomian angle produced in prominent spine. Ventral margin of abdominal pleura lacking sclerotized denticles; caudoventral angle of

fourth and fifth pleura usually produced in spines. Fifth abdominal segment with median tubercle on sternum moderately to strongly developed; sternum of sixth abdominal segment less than half as long as wide. Preanal carina in form of subconical spine directed caudally to caudoventrally. Telson 1.2 to 1.4 times as long as broad and bearing paired arched dorsal rows of 4 to 6 spines. Antennular peduncle with dorsal surface of proximal article lacking sclerotized spinules proximal to transverse distal row; penultimate article 1.5 to 2.2 times as long as wide and bearing dorsolateral longitudinal row of spinules. Coxa of third and fourth pereiopods with prominent ventrolateral spine, that of third also with strong mesial caudoventral prominence. Third pereiopod with merus subplane ventrally, 1.5 to 2.3 times as long as high, ventromesial margin subangular and parallel to that of corresponding podomere of other third pereiopod, and lateral surface bearing irregular rows of spines, many of which with flattened corneous extremities; propodus 1.3 to 1.6 times as long as broad, studded with scalelike tubercles on extensor surface and with few similar ones of flexor surface, latter largely obscured by conspicuous tufts of long plumose setae; dactyl apparently inflexibly fused with propodus and bearing 1 or 2 small scalelike tubercles on flexor surface just proximal to corneous tip.

MALE (Río Chucunaque, Darién Province, Panama).—Rostrum (Figure 16*a*,*c*) with margins tapering from base to corneous, acute apex, latter almost reaching distal end of antennular peduncle; dorsal median carina rounded and bearing row of 7 corneous-tipped spines, 4 of which situated behind orbit, directed dorsally, and decreasing in size posteriorly; those on rostrum subequal in size, 2 more posterior ones directed dorsally, and anteriormost anterodorsally. Ventral surface of rostrum evenly rounded transversely, lacking clearly defined carina; lateral carinae very small, becoming obsolete at base of anteriormost spine. Ocellar beak upturned and so well concealed beneath rostrum and between eyes that hardly noticeable. Antennal and pterygostomian spines acute, and cephalic border of carapace between them bearing 2 large, acute, corneous-tipped spines. Entire surface of carapace densely punctate, and cephalic half very ornate dorsally and dorsolaterally, bearing paired ridges studded with rows of corneous-tipped spines; ventrolateral punctations bearing conspicuous setae.

Pleura of first and second abdominal segments (Figure 16*i*) with rounded posteroventral extremities, corresponding parts of third obtuse, and those of fourth and fifth acute with corneous apices; anteroventral angle of sixth also with acute, corneous, caudoventrally directed tip. All pleura lacking corneous denticles on ventral margin, but fourth and fifth with row of prominent plumose setae. Fourth abdominal tergum approximately 1.2 times as long as fifth, length of sixth subequal to that of fifth and almost 0.9 as long as telson. Sternum of fifth abdominal segment (Figure 1*m*) with very prominent, corneous-tipped, acute median spine directed caudoventrally; sternum of sixth segment about 0.42 times as long as broad. Preanal carina (Figure 16*k*) represented by strong, caudally directed, corneous-tipped spine. Telson (Figure 16*b*) about 1.3 times as long as wide, its dorsal surface bearing paired rows of 6 corneous denticles and with posteromedian tubercle slightly overhanging caudal margin.

Proximal podomere of antennule (Figure 16*a*,*l*) with strong stylocerite overreaching midlength of segment, dorsal surface with few setae but lacking corneous spinules; distal margin studded with row of 5 corneous spinules; penultimate segment of peduncle 1.5 times as long as wide and provided with 4 spinules on dorsolateral surface and row of 3 (right) or 4 (left) on distal margin; ultimate podomere with no spinules on dorsal surface but with row of 5 flanking dorsal base of lateral flagellum and 2 at dorsal base of mesial flagellum. Antenna with ventrolateral spine on basis reaching proximal end of penultimate podomere of antennular peduncle, distinctly overreaching stylocerite; lateral spine on scaphocerite strong, extending to level of tip of rostrum; lamella overreaching peduncles of antennule and antenna; flagellum of antenna reaching caudal margin of telson.

Third maxilliped overreaching antennular pe-

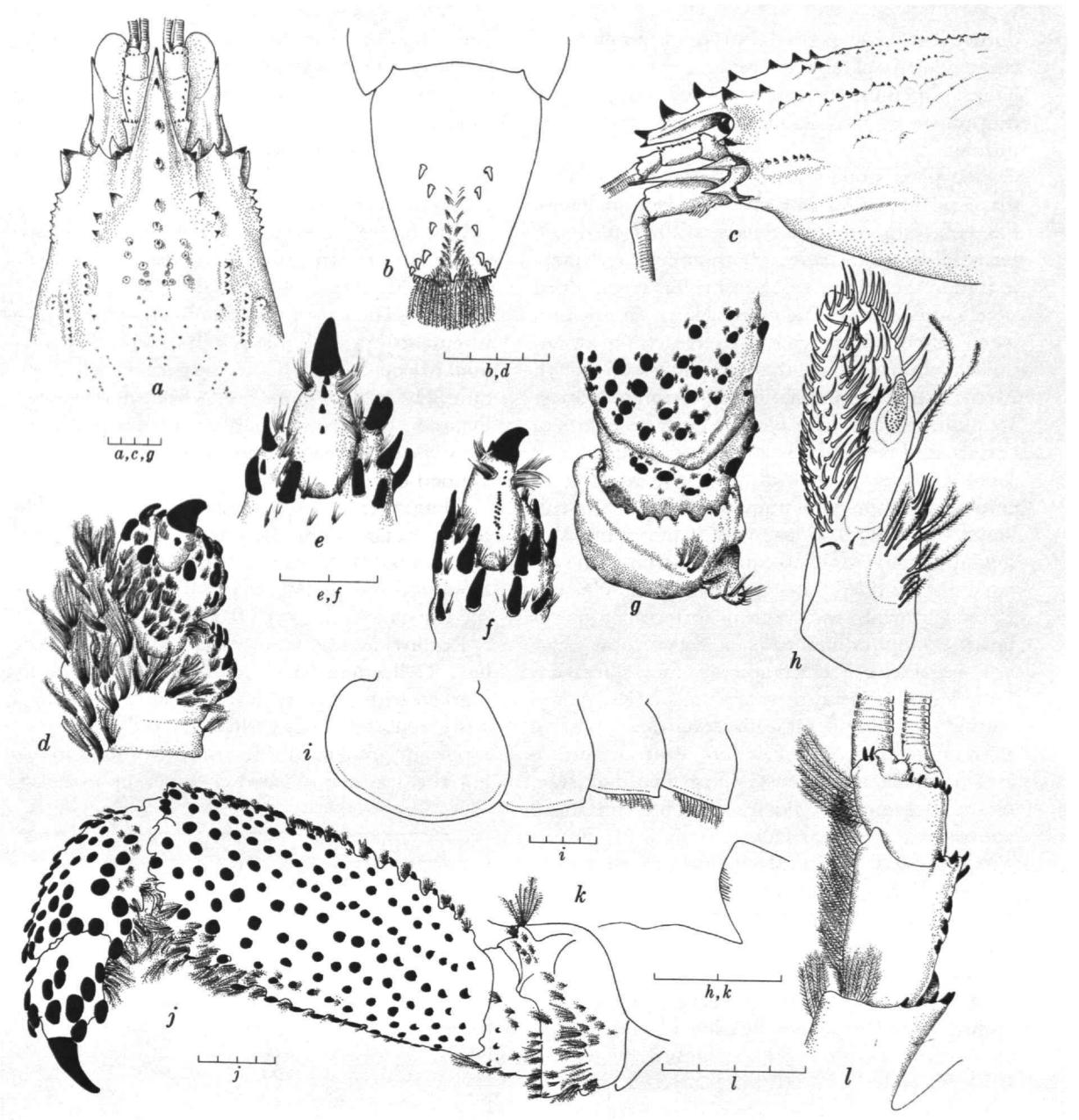

FIGURE 16.—*Atya crassa* (all from male from Río Chucunaque, Panama, except *b* from male from Río Lempa, El Salvador): *a*, dorsal view of cephalic region; *b*, dorsal view of telson; *c*, lateral view of cephalic region; *d*,*e*,*f*, flexor surface of distal part of third, fourth, and fifth pereiopods, respectively; *g*, ventral view of base of right third pereiopod; *h*, mesial view of appendices masculina and interna; *i*, lateral view of second through fifth abdominal pleura; *j*, lateral view of third pereiopod; *k*, lateral view of preanal carina; *l*, dorsal view of antennular peduncle. (Scales marked in 1 mm increments.)

duncle by 0.25 length of ultimate segment of endopod; tip of exopod almost reaching mid-length of penultimate podomere of endopod; penultimate segment about 1.6 times as long as ultimate.

First pereiopod reaching level of base of ultimate podomere of antennule, second reaching base of distal fifth of dactyl of first pleopod; terminal brush of setae of both appendages lacking scraping denticles. Except for coxa, third pereiopod (Figure 16*d,g,j*) lacking spines and when extended anteriorly, overreaching antennular peduncle by length of propodus and dactyl. Merus with ventromesial margin straight, almost 1.5 times as long as high, 14.1 times length of carpus, and 4.4 times as long as propodus; latter slightly longer than wide and 0.48 as long as carpus; distoventral margin of coxa strongly scalloped, distolateral surface with strong spine, and mesial caudoventral prominence strongly developed and studded with prominent setal clusters. Lateral, dorsal, and ventral surfaces of merus bearing longitudinal rows of conspicuous, corneous tubercles of which apices of most somewhat flattened and bearing sharp free edge; paired clusters of plumose setae flanking distal base of most tubercles; tubercles on ventral surface largely concealed by dense, shaggy beard of setae; mesial extremity of podomere slightly produced at level of mesial articular condyle of carpus; strong tubercle on distal mesioventral angle opposing tubercle on carpus. Ventral and ventromesial surface of carpus heavily bearded. Flexor surface of propodus with few widely spaced tubercles, almost all obscured by tufts of setae borne proximally on podomere; dactyl fused with propodus, its flexor surface bearing median cluster of small, corneous denticles flanked by pair of setal clusters.

Fourth pereiopod with dactyl reaching base of distal third of merus of third pereiopod; length of merus slightly greater than twice that of carpus, latter 1.1 times longer than propodus; coxa with strong distolateral spine. Fifth pereiopod reaching end of basal fifth of carpus of fourth; merus about 1.5 times as long as carpus, and latter 0.86 as long as propodus. Ornamentation of merus, carpus, and propodus of fourth pereiopod similar to that of third except ventral surface of merus with 3 articulated spines, and ventrolateral surface of carpus with 1; only 2 such spines present on merus of fifth pereiopod, and flexor surface of dactyl with row of many more spinules, ornamentation otherwise similar to that of fourth.

Diaresis of lateral ramus of uropod flanked proximally by 16 articulated corneous denticles and slightly larger fixed lateral spine.

Size.—The largest specimen for which measurements are available is a male from Río Presidio, Mexico, which has a carapace length of 60.0 mm. The largest female, one from northwestern Ecuador, has a corresponding length of 41.4 mm. No ovigerous females have been reported or examined by us.

Distribution and Specimens Examined.—This species ranges along the Pacific slope from Presidio (probably Sinaloa), Mexico, southward to Ecuador, and in Panama it has been found on the Caribbean slope (Doflein, 1900) (Figure 17).

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

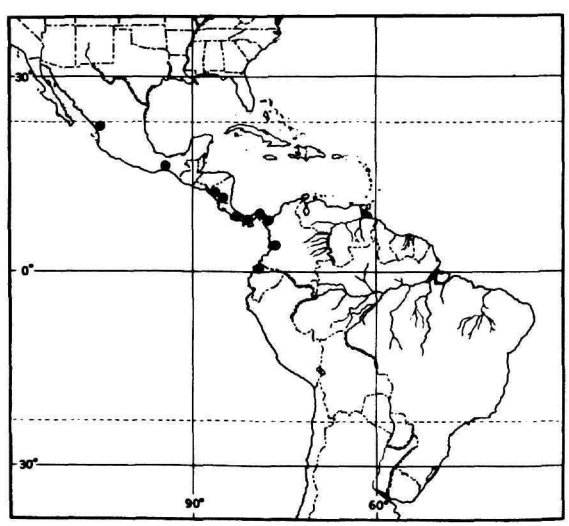

Figure 17.—Distribution of *Atya crassa*.

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.

MEXICO: (1) *BM, Río Presidio (?Sinaloa) (Koelbel, 1884:318), 1♂ (60.0), 2♀ (17.7, 23.3), A. Forrer; MHNP, 1 specimen (35.5). (2) †USNM, Río Tehuantepec, Oaxaca, 1♂ (50.5), T. MacDougall.

EL SALVADOR: †USNM, Río Lempa at Suchitoto, 2♂ (29.3, 28.7), 1♀ (29.0), 9 Feb 1924, C.A. Hildebrand and Foster; USNM, 2♂ (22.6, 32.8), 5 Feb 1924, CAH and F.

NICARAGUA: (1) *USNM, freshwater streams, El Polvón (12°27'N, 87°05'W) or Río Fulva, 2.5 mi NW of Realejo (Smith, 1871), 1♀ (40.0), syntype, 1869, J.A. McNeil. (2) †PM, "Rio Frilo," (probably Río Frío), about 1.8 km NW of Realejo, 1♂ (11.2), 2♀ (8.5, 15.0), 1869, J.A. McNiel.

COSTA RICA: Río Nuevo (Halbinsel Osa), Golfo Dulce (Pesta, 1931:178), 1♂ (120, t.l.), 4 juv, 1 Apr 1930.

PANAMA: (1) "Atlantic side" (Doflein, 1900: 127). (2) †USNM, Río Chucunaque near Río Sansón, Provincia de Darién, 3♂ (47.5, 50.8, 56.3), 27 Apr 1958, C.E. Bennett, Jr. (3) †USNM, Río Chucunaque above Membrillo, Provincia de Darién, 1♂ (38.9), 4♀ (15.3–38.6), 7 Apr 1924, J.L. Baer. (4) †LGA, Río Bayano at ford, Provincia de Panamá, 1♀ (6.3), 6 Mar 1973, R.L. Dressler. (5) †LGA, headwaters of Río Bayano 1♂ (28.0), 1♀ (9.6), Dec 1974, L.G. Abele.

COLOMBIA: †USNM, Río Dagua at bridge, 0.25 km from Buenaventura, 6♂ (30.8–41.0), 5♀ (28.7–39.3), 17 Jul 1939, Karl P. Schmitt.

ECUADOR: (1)†BM, NW Ecuador, alt 136 m, 2♂ (38.1, 39.0), 4♀ (32.1–41.4). (2) †MCZ, Ríos Cayapas, Hoja Blanca, and San Miguel, in immediate vicinity of village of San Miguel, Provincia de Esmeraldas, 2♀ (32.9, 37.9), Miyata and Rand. (3) †USNM, junction of Río Cayapas and Río San Miguel, Provincia de Esmeraldas, 1♀ (37.2), Jun 1977, Andris Rankis.

VARIATIONS.—The following few remarks are based on such a limited series of specimens, 11 constituting the greatest number from a single locality, that they should not be considered as conclusive. The specimens from Colombia and Ecuador differ from those from the Middle American region in possessing fewer tubercles on the lateral surface and dorsal margin of the merus of the third pereiopod. In the South American specimens, the dorsal row consists of 12 to 14 (rarely 13 or 14) and in those from Middle America, 15 to 19. Six to 10 spines constitute the median row on the rostrum, and, whereas in the specimens from Ecuador, Colombia, and Panama there are usually six or seven, as contrasted with eight to 10 in the more northern part of the range, the numbers are not consistent, for specimens from both El Salvador and Nicaragua have as few as seven and at least one from each of Colombia and Panama exhibit eight or nine. Of the other features compared in specimens from throughout the range, there seems to be no correlation of a variation with a limited part of the area occupied by the species.

ECOLOGICAL NOTES.—The only data available as to the habitat occupied by *Atya crassa* are in the short statement of Smith (1871:97), "Fresh water streams . . . and 'Rio Fulva' . . . ," citing the localities from which his specimens were taken, and the inclusion of "Rio" among the data accompanying most subsequent collections (see "Distribution"). Some of the specimens cited herein from Ecuador were collected at an altitude of 150 m.

LIFE HISTORY NOTES.—There are no published data relative to the life history of members of this species. Of the specimens known to us, not one is ovigerous, and even the dates collections were made are few. Among the previously recorded localities, only that in Costa Rica (Pesta, 1931) was accompanied by the date on which the collection was made, 1 April 1930.

REMARKS.—Fortunately, *Atya crassa* is the most distinctive member of the genus, for one cannot be certain that any of the existing specimens collected by McNiel in Nicaragua were among the specimens on which Smith based his description. The female in the Smithsonian (USNM 84261) that was formerly in the Kingsley collection is likely one of Smith's specimens. It bears a hand written label carrying the following: "Evatya Crussa [the "u" probably an intended "a"]

Smith (type) for Locality s II & III Ann. Rep. Peabody Aca. Science," and number "216" is included on a second small slip of paper. The smaller male and two females in the Peabody Museum (no. 6083) from "Rio Frilo" are perhaps less likely to have been examined by Smith, for this stream is not mentioned at the end of the description as is Río Fulva. Inasmuch as the latter specimens were collected within such a short distance from Realejo, they are at least virtual topotypes.

Atya dressleri Abele

FIGURES 1*g*, 9, 10, 12*f*, 18, 19

Atya dressleri Abele, 1975:51–57, figs. 1, 2 [type-locality: Río San Juan, 15 km above town of Calobre (566 m elevation), Provincia de Veraguas, Panama; types, USNM 184856, ♂ holotype; USNM 141845, 8♀ paratypes, 1♂ paratype].

REVIEW OF LITERATURE.—Abele's original description and notes on the range and habitat (see below) of this Panamanian species constitute the only published record of its existence.

PUBLISHED ILLUSTRATIONS.—The illustrations accompanying the original description include dorsal and lateral views of the cephalic region, dorsal view of the telson, illustrations of the antennule, third pereiopod, first pleopod of the male, appendices interna and masculina, preanal carina, and a lateral view of an entire animal showing the color pattern.

DIAGNOSIS.—Cephalic region of carapace not conspicuously sculptured, glabrous, lacking spines other than antennal, pterygostomian, and usually ventral rostral; pterygostomian spine absent or rather small; rostrum with margins tapering from base, sometimes with slight irregularity but never angulate. Ventral margin of all abdominal pleura without sclerotized denticles, and caudoventral angles of fourth and fifth pleura not produced in spines. Sternum of fifth abdominal segment with small median tubercle, that of sixth 1.4 to 1.5 times as broad as long. Preanal carina with well-developed curved spine. Telson almost twice as long as wide and with 8 to 10 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, its dorsal surface usually provided with linear series of spinules. Coxae of third and fourth pereiopods lacking prominent anterolateral spines. Third pereiopod with merus rounded ventrally, more than 5 times as long as high; ventromesial surface bowed, never parallel to that of corresponding podomere of other third pereiopod; lateral surface with linear series of subsquamous, comparatively large tubercles, those constituting median series rather larger than others but none heavily sclerotized; propodus 3 to 4 times as long as broad, extensor surface bearing rather large subsquamous tubercles, flexor surface also with large tubercles bearing sclerotized spines, more lateral tubercles forming row and all flanked by horseshoe-shaped row of setae (latter sometimes absent in later intermolt stage); dactyl about twice as long as broad, freely movable, and usually bearing 2 oblique rows of sclerotized spines on flexor surface, occasional members slightly displaced from either series and rarely spines arranged in single row; except in middle to late intermolt individuals, conspicuous band of setae extending from basal third of lateral surface of merus to distal margin of propodus.

HOLOTYPIC MALE.—Rostrum (Figure 18*a*,*d*) with margins tapering from base, and hardly hint of angle at base of long acumen; apex of latter slightly overreaching extremity of proximal podomere 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 on acumen; ocellar beak well hidden between eyes, reaching little beyond level of base of stylocerite, its cephalic border broadly rounded, and dorsal margin embraced by sides of ventral rostral groove. Antennal spine strong; pterygostomian spine rather small; no spine present between them. Surface of carapace bearing crowded minute punctations supporting very short, erect, fine setae, latter nowhere conspicuous; devoid of ridges and spines other than those just mentioned.

Pleura of first 3 abdominal segments (Figure 18*e*) with rounded posteroventral extremities; cor-

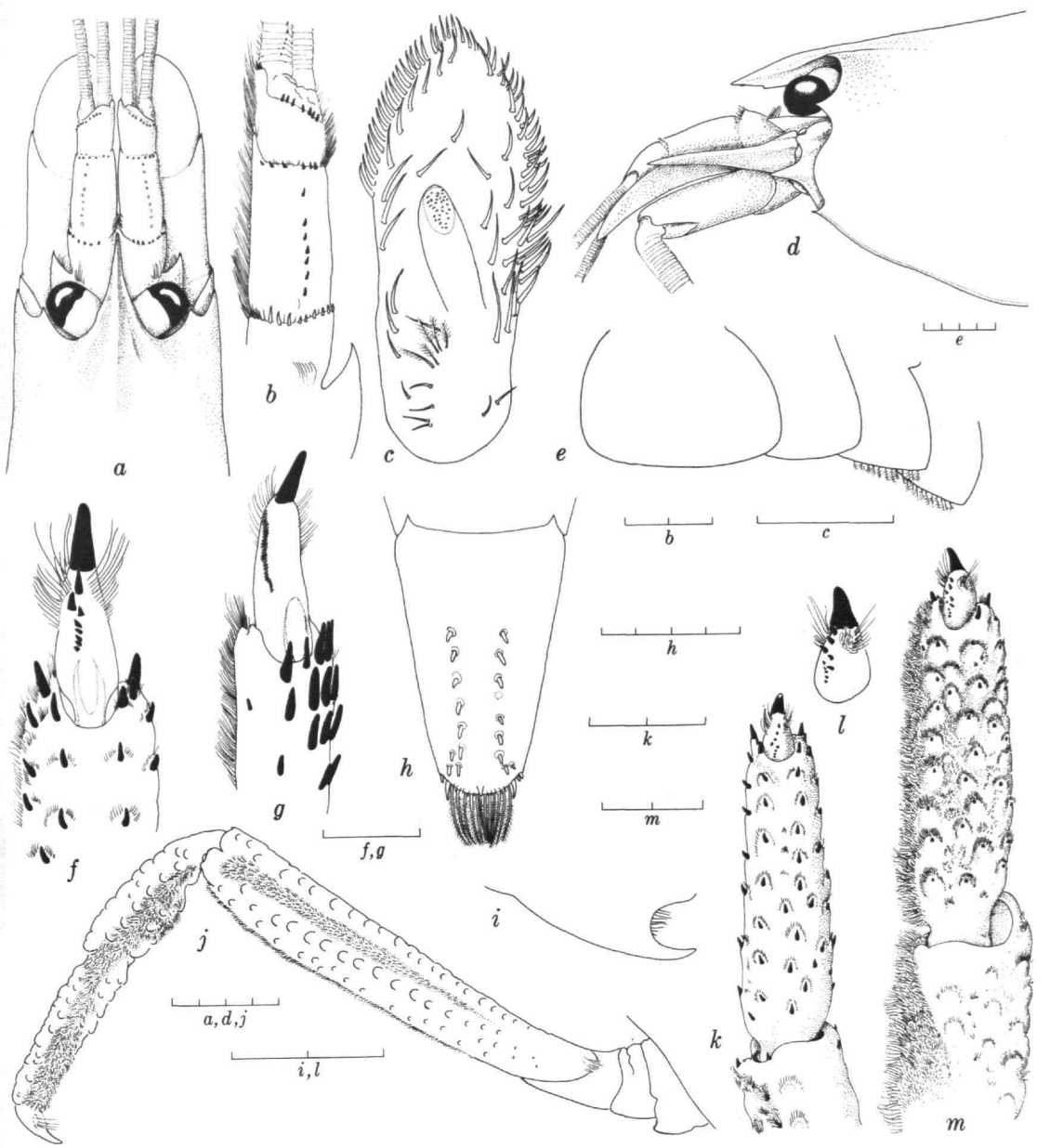

FIGURE 18.—*Atya dressleri* (all from holotype except *k,l* from Santa Fe, Panama): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view of cephalic region; *e*, lateral view of second through fifth abdominal pleura; *f*, flexor surface of distal part of fourth pereiopod; *g*, subflexor surface of distal part of fifth leg; *h*, dorsal view of telson; *i*, lateral view of preanal carina; *j*, lateral view of third pereiopod; *k,l,m*, flexor surface of distal part of third pereiopod. (Scales marked in 1 mm increments.)

responding parts of fourth and fifth angular but not produced in spines. All pleura lacking corneous spinules on ventral margin, but fourth and fifth with moderately prominent fringe of plumose setae. Fourth abdominal tergum slightly more than 1.1 times as long as fifth, 1.2 times as long as sixth, and tergum of fifth subequal in length to telson. Sternum of fifth abdominal segment with small acute median tubercle (Figure 1*g*). Sternum of sixth abdominal segment about 0.7 as long as broad. Free part of preanal carina (Figure 18*i*) spiniform, curved, and slightly overreaching caudal border of basal part of sclerite. Telson (Figure 18*h*) little less than 1.6 times as long as broad, its dorsal surface bearing paired, concave rows of 7 corneous denticles flanked posteriorly by 1 (right) or 2 (left) ones; posteromedian tubercle slightly overhanging caudal margin.

Proximal podomere of antennule (Figure 18*b*) with stylocerite reaching between base of distal fourth and fifth of segment; dorsal surface with linear cluster of setae but lacking corneous spinules; distal margin bearing row of 9 (right) or 6 (left) corneous spinules; penultimate segment of peduncle slightly less than twice as long as wide and bearing dorsal longitudinal row of 7 corneous spinules and transverse distal row of 6; ultimate podomere without spinules on dorsal surface and with row of 7 (right) or 8 (left) at base of lateral flagellum and another of 2 at mesial base of mesial flagellum. Antenna with ventrolateral spine on basis reaching almost as far anteriorly as stylocerite; lateral spine on scaphocerite rather strong, reaching about midlength of ultimate podomere of antennular peduncle; lamella far surpassing latter; flagellum extending to fifth abdominal tergum.

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

First pereiopod reaching level of base of ultimate podomere of antennular peduncle, second extending to base of distal fifth of fingers of first pereiopod; terminal brush of both appendages lacking setae with scraping denticles. Third pereiopod (Figure 18*j*,*m*) without lateral distoventral spine on merus and carpus, ventral spine absent from merus, and carpus lacking distolateral spines; when appendage extended anteriorly, overreaching antennular peduncle by dactyl, propodus, and distal third of carpus. Merus with ventromesial margin bowed, almost 7 times as long as high, 2.6 times as long as carpus, and 2.3 times as long as propodus; propodus 3.4 times as long as wide and almost 0.9 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 moderate number of rather large tubercles little if any cornified and, for most part, arranged in linear series; longitudinal band of setae present on lateral surface of merus; mesial extremity of podomere noticeably produced in rounded lobe at level of mesial articular condyle of carpus. Latter strongly tuberculate, almost all tubercles flanked distally by subsemicircular row of setae; lateral and ventrolateral surfaces matted with tufts of plumose setae. Propodus also strongly tuberculate, almost all tubercles with small cornified spines and, like those of carpus, flanked by setae; those on flexor surface not in well-defined rows proximally; lateral surface with tufts of setae arranged in longitudinal band. Dactyl movable, its flexor surface with 2 oblique rows of denticles flanked distally by usual setal clusters.

Fourth pereiopod with dactyl reaching end of proximal fourth of propodus of third pereiopod; length of merus slightly more than twice as long as carpus; latter approximately 0.9 as long as propodus. Fifth pereiopod reaching anteriorly to end of proximal third of propodus of third pereiopod; merus 1.4 times as long as carpus, latter almost 0.7 as long as propodus. Ornamentation of merus, carpus, and propodus of fourth pereiopod consisting of distolateral spine and 2 more proximal ones on ventral surface of merus (more distal spine of latter very long), distal ventrolateral spine and 2 small distolateral spines on carpus; lateral surface of merus, carpus, and propodus with conspicuous band of plumose setae. Ornamentation of corresponding podomeres of fifth pereiopod quite similar to that of fourth

except distalmost of ventral spines on merus not nearly so large.

Diaresis of lateral ramus of uropod flanked proximally by row of 21 articulated corneous denticles, and fixed spine at lateral end of row.

COLOR NOTES (paraphrased from Abele, 1975:55, 56).—Ground color light brown with yellow and black specks. Carapace light brown with dark brown oblong area on anterolateral surface just dorsal to elongate black spot. Short yellow rectangular area with black posterior border posterodorsal to latter. Posteroventral part of carapace with long yellow stripe margined in black. First abdominal segment with sinuous black area covering anterior part of segment; black area bordered by distinct narrow yellow band. Second abdominal segment with anterior and posterior pleural angles outlined in black and with oblique black stripe medial to each; distinct yellow area with black border situated posterodorsally. Third segment with pleural angle black and bearing oblique stripe anterior to it. Fourth segment bearing hourglass-shaped yellow area bordered in black on posterodorsal surface; pleural angle black and oblique black stripe lying anterior to it. Pleural angle of fifth segment like that of fourth. Almost entire dorsal surface of sixth segment yellow with black border. Distinct black spot present at base of uropods. Antennular peduncle with dorsal surface of antepenultimate and penultimate segments bearing yellow markings; flagella brown. Third through fifth pereiopods with 7 yellow bands: 1 at coxa-ischium, 1 about midlength and another toward distal end of merus, 1 at merus-carpal joint, 1 distally on carpus, and 1 at each end of propodus. Remainder of shrimp concolorous brown.

Some individuals lack, or have a modification of, the pattern described; others have a mid-dorsal longitudinal stripe; and the smaller specimens were concolorous light brown.

SIZE.—The carapace length of the males ranges from 12.1 to 20.4 mm, and that of the females, from 9.3 to 18.4 mm. No ovigerous females are available.

DISTRIBUTION AND SPECIMENS EXAMINED.—Known only from the Pacific slope of Panama in Panamá and Veraguas provinces at elevations of 566 to 650 m (Abele, 1975:56) (Figure 19).

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; this could not be determined.

PANAMA: *Provincia de Panamá*—(1) Río Cabra above Cerro Azul, alt 650 m (Abele, 1975), 2♂ ("molts of aquarium specimens"). (2) †LGA, Cerro Jefe, Pacora Basin, 1♂ (exuviae only), 1969, R.L. Dressler. (3) †USNM, stream between Pacora and Chepo, 17 km E of Río Pacora, 1♂ (12.2), 1 exuviae, 20 Feb 1971, RLD. *Provincia de Veraguas*—(4) *USNM, "Probably near 'Goofy Lake,'" 1♂ (exuviae, 15.1), RLD. (5) *USNM, trib of Río Santa María N of Santa Fe, alt 600 m (Abele, 1975), 6♀ paratypes (10.7, 14.1, 16.4, 17.0, 17.0, 18.2), 9 Feb 1962, H. Loftin and E.W. Tyson. (6) *USNM, headwaters of Río San Juan about 15 km above Calobre, alt 566 m (Abele, 1975), 2♂ (20.0, paratype; 20.4, holotype), 2♀

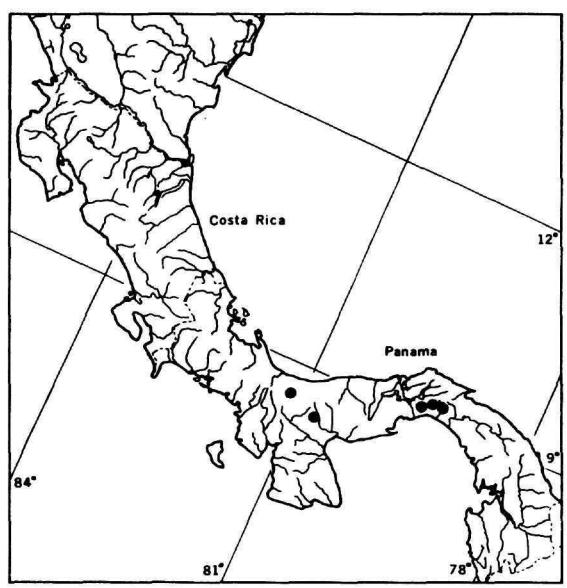

FIGURE 19.—Distribution of *Atya dressleri*.

paratypes (9.3, 18.4), 20 Feb 1973, L.G. Abele and H. Robinson.

VARIATIONS.—The most conspicuous variations occur in the spination of the rostrum, the ventral margin bearing one to three spines or serrations, and, whereas the dorsal surface is usually entire, the rostra of the exuviae of one specimen and of a paratypic female exhibit a row of four serrations. The pterygostomian angle may be strongly reduced and rounded, or it may be moderately produced, ending in an acute spine. The telson bears seven to 10 spines in each of the paired dorsal rows. Although in most of the specimens the spines (usually about eight) on the flexor surface of the dactyl of the third pereiopod are arranged in two rows, in two individuals examined they occur in a single median series or in a row with one or two spines flanking it.

ECOLOGICAL NOTES.—Abele (1975:56) stated that this shrimp "occurs in small fast running freshwater streams from about 560 to 650 m elevation. All of the specimens were collected from vegetation or overhanging roots in areas where the current was swift."

LIFE HISTORY NOTES.—The only information concerning the life history of members of this species is that offered by Abele (1975:56): "This species is fairly long lived. Robert Dressler has kept adult individuals alive in an aquarium for more than 5 years."

Atya gabonensis Giebel

FIGURES 1*n*, 3, 9, 10, 11*f*, 20, 21

Atya gabonensis Giebel, 1875:52-55 [type-locality: Gabon; types: disposition unknown].—Thompson, 1901:22.—Bouvier, 1904:138; 1905:110, 112, 123, 124, 128, fig. 26; 1925:20, 22, 26, 27, 29, 293, 317-323, 357, figs. 707, 708.—Monod, 1928:205; 1933:461; 1967:110, 119, 135, pl. 7: fig. 8; pl. 9: figs. 25, 26; 1977:1203, 1204; 1980: 375.—Oliveira, 1945:179.—Irvine, 1947:306, fig. 211.—Holthuis, 1951:9, 25; 1980:69, 71, 181.—Gordon, 1967:52.—Reed, 1967:120, fig. 153.—Motwani and Kanwai, 1970:34.—Rutherford, 1971:87, 90.—Lemasson, 1973:68, 70.—Powell, 1979:116, 134-138.—Hobbs, 1980:111.

Euatya sculptilis Koelbel, 1884:317-321, 323, pl. 2: fig. 8; pl. 3: figs. 1-8 [type-locality: Orinoco; type: NMW, 1 specimen].—Hobbs, 1980:111.

Atya sculptata Ortmann, 1890:465, 466 [type-locality: Africa, "Vielleicht aus West-Africa . . . "; type: Strassburg Museum].—Aurivillius, 1898:14.—Oliveira, 1945:179.

[*Atya*] *sculptipes*.—Ortmann, 1890:466 [erroneous spelling].

Atya (Atya) gabonensis.—Ortmann, 1895:410, 414, 415 [by implication]; 1897:184, 185, 186 [by implication].

Evatya sculptilis.—Ortmann, 1897:185 [erroneous transcription of *Euatya*].

Atya scabra.—Rathbun, 1900:313, 314 [in part].—Balss, 1914:98 [in part].

Atya.—Yaro, 1967:210.—Monod, 1967:176.

REVIEW OF LITERATURE.—This shrimp was described in considerable detail by Giebel (1875) on the basis of four specimens that had been sent to him by Baron von Koppenfels from Gabon. Almost a decade later, Koelbel (1884) presented a description and beautiful illustrations of an atyid from the Orinoco Basin of South America that he designated *Euatya sculptilis*, employing a generic name that is an invalid emendation of *Evatya* Smith (1871:95).

In recording the decapod crustaceans housed in the Strassburg Museums, Ortmann (1890) included a brief description of an African shrimp, proposing the name *Atya sculptata* and assigning it to "die *margaritacea*-Gruppe (zu der *margaritacea*, *robusta*, *scabra* und *sculptipes* [sic] gehören)" (p. 466). In a subsequent study of the geographical distribution of the family Atyidae, Ortmann (1895) placed Koelbel's *Euatya sculptilis* and his *Atya sculptata* in the synonomy of *Atya gabonensis* and employed the subgenus *Evatya* in referring to *Atya crassa* (p. 184), thereby implying that the other members of the genus belong to the nominate subgenus. In addition, he reviewed the ranges of *A. gabonensis*, *A. crassa*, and *A. scabra*. In his account of the freshwater shrimps of South America (1897), he included a diagnosis of this species and stated that it is possible that it occurs only in the Orinoco and in Gabon. A single male specimen in the National Museum of Natural History collected by O.F. Cook at Mt. Coffee, Liberia, provides evidence that Rathbun (1900) perhaps had a specimen of *A. gabonensis* before her in preparing her account of the decapod crustaceans of West Africa; however, there was no identification accompanying the uncatalogued

specimen. She did not misidentify one of the specimens of *Atya scabra* she reported from St. Paul's River near Mt. Coffee, Liberia (see "Distribution" of *A. scabra* herein). She erred, however, in considering specimens of *A. africana* to be conspecific with *A. scabra* in synonymizing *A. gabonensis* with the latter, listing the Orinoco and "Gabun" as localities for *A. scabra.* Thompson (1901) reported the presence of *Atya gabonensis* among the Crustacea "contained in the Museum of University College, Dundee," but noted the absence of locality data.

In recording the specimens of atyids in the Muséum d'Histoire Naturelle (Paris), Bouvier (1904) stated that this shrimp is the most beautiful and largest species belonging to the genus *Atya.* He listed specimens from three localities (see "Distribution and Specimens Examined"). The following year (1905) he elaborated upon information offered in 1904, grouped *A. gabonensis* with the advanced members of the genus, and presented illustrations of the rostrum and cephalolateral region of the carapace. In his monograph of the family Atyidae, Bouvier (1925) first questioned the reported source of Koelbel's specimens, stating that "l'Orénoque, ce qui tient peut être à une fausse indication de provenance" (p. 319). Following a detailed description and a presentation of the same figures published in 1904, he summarized the range, restated the sizes (45 to 124 mm) of the specimens available to him, and discussed the relationships, stating that the most highly evolved stock of the genus "à produit en Afrique occidentale et en Amérique l'*A. gabonensis* et dans la région de l'isthme américain l'*A. crassa* qui représente avec l'espêce précédente le point terminal" (p. 357).

Monod (1928 and 1967) listed this shrimp as being fished in Cameroon and later (1933) reported it from the "Yabassi riv. Wouri," Cameroon. In updating our knowledge of the crustacean fauna of West Africa, Monod (1933) presented a new locality record for *A. gabonensis* and questioned its occurrence in the Orinoco. Oliveira (1945) added no new data. Another locality was cited by Irvine (1947) who provided an illustration of the shrimp and stated that this species is thought to be confined to rocky sections of the river (Volta).

In his review of the caridean Crustacea of tropical West Africa, Holthuis (1951) provided a nearly complete synonomy for the species and listed all of the known locality records, expressing doubt, however, of the validity of the reported occurrence of the species in the Orinoco River, and erring in treating Rathbun's (1900), and perhaps Johnston's (1906), records for *A. scabra* in Liberia as those of *A. gabonensis.* Monod (1967) cited the range of this shrimp as extending from Senegal to Gabon; his illustrations were taken from Bouvier (1925) and Irvine (1947). Gordon (1967) included no information concerning this shrimp. Reed (1967) reported its presence in most parts of northern Nigeria but noted that it is not common; it inhabits rocky areas of the "main river" and its tributaries. Yaro (1967) recorded the common names in several of the local dialects.

Motwani and Kanwai (1970) reported the occurrence of large numbers of *Atya gabonensis* in the coffer-dammed right channel of the Niger River on 4 and 5 August 1966. Gill nets ensnared them at depths as great as 11.4 m. Rutherford (1971) added no new information other than his failure to find members of the species along the Cape Coast of Ghana. Lemasson (1973), noting that this shrimp attains a total length of 12.4 cm, believed that it might lend itself to commercial cultivation. Monod (1977) reported the range of *A. gabonensis* to include the coastal streams of West Africa and the islands of Fernando Poo and São Tomé; also he suggested that the distribution of the species may be associated with rocky substrates.

Powell (1979) noted that *A. gabonensis* occurred in company with *Potamalpheops haugi* (Coutière, 1906) in "whitewater mollusc rivers" (p. 116) of the Niger Basin in Nigeria. Juveniles were found "in the Nun branch of the Niger near Kaiama (about 95 km inland and 15 km upstream from the extreme dry-season tidal-limit) . . . " (p. 134). He pointed out that the locality Bouvier (1925:319) cited on the Ogooué River lies about

125 air-km from the coast. The similarity in body form of migrating juveniles of *A. gabonensis* and of individuals of *P. haugi* of equal size render them "difficult to separate with the naked eye" (p. 136). Like *P. haugi*, according to Powell (p. 137), *A. gabonensis* "is perhaps restricted to relatively hard waters," and he implied that it is present in the Osse watershed. Holthuis (1980) summarized our knowledge of this shrimp, providing FAO (Food and Agriculture Organization of the United Nations) names, local names, geographical and habitat distribution, and maximum size (total length: 124 mm for males and 92 mm for females). References to its importance in fisheries are also included. Hobbs (1980:111) reported the presence of this species in Rio Piaui, Brazil.

PUBLISHED ILLUSTRATIONS.—The first and best illustrations of *Atya gabonensis* are those of Koelbel (1884) and include a beautifully executed lateral view of the entire body and appendages along with a ventral view of the third pereiopod, lateral view of the first pereiopod, and a posterior view of each of the gnathal appendages. Bouvier (1905) provided a dorsal view of the rostrum, and the rostral, orbital, and pterygostomian regions of the carapace were presented in lateral aspect. The latter figures were used by Bouvier (1925) in his monograph. The most recent illustration is that of Irvine (1947), a lateral view of the entire animal that is much less detailed than Koelbel's figure 1 on plate 3. Bouvier's figure has been reproduced by Monod (1967) and Reed (1967).

