

The Shrimp Genus *Atya*  
(Decapoda: Atyidae)

HORTON H. HOBBS, JR.  
and  
C.W. HART, JR.

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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 synonymy, 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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# The Shrimp Genus *Atya* (Decapoda: Atyidae)

*Horton H. Hobbs, Jr.*  
*and C. W. Hart, Jr.*

## 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 synonymy 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 out 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 Riksmuseet, 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. innocuous* 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: antierius par crurum quasi suras habet, crassius relinquit & vicem brachiorum fungens; paulo plus duobus digitis longum: medium parses quidigitum longum, ultimum paulo plus uno, omnia aculeata seu spinosa. Cirrhus 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) Innocuus" 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 *Atya 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 claviger*" 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. innocuus* Herbst. The validation of this name and Holthuis' clarification of its synonymy 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. innocuus* by Hunte (1975, 1977, 1979b), and the work on functional morphology and ecology of *A. innocuus* 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
<i>Atya africana</i> Bouvier, 1904	<i>Atya africana</i>	<i>Atya africana</i>
<i>Atya intermedia</i> Bouvier, 1904	<i>Atya intermedia</i>	<i>Atya intermedia</i>
	<i>Atya innocous</i>	<i>Atya innocous</i>
	(Herbst, 1792)	
<i>Atya robusta</i> A. Milne-Edwards, 1864	( <i>Atya robusta</i> )	( <i>Atya robusta</i> )
<i>Atya occidentalis</i> Newport, 1847	( <i>Atya occidentalis</i> )	( <i>Atya occidentalis</i> )
( <i>Atya tenella</i> Smith, 1871)	<i>Atya tenella</i>	( <i>Atya tenella</i> )
<i>Atya scabra</i> (Leach, 1815)	<i>Atya scabra</i>	<i>Atya scabra</i>
( <i>Atya mexicana</i> Wiegmann, 1836)	( <i>Atya mexicana</i> )	( <i>Atya mexicana</i> )
( <i>Atya punctata</i> Kingsley, 1878a)	( <i>Atya punctata</i> )	( <i>Atya punctata</i> )
		( <i>Atya sulcatipes</i> )
		( <i>Atya margaritacea</i>
		<i>claviger</i> )
( <i>Atya margaritacea</i> A. Milne-Edwards, 1864)	( <i>Atya margaritacea</i> )	<i>Atya margaritacea</i>
( <i>Atya sulcatipes</i> Newport, 1847)	<i>Atya sulcatipes</i>	
( <i>Atya margaritacea</i> var. <i>claviger</i> Aurivillius, 1898)	( <i>Atya margaritaria</i> <i>claviger</i> )	
( <i>Atya rivalis</i> Smith, 871)	<i>Atya rivalis</i>	( <i>Atya rivalis</i> )
<i>Atya gabonensis</i> Giebel, 1875	not mentioned	<i>Atya gabonensis</i>
( <i>Euatya sculptilis</i> Koelbel, 1884)	not mentioned	( <i>Euatya sculptilis</i> )
( <i>Atya sculptata</i> Ortmann, 1890)	not mentioned	( <i>Atya sculptata</i> )
<i>Euatya crassa</i> Smith, 1871	not mentioned	<i>Atya crassa</i>
	not mentioned	<i>Atya ortmannioides</i>
		Villalobos, 1956
		<i>Atya lanipes</i>
		Holthuis, 1963
		<i>Atya dressleri</i>
		Abele, 1975
		<i>Atya brachyrhinus</i> ,
		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 pterygostomial 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. dres-*

