

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'espèce 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 illustra-

tion 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 synonymy 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 pereopod, lateral view of the first pereopod, 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 pereopods lacking prominent spine anterolaterally. Third pereopod with merus somewhat flattened ventrally, about 2.5 times as long as high; ventromesial surface parallel to that of corresponding podomere of other third pereopod, 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 podomers 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 postero-median 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 pereopod reaching ultimate podomere of

antennular peduncle, second reaching base of distal fourth of fingers of first pereopod; terminal brush of setae of both appendages lacking scraping denticles. Third pereopod (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 pereopod with dactyl reaching base of distal third of merus of third pereopod; length of merus slightly less than twice that of carpus, and latter little longer than propodus. Fifth pereopod reaching just beyond merocarpal joint of fourth pereopod; 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 pereopod 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 pereopod similar to that of fourth but with additional smaller spine on merus proximal to ventral spine.

Diagnosis 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-

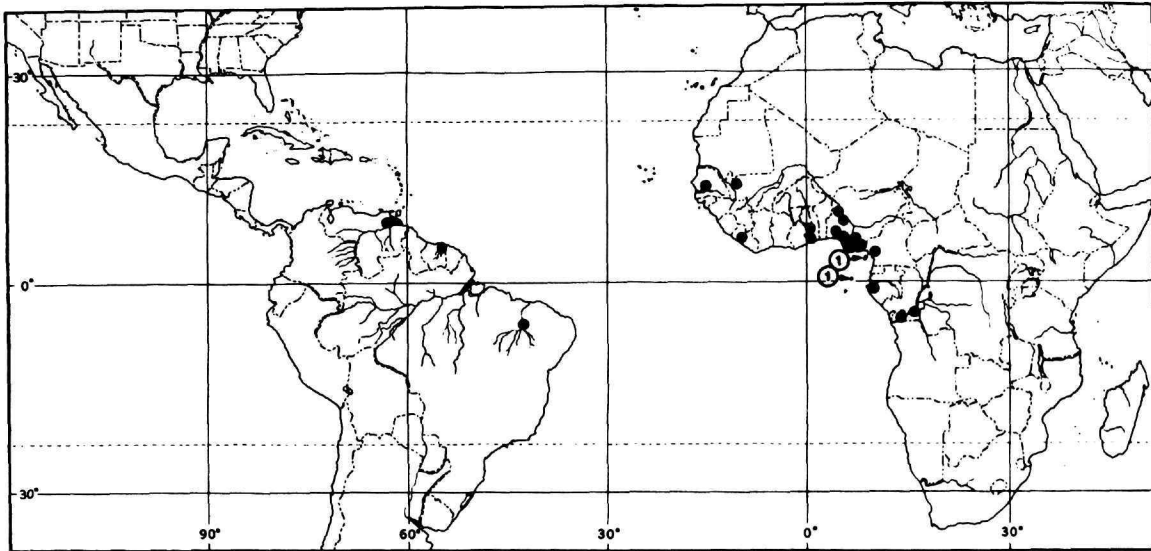


FIGURE 21.—Distribution of *Atya gabonensis* (circled numerals = number of localities).

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 Parnaíba, 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 Férou," 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, com-

parable 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-toruôpuru (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)
 Oporu (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 innocuus (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) Innocuus 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.—Gibbel, 1875:52.—Kingsley, 1878a:92, 93; 1878b:57.—Bate, 1888:693.—Pocock, 1889:11–16, pl. 2: fig. 3, 3*a*; 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 innocuus.—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, 10*a-c*, 14*a,b*, pl. 1.—Chace, 1972:14.—Bonnely de Calventi et al., 1973:1338.—Upatham and Sturrock, 1973:448–452.—Bonnely 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).
Atya occidentalis.—Vélez, 1967:42 [erroneous spelling].
Atya innocuus.—Alayo, 1974:25 [erroneous spelling].—Bonnely 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) Innocuus* 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. McNeil 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 pereopods 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 synonymy 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 8b,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 synonymy 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 synonymy, 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