DIAGNOSIS.—Cephalic region of carapace strongly sculptured, but spines limited to antennal, pterygostomian, and occasional ventral and often lateral rostral; pterygostomian spine rather weak. Rostrum with margins suddenly contracted, forming distinct angle anterior to orbit, angle often produced anteriorly; dorsal surface without row of strong spines but with low median carina. Ventral margin of abdominal pleura lacking sclerotized spinules. Sternum of fifth abdominal segment with median tubercle produced in curved hornlike projection usually overreaching midlength of sixth sternite when abdomen flexed. Sternum of sixth abdominal segment approximately one-half as long as wide. Preanal carina subconical and directed almost ventrally. Telson 1.2 to 1.4 times as long as broad and bearing paired arched dorsal rows of 4 or 5 spines. Antennular peduncle with dorsal surface of proximal article bearing 1 to 6 spinules proximal to distal row; penultimate article 1.4 to 1.5 times as long as wide and bearing scattered sclerotized spinules in lateral half of dorsal surface. Coxae of third and fourth pereiopods lacking prominent spine anterolaterally. Third pereiopod with merus somewhat flattened ventrally, about 2.5 times as long as high; ventromesial surface parallel to that of corresponding podomere of other third pereiopod, and lateral surface bearing irregular rows of heavy corneous tubercles with flattened, often frayed, scalelike extremities; propodus 1.6 to 1.9 times as long as broad; extensor surface studded with stalked corneous tubercles similar to those on merus and with very few widely spaced ones on flexor surface, most tubercles on latter surface flanked distally by clusters of plumose setae; dactyl at least slightly movable, its flexor surface bearing 1 to several tubercles in cluster just proximal to corneous tip.

MALE (Volta River at Kpong Rapids, Ghana).—Rostrum (Figure 20*a,d*) with margins somewhat tapering, but thickened and appearing concave laterally, to base of acumen where produced in spines reaching slightly beyond midlength of proximal podomere of antennule; apex of acumen overlying midlength of penultimate podomere of antennule; dorsal median carina, although prominent, dipping below level of lateral carinae posterior to acumen and reaching apex of latter; ventral carina poorly developed, ventral surface of rostrum grooved posteriorly, receiving ocellar beak which strongly produced anteriorly, ending in acute apex almost reaching level of tip of stylocerite. Antennal and pterygostomian spines moderately strong and acute, no spines present between them. Surface of carapace densely punctate and rather ornate, marked by strong ridges; submarginal punctations along ventral edge of carapace bearing conspicuous setae.

Pleura of first 3 abdominal segments (Figure 20*i*) with rounded posteroventral extremities, cor-

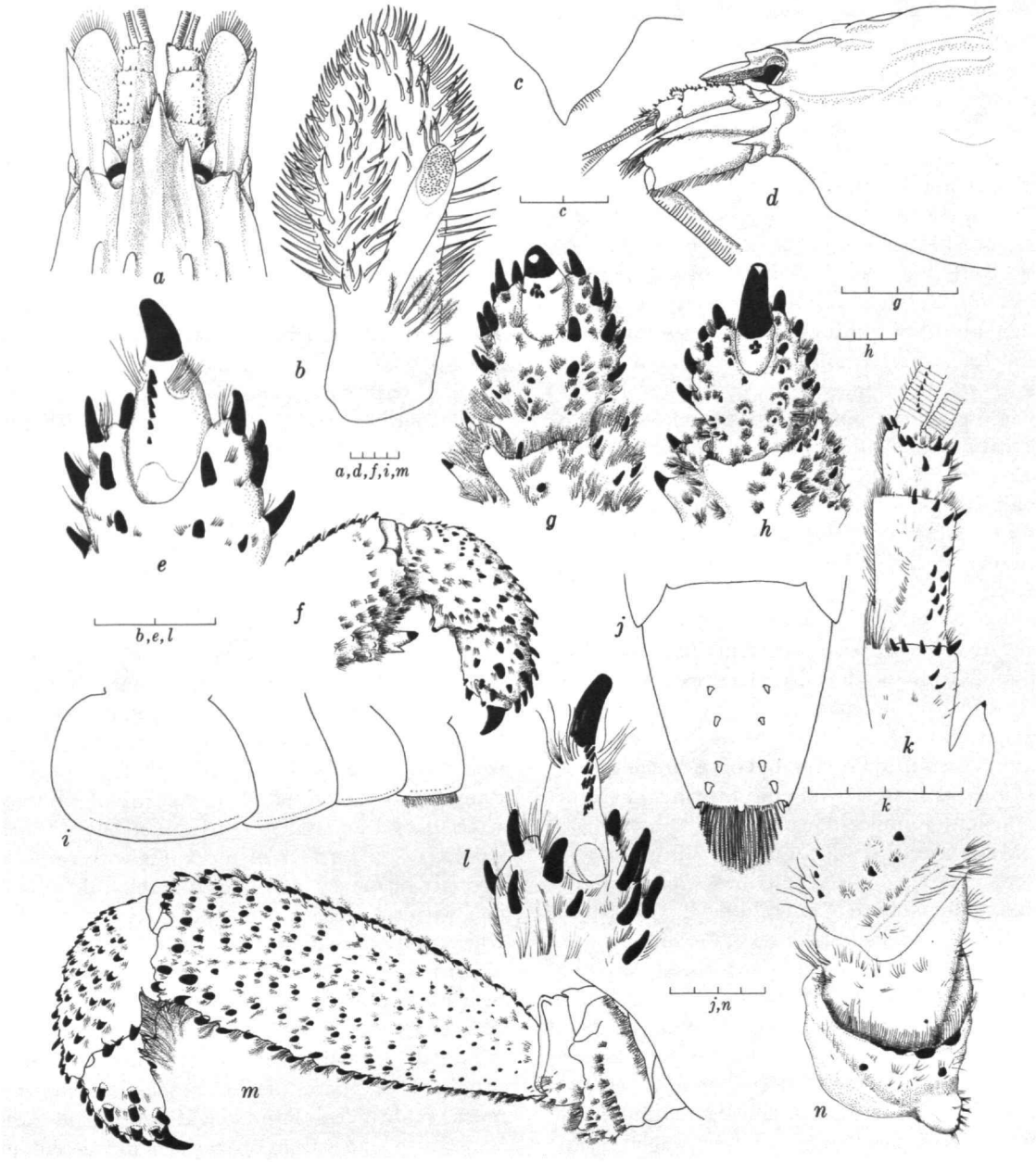

FIGURE 20.—*Atya gabonensis* (all from male from Kpong rapids of Volta River, Ghana, except *h* from Rio Piaui, Brazil): *a*, dorsal view of cephalic region; *b*, mesial view of appendices masculina and interna; *c*, lateral view of preanal carina; *d*, lateral view of cephalic region; *e*, flexor surface of distal part of fourth pereiopod; *f*, lateral view of distal part of third pereiopod; *g,h*, flexor surface of distal part of third pereiopod; *i*, lateral view of second through fifth abdominal pleura; *j*, dorsal view of telson; *k*, dorsal view of antennular peduncle; *l*, flexor surface of distal part of fifth pereiopod; *m*, lateral view of third pereiopod; *n*, ventral view of basal podomeres of right third pereiopod. (Scales marked in 1 mm increments.)

responding parts of fourth and fifth segments rounded to subangular but not produced. All pleura lacking corneous spinules on ventral margin but fifth with conspicuous row of plumose setae. Fourth abdominal tergum about 1.2 and 1.1 times as long as fifth and sixth, respectively, and subequal in length to telson; length of sixth only slightly greater than that of fifth and 0.9 as long as telson. Sternum of fifth abdominal segment with very large median, curved, hornlike projection (Figure 1*n*) which, when abdomen flexed, abutting sternum of sixth abdominal segment immediately anterior to preanal carina. Latter sternum approximately 0.4 as long as broad. Preanal carina (Figure 20*c*) represented by sclerite bearing strong ventrally directed spine. Telson (Figure 20*j*) about 1.3 times as long as broad, its dorsal surface bearing paired concave rows of 4 corneous denticles and with posteromedian tubercle slightly overhanging caudal margin.

Proximal podomere of antennule (Figure 20*k*) with strong stylocerite reaching base of distal third of segment; dorsal surface with cluster of setae and 2 or 3 corneous spinules; distal margin bearing row of 5 (right) or 4 (left) corneous spinules; penultimate segment of peduncle almost 1.5 times as long as wide and bearing 12 (right) or 10 (left) spinules dorsolaterally and row of 7 (right) or 6 (left) on distal margin; ultimate podomere with row of 4 (right) or 6 (left) spinules flanking dorsal base of lateral flagellum, 2 (right) or 3 (left) at dorsomesial base of mesial flagellum and 3 (right) or 4 (left) more proximally situated. Antenna with lateral spine on basis reaching slightly beyond apex of stylocerite (base of distal third of proximal podomere of antennular peduncle); lateral spine on scaphocerite strong, extending to level of end of peduncle of antennule, lamella much overreaching latter; flagellum attaining fourth abdominal tergum.

Third maxilliped overreaching antennular peduncle by about half of distal podomere of endopod; tip of exopod reaching midlength of penultimate podomere of endopod.

First pereiopod reaching ultimate podomere of antennular peduncle, second reaching base of distal fourth of fingers of first pereiopod; terminal brush of setae of both appendages lacking scraping denticles. Third pereiopod (Figure 20*f,g,m,n*) lacking spines, and when extended anteriorly overreaching antennular peduncle by length of carpus, propodus, and dactyl; merus with ventromesial margin straight, about 2.5 times as long as high and almost twice length of carpus; latter 2.3 times as long as propodus; length and width of propodus subequal and its length 1.5 times that of dactyl; distoventral margin of coxa very weakly scalloped and mesial caudoventral prominence studded with conspicuous setal clusters. Lateral, dorsal, and ventral surfaces of merus with sublinear series of distally flattened corneous tubercles bearing sharp free edge; paired clusters of plumose setae flanking distal base of most tubercles; proximoventral and ventromesial parts of merus with conspicuous tufts of setae obscuring and/or replacing tubercles occurring elsewhere on ventral, lateral, and dorsal surfaces; mesial extremity of podomere weakly produced at level of mesial articular condyle of carpus; strong tubercle on distal mesioventral angle opposing tubercle on carpus (Figure 20*f*). Ventral and ventromesial surfaces of carpus with few corneous tubercles but studded with clusters of plumose setae, dorsal and lateral surfaces strongly tuberculate; dorsal surface of propodus with series of strongly produced, corneous tubercles; flexor surface with tubercles much smaller than those elsewhere on podomere, ventrolateral ones occurring in irregular row; dactyl movable, its flexor surface bearing median group of small corneous tubercles flanked by pair of setal patches.

Fourth pereiopod with dactyl reaching base of distal third of merus of third pereiopod; length of merus slightly less than twice that of carpus, and latter little longer than propodus. Fifth pereiopod reaching just beyond merocarpal joint of fourth pereiopod; merus about 1.6 times as long as carpus and latter slightly more than 0.7 length of propodus. Ornamentation of merus, carpus, and propodus of fourth pereiopod similar to those of third except dorsal and ventral surfaces more

setose, merus bearing single large distolateral spine and more proximal ventral one, and carpus with 1 ventrolateral and 2 distolateral spines. Ornamentation of fifth pereiopod similar to that of fourth but with additional smaller spine on merus proximal to ventral spine.

Diaresis of lateral ramus of uropod flanked proximally by row of 17 articulated, corneous denticles and slightly larger fixed spine at lateral end of row.

COLOR NOTES.—The only available observations on color is a brief statement by Irvine (1947:306) describing this shrimp as being "dark grayish" in color. Accompanying specimens from the Volta River, Ghana, is the following note: "brown in colour with crab-like claw of a blue shade."

All individuals observed in Nigeria by C.B. Powell (pers. comm.) were uniform slate-gray to black. He informed us that none of the specimens seen by him, except preserved ones, match the color recorded here for members of the species in the Volta River, Ghana.

SIZE.—According to Bouvier (1904:138), this shrimp is "la plus belle et la plus grande espèce du genre, peut atteindre 14 centimètres de longueur." Presumably this record-sized specimen from Africa was among the five reported from "Chutes de Félou," some of which he described (1904) as "enormes." The largest of Koelbel's (1884:321) specimens from the Orinoco measured 137 mm from the tip of the rostrum to the end of the telson. Of those from Brazil (all males) reported by Hobbs (1980), the largest and smallest have postorbital carapace lengths and total lengths (latter in parentheses) of 52.3 (130) and 50 (121) mm. The largest female available to us has a carapace length of 39.0 mm; that of the smallest ovigerous female, 29.7 mm. In Nigeria, according to C.B. Powell (pers. comm.), the largest specimens observed by him were those collected farthest inland.

DISTRIBUTION AND SPECIMENS EXAMINED.—*Atya gabonensis* has a discontinuous distribution: in western Africa it ranges from Senegal southward to Zaire (most of the localities are in the Niger and Volta river basins), and in northern South America it has been found in the Parnaiba, Suriname, and Orinoco basins in Brazil, Surinam, and Venezuela, respectively (Figure 21).

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 or, if followed by "t.l.," total length. Some listings lack dates and/or collectors; these could not be determined.

SENEGAL: *MHNP, "Chutes de Félou" (Bouvier, 1904:138), 3♂ (34.9, 36.0, 37.4), 1890, Archinard; *BM, 2♂ (38.0, 49.5).

LIBERIA: †USNM, Mt. Coffee, 1♂ (34.8), 1896, O.F. Cook.

MALI: Kayes (Bouvier, 1904:138).

FRENCH SOUDAN: *MHNP, no locality, 1♂ (24.6), 1♀ (39.0), 1907, A. Chevalier.

GHANA: *RNHL, no locality, 2♂ (42.3, 44.2), W. Schlüter. (1) *Volta River at Kpong (Irvine, 1947:306); USNM, 6♂ (21.2–42.3), 3 ovig ♀ (29.7–30.6), 20 Jul 1950, L. Berner. (2) †BM, Volta River at Senchi, 8♂ (32.2–47.8), 1♀ (26.4), 1935, F.R. Irvine. (3) †BM, Volta River at Senchi, 8.0 km above Kpong, 10.4 km from sea, 1♂ (42.0), 25 May 1948, M.N. Buxton. (4) †RNHL, rapids in Volta River at Senchi, 2♂ (37.1, 38.8), 1969, T.C. Rutherford. (5) *BM, Volta River, 6♂ (21.8–35.9), 11♀ (19.2–27.1), W. Foote; USNM, 1♂ (24.2), 2♀ (22.5, 27.8). (6) †USNM, Senchi River, 1♂ (35.0), 19 Jan 1962, Amegah.

NIGERIA: (1) Nun Branch of Niger River near Kaiama, about 152 km inland (Powell, 1979:134), 9 juv ♂ (5.8–10.8), 11 juv ♀ (4.4–9.0), 25–26 May 1977, C. B. Powell. (2) †BM, Niger River, Jebba, 1♂ (33.9), C.H. Firmin. (3) Ogun River at Abeokuta, approximately 7°05′N, 3°20′E (CBP, pers. comm.). (4) Osse River at Iguoriakhi, W of Benin City, 6°29′N, 5°28′E (CBP, pers. comm.). (5) Niger River at Kainji, approximately 10°N, 4°40′E (CBP, pers. comm.). (6) Niger River at Jebba, approximately 9°05′N, 4°55′E (CBP, pers. comm.). (7) Niger River at Onitsha, approxi-

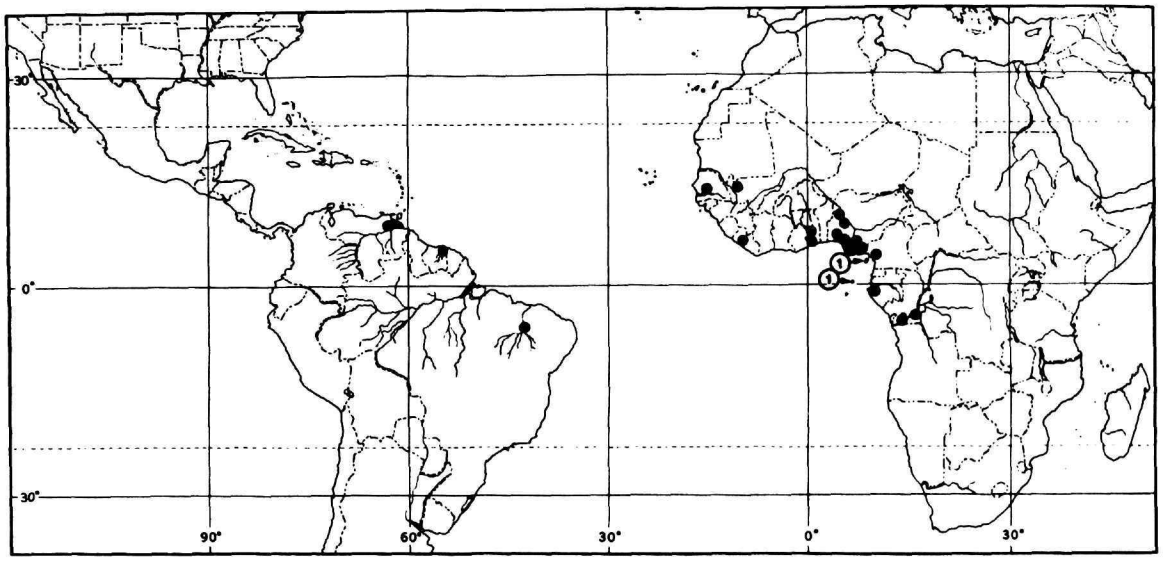

FIGURE 21.—Distribution of *Atya gabonensis* (circled numerals = number of localities).

mately 6°29′N, 6°55′E (CBP, pers. comm.). (8) Cross River at Itigi, 5°53′N, 8°01.5′E (CBP, pers. comm.). According to C.B. Powell, it has not been found in the Benin, Sombreiro, or New Calabar rivers, nor are there records of its occurrence in Sierra Leone or Ivory Coast.

CAMERON: Wouri River, Yabassi (Monod, 1933:461).

GABON: *BM, no locality, 1♂ (42.1). (1) *MHNP, Ngómó dans la riviere Ogôoué (Bouvier, 1925:319), 2♂ (12.6, 18.7), 3♀ (19.0, 39.4, 40.0), 1906, E. Haug.

ZAIRE: (1) †RNHL, Rapids of lower Congo River at Kinsuka near Kinshasa, 1♀ (43.4), 21 Jun 1971, P. Brichard. (2) †MCZ, Zaire River near Inga Hydroelectric Dam, 5°31.5′S, 13°37.5′E, 1♂ (45.3), 4 Aug 1973, T.R. Roberts, D.J. Stewart.

FERNANDO POO: No locality (Monod, 1977: 1204).

SAO TOME: No locality (Monod, 1977:1204).

WEST AFRICA (probably Ghana): *BM, 3♂ (31.5–42.0), FRI.

MEXICO: †BM, 1 dry specimen (43.9). (We question data.)

VENEZUELA: Orinoco River (Koelbel, 1884: 321).

SURINAM: *RNHL, rapids in Suriname River near Brokopondo (Holthuis, pers. comm.), 1♀ (27.5), 14 Feb 1964, M. Boeseman.

BRAZIL: *USNM, Rio Piaui, trib of Rio Parnaiba, at Boa Esperanza Dam, state of Piaui (Hobbs, 1980:111), 5♂ (50.0–52.7), 31 May 1968, J.W. Bezerra e Silva.

NO DATA: *BM, label reads "?Type of *Atya scabra* Leach. Trans. Linns. Soc. Lond. xi p. 345," 1♂ (38.8).

The presence of the species in Liberia (Holthuis, 1951:25) is confirmed by the recent discovery of an uncatalogued specimen from Mt. Coffee in the collection of the Smithsonian Institution. We have examined the specimens from the St. Paul River and from Beulah reported by Rathbun (1900:313) as *Atya scabra*, and later cited by Holthuis as members of *A. gabonensis*, and we concur in Rathbun's determinations. Her specimen from "Muhlenburg Mission," as pointed out above, is a member of *Atya africana*. The Johnston (1906:862) record for *A. scabra* in Liberia (reported as *A. gabonensis* by Holthuis, 1951:25) included no locality and conceivably was based on Rathbun's (1900) report. In any event, to our knowledge, there are no extant specimens of *A. gabonensis* from Liberia except the male from Mt. Coffee (USNM).

The record for Mexico cited here is also in need

of confirmation. In the absence of more precise locality data, we are not including Mexico within our summary statement of the range of the species.

As for the specimen in the British Museum that bears the questionable label "Type of *Atya scabra*," we are convinced as was Holthuis (1966:234) that this specimen was not that (or one of those) before Leach when he described *Atya scabra*. Supporting this conclusion is the illustration in plate 21 of Leach's 1816 account of this species.

VARIATIONS.—The variations noted by us are hardly noteworthy, and none seems to be restricted to populations occupying a restricted part of the range of the species. The rostral margins may be almost straight or distinctly concave. Whereas the ornamentation of the cephalic and ambulatory appendages exhibits variations in number and position of the spines and tubercles and in the condition of the setation borne by them, the differences are indeed minor.

ECOLOGICAL NOTES.—The first note on the type of habitat occupied by this shrimp was Bouvier's (1904:138) record "Chutes de Félou," and repeated by him (1905:124; 1925:319). He added (1925) that the specimens reported from "Ngomo, dans Ogooué" were captured from crevices in rocks on the river bed. That at least the adults of the species may well be largely restricted to rapids is suggested by Irvine (1947:306) who stated that it "is said to inhabit only those parts of the river where the bottom is rocky." Reed et al. (1967:120) also noted that the usual habitat is in rocky parts of streams, and Motwani and Kanwai (1970) reported the occurrence of this shrimp in an impounded channel of the Niger River where it was taken in gill nets set at depths of as great as 11.4 m. The most recent observations are those of Powell (1979) who remarked that *A. gabonensis* occurs in "whitewater mollusc rivers" (p. 116), "is perhaps restricted to relatively hard waters" (p. 137), and that juveniles had been found "among loose vegetation and other debris caught in the current by parts of fallen trees projecting out of the water" (p. 134). He also stated that "migrating juveniles of *Atya gabonensis* . . . can swim steadily forward with surprising speed, comparable to the speed of darting fish" (p. 136). The specimens collected from the Kpong Rapids of the Volta River by Berner (see "Distribution and Specimens Examined") were found "under rocks three to five feet deep in swiftly flowing, murkey water." According to C. B. Powell (pers. comm.), this shrimp is not confined to rapids in Nigeria. "The localities I know them from are wide deep rivers with a large seasonal change in water level and discharge—in the dry season the rivers are sluggish, and in the Nun and lower Osse rivers there are no rocks at all."

LIFE HISTORY NOTES.—The only ovigerous females of which we are aware are the three (c.l. 29.7, 30.0, and 30.6 mm) noted here that were collected from the Volta River in Ghana, on 20 July 1950. The diameters of the eggs borne by them range from 0.4 × 0.5 to 0.4 × 0.7 mm. The juveniles as noted in "Ecological Notes" have been found in loose vegetation, and they have not been reported as taken on rocky substrates as have the adults.

We were informed by C.B. Powell (pers. comm.) that during the low-water season (December to April) in Nigeria, ovigerous females are quite common. During the rest of the year, however, collecting is not possible. He attempted to rear larvae obtained from females collected in the Osse River, but in fresh water they failed to molt and died after about 10 to 12 days. With the addition of salt water, some of the larvae molted to the second instar. He suggested that the 10-day survival period might allow the larvae time to reach estuaries from such far inland localities as Kainji. Juveniles that were placed in round plastic containers swam continuously round and round the edge at remarkable speeds, and when blocked, they scrambled over the obstacle, leaving the water, if necessary, to continue their course. Powell suggested further that young *Atya*, like at least some young *Macrobrachium*, may avoid the stronger currents by moving upstream close to the shore.

COMMON NAMES.—The following common names have been reported for this shrimp (no distinction is apparently made between it and the African *Atya scabra*).

Bomingomô (in Batanga), Cameroon (Monod, 1928:206)
Crevette gros-doigt (in French), Cameroon (Monod, 1928:458)
Dikuta (in Bassa Bania), Cameroon (Monod, 1928:206)
Èkusa (in Soubou), Cameroon (Monod, 1928:206)
Jaten lendi (in Hausa), in Nigeria (Yaro, 1967:210)
Kalama-toruõpuru (in the Kolokuma dialect of Ijaw), around Kaiama, Nigeria (C.B. Powell, pers. comm.)
Mobèngomô (in Douala), Cameroon (Monod, 1928:205)
Ndakansa (in Nupe), in Nigeria (Yaro, 1967:210)
Opuru (in the Akpada dialect of Ijaw), in Nigeria (Yaro, 1967:210)

FAO names were recorded by Holthuis (1980:69) as follows: Gabon shrimp (English), Saltarelle gabonaise (French), and Camarón gabonés (Spanish).

Atya innocous (Herbst)

FIGURES 1*d,e*, 2, 4*a*, 5–10, 12*a,b*, 22–30

Astacus 988 Gronovius, 1764:231, pl. 17: fig. 6.

Astacus Nasoscopus Meuschen, 1778:86; 1781:[9].—Holthuis, 1966:237.

Cancer (Astacus) Innocous Herbst, 1792:62, pl. 28: fig. 3 [type-locality: Martinique; type: not extant].—Holthuis, 1966:237.

canc[er] innocuus.—Latreille, 1817:37.

Atya occidentalis Newport, 1847:159 [type-locality: Jamaica; types: not extant].—White, 1847:74.—Gosse, 1851:85.—A. Milne-Edwards, 1864:147.—Martens, 1872:135.—Giebel, 1875:52.—Kingsley, 1878a:92, 93; 1878b:57.—Bate, 1888:693.—Pocock, 1889:11–16, pl. 2: fig. 3, 3a; 1894:408.—Rathbun, 1897:44.—Ortmann, 1897:184.—Bouvier, 1904:137; 1905:110, 112, 113, 117–119, 121–123, fig. 22; 1909:333; 1925:293, 311–314, 322, 323, 356, figs. 700–702.—Hansen, 1925:140.—Allee and Torvik, 1927:67.—Boone, 1931:187–189, fig. 23.—Schmitt, 1935:135, 136, fig. 9.—Oliveira, 1945:179.—Villalobos, 1956:474.—Burgers, 1958:584.—Hart, 1961b:61, 63, 67, 72, 73, fig. 10; 1964:334.—Davant, 1963:42, 44, 98, 100.—Vélez, 1967:42.—Straskraba, 1969:17.—Odum, 1970:H-6.—Hunte, 1975:66.—Villamil and Clements, 1976:1.

Atya robusta A. Milne-Edwards, 1864:148, pl. 3: fig. 1 [type-locality: New Caledonia; syntypes: MHNP 600 (♂), 1003 (♂)].—Bate, 1888:693.—Ortmann, 1890:466; 1895:409.—Bouvier, 1904:137; 1905:110, 112, 116, 117, 119, 120, 122, 128, fig. 21; 1925:292, 310–312, 314–317, 322, 323, 356, figs. 697–699.—J. Roux, 1926b:217, 218.—Holthuis, 1966:237, 238; 1969:92.—Chace and Hobbs, 1969:58.

Atya tenella Smith, 1871:94, 95 [type-locality: Hacienda El Polvón, Departamento Occidental, Nicaragua; syntypes: MCZ 315 (4♀), PM 1785 (♂, ♀)].—Kingsley, 1878a:92; 1878b:57.—Pocock, 1889:16.—Bouvier, 1905:121; 1925:312.—Oliveira, 1945:179.—Holthuis, 1966:238.—Chace and Hobbs, 1969:61.—Abele, 1975:56, 57.—Abele and Blum, 1977:240, 242–245, 250.

Atya scabra.—Ortmann, 1895:409 [in part]; 1897:184 [in part].—Rathbun, 1901:119 [in part].—Bouvier, 1905:121 [in part]; 1925:314 [in part].

Atya innocous.—Holthuis, 1966:237, 238; 1969:92; 1980:69, 181.—Beatty, 1968:263.—Chace and Hobbs, 1969:5, 15, 19, 33, 36, 44, 46, 47, 57–62, 66, figs. 8, 10a–c, 14a,b, pl. 1.—Chace, 1972:14.—Bonnelly de Calventi et al., 1973:1338.—Upatham and Sturrock, 1973:448–452.—Bonnelly de Calventi, 1974b:35, 38, 39, figs. 6, 12.—Lévêque, 1974:42, fig. li.—Alayo, 1974:22, pl. v: fig. 9; pl. vi: fig. 12.—Abele, 1975:56, 57.—Peck, 1975:308.—Hunte, 1975:66; 1977:373–376; 1978:135, 136, 139, 144–146, 148, fig. 2; 1979b:231–241, figs. 1–5; 1979c:70.—Villamil and Clements, 1976:1, 4, 20, 25–28, 32, 34, 36, 37, 52, 59.—Carvacho and Carvacho, 1976:213, pl. 2: fig. vii.—Fryer, 1977:57, 58, 62, 63, 69–74, 90, 92–94, 98, 111–117, 125, figs. 2, 7, 12–14, 36–38, 40–44, 51, 55–69, 72, 73, 75, 76, 78, 83–86, 89–92, 95–112, 114–119.—Hobbs, Hobbs, and Daniel, 1977:150.—Hart, 1980:845, 847, 848.—Felgenhauer and Abele (in press).

Atyia occidentalis.—Vélez, 1967:42 [erroneous spelling].

Atyia innocous.—Alayo, 1974:25 [erroneous spelling].—Bonnelly de Calventi, 1974a:16.

REVIEW OF LITERATURE.—More than 100 years elapsed between the appearance of Marcgrave's (1648) account of "guaricuru" (= *Atya scabra*) in Brazil and the report of the second shrimp now assigned to the genus *Atya*. Gronovius (1764), in his *Zoophylacium Gronovicianum*, presented a description of "Astacus 988," in Latin, and noted its occurrence in "Oceano Americano ad Martinicam." Fourteen years later, Meuschen (1778) proposed the name "Astacus Nasoscopus" for it, which, as Holthuis (1966:237) pointed out, "is a senior objective synonym of *Cancer (Astacus) Innocous* Herbst (1792), but is unavailable as Meuschen's publication is ruled invalid under Opinion 260 of the International Commission on Zoological Nomenclature (1954, Opin. Decl. Int. Comm. Zool. Nomencl., vol. 5, pt. 21, p. 267)." The names proposed by both Meuschen and Herbst were based upon the specimen described and illustrated by Gronovius, and whereas Meuschen simply applied a name to Gronovius' species, Herbst presented a translation of Gronovius' description and copied his illustration. He erred, however, in noting that the locality from which the shrimp was collected was unknown (see

above). Latreille (1817) did nothing more than call attention to the species. Not until 30 years later was it mentioned in the literature again when Newport (1847) presented a brief description of specimens from Jamaica that he designated *Atya occidentalis*, noting that "the species seems to be common to the West India Islands, and appears to be that which is figured and described, but not named, by Gronovius . . . ." Obviously he was unaware of the proposed names of Meuschen and Herbst. The discovery of this shrimp on Jamaica by Gosse (1851:85) was recorded by him as follows: "Some interesting *Crustacea* are also found in Bluefields rivulet. I obtained in some numbers a new *Atya* which has been since described by Mr. Newport under the name of *occidentalis*, ..." The opinion was expressed by A. Milne-Edwards (1864) that the characters on which *A. occidentalis* was established were insufficient to distinguish it from *Atya scabra* (Leach, 1815), yet he described *Atya robusta*, believed by him to have been collected on New Caledonia.

One of three new members of the genus that had been collected on the Pacific slope of Nicaragua by J.A. McNiel was designated *Atya tenella* by Smith (1871). Neither White (1847), Giebel (1875), nor Bate (1888) added to our knowledge of the species, and whereas Kingsley (1878a) contrasted it with his *A. punctata* (= *A. scabra*), no new information was offered in that publication or in another (1878b).

Pocock (1889) presented a detailed description of *Atya occidentalis* from two localities on Dominica and pointed out the most obvious differences between it and *A. scabra*. In his report of 1894, he cited two new locality records for the species on the island of Saint Vincent. Ortmann (1890, 1895) added no new information; soon thereafter (1897:184), however, he listed *Atya occidentalis*, *A. punctata*, and *A. tenella* among the synonyms of *A. scabra* but again presented no original data. Rathbun (1897) also considered *A. occidentalis* to be a probable synonym of *A. scabra*.

Bouvier (1904) added three new localities for *A. occidentalis* on the island of Martinique and in 1905 included it in his key, described it, illustrated the rostrum and orbital region, and summarized its distribution: Jamaica, Dominica, Martinique, and questionably Saint Thomas. The island of Cuba was added within the range by him (1909:333). Hansen (1925), in comparing the appendages of crustaceans, found that the "preischium" is not clearly defined in any of the pereiopods of *A. occidentalis*. In his monograph of the family Atyidae, Bouvier (1925) continued to use the combination *Atya occidentalis;* following his key, he presented a synonomy including, in addition to citations to Newport (1847), A. Milne-Edwards (1864), Von Martens (1872), Kingsley (1878a), Pocock (1889), and Bouvier (1904, 1905), Smith's (1871) *Atya tenella* and part of Ortmann's (1895) *A. scabra*. A description of the species was offered, affinities were discussed, and Nicaragua was added to the range given in 1905. *Atya robusta* was recognized by him as a distinct species. Jean Roux (1926b) also considered the latter to be a valid species but questioned its occurrence on New Caledonia because of 150 atyids collected there from six localities not one was a member of the genus *Atya* (as restricted herein). Allee and Torvik (1927) reported the occurrence of this shrimp in Panama as did Boone (1931) who presented a long, detailed description based on six specimens from Isla Barro Colorado. Schmitt (1935) added Puerto Rico to the range of the species, but Oliveira (1945) contributed no original information.

Villalobos (1956), in describing *Atya ortmannioides*, pointed out its affinities with *A. occidentalis*. Burgers (1958) reported that an extract from the eyestalk of this animal, when injected into an "eyestalkless" fiddler crab *Uca rapax*, caused pigment dispersion in the walking legs of the crab. Hart (1961b) reported the distribution of this shrimp on Jamaica and noted that it is used by the local inhabitants as food. There the animals are collected by "holding baskets made of reeds in the swift waters and then turning over rocks a few feet upstream" (p. 73) (see Figure 8*b*,*e* herein). No new information was added by Davant (1963) who suspected the occurrence of this shrimp in Venezuela. Hart (1964) suggested that the delicate texture of the carapaces of Puerto Rican

specimens of *A. occidentalis* was associated with the small amount of calcium available in the water from which they were collected.

Apparently unaware of Holthuis' (1966) lucid discussion of the synonomy of *A. occidentalis* with *A. innocous*, Vélez (1967) included the species in his checklist of the freshwater decapods of Puerto Rico under the former combination. Likewise, Straskraba (1969) employed the same combination in listing the freshwater crustaceans of Cuba. The most recent references to this shrimp as *A. occidentalis* were that of Hunte (1975:66) mentioning Hart's (1961b) report of the species on Jamaica and that of Villamil and Clements (1976), who cited Schmitt's (1935) account of its presence on Puerto Rico.

The delayed acceptance of the name *Atya robusta* as a synonym of *A. occidentalis* (and ultimately of *A. innocous*) no doubt resulted from the belief that the source of the types was New Caledonia. Even Ortmann (1890), who all too frequently invoked synonomy, recognized the species and assigned it to his "*margaritacea*-Gruppe" (based on rostral characters) of the genus. The identity of A. Milne-Edwards' *A. robusta* became evident when Holthuis (1966) presented a convincing explanation that New Caledonia was not likely the source of the types of either *Atya robusta* or *A. margaritacea*. Whereas it was Holthuis' opinion that the types of both came from the same locality in "eastern America," in view of the fact that we have discovered that the types of the latter are conspecific with Smith's *Atya rivalis*, a species known only from the Pacific versant of the Americas that shares stream habitats with *A. tenella* (= *A. innocous*), which, in turn, appears to be inseparable from *A. robusta*, we suggest that if these specimens shared a common locality it is situated somewhere along the Pacific slope of Middle America. Strengthening Holthuis' conclusion that the type-locality of the two species is somewhere other than on New Caledonia is the fact that no unquestioned records exist for members of the genus *Atya* (as restricted herein) in Oceania or the Indo-Pacific. Beatty (1968) recorded this shrimp from several localities on Saint Croix.

Chace and Hobbs (1969) reported the occurrence of *Atya innocous* in 49 stations on Dominica, on nine additional West Indian islands, and from Nicaragua to Panama. They presented a key to the *Atya* occurring in the West Indies and, for each, included a diagnosis and notes on color, size, ecology, and life history. Odum (1970) and Chace (1972) did not add to the information contained in previous references. Bonnelly de Calventi et al. (1973) and Bonnelly de Calventi (1974a) recorded the shrimp in the Cañada Madrigal, in the Dominican Republic. The latter author (1974b) presented a brief diagnosis, illustrations, and statements relating to color, size, habitat, and distribution. She found it to be less common in the Dominican Republic than *A. scabra*. Upatham and Sturrock (1973) investigated the effectiveness of this shrimp along with several other animals as decoys to miracidia of *Schistosoma mansoni*. They concluded that it is unlikely that the shrimp would prevent natural transmission of the fluke but might "limit its severity" since some miracidia were found on the exoskeleton. Alayo (1974) stated that *A. innocous* and *A. scabra* are common in the eastern part of Cuba, and Lévêque (1974) reported the presence of the former on Guadeloupe where he found ovigerous females in May. Peck (1975) cited this shrimp as a cave inhabitant on Jamaica but did not designate a specific locality. Abele (1975), in describing *Atya dressleri*, noted the occurrence of *A. innocous* in streams of the Atlantic Basin of Panama, pointing out the presence of short, strong denticles on the ventral margin of the third through the fifth abdominal pleura as a feature that might be used to separate the latter from the former. He was of the opinion that *Atya tenella* is distinct from *A. innocous* and called attention to the absence in the former of "strong short denticles" on the ventral margins of the third through fifth pleura that are present in *A. innocous*. Differences were also suspected by him in the "spination and form of the antennal peduncles, in the shape of the preanal carina and in the robustness of the legs . . . ." (p. 57). Hunte (1975) added no new data concerning this shrimp. Villamil and Clements (1976) stated that in their study of the shrimp in the upper

Espíritu Santo River they encountered only one specimen of *A. innocous*, that in a riffle area (p. 26), and they concluded that the species appears to be "restricted to lower elevations," at least during the time of their study (p. 28). They reported that Gifford and Cole (1970) found that this shrimp tends "to favor the slower flowing streams." "Zoea" are reported by Villamil and Clements (p. 37) "to live in 15% sea water." Hobbs, Hobbs, and Daniel (1977) called attention to Peck's report of the occurrence of this shrimp in the cave fauna of Jamaica.

The study of this species by Fryer (1977), relating certain morphological features to the mode of life of the animal, is beautifully presented. This report, based largely on a study of Dominican members of the species, endeavors to correlate body structure with behavior, adaptations to their environment, and with capture and mechanical manipulation of food through the foregut. As a result of Fryer's study, that of Hunte (1977, see below), and Felgenhauer and Abele (in press), more is known of the biology of *A. innocous* than of any other member of the genus. Hunte (1977), in recounting his rearing this shrimp stated that it is the largest of the West Indian atyids, attaining a length of about 85 mm. He found that while the first larvae did not feed, subsequent instars thrived best, in the laboratory, on wheat germ and Tetramin that were given them every 12 hours. Of the salinities and temperatures provided, 30‰ and 27° C produced maximum survival. Moults occurred about four to five days apart, and growth was irregular. Approximately 80 days were required from hatching to metamorphosis to the juvenile stage. The ecological and geographical distribution of this shrimp on Jamaica was discussed by Hunte (1978). His study of larval development was detailed by him the following year (1979b; see "Life History Notes" herein), and he included *A. innocous* in his list of atyid and palaemonid shrimps of Jamaica (1979c). Hart (1980) summarized the distribution of the freshwater atyids and palaemonids occurring in the Lesser Antilles, citing the first record of the occurrence of *A. innocous* on Tobago.

The recent study of Felgenhauer and Abele (in press) provides the first recorded observations on mating behavior among members of the genus *Atya*. They observed that in an aquarium, a newly molted female of *Atya innocous* attracted (perhaps by a pheromone) males that followed her in swimming about the tank. When she came to rest on a rock, a male approached, touching her with his antennae and third, fourth, and fifth pereiopods, and, moving parallel to her body, repeatedly touched her with his extended third and fourth pereiopods. He then climbed onto her cephalothorax only to be thrown off; the same ritual was followed by other suitors. After other prenuptial meanderings of the female and an accepted partner, he moved almost directly behind her, and as she moved backward, he walked forward climbing upon her body. Shortly thereafter, his abdomen was shifted to the side and then under hers, and, continuing in an upside-down position, he aligned his body with hers at which time it was assumed that the spermatophore was transferred to the female. Presumably this was accomplished with the aid of the first and second pleopods of the male. Some 24 hours later eggs (0.6 × 0.7 mm) were deposited on the pleopods of the female. The courtship and amplexus are effectively illustrated by line drawings and photographs depicting events observed in the aquarium. The authors also presented excellent photographs, made with the aid of a scanning electron microscope, of parts of the first and second pleopods of the male and proposed a hypothesis as to how the spermatophore is transferred to the body of the female.

PUBLISHED ILLUSTRATIONS.—The earliest illustrations of this species are that of Gronovius (1764), a dorsolateral view of an entire animal, and a redrawn, hand-colored copy of this figure presented by Herbst (1792). The original description of *Atya robusta* by A. Milne-Edwards (1864) was accompanied by a lateral view of the animal and dorsal and lateral views of the rostrum. Pocock (1889) presented a detailed lateral view of the shrimp along with a drawing of the third pereiopod. Bouvier (1905) illustrated *Atya robusta* (fig. 21) by a dorsal view of the rostrum and a lateral view of the cephalic region of the carapace;

the same characters were illustrated for *A. occidentalis* (fig. 22) along with drawings of the first pleopod of the male and female. In his monograph, Bouvier (1925) included figures similar to those published earlier but added an illustration of the terminal part of the fifth pereiopod of *A. robusta* and omitted that of the first pleopod of the female of *A. occidentalis*. Boone (1931) presented a lateral view of an entire animal, and Schmitt (1935) redrew Bouvier's (1905) figure of *A. occidentalis*. Photographs of a Jamaican specimen in dorsal and lateral views were presented by Hart (1961b). Chace and Hobbs (1969) depicted a dorsolateral view of a male showing the color pattern (Figure 24 herein), a dorsal view of the cephalic region, lateral views of the preanal carina and third abdominal pleuron, mesial views of the distal part of the second pleopod and appendix masculina, and a view of one of its habitats on Dominica. Bonnelly de Calventi (1974b) included photographs of this shrimp in dorsal and lateral views and drawings of the rostrum in dorsal aspect, the appendices masculina and interna, and of the antennular peduncles. Fryer (1977) presented a line drawing of a lateral view of an animal; others include the distal parts of the third through fifth pereiopods, details of the structure, musculature, and setae of the first pereiopod, and photographs of a feeding animal: filtering, sweeping, and scraping (some showing color pattern). In addition, drawings of the setation of the gnathal appendages and detailed renditions of the anatomy of the foregut are included. The most recent illustrations pertaining to this shrimp are those of the larvae and their appendages presented by Hunte (1979b) and of courtship and details of the first and second pleopods of the male by Felgenhauer and Abele (in press).