*sleri* 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-

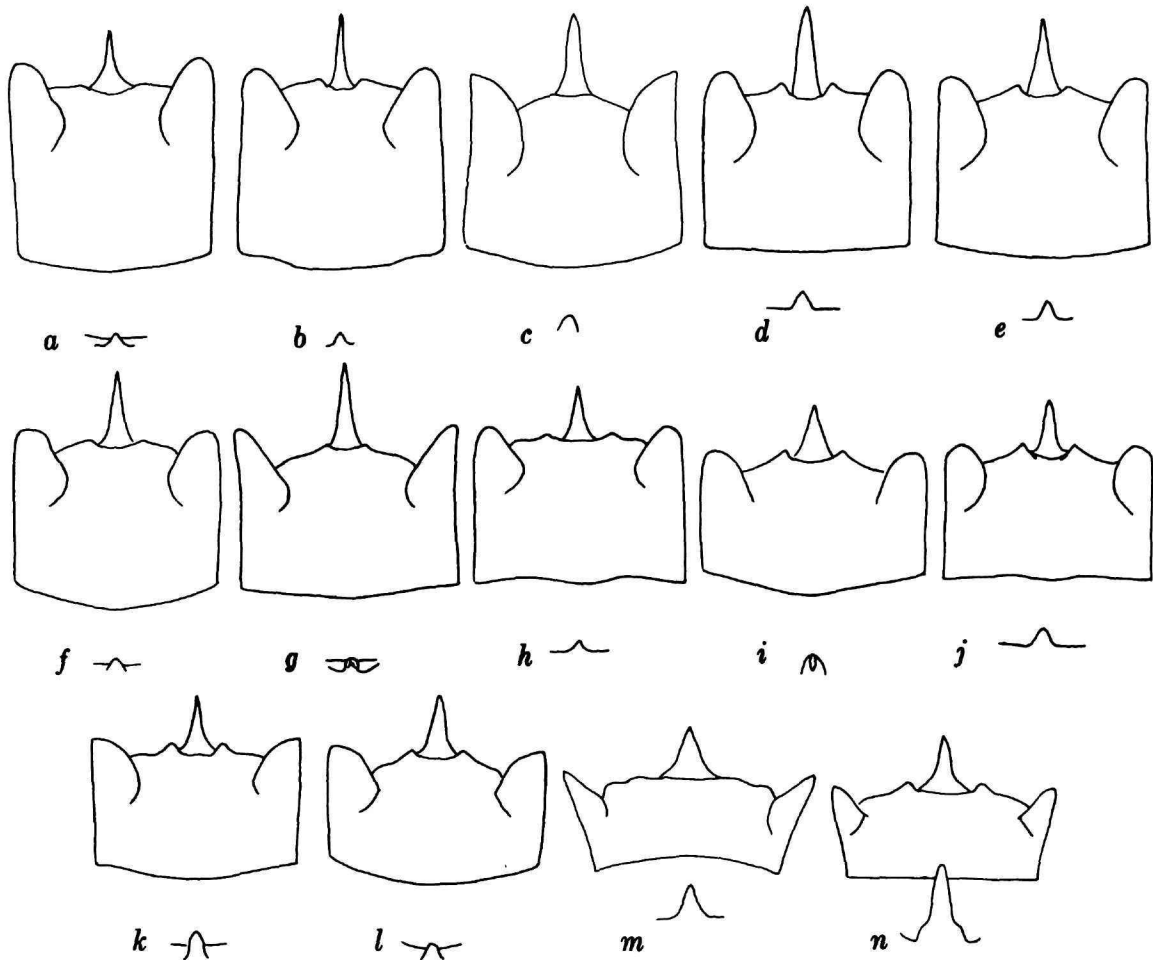


FIGURE 1.—Ventral view of preanal carina, sternum of sixth abdominal segment, and median tubercle (or projection) on fifth abdominal segment in: a, *Atya lanipes*; b, *A. ortmannioides*; c, *A. brachyrhinus*; d, *A. innocous*; e, *A. tenella* (= *A. innocous*); f, *A. intermedia*; g, *A. dressleri*; 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 alpheidids 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 pereopod 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 pereopod 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 pereopods 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 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.