Esperito 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 pereopods, and, moving parallel to her body, repeatedly touched her with his extended third and fourth pereopods. 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 pereopod. 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 pereopod 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 pereopods, details of the structure, musculature, and setae of the first pereopod, 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 pereopods lacking prominent anterolateral spine. Third pereopod 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 pereopod, 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 22a,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

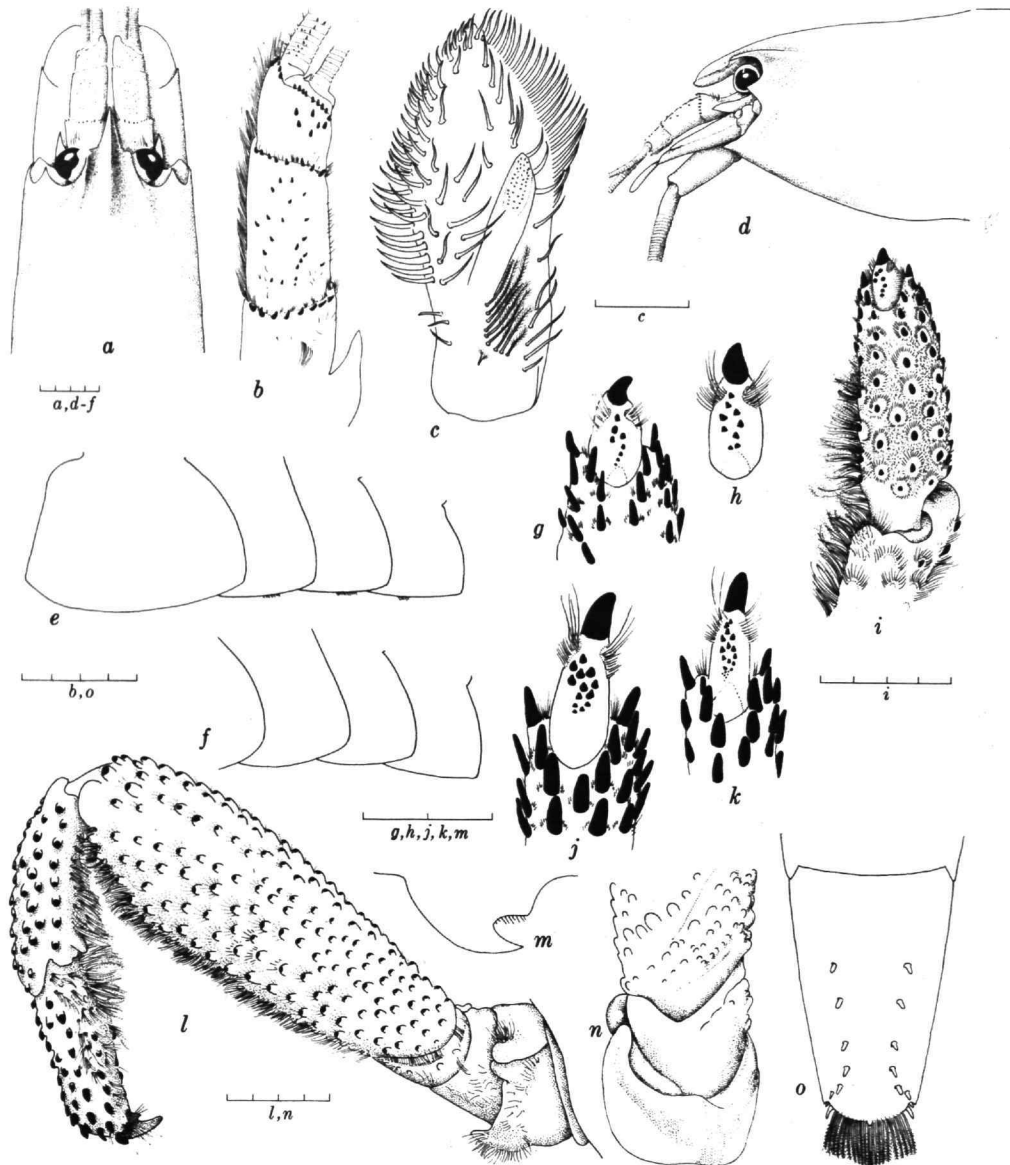


FIGURE 22.—*Atya innocens* (all from males from Mannet's Gutter, Dominica): a, dorsal view of cephalic region; b, dorsal view of antennular peduncle; c, mesial view of appendices masculina and interna; d, lateral view of carapace; e, f, lateral view of second through fifth abdominal pleura; g, flexor 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 pterygostomial 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 pereopod 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 pereopod (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 pereopod with dactyl reaching distal end of proximal third of carpus of third pereopod; merus about 1.8 times as long as carpus; latter subequal in length to propodus. Fifth pereopod reaching distal extremity of carpus of fourth pereopod; merus 1.3 times as long as carpus, latter approximately 0.8 as long as pro-