DIAGNOSIS.—Cephalic region of carapace not conspicuously sculptured, glabrous; antennal and pterygostomian spines prominent. Rostrum with margins suddenly contracted at base of acumen forming subangular bends; angles never produced acutely anteriorly. Ventral margin of third through fifth abdominal pleura usually, except in Pacific watershed, provided with rows of sclerotized denticles (such never present on second); caudoventral angle of fourth and fifth pleura subacute to acute but not produced. Sternum of sixth abdominal segment more than half as long as wide; compressed median tubercle on sternum of fifth abdominal segment small and comparatively inconspicuous. Preanal carina with compressed spine overreaching posterior extremity of basal part. Telson 1.9 to 2.2 times as long as wide with 6 to 8 spines in each of 2 dorsal rows. Antennular peduncle with dorsal surface of proximal article usually devoid of (rarely with 1) sclerotized denticles proximal to distal row; penultimate article 1.3 to 1.8 times as long as wide and dorsal surface with several to many scattered spinules. Coxae of third and fourth pereiopods lacking prominent anterolateral spine. Third pereiopod with merus rounded ventrally, 3 to 6 times as long as high, ventromesial surface slightly to strikingly bowed, never parallel to that of corresponding podomere of other third pereiopod, and lateral surface bearing corneous, subsquamous tubercles, latter frequently crowded, and, at least in part, linearly arranged; propodus 2.5 to 3.5 times as long as broad, its extensor surface studded with strongly sclerotized spines or tubercles, and flexor surface with similarly sclerotized spines or tubercles where if any arranged in row those comprising latter never contiguous or overlapping; spines and/or tubercles flanked distally and to the sides by semicircular, often conspicuous, patches of plumose setae; dactyl freely movable and bearing 2 oblique rows of scale- or spikelike denticles on flexor surface.

MALE (Mannet's Gutter, Dominica, WI).—Rostrum (Figure 22*a,d*) with margins strongly contracted at base of acumen (often forming angles); apex of acumen slightly overreaching proximal podomere of antennular peduncle; dorsal median carina gently curved, not excavate dorsally (not dipping below level of lateral carinae posterior to acumen), and ending preapically on acumen; ventral carina with 3 small teeth near apex of acumen; ocellar beak hidden in lateral aspect by eyes, reaching level of about midlength of stylocerite, its cephalic border vertical, and rounded dorsal margin embraced by sides of ventral rostral groove. Antennal and pterygostomian

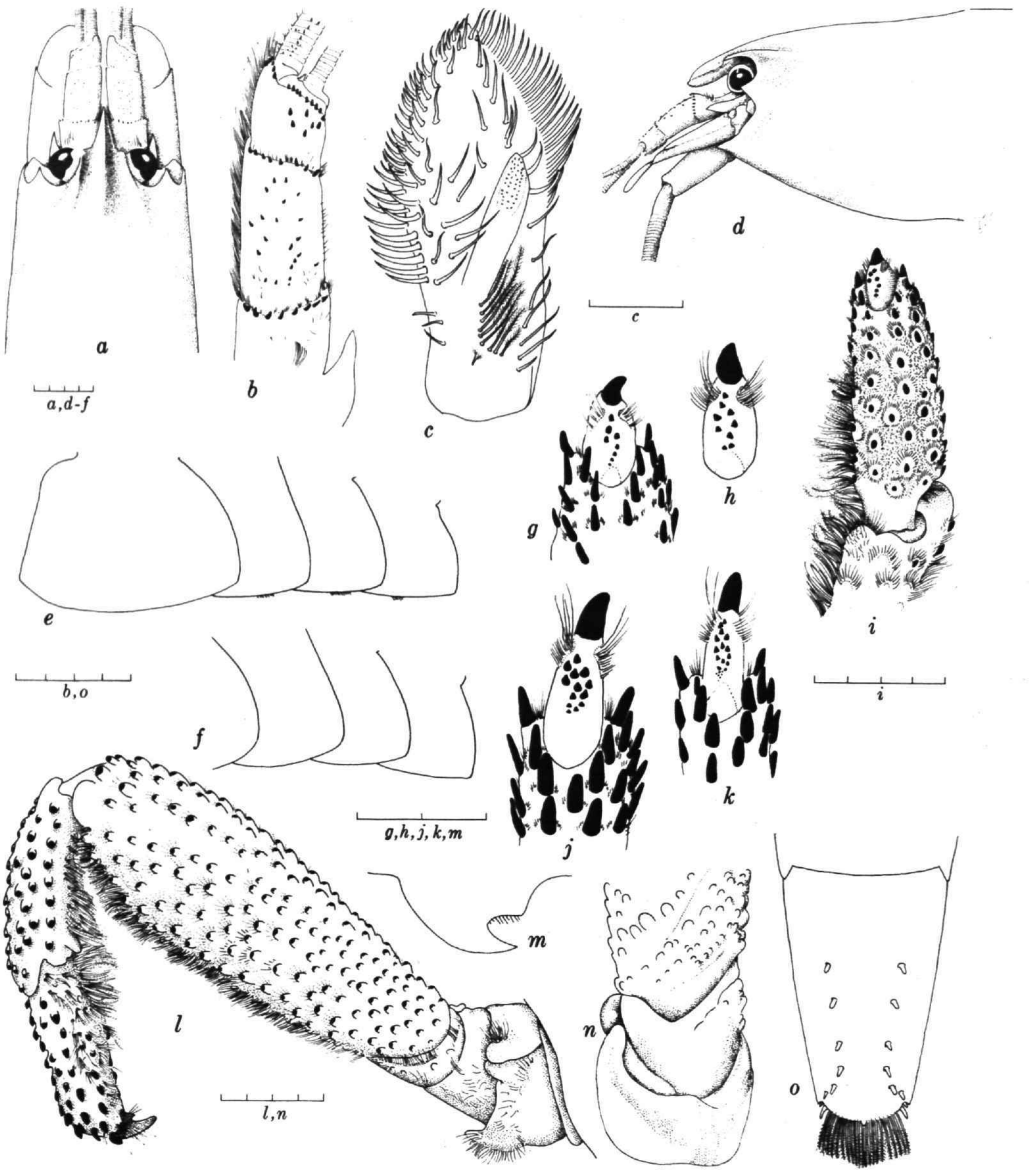

FIGURE 22.—*Atya innocous* (all from males from Mannet's Gutter, Dominica): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view of carapace; *e*,*f*, lateral view of second through fifth abdominal pleura; *g*, flexor surface of distal part of fourth pereiopod; *h*, flexor surface of dactyl of fourth pereiopod; *i*, flexor surface of distal part of third pereiopod; *j*,*k*, flexor surface of distal part of fifth pereiopod; *l*, lateral view of third pereiopod; *m*, lateral view of preanal carina; *n*, ventral view of basal podomeres of third pereiopod; *o*, dorsal view of telson. (Scales marked in 1 mm increments.)

spines strong; no spines present between them. Surface of carapace with crowded punctations supporting very short, erect, fine setae dorsally, latter nowhere conspicuous; devoid of ridges and spines other than those just mentioned.

Pleura of first 4 abdominal segments (Figure 22*e*) with rounded to subacute posteroventral extremities; corresponding parts of fifth acute but not produced in spine. Third through fifth pleura with fine corneous denticles on ventral margin and fifth with moderately conspicuous fringe of plumose setae. Fourth abdominal tergum almost 1.3 times as long as fifth (latter subequal to sixth) and 1.1 times as long as telson. Sternum of fifth abdominal segment with small compressed median tubercle (Figure 1*d*). Sternum of sixth abdominal segment about 0.8 as long as broad. Free part of preanal carina (Figure 22*m*) spiniform, curved, and slightly overreaching angle of basal part of sclerite. Telson (Figure 22*o*) about 1.4 times as long as broad, its dorsal surface bearing paired concave rows of 6 corneous denticles and posteromedian tubercle, latter overhanging caudal margin.

Proximal podomere of antennule (Figure 22*b*) with stylocerite reaching distal fourth or fifth of segment; dorsal surface with linear cluster of setae but lacking corneous spinules; distal margin bearing row of 9 corneous spinules; penultimate segment of peduncle about 1.4 times as long as wide and provided with 23 (right) or 24 (left) scattered corneous spinules on dorsal surface and row of 11 (right) or 10 (left) on distal margin; ultimate podomere with 10 (right) or 9 (left) spinules on dorsal surface, row of 9 (right) or 8 (left) at base of lateral flagellum, and row of 6 at base of mesial flagellum. Antenna with ventrolateral spine on basis reaching as far anteriorly as pterygostomian spine but not quite so far as stylocerite; lateral spine on scaphocerite strong, reaching about midlength of ultimate podomere of antennular peduncle; lamella far surpassing latter; flagellum extending slightly beyond midlength of telson.

Third maxilliped overreaching antennular peduncle by two-thirds of distal podomere of endopod; tip of exopod attaining base of ultimate podomere; penultimate segment about 1.1 times as long as ultimate.

First pereiopod reaching distal end of antennular peduncle; second overreaching first by about one-third length of fingers; terminal brush of both appendages containing setae with scraping denticles. Third pereiopod (Figure 22*i,l,n*) without lateral distoventral spine on merus and carpus, ventral spine absent from merus, and carpus lacking distolateral spines; when appendage extended anteriorly, overreaching antennular peduncle by dactyl, propodus, and half length of carpus. Merus with ventromesial margin bowed, almost 3 times as long as high, 2.2 times as long as carpus, almost 2.4 times as long as propodus; propodus 2.8 times as long as wide, 0.9 as long as carpus; distoventral margin of coxa entire (evenly rounded), and mesial caudoventral prominence virtually absent, distal ventrolateral spine also lacking. Lateral, dorsal, and ventral surfaces of merus studded with linear series of large tubercles, most bearing cornified discs apically and flanked by distal arc of setae; conspicuous tufts of long plumose setae present ventrolaterally; mesial extremity of podomere produced in rounded lobe at level of mesial articular condyle of carpus. Latter strongly tuberculate, and tubercles tipped with corneous discs and flanked distally by arc of 3 or more setae; setae long and forming conspicuous tufts ventrolaterally. Propodus also strongly tuberculate with corneous elements (discs) produced in conspicuous corneous spines; tubercles on flexor surface somewhat irregularly arranged in proximal half of podomere, tending toward biserial arrangement in distal half; lateral surface bearing tufts of plumose setae. Dactyl movable, its flexor surface with 2 irregular, oblique rows of denticles flanked distally by paired clusters of setae.

Fourth pereiopod with dactyl reaching distal end of proximal third of carpus of third pereiopod; merus about 1.8 times as long as carpus; latter subequal in length to propodus. Fifth pereiopod reaching distal extremity of carpus of fourth pereiopod; merus 1.3 times as long as carpus, latter approximately 0.8 as long as pro-

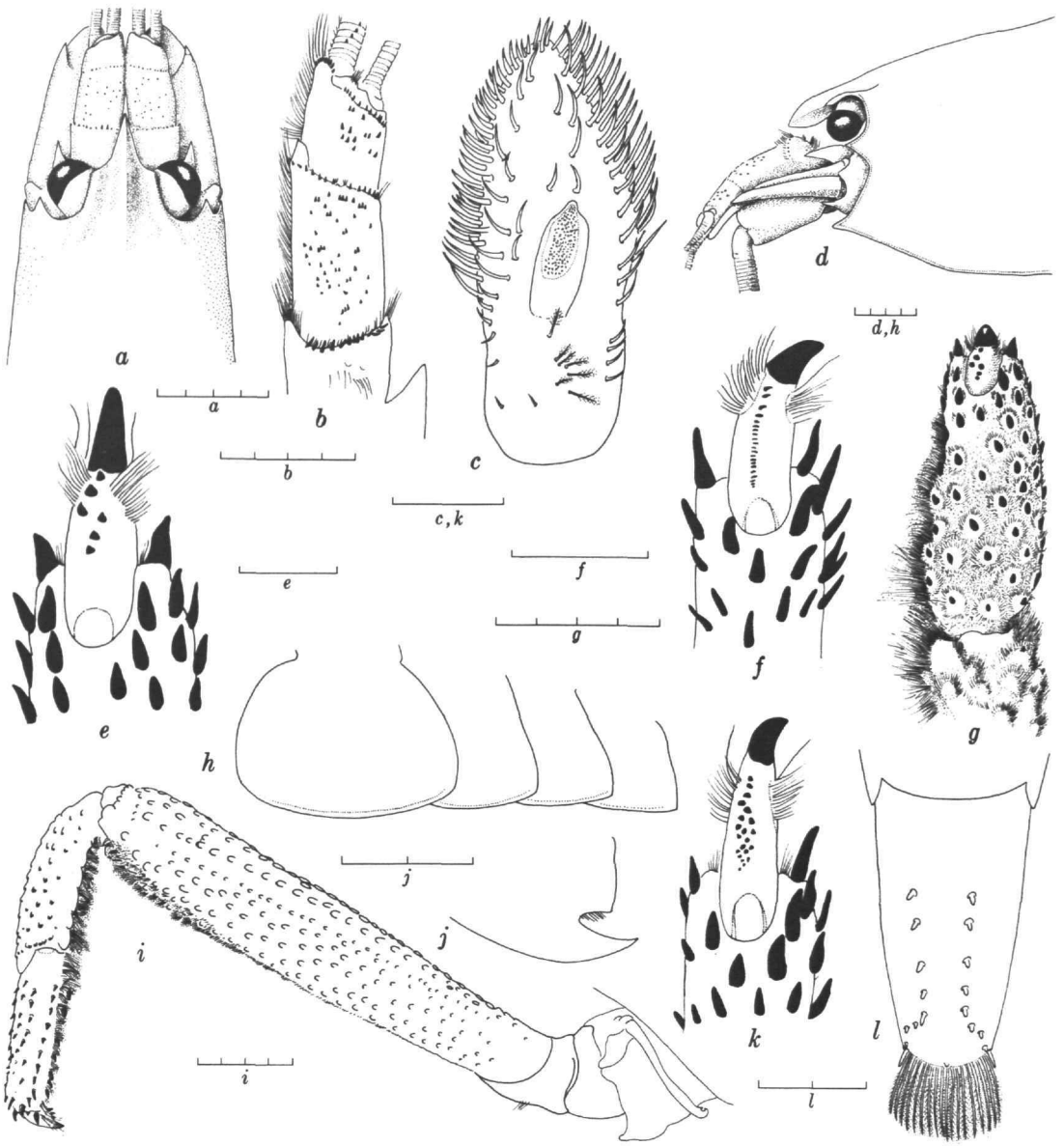

FIGURE 23.—*Atya innocous* (*a*, male syntype of *A. tennella*; *b–d,h–j,l*, male from Cerro Azul area, Panama; *e–g,k*, male from Río Guabas, Panama): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view of cephalic region; *e*, flexor surface of distal part of fourth pereiopod; *f*, flexor surface of distal part of fifth pereiopod; *g*, flexor surface of distal part of third pereiopod; *h*, lateral view of second through fifth abdominal pleura; *i*, lateral view of third pereiopod; *j*, lateral view of preanal carina; *k*, flexor surface of distal part of fifth pereiopod; *l*, dorsal view of telson. (Scales marked in 1 mm increments.)

podus. Ornamentation of merus, carpus, and propodus of fourth pereiopod consisting of distal ventrolateral spine, 2 more proximal ventral ones on merus, and distal ventrolateral and 3 distolateral spines on carpus; ventrolateral surface of merus, carpus, and propodus with conspicuous band of plumose setae. Ornamentation of corresponding podomeres of fifth pereiopod similar but with 3 ventral spines on merus and 2 distolateral spines on carpus.

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

COLOR NOTES.—The most complete account of the color of *Atya innocous* is that of Chace and Hobbs (1969:58–60).

Two phases, green and brown.

Brown Phase: Ground color of cephalothorax dark brown (brownish black chromatophores forming reticulate pattern over tan). Dorsum of carapace with dark brown longitudinal stripe extending from base of rostrum to posterior margin, becoming broader posteriorly. Stripe continuing onto abdomen but broken by very narrow transverse tan bands across posterior margins of anterior five terga; sixth tergum tan anteriorly and dark brown posteriorly; broadest portion of stripe on first and second somites, in both becoming narrower posteriorly. Lateral surface of carapace straw brown with several obliquely directed dark brown lines, posterior and ventral ones directed posteroventrally; posterolateral area with lateral and ventrolateral pale tan spots outlined above and below by aforementioned pairs of dark brown lines. Ventrolateral portion of abdominal terga and pleura mottled straw brown with short dark brown lines (in anterior somites) or spots (in posterior somites) adjacent to articular knobs at posterior bases of pleura: second pleuron with prominent pale tan spot at base and succeeding three pleura with similar, progressively smaller ones, all forming row with lateral spot on carapace; each spot on pleura with dark border. Ventral and posterior margins of pleura very light with dark submarginal line.

Antennular peduncle straw brown with dark brown rings, antennal peduncle straw brown with dark brown markings just proximal to, and on lateral margin of, antennal scale; flagella dark brown to tan. Third maxillipeds pale, translucent, with narrow black lateral margins on more distal podomeres. First two pereiopods translucent to straw brown with dark brown lateral line on merus; carpus straw brown with orange spot on articular surface; bases of two distal podomeres orange, followed by bluish cream throughout most of their lengths, with subterminal narrow, vivid orange band and terminal white one bearing setal tufts; setae dark gray at base fading to cream distally. Basal podomeres (coxa through ischium) of third leg cream with irregular dark brown splotches; merus light basally, becoming dark brown distally and bearing very dark brown tubercles, few with corneous tips; carpus dark brown with light tan band at midlength, propodus light tan in proximal fourth and dark brown in distal three-fourths, tubercles on carpus and propodus dark at base but with corneous (yellow) tips; dactyl mostly corneous. Fourth and fifth pereiopods with basal podomeres as in third pereiopod; merus with flexor portion, proximal and distal ends dark brown, remainder tan; carpus with proximal extensor surface tan, otherwise dark brown; propodus and dactyl as on third pereiopod.

In most young specimens, light dorsomedian stripe extending from tip of rostrum almost to, or to, distal [sic, = posterior] margin of telson; on cephalothorax, stripe of uniform width; on first abdominal somite, expanded in posterior half; in succeeding three somites, narrow anteriorly and broadening posteriorly; in fifth somite narrow and of uniform width; in sixth, essentially similar to that in second through fourth; and on telson, narrower posteriorly. In older individuals, dark pigment forming variable, mostly bilaterally symmetrical, patterns along lateral margins of dorsomedian stripe; with increasing age patterns coalescing and infringing on stripe to extent that in individuals of intermediate size, stripe usually narrower, irregular, and interrupted, and largest individuals usually without trace of stripe.

Green Phase: Pattern essentially identical; color, however, ranges from pale bluish green to greenish black.

The pattern of a male with a carapace length of 25.8 mm is reproduced from Chace and Hobbs in Figure 24. Bonnelly de Calventi (1974b:39) observed that the median dorsal stripe "desaparece con los cambios de luz del medio ambiente."

Fryer (1977:70) confirmed the observations of Chace and Hobbs that the color pattern changes with age and added that "many individuals, especially larger ones appear to be almost black." Several of the photographs therein show the color patterns mentioned above.

The color pattern of specimens from El Vallé, Panama, differs in no conspicuous way from that described above. The most obvious difference between the color photographs lent to us by Bruce E. Felgenhauer and the pattern illustrated in Figure 24 is the presence of a broad, median, longitudinal, light stripe extending from the apex of the rostrum onto the telson; flanking the stripe is a pair of irregular, narrow, very dark brown to blackish lines. Also, the more ventral of the two

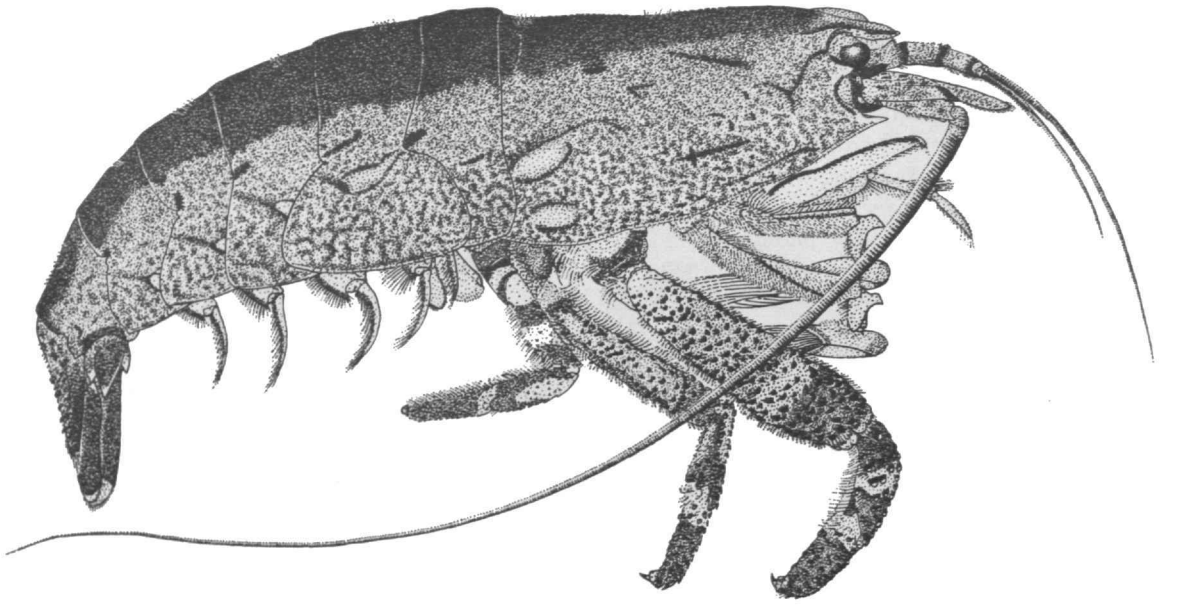

FIGURE 24.—Lateral view of *Atya innocous* (from Chace and Hobbs, 1969).

light spots on the posterolateral surface of the carapace of the Dominican specimen is lacking in that from Panama, and the bands on the antennal peduncle of the latter are not so clearly defined, rather the two distalmost podomeres are dark brown dorsally with only faint suggestions of the bands laterally.

Hunte (1979b) recorded the positions of chromatophores in the first larval stage of *A. innocous*, noting that on a "virtually transparent" animal, reddish chromatophores were present as follows: one on the antennular peduncle, one on the carapace posterior to each eye, three on the first abdominal segment, and at least one on each of the following segments. Heavy pigmentation occurred at the junction of the carapace and abdomen and at that between the latter and the telson. Four chromatophores were found on the telson.

SIZE.—Although he provided only one measurement of an adult, about 85 mm total length, Hunte (1979b:231) stated that *Atya innocous* is the largest atyid shrimp occurring in the West Indies. Of the almost 700 specimens from Dominica examined by Chace and Hobbs (1969), 232 males had carapace lengths of 5.0 to 33.7 mm; the range in 246 females was 2.5 to 20.6 mm, including 80 ovigerous ones, which measured 8.8 to 20.6 mm. The carapace length of 215 juveniles ranged from 1.1 to 5.0 mm. Fryer (1977:69) noted that the maximum total length of members of this species is about 12.2 cm. Of the specimens measured by us, the largest is a male from Dominica, having a carapace length of 40.9 mm. The ovigerous females ranged from 7.9 to 24.9 m·

DISTRIBUTION AND SPECIMENS EXAMINED.—This shrimp, described from Jamaica, has a range in the Americas almost as great as that of *Atya scabra* and, where it occurs, appears to be far more abundant. It has been reported on the Pacific slope as *A. tenella*, from Nicaragua to Panama; in the Atlantic watershed, it ranges from Nicaragua to Panama, and in the West Indies it has been recorded from the Greater Antilles and from the Virgin Islands southward to Curaçao. Chace and Hobbs (1969) reported its presence on the island of Dominica in some 49 localities ranging from sea level to 925 m above sea level (Figures 25–28).

Records for the known localities are listed below. Collections that we have examined are

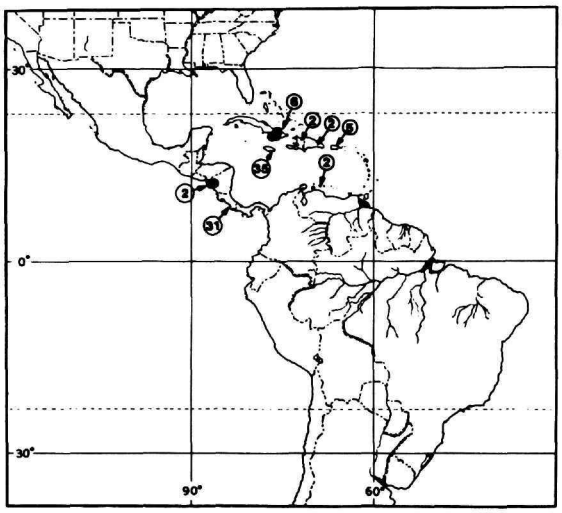

FIGURE 25.—Distribution of *Atya innocous* (circled numerals = number of localities; see Figures 26–28).

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 or, if followed by "t.l.," total length. Some listings lack dates and/or collectors; these could not be determined.

CUBA (all localities in Provincia de Oriente): No specific locality, (Bouvier, 1909:333). (1) *MHNP, eastern extremity of Cuba (Bouvier, 1925:313), 1 ovig ♀ (15.6), 1910. (2) †USNM, Río Santa María de Loreto, Ramón de las Yaguas at about 480 m, 1♀ (11.6), C.J. Ramsden. (3) †USNM, Arroyo de la "Alcachofa" (probably Alcahuete) at about 360 m, 2♀ (8.5, 14.4), 3 Mar 1919, CJR. (4) †USNM, Río Los Hondones, Guantánamo, at about 490 m, 1♀ (25.2), CJR. (5) †USNM, Arroyo Los Machitos, El Corojo de San Carlos, Guantánamo, 1♂ (26.2), CJR. (6) †MCZ, Pico Turquino, 1♂ (24.8), 10–19 Jun 1936, J. Acuña.

JAMAICA: No specific locality (Newport, 1847:159); *USNM, 1♂ (22.2), 1♀ (19.5), 1–11 Mar 1884, Str. *Albatross*. *Manchester Parish*—(1) *USNM, One Eye River S of Auchtembeddie at 230 m (Hart, 1961b:72), 2♀ (18.0, 22.0), 13 Jan 1960, CWH, T. Farr. *Portland Parish*—(2) *USNM, trib to Black River near Elysium at 76 m (Hart, 1961b:72), 1♂ (10.5), 2♀ (6.5, 13.9), 1 ovig ♀ (10.4), 8 Apr 1959, CWH, G. Thomas. (3) Drivers River at 362 m (Hunte, 1978:140). (4) Rio Grande River at 300 m (Hunte, 1978:140). (5) Buff Bay River at 910 m (Hunte, 1978:140). (6) †MCZ, brook at Spring Bank 4.2 km W of Port Antonio, 1♂ (23.4), 1 ovig ♀ (16.2), 28 Mar 1906, A.E. Wright. (7) †MCZ, Brook Port 3.4 km W of Port Antonio, 5♂ (8.5–15.5), 27 Mar 1906, AEW. (8) †USNM, Mabess River, 2♂ (approx 31.0, 36.0), 26 Jul 1926, D.S. Johnson. (9) †USNM, Spanish River Falls, 3♂ (10.5–13.3), 1♀ (13.8), 1 ovig ♀ (16.6), 11 Jul 1948. (10) †LGA, John Crow Mts at about 600 m, 1 ovig ♀ (23.9). *Saint Andrew Parish*—(11) *USNM, Mammee River near Maryland at 380 m (Hart, 1961b:72), 1♂ (15.2), 5♀ (6.2–13.5), 4 Jun 1959, CWH, TF. (12) Hope River at 1050 m (Hunte, 1978:140). (13) Cane River at 575 m (Hunte, 1978:140). (14) †USNM, Yallahs River near Cinchona at 1200 m, 2♂ (32.0, 36.1), 3 ovig ♀ (23.6–24.0), 1910, E.A. Andrews. (15) †USNM, Yallahs River near Cinchona, 1♂ (33.0), 1 ovig ♀ (24.9), 10 Jun 1910, EAA. (16) †USNM, Upper Ginger River, Tweed-

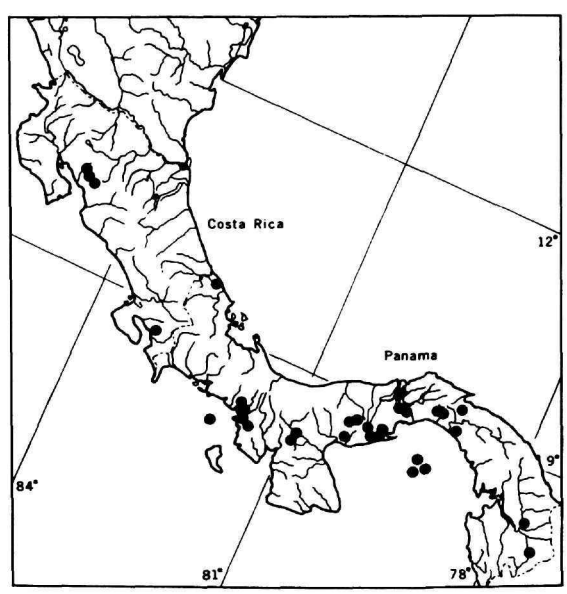

FIGURE 26.—Distribution of *Atya innocous* in Costa Rica and Panama.

side at 600 m, 3♂ (29.0–32.2), 2♀ (16.4, 21.0), 2 ovig ♀ (20.9, 21.0), 13 Apr 1903, W.R. Maxon. (17) †USNM, Clyde River at Chestervale, 1♂ (30.3), 1♀ (22.5), 30 Jun 1948. *Saint Ann Parish*—(18) *USNM, Great River at Llandovery at 30 m (Hart, 1961b:72), 7♂ (11.1–17.4), 5♀ (6.0–12.1), 6 ovig ♀ (9.0–12.6), 10 Apr 1959, CWH, GT. (19) Laughland's Great River at 15 m (Hunte, 1978:140). (20) Laughland's Great River at 304 m (Hunte, 1978:140). (21) Rio Bueno at 152 m (Hunte, 1978:140). (22) †BM, Ocho Rios, 2♀ (10.9, 15.4), 16 Jan 1937, I. Sanderson. *Saint Catherine Parish*—(23) Rio D'Oro at William's Field at 150 m (Hart, 1961b:72). *Saint James*

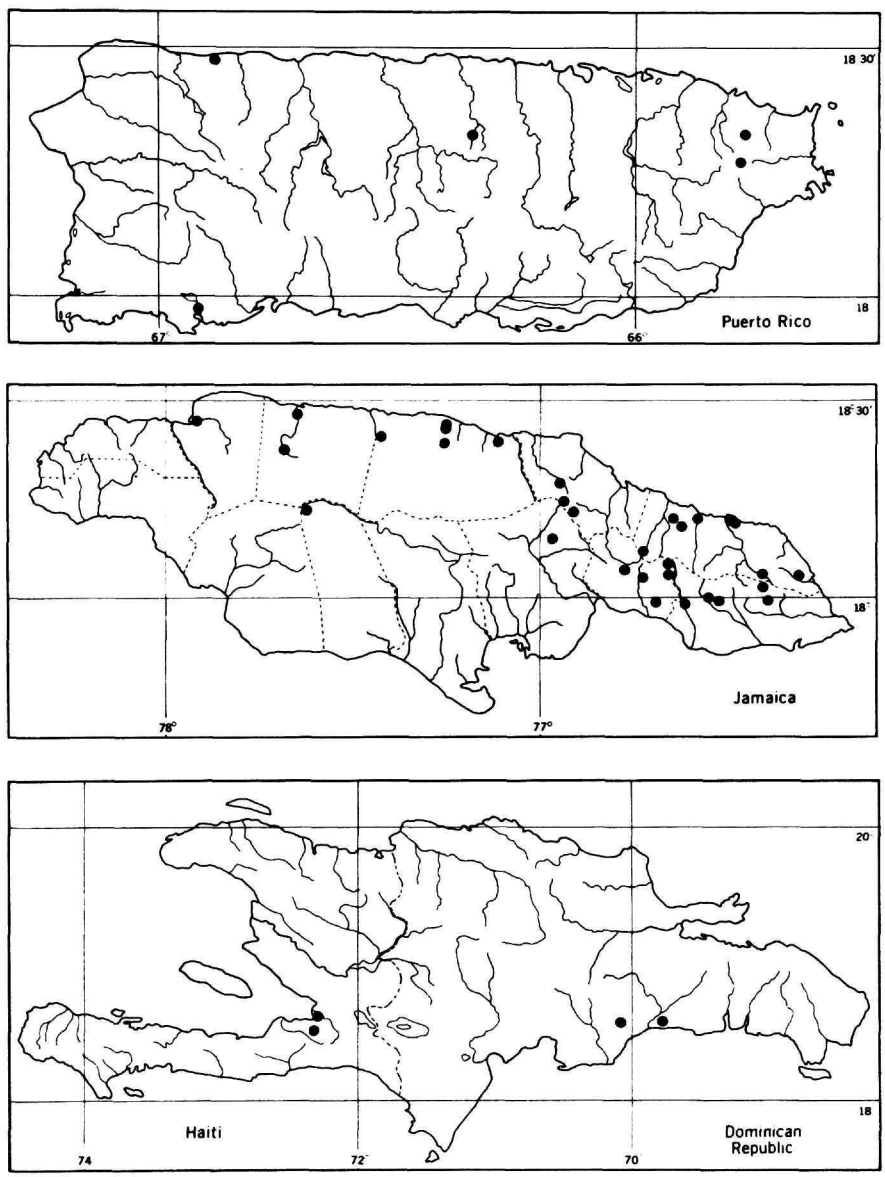

FIGURE 27.—Distribution of *Atya innocous* in the Greater Antilles.

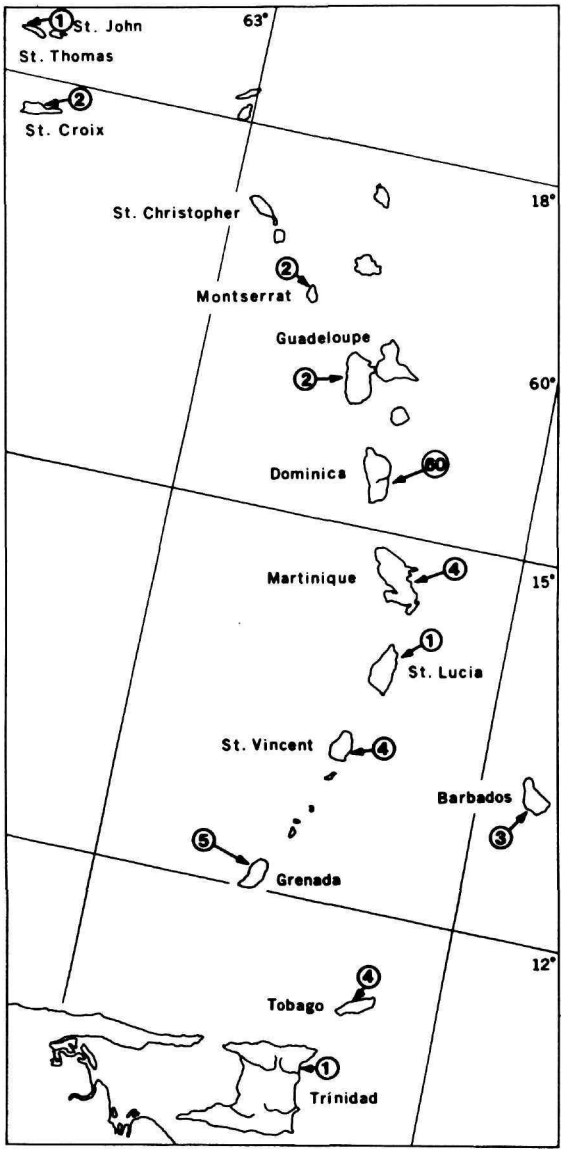

FIGURE 28.—Distribution of *Atya innocous* in the Lesser Antilles (circled numerals = number of localities).

Parish—(24) †USNM, Montego River near Tannery, 1♂ (28.3), 10 Jul 1910, EAA (?). *Saint Mary Parish*—(25) *USNM, trib to Trunnels River 6.8 km S of Richmond at 230 m (Hart, 1961b:72), 2♂ (10.5, 13.2), 2 ovig ♀ (8.4, 15.4), 7 Apr 1959, CWH; 2♂ (8.5, 12.2), 1♀ (12.3), 1 ovig ♀ (16.6), 7 Jan 1960, CWH. (26) Rio Nuevo at 454 m (Hunte, 1978:140). (27) †USNM, Rock Spring Cave, Pear Tree Grove, 4♂ (15.7–31.7), 7♀ (16.2–18.7), 1 ovig ♀ (20.8), 21 Aug 1974, S. Peck. *Saint Thomas Parish*—(28) Bugaboo River 0.3 km below Corn Puss Gap at 600 m (Hart, 1961b:73). (29) Negro River 4.3 km NW of Trinity Ville at 450 m (Hart, 1961b:73). (30) *USNM, Banana River 1.7 km N of Richmond Vale at 450 m (Hart, 1961b:73), 29♂ (9.8–22.5), 5♀ (9.1–13.6), 27 ovig ♀ (9.9–18.0), 6 Jan 1960, CWH, R. Bengry. (31) Morant River at 300 m (Hunte, 1978:140). (32) Bugaboo River at 543 m (Hunte, 1978:40). (33) Yallahs River at Ramble Bridge at about 82 m (Hart, 1961b:73). *Trelawny Parish*—(34) Martha Brae River below dam near Martha Brae at 15 m (Hart, 1961b:73). (35) †RNHL, Martha Brae River S of Bunkershill, 2♂ (15.7, 22.8), 17♀ (7.8–14.4), 10 Jan 1960, CWH.

HISPANIOLA: *Haiti*—no specific locality (Kingsley, 1878a:92); *MCZ, 3♂ (11.3–18.6), 8 Sep 1858, D.F. Weinland. (1) †BM, Thorlands, 8♂ (7.8–11.6), 3♀ (8.0–9.7), 1 ovig ♀ (11.8), 17 May 1937, IS. (2) †USNM, Port au Prince, 1♀ (injured), 20 May 1930, W.M. Parrish. *Dominican Republic*—no specific locality, †USNM, 3♂ (17.0–25.1), 2♀ (13.4, 18.1), 4 ovig ♀ (13.9–17.4), 1878, W. Gabb. (3) Cañada Madrigal, Distrito Nacional (Bonnelly de Calventi et al., 1973: 1338); 6♂ (13.8–25.4), Bonnelly de Calventi, 1974a:16.

PUERTO RICO: (1) Luquillo Forest (Schmitt, 1935:136). (2) †RNHL, Río Guánica, 5 juv (2.0–2.1), 15 Sep 1965, P.W. Hummelinck. (3) †USNM, Río Manatí between Corozal and Orocovis, 2♂ (9.5, 10.3), 1♀ (9.8), 23 Nov 1954. (4) †USNM, trib to Río Mameyes at Rte 112, 2.7 and 1.8 km N of El Yunque summit, 1♂ (21.3), 8 Jun 1953. (5) †USNM, Río Maracayo, pool below fish hatchery, 2♂ (36.8, 37.0), 1 Feb 1971, D.S. Erdman.

SAINT CROIX: Beatty (1968:263) cited the following: "Upper Love, Fairplain, Caledonia, Crique, La Grange, streams, Mt. Welcome Swamp." Chace and Hobbs, (1969:60) cited no specific locality; *USNM, 1♂ (20.4), H.A. Beatty. (1) †USNM, Caledonia Street, 1♂ (8.4), 2♀ (11.2,

17.0), HAB. (2) †RNHL, Canaan Stream, 4♂ (7.1–15.5), 5♀ (7.7–10.4), 10 Jun 1955, PWH.

SAINT THOMAS: No specific locality (Bouvier, 1905:119).

MONTSERRAT: No specific locality (Chace and Hobbs, 1969:60); *USNM, spring, alt about 450 m, 1♂ (8.2), 1♀ (8.3), 1894, Hubbard and Schwartz.

GUADELOUPE: No specific locality (Chace and Hobbs, 1969:60); *USNM, stream, 1♂ (11.4), 1♀ (14.2), 1 ovig ♀ (12.7), Mar 1937, HAB. (1) †MHNP, second chute du Carbet, Basse Terre, alt 600 m, 4♂ (16.8–22.0), 1♀ (11.9), 14 Jun 1978; 25♂ (9.1–25.2), 6♀ (8.6–11.5), 3 ovig ♀ (11.9–14.6), 24 Jun 1978. (2) †MHNP, Rivière Belle Eru (Grand Etard), alt 180 m, Basse Terre, 4♂ (14.1–23.0), 1♀ (15.4), 1 ovig ♀ (13.6).