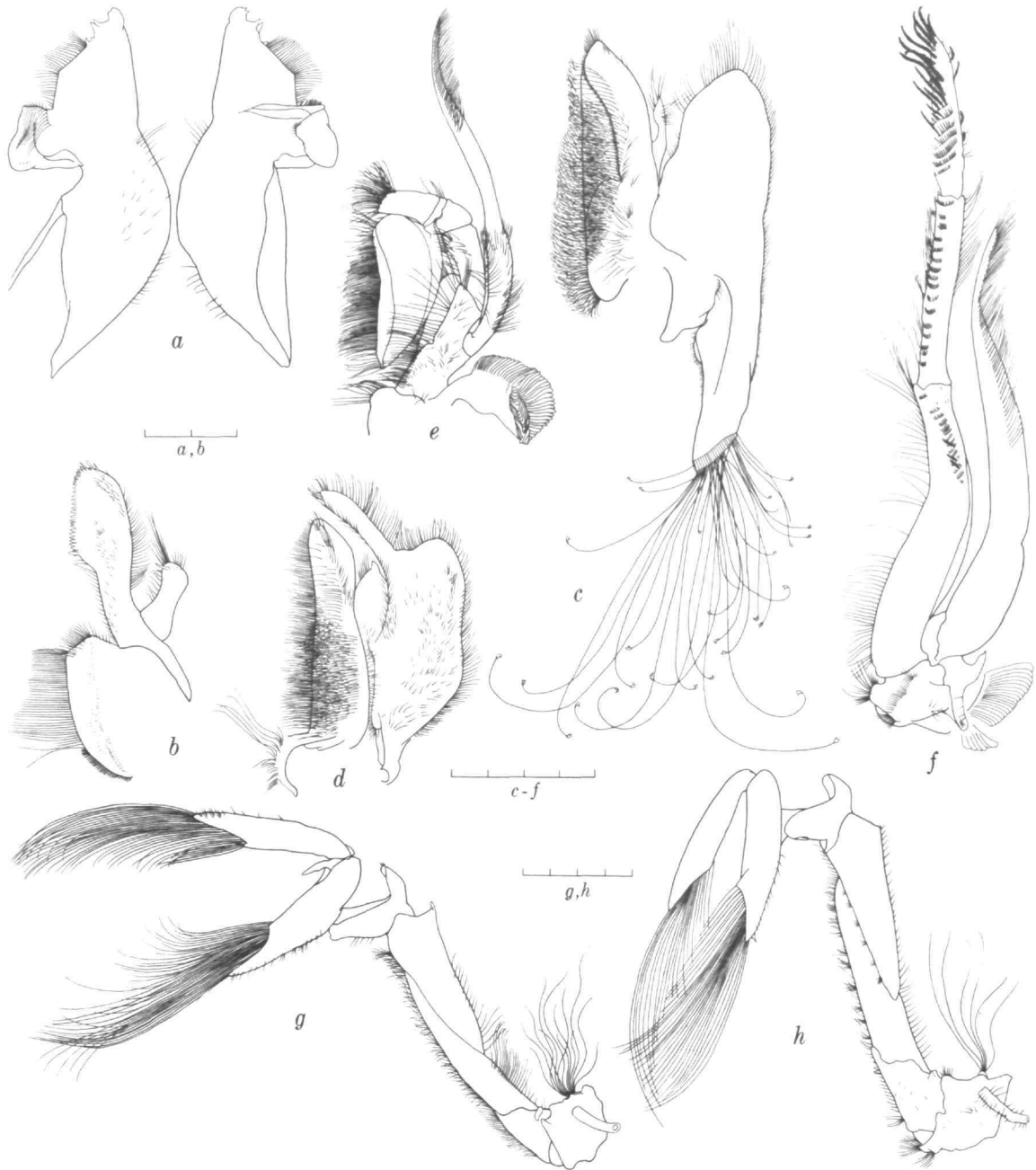


FIGURE 2.—Appendages of *Atya innocuus* (all from male, Mannet's Gutter, Dominica): *a*, lateral and submesial views of mandible; *b*, first maxilla; *c*, second maxilla; *d*, first maxilliped; *e*, second maxilliped; *f*, third maxilliped; *g*, first pereiopod; *h*, second pereiopod. (Scales marked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

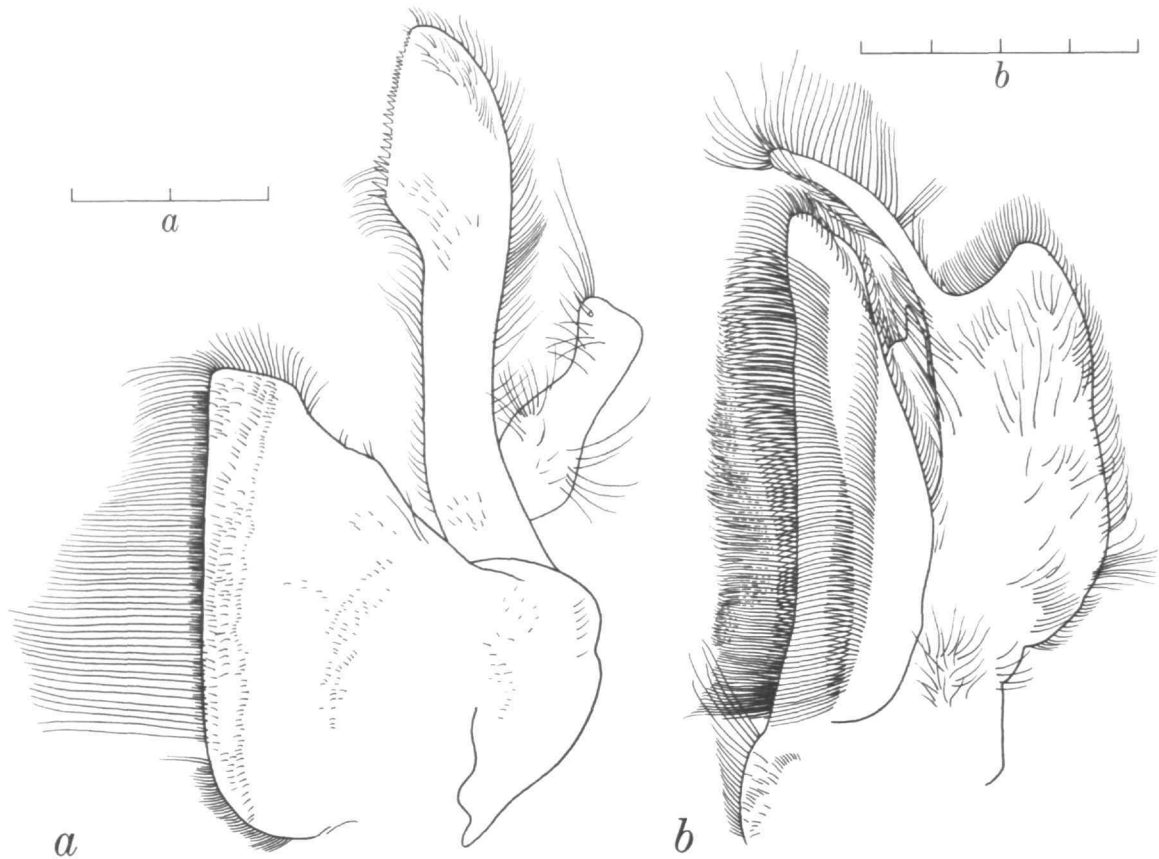


FIGURE 3.—Gnathal appendages of male of *Atya gabonensis* from Volta River, Ghana: *a*, first maxilla; *b*, first maxilliped. (Scales marked in 1 mm increments.)