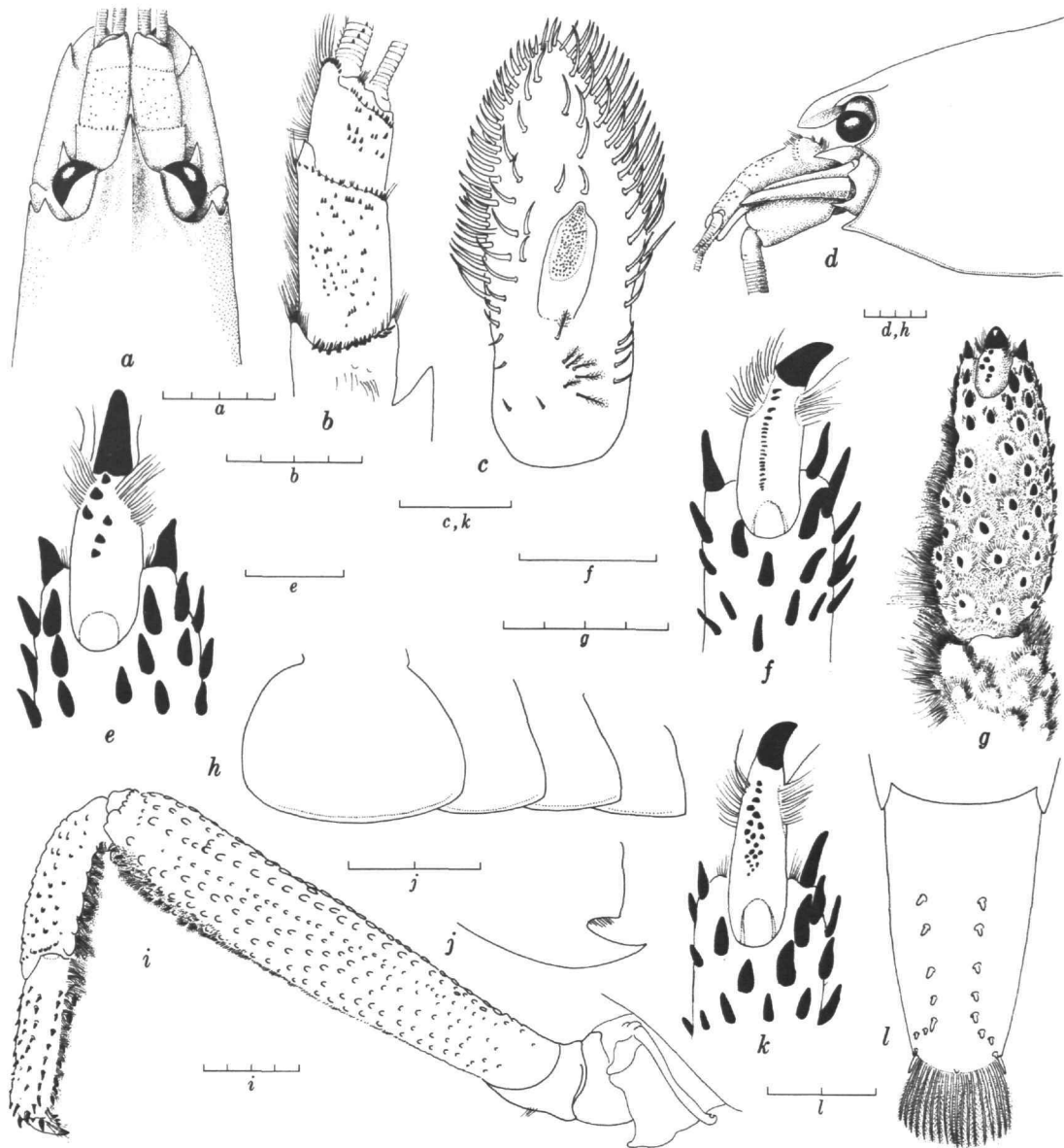


FIGURE 23.—*Atya innocous* (a, male syntype of *A. tennella*; b–d,h–j,l, male from Cerro Azul area, Panama; e–g,k, male from Río Guabas, Panama): a, dorsal view of cephalic region; b, dorsal view of antennular peduncle; c, mesial view of appendices masculina and interna; d, lateral view of cephalic region; 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 pereopod 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 pereopod similar but with 3 ventral spines on merus and 2 distolateral spines on carpus.