DOMINICA: (Except for localities 2–6, 12, 20–24, 37, 39–44, 58, and 59, all of those from the island were included in Chace and Hobbs, 1969:9–12.) Unknown locality, *USNM, 8♂ (21.2–32.2), 4 ovig ♀ (15.4–17.2), 17 Jul 1877, F.A. Ober. *Saint Andrew Parish*—(1) *USNM, trib of Pagua River 3.4 km N of Deux Branches, alt 106 m, 3♂ (5.5–10.3), 4 Mar 1966, HHH. (2) Trib to Kasiobna River, alt 91 m. (3) Toulaman River, alt 15 m. (4) Hodges River, alt 7.5 m. (5) †USNM, trib to Melville Hall River 2.6 km N of airport, alt 91 m, 1♀ (10.5), 1 ovig ♀ (14.2), 3 Feb 1964, HHH III, HHH. *Saint David Parish*—(6) *USNM, trib to Fond Figues River, to Castle Bruce River, alt 410 m, 1♂ (10.2), 2♀ (8.3–11.3), 4 ovig ♀ (12.4–16.1), 62 juv (5.0–7.0), 6 Mar 1966, HHH. (7) *USNM, Fond Figues River at 105 m, 2♂ (12.3, 13.5), 1 ovig ♀ (14.5), 2 juv (5.0, 5.5), 22 Mar 1964, HHH. (8) *USNM, trib to Castle Bruce River W of Raymond Stone River, alt 76 m, 3♂ (8.3–14.4), 4♀ (8.4–12.3), 22 Mar 1964, CWH, HHH. (9) *USNM, trib to N Branch of Ravine Deux Dleau, alt 180 m, 14♂ (7.0–21.3), 11♀ (6.9–12.0), 3 ovig ♀ (9.3–12.1), 3 juv (5.0–6.1), 14 Feb 1964, HHH III, HHH. (10) *USNM, N Branch of Deux Dleau, alt 242 m, 1♂ (11.1), 1♀ (12.5), 29 Jan 1964, HHH III, HHH; 4♂ (6.8–18.7), 1♀ (8.2), 14 Feb 1964, HHH III, HHH. (11) *USNM, trib to Rosalie River near Bori Lake, alt 920 m, 1♂ (18.9), 23 Mar 1964, CWH, HHH III, HHH; 5♂ (9.4–22.7), 3♀ (13.0–15.2), 1 ovig ♀ (16.7), 10 Nov 1964, P.J. Spangler. (12) Mill Race to Rosalie River at 15 m. (13) †USNM, trib to Fond Figues River, alt 410 m, 1♂ (10.2), 2♀ (8.3–11.3), 4 ovig ♀ (12.4–16.1), 62 juv (5.0–7.0), 6 Mar 1966, HHH. *Saint George Parish*—(14) *BM, Laudat (Pocock, 1889:11), alt 300 m, 4♂ (26.1–40.9), J.A. Remage. (15) *USNM, stream at Fond Baron Estate 1 mi E of Loubiere, alt 135 m, 7♂ (11.7–22.8), 4♀ (12.2–13.8), 1 juv (6.2), 21 Feb 1964, HHH III, HHH. (16) *USNM, trib to Roseau River below Trafalgar Falls, alt 300 m, 6♂ (6.0–34.2), 1♀ (21.1), 1 ovig ♀ (20.5), 5 juv (no more than 5.0), 26 Mar 1964, CWH, HHH. (17) *USNM, pool below Trafalgar Falls, alt 300 m, 1♂ (21.5), 1 ovig ♀ (14.3), 8 Jan 1964, HHH III; 2♂ (25.9, 32.5), 25 Oct 1964, PJS. (18) *USNM, stream near Freshwater Lake, trib to Rosalie River, alt 760 m, 1♂ (21.3), 23 Feb 1964, purchased by D.L. Bray. *Saint John Parish*—(19) *USNM, Hermitage River N of Portsmouth, alt 90 m, 13♂ (8.0–18.3), 11♀ (5.5–17.6), 21 juv (about 5.0), 5 Mar 1964, HHH. (20) Headwaters of Picard River, alt 450 m. (21) Lamonthe River, alt 121 m. (22) Cario River, alt less than 8 m. (23) Barry River to Indian River, alt about 3 m. (24) †USNM, headwaters of Espagnole River on slope of Morne Diablotin, alt 450 m, 1♂ (17.2), 6♀ (10.3–17.3), 26 Jan 1964, HHH. *Saint Joseph Parish*—(25) Layou River (Pocock, 1889:11). (26) *USNM, Mannet's Gutter near mouth, alt 15 m, 5♂ (15.1–26.6), 7♀ (11.4–17.5), 38 juv (3.0–5.0), 25 Jan 1964, HHH; 1♂ (10.0), 1♀ (14.9), 1 juv (5.2), 19 Feb 1966, HHH; 2♂ (18.0, 20.1), 2♀ (12.4, 16.1), 21 Feb 1966, HHH; 14♂ (14.0–29.2), 9♀ (13.2–16.5), 7 ovig ♀ (14.4–19.0), 2 Feb 1967, C. Rhyne. (27) *USNM, Mannet's Gutter at upper bridge, alt 21 m, 9♂ (15.3–29.6), 5♀ (13.0–19.9), 4 ovig ♀ (14.1–21.1), 29 Jan 1964, HHH; 3♂ (14.7–22.8), 2♀ (10.2, 17.8), 3 ovig ♀ (17.5–20.0), 7 juv (4.7–7.0), 17 Mar 1966, HHH; 1♂ (23.0), 1♀ (21.5), 1 ovig ♀ (17.6), 8 Aug 1965, D.M. Anderson; 1♂ (18.3), 1 Sep 1965, DMA; 2♂ (16.1, 31.3), 1♀ (18.4), 4 juv (about 5.0), 7 Mar 1966, R.B. Manning, HHH. (28) *USNM, trib of Layou River across from Clarke Hall, alt 15 m, 7♂ (12.0–25.5), 2♀ (16.5–17.1), 15 juv (5.0), 7

Feb 1964, HHH III, HHH; 2♂ (10.2, 17.8), 2♀ (9.5, 14.4), 13 Mar 1964, HHH; 3♂ (7.2–19.8), 2♀ (17.2, 17.3), 29 juv (4.0–5.0), 22 Feb 1966, HHH. (29) *USNM, trib to Layou River at Cassada Gardens, alt 150 m, 3♂ (13.2–24.3), 4♀ (10.6–16.2), 5 juv (about 5.0), 19 Feb 1964, HHH; 1♂ (21.2), 4 ovig ♀ (15.0–17.2), 11 juv (about 5.0), 3 Mar 1964, H. Robinson, HHH. (30) *USNM, Dleau Morne Laurent to Layou River, alt 210 m, 2♂ (20.8, 28.0), 2♀ (18.4, 25.9), 2 ovig ♀ (13.1, 18.5), 29 Feb 1964, HHH III, HHH. (31) *USNM, trib to Layou River just N of Dleau Manioc, alt 210 m, 8♂ (14.6–27.5), 1♀ (16.5), 4 ovig ♀ (12.1–16.4), 20 Feb 1964, HHH III, HHH. (32) *USNM, Warner River 3.4 km N of Pont Casse, alt 410 m, 1 ovig ♀ (12.3), 4 Mar 1966, HHH. (33) *USNM, trib of Laurent River E of Pont Casse, alt 485 m, 6♂ (7.2–12.2), 4♀ (8.2–18.3), 8 ovig ♀ (11.0–13.1), 4 Mar 1966, HHH. (34) Layou River at lowest riffle, approximately 2 to 3 m. (35) North bank of Layou River about 30 m above mouth at sea level. (36) Batali River near mouth at sea level. (37) Trib to Layou River just N of Dleau Manioc. (38) Mouth of Layou River to 200 m upstream on S bank, sea level. (39) Macoucheri River in vicinity of bridge, alt 1 to 3 m. (40) Trib of Macoucheri River, mill race, alt about 2 m. (41) Trib to Layou River just S of River D'Or, alt 212 m. (42) Mannet's Gutter, Clarke Hall Estate, alt 106 m. (43) Ravine Neiba to Layou River, alt 76 m. (44) †USNM River D'Or, to Layou River, alt 230 m, 1♂ (30.2), 1 ovig ♀ (16.4), 29 Feb 1964, HHH III, HHH. *Saint Patrick Parish*—(45) *USNM, Ravine Cacao, alt 120 m, 1♂ (20.0), 24 Mar 1964, CWH, HHH. (46) *USNM, Ravine Irene, alt 15 m, 1♂ (13.0), 26 Mar 1964, CWH, HHH. (47) *USNM, trib to Stewart's River 4.4 km N of Berekua, alt 45 m, 2♂ (8.2, 9.0), 3♀ (6.2–17.1), 3 juv (6.0–6.5), 21 Feb 1964, HHH. (48) *USNM, Pichelin River below Logge, alt 106 m, 2 ovig ♀ (13.8, 16.0), 1 juv (6.5), 26 Mar 1964, CWH, HHH. (49) *USNM, trib to Perdu Temps River, alt 106 m, 7♂ (6.0–21.9), 9♀ (6.9–14.2), 3 ovig ♀ (10.6–13.5), 4 juv (about 5.0), 26 Mar 1964, CWH, HHH. (50) *USNM, La Ronde River, alt 75 m, 8♂ (10.8–23.7), 1 ovig ♀ (10.5), 15 Oct 1964, A. La Ronde; 1♂ (14.1), 1♀ (13.0), 1 ovig ♀ (9.4), 3 Sep 1965, AL; 2♂ (6.0, 8.8), 1 ovig ♀ (10.0), 15 Mar 1966, HHH. *Saint Paul Parish*—(51) *USNM, headwater trib of Belfast River, Pont Casse, alt 600 m, 1♂ (20.2), 1♀ (15.9), 1 juv (7.6), 16 Feb 1964, HHH III, HHH. (52) *USNM, trib to Belfast River at Sylvania, alt 575 m, 3♂ (8.9–17.5), 4♀ (10.0–17.2), 28 Jan 1964, R. Zusi, HHH III. (53) *USNM, Check Hall River at Springfield, alt 350 m, 10♂ (7.9–19.3), 12♀ (7.6–19.8), 4 juv (about 5.0), 1 Feb 1964, HHH III, HHH. (54) *USNM, trib to Check Hall River, alt 460 m, 11♂ (7.2–23.2), 14♀ (12.4–16.2), 2 ovig ♀ (10.7–12.5), 1 juv (6.0), 1 Feb 1964, R. Patrick, HHH. (55) Belfast River, alt 23 m. (56) Mouth of Belfast River at sea level. (57) Mouth of Check Hall River at less than 2 m. *Location Uncertain*—(58) †USNM, Du Blanc River, the Jungle Biol Sta, 2♀ (9.9, 14.0), 3–19 Mar 1929, P.G. Howes. (59) †BM, Emerald Pool, beneath waterfall, 1♀ (15.1), 1 juv (5.7), 2 Aug 1977, Michael New.

MARTINIQUE: No specific locality (Gronovius, 1764:231). (1) *MHNP, "Rousseau" (Bouvier, 1904:137), 7♂ (15.5–30.5), 5♀ (17.6–19.0), 1 ovig ♀ (15.1). (2) *MHNP, "Bellanger" (Bouvier, 1904:137), 7♂ (21.3–27.4), 2 ovig ♀ (18.9, 19.6). (3) Chaffanjon (Bouvier, 1904:137), (4) †RNHL, Dumauze, 2♂ (15.1, 22.0), 13 Jun 1955, R. Pinchon.

SAINT LUCIA: (1) †BM, Marc stream, 1♂ (14.0), 1 ovig ♀ (16.3), 15 juv (3.2–6.0), 18 May 1971, G. Barnish.

SAINT VINCENT: No specific locality, *RNHL, 3♂ (18.7–31.8), 1 ovig ♀ (17.0), 1975, S.P. Meyers. (1) *USNM, Cumberland River (Pocock, 1894:408), 17♂ (16.1–23.4), 2♀ (13.0, 14.9), 2 ovig ♀ (14.1, 16.3); *BM, 12♂ (14.3–19.2), 4♀ (11.4–14.5), 5 ovig ♀ (13.0–15.1), H.H. Smith. (2) *BM, Fitzhughes River (Pocock, 1894:408), 31♀ (8.2–16.4), 10 ovig ♀ (10.4–11.9). (3) †RNHL, Greathead River, 2 km from Kingston, 1 juv (3.6), 10 Jul 1967, PWH. (4) †USNM, Teviot River at Montreal Estate, 1♂ (17.8), 1♀ (13.7), 31 Mar 1971, A.P. Harrison.

BARBADOS: (1) †RNHL, Wiltshire's Spring, Marley Vale, St. Philip, 20♂ (9.8–19.9), 9♀ (5.9–17.1), 3 ovig ♀ (7.9–8.8), 1 juv (4.8), 6 Jul

1967, PWH. (2) †RNHL, Conset River at St John, 9♂ (6.3–16.5), 4♀ (6.3–9.0), 6 ovig ♀ (9.3–13.4), 26 juv (3.6–6.1), 7 Jul 1967, PWH. (3) †RNHL, Joe's River at Frizers, W of Bathsheba, 13♂ (6.2–11.6), 7♀ (7.4–16.7), 64 juv (2.9–6.0), 16 Feb 1964, PWH.

GRENADA: (1) †RNHL, Titivee, Victoria, 1 juv (4.1), 16 Jan 1958, PWH. (2) †RNHL, Beaulieu, examined but sex and c.l. not recorded, 3 Oct 1965, J.R. Groome. (3) †RNHL, La Sagesse River, Coats Gap, St. Davids, 1♂ (15.9), 1 Jan 1966, Justin Francis, JRG. (4) †RNHL, St. Marks River, 5♂ (16.8–21.5), 3♀ (11.0–13.6), 55 juv (1.0–5.3), 25 Jan 1966, C.A.O. Philips, JRG. (5) †RNHL, Irwin's River, Z.O. van Santenos, 40 juv (2.2–4.0), 7 Jul 1967, PWH.

TOBAGO: No specific locality, †BM, 1 ovig ♀ (13.4), P.L. Guppy. (1) *USNM, Doctor's River, in small dammed pond near Speyside, 11°18′N, 60°31′W (Hart, 1980:847), 4♂ (17.0–29.0), 9 Apr 1978, F.D. Martin et al. (2) †BM, Mt. Irvine River SW of Plymouth, 5♂ (17.2–24.0), A.K. Totten. (3) †RNHL, Frenchman's River at Speyside, 3♂ (8.0–11.9), 7♀ (6.0–12.8), 3 juv (6.3–6.5). (4) †USNM, cascading stream on Roxborough, Parlatuvier Road, vic. Bloody Bay, 1♂ (23.3), 31 Aug 1972, R.G. Tuck, Jr., W. Flowers; 1♂ (27.6), 4 Sep 1972, RGT.

TRINIDAD: (1) †BM, Mt. Aripo, 2♂ (8.3, 11.1), IS.

CURAÇAO: No specific locality (Holthuis, 1980:69). (1) †RNHL, stream in mango plantation at Santa Cruz, 22♂ (6.1–21.7), 11♀ (5.7–12.9), 2 ovig ♀ (11.0–11.7), 12 juv (3.1–5.9), 4 Jan 1957, L.B. Holthuis; RNHL, 64♂ (7.5–23.6), 30♀ (7.2–13.6), 14 ovig ♀ (10.9–16.0), 67 juv (3.0–8.0), 11 Feb 1957, LBH; RNHL, 41♂ (8.1–20.9), 22♀ (5.8–14.5), 3 ovig ♀ (11.3–13.4), 8 May 1957, A.C.J. Burgers, F.L. Hermans. (2) †RNHL, stream near Hato airport, 20♂ (12.1–23.4), 18♀ (9.2–21.8), 36 ovig ♀ (10.2–14.9), 10 Jul 1957, ACJB.

NICARAGUA: (1) †PM, Hacienda El Polvón, Departamento Occidental (Smith, 1871:95), syntypes of *Atya tenella*, 1♂ (16.2), 1♀ (9.4), summer 1868, J.A. McNiel; MCZ, 4♀ (11.2, 13.7, 13.7, 18.2), 1871(?), J.A. McNiel, (2) †MCZ, Corcuera, 1 juv ♂, Jul 1868, J.A. McNiel.

COSTA RICA: (1) †USNM, Río de los Platanales, Golfo Dulce, 1♂ (13.8), 2♀ (15.0, 17.4), Apr 1896, H. Pittier. (2) †USNM, Río Barranca, 1♀ (17.7), 4 Aug 1928, M. Caleris.

PANAMA: *Provincia de Bocas del Toro*—(1) †USNM, Río Sixaola and creek near Finca Calif. pumping station, 2 juv (2.8, 3.0), 2 Sep 1962, H. Loftin. *Zona del Canal*—(2) *USNM, Shannon Creek on Isla Barro Colorado (Allee and Torvik, 1927:67 for *A. occidentalis*) 1♀ (19.4), Mar 1924, W.C. Allee. (3) †MCZ, "Limones" (= El Limón?), 1 ovig ♀ (about 11.0), 8 Jun 1929. (4) *USNM, Isla Barro Colorado, 1♂ (18.3), 26 Jun 1969, L.G. Abele. (5) †USNM, Pedro Miguel Locks, 2 juv (1.2, 1.9), 3 Feb 1969, LGA. (6) †USNM, Pedro Miguel, Madden Forest, Green Memorial, 1♂ (17.5), 23 Jul 1969, LGA; LGA, 4♂ (11.0–20.7), 4♀ (15.6–17.5), 1 Mar 1973, LGA, M.H. Robison, F. Quieros; LGA, 4♂ (16.0–18.1), 2♀ (14.5, 16.8), 4 Apr 1973; LGA, MHR. *Provincia de Chiriquí*—(7) †USNM, trib to Río Tabasará 22 km W of El María on Soná-Remedios Rd, 3♂ (13.1–21.3), 11 Nov 1961, HL. (8) †USNM, creek 17 km W of David, 3♂ (10.6–18.3), 1♀ (18.0), 2 Dec 1961, HL. (9) †USNM, 8.5 km W of David on Carretera Interamericana, 2♂ (13.9, 14.4), 1 ovig ♀ (16.1), 12 Dec 1961, HL. *Provincia de Coclé*—(10) †MCZ, Río Las Lajas, 3♂ (7.3–11.0), 22 Oct 1939, G.B. Fairchild. (11) †USNM, Río Antón in El Vallé Crater, 6♂ (11.2–21.0), 1♀ (13.9), 7 Apr 1962, HL. (12) †USNM, Río Arenal at Carretera Interamericana, 5♂ (9.1–11.3), 1♀ (15.4), 5 ovig ♀ (10.1–16.2), 13 Oct 1961, HL. (13) †USNM, Río Guabas, 1.7 km W of Antón, 7♂ (8.6–21.9), 3♀ (10.3–16.6), 6 ovig ♀ (13.3–15.6), 14 Oct 1961, HL. (14) †USNM, Río Arenal 5.1 km E of San Carlos, 1♀ (16.2), 11 Mar 1962, HL. (15) †USNM, Río Las Lajas E of San Carlos, 1♂ (19.0), 5♀ (8.8–16.4), 24 Mar 1962, HL. (16) †LGA, El Vallé, 2♂ (10.5, 12.1), 2 ovig ♀ (14.2, 21.1), 5 juv (4.3–5.5), May 1978, LGA, B.E. Felgenhauer. (17) †LGA, El Vallé, Mosa Cham, 2♀ (14.5, 15.3), 14 Apr 1973, LGA; LGA, 9♂ (7.1–11.4), 14♀ (5.8–17.9), 14 Apr 1973, LGA. (18) †LGA, Río Antón, El Vallé, 1 ovig ♀ (14.5), 30 Jan 1974, D.C. Darling. *Provincia de Colón*—(19) †LGA,

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

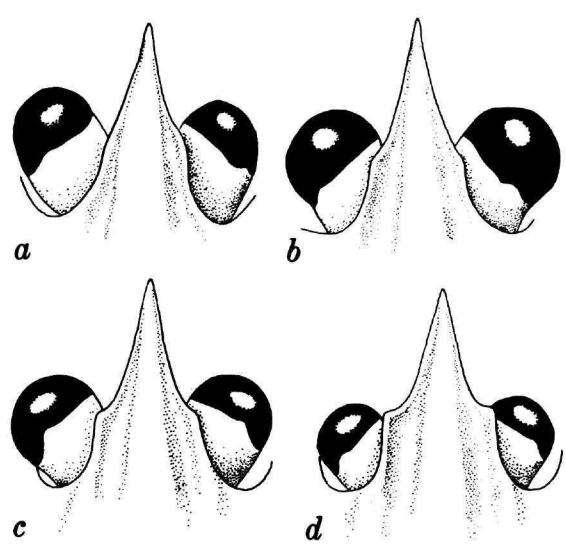

FIGURE 29.—*Atya innocous*, variations in rostrum and eyes with increase in size of animal (scaled to approx. same size; numbers in parentheses = carapace length in mm): *a*, male (7.8); *b*, male (9.9); *c*, female (15.1); *d*, male (24.7).

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

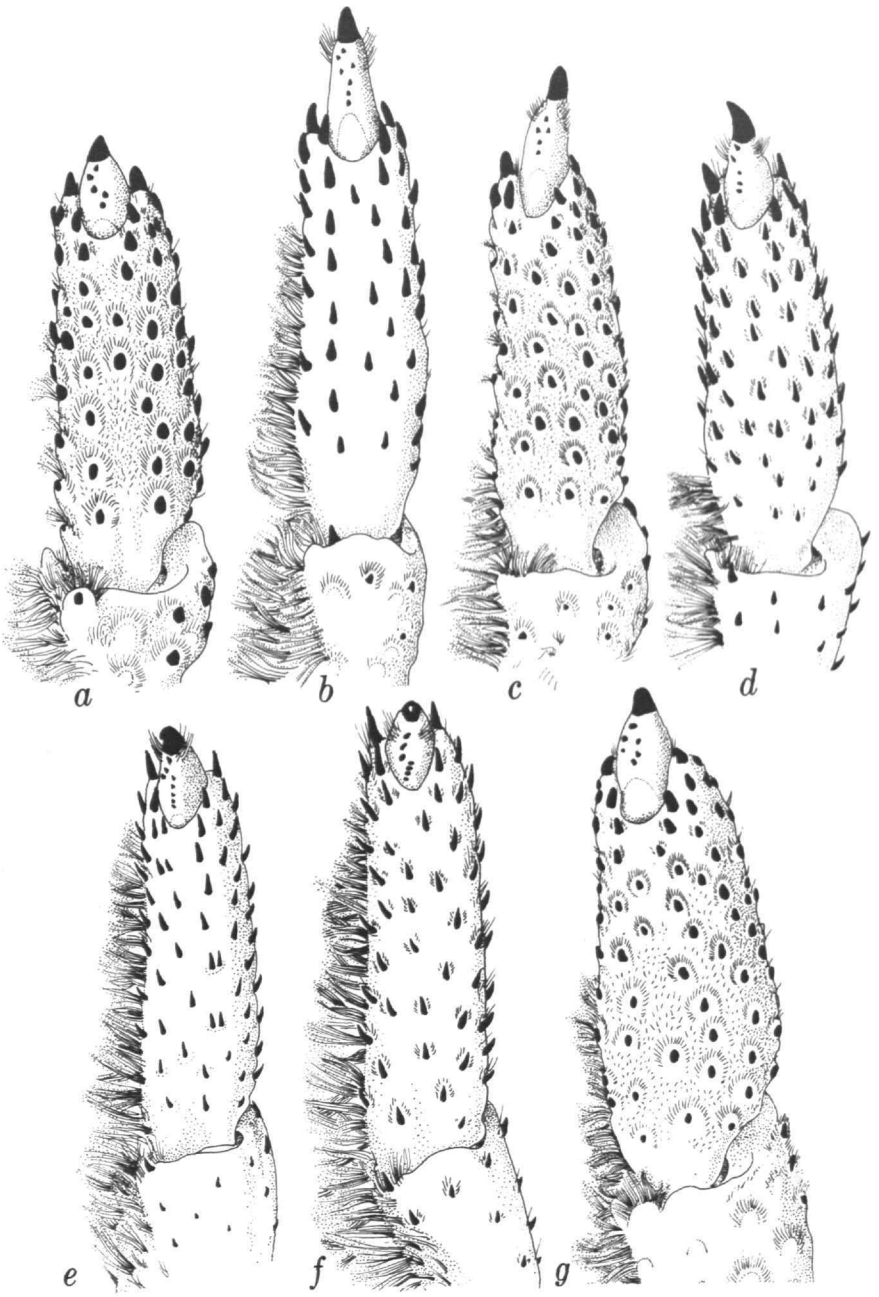

FIGURE 30.—*Atya innocous*, variations in flexor surface of distal part of third pereiopod (numbers in parentheses = carapace length in mm): *a*, Saint Croix, Virgin Islands (♂, 20.4); *b*, Banana River, Jamaica (♂, 18.3); *c*, Banana River, Jamaica (♂, 22.2); *d*, Río de los Platanales, Costa Rica (♀, 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 tol-

erates 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: "Af-

rique 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

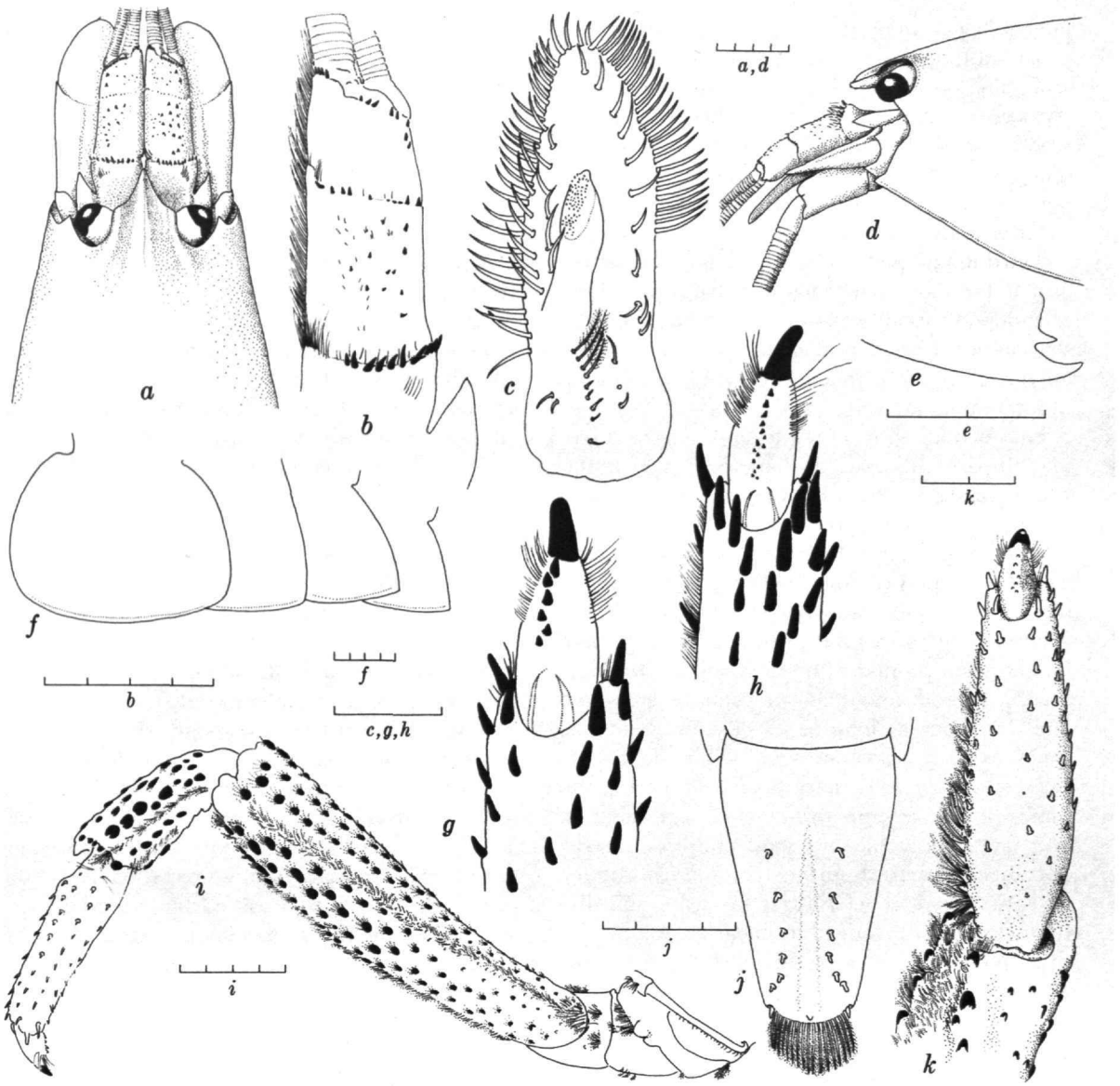

FIGURE 31.—*Atya intermedia* (all from male from Annobón): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view of cephalic region; *e*, lateral view of preanal carina; *f*, lateral view of second through 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:

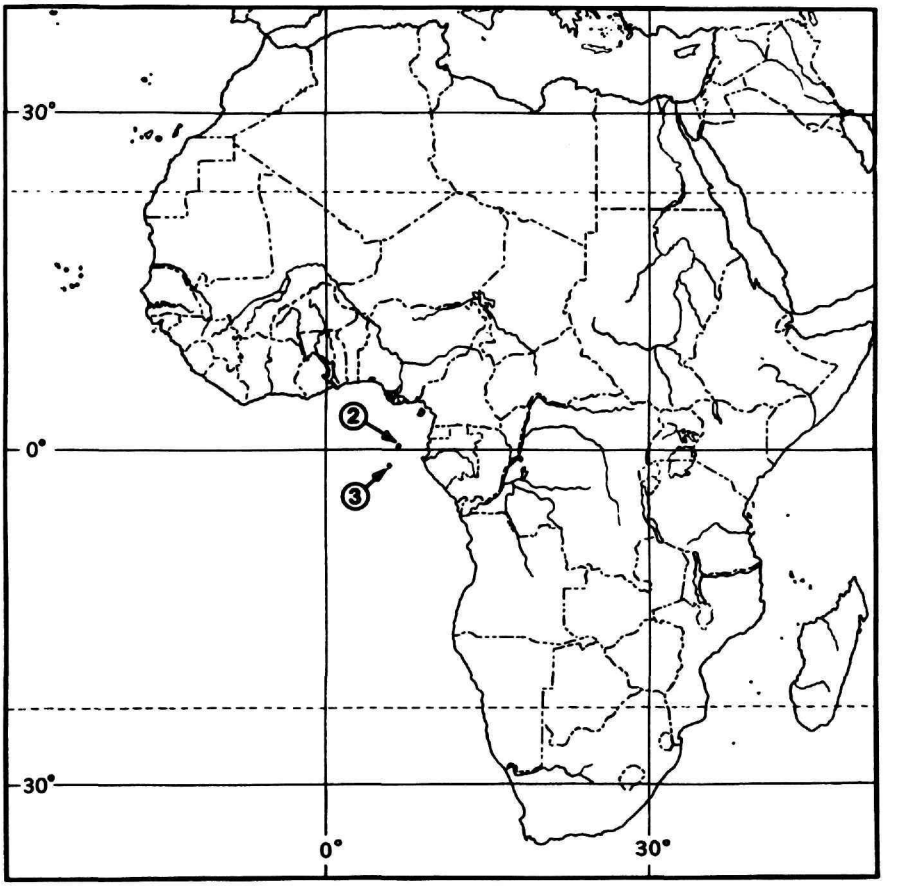

FIGURE 32.—Distribution of *Atya intermedia* (circled numerals = number of localities).

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.l), 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 sur-

faces 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

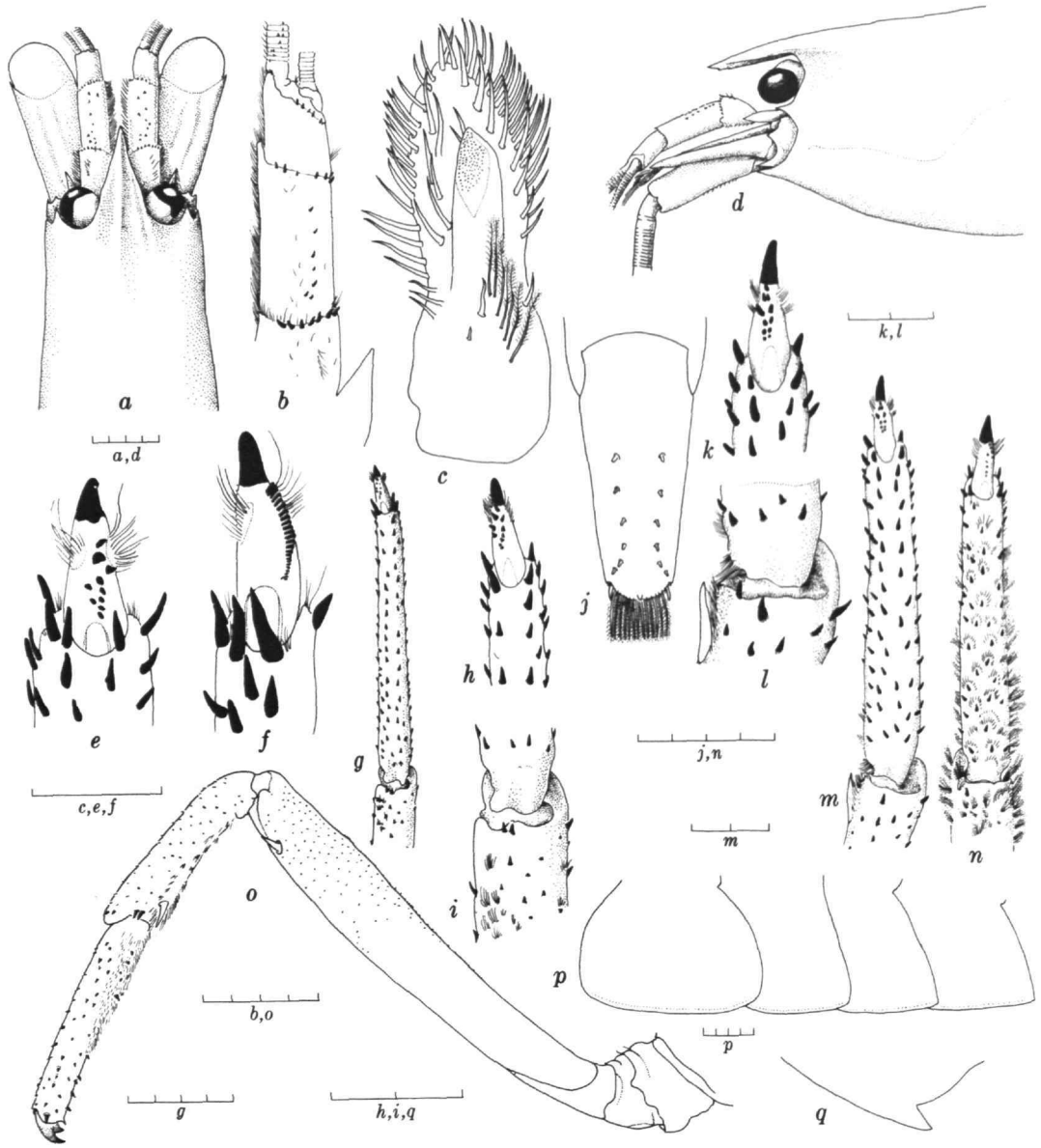

FIGURE 33.—*Atya lanipes* (all from male from Río Maricao, Puerto Rico, except *g,h,i* from Río Mameyes, Puerto Rico, and *n* from Rock Springs, Jamaica): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view 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

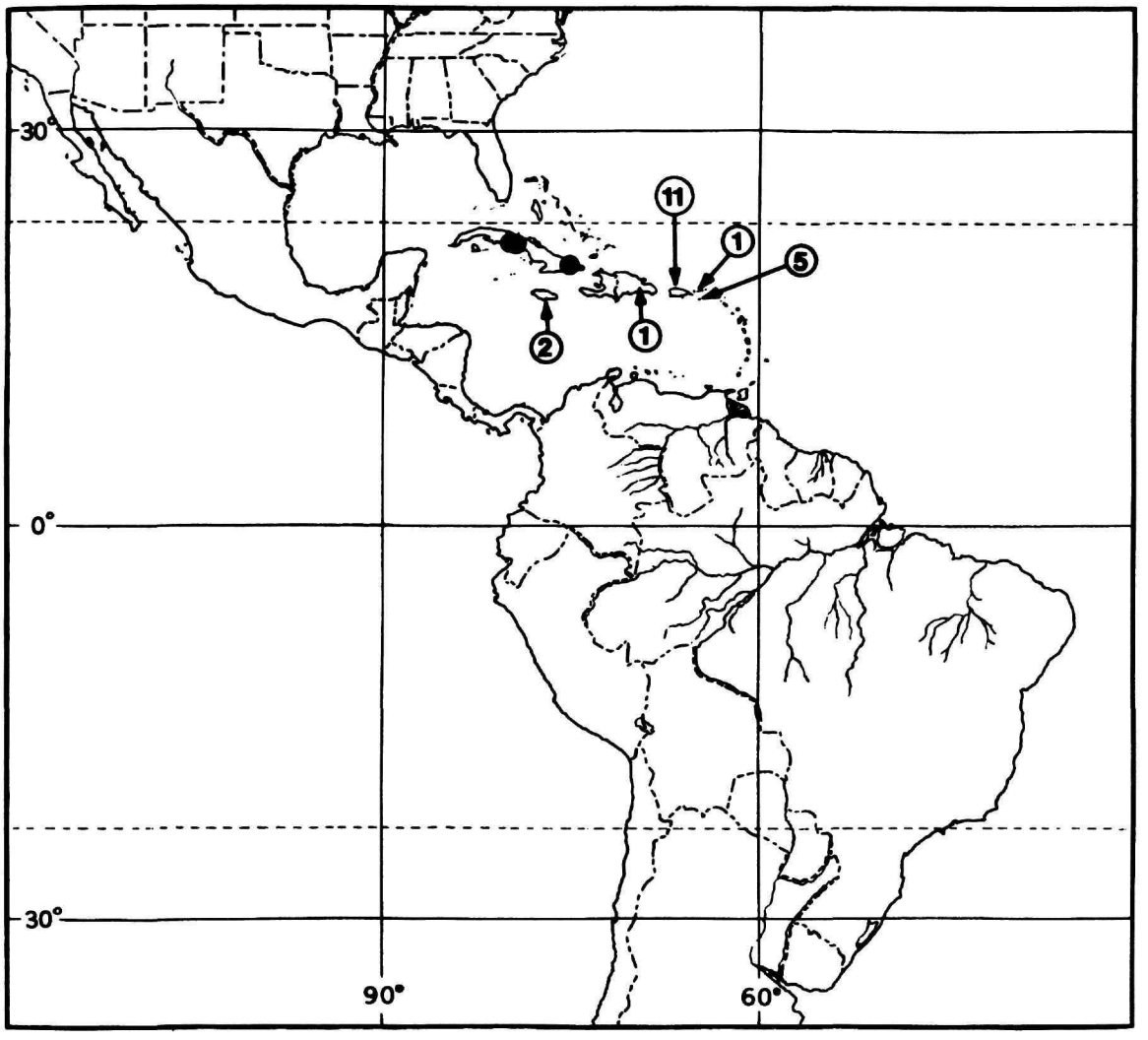

FIGURE 34.—Distribution of *Atya lanipes* (circled numerals = number of localities; see Figure 35).

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),

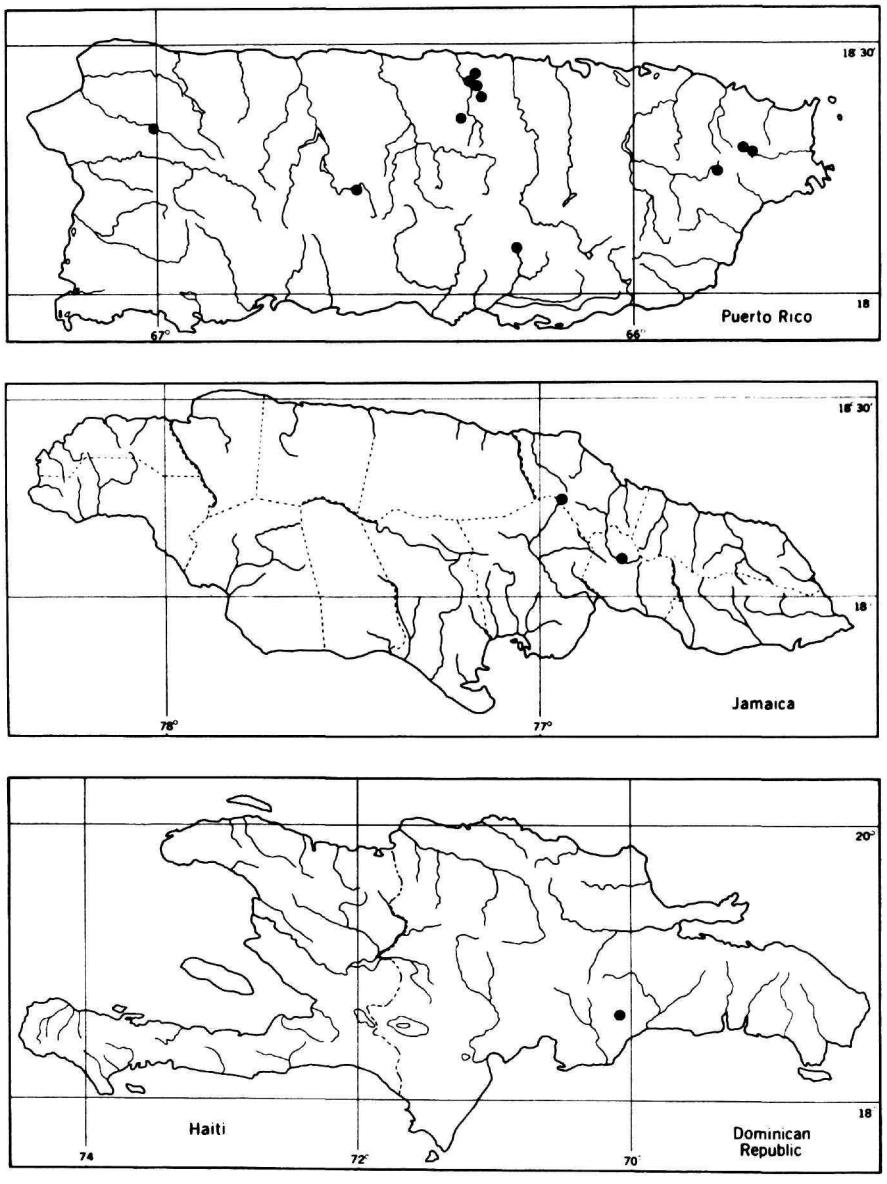

FIGURE 35.—Distribution of *Atya lanipes* in the Greater Antilles.