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 pereopods 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 4a,b),

**THIRD PEREIOPOD.**—Among the most useful characters for distinguishing between the several species are those associated with the third pereopod. The coxa of *Atya crassa* is unique in two respects: the ventrodistal margin is distinctly scal-

loped, and the anterolateral angle of this podomere on both the third and fourth pereopods 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

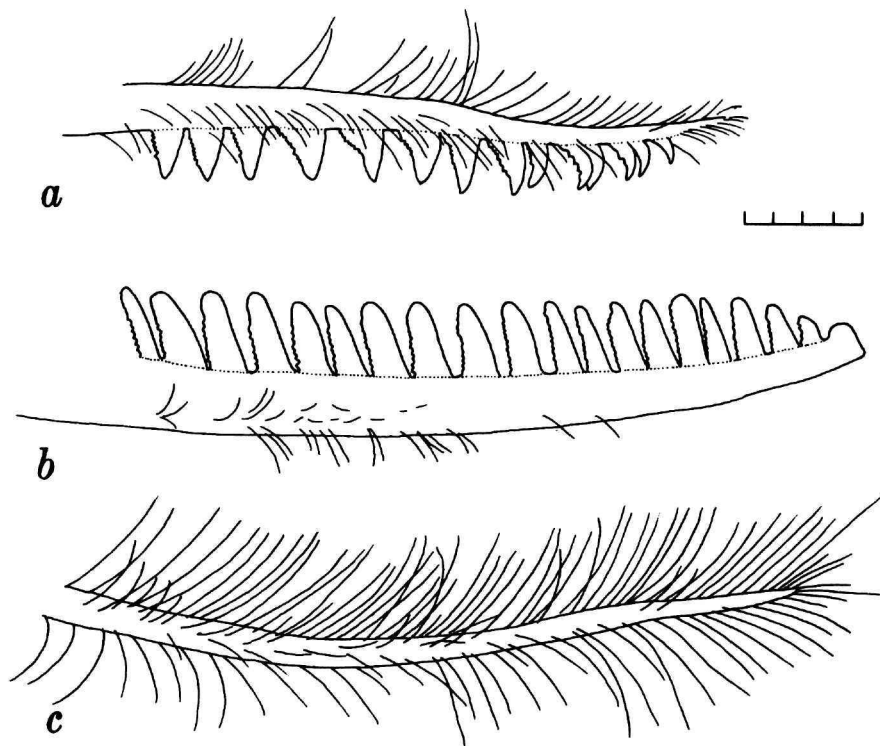


FIGURE 4.—Bristles from distal tufts of first pereopod: a, distal part of bristle bearing scraping denticles in *Atya innocous*; b, same in *A. lanipes*; c, distal part of bristle that serves as a brush seta in *A. lanipes*. (Scales marked in 1 mm increments.)



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 pereopods are variable as pointed out by Chace and Hobbs (1969:63), who noted that in none of their specimens of *Atya lanipes* from Puerto Rico are the pereopods "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 pereopods 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 pereopod 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 PEREIPODS.**—Further study should be accorded the fourth and fifth pereopods. 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 pereopods 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 pereopod of *A. ortmannioides* (Figure 43c) 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 5d and 5e,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

