The *Atya*-like Shrimps of the Indo-Pacific Region (Decapoda: Atyidae)

FENNER A. CHACE, JR.

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 384

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 384

The *Atya*-like Shrimps of the Indo-Pacific Region (Decapoda: Atyidae)

Fenner A. Chace, Jr.

SMITHSONIAN INSTITUTION PRESS
City of Washington
1983

ABSTRACT

Chace, Fenner A., Jr. The *Atya*-like Shrimps of the Indo-Pacific Region (Decapoda: Atyidae). *Smithsonian Contributions to Zoology*, number 384, 54 pages, 24 figures, 1983.—The shrimps recognized in this study comprise six freshwater species that have often been referred, untenably and sometimes in synonymy, to the genus *Atya*. Three of the species are here assigned to the re-established genus *Atyoida: A. bisulcata*, confined to Hawaii; *A. pilipes*, ranging eastward from eastern Indonesia and the Philippines to the Marquesas and Gambier islands; and *A. serrata*, possibly limited to Madagascar and smaller islands in the tropical western Indian Ocean. Two closely related forms compose the new genus *Atyopsis: A. moluccensis*, ranging through Thailand and Malaya to Indonesia and perhaps westward to Sri Lanka and northeastward to the Philippines; and *A. spinipes*, apparently inhabiting the eastern Lesser Sunda Islands and extending northward through the Philippines to Okinawa and eastward as far as Samoa. *Atya striolata*, occupying streams along the east coast of Australia, is assigned to the new genus *Australatya*. Keys are provided to the genera and species and, for each of the latter, there are a complete synonymy, review of the literature, references to published illustrations, a diagnosis, color notes if available, size limits, the known range and material examined, variations observed, ecological information, life-history notes if any, common names, and economic importance. Special attention is paid to the heteromorphism of the chelipeds in *Atyoida*, especially as displayed by a series of several hundred specimens of *A. pilipes* from Palau, Caroline Islands.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Chace, Fenner Albert.
The Atya-like shrimps of the Indo-Pacific region (Decapoda: Atyidae)
(Smithsonian contributions to zoology ; no. 384)
Bibliography: p.
Supt. of Docso. no.: SI 1.27:384
1. Atyidae. 2. Crustacea—Indian Ocean. 3. Crustacea—Pacific Ocean. I. Title. II. Series.
QL1.S54 no. 384 591s [595.3'843] 83-600083 [QL444.M33]

Contents

The *Atya*-like Shrimps of the Indo-Pacific Region (Decapoda: Atyidae)

Fenner A. Chace, Jr.

Introduction

A protracted study of the caridean shrimps collected during the *Albatross* Philippine Expedition of 1907–1910 has made it clear to me that the Indo-Pacific freshwater shrimps commonly referred to the genus *Atya* Leach, 1816, for up to 100 years or more are not only quite distinct from the typical Afro-American species of that genus but also that they are not even congeneric among themselves. When Hobbs and Hart (1982) recently reviewed the typical members of the genus *Atya*, they reached a similar conclusion but limited their study to Leach's genus in the restricted sense and urged me to publish my opinion separately. This, then, is a sequel to the Hobbs and Hart revision and extends their undertaking to the *Atya*-like shrimps inhabiting the lands of the Indian and western Pacific oceans.

In keeping with its role as a sequel to the Hobbs and Hart review, the present report follows the general format of its predecessor but in less detail; I do not believe that current taxonomic or distributional knowledge of the Indo-Pacific species is sufficient to substantiate precise analysis. Each of the species accounts consists of a synonymy and list of references as complete as I have been able to compile, a review of the more important elements in that literature, an appraisal of the published illustrations of the species, a concise diagnosis, information on color in life when available, size, the known range and a list of the material examined, what is known of the variability, ecology, and life history of the species, common names, economic importance, and occasional general remarks. Each species is illustrated rather fully, but no consummate verbal descriptions have been attempted.

ACKNOWLEDGMENTS.—My carcinological Smithsonian colleagues, particularly C.W. Hart, Jr., Horton H. Hobbs, Jr., and Raymond B. Manning, furnished hortatory and practical support almost daily during the year devoted to this study. L.B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden, was similarly helpful, both by correspondence and by direct communication during visits in August and September 1982; in particular, he furnished a photograph of the larger of the type-specimens of *Atya moluccensis* and no less than a score of the references cited. R.W. Ingle of the British Museum (Natural History) kindly provided indispensable material of two of the species. Lawrence G. Abele of Florida State University donated a fine series of *Archaeatya* that was important to an understanding of that eastern Pacific genus. The staff

Fenner A. Chace, Jr., Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

of the Smithsonian Library, especially Jack F. Marquardt and Carolyn S. Hahn, strove mightily in their successful efforts to locate and deliver numerous obscure publications. Lilly King Manning graciously shared her expertise on the arrangement and reproduction of illustrations. Finally, C.W. Hart, Horton Hobbs, L.B. Holthuis, and W.D. Williams of the University of Adelaide reviewed the penultimate draft of the manuscript. All of these, and others, contributed materially to the final draft of the study. I am most grateful to them as well as to the authorities of the National Museum of Natural History for providing space and facilities that are essential to the completion of this and other post-retirement commitments.

GENERAL CONSIDERATIONS.—A study of this kind is bound to reveal provocative gaps in our knowledge of the animals involved. Some of those that appeared as this project unfolded can be solved only by additional collecting, others by comparative population analyses, and still others by laboratory observations that should be easily made on animals, like these, that seem to be aquarium-hardy and long-lived. As a descriptive zoologist, I have neither the talent nor the desire to pursue any of the following problems, but I do have an interest in promoting their solution.

What is the actual range of *Atyoida serrata*? Is it really confined to the high islands of the tropical western Indian Ocean, as currently available information would seem to indicate?