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 Ai-

bonito, 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-

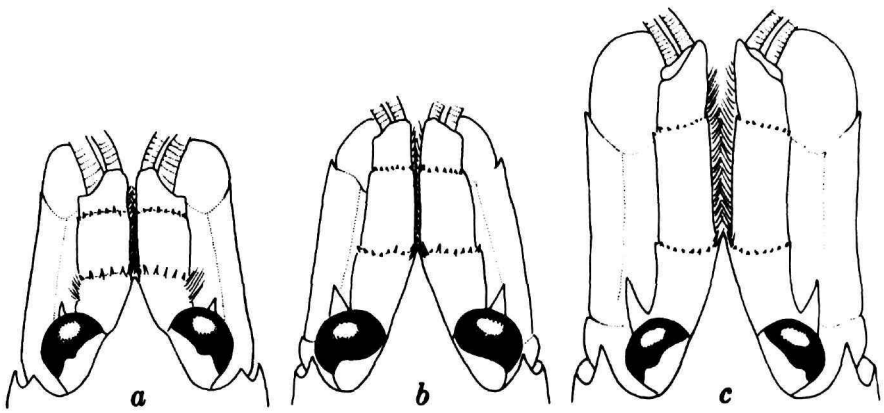

FIGURE 36.—*Atya lanipes*, variation in the rostrum of 3 specimens from Río Mantí, Puerto Rico (numbers in parentheses = carapace length in mm): *a*, ovigerous female (14.9); *b*, ovigerous female (18.0); *c*, male (23.4).

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 syn-

onyms 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

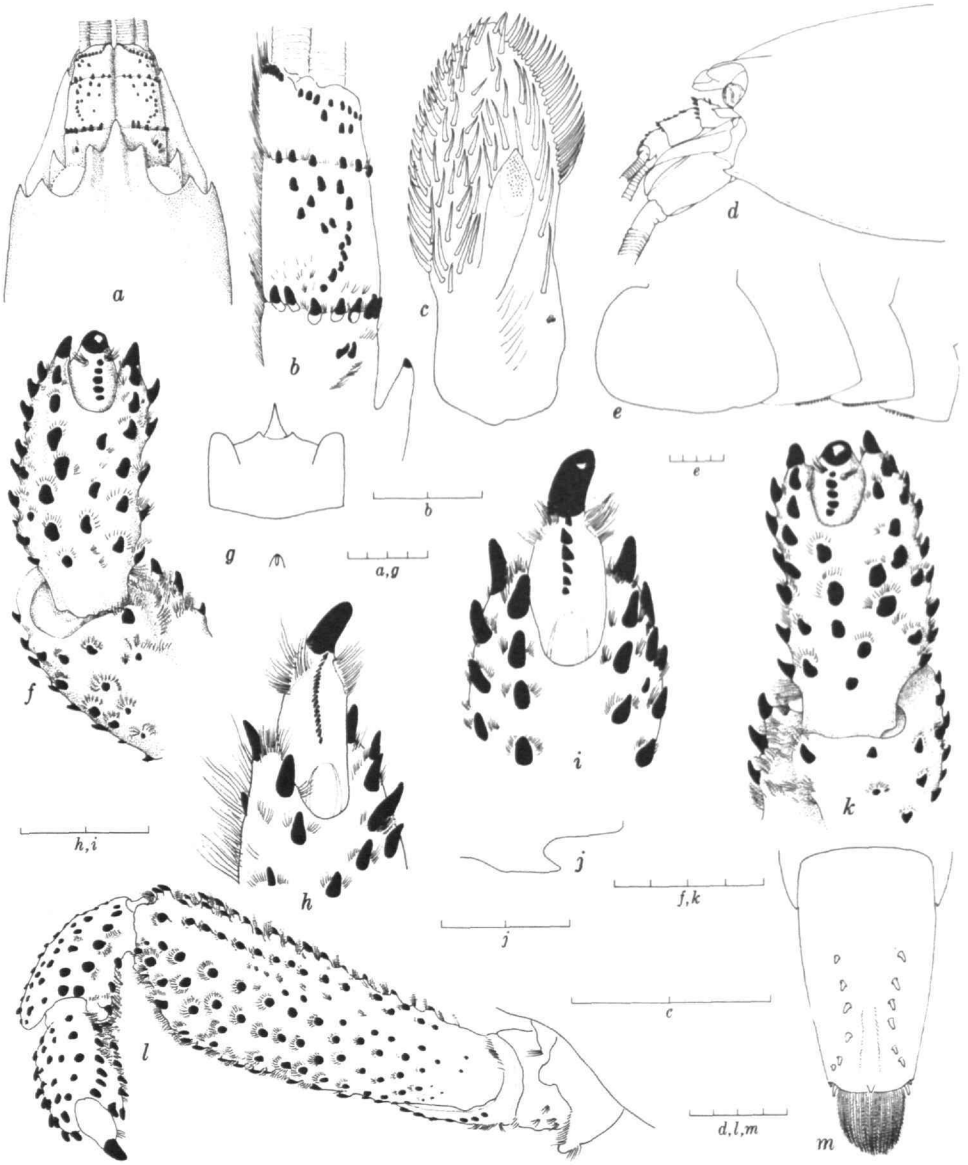

FIGURE 37.—*Atya margaritacea* (all from syntypic male): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, mesial view of appendices masculina and interna; *d*, lateral view of cephalic region; *e*, lateral view of second through fifth abdominal pleura; *f*, flexor surface 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

carapace length agrees very well with the illustration of *A. scabra* herein (Figure 47) except that the dark distal part of the third pereiopod is not so strikingly conspicuous, and there are a few dark spots on the lateral surface of the carapace that are not present in the illustration of *A. scabra.* Whether or not there is a dorsomedian longitudinal stripe cannot be determined from the transparency because of the position of the animal in the photograph. The uniform, very dark-blue coloration, even extending onto the basal section of the eyestalks of an animal with a 30 mm carapace length suggests that an encrustation of some kind is at least partly responsible for the intensity of the dark color.

SIZE.—Of the 98 males measured, the largest specimen has a carapace length of 38.0 mm; the average was 18.6 mm. The largest of 54 females has a corresponding length of 24.4 mm, the average 14.3 mm. The smallest and largest ovigerous females have carapace lengths of 7.3 and 20.8, average 12.7 mm.

DISTRIBUTION AND SPECIMENS EXAMINED.—Disregarding the almost certain erroneous data (New Caledonia) recorded by A. Milne-Edwards for his types as well as for those reported for Argentina and Australia, this American species ranges from Baja California southward on the Pacific versant to Peru (Figures 38, 39).

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 or, if followed by "t.l.," total length. Some listings lack dates and/or collectors; if so, these could not be determined.

MEXICO: (1) †USNM, La Paz, Baja California Sur, 1♀ (9.6), Jun 1882, L. Belding. (2) †MCZ, San José, Baja California Sur, 2♂ (6.1, 8.2), 2♀ (7.5, 7.9), 3 juv, Gustav Eisen. (3) †BM, San Ramón, 3♂ (28.8–35.6), 1♀ (22.7), A.C. Butler. (4) †USNM, Río San Nicholás between Chamela and Tomatlán, Jalisco, 8♂ (6.1–12.0), 2♀ (7.8–9.9), 4 ovig ♀ (7.3–8.4), 1 juv (3.1), 6 Apr 1965, R.R. Miller and Sable. (5) †BM, San Isidro, 3♂ (14.8–19.3), F.D. Godman. (6) †BM, Río Machiro, trib to Río Grande, near San Mateo, Oaxaca, alt 300 m, 2♂ (27.9, 28.3), H. Pittier de Fahega.

GUATEMALA: (1) †BM, Pentalion, 10♂ (13.1–

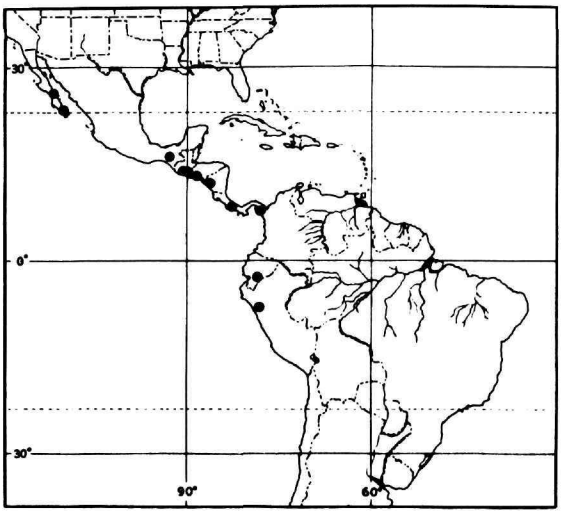

FIGURE 38.—Distribution of *Atya margaritacea* (for locality records in Costa Rica and Panama, see Figure 39).

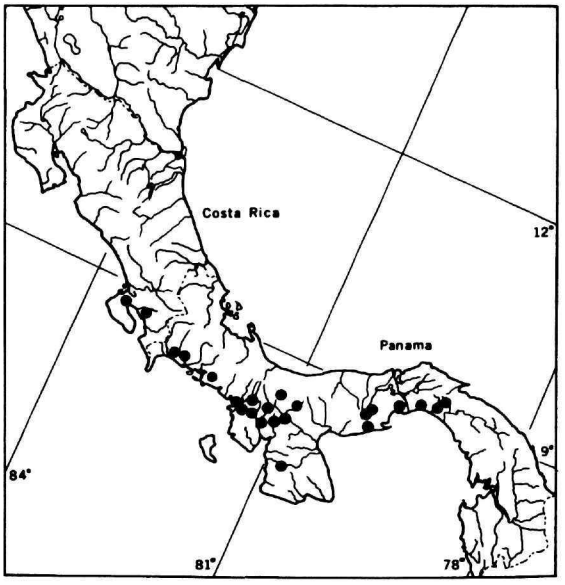

FIGURE 39.—Distribution of *Atya margaritacea* in Costa Rica and Panama.

22.5), 10♀ (9.1–16.8), Champion. (2) †USNM, Río La Paz at San Diego on Carretera Interamericana, 20+ km W of Jutiapa, 4♂ (14.6–30.8), 13 Mar 1946, R.R. Miller and Holloway.

EL SALVADOR: †USNM, Santo Tomás in flooded river, 7♂ (11.8–15.0), 1♀ (8.4), 13 Mar 1939, Calderón.

NICARAGUA: †MCZ, El Polvón, 4 specimens (syntypes of *Atya rivalis*, in very poor condition), 1871, J.A. McNiel.

COSTA RICA: (1) †USNM, Río Riryto, 13.6 km from Rincón de Osa, 4♂ (10.6–17.5), 3♀ (11.4–17.3), 1 ovig ♀ (10.1), 15 Sep 1966, S.B. Peck. (2) †USNM, Río de los Platanales, Golfo Dulce, 1 ovig ♀ (9.5), Apr 1896, H. Pittier.

PANAMA: *Provincia de Chiriquí*—(1) †USNM, rivers flowing from Mt. Chiriquí, alt 426 m, 8°27'N, 82°24'W, 17♂ (20.3–30.6), 1♀ (20.6), 1 ovig ♀ (20.8), Jul 1883.(2) †USNM, 17 km W of Río David at Carretera Interamericana, 2♂ (16.6, 23.0), 1♀ (24.4), 15 Apr 1962. (3) †USNM, Río Tinta, 4.8 km W of Río Tabasará on Soná-Remedios Rd (Tabasará Basin), 1 ovig ♀ (9.1), 11 Nov 1961, H. Loftin. (4) †USNM, upper trib of Río Jacaque, 8♂ (10.2–23.4), 1♀ (11.6), HL and Dean. (5)?Mt. Sapo, Piñas Bay (Coventry, 1944:534), 1 specimen, 21 May 1941, Fifth George Vanderbilt Expedition. *Provincia de Coclé*—(6) †MCZ, Río Las Lajas, 3♂ (7.3–8.1), 3♀ (11.1–12.6), 3 ovig ♀ (11.6–13.1), 22 Oct 1939, G.B. Fairchild. (7) †LGA, Río Cocoli (Coclé?) at K-6 crossing, 2♂ (14.0, 21.6), 3♀ (9.1–12.8), 26 Feb 1973, L.G. Abele, M.H. Robinson. (8) †LGA, El Vallé, Masso Charro?, 1♂ (13.3), 14 Apr 1973, LGA, L.R. Abele; 1♂ (22.5), 1♀ (19.9), 18 Apr 1973, LGA, LRA. (9) †LGA, El Vallé in fast riffles, 1 ovig ♀ (14.0), May 1978, LGA, B.E. Felgenhauer, L. Deaton. *Provincia de Panamá*—(10) †LGA, 12 km N of El Llano on Cartí Rd, 6♂ (10.2–21.8), 2♀ (10.2, 12.7), 10 Mar 1973, McPhail, R.L. Dressler. (11) †USNM, creek 1.7 km E of El Llano (Bravana Basin), 1♀ (16.0), 17 Mar 1962, HL. (12) †LGA, Río Mamoni (Bayano Basin), 2♂ (25.6, 26.1), 2♀ (10.2, 14.7), 16 Apr 1973, LGA, RLD; 1♂ (29.0), 16 May 1973, LGA, RLD; 2♂ (11.8, 13.1), Apr 1974, J. Gee, D. Kramer; 1♂ (20.0), 1♀ (13.3), 3 Aug 1974, LGA, K.L. Heck. (13) †LGA, first stream on Cartí Rd, km 11, 2♂ (15.3, 18.3), 15 Jan 1975, DK. (14) †LGA, second stream on rd to Chepo, 3♂ (7.0–31.2), 1♀ (approx 8.5), May 1978, LGA, BEF, LD. *Provincia de Los Santos*—(15) †USNM, Río Tonosi, halfway between Llano de Piedra and Tonos Plain, 1♂ (16.0), 1♀ (14.4), Mar 1963, HL. *Provincia de Veraguas*—(16) †USNM, creek 13.6 km W of El María on Soná-Remedios Rd (Tabasará Basin), 6♂ (7.6–21.4), 4♀ (about 10.0–15.2), 2 ovig ♀ (9.3, 11.4), 11 Nov 1961, HL. (17) †USNM, Río Calixto, 11.9 km W of El María on Soná-Remedios Rd (Tabasará Basin), 1♂ (10.7), 11 Nov 1961, HL. (18) †USNM, creek just before entering Santa Fe (Santa María Basin), 5♂ (17.4–28.0), 1♀ (12.5), 9 Feb 1962, HL. (19) †LGA, Río San Pablo, 3♂ (20.4–23.2), 2♀ (12.1, 13.9), 30 Mar 1973, LGA, P. Campanella, J.B. Graham. (20) †USNM, 8.5 km E of Soná on San Remedios Rd (San Pablo Basin), 2♂ (13.4, 15.8), 1♀ (14.0), 28 Jan 1962. (21) †USNM, Río San Martín Grande, 6.8 km S of Santiago on Montigo Rd, 3♂ (13.3–25.6), 14 Jan 1962, HL. (22) †USNM, Río Curvibora, 3.4 km E of Santiago on Carretera Interamericana (San Pedro Basin), 2♂ (16.8, other injured), 21 Oct 1961, HL. (23) †LGA, Río Las Guías at Rd from Calobre, 2♂ (8.2, 28.9), 4♀ (15.3–17.7), 21 Feb 1973, LGA, MHR. (24) †LGA, Río Vigui [= Río Tabasará], 1♂ (26.9), 29 Mar 1973, LGA, PC, JBG.

ECUADOR: (1)†RNHL, Chula, 3♂ (14.5–17.7), 2♀ (11.1, 14.6), 3 ovig ♀ (11.2, 14.1, 19.1), Sep 1956, W. Forster. (2) †BM, Río Sapayo, NW Ecuador, 3♂ (23.9–24.7).

PERU: (1) †RNHL, Río Tumbes, 1♂ (24.3), Mario Peña. (2) †RNHL, "don Museo Historia Natural de Lima, Peru," 1♂ (28.6). (3) †USNM, Río Chicama, near Trujillo, 1♂ (27.4), Jul 1970, F. Ancieta. (4) *USNM, purchased at market in Salaverry, 1♂ (26.7), 24 Oct 1926. (5) Río Jequetepeque, near Pacasmayo (Solar, 1972:8). (6) Río Chicama, near Pacasmayo (Solar, 1972:8). In addition to the rivers listed here, Méndez (1981:70) also reported its occurrence in ríos Chira, Supe, and Huaura, but no specific localities were cited.

There is every reason to believe that the follow-

ing locality data are erroneous:

ARGENTINA: *BM, Buenos Aires, 1♂ (38.0), 1♀ (13.4), March 1892, H. Pittier. (Perhaps pertinent is the fact that H. Pittier collected in Oaxaca, Mexico; see locality 6 under "Mexico," above.)

NEW CALEDONIA: *MHNP, syntypes of *Atya margaritacea*, 2♂ (24.5, 30.6), 1♀ (16.6).

AUSTRALIA: *MHNP, Victoria, 1♂ (21.8), von Müller.

VARIATIONS.—The carapace of freshly molted individuals is studded with a dense pile of short, comparatively stiff setae, but frequently specimens are encountered in which the pile is so abraded as to be hardly noticeable. Among other variations are features of the rostrum, the margins of which may be very weakly or strongly concave, and whereas always angular at the base of the acumen are sometimes produced with acute or rounded apices. The apex of the acumen always lies at or near the articulation of the basal and penultimate podomeres of the antennule, and the high to moderately low concave dorsal carina almost or quite reaches the apex; the ventral carina may lack or possess a small preapical tooth. The posteroventral angle of the pleuron of the third abdominal segment may be angular or rounded, and the number of denticles on the ventral margin of the third, fourth, and fifth pleura are quite variable, at least in part due to loss of one or more of them. The number of spines in each of the curved rows on the dorsal side of the telson varies from five to seven, and the posteromedian tubercle, always premarginal, may or may not overreach the caudal margin. The preanal spine appears usually to be proportionately longer in smaller individuals; with respect to the dorsal base of the carina, becoming shorter with increase in size of the animal. The basal podomere of the antennule may bear one, two, or no corneous spinules among the plumose setae on the dorsal surface, and the number of spinules in the transverse distal row varies from six to 10; even more variable is the number of spinules on the dorsodistal margin of the penultimate podomere; frequently gaps occur in both rows suggesting a loss due perhaps to injury. The same is true of the two distal rows of spinules on the ultimate podomere of the peduncle. Variations in the arrangement of tubercles on the flexor surface of the propodus and dactyl of the third pereiopod are illustrated in Figures 37*f,h,i,k*, 40*b*, 41. The merus of the fourth and fifth pereiopods of most small individuals bears two or three movable ventral spines and a subterminal ventrolateral one, and there is a large one present on or near the distal ventrolateral extremity of the carpus; any one or all may be lacking in larger representatives of the species.

None of the variations noted have been discovered to be helpful in recognizing the geographical source of a specimen. Virtually all of the limits of variations noted are exhibited by a series of specimens from a single Panamanian locality.

ECOLOGICAL NOTES.—Ecological observations pertaining to this shrimp are indeed few. Smith (1871) noted that his specimens of *Atya rivalis* were collected in freshwater streams, and Abele and Blum (1977) stated that it is found only in riffle areas of fast-flowing, clear streams. In their study of the freshwater decapods in the Archipiélago de las Perlas, the latter found that *A. rivalis* seemed to be limited to the larger islands where such a habitat exists throughout the year.

Of the specimens examined by us, all of them that are accompanied by data other than that citing the locality include a reference to a creek, river, or stream. The greatest altitude at which specimens are known to have been obtained was in Panama where they were found at 426 m above sea level.

We have discovered no comb-bearing scrapers among the terminal clusters of setae on the fingers of the first and second pereiopods of this shrimp, and the terminal brush on the "bristles," like those of *A. scabra*, are comparatively inconspicuous as compared with those of *A. innocous*. As pointed out in the introductory section of this study, Fryer (1977:93) associated these features with the feeding behavior of the shrimp, correlating (p. 73) such bristles as those possessed by *A. margaritacea* with predominance of filtering over scraping.

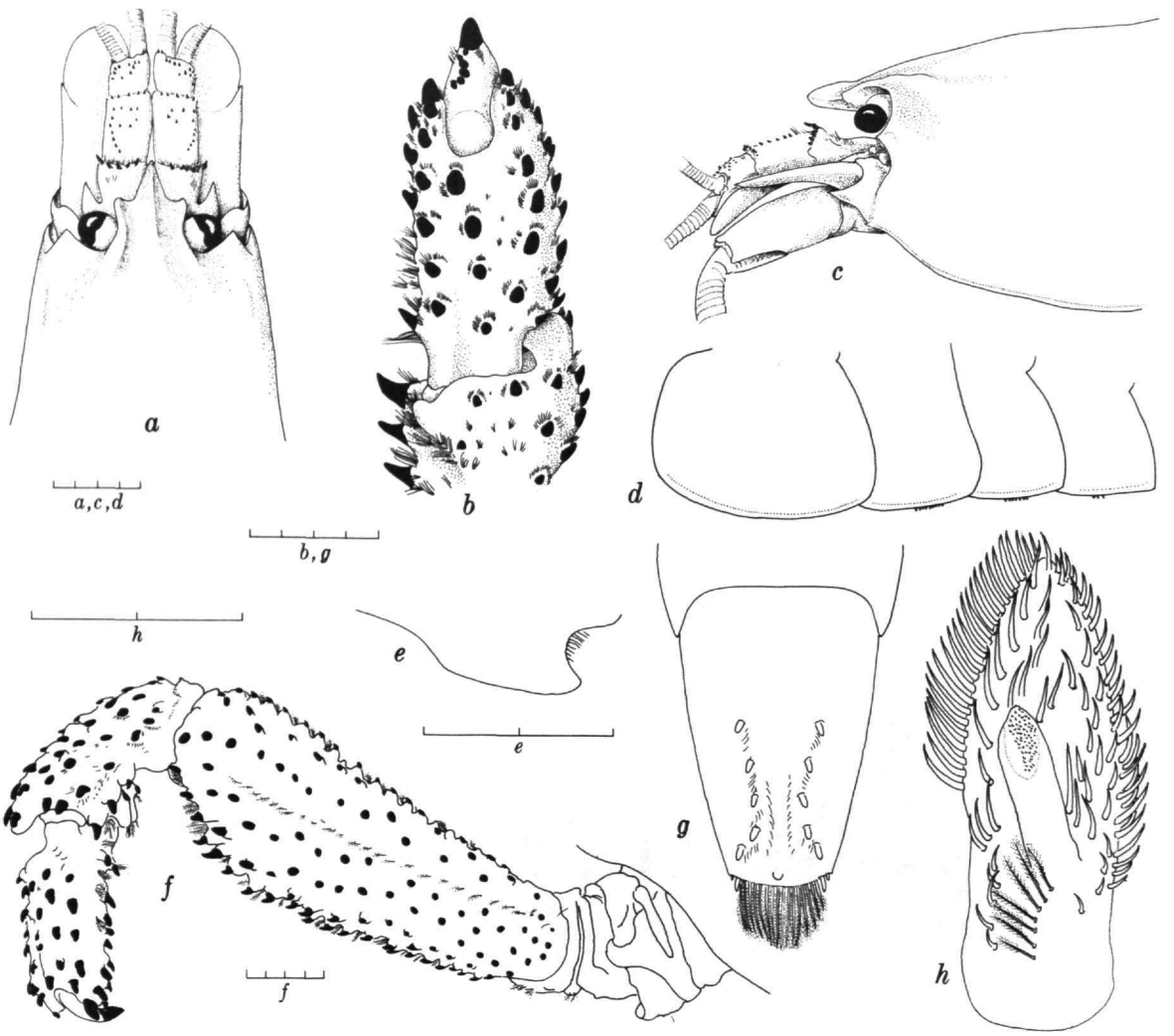

FIGURE 40.—*Atya margaritacea* (all from male from Mt. Chiriquí, Panama): *a*, dorsal view of cephalic region; *b*, flexor surface of distal part of third pereiopod; *c*, lateral view of cephalic region; *d*, lateral view of second through fifth pleura; *e*, lateral view of preanal carina; *f*, lateral view of third pereiopod; *g*, dorsal view of telson; *h*, mesial view of appendices masculina and interna. (Scales marked in 1 mm increments.)

LIFE HISTORY NOTES.—Even less is known of the life history of this shrimp than about the habitats in which it lives. Ovigerous females have been collected in April, May, July, September, October, and November. The numbers of eggs carried by three females were as follows: carapace length 9.3 mm, 1770 eggs; 9.5 mm, 1798 eggs; 11.4 mm, 3010 eggs. Such a high biotic potential suggests that like *Micratya poeyi* and *Atya innocous*, studied by Hunte (1979a,b), which require an increased salinity in their early larval stage, the hatchlings of members of this species probably travel downstream for at least a temporary sojourn in an estuarine, if not marine, habitat. The

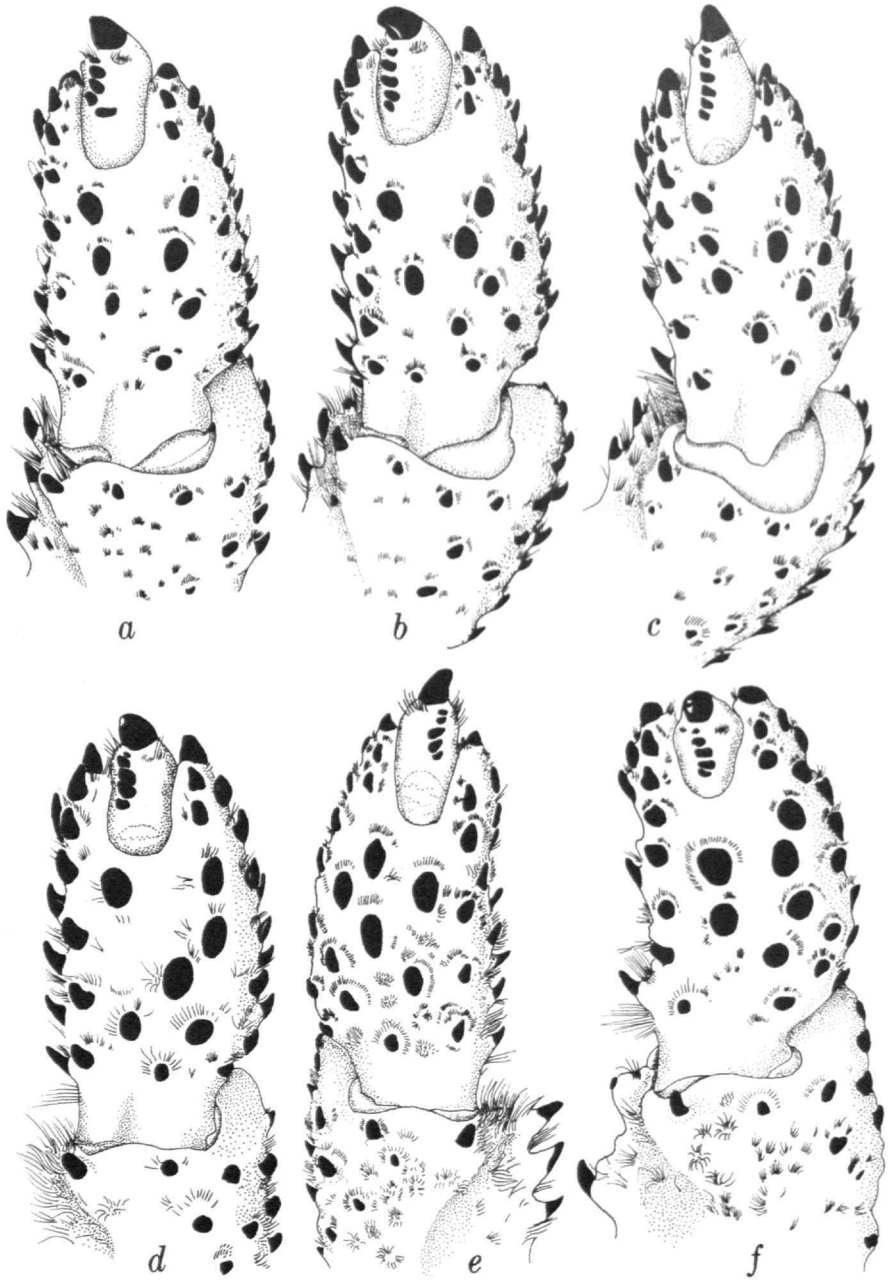

FIGURE 41.—*Atya margaritacea*, variations in flexor surface of distal part of third pereiopod (numbers in parentheses = carapace length in mm): *a*, Río Machiro, San Mateo, Mexico (♂, 28.5); *b*, San Ramón, Mexico (♀, 33.5); *c*, Pentalion, Guatemala (♂, 22.7); *d*, Río Riryto, Costa Rica (♂, 17.5); *e*, Río San Martín Grande, Panama (♂, 25.6); *f*, Río Chicamo, Peru (♂, 27.4).

dimensions of the eggs carried by the syntypic female of *A. margaritacea* were reported by Bouvier (1925:315) to be 0.51 by 0.31 mm, measurements that are in keeping with those noted among the ovigerous females examined by us.

REMARKS.—Because of the confusion surrounding the identity and range of this shrimp, we are illustrating both a syntypic male of Milne-Edwards' species and a male specimen from the Pacific watershed of Guatemala. The syntypes of *Atya rivalis* are in such poor condition, and we have no specimens from Nicaragua, that this specimen from Guatemala has been chosen to represent Smith's species. Inasmuch as the syntypes of *A. margaritacea* appear to us to be indistinguishable from the syntypes of *A. rivalis* as well as from other specimens collected on the Pacific versant from Baja California to Peru and are obviously different from specimens of *Atya scabra* from throughout its range, we are convinced that the name *Atya rivalis* should be removed from the synonomy of *A. scabra* and treated as a junior subjective synonym of Milne-Edwards' *Atya margaritacea*.

In our opinion, *A. margaritacea* is more closely related to *A. scabra* than to any other member of the genus. It may be distinguished from the latter by several features, among the most conspicuous of which are (1) the arrangement of the tubercles on the flexor surface of the propodus of the third pereiopod; in the former the tubercles are scattered over the entire surface, and if a few tend to lie in a linear series they are never contiguous or overlapping (cf. Figures 41, 53), (2) the distomesial extremity of the merus of the third pereiopod is produced in a prominent rounded lobe in *A. margaritacea*, one that is far more conspicuous than the comparatively small corresponding bulge in *A. scabra*, and (3) spinules are never present on the ventral margin of the second abdominal pleuron in *A. margaritacea* but in the Western Hemisphere are rarely absent in *A. scabra*.

Atya ortmannioides Villalobos

FIGURES 1*b*, 9, 10, 12*c*, 42–44

Atya ortmannioides Villalobos, 1956:459–475, pls. 1–6 [type-locality: Río de las Truchas, La Mira, 52.5 km SSE of Arteaga, Michoacán, Mexico; types: IBM 21153, holotype (♀), allotype (♂); paratypes, USNM 99527 (1♂, 1♀); Instituto Politécnico Nacional (2 specimens)].

The above citation is the only reference that we have encountered to this shrimp; it consists of a description and illustrations that were based upon four males and five females from the type-locality. Villalobos did not account for three of the specimens listed in his measurements but which were not included among the types (see pp. 472, 474).

PUBLISHED ILLUSTRATIONS.—The excellent illustrations provided with the original description depict a lateral view of the entire female, a lateral view of the carapace, dorsal view of the cephalic region and of the telson and uropods, drawings of the gnathal and ambulatory appendages, the first and second pleopods of the male, and mesial views of the appendix interna and appendix masculina. Setae from the scaphognathite, second maxilla, and first and second pereiopods, including those with biserial arrangement of denticles, are also presented.

DIAGNOSIS.—Cephalic region of carapace not conspicuously sculptured, with anteriorly converging flat (not convex), glabrous lateral surfaces; antennal and pterygostomian spines prominent. Rostrum projecting anteriorly, not arched or directed ventrally, with margins suddenly contracted at base of acumen forming angular to subangular bends; angles never produced anteriorly; acumen longer than remainder of rostrum. Ventral margin of third through fifth abdominal pleura lacking rows of sclerotized denticles; caudoventral angle of fourth and fifth pleura weakly obtuse to acute but not produced. Sternum of sixth abdominal segment distinctly more than half as long as wide; compressed median tubercle on sternum of fifth abdominal segment small and comparatively inconspicuous. Preanal carina with compressed spine reaching to or beyond caudal extremity of basal part of sclerite. Telson slightly more or less than twice as long as wide with 6 to 8 denticles in each of 2 dorsal rows. Antennular peduncle with dorsal surface of proximal article devoid of sclerotized denticles proximal to distal row; penultimate article 1.5 to 1.8

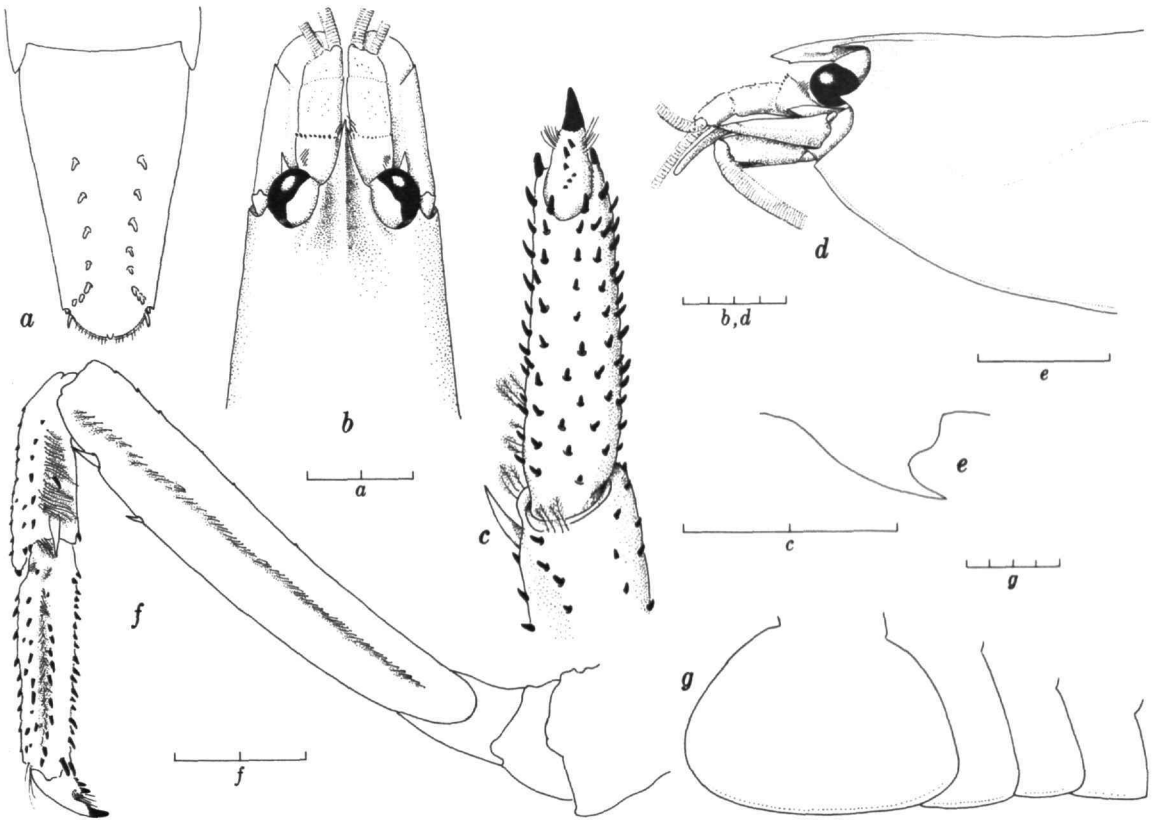

FIGURE 42.—*Atya ortmannioides* (all from paratypic female): *a*, dorsal view of telson; *b*, dorsal view of cephalic region; *c*, flexor surface of distal podomeres of third pereiopod; *d*, lateral view of cephalic region; *e*, preanal carina; *f*, lateral view of third pereiopod; *g*, lateral view of second through fifth pleura. (Scales marked in 1 mm increments.)

times as long as wide, and dorsal surface with about 15 scattered spinules. Coxae of third and fourth pereiopods lacking prominent anterolateral spines. Third pereiopod with merus rounded ventrally, approximately 5.5 to 6.5 times as long as high, entire podomere bowed, never parallel to merus of other member of pair, and lateral surface bearing weakly sclerotized (none cornified) tubercles, some of which sublinearly arranged; propodus about 3 times as long as wide, its extensor surface studded with acute to subacute cornified denticles, and flexor surface with similar denticles, some linearly arranged but those in rows neither contiguous nor overlapping; flanking setae not conspicuous; dactyl freely movable and bearing 2 irregular rows of sclerotized denticles.

MALE (Río Murga, Estado de Guerrero, Mexico).—Rostrum with margins strongly contracted at base of acumen forming angle of slightly more than 90 degrees; acumen about 1.5 times as long as basal part of rostrum and reaching distal end of proximal third of penultimate podomere of antennule; dorsal median carina gently curved, not excavate dorsally (not dipping below level of lateral carinae posterior to acumen), and reaching base of corneous tip of acumen; ventral carina with single small preapical tooth; ocellar beak largely hidden by eyes, falling short of midlength of stylocerite, its cephalic margin vertical, and dorsal one subtruncate, abutting shallow ventral rostral groove. Antennal spine strong, pterygostomian spine less conspicuous. Surface of cara-

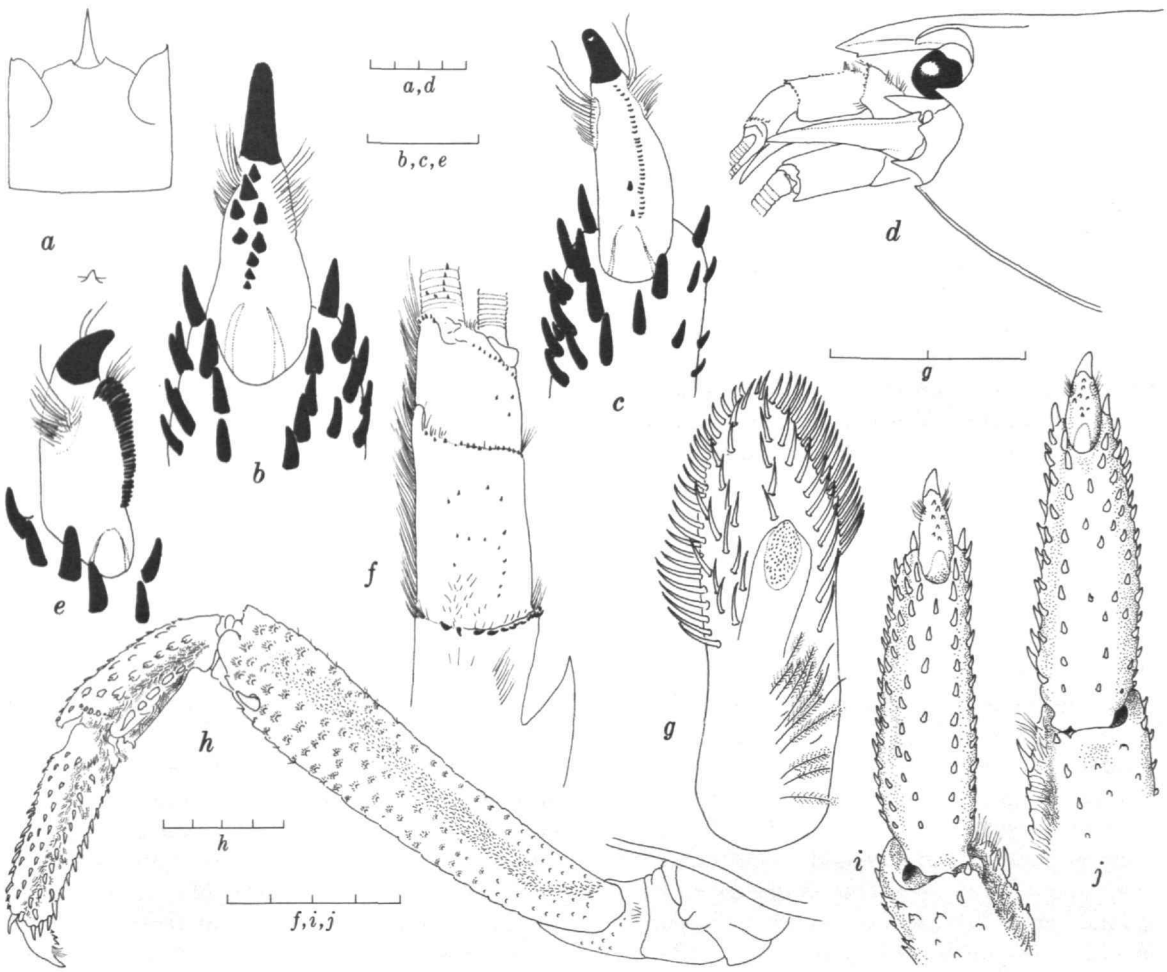

FIGURE 43.—*Atya ortmannioides* (all from male from Río Murga, Estado de Guerrero, Mexico): *a*, preanal carina, sternum of sixth abdominal segment, and median tubercle of fifth; *b,c*, flexor surface of distal part of fourth and fifth pereiopods, respectively; *d*, lateral view of cephalic region; *e*, preaxial view of distal part of fifth pereiopod; *f*, dorsal view of antennular peduncle; *g*, mesial view of appendices masculina and interna; *h*, lateral view of third pereiopod; *i,j*, flexor surface of distal part of right and left third pereiopods. (Scales marked in 1 mm increments.)

pace glabrous, densely but finely punctate, punctations bearing very short fine setae except just dorsal to ventral marginal sulcus where setae long; ridges and spines other than those just mentioned lacking.

Pleura of first 4 abdominal segments with rounded to subacute posteroventral extremities, corresponding part of fifth forming almost right angle, not produced. Third through fifth pleura lacking denticles on ventral margin and fifth with moderately conspicuous fringe of plumose setae. Fourth abdominal tergum 1.2 times as long as fifth, latter subequal in length to sixth and almost 0.9 as long as telson. Sternum of fifth abdominal segment with small compressed median tubercle (Figure 43*a*); that of sixth 1.2 times as broad as long. Free part of preanal carina spiniform, curved, and only slightly overreaching angle of

basal part of sclerite. Telson about twice as long as broad, its dorsal surface bearing paired concave rows of 6 corneous denticles and posteromedian tubercle, latter overreaching caudal margin of telson.

Proximal podomere of antennule (Figure 43*f*) with stylocerite reaching about distal fifth of segment; dorsal surface with linear cluster of setae but lacking corneous denticles; distal margin bearing row of 13 (right) or 12 (left) corneous denticles; penultimate podomere about 1.5 times as long as wide and provided with 15 (right) or 16 (left) corneous denticles on dorsal surface and row of 18 on distal margin; ultimate podomere with 3 (right) or 2 (left, one of which broken) denticles on dorsal surface and row of 11 (right) or 9 (left) at base of lateral flagellum and 4 at base of mesial flagellum. Antenna with ventrolateral spine on basis reaching much farther anteriorly than pterygostomian spine but not quite so far as stylocerite; lateral spine on scaphocerite almost reaching lateral extremity of antennular peduncle; lamella far surpassing latter; flagella broken but in accompanying female reaching third abdominal tergum.