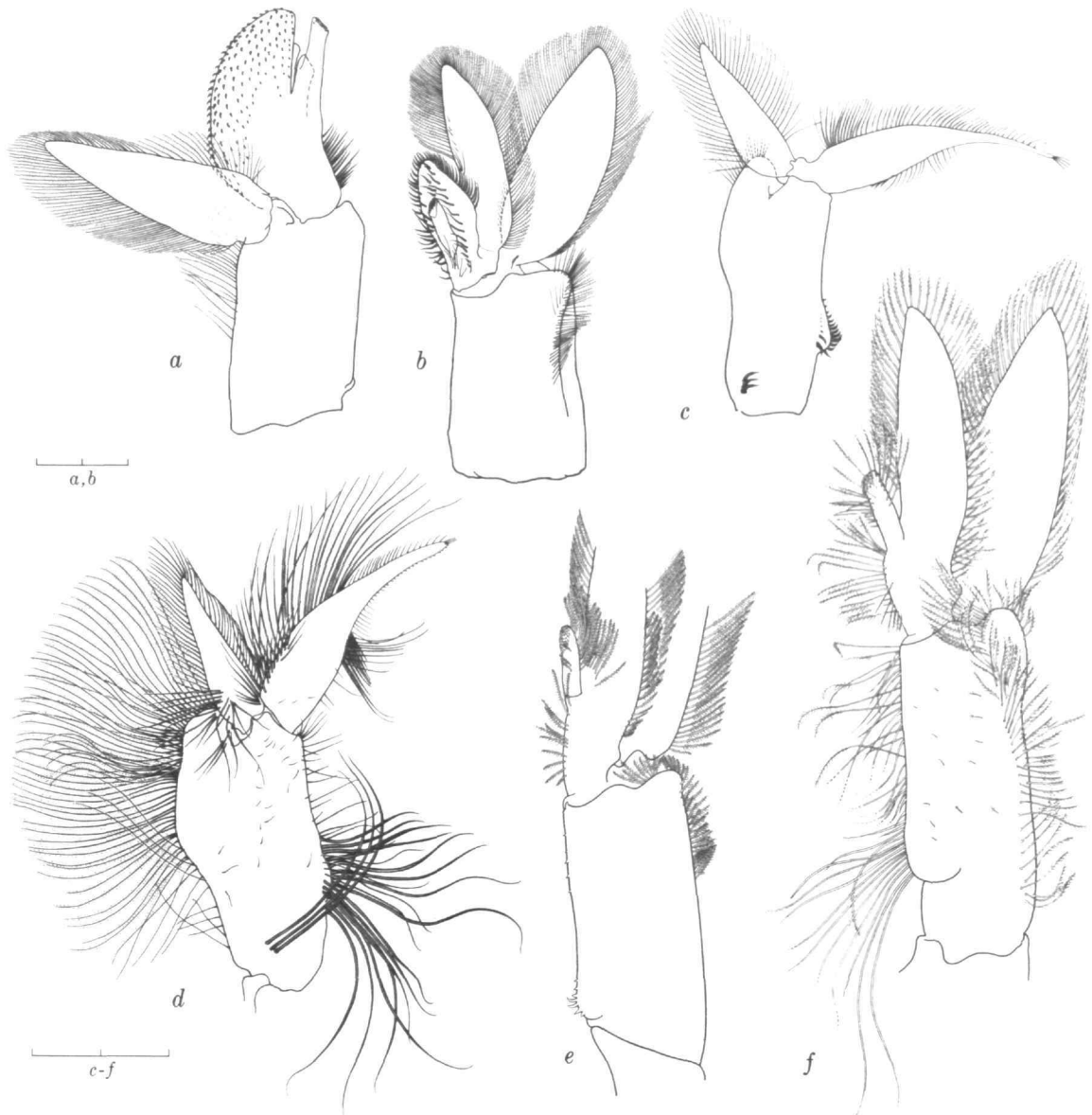


FIGURE 5.—Appendages of *Atya innocous* (all from Mannet's Gutter, Dominica); *a*, first pleopod of male; *b*, second pleopod of male; *c*, first pleopod of female; *d*, first pleopod of ovigerous female with ovigerous setae; *e*, basal part of third pleopod of nonovigerous female; *f*, third pleopod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

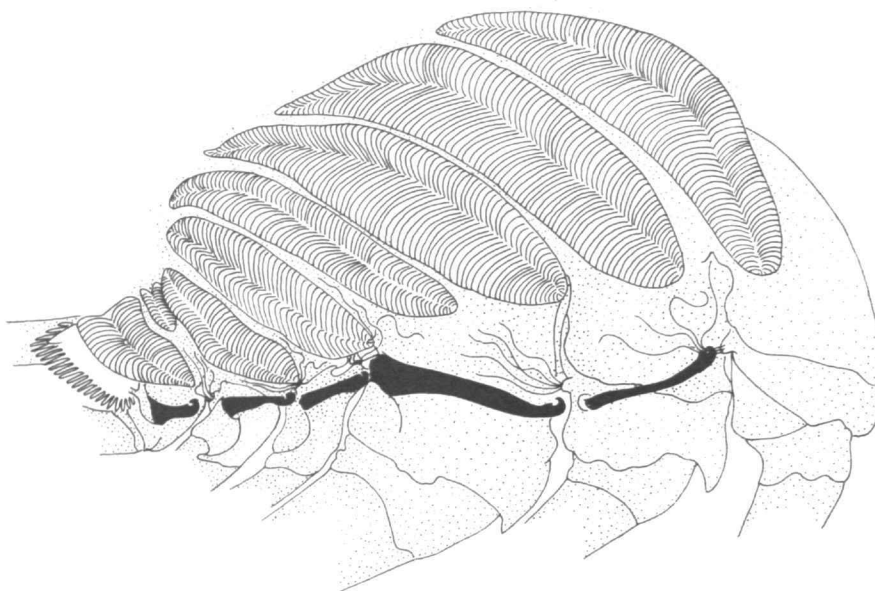


FIGURE 6.—Branchial apparatus of left side of *Atya innocous* (epipods black).

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:

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

The regression lines  $y = 3.41925 + 3.03262x$  and  $y = -0.77307 + 0.32241x$  are shown in Figure 7a 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-