Diarsis 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 pereopods 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 pereopods with basal podomeres as in third pereopod; 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 pereopod.

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

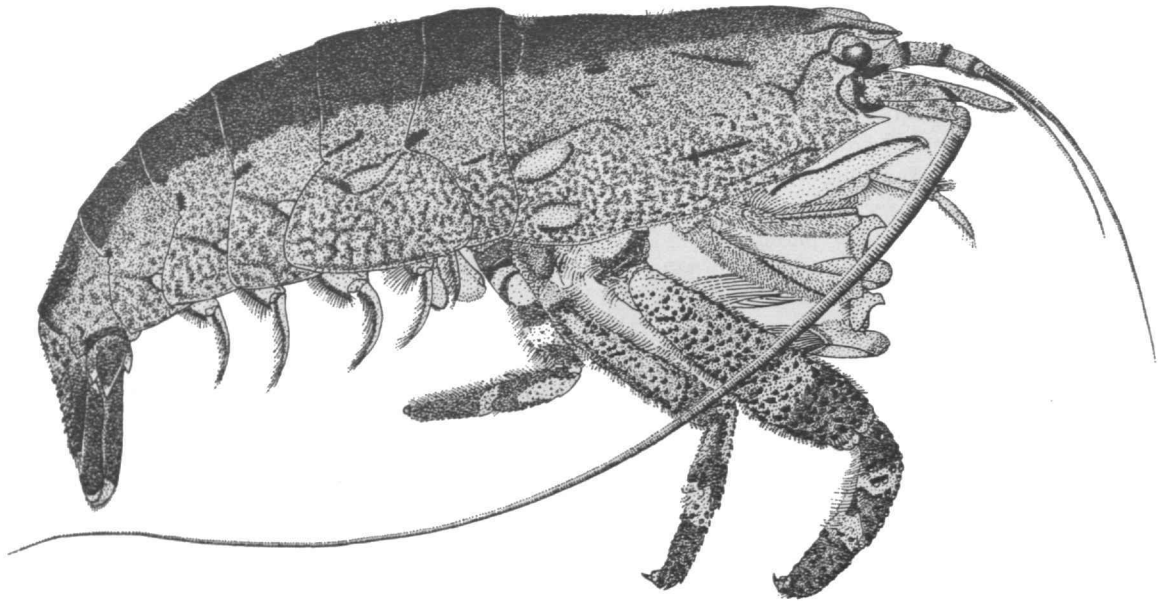


FIGURE 24.—Lateral view of *Atya innocuous* (from Chace and Hobbs, 1969).

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. innocuous*, 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 innocuous* 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 mm.