Third maxilliped only slightly overreaching antennular peduncle; tip of exopod attaining base of distal podomere of endopod; penultimate segment about 1.1 times as long as ultimate.

First pereiopod reaching base of distal third of penultimate podomere of antennular peduncle, second almost attaining end of same podomere. Terminal brush of both fingers with some bristles bearing scraping denticles. Third pereiopod (Figure 43*h–j*) with lateral distoventral spine on merus and carpus, ventral spine lacking on both podomeres; when appendage extended anteriorly overreaching antennular peduncle by dactyl and slightly more than half length of propodus. Merus with ventromesial margin bowed, about 5.4 times as long as high, 2.3 times as long as carpus, and 2.2 times as long as propodus. Latter 3.1 (right) or 3.3 (left) times as long as wide and 0.9 as long as carpus; distoventral margin of coxa entire, mesial caudoventral prominence and distal ventrolateral spine lacking. Lateral, dorsal, and ventral surfaces of merus studded with sublinear series of prominent but noncornified tubercles flanked by arcs of plumose setae; moderately conspicuous longitudinal band of short setae present laterally; mesial extremity of podomere produced in small rounded lobe at level of mesial articular condyle of carpus. Latter bearing strong tubercles capped with corneous discs, tubercles flanked distally by arcs of plumose setae, setae on ventrolateral surface somewhat longer but not forming conspicuous tufts. Propodus also strongly tuberculate, tubercles capped with corneous spines; some tubercles on flexor surface forming mesial and lateral series and with more irregularly dispersed ones between, those in rows neither contiguous nor overlapping; lateral and ventrolateral surfaces with tufts of plumose setae. Dactyl movable, its flexor surface with denticles forming 2 irregular oblique rows flanked by paired setal clusters.

Fourth pereiopod with dactyl reaching end of proximal fourth of propodus of third pereiopod; merus about twice as long as carpus and latter only slightly shorter than propodus. Fifth pereiopod reaching distal end of proximal fourth of propodus of fourth pereiopod, merus 1.4 times as long as carpus and latter 0.65 length of propodus. Ornamentation of merus, carpus, and propodus of fourth pereiopod consisting of distal ventrolateral spine and 1 more proximal ventral spine on merus, and distal ventrolateral and 2 smaller distolateral spines on carpus; lateral surface of distal part of merus and of carpus and propodus with longitudinal narrow band of plumose setae. Ornamentation of corresponding podomeres of fifth pereiopod similar but with 3 distolateral spines on carpus instead of 2 and lacking setal band on distal part of merus.

Diaresis of lateral ramus of uropod flanked proximally by row of 20 (right) or 19 (left) articulated, corneous denticles, and fixed spine present at lateral end of row.

Color Notes.—No observations on the color of this shrimp have been reported.

Size.—Among the measurements recorded by Villalobos (1956:472) of four males and five fe-

males were the total length and carapace length (the latter was apparently made from the tip of the rostrum to the posterior margin of the carapace). His largest specimen was a female having a carapace length of 21.0 mm and a total length of 59.0 mm. Corresponding measurements of the largest male were 11.5 and 32.7 mm. Among the specimens measured by us, the largest was a male having a carapace length (measured from the orbit to the posterior margin of the carapace) of 24.6 mm, and that of the largest female was the holotype with a carapace length of 15.9 mm. No ovigerous females have been reported.

DISTRIBUTION AND SPECIMENS EXAMINED.—This shrimp has been found in four localities between Estado de Guerrero, to La Paz, Baja California.

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. One lot lacks the date it was collected; this could not be determined.

MEXICO: *Estado de Baja California Sur*—(1) †USNM, La Paz, 2♂ (9.9–10.0), Jun 1882, L. Belding. *Estado de Guerrero*—(2) †USNM, Acapulco, 1♀ (14.2), 22 Jan 1895, Nelson and Goldman. (3) †IBM, Río Murga, 16 km de la carretera Petatlán-Zihuatanejo, 3♂ (9.7–24.6), 1♀ (15.0). G. Malagrino J. *Estado de Michoacán*—(4) *IBM, Río de las Truchas, La Mira (Villalobos, 1956:474), holotypic ♀ (15.9), paratypic ♂ (8.8); *USNM, paratypic ♀ (12.9), paratypic ♂ (7.7), 11 Feb 1953, B.F. Osorio-Tafall, R. Ramírez, T. Gutiérrez.

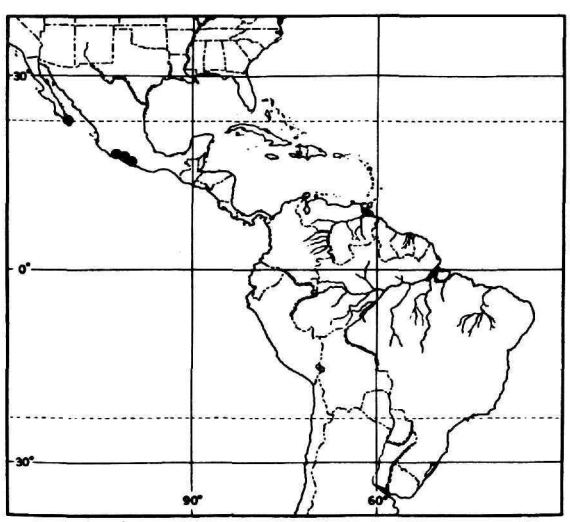

FIGURE 44.—Distribution of *Atya ortmannioides*.

VARIATIONS.—The variations noted in the specimens of this shrimp just listed are hardly noteworthy. In all of them, the rostrum reaches to at least the base of the penultimate podomere of the antennule, and the acumen, although poorly delimited (the angles rather strongly obtuse) basally in the smaller specimens, is clearly longer than the basal part. The spine on the ventral carina may or may not be present. As might be expected, fewer denticles are present on the antennular peduncle of the small individuals than on those of the comparatively large male described. As has been observed in other species, the number of spines on the ventral surface of the merus of the ambulatory appendages, especially that of the fourth and fifth pereiopods, in small specimens is greater than in larger individuals; in *A. ortmannioides* the small individuals have three, whereas the male that is described has only one.

We are unable to discover a single feature in the two specimens from Baja California Sur that serves to distinguish them from the specimens from the more southern localities in Guerrero and Michoacán.

ECOLOGICAL NOTES.—Except that two of the lots examined by us bore labels noting that the specimens had been collected in rivers, there are no ecological data available other than those recorded by Villalobos (1956:474). The following is a free translation of the information quoted from the collectors by Villalobos: The exact place where the shrimp were collected lies at the foot of Las Truchas hill, which seems to be the site of the most important iron-ore deposit in Mexico. The river before entering onto the alluvial plain courses through a series of canyons carved through granite, forming rapids, small cataracts, and extensive potholes. At the edge on which the

slope begins, in the rapids and cataracts, plants are firmly rooted among the rocks, and their leaves are constantly drenched by the flowing water. The crustacean (shrimp) clings firmly to the leaves of these plants. In order to dislodge it, it is necessary to shake the leaves over a ring net or, exerting pressure, to run the net over the mats of such plants several times. In this section of Las Truchas River, the so-called trout, which are freshwater mugilids belonging to *Agonostoma monticola*, were also collected. Moreover several large specimens of *Macrobrachium* were obtained.

Whereas there are records of other *Atya* occurring among aquatic vegetation, this is the only account of their clinging to leaves of plants. Whether or not a search for specimens among the rocks was undertaken was not stated, thus one cannot be certain that this microhabitat of *Atya ortmannioides* is occupied to the exclusion of others by this shrimp.

Life History Notes.—No ovigerous females have been reported, and nothing is known about aspects of its life cycle.

Remarks.—Villalobos (1956:474) compared *Atya ortmannioides* with *A. scabra* and *A. occidentalis* (= *A. innocous*), stating that it differs from them in (1) lacking any sculpture of the carapace and the proportions of the latter, (2) by the strong development of the abdominal pleural region, (3) by the sharp, long rostrum, (4) by the presence of dentiform bristles among the terminal clusters of the first and second pereiopods, (5) by the pectinate series of spines on the dactyl of the fifth pereiopods, (6) by the absence of spines on the external margin of the endopodite of the first pleopod of the male, and (7) by the form of the appendices masculina and interna of the second pleopod of the male.

Of these features, except for certain proportions, the first is not unique, and many specimens of *A. innocous* lack any visible sculpture other than punctations that are also present in *A. ortmannioides*; the pleural region seems to be no more strongly developed than are those of some *A. innocous*, particularly those of members of the species occurring on the Pacific versant of Middle America, the form that was designated *A. tenella* by Smith. As shown by Fryer (1977), *A. innocous* also exhibits dentiform bristles among the terminal setal clusters of the first and second pereiopods. The males available to Villalobos were rather small (carapace lengths, 7.7 and 8.8 mm, tip of rostrum to posterior margin of carapace) and perhaps juvenile; if so, it is not surprising that the spines on the margin of the endopod of the first pleopod were not evident. The spines are present on the largest male examined by us.

The most distinctive features of this shrimp occur in the rostrum and in the dactyl of the fifth pereiopod. The rostrum extends almost horizontally instead of being arched or directed anteroventrally, and the acumen is longer than the basal part. The consistent pectinate arrangement of the denticles on the flexor surface of the dactyl of the fifth pereiopod seems to be unique among the American members of the genus, but such an arrangement has been observed on a few individuals of *A. innocous* and on several specimens of other species. Slightly less conspicuous are the anteriorly converging, rather than arched, lateral surfaces of the cephalic region of the carapace of *A. ortmannioides*. As for the apparently unique features of the appendix masculina, there are too few males available to be confident that such features are unique.

Atya scabra (Leach)

Figures 1*k,l*, 8–10, 11*b,c*, 45–53

Guaricuru.—Marcgrave, 1648:187, unnumbered fig.; 1942:187, unnumbered fig.—Jonstonus, 1650:35, 36, pl. ix: fig. 16; 1657:27, 28, pl. ix: fig. 16; 1665:27, 28, pl. ix: fig. 16; 1767:35, 36, pl. ix: fig. 16.—Piso, 1658:78.—Jonston, 1660, pl. ix: fig. 16.—Ruysch, 1718:27, 28, pl. ix: fig. 16.—Sawaya, 1942:lxiii.—Lemos de Castro, 1962:41, pl. 4: fig. 26.

Poti.—Piso, 1658:78, fig; 1957:188, fig.

Gaurikuru.—Jonston, 1660:27.

Guarikuru.—Jonston, 1660:27.

Atys scaber Leach, 1815:345 [type-locality: unknown ("Habitat _____"; Leach, 1815:345); restricted to "the area of Veracruz, Mexico" (Holthuis, 1966:234); fixed by the present neotype selection to Misantla, Estado de Veracruz, Mexico, 19°56′N, 96°50′W; types: not known to exist,

neotype designated herein].—Holthuis, 1955a:208, 221; 1955b:26; 1957:167, 180.—Hemming, 1957:133, 150, 167, 180.

Atya scabra.—Leach, 1816, pl. 21; 1817:29, 30, pl. 131; 1824:421, pl. 21.—H. Milne Edwards, 1816:138, 139, pl. 51: fig. 4; 1837:348, pl. 24: figs. 15–19; 1838:352; 1839:386; 1840, pl. 51: fig. 4–4ᵉ; 1842:138.—Latreille, 1817:37.—Desmarest, 1823:313, pl. 37: fig. 2; 1825:217, pl. 37: fig. 2.—Guilding, 1825:338.—Guérin-Méneville, 1825:329; 1837, vol. 2, pl. 20: fig. 2; 1844, vol. 3, p. 15; 1856–1857a:xlvi, xlvii, pl. 2: fig. 7c; 1856–1857b:xviii, pl. 2: fig. 7c.—P. Roux, 1831:27.—Lucas, 1833–1834:333; 1840:182, pl. 11: fig. 1; 1842:182, pl. 11: fig. 1; 1851:182, pl. 11: fig. 1.—Griffith and Pidgeon, 1833:190.—Broderip, 1835:71, fig.—Griffith, 1835:223, lxiii.—Wiegmann, 1836:146, 147.—White, 1847:74.—Newport, 1847:158, 159.—Stimpson, 1857:498.—A. Milne-Edwards, 1864: 146, 147.—Costa, 1864:89.—Capello, 1867, explanation of pl. 1: fig. 1f.—Giebel, 1875:53, 54.—Brocchi, 1875:32, figs. 33, 34.—Vilanova y Piera, 1875:385.—Kingsley, 1878a:92; 1878b:56, 57.—Greeff, 1882:35–37; 1884: 54.—Albert, 1883a:469–471, 534, pl. 29: figs. 4–6; 1883b:27–29.—Mocquard, 1883:190–199, 307, pl. 8: figs. 183–191.—Claus, 1885:57, 107, pl. 4: fig. 35.—Gundlach, 1887:131.—Osorio, 1887:222, 230; 1888:188; 1889:129, 137, 139; 1891a:47; 1891b:140; 1892:200; 1895a:249; 1895b:251; 1898:186, 187, 194; 1905:102; 1906:150.—Bate, 1888:693, 694, 698.—Pocock, 1889:16.—Ortmann, 1890:466; 1895:408–410, 415, 416 [in part]; 1897:183–185 [in part].—Sharp, 1893:111.—Stebbing, 1893:240.—Nobili, 1897:5.—Rathbun, 1897:44; 1900:313–314 [in part]; 1901:119 [in part].—Doflein, 1900:127.—Young, 1900: 473.—Thompson, 1901:22.—Bouvier and Lesne, 1901:13 (or 332).—Gerstaecker and Ortmann, 1881–1901, pl. 91: figs. 5, 6, 6a; pl. 115; figs. 8–11.—Bouvier, 1904:138 [in part]; 1905:110, 112, 119–123, 128 [in part], fig. 25s; 1906:492; 1909:333; 1925:22, 27, 29, 293, 312–319, 322, 323, 356, 358 [in part], figs. 55–67.—Johnston, 1906: 862.—Balss, 1914:97, 98; 1925:239.—Tesch, 1914: 247, 250.—Pearse, 1915:551.—Torralbas, 1917, fig. 60.—De Man, 1925:27–28 [in part], fig. 4a–c.—J. Roux, 1926a:238, 253; 1926b:217, 218.—Allee and Torvik, 1927:67.—Monod, 1928:121, 205; 1933:461, 462 [in part]; 1967:110, 119, 135, pl. ix: figs. 11, 12, 15–17 [not figs. 13, 14 as noted in explanation of plate]; 1980:375, 376, figs. 5, 6.—Schmitt, 1935:135, 136 [in part].—Villalobos, 1943:1–67, pls. 1–22; 1956:474; 1959:328, 329.—Oliveira, 1945:177–189 [in part], pl. 1: figs. 1–4; pl. 2.—Holthuis, 1951:9, 22, 24, 25 [in part]; 1955b:26; 1959:16; 1966:233, 234, 238 [in part]; 1974:231; 1980:70, 181.—Parodiz, 1960:38, 39 [in part], figs. 1–3.—Rioja, Ruiz, and Larios, 1955, fig. 316.—Darnell, 1956:131–138, 3 figs.; 1962: 440.—Hart, 1961b:61–64, 67, 73, fig. 11; 1980:845, 846, 848.—Lemos de Castro, 1962:41, pl. 4: fig. 27.—Davant, 1963:42–44, 98–100, figs. 27, 28 [both figs. on pp. 43 and 49].—Chapa, 1964:34.—Pericchi Lopez, 1965: 25.—Holthuis and Rosa, 1965:9.—Pinchon, 1967:161.—Coelho and Ramos, 1968:3.—Fausto Filho, 1968:28.—Straskraba, 1969:17, 25.—Chace and Hobbs, 1969:5, 15, 19, 33, 36, 57, 61, 63–66 [in part], 73, figs. 9, 10d–f, 14d,e.—Cendrero, 1971:524.—Disney, 1971:84, 85; 1975: 69.—Hobbs, 1971:27.—Chace, 1972:14.—Lemasson, 1973:68.—Bonnelly de Calventi et al., 1973:1338; 1974: 104, 106, 111, 123, fig. 17.—Lêveque, 1974:42, fig. 1j.—Bonnelly de Calventi, 1974b:35, 38, 40, 54, fig. 7.—Alayo, 1974:22, pl. vi: fig. 11.—Scelzo, 1974:12.—Abele, 1975:56, 57.—Hunte, 1975:66; 1978:135, 136, 139, 144, 145, 147, fig. 7; 1979c:70.—Carvacho and Carvacho, 1976: 213, pl. 2: fig. 8.—Villamil and Clements, 1976:5, 59.—Fryer, 1977:57, 58, 62, 63, 72, 73, 90, 93, 94, 98, 125, figs. 3, 45, 49, 50, 52, 74, 79–82.—Burkenroad, 1981: 261.—Rodríguez, 1981:46.

Atya Scabra.—Leach, 1816:421.—A. Milne-Edwards, 1864: 150.—Valdés Ragués, 1909:180.—Hart and Hart, 1974:142.

Atia scabra.—Latreille, 1817:37 [erroneous spelling, combination by implication]; 1837:xvii, Crustacea pl. 31 (bis): fig. 2 [erroneous spelling].

Atie épineuse.—Audouin and H. Milne Edwards, 1829:14, pl. 25: fig. 1.

Atya.—Broderip, 1835:71.—Capello, 1866:6.—Gerstaecker and Ortmann, 1881–1901:886, 887, 1127.—Johnston, 1906:843.—Sawaya, 1942:lxiii.—Darnell, 1962:440.

Astacus (Atya) scabra.—Voigt, 1836:178.

Atya mexicana Wiegmann, 1836:145 [type-locality: Misantla, Estado de Veracruz, Mexico; types: ZBM, 2 specimens].—Newport, 1847:158, 159.—Guérin-Méneville, 1856–1857a: xlvi.—A. Milne-Edwards, 1864:147.—Martens, 1868: 49.—Giebel, 1875:52.—Bate, 1888:693.—Holthuis, 1966: 234.

Athys scabra.—H. Milne Edwards, 1838:352; 1839:386 [erroneous spelling].

"*Atya sulcatipes?*" Newport, 1847:159, pl. 8: fig. 1 [type-locality: São Nicolau, Cape Verde Islands; types: stated to be in the British Museum but could not be located in April 1980].

Atya sulcatipes.—White, 1847:74.—A. Milne-Edwards, 1864:147.—Martens, 1868:49.—Giebel, 1875:52, 55.—Gerstaecker and Ortmann, 1881–1901, pl. 73: fig. 6a–c; pl. 74: figs. 4, 5.—Bate, 1888:693–699, 701–704, pls. 118, 119: fig. 1, 1p, 1q.—Hickson, 1889:222, 223, 362.—Stebbing, 1893:240.—Oliveira, 1945:179, 180, 188.—Holthuis, 1966:232–237, fig. 4; 1980:71, 181.—Rutherford, 1971:87, 88, 90, fig. 2a,b.—Disney, 1975:69.

Atya Mexicana.—Stimpson, 1857:498.

Atya scalva.—Martens, 1872:135 [erroneous spelling].

Atya scaber.—Giebel, 1875:52 [erroneous spelling].

Atya punctata Kingsley, 1878a:91–92 [type-locality: Haiti;

type: ?USNM 84327, ♀]; 1878b:57.—Pocock, 1889:16.—Oliveira, 1945:179.—Holthuis, 1966:237.—Chace and Hobbs, 1969:63.

Atya sculptipes.—Ortmann, 1890:466 [erroneous spelling].

Atya margaritacea var. *claviger* Aurivillius, 1898:14–16, pl. 3: figs. 5–8 [type-locality: "Etome, in Bächen," Cameroon; types: SMNH, 2 specimens].

"*Atya scabra*, type de *margaritacea.*"—Bouvier, 1925, figs. 703, 704 [not 705, 706 as indicated].

Atya sacabra.—Villalobos, 1943:66 [erroneous spelling].

Atya margaritaria clavipes.—Holthuis, 1966:234 [erroneous spelling].

Atyia scabra.—Vélez, 1967:42.—Bonnelly de Calventi, 1974a:16.—Alayo, 1974:25 [erroneous spelling].

Atya innocous.—Chace and Hobbs, 1969:66 [lapsus for *Atya scabra*].

Atya sulzatipes.—Rutherford, 1971:90 [erroneous spelling].

Atya sulcaltipes.—Rutherford, 1971:89 [erroneous spelling].

Atya scubra.—Bonnelly de Calventi, 1974b:54 [erroneous spelling].

REVIEW OF LITERATURE.—The first record of the existence of a member of the genus *Atya* is that of Marcgrave (1648), who recorded it by the vernacular name "Guaricuru" in his "Historia Naturalis Brasiliae," presenting an illustration of an unmistakable member of the genus. Lemos de Castro (1962) pointed out that this figure almost certainly depicts a representative of *Atya scabra.* The description, which is in Latin, was republished by Jonstonus (1665) along with a slightly modified figure.

This shrimp, from an unknown locality, was briefly described by Leach (1815) as *Atys scaber*; the whereabouts of the type, if extant, is also unknown. Apparently Leach discovered that the name "*Atys*" had been employed by De Montfort (1810:343) for a gastropod mollusk, and in 1816 Leach illustrated and referred to his shrimp as *Atya scabra.* The latter designation was adopted the same year by H. Milne Edwards (1816:138), who presented an expanded description and well-executed illustration of a specimen. The only addition of significance offered by Leach (1817) is the hand-colored dorsosinistral view of an entire animal. Latreille (1817) introduced the synonym *Atia* in stating that although Leach's species was unknown to him, it "appears to connect the penaeids and alpheids." He also called attention to Herbst's "canc. innocous." Desmarest (1823 and 1825) added no new information but presented a lateral view of an entire animal in both publications. The earliest locality cited is that by Guilding (1825) who recorded the presence of the species in mountain streams of Saint Vincent "in incredible numbers." Whereas there is no reason to doubt that the species occurs on this island, we suspect that most of the shrimps that Guilding identified as *Atya scabra* were members of the more common *A. innocous.* Guérin-Méneville (1825) presented a brief diagnosis of his "Atye Raboteuse," and in a subsequent work (1829–1844) included a lateral view of a specimen and reported (p. 15) the presence of the species in "les côtes du Mexique." Polydore Roux (1831), Griffith and Pidgeon (1833), Lucas (1833–1834), Broderip (1835), Griffith (1835), and Voigt (1836) added nothing to our knowledge of the species. Wiegmann (1836) described this shrimp, employing the name *Atya mexicana*, from Misantla, Veracruz, Mexico. The following year, H. Milne Edwards (1837) cited previous references, briefly described the species, and under "Habite" listed only "côtes du Mexique." The latter, together with the similar reference by Guérin-Méneville, led several subsequent authors to assume that this shrimp frequents marine habitats. Nothing new related to *A. scabra* appeared in H. Milne Edwards' 1838 and 1839 publications, but in that of 1840 he included a hand-colored lateral view of a specimen along with detailed illustrations of several body parts. Latreille (1837) also presented a hand-colored dorsolateral view of an entire animal. Lucas (1840, 1842, 1851) included additional features in his diagnosis of the species and presented a lateral view of an entire animal; otherwise he added nothing new. Newport (1847), apparently with hesitation, described *Atya sulcatipes* from San Nicolas, Cape Verde Islands, stating that "it may prove to be only a variety" of *Atya scabra.* In the same year, White (1847), in listing the Crustacea in the British Museum, included *A. scabra* from Mexico (from the Leach collection) and another lot from the Cape Verde Islands (from the collection of Newport). Whereas

he listed *A. sulcatipes*, he gave no locality and made no comment concerning the collection. Guérin-Méneville (1856–1857a,b) contrasted this shrimp with his *Atya poeyi* (= *Micratya poeyi*). Stimpson (1857) "ventured to cite Wiegmann's name [*Atya mexicana*] as a synonym" of *A. scabra*. To Wiegmann's locality, he added western Mexico as a new record for the species, and he also expressed the belief that no member of the genus is found in the sea. On what basis the "western Mexico" record is founded is not known; perhaps he had specimens of *A. margaritacea* or *A. ortmannioides* that were misidentified. That *A. mexicana* and *A. scabra* are conspecific was pointed out by A. Milne-Edwards (1864), who also stated that except for the occurrence of *A. sulcatipes* in the Cape Verde Islands, "one would not hesitate to see in it a variety of *A. scabra*; in effect it seems to differ only in the legs which are slightly grooved, by the rostrum which exhibits a more marked depression, and by the antennae which are not more than half the length of the body" (p. 147, translation). In this work he presented a key to all of the species belonging to the genus. Costa (1864) and Capello (1867) provided no new information. Von Martens (1868) added more complete data for the specimens on which Wiegmann described *Atya mexicana*: a small coastal stream flowing into the Gulf of Mexico south of Tecolutla, about 20 km from the sea. Giebel (1875) summarized the composition of the genus *Atya* and in his description of *A. gabonensis* made comparisons with *A. scabra*. In Brocchi's study (1875) of the genital organs of decapod Crustacea, he mentioned and figured the first and another (no statement as to which) pleopod of *A. scabra*. Kingsley (1878a) described *Atya punctata* from Haiti and in the same year (1878b) listed *A. scabra* among the North American caridean shrimps, reporting it from fresh water in western Mexico (perhaps a misidentification of *A. margaritacea*); *A. mexicana* was cited as a synonym. Greeff (1882, 1884) reported the occurrence of *A. scabra* on São Tomé. Mocquard (1883), in an investigation of the stomachs of a number of crustaceans, described and illustrated that of *A. scabra*, and Albert (1883a) also provided an anatomical description of this organ. In an excellently illustrated study of the branchial apparatus of crustaceans, Claus (1885) presented the gill formula of *A. scabra* and a well-executed drawing of the branchiae. The presence of this shrimp in a tributary of Río Añasco and in the San Juan, Puerto Rico, market was noted by Gundlach (1887) who also mentioned its occurrence in Cuba and Mexico. In a series of reports dealing with the fauna of the then Portuguese West Africa (1887–1906), Osorio listed *A. scabra* from a number of localities in Angola, Annobón, Ihla do Principe, and São Tomé. Bate (1888) reported *A. sulcatipes* from San Antonia, "San Iago," Cape Verde Islands, presented a detailed description accompanied by illustrations, and stated that it differs from *A. scabra* "in having a prominent tooth on the inner distal angle of the carpus," (p. 694) and a longer second antenna (p. 698). Hickson (1889) added no new information on the species. Pocock (1889) commented that the only features selected by Kingsley (1878a) to distinguish his *A. punctata* from other species were probably individual variations or due to differences in age.

Ortmann (1890) included *Atya scabra* and *A. sulcatipes* in his *margaritacea* group on the basis of the shape of the rostrum. In his study of the family Atyidae (1895), he grouped the following in his synonomy of *A. scabra*: *A. mexicana* Wiegmann, *A. sulcatipes* Newport, *A. occidentalis* Newport, *A. rivalis* Smith, *A. tenella* Smith, and *A. punctata* Kingsley. This synonomy set the stage for repeated erroneous interpretations of the species involved. The range cited for *A. scabra* by him was based, at least in part, as follows: Nicaragua on records for *A. rivalis* (= *A. margaritacea*) and *A. tenella* (= *A. innocous*) by Smith (1871); Jamaica on that for *A. occidentalis* (= *A. innocous*) by Newport (1847); and Dominica on that for *A. occidentalis* by Pocock (1889). The Haitian record is that of Kingsley (1878a) for *A. punctata*, and the Cape Verde Islands localities are those for *A. sulcatipes* reported by Newport (1847) and Bate (1888). Inasmuch as both *A. scabra* and *A. occidentalis* (= *A. innocous*) occur on Tobago, which of the two

was examined by him is not known. Stebbing (1893) expressed the opinion that *A. sulcatipes* "is perhaps only a variety of the older *Atya scabra*." Ortmann continued to recognize *A. margaritacea* as a distinct species in his 1895 report but stated: "The differences between the New Caledonian species *A. margaritacea* and *robusta* and the West Indian *A. scabra* are very doubtful . . . " (p. 408).

Except for a diagnosis of the species in Portuguese, nothing new relative to *A. scabra* was recorded by Ortmann (1897). The occurrence of this shrimp in Río Macuto, near La Guaira, Venezuela, was noted by Nobili (1897). In the same year, Rathbun (1897) cited Jamaica as a locality for it, but her statement, "This species is probably identical with *A. occidentalis* Newport," leaves some doubt as to the identity of the material before her. Aurivillius (1898) described and illustrated *A. margaritacea* var. *claviger*, another synonym of *A. scabra*, from Cameroon.

In her study of the West African decapods, Rathbun (1900) erred in several respects: she apparently agreed with Ortmann's synonomy for *A. scabra* adding *A. gabonensis* and Aurivillius' *A. margaritacea* var. *claviger* to the list. One of the specimens cited from St. Paul River, Mount Coffee, and that from Beulah were misidentified. The Costa Rican record is new and may or may not be based upon a correct identification. All of the specimens from Costa Rica now in the Smithsonian collection that would have been available to her are members of *A. margaritacea*. The only record of *Atya* from the Orinoco of which we are aware is that of Koelbel (1884) for *Atya sculptilis* (= *A. gabonensis*). Therefore, in all probability her inclusion of Costa Rica, Nicaragua, and Orinoco in the range was based on erroneous determinations. The Liberian and "Gabun" records seem to have been founded, at least in part, on collections of *A. africana* and *A. gabonensis*, respectively. The inclusion of Cameroon, Ihla do Principe, São Tomé, and Rolas, cited originally by other authors (and some based on records previously given for *A. sulcatipes*) have been confirmed. In her study of the Brachyura and Macrura of Puerto Rico, Rathbun (1901) almost certainly treated three species under *A. scabra*. Her statement that "this species is extremely variable in the form of the rostrum and more noticeably in the shape of the last three pairs of thoracic feet which may all be slender and nearly equal in length; and their spines very feeble and appressed" suggests that among her material were *A. scabra*, *A. lanipes*, and, in all probability, *A. innocous*. Specimens of *A. lanipes* from Puerto Rico collected by the *Fish Hawk* in 1899 may not have been examined by Rathbun until much later, for they were not entered in the Smithsonian catalogue until 1913, at that time identified by her as *A. occidentalis*. Her summary of the distribution of *A. scabra* was almost identical to that recorded by her in 1900.

The first report of the occurrence of *Atya scabra* in Panama was that of Doflein (1900), who recorded it from the Atlantic watershed. No original data were offered by Young (1900), Thompson (1901), or Bouvier and Lesne (1901). Gerstaecker and Ortmann (1901) illustrated a lateral view of an animal together with several appendages. Bouvier (1904), considering *A. margaritacea* and *A. sulcatipes* as synonyms of *A. scabra*, recorded the species from the following localities, several of which were new: New Caledonia; Victoria, Australia; Darién, Colombia; San Esteban and Naricual, Venezuela; Valley Nacional, Oaxaca, Mexico; Cape Verde Islands; Fernando Poo; and São Tomé. In his synoptic treatment of this shrimp (1905), Bouvier included the following as synonyms: *A. sulcatipes*, *A. rivalis*, *A. tenella*, *A. punctata*, and *A. margaritacea*. This list differed from Ortmann's in the recognition of *A. occidentalis* as a valid species and relegating *A. margaritacea* to the synonomy of *A. scabra*. Its range, essentially the same as that presented in 1904, differed only by the addition of the Antilles and west Africa. He noted that many of the specimens from the Antilles probably belong to *A. occidentalis* and that several of the African specimens should be referred to *A. intermedia* and *A. africana*. *Atya margaritacea* var. *claviger* was considered by him to be an unquestioned synonym of *A. scabra* (p. 122).

Nothing of importance was added to our knowledge of this shrimp by Bouvier or by John-

ston in 1906, or by the former or Valdés Ragués in 1909. Balss (1914), following Rathbun, included in the range of the species the Atlantic versant of the Americas, the West Indies, and in and off Africa: Gabon, São Tomé, Principe, Annobón, and Rolas. Tesch (1914) predicted that *A. scabra* would be found in Surinam. Pearse (1915) recorded 79 specimens from Santa Marta, Colombia. Other than presenting a lateral view of the entire animal, Torralbas (1917) offered no information.

Bouvier's (1925) monograph of the family Atyidae has served as the principal source for all subsequent work on members of the family. In it he reviewed the previously reported localities, adding a number of new ones, and in his key and text contrasted and compared *A. scabra* with related species. Balss (1925) reported the presence of the species in Victoria, Cameroon, and cited Valdivia as a new locality, and De Man (1925) recorded its occurrence in the Belgian Congo. Jean Roux (1926a) stated that if the species occurs in Australia it must be rare. Working on Isla Barro Colorado, Panama, Allee and Torvik (1927) found this shrimp in Shannon Creek, and Monod (1928), in a report on the fisheries of Cameroon, noted that *A. scabra* was of economic importance and pointed out its occurrence in the Bimbia River. Later (1933), he recorded two new localities in Cameroon and cited a more precise station on the Bimbia River. Schmitt's review (1935) of the Macrura and Anomura of Puerto Rico contains no new data on the species. In a note on Marcgrave's treatment of "Guaricuru," Sawaya (1942) suggested that the shrimp was a member of the genus *Atya*.

The beautifully illustrated morphological study by Villalobos (1943), together with locality and ecological data, is an invaluable contribution. Oliveira (1945) compared *A. sulcatipes* with *A. scabra*, including a list of differences that subsequently have not proven to be consistent. Holthuis (1951) presented the most nearly complete synonomy previously available and cited all of the localities offered by earlier investigators. In this study, *Atya sulcatipes* and *A. margaritacea claviger* are the only synonyms listed for *A. scabra* other than Leach's original combination *Atys scaber*. No new data were offered by Holthuis (1955b) in his synopsis of the recent caridean and stenopodidean genera; however, he (1955a) requested the International Commission on Zoological Nomenclature to place "*Atys*," of which *Atys scaber* Leach is the type, on the "Official List of Generic Names." This was done by the Commission in Opinion 470 (Hemming, 1957). Villalobos' (1943) illustration of a specimen in lateral view was reproduced by Rioja, Ruiz, and Larios (1955). In his description of *A. ortmannioides*, Villalobos (1956) contrasted it with *A. scabra*. Darnell (1956) analyzed a population of *A. scabra* frequenting a small stream in Tamaulipas, Mexico, the most northern locality known for the species. In this study, he presented observations of their habitat, distribution, population structure, food, and life history and related his findings to those of Villalobos (1943).

Holthuis (1959:16) pointed out that "Tesch's supposition that *Atya scabra* (Leach) might be found in Surinam has not yet been substantiated." Villalobos (1959) reported capturing juvenile forms of *Atya scabra* in the Río Papaloapan, and stated that the earlier part of their development occurs near the coast, and afterward they migrate upriver into areas far removed from the mouths of the streams, in this respect resembling *Potimirim mexicana* (De Saussure, 1857:505). Parodiz (1960) cited a new locality for *A. scabra* in Brazil and provided illustrations. In his study of the freshwater shrimps of Jamaica, Hart (1961b) presented photographs of a specimen and reported three new localities. Darnell (1962) tabulated data from his previous study (1956). *Atya scabra* was the only member of the family Atyidae considered by Davant (1963) to be of economic importance in Venezuela, and he reported it to be a common inhabitant of the Río Manzanares. Lemos de Castro (1962), in reviewing the Crustacea included by Marcgrave in his "História Naturalis Brasiliae," called attention to the inclusion of "Guaricuru" with which Lemos de Castro associated *Atya scabra*. The illustration of Marc-

grave is reproduced and is accompanied by a photograph of *A. scabra* from Río Serinhaem, Estado de Pernambuco, Brazil. Holthuis and Rosa (1965) noted that this shrimp is used for food in Mexico, Costa Rica, Panama, Nicaragua, British Caribbean Federation, Cuba, Haiti, Puerto Rico, Netherlands West Indies, Venezuela, and Peru. The lattermost is based on the misidentification of *A. margaritacea.* No new information was added by Pericchi Lopez (1965).

Even though Holthuis (1966) found that the differences between *A. sulcatipes* and *A. scabra* compiled by Oliveira were not reliable when larger series were compared, on the basis of differences noted in the shape of the antennule, he assigned the West African collections that had been designated as *A. scabra* by him in 1951, and earlier by Bouvier and others, to *A. sulcatipes.* He also considered *A. margaritaria clavipes* [sic] to be a synonym of *A. sulcatipes*, and cited the known West African localities, including a number of new ones, for the latter. The type of *Atya scabra* was discussed by him, and he concluded that it is not among the specimens in the British Museum. The type-locality was restricted to "the area of Veracruz," Mexico. *Atya mexicana*, *A. margaritacea*, and *A. punctata* were recognized as synonyms of *A. scabra.* He also listed four differences between the latter and *A. rivalis* (p. 234). Monod (1967) recorded *A. scabra* from the Cape Verde Islands, Fernando Poo, São Tomé, and Annobón; his illustrations were taken from Bouvier (1925) and De Man (1925). Neither Vélez (1967) nor Straskraba (1969) added to our knowledge of the species in pointing out its occurrence on Puerto Rico or Cuba, respectively. Except for recording the common name "Bouc," no new data were added by Pinchon (1967). Coelho and Ramos (1968) reported that this shrimp is sold in the markets of Recife, Brazil, and Fausto Filho (1968) noted its use as a food item in northeastern Brazil.

Chace and Hobbs (1969) followed Holthuis (1966) in their synonomy of *A. scabra.* They diagnosed and illustrated the species, described the color pattern, reviewed its range, and commented on its ecological distribution on Dominica. They also pointed out a number of characteristics in which this shrimp differs from the sympatric *A. innocous.* Disney (1971) noted that he had found this shrimp in limited numbers in two localities in the vicinity of Kumba, Cameroon: the Bille River (a tributary of the Meme River) and the Blackwater River (a tributary of the Mungo River). It was infested with the larvae and pupae of the blackfly *Simulium atyophilum.* Rutherford (1971) reported the occurrence of *A. sulcatipes* in Ghana, noting that in addition to frequenting the Cape Verde Islands, São Tomé and Annobón, it ranges on the African continent from Liberia to Congo-Kinshasa. He stated that this dark greenish gray shrimp occurs in rocky stream rapids. Cendrero (1971) added no new data. In considering the possibility that individuals of *A. scabra* occurring in a small stream at Tapalapan, Santiago Tuxtla, Veracruz, serve as a host to the entocytherid ostracod *Uncinocythere zaruri*, Hobbs (1971) reported a new locality for the shrimp. Lemasson (1973) pointed out that *A. scabra* attains lengths of eight to 10 centimeters. Bonnelly de Calventi et al. (1973) cited its presence in the Haina, Mana, Isa, and Nigua rivers and Cañada Madrigal in the Dominican Republic. They also noted that it "yields relatively little edible mass (13% total body weight) as compared with peneids, but has a comparable content of water (74.5%) and protein (16.99%). Lipids represent 0.82–2.94%, ash 31.0%, calcium 0.232%, phosphorus 1.033%, and iron 0.25%. *Atya scabra* muscle provides 88.3 dietary calories per 100 g while peneid muscle provides 78.3." In their joint study (1974), Bonnelly de Calventi et al. pointed out that in the Dominican Republic this shrimp is eaten only in some regions of the southern part of the country. Bonnelly de Calventi (1974a) listed two additional rivers (Río Jurá and Río Nizao) where it occurs in the Dominican Republic. In another report (1974b) she presented a diagnosis of the species, illustrations, notes on color, size, habitat, life history, and distribution in the Dominican Republic.

Holthuis (1974) recorded a new locality in the province of Pinar del Río, Cuba. The following

references to *A. scabra* contain no new data: Chace (1972), Hart and Hart (1974), Scelzo (1974), Hunte (1975), and Abele and Blum (1977). Lévêque (1974) noted the occurrence of this shrimp on the island of Guadeloupe and stated that ovigerous females had been found in June. It was reported to be common in the eastern part of Cuba by Alayo (1974). Abele (1975) recorded the presence of the species in streams of the Atlantic Basin in Panama, and, the following year, Villamil and Clements (1976) stated that on Puerto Rico it appears to be ecologically the most restricted and the most specialized of the crustaceans occurring in the area. Fryer (1977), in his impressive study of the Dominican atyids, related the presence on the chelae of the first and second pereiopods of bristles with scraping denticles to "scraping" and "sweeping" for food. Their absence in *A. scabra* is correlated with the infrequency of its resorting to scraping; it usually employs filter techniques. He included a brief but exhaustive summary of available knowledge of their ecological distribution and habits. The excellent illustrations, particularly photographs of sections through the mouth parts and of a living animal, greatly enhance his contribution. Among the most recent references to this shrimp are those of Hunte (1978, 1979c). Although the latter introduces no new information, the former provides not only additional locality records but also contains valuable ecological data. *Atya scabra* was found by him on Jamaica only in the eastern parishes where there is a mountainous terrain. Data on tolerance of individuals to lowered temperature and oxygen concentrations were offered in his effort to determine what environmental factors affected their distribution. In discussing relationships among the Decapoda, Burkenroad (1981:261) mentioned that *A. scabra* does not possess "tack-like" sperm.

PUBLISHED ILLUSTRATIONS.—The earliest illustration of this shrimp is that of Marcgrave (1648), who presented a lateral view of the entire animal (presumably from Brazil), identifying it by the vernacular name "guaricuru." This drawing was later employed by Piso (1658) and others. Almost two centuries elapsed before Leach (1816) presented a dorsodextral view of the shrimp. Much better executed and more detailed illustrations were furnished by H. Milne Edwards (1816); these consist of a lateral view of the entire animal, a dorsal view of the cephalic region, the mandible, the first pleopod together with another unidentified one, and a dorsal view of the sixth abdominal segment, telson, and uropods. The following year, Leach (1817) published a hand-colored dorsosinistral view of a shrimp that appears to have been redrawn in reverse from the figure in his 1816 publication. In his "Dictionary of Natural Science," Desmarest (1823) included a dorsodextral view of an entire animal and in 1825 republished the same figure. Guérin-Méneville's (1829–1844) illustration of an entire animal was apparently redrawn from Desmarest's figure, Broderip's (1835) from Leach (1817), and Latreille (1837) used a hand-colored reproduction of Desmarest's illustration. The figures included in H. Milne Edwards (1837 and 1842) are the same as those published by him in 1816. Lucas' (1851) illustration of an entire animal was apparently redrawn from Desmarest (1823). A small likeness of the cephalic region in lateral aspect was depicted by Guérin-Méneville (1856–1857a,b). Capello (1867) included sketches of the first (or second?) pereiopod. Mocquard (1883) and Albert (1883 a,b) presented several figures illustrating the anatomy of the stomach of this shrimp.