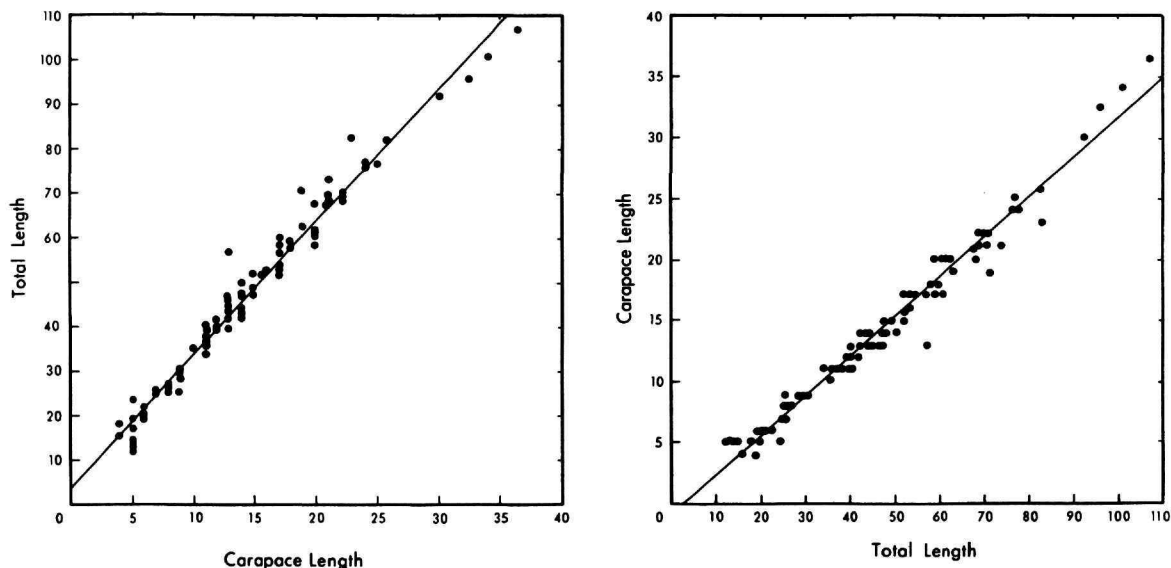


FIGURE 7.—Correlations of carapace length and total length in *Atya innocous*. (See "Measurements and Size Correlations" for explanation.)

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

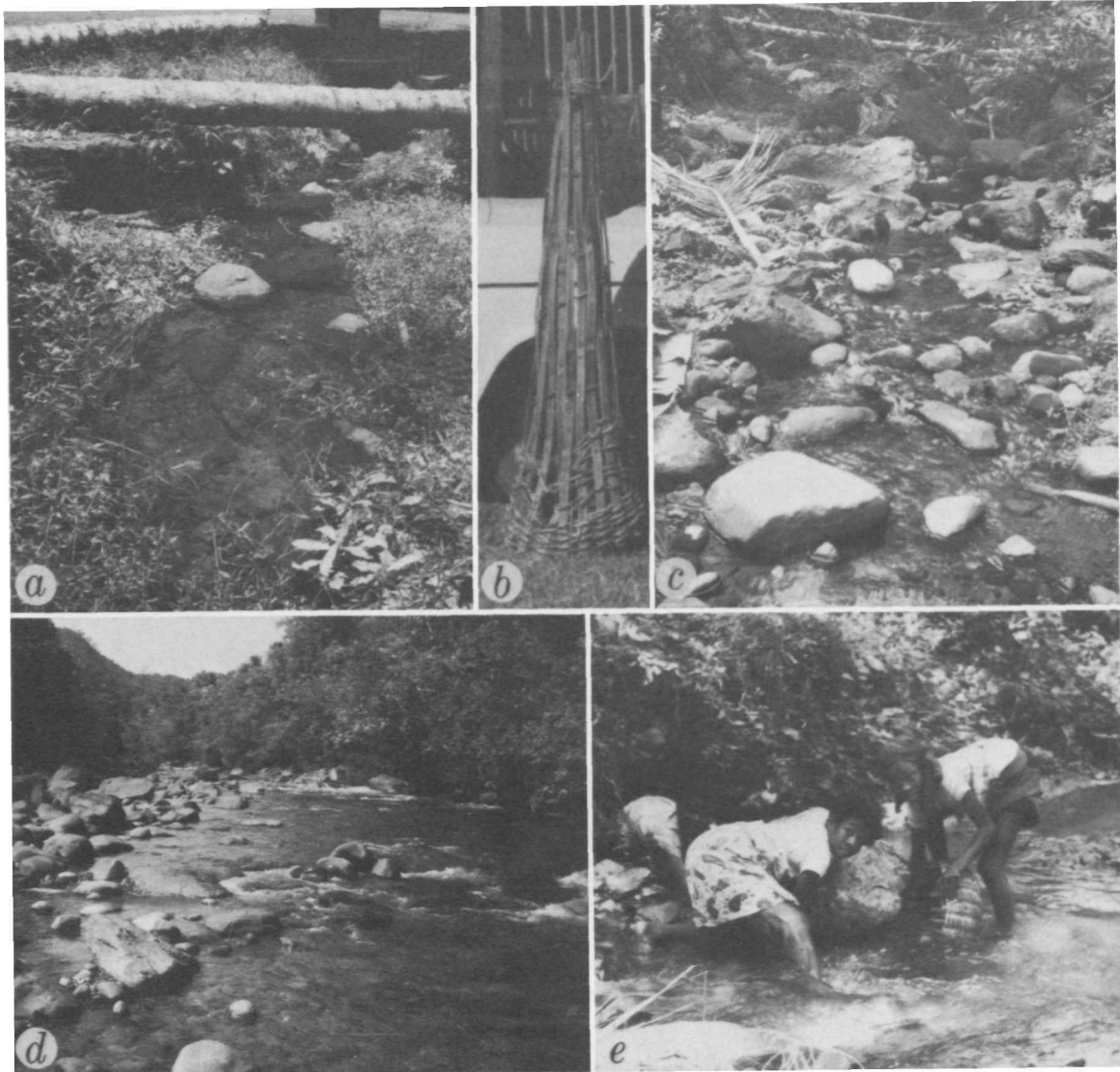


FIGURE 8.—Habitats exploited by members of the genus *Atya*, and implements used in Jamaica to catch freshwater shrimps: *a*, Mannet's Gutter, near mouth, in Dominica, frequented by *Atya innocous*; *b*, basket employed in Jamaica in catching both atyid and palaemonid shrimps; *c*, an upstream locality 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 head-water 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.