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

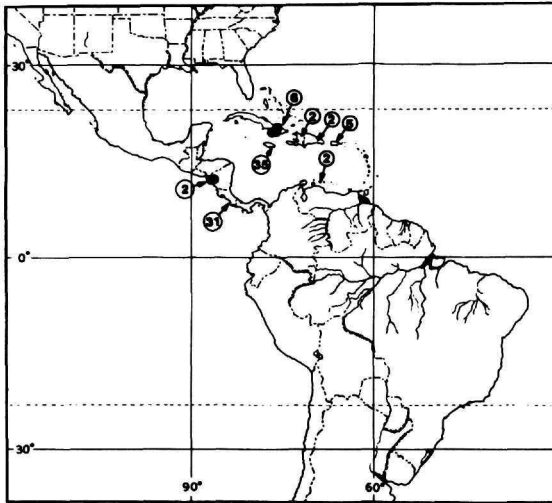


FIGURE 25.—Distribution of *Atya innocuus* (circled numerals = number of localities; see Figures 26–28).

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-

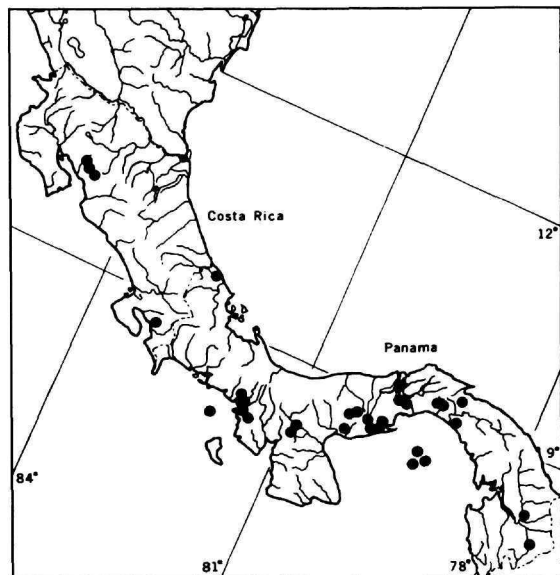


FIGURE 26.—Distribution of *Atya innocuus* in Costa Rica and Panama.