Claus (1885) presented an excellent rendition of the gills and basal parts of the thoracic appendages. Bate's (1888) figures of *A. sulcatipes* include a lateral view of an entire animal, others of the first and second antennae, mandible, second maxilla, first through third maxillipeds, first pereiopod, telson, uropod, branchiae, and first and second pleopods of a male. Aurivillius (1898) illustrated his *A. margaritacea* var. *claviger* as follows: the telson, the third pereiopod, and dorsal and lateral views of the carapace. Gerstaecker and Ortmann (1901) figured an animal in lateral aspect along with views of the antenna, mandible, first and third maxillipeds, and first pereiopod. Bouvier (1905) presented drawings of the rostrum

of *A. scabra* in dorsal aspect and a lateral view of the cephalic part of the carapace. The drawing of Torralbas (1917) was of a specimen in lateral view. In his monograph, Bouvier (1925) illustrated the eyes, basal segment of the antennule, the antennular carina (= ocellar beak), the first and second maxillae, dactyls of the fourth and fifth pereiopods, and reprinted drawings of the rostrum in dorsal aspect and a lateral view of the cephalic region of the carapace. The latter two are mislabeled, for figures 705 and 706 (not 703 and 704) correspond to figure 25s of *A. scabra* in Bouvier (1905). Monod (1967), employing Bouvier's (1925) figures, repeated the latter's error. Illustrations of a specimen of *A. scabra*, presumably from the Belgian Congo, by De Man (1925) include the rostrum in dorsal and lateral aspects and the telson in dorsal view.

The most completely illustrated work on *Atya scabra* is that of Villalobos (1943) in which virtually the entire exoskeleton is depicted. Oliveira (1945) presented drawings of the animal in lateral aspect, a dorsal view of the carapace, the caudal area in dorsal and ventral aspects, and the maxillae and maxillipeds. Rioja, Ruiz, and Larios (1955) reproduced the lateral view of the entire animal as illustrated by Villalobos (1943). The illustrations provided by Parodiz (1960) include the cephalic region in lateral aspect, a lateral view of the third pereiopod from the merus distally, and the distal part of the first or second (not third as labeled) pereiopod.

Hart (1961b) presented a photograph of a Jamaican specimen in lateral aspect. A similar photograph along with a dorsal view of the rostrum and a lateral view of the cephalic region are recorded by Davant (1963). Chace and Hobbs (1969) included a lateral view of a male from Dominica showing the color pattern, a dorsal view of the cephalic region, lateral views of the preanal carina and of the ventral margin of the second abdominal pleuron, and mesial views of the distal part of the second pleopod of the male and of the appendix masculina. Rutherford (1971) presented illustrations of the rostrum in dorsal view and of the cephalic region in lateral aspect. Bonnelly de Calventi (1974b) included a photograph of an entire animal in lateral and dorsal views along with drawings of the rostrum, appendices masculina and interna, and of the antennular peduncles. Bonnelly de Calventi et al. (1974) provided a photograph of a shrimp in lateral view. Lévêque (1974) figured the rostrum in dorsal aspect as did Alayo (1974). Fryer's (1977) illustrations include a lateral view of a specimen, setal structural features, and photographs of a Dominican animal filter feeding and of sections through the mouth parts.

DIAGNOSIS.—Cephalic region comparatively weakly sculptured except nodose in larger individuals; much of carapace studded with pile of short stiff setae (conspicuous in early postmolt stages); antennal and pterygostomian spines prominent. Rostrum with margins bearing paired preapical angles, latter almost always slightly produced anteriorly; dorsal surface with rather sharp median carina. Ventral margin of second through fifth abdominal pleura with row of sclerotized denticles (occasionally absent on second and fifth pleura throughout the range of the species and almost characteristically wanting on the second in members of African populations); caudoventral angle of fourth and fifth pleura acute but rarely produced. Sternum of sixth abdominal segment little more than half as long as wide; compressed median prominence on sternum of fifth abdominal segment conspicuous but never forming hornlike element overlapping sixth abdominal sternite. Preanal carina acute to rounded apically and directed caudoventrally, apex rarely reaching caudal margin of basal part of carina. Telson about 1.5 to 1.7 times as long as broad with paired dorsal rows of 5 to 7 spines. Antennular peduncle with dorsal surface of proximal article bearing 1 to 3 sclerotized spinules proximal to transverse distal row; penultimate article 1.3 to 1.6 times as long as wide and bearing scattered spinules on dorsal surface. Coxae of third and fourth pereiopods lacking prominent anterolateral spine. Third pereiopod with merus rounded ventrally, about 3 times as long as high, ventromesial surfaces of paired articles not touching when appendages brought together, and lateral surface bearing irregular rows of prominent

corneous-tipped tubercles; propodus 1.7 to 2.1 times as long as broad and studded with rows of sclerotized tubercles on both extensor and flexor surfaces, tubercles in row on flexor surface mesial to median line of article quite or almost contiguous; dactyl freely movable and bearing single row of usually 6 or 7 tubercles on flexor surface.

REMARKS.—Much of the misunderstanding of the range and variations in *Atya scabra* no doubt resulted from the fact that Leach described the species from specimens obtained from an unknown locality. Despite the existing confusion, most previous authors have agreed that the American atyids with a heavily pubescent body and the third pereiopods studded with large corneous tubercles are members of Leach's species. Clouding this general concept of *A. scabra*, however, is a dry specimen in the British Museum identified as *A. scabra* and bearing a label on which is written "Type." The specimen is clearly identifiable with *Atya gabonensis* Giebel and exhibits characteristics that would hardly have been ignored by the delineators of the illustrations presented by Leach (1815, 1816) and H. Milne Edwards (1816). The label is therefore strongly suspect.

As Holthuis (1966:234) has pointed out, Newport (1847:158) noted that there were four specimens of this species "in the cabinets of the British Museum, but nothing whatever is known of their habits, or from whence they were obtained." Continuing his remarks on the types of this shrimp, Holthuis stated:

> In White's (1847:74) list of the Crustacea in the British Museum, however, is indicated under *Atya scabra* "a–d. Mexico. From the collection of Dr. Leach." It is impossible [inasmuch as Leach's specimens lacked data] therefore that the locality of Leach's type material has been discovered later and that the material listed by White indeed is the type material.

Although Holthuis did not designate a neotype for the species, he stated (p. 234): "It seems safe to restrict the type locality to the Atlantic drainage of Mexico and more accurately to the area of Veracruz." In order that stability in the action of Holthuis be more assured, we are designating a male specimen in the British Museum from Misantla (the location of which is in the area designated by Holthuis) as the neotype of Leach's *Atys scaber*.

NEOTYPIC MALE.—Rostrum (Figure 45*a,d*) with concave lateral margins slightly produced at base of acumen in angles little less than 90 degrees; acumen just overreaching proximal podomere of antennule; dorsal median carina high, rather sharp, excavate dorsally (dipping to or below level of lateral carina posterior to acumen), and reaching apex of acumen; ventral carina with single anteriorly directed corneous-tipped tooth. Ocellar beak, largely obscured by eyes, tuberculiform with anterior margin almost vertical and apex directed dorsally, latter fitting into shallow subrostral groove. Antennal spine acute; pterygostomian spine slender and acute, no spines present between them. Carapace (length 29.8 mm) devoid of other spines, but surface somewhat nodose dorsally; most conspicuous nodules arranged in 1 to 3 subparallel rows extending anteroventrally, and almost entire surface bearing punctations studded with clusters of 2 to 5 short, erect setae. Conspicuous subcircular obliquely impressed area present at cephalic end of branchiocardiac groove, and 2 smaller flat ones situated posterodorsal to it, these areas smooth and lacking punctations and setae.

Pleuron of second abdominal segment (Figure 45*e*) with rounded posteroventral extremity, that of third, fourth, and fifth weakly produced in very short subspiniform corneous prominences. Ventral margins of second through fifth pleura with linear clusters of 14, 17, 11, and 8 corneous denticles on right side of body, respectively, and 6, 18, 11, and 7 on left; margin of fifth lacking prominent setal fringe. Fourth, fifth, and sixth abdominal terga approximately subequal in length and 0.9 as long as telson. Sternum of fifth abdominal segment (Figure 45*f*) with rather large, median, laterally compressed projection having irregular oblique ventral extremity bearing row of 3 very small corneous tubercles; sternum of sixth about 0.67 as long as broad. Preanal carina with caudally directed apex almost reaching level of posterior margin of basal (dorsal) part of carina. Telson injured, but that of male in same lot of specimens (Figure 45*h*) about 1.6

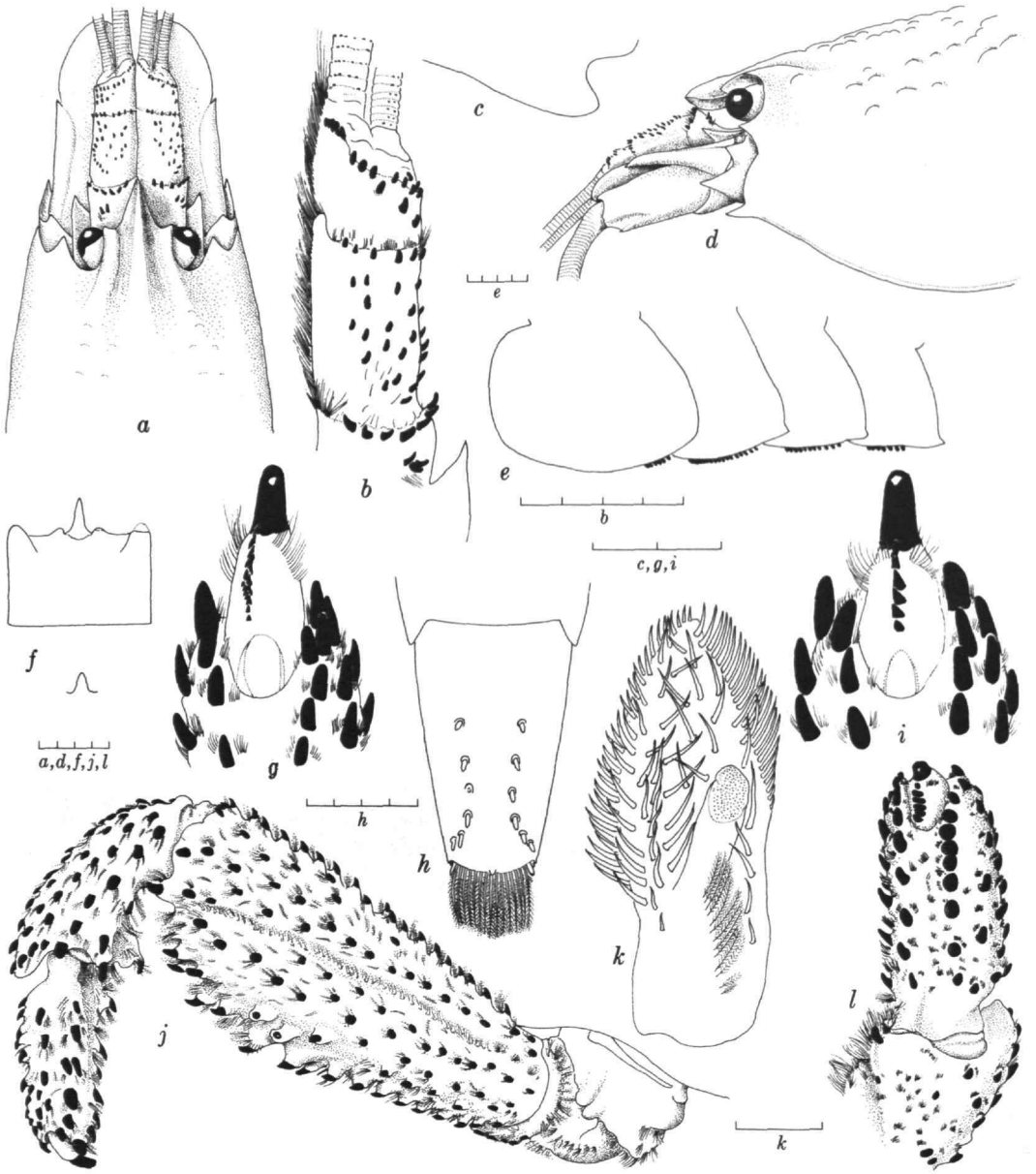

FIGURE 45.—*Atya scabra* (all from neotype except *h* from topotype): *a*, dorsal view of cephalic region; *b*, dorsal view of antennular peduncle; *c*, lateral view of preanal carina; *d*, lateral view of cephalic region; *e*, lateral view of second through fifth abdominal pleura; *f*, preanal carina, sternum of sixth abdominal segment, and median tubercle on that of fifth; *g*, flexor surface of distal part of fifth pereiopod; *h*, dorsal view of telson; *i*, flexor surface of distal part of fourth pereiopod; *j*, lateral view of third pereiopod; *k*, mesial view of appendices masculina and interna; *l*, flexor surface of distal part of third pereiopod. (Scales marked in 1 mm increments.)

times as long as wide, its dorsal surface bearing paired, mesially concave rows of 6 corneous denticles each and posteromedian tubercle, latter very slightly overreaching caudal margin of telson.

Proximal podomere of antennule (Figure 45*b*) with stylocerite bearing acute, corneous tip almost reaching distal end of segment, dorsal surface with linear cluster of setae and 3 corneous denticles; distal margin studded with row of 7 (right) or 6 (left) cornified spinules; penultimate segment of peduncle 1.6 times as long as wide, its dorsal surface bearing 22 small, irregularly arranged, corneous spinules, dorsodistal margin

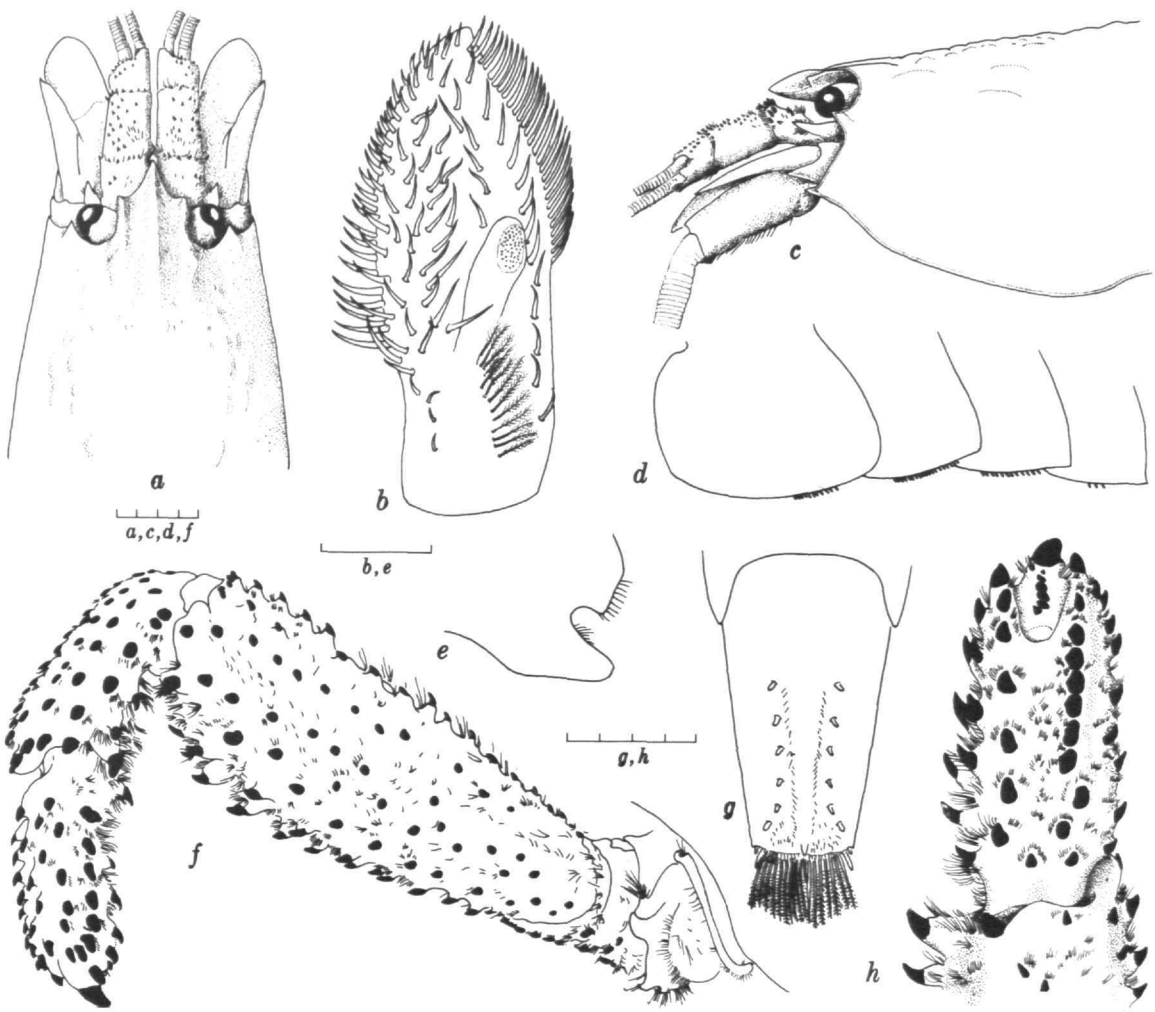

FIGURE 46.—*Atya scabra* (all from male from Río Sabinas, Estado de Tamaulipas, Mexico): *a*, dorsal view of cephalic region; *b*, mesial view of appendices masculina and interna; *c*, lateral view of cephalic region; *d*, lateral view of second through fifth abdominal pleura; *e*, lateral view of preanal carina; *f*, lateral view of third pereiopod; *g*, dorsal view of telson; *h*, flexor surface of distal part of third pereiopod. (Scales marked in 1 mm increments.)

with row of 8; dorsum of ultimate segment of peduncle about 0.5 as long as penultimate podomere, 3 or 4 spinules on dorsal surface, oblique row of 8 and 2 eccentric distolateral spinules flanking dorsal base of lateral flagellum; similar rows of 4 (right) and 5 (left) at dorsomesial base of mesial flagellum, and 3 or 4 on dorsal surface proximal to latter rows. Antenna with lateral spine on basis clearly overreaching stylocerite; lateral spine on scaphocerite extending to slightly beyond midlength of ultimate podomere of antennule and falling considerably short of distal extremity of antennal peduncle; lamella far surpassing latter; flagellum broken but reaching at least to midlength of second abdominal tergum.

Third maxilliped extending anteriorly to about same level as antennular peduncle; penultimate segment about 1.5 times as long as ultimate; tip of exopod reaching base of distal fifth of penultimate podomere of endopod.

First pereiopod reaching only slightly farther anteriorly than second and attaining level (neglecting terminal setae) of about midlength of penultimate segment of antennular peduncle; bristles composing terminal brush of both pereiopods lacking scraping denticles. Third pereiopod (Figure 45*j*,*l*) lacking spines, and, when extended anteriorly, overreaching antennular peduncle by distal 3 podomeres; merus with ventromesial margin bowed, 2.3 times as long as high, 1.8 times as long as carpus, and 1.6 times as long as propodus; latter almost twice as long as wide and about 0.9 as long as carpus; distoventral margin of coxa entire and with conspicuous mesial caudoventral prominence bearing corneous tip and studded with tufts of plumose setae. Lateral, dorsal, and ventral surfaces of merus studded with conspicuous corneous tubercles of which many, if not most, somewhat flattened distally and bearing sharp free edge; plumose setae, either singly or in groups, present at distal base of tubercles, some setal groups partly encircling tubercles; median longitudinal row of setae on lateral surface of podomere well defined; distomesial extremity of podomere produced in broad rounded lobe bearing row of 5 (right) or 7 (left) corneous denticles. Carpus strongly tuberculate except ventrally and ventromesially, there mostly studded with conspicuous tufts of plumose setae borne in punctations. Propodus entirely tuberculate, those on flexor surface arranged in 2 longitudinal series, 5 of those in mesial row contiguous. Dactyl not fused with propodus, flexor surface with single row of 6 tubercles flanked distally by setal clusters.

Fourth pereiopod with dactyl almost reaching distal end of merus of third; length of merus about twice that of carpus, and latter only slightly shorter than propodus. Fifth pereiopod almost reaching midlength of merus of third; merus about 1.5 times as long as carpus, and latter 0.65 as long as propodus. Ornamentation of fourth pereiopod similar to that of third, except merus with articulated distal ventrolateral spine and ventral one proximally, and carpus with similar large distolateral spine. Ornamentation of fifth pereiopod like that of fourth, except merus with 2 articulated ventral spines, and flexor surface of dactyl with row of many more spinules.

Diaresis of lateral ramus of uropod with 19 (right) or 20 (left) articulated corneous denticles and fixed lateral spine, latter about same size as spinules.

Color Notes.—The most complete notes on the color of this shrimp are those of Chace and Hobbs (1969:63–66) based upon specimens collected on the island of Dominica (Figure 47).

Green Phase: Ground color of cephalothorax and abdomen dark green (chromatophores forming reticulate pattern), darker dorsally, gradually fading ventrolaterally to olive interspersed with dark cream. Dorsum with broken, narrow, median, longitudinal, greenish-cream stripe extending from anterior part of rostrum to posterior margin of fifth abdominal tergum. (In some larger individuals, dorsal light stripe obliterated.) Three dorsally situated transverse bands of dark forest green as follows: (1) immediately posterior to base of rostrum and extending ventrally almost to level of antennal spine; (2) on posterior margin of carapace, continuing onto anterior portion of first abdominal tergum, and extending ventrally on both to level of base of abdominal pleura; and (3) on anterior half of sixth abdominal tergum extending ventrally to margin. Carapace with dark green spot immediately below second band and cream one immediately anterior to spot, studded with pile of short golden setae, one to three setae in each punctation.

Antennular and antennal peduncles forest green; flagella

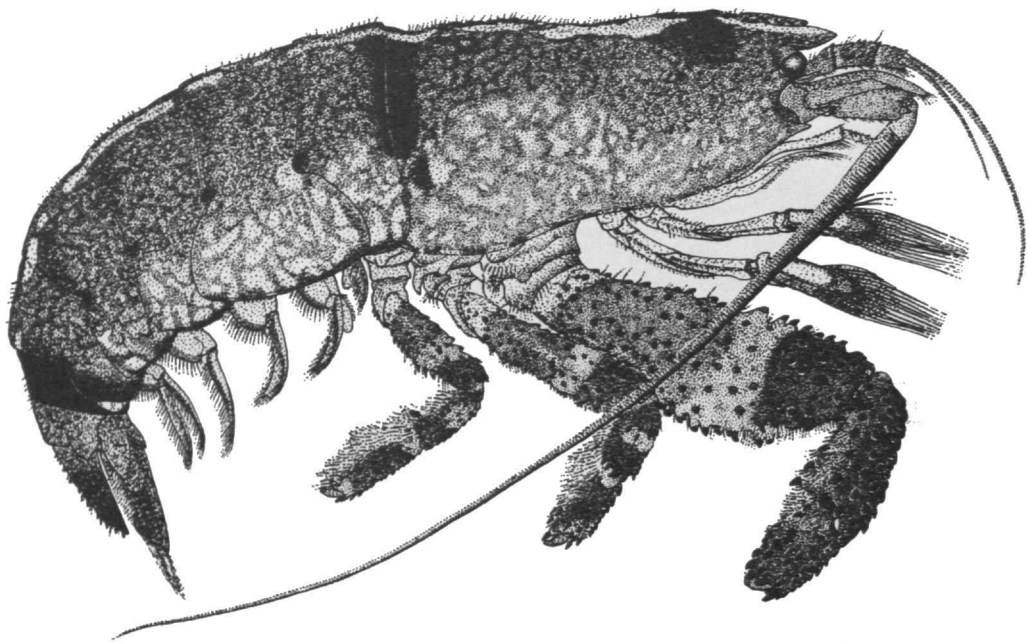

FIGURE 47.—Lateral view of *Atya scabra* (from Chace and Hobbs, 1969).

tan to brown. Third maxillipeds and first two pairs of pereiopods lavender cream with bright green longitudinal lines on ischium and merus; proximal portions of chelae of first two pereiopods lavender, distal portions vermilion; distal setal tufts dark gray proximally fading to beige distally. Proximal three podomeres of third, fourth, and fifth pereiopods cream with irregular green markings; merus with cream-colored base followed distally by broad green band, narrower cream one, and distal green one; carpus and propodus of third pereiopods forest green; those of fourth and fifth cream proximally and dark green distally; dactyls of three orange brown (corneous); tubercles on all three legs progressively darker from proximal to distal podomeres. Basal portions of pleopods cream with greenish-tan lateral margin; rami tan with brown borders. Uropod light green proximally, dark green distally with patches of brownish pigment alternating with aqua spots in distal portions of both rami; marginal setae golden. Telson light green anteriorly, dark green posteriorly with brownish spots and brown tip.

Brown Phase: Pattern essentially identical; colors, however, range from cream through pale buff to dark brown.

SIZE.—The largest specimen that we have examined is a male from Brazil exhibiting a carapace length of 46.3 mm, and the largest in African waters is also a male with a corresponding length of 34.4 mm. The largest female, which is ovigerous and is also from Brazil, has a carapace length of 29.5 mm; the corresponding length of the smallest ovigerous female is 7.1 mm.

DISTRIBUTION AND SPECIMENS EXAMINED.—*Atya scabra* ranges from Liberia to northern Angola, in the islands off the west coast of Africa from the Cape Verde group southward to Annobón, in the West Indies from Cuba and Hispaniola to Curaçao and Trinidad, and from Tamaulipas, Mexico, to Santa Catarina, Brazil. In Panama it has apparently crossed the continental divide, occurring in the Río Frijoles Basin (Figures 49–52). Its presence elsewhere on the Pacific slope perhaps resulted from introductions.

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 or, if followed by "t.l.," total length. Some listings lack dates and/or collectors; these could not be determined.

LIBERIA: (1) *USNM, St. Paul River, Mt. Cof-

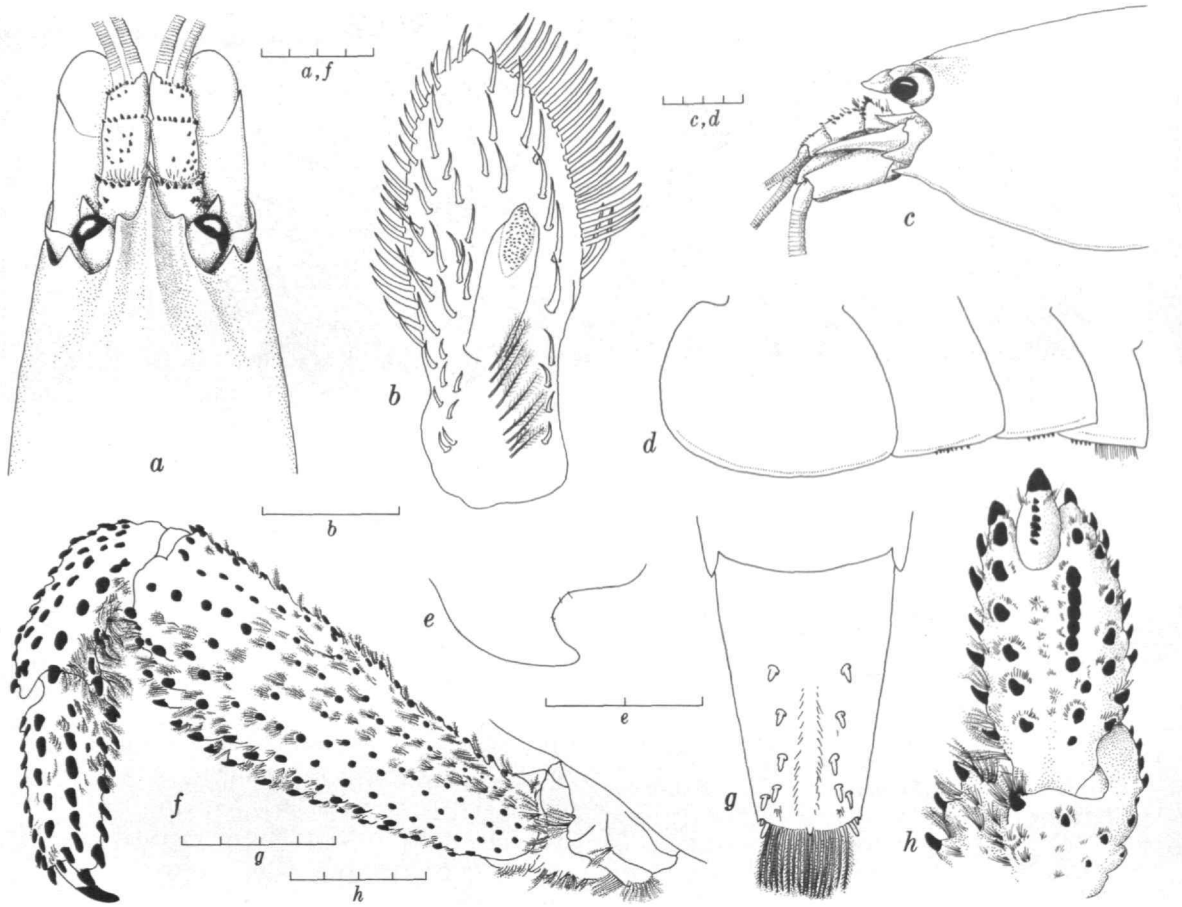

FIGURE 48.—*Atya scabra* (from male from São Tiago, Cape Verde Islands): *a*, dorsal view of cephalic region; *b*, mesial view of appendices masculina and interna; *c*, lateral view of cephalic region; *d*, lateral view of second through fifth abdominal pleura; *e*, lateral view of preanal carina; *f*, lateral view of third pereiopod; *g*, dorsal view of telson; *h*, flexor surface of distal part of third pereiopod. (Scales marked in 1 mm increments.)

fee (Rathbun, 1900:313), 1♂ (17.3), 22 Mar 1897, R.P. Currie. (2) †BM, St. Paul River near Handi (6°54′N, 10°22′W), 1♀ (24.3), 6 Mar 1970, R. Garms. (3) *RNHL, Sheffelinsville between Monrovia and Marshall (Holthuis, 1966:235), 1♂ (12.2), 1887, J. Büttikofer. (4) †BM, Cavalla River near Nyaake, Grand Gedeh Co (4°51′N, 7°35′W), 1♂ (23.1), 13 Dec 1970, RG. (5) †USNM, Liberia Harbel, 64 km inland from Monrovia, 1♀ (17.7), "Smithsonian Firestone Exped. to Liberia." (6) †USNM, Cavalla River at Bolobo, 2♂ (20.1, 23.3), 1♀ (10.2), H.A. Beatty.

GHANA: (1) Environs of Cape Coast between Elmina and Anomabu (Rutherford, 1971:87, 88).

CAMEROON: (1) "Etome in Bächen" (Aurivillius, 1898:16). (2) Victoria (Balss, 1925:239). (3) Bimbia River near Dikullu (Monod, 1928:121; 1933:462). (4) stream near Tiko (Monod, 1933:462). (5) Kienke River near Kribi (Monod, 1933:462), (6) †RNHL, about 3 km N of Kribi, 1 juv (3.9), 5 Aug 1964, B. de Wilde-Duyfjes. (7) *RNHL, pools and waterfalls of the Lobé River about 9.0 km S of Kribi (Holthuis, 1966:235), 5♂ (6.2–8.9), 6♀ (5.1–9.8), 3 ovig ♀ (7.1–8.8), 23 juv

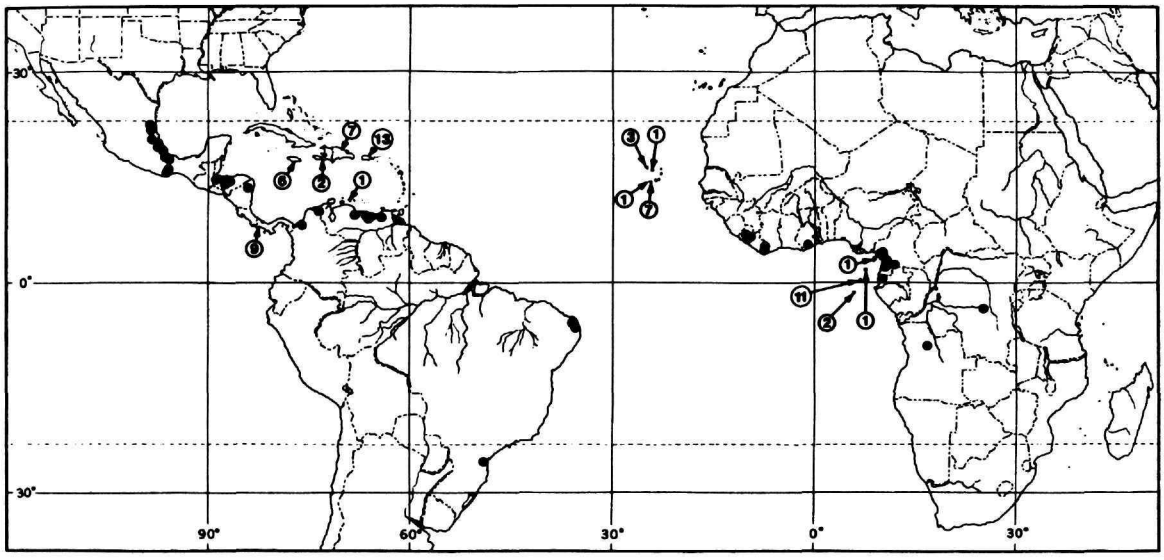

FIGURE 49.—Distribution of *Atya scabra* (circled numerals = number of localities; see Figures 50–52).

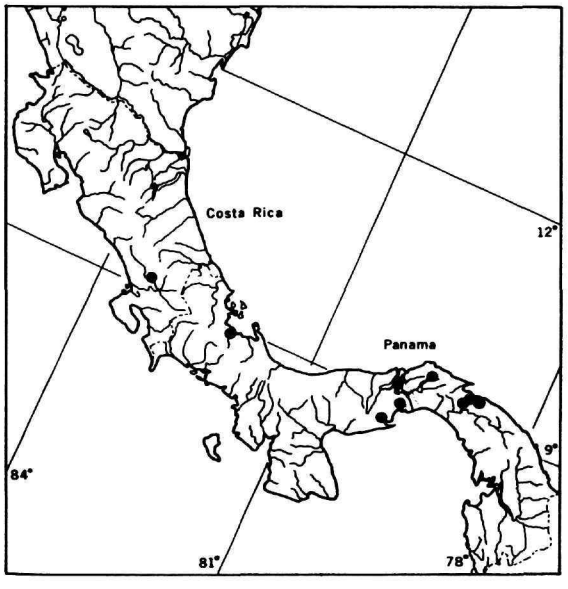

FIGURE 50.—Distribution of *Atya scabra* in Costa Rica and Panama.

(2.7–4.8), 7 Aug 1964, BWD; 5 juv (2.5–2.7) 9 Aug 1964, BWD. (8) †RNHL, Kribi, caught by fishermen with beach seine, 3 juv (2.8–3.0), 9 Aug 1964, BWD. (9) †BM, Bille River, 1♂ (18.4), 19 May 1969, R.L.H. Disney. (10) †BM, Blackwater River (4°22′N, 9°47′E), 1♂ (20.7), 19 Nov 1968, RLHD; 1♂ (21.8), 13 Feb 1969, RLHD.

GABON: †RNHL, Gabon River at Ororendo Point, 1♀ (16.3), 27 Aug 1956, J.H. Logemann.

ZAIRE: "MBuma dans le Mayumbe" (De Man, 1925:27, 28), 1♂ (80, t.l.), 25–26 Oct 1920, Dr. Schouteden.

NORTH ANGOLA: Duque de Bragança (Osorio, 1887:230).

CAPE VERDE ISLANDS: (White, 1847:74). *MHNP (Bouvier, 1904:138), 1 ovig ♀ (23.7), 1866. *BM, 1 dry specimen (22.3); 9♂ (12.0–17.3), 1♀ (18.6); *BM, 1♂ (28.1), *Challenger. Santo Antão*—(1) *RNHL, Ribeira de Paul (Holthuis, 1966:234), 3♂ (13.5–23.7), 1 ovig ♀ (14.0), May 1950, J. Cadenat. (2) *RNHL, Ribeira Grande (Holthuis, 1966:234), 1♂ (14.4), 1♀ (9.0), 27–28 Dec 1953, H. Lindberg. (3) *MHNP, no locality (Bouvier, 1904:138), 3♂ (21.5–28.5), 1♀ (15.9), 2 ovig ♀ (15.2, 17.8), 1900, A. de Cessac. *São Nicolau*—(Newport, 1847:159). (1) Ribeira Brava (Osorio, 1905:102). (2) *RNHL, Cha da Prequiça (Holthuis, 1966:235), 1 juv (3.9), 13–17 Dec 1953, HL. *Brava*—*RNHL, Faja Agua (Holthuis, 1966:235), 3 juv (3.4–7.1) 5 Feb 1954, HL. *São Tiago*—(1)

São Antonio Valley (Bate, 1888:694). (2) †BM, Ribeira Picos, 8♂ (13.9–23.3), 1♀ (12.9), C. Stoner; 36♂ (14.6–25.3), 6♀ (11.5–16.6), CS. (3) †USNM, river, 4♂ (19.7–24.9), CS. (4) †MHNP, Ruisseaux descendant de Pics de Antonia au dessus de 500 m alt, 11♂ (19.6–34.4), 1♀ (13.9), 10 ovig ♀ (15.9–20.3), A. Chevalier. (5) *RNHL, Lagoa (Holthuis, 1966:235), 4♂ (12.1–17.1), 15 Feb 1954, HL. (6) *RNHL, Praia (Holthuis, 1966:235), 20 juv (2.9–4.9), 5–19 Feb 1954, HL. (7) *RNHL, Ribeira Picos, near Picos (Holthuis, 1966:235), 8♂ (6.6–24.8), 12♀ (6.0–14.3), June 1950, JC.

FERNANDO POO: (Bouvier, 1904:138). *BM, 3♂ (10.1–14.4), 3♀ (7.0–10.0), 1 ovig ♀ (13.5).

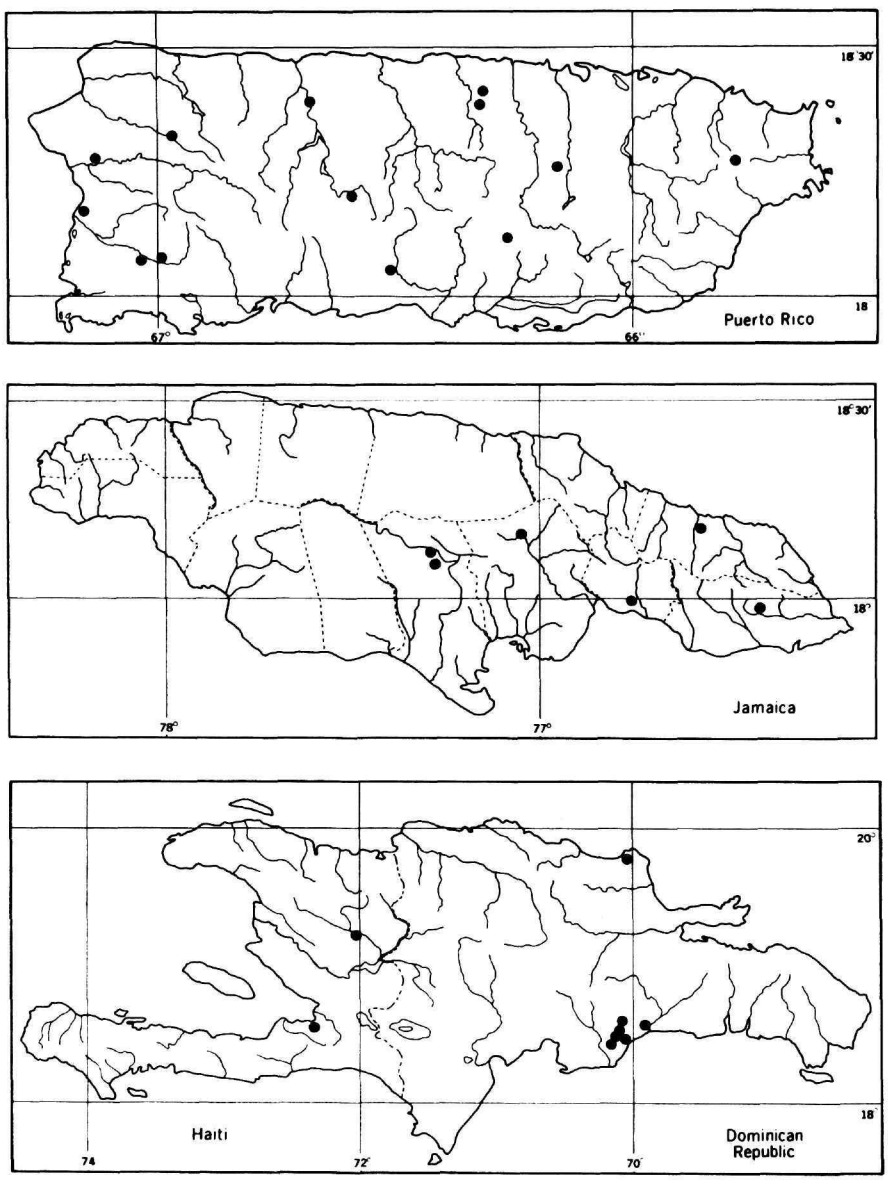

FIGURE 51.—Distribution of *Atya scabra* in the Greater Antilles.

IHLA DO PRINCIPE: (Osorio, 1898:194). (1) Rio Papagaio (Osorio, 1889:139). (2) Rio Banzu (Osorio, 1895b:251).

SÃO TOMÉ: (Greeff, 1882:35). (1) Rivière Agua Grande (Osorio, 1887:222). (2) Batipa (Osorio, 1889:137). (3) Obó Vermelho (Osorio, 1889:137). (4) Rio Quija (Osorio, 1891a:47). (5) Fleuve Manuel Jorge (Osorio, 1891b:140). (6) Rio Gumoela (Osorio, 1892:200). (7) Portinho (Osorio, 1892:200). (8) Rio Agua Izé (Osorio, 1906:150). (9) *RNHL, Bombom (Holthuis, 1966:235), 1♂ (18.1), 1♀ (13.3). (10) *MHNP, A. Negreiros (Bouvier, 1925:316), 1♂ (20.3), 1900. (11) †MHNP, Rio de Ouro, 1 ovig ♀, 24 Jul 1906.