### 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.

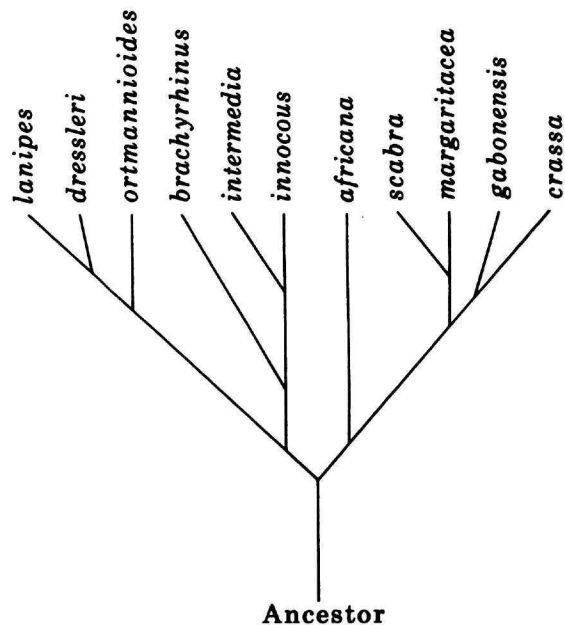


FIGURE 9.—Dendrogram depicting relationships of members of the genus *Atya*.

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 pterygostomial 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 pereopods 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 pereopod are arranged in a contiguous or subcontiguous 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 pereopod 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 pereopod are arranged in a linear series. That *A. scabra* has digressed slightly more from the supposed ances-

tral 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 blade-like, 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



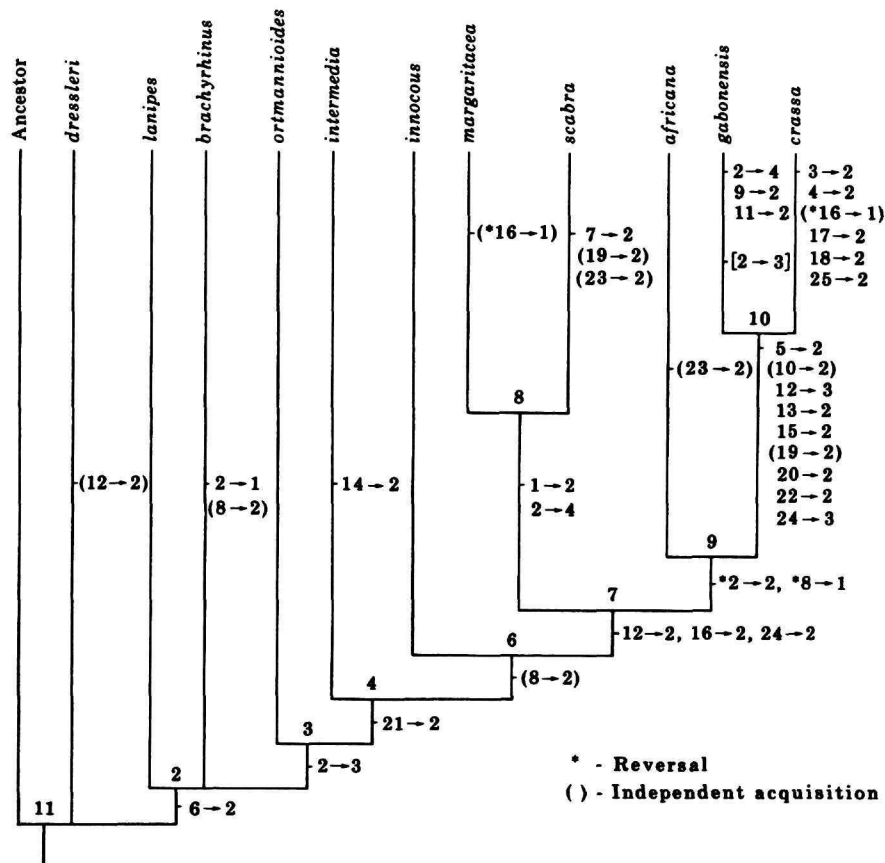


FIGURE 10.—Cladogram expressing relationships of members of the genus *Atya*.

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 blade-like
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, pereopod III	(1) ventrodiscal margin not scalloped, (2) scalloped
18. Coxa, pereopod III	(1) anterolateral spine absent, (2) present
19. Coxa, pereopod III	(1) caudomesial projection small or absent, (2) strong
20. Merus, pereopod III	(1) bowed, (2) straight
21. Merus, pereopod III	(1) lateral tubercles not strongly cornified, (2) strongly so
22. Merus, pereopod III	(1) distoventral prominence absent or not opposed; (2) strong and opposed by tubercle on carpus
23. Propodus, pereopod III	(1) flexor surface with tubercles scattered or not contiguous in mesial row, (2) those of mesial row contiguous
24. Dactyl, pereopod 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 disjointed 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 head-water 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 pereopod, 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