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*

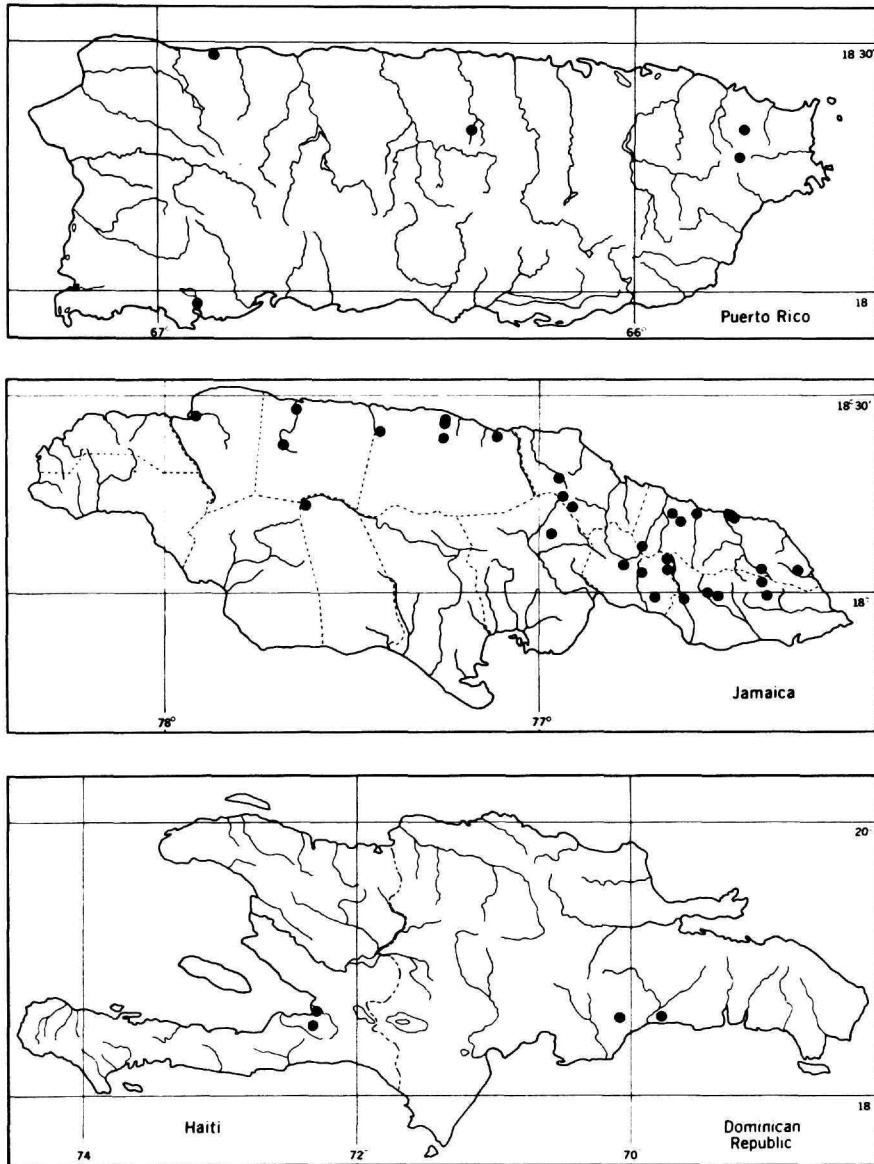


FIGURE 27.—Distribution of *Atya innocous* in the Greater Antilles.

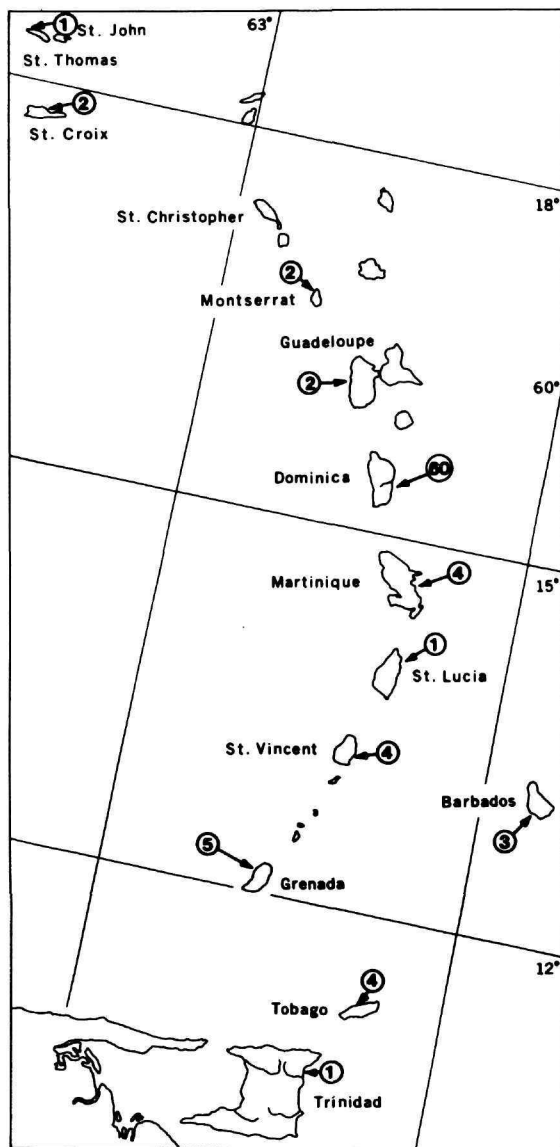


FIGURE 28.—Distribution of *Aya innocuus* in the Lesser Antilles (circled numerals = number of localities).

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 Orcovis, 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 Kasibna 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 Figue 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 Figue 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 Figue 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) Lamonthé 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 Berekuva, 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. McNeil; MCZ, 4♀ (11.2, 13.7, 13.7, 18.2), 1871(?), J.A. McNeil, (2) †MCZ, Corcuera,

1 juv ♂, Jul 1868, J.A. McNeil.

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,