ANNOBÓN: (Osorio, 1898:194). (1) Rio São João (Osorio, 1895a:249). (2) *RNHL, Crater Lake (Balss, 1914:97), effluent from (01°25'S, 05°36'E), 55♂ (7.0–25.1), 28♀ (6.1–11.2), 16 ovig ♀ (7.2–16.7), 20 Mar 1965, *Pillsbury* sta 278; USNM, 3♂ (9.0–21.1), 1♀ (8.8), 2 ovig ♀ (11.0, 19.6).

CUBA: (Martens, 1872:135). (1) Río Almendares at Calabazar, Provincia de la Habana (Bouvier, 1925:317); *USNM, 3♂ (8.0–19.2), C.F. Baker. (2) Calabazar, Provincia de la Habana (Bouvier, 1909:333). (3) †MHNP, La Habana, Provincia de la Habana, 4♂ (11.8–17.7), 1♀ (12.1), 1909. (4) Río San Vincente near Viñales, Provincia de Pinar del Río (Holthuis, 1974:231).

JAMAICA: (Ortmann, 1895:410, in error for Newport's *Atya occidentalis*). *USNM, 2♀ (20.9, 21.0), 1–11 Mar 1884, *Albatross*. (1) Thomas River 1 mi N of Summerfield, Clarendon Pr (Hart, 1961b:64). (2) *RNHL, Río Minho at confluence with Pennants River, Clarendon Pr (Hart, 1961b:64), 2♂ (23.5, 26.8), 9 Apr 1959, C.W. Hart. (3) *USNM, Byndloss Gully, 1.5 mi N of Linstead on road to Ewarton, St. Catherine Pr (Hart, 1961b:66), 4♂ (18.0–26.2), 1♀ (18.2), 7 Apr 1959, G. Thomas, CWH. (4) Cane River, St. Andrew Pr (Hunte, 1978:142). (5) Morant River, St. Thomas Pr (Hunte, 1978:142). (6) Bugaboo River, St. Thomas Pr (Hunte, 1978:142). (7) Swift River, Portland Pr, alt 80 m (Hunte, 1978:142).

HISPANIOLA: *Haiti*—(Kingsley, 1878a:92). (1) †BM, Hinche, 2♂ (20.4, 30.1), I. Sanderson. (2) †BM, Thorlands, 1♂ (18.0), 1♀ (18.9), 2 ovig ♀ (12.4, 16.3), 17 May 1937, IS. *Dominican Republic*—(1) *USNM, "San Domingo," 1♂ (16.0), 1878, W.M. Gabb. (2) Río Haina (Bonnelly de Calventi et al., 1973:1338), 1♂ (30.5), I. Bonnelly de Calventi. (3) *MCZ, Río Nigua (Bonnelly de Calventi et al., 1973:1338) near San Cristóbal, Tru-

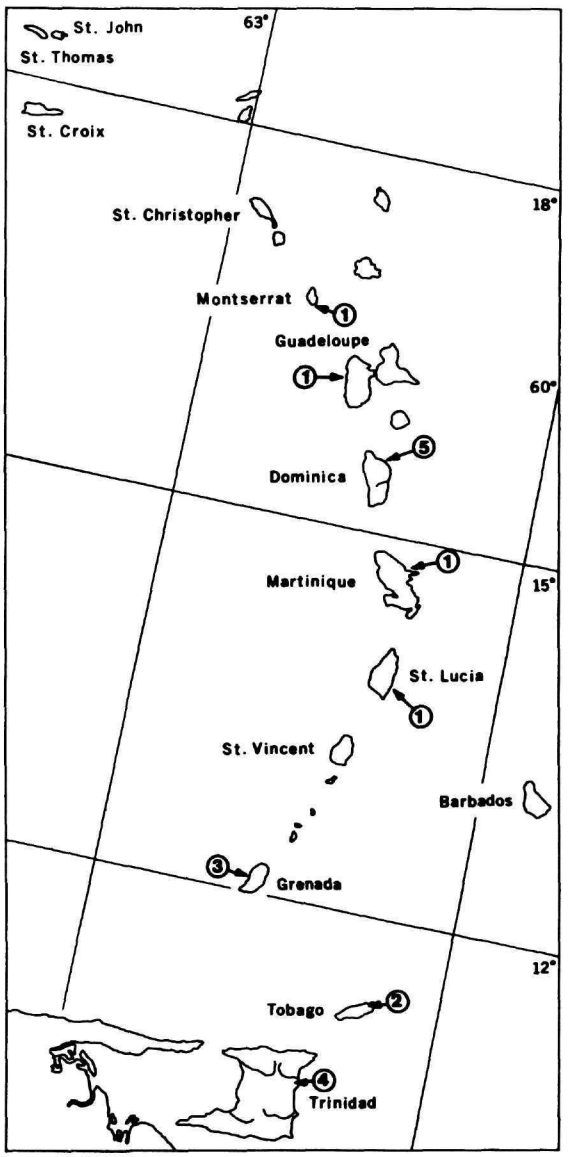

FIGURE 52.—Distribution of *Atya scabra* in the Lesser Antilles (circled numerals = number of localities).

jillo Pr, 5♂ (14.2–18.2), 3♀ (10.2–11.5), 5 ovig ♀ (10.1–11.3), P.J. Bermúdez. (4) †USNM, Río San Juan, 1♂ (9.6), S.G. Miller, Jr. (5) Río Mana (Bonnelly de Calventi et al., 1973:1338). (6) Cañada Madrigal (Bonnelly de Calventi et al., 1973:1338). (7) Río Isa (Bonnelly de Calventi et al., 1973:1338). (8) Río Jura (Bonnelly de Calventi, 1974a:16). (9) Río Nizao (Bonnelly de Calventi, 1974a:16).

PUERTO RICO: *USNM, San Juan Market (Gundlach, 1887:131), 1♂ (18.5), 14 Jan 1899. (2) *USNM, falls of Río Grande de Aibonito (Rathbun, 1901:119), 1♂ (22.9), 26 Jan 1899, *Fish Hawk.* (3) Falls of Río Grande de Arecibo (Rathbun, 1901:119). (4) El Yunque (Rathbun, 1901:119). (5) Trib to Río Añasco (Rathbun, 1901:119). (6) Río Espíritu Santo at El Verde (Villamil and Clements, 1976:5). (7) †USNM, Maricao, creek below town, 3♀ (11.0–12.5), 7 Feb 1934, S.F. Hildebrand. (8) †USNM, Río Maricao, 2♂ (28.0, 29.8), 1♀ (14.4), 9 Feb 1951, N.T. Mattox. (9) †USNM, (?) Maricao, Río Grande de Añasco, 1♂ (about 20), 21 Feb 1934, SFH. (10) †USNM, Juana Díaz, 8♂ (24.4–33.3), 1♀ (15.1), 26 Feb 1934, SFH. (11) †USNM, Río Comerío above S dam, 5♂ (36.5–40.9), 6 Mar 1934, SFH. (12) USNM, Río Culebrinas at Rte 13, 100 m S and 300 m E of San Sebastián, 4♂ (18.0–26.4), 2 Jun 1953, H.W. Harry. (13) †USNM, Río Cruces at Rte 2, 1500 m W of Sabana Grande, 2♂ (18.4, 22.7), 16 Jun 1953, HWH. (14) †USNM, Mayagüez, 1 ovig ♀ (13.3), 20 Jan 1899, *Fish Hawk.* (15) †USNM, Río Guanajibo, about 2,000 m E of San Germán, 1♂ (22.6), 16 Jun 1953, HWH. (16) †USNM, stream at Jayuya, 1♂ (42.2), Spring 1954, L.A. Costas.

SAINT KITTS: †RNHL, Wingfield, 5 juv (3.2–3.5), 30 Jun 1949, P.W. Hummelinck.

MONSERRAT: †BM, river at Monserrat, 4♂ (20.4–26.1), 1♀ (21.0), 2 ovig ♀ (16.4, 19.8), F.H. Mansell.

GUADELOUPE: Rivière Bras David (Lévêque, 1974:42).

DOMINICA: (Oliviera, 1945:177). *USNM, 2♂ (17.5, 22.3), 1♀ (18.0). (1) *USNM, trib to Layou River across from Clarke Hall (Chace and Hobbs, 1969:66), 1♂ (20.1), 4 Feb 1964, HHH. (2) *USNM, Mannet's Gutter near mouth (Chace and Hobbs, 1969:66), 1♂ (27.8), 1 Apr 1964, HHH; 1♂ (23.4), 19 Feb 1966, HHH; 2♂ (22.1, 23.6), 1♀ (15.6), 21 Feb 1966, HHH. (3) *USNM, Mannet's Gutter at upper bridge (Chace and Hobbs, 1969:66), 1♂ (21.1), 13 May 1966, Nichols and Oliver. (4) *USNM, Fond Figues River (to Castle Bruce River) (Chace and Hobbs, 1969:66), 1♂ (11.5) 22 Mar 1964, HHH. (5) *USNM, Pichelin River below Logge (to Stewart's River) (Chace and Hobbs, 1969:66), 1♂ (31.2), 26 Mar 1964, CWH, HHH.

MARTINIQUE: (Sharp, 1893:111). †MHNP, La Trinité, 3♂ (27.4–37.5), 2♀ (17.0, 18.8), 1 ovig ♀ (17.2), 1916.

SAINT LUCIA ISLAND: †BM, Marc Stream, 2 ovig ♀ (11.4, 12.1), 18 Jun 1971, G. Barnish and R.F. Sturrock.

GRENADA: (1) †RNHL, La Sagesse River, Coats Gap, St. Davids, 1 ovig ♀ (17.9), 9 Jan 1966, Justin Francis. (2) †RNHL, Beaulieu, 1 ovig ♀ (16.9), 3 Oct 1965, J.R. Groome. (3) †RNHL, St. Marks River, Bonaire Estate, 1♂ (11.5), 25 Jan 1966, C.A.O. Philips.

TOBAGO: (Ortmann, 1895:410). *BM, 2♂ (13.4, 14.9), 1 ovig ♀ (11.0), P.L. Guppy. (1) †RNHL, Frenchman's River at Speyside, 1♂ (17.3), 1♀ (10.1), 1 ovig ♀ (11.5), 18 Jan 1955, PWH.

TRINIDAD: *BM, 2♂ (34.0, 40.0), PLG. (1) *MHNP, Port of Spain (Bouvier, 1925:316), 1♂ (31.8), 1♀ (22.0), 1914, Paul Serre. (2) †MCZ, brook at Maguerepe Bay, 1♂ (18.0), 7 ovig ♀ (10.4–13.2), 24 Jul 1937, E. Deichmann. (3) †BM, Mt. Aripo, in small, clear, rocky river, 1♂ (16.1), 1♀ (20.0), 10 Aug 1937, IS. (4) †BM, Maracas River, 4♂ (26.1–35.2), 1♀ (19.5), 2 ovig ♀ (18.6, 20.3).

CURAÇAO: †RNHL, Santa Cruz Plantation near Santa Cruz, 1♀ (9.7), 1 ovig ♀ (11.0), 11 Jan 1957, L.B. Holthuis.

MEXICO: (Guérin-Méneville, 1829–1844:15). *RNHL, 2 dry spec (29.5, 34.8). *USNM, 1♂ (35.1). *Tamaulipas*—(1) †MCZ, Río Frío, 16 km N of Mante, 2♂ (15.0, 18.3), 21 Dec 1939, W.A. McLane. (2) *USNM, Río Sabinas (to Río Tamesi) at Storm's Ranch, km 619 Carretera Interamericana, 4.8 km NE of Gómez Farías (Darnell,

1956:131), 3♂ (22.7–25.5), 1 ovig ♀ (16.2), 27 Apr 1950, M. Darnell. *Veracruz*—(1) †USNM, Santa María, 2♂ (18.0, 19.5), 14 Feb, Nelson and Goldman. (2) †USNM, Orizaba, 1 ovig ♀ (14.4). (3) *BM, Misantla (Wiegmann, 1836:145), 3♂ (21.9–29.8), 1 ovig ♀ (18.6), 1888, F.D. Godman. (4) Río Necaxa near Coyutla (Villalobos, 1943:11). (5) Río Papaloapan (Villalobos, 1959:328). (6) Tapalapan, Santiago Tuxtla (Hobbs, 1971:27). (7) †BM, Hacienda El Hobo, Río de los Bobos, 1♂ (16.6), 1 ovig ♀ (21.1), Nov 1897, P. Geddes. *Oaxaca*—(1) *MHNP, Río Chacalapa near Pochutla (Bouvier, 1925:316), 1♂ (22.3), 1903, Diguet. (2) *MHNP, Valle Nacional (Bouvier, 1904:138), 3♂ (23.6–25.5), 4♀ (20.1–21.4).

GUATEMALA: (1) *USNM, Río Gualán at Gualán (Bouvier, 1925:317), 3♂ (17.5–33.5), 1♀ (20.0), 1 ovig ♀ (injured), 4 Jun 1909, C.C. Dean. (2) †RNHL, in drinking water on KNSM ship *Breda*, water last filled at Puerto Barrios, 1 juv (3.0), March 1966, J. Geÿskes.

HONDURAS: (1) †USNM, Lancetilla, 1♂ (21.1), 14 May 1946, A.F. Carr, Jr. (2) †USNM, Río Guayabal, trib to Río Comayagua, Dept de Cortés, alt about 100 m, 2♂ (28.9, 33.3), 22 May 1948, A.C. Chable. (3) †USNM, Lago de Yojoa, 1♂ (32.2), 7 Nov 1954, S.Y. Lin, Jr.

NICARAGUA: †USNM, Waspuc River at Musawas, 3♂ (20.0–32.5), 2 ovig ♀ (13.5, 16.7), Oct 1955, B. Malkin.

COSTA RICA: †BM, Salamanca, 1♂ (20.1), March 1895, HP.

PANAMA: *LGA, 9♂ (14.1–23.9). (1) Atlantic side (Doflein, 1900:127). (2) *USNM, Río Chagres Basin, Isla Barro Colorado (Allee and Torvik, 1927:67), 8♂ (6.2–15.0), 20 ovig ♀ (9.2–11.4), Aug 1962, H. Loftin. (3) †USNM, large river on mainland opposite Isla Multatupo, 6♂ (6.0–14.1), 4♀ (5.0–9.8), 1 ovig ♀ (9.4), 2 Dec 1962. (4) †USNM, San Blas area, creek just W of Puerto Obaldía, 7♂ (6.5–8.2), 4 ovig ♀ (10.1–10.4), 9 Feb 1963, HL. (5) †USNM, San Blas area, small river opposite Isla Ustupo (Portogandí), 1♂ (10.8), 1♀ (11.6), 1 ovig ♀ (9.3). (6) †USNM, Chiriquicito, backwaters and banks of Río Guarumo, 2♂ (16.8, 18.3), 1♀ (15.4), 3 ovig ♀ (9.2–13.7), 18 Apr 1963, HL. (7) †USNM, Río Lagarto between La Campana and Bejuco, 2♂ (9.6, 12.2), 2♀ (8.4), 1 ovig ♀ (9.5). (8) †LGA, "Atlantic Pipeline Road," 2♂ (28.6, 31.4), 1973, L.G. Abele and Robinson. (9) †LGA, stream 20–23 km N of El Llano on Cartí Hwy, 1♂ (11.3), 30 Mar 1973, R.L. Dressler. (10) †LGA, Río Frijoles, 1♀ (19.1), 14 May 1975, Kramer; 1♂ (25.1) Aug 1974.

COLOMBIA: (1) Río Carabalí, affluent of Río Chagri, Darién (Bouvier, 1904:138). (2) Santa Marta (Pearse, 1915:551).

VENEZUELA: (1) Río Macuto near La Guaira (Nobili, 1897:5). (2) †USNM, freshwater rocky branch at Macuto (cited by Rathbun, 1901:119, as "Venezuela"), 5♂ (13.5–25.1), 1 Aug 1900, Lyon and Robinson. (3) San Esteban (Bouvier, 1904:138). (4) *MHNP, Naricual (Bouvier, 1904:138), 5♂ (20.0–24.3), 1♀ (15.6), 1 ovig ♀ (20.8), 1885. (5) †RNHL, Río Tuy, Santa Teresa del Tuy, Estado de Miranda, 1♀ (18.6), Feb 1949, G. Marcuzzi. (6) †USNM, Río Cumboto near mouth, 2 km NW of Ocumare, 1♂ (7.3), 5 May 1939, F.F. Bond. (7) Río Manzanares, Cumaná, Estado de Sucre (Davant, 1963:100).

BRAZIL: (1) Rio Prangí, Estado do Pernambuco (Oliveira, 1945:177). (2) Rio Serinhaem, Estado do Pernambuco (Lemos de Castro, 1962:50). (3) †USNM, Blumenau, Estado do Santa Catarina, 1♂ (46.3), 1 ovig ♀ (29.5), Feb 1926, Paula Paul.

ERRONEOUS OR PROBABLY ERRONEOUS LOCALITIES.—There is reason to question the following localities as noted for each.

AUSTRALIA: Victoria (Bouvier, 1904:138). Two specimens reported by Bouvier, if correctly identified, almost certainly bore erroneous data, for no member of the genus, as defined herein, has since been reported from the continent.

NEW CALEDONIA: (Ortmann, 1890:465). The three syntypes of *Atya margaritacea* A. Milne-Edwards (1864), considered by Ortmann to belong to *A. scabra*, constitute the basis for this erroneous record. As pointed out elsewhere, that the specimens were collected on New Caledonia is highly improbable.

ROLAS ISLAND: (Rathbun, 1900:314). Apparently Rathbun erred in recording Rolas Island as having been cited to be frequented by *A. scabra*

by Greeff, and her error was repeated by Balss (1914:98).

BAJA CALIFORNIA: (Holthuis, 1951:25). Considering *Atya rivalis* (= *A. margaritacea*) to be a synonym of *A. scabra*, Holthuis cited Lower California as marking the northern limit of the range of the latter on the west coast of the Americas.

WESTERN MEXICO: (Stimpson, 1857:498). We have not located the specimens in the Smithsonian collections on which Stimpson based this record. Perhaps it is a valid one, for the lot cited here from Río Chacalapa, Oaxaca, contains a male of this species rather than one of *A. margaritacea* as we had anticipated.

NICARAGUA: (Rathbun, 1900:313). The Nicaraguan record was based upon the assumed synonomy of *A. rivalis* with *A. scabra*. The types of the former were from Nicaragua. A new locality on the eastern versant (see above) has established the presence of *A. scabra* in the country.

COSTA RICA: (Rathbun, 1900:313). The locality record for Costa Rica by Rathbun, and elaborated upon by Bouvier (1925:316), was based on a collection of *A. margaritacea* from Río Platanales, Mt. Chiriquí, which is in Panama. To our knowledge, the first valid record of the occurrence of the species in this country is the new one cited herein.

VENEZUELA: (Rathbun, 1900:313). Rathbun's recording the presence of *A. scabra* in the Orinoco was based on the assumed synonomy of Koelbel's *A. sculptilis* (= *A. gabonensis*) from the Orinoco River with *A. scabra*. Apparently she was unaware of the locality "Rio de Macuto" that had been reported by Nobili (1897:5).

ARGENTINA: †BM, Buenos Aires, 1♂ (22.5), Mar 1892, H.P. Hirt. Within the lot containing this specimen of *A. scabra* were two specimens of *A. margaritacea*. Inasmuch as the latter has been found elsewhere only in the Pacific watershed and has not been collected in other localities with *A. scabra*, the source of the specimens contained in this lot must be questioned.

VARIATIONS.—Try as we may, we have found no character or group of characters that enable us to distinguish the African *Atya sulcatipes*, *A. margaritacea* var. *claviger*, and the American *A. punctata* from the insular and continental American *Atya scabra* (including *A. mexicana*). Furthermore, the nature of the variations that have been reported to serve as a means of separating them, even were they reliable, seems to us to be so minor that they are hardly noteworthy. Most of the specimens that we have examined from Africa and the eastern Atlantic islands lack corneous denticles on the ventral margin of the second abdominal pleuron, but individuals in several lots possess one or more of them. The reverse is true of specimens from the Americas (including the West Indies). Comparisons of proportions of several features of the antennules and pereiopods resulted in the discovery of no feature that could be associated with a restricted part of the range.

The setal pile so conspicuous in recently molted individuals is sometimes exceedingly sparse. The rostral margins may be subparallel or rather strongly concave; the dorsal carina varies from being moderately high and rounded to high and sharp and frequently concave, sloping over the main body of the rostrum to the level of the lateral carinae; toward the apex, it may be smooth or scalloped but terminates at, or almost at, the tip of the acumen. The width and depth of the furrows flanking the median carina are also quite variable but, in general, are rather broad and shallow in small individuals, becoming deeper and the fundal area narrower (as a result of thickening of the basal parts of the lateral and median carinae) in larger, presumably older, individuals. The ventral carina may bear one or no spine along the anterior half.

The width of the penultimate podomere of the antennule ranges from only slightly less than the length to a little less than half as long. The basal podomere of that appendage bears none to three corneous spinules dorsally, and the premarginal spinules on the dorsal surface of the penultimate and ultimate podomeres vary both in number and position, the more laterally situated ones on the penultimate segment sometimes occurring in a linear series.

The merus of the third pereiopod ranges from about 2.0 to 2.7 times as long as high; the pattern of distribution of the tubercles on its lateral sur-

face follows somewhat that illustrated in Figures 45*j*, 46*f*, 48*f*, but the details are apparently never identical. In small individuals, a single ventrolateral spine occurs near the distal end of the podomere but is absent or reduced to a vestige in virtually all individuals with a carapace length greater than 20 mm. Whereas the number of tubercles on the flexor surface of the propodus of the third pereiopod may vary, some of those forming the row on the mesial side of the median line are contiguous or overlap (Figures 45*l*, 46*h*, 48*h*, 53). The spines on the merus and carpus of the ambulatory appendages in many, if not most, individuals with carapace lengths under 20 mm are dispersed as follows: the merus of the third pereiopod exhibits one distal ventrolateral spine, and the carpus lacks spines; the merus of the fourth pereiopod possesses in addition to one spine corresponding to that on the third another proximoventral to it, and the carpus bears one distal ventrolateral spine; the spination of the fifth pereiopod differs from that of the fourth in the presence of an additional spine on the ventral surface of the merus. Whereas spines are lacking on the third pereiopod in virtually all individuals with a carapace length of as much as 20 mm (and in some others that are smaller), in the largest specimen available the distolateral one is present on both the merus and carpus of the fourth and fifth; in some of the larger individuals, at least one of the ventral spines is present on the merus of the fifth, and in some individuals two are present on the merus of both the fourth and fifth legs.

Ecological Notes.—Ten years after this shrimp had been described from an unknown locality, Guilding (1825:338) reported its occurrence "in incredible numbers in the mountain streams" of Saint Vincent. As expressed in the "Review of Literature" above, Guilding probably did not distinguish this shrimp from the more commonly occurring *Atya innocous*. Newport (1847:159) noted that *Atya sulcatipes* had been found "300 feet above the level of the sea on San Nicolas, Cape Verde Islands." The reported occurrence of members of the species from "les côtes du Mexique" by Guérin-Méneville (1829–1844:15), H. Milne Edwards (1837:348), and others apparently gave some subsequent authors the impression that *A. scabra* occurred in salt water, for Stimpson (1857:498) stated that "Milne-Edwards considers *A. scabra* to be a marine form, but there is great doubt that any species of the genus is found in the sea." Gundlach (1887:131) found this shrimp in a tributary to Río Añasco in the interior of Puerto Rico. Osorio (1887–1906) reported its occurrence in several streams in the Cape Verde Islands and on other islands off the West African coast at altitudes of 200 (1892:200) to 300 m (1891b:140). Rathbun (1897:44) reiterated its presence in "Fresh waters of tropical America and Cape Verde Islands," and Aurivillius (1898:16) reported his *Atya margaritacea* var. *claviger* from "brooks." Pearse (1915:551) noted that in the area of Colombia in which he was exploring, "This peculiar shrimp was quite common in the swift streams flowing among bowlders [sic] over sandy bottoms near 'La Rosa.' It was found among or under bunches of dead leaves which had accumulated against sticks or stones."

Allee and Torvik (1927:67) stated that in Shannon Creek on Isla Barro Colorado, *A. scabra* was limited to the lower 24 pools. Villalobos (1943:11), in describing the locality on the Necaxa River from which his specimens were obtained, stated that it was situated 100 km from the sea, at an elevation of about 800 m in a tropical area surrounded by mountains. The stream at this site is shallow, and the shrimp live under the rocks in places where there are riffles. A collection made in this locality with a U-shaped net placed below the rocks as they were turned yielded 127 specimens in less than a half hour. Darnell (1956) conducted a populational study of *A. scabra* in Tamaulipas, Mexico. In describing the locality (pp. 131–132), he stated:

> The habitat of the shrimp was a turbulent riffle, 0–1 meter in depth, with a rock and boulder bottom. . . . Filamentous algae (*Lyngbya* and *Oscillatoria*) made up the only endogenous vegetation. This, however, constituted less than 5 percent of the total vegetation in the riffle, the remainder being composed of exogenous river borne branches, twigs, leaves, and seedpods. Vegetation from the two sources together amounted to 45.1 grams per square meter of riffle bottom.

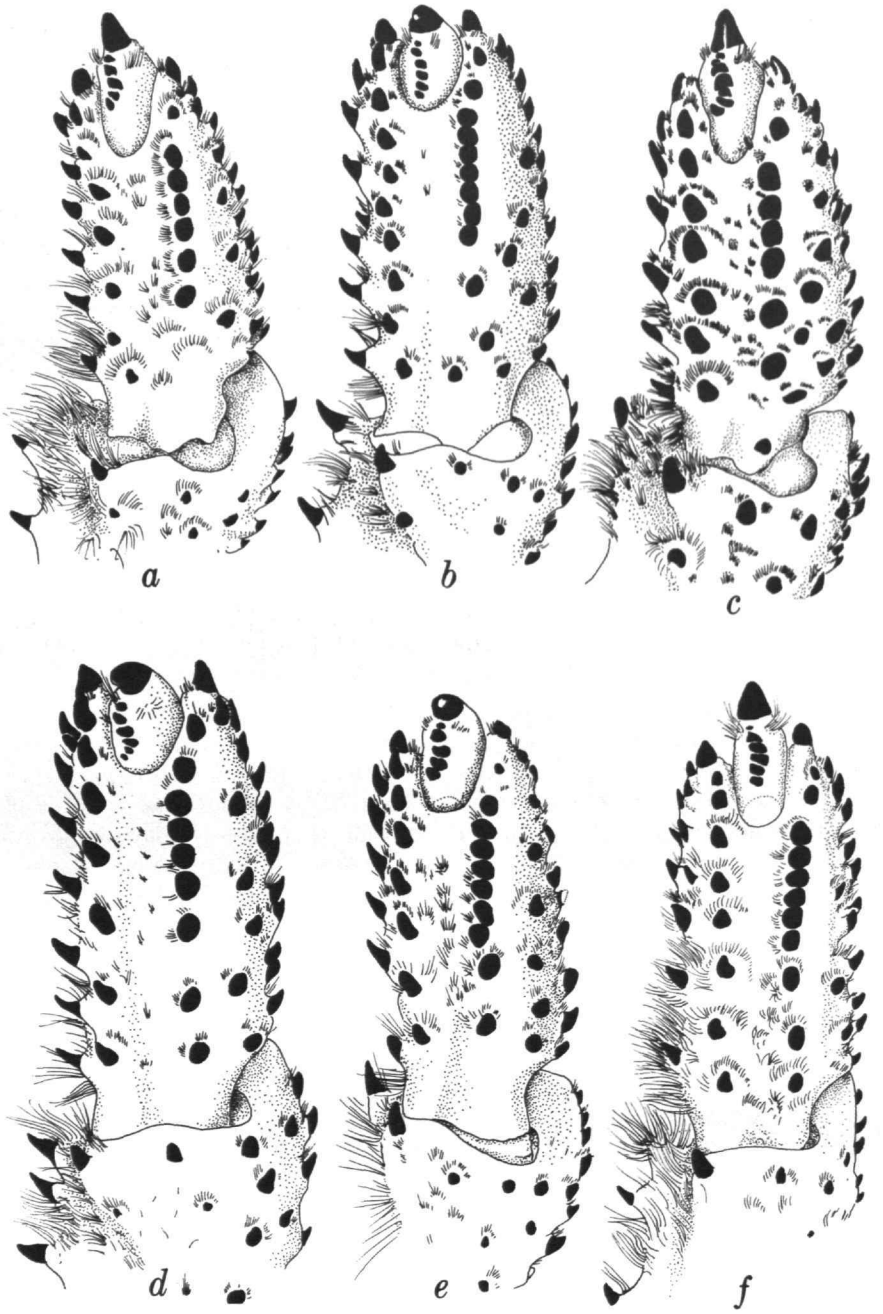

FIGURE 53.—*Atya scabra*, variations in flexor surface of distal part of third pereiopod (numbers in parentheses = carapace length in mm): *a*, Cavalla River, Liberia (♂, 23.1); *b*, Río Haina, Dominican Republic (♂, 30.5); *c*, Río Culebrinas, Puerto Rico (♂, 27.3); *d*, Lago de Yojoa, Honduras (♂, 32.2); *e*, Macuto, Venezuela (♂, 25.1); *f*, Blumenau Estate, Estado do Santa Catarina, Brazil (♂, 46.3).

In addition to the shrimp, an abundant and varied gastropod and insect fauna was present. . . .

Throughout six discontinuous months of field work during the winter, spring, and early summer no specimens of this shrimp were observed outside the riffle during daylight hours. At night, however, they were occasionally noted on rocky bottoms in adjacent shallow backwaters, particularly in the vicinity of weed beds.

Juveniles and some adult females were found along the edges of the riffle. An examination of stomach content revealed that 91.3% (by volume) consisted of unidentified detritus, 6.9% of plant remains, and 1.0% arthropod remains. Among the plants were diatoms, two of which he attributed to upstream sources, "*Spirogyra* sp., desmids, and epiphytic diatoms" were thought to have originated in weed beds, and *Oscillatoria* sp. in "the local riffle" (p. 135). The small amounts of *Oscillatoria* and *Lyngbya* present in the stomachs suggested to Darnell that the shrimp "were not feeding from the uppermost rocks but remained at the lowermost levels, consuming bits of detritus and other incidental material which filtered through to the bottom of the riffle" (pp. 135, 136). Few insect parts were present, but among the arthropod remains were parts of *Atya scabra*.

In collecting *Potimirim mexicana* (De Saussure, 1857) in the littoral zone of Río Papaloapan, Veracruz, Villalobos (1959:328) found juvenile specimens of *Atya scabra* and members of the genus *Macrobrachium* to be abundant among the submerged roots of the willow (*Salix humboldtiana*), which grows along the banks of the stream. He also reported discovering that *Atya scabra* spends the early stages of its development near the coast, later emigrating up river, becoming dispersed in areas far removed from the river mouths. He stated further that such juvenile forms have general similarity to individuals of *Potimirim mexicana*, and that in order to distinguish between them a certain knowledge of the distinctive features of the two genera is needed.

In their ecological classification of the freshwater decapods of the West Indies, Chace and Hobbs (1969:33) categorized *A. scabra* as a "typically freshwater species that invades marine habitats or have, or probably have, marine larvae." They reported that on Dominica this shrimp had been found in only a few localities, those at elevations between 17 and 117 meters where it "frequents cascading reaches and riffles of small streams . . . [secreting] itself among the stones over and among which water is rushing. Although it must travel through pools in moving from one congenial niche to another, it was neither observed nor collected in a pool during this study" (p. 66).

Hart and Hart (1969) recorded chemical and physical data collected in two seasons (March and November) from a station in Dominica from which *Atya scabra* was taken; Hunte (1978) provided additional data from two stations in Jamaica. The data from the two localities are summarized in Table 1.

Villamil and Clements (1976:5) believed *A. scabra* "to be the most ecologically restricted and most specialized member of the crustacean fauna of the area [upper Río Espíritu Santo at El Verde, Puerto Rico]. The females were collected only from rocky riffles and the males only from crevices between rocks over which a fast current was flowing."

Fryer (1977) also found *A. scabra* to be comparatively rare on Dominica and limited to habitats similar to those mentioned by Chace and Hobbs. He observed that an adult specimen kept in an aquarium "by day at least . . . had more retiring habits than *A. innocous*, making few appearances from the stones under which it took refuge, save to filter . . . " (p. 72). He found members of the species to feed primarily by filtering the water with the aid of its first and second pereiopods. The entrapped "food is transferred and manipulated by the extremely complex oral machinery . . . one of the most elaborate parts of this is a teaselling device in which components of the maxillae and first maxillipeds participate" (p. 58). The feeding mechanism is described by Fryer (pp. 98–104).

Hunte (1978) reported the results of his survey of the freshwater shrimps on the island of Jamaica; in each stream he made collections at high and low altitudes. *Atya scabra* appears to have been found at altitudes in the four localities cited of 335, 152, 380, and 380 meters (the latter two

TABLE 1.—Chemical and physical data for one station on the Pichelin River, Dominica (from Hart and Hart, 1969), and two stations in Jamaica, the Cane and Morant rivers (from Hunte, 1978), from which *Atya scabra* was taken

	Pichelin River		Cane River	Morant River
	Mar 1964	Nov 1966		
pH	7.7	7.6	7.5	7.7
Temperature (°C)	24.0	24.0	22.8	22.3
Dissolved oxygen (ppm)	8.0	7.9	8.5	8.7
Alkalinity (ppm)	42.0	58.6	-	-
CO_2 (ppm)	1.6	3.7	-	-
Cl (ppm)	13.6	13.6	-	-
Total hardness (ppm)	36.0	36.6	-	-
Calcium hardness (ppm)	22.2	25.0	-	-
Magnesium hardness (ppm)	13.8	11.6	-	-
SO_4 (ppm)	6.6	6.4	-	-
Ca (ppm)	8.9	10.0	-	-
Mg (ppm)	3.4	2.8	-	-
SiO_2 (ppm)	-	68.2	-	-
Specific conductivity (micromhos/cm)	-	127.3	-	-
NO_3 (ppm)	-	-	0.008	0.265
PO_4 (ppm)	-	-	0.384	0.362

the maximum altitude at which collections were made); however, Hunte (p. 139) stated that this shrimp was found at lower altitudes. Classifying it as a high-gradient species, he also subjected specimens to temperatures of 10°, 15°, 35°, and 40° C and recorded the survival time. They were as follows: 7.7 (±.07), 31.3 (±2.7), 26 (±7.6), and 4.7 (±2.1) hours, respectively. The temperature of the water in two of the localities where the shrimp was collected was 22.8° and 22.3° C. Three specimens were placed in an unaerated aquarium maintained at 25° C. The time of death ranged from 4.2 to 8.0 hours (mean 5.6 hours) when the oxygen tensions reached a level of a little less than 1.5 to 0.5 mg/l. The oxygen, NO_3, and PO_4 concentrations and pH at two of the localities where the shrimp was found are noted in Table 1, herein. Salinities of the sea near the mouths of the two streams were 31.9‰ and 28.3‰.

There is general agreement among almost all of the observers that *Atya scabra* frequents comparatively shallow (records include no more than one meter), swiftly flowing water where a rocky substrate exists, although some adult females and juveniles may frequent pools adjacent to riffle areas; young shrimp may also be found among submerged roots of shoreline plants. The altitude at which this shrimp has been collected ranges from sea level to 800 meters.

Should the larval requirements prove to be similar to those of *A. lanipes* and *A. innocous* reported by Hunte (1975, 1979b), then the first molt after hatching must occur in estuarine conditions or at least in brackish water.

LIFE HISTORY DATA AND POPULATION STRUCTURE.—The earliest report of ovigerous females accompanied by date of observation is that of Pearse (1915:551), who observed such females "often during the first week in August" in Santa Marta, Colombia. Villalobos (1943) sampled a population of *A. scabra* inhabiting Río Necaxa at Coyutla, Veracruz, Mexico, during March. His catch included 100 males and 27 females that exhibited a mean carapace length of 28.9 (total length, 68.5) mm and 19.0 (50.0) mm, respectively. In November, he obtained about 400 additional individuals among which there were

about 10% more males than were present in the collection made in March. He measured 100 males that had a mean carapace length of 29.2 (total length, 70.0) mm; some were "individous gigantes" having a carapace length as great as 38.8 (94.5) mm; smaller adult individuals had corresponding lengths of 23.2 (59.9) mm. Villalobos noted that his collections contained more males than females. Ovigerous individuals were found in both March and November.

In studying a population of *Atya scabra* in the Río Sabinas in southern Tamaulipas, Mexico, Darnell (1956) found the ratio of males to females to be 61:39. He also reported the males to be larger: the average total length was 68.5 mm with a maximum of 94.5 mm, and the average length of the females 50.0 mm. Of 23 females collected in late April, four were ovigerous; their total length and number of eggs (in parentheses) carried were as follows: 57.5 mm (8000 estimated), 50.5 mm (1111), 47.5 mm (1865), and 43.0 mm (746). The smallest female with ovarian eggs "large enough to be considered mature" had a total length of 39.0 mm. Two females of comparable size had "what appeared to be recently spent ovaries" (p. 137). Basing his opinion on the varied stages of development of the ovarian eggs, he expressed the belief, formerly stated by Villalobos, that "breeding takes place during most of the year" (p. 137). The average length of the eggs was 0.84 mm. Ovarian eggs of 13 nonovigerous females collected at that time had average lengths ranging from 0.38 to 0.87 mm. He suggested that a logarithmic relationship exists between body size and number of undeveloped eggs carried on the abdomen of the female. Assuming this to be factual, he calculated that the female with a total length of 50.5 mm should have carried about 3000 eggs instead of 1111 and concluded that "about 60 percent mortality is indicated for a group of eggs which had reached the eye pigment stage" (p. 137).

The dimensions of the eggs carried by specimens from the Cape Verde Islands and Venezuela were reported by Bouvier (1925:316) to be 0.58–0.64 × 0.40 and 0.65 × 0.37 mm, respectively.

Chace and Hobbs (1969:66) reported collections on Dominica of 15 males and four females of which one among the latter, collected on 29 January, was ovigerous. Lévêque (1974) observed ovigerous females on Guadeloupe in June. Bonnelly de Calventi (1974b:40) reported the occurrence of ovigerous females in March, April, May, June, July, September, October, and November.

The only information on longevity is that of Fryer (1977:72), who reported maintaining an adult individual in an aquarium with several specimens of *A. innocous* for 2.5 years.

Summarizing the data presented here, ovigerous females have been found in African waters in March, May, July, and August and in American waters in every month of the year. The smallest and largest ovigerous females that we have examined have carapace lengths of 7.1 and 29.5 mm, respectively.

COMMON NAMES.—The following common names have been applied to *Atya scabra*.

Bomingomô (in Batanga), Cameroon (Monod, 1928:206)
Bouc on Martinique (Pinchon, 1967:161)
Cacador in Guadeloupe (Holthuis, 1980:70) and in Dominica; also applied to *A. innocous* in Guadeloupe (Lévêque, 1974:42) and in Dominica
Camacuto in Venezuela (Davant, 1963:42)
Camarão on São Tomé (Osorio, 1889:139)
Chacales (probably derived from the Nauatl word "chacalli," according to Villalobos) in Veracruz, Mexico (Villalobos, 1943:12)
Conca, Cruca, or Camarão de pedra in northern Brazil (Fausto Filho, 1968:28)
Coruca in Pernambuco, Brazil (Holthuis, 1980:70)
Crevette gros-doigt in Cameroon (Monod, 1928:458)
Dikuta (in Bassa Bania), Cameroon (Monod, 1928:206)
Èkusa (in Soubou), Cameroon (Monod, 1928:206)
Guábaras on Cuba (Gundlach, 1887:131)
Guaricuru in Brazil (Marcgrave, 1648:187)
Inzé on Annobón (Osorio, 1895a:249)
Janga or Jonga on Jamaica; apparently applied to any freshwater shrimp on the island (Hart, 1961a:3)
Langostino in Dominican Republic (also applied to *A. innocous*; Bonnelly de Calventi, 1974b:40)
Langosta in Dominican Republic (also applied to *A. innocous* and *A. lanipes*; Bonnelly de Calventi, 1974b:40)
Mobéngomô (in Douala), Cameroon (Monod, 1928:205)
Patúa in Dominican Republic (Bonnelly de Calventi, 1974b:40)
Pepeluña in Dominican Republic (Bonnelly de Calventi, 1974b:40)

Sutu-feelee or "Bitter crayfish" in Africa (Rathbun, 1900:313)
Vieja in Dominican Republic (Bonnelly de Calventi, 1974b:40)
Viejitas in Cuba (also applied to *Atya innocous*) (Alayo, 1974:22)
Zapata in Dominican Republic (Bonnelly de Calventi, 1974b:40)

According to Holthuis (1980), the FAO names for the American *Atya scabra* are: Camacuto shrimp (English), Saltarelle camacuto (French), Camerón camacuto (Spanish). For the African representatives (formerly assigned to *Atya sulcatipes*), the FAO names are: Ekusa shrimp (English), Saltarelle ekusa (French), and Camerón ecusa (Spanish).

ECONOMIC IMPORTANCE.—Guilding (1825:338) stated that *Atya scabra* were caught for the market on Saint Vincent, and Gundlach (1887:131) reported their being in the market in San Juan, Puerto Rico. They were mentioned as being "excellent for eating" by Johnston (1906:843) in treating the fauna of Liberia. In their list of the shrimps and prawns of economic importance, Holthuis and Rosa (1965:9) reported that they were fished in the following: Mexico, Costa Rica, Panama, Nicaragua, British Caribbean Federation, Cuba, Haiti, Puerto Rico, Netherlands West Indies, and Venezuela. (Their Peruvian citation is for *Atya margaritacea*.) Chace and Hobbs (1969:45) also noted that they were eaten on Dominica. One of us (CWH) was informed that this shrimp is a food item on Jamaica.

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Part	*Pages*	*Plates*	*Year*
1–3	1–96	1–8	1881
4–8	97–240	9–22	1882

9, 10	241–304	23–28	1883
11–15	305–416	29–48	1884
16, 17	417–512		1886
18, 19	513–592	49, 50	1888
20–27	593–752	51–68	1889
28	753–800		1890
29–31	801–816	69–76	1891
32–34	817–896	77–82	1892
35–37	897–960	83–88	1893
38–40	961–976	89–96	1894
41–46	977–1056	97–108	1895
47–49	1057–1120	109–111	1898
50–52	1121–1168	112–116	1898
53–56	1169–1232	117–122	1899
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