- Atya* Leach, 1815:345 [type-species by monotypy: *Atya scaber* Leach, 1815:345; gender masculine; junior homonym of *Atya* De Montfort, 1810:342 (Mollusca)].  
*Atya* Leach, 1816:421 [substitute name for *Atya* Leach, 1815:345; type-species by monotypy: *Atya scaber* Leach, 1815:345; gender feminine].  
*Atia*.—Latreille, 1817:37 [erroneous spelling].  
*Athys*.—H. Milne Edwards, 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
<i>Atya africana</i>			x
<i>Atya brachyrhinus</i>		x	
<i>Atya crassa</i>	x	x	
<i>Atya dressleri</i>	x		
<i>Atya gabonensis</i>		x	x
<i>Atya innocous</i>	x	x	
<i>Atya intermedia</i>			x
<i>Atya lanipes</i>		x	
<i>Atya margaritacea</i>	x		
<i>Atya ortmannioides</i>	x		
<i>Atya scabra</i>	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."

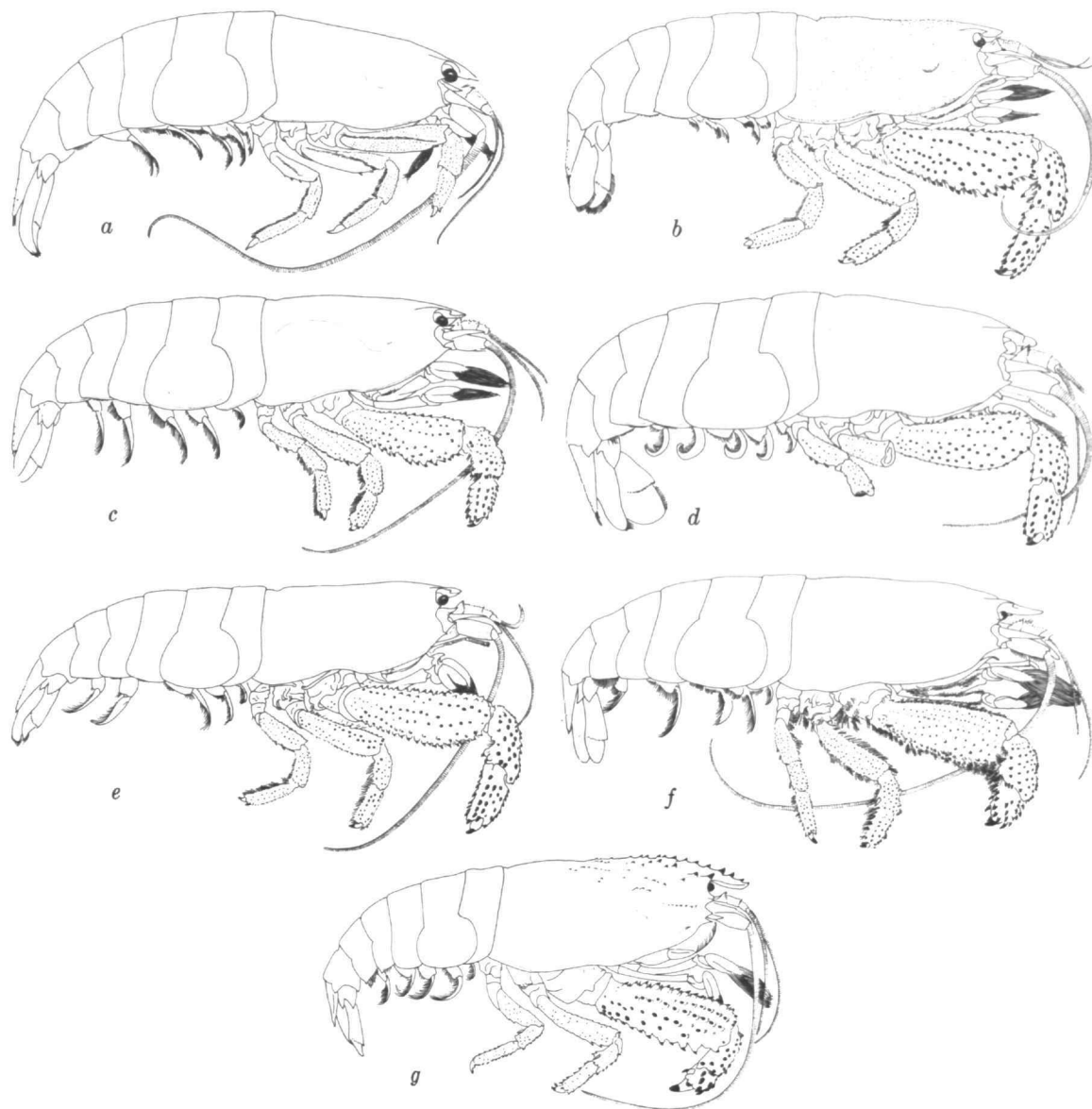


FIGURE 11.—Lateral views of members of genus *Atya* (numbers in parentheses = carapace length in mm): a, *A. africana*, Mount Coffee, Liberia (♂, 22.6); b, neotype of *A. scabra*, Misantla, Mexico (♂, 29.8); c, *A. scabra*, São Tiago, Cape Verde Islands (♂, 24.5); d, syntype of *A. margaritacea* (♂, 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).