Is *Atyoida pilipes* truly absent west of approximately 120° east longitude and, therefore, from the larger Indonesian islands and the Asiatic mainland? Is it a single taxon or are other species or subspecies discernible in parts of its extensive Pacific range?

Is the endopod of the first pleopod in old males of *Atyopsis spinipes* different from the one in *A. moluccensis* of comparable size? In other words, are the two forms species or subspecies? Also, does *A. moluccensis* occur in the Philippines? If so, to which form does the incomplete holotype of *Atya spinipes* belong?

What are the life-history adaptations of shrimps that inhabit swift mountain streams? Is it true, as observed by Hunte (1978:135) in Jamaica, "that species in high-gradient streams had larvae which required high salinity for development, and those in low-gradient streams had larvae with low salinity requirements?" Are the larval stages actually abbreviated during torrential periods, as suggested by Edmondson (1929:16)? If larvae are estuarine or marine, how do they manage to migrate the hundreds of arduous kilometers upstream to the adult habitat?

Are the species of *Atyoida* protandrous, either totally or partially, as maintained by Carpenter (1978:349)?

Is the heteromorphism displayed by the species of *Atyoida* of survival importance, as suggested by Fryer's statement (1977:125) that *Atya innocous* (Herbst, 1792), a species with chelae adapted for either sweeping the substrate or filter feeding, may compete successfully with *Atya scabra* (Leach, 1815), which is specialized for filter feeding? Or does the apparently sex-associated heteromorphism in *Atyoida* negate that possibility? Finally, what is the mechanism for color change in *Atyoida bisulcata*?

Key to Atya-like Genera of Atyid Shrimps

(Carpus of second pereopod deeply excavate and little longer than broad)

1. Rostrum with series of median dorsal spines; pleurobranchs on somites bearing 4 anterior pairs of pereopods only. (Pterygostomian margin of carapace rounded; telson with posterolateral angles not overreaching setigerous posterior margin; chelae not heteromorphic; 3rd pereopod of large males not armed with massive spur on merus; epipods on 3 anterior pairs of pereopods only; 1st pereopod without arthrobranch.) 2

Rostrum without median dorsal spines (except *Atya crassa* (S.I. Smith, 1871)); pleurobranchs on all 5 somites bearing pereopods. (Third maxilliped with 2 arthrobranchs.) 3

2. Rostrum with more than 12 dorsal teeth; antennular peduncle with distolateral spine of proximal segment reaching midlength of 2nd segment; 3rd maxilliped with 1 rudimentary arthrobranch ..... **Atyella** Calman, 1906 (Lake Tanganyika)

Rostrum with no more than 10 dorsal teeth; antennular peduncle with distolateral spine of proximal segment not even nearly reaching midlength of 2nd segment; 3rd maxilliped with 1 well-developed and 1 rudimentary arthrobranch. (Third maxilliped without stout terminal spine; endopod of 1st pleopod of male expanded in proximal half, not tapering regularly from base to tip; appendix masculina spinose near distal end only; mastigobranchs on 4 anterior pereopods.) ..... **Micratya** Bouvier, 1913b (West Indies; Costa Rica; and Panama)

3. Third maxilliped with terminal spine (sometimes partially concealed by setae); endopod of 1st pleopod of male tapering from base to tip; females exceeding males in size, possibly protandrous. (Telson with posterolateral angles not overreaching setigerous posterior margin; 3rd pereopod of large males not armed with massive spur on merus.) 4

Third maxilliped terminating in numerous stout setae but lacking single terminal spine; endopod of 1st pleopod of male expanded into broad lamina, not tapering from base to tip; males equalling or exceeding females in size, not protandrous. (Pterygostomian margin of carapace dentate or angular; chelae not heteromorphic; appendix masculina spinose over more than distal half of length; 1st pereopod with arthrobranch.) 6

4. Pterygostomian margin of carapace broadly rounded; chelae not heteromorphic, adapted for filter feeding; appendix masculina with spinose area distinctly distal to apex of appendix interna; epipods on 3rd and 4th pereopods much reduced, vestigial; no mastigobranchs ..... **Australatya**, new genus

Pterygostomian margin of carapace narrowly rounded to sharply acute; chelae heteromorphic, adapted for filter or substrate feeding; appendix masculina with spinose area overlapped by at least distal part of appendix interna; well-developed epipods on 4 anterior pairs of pereopods; mastigobranchs on all 5 pereopods 5

5. Pterygostomian margin rounded; 1st pereopod without arthrobranch ..... **Archaeatya** Villalobos, 1960 (Costa Rica; Isla del Coco; and Perlas Archipelago, Gulf of Panama)

Pterygostomian margin dentate or angular; 1st pereopod with arthrobranch ..... **Atyoida** Randall, 1840

6. Telson with posterolateral angles not overreaching setigerous posterior margin; 3rd pereopod of large males without massive spur on merus;

endopod of 1st pleopod of male semicircular, spinulose, flexible; well-developed epipods on 4 anterior pairs of pereopods; mastigobranchs on all 5 pereopods ..... **Atya** Leach, 1816
(America: Pacific drainage from northern Mexico to Peru, Atlantic drainage from northern Mexico and West Indies to southern Brazil; Africa: Atlantic drainage from Senegal to northern Angola)

Telson with posterolateral angles overreaching setigerous posterior margin; 3rd pereopod of large males armed with massive spur on merus; endopod of 1st pleopod of male rhomboidally oval, submarginally spinose, rigid; epipods on 3rd and 4th pereopods reduced, vestigial; no mastigobranchs ..... **Atyopsis**, new genus

Genus *Atyoida* Randall, 1840

Atyoida Randall, 1840:140 [type-species by monotypy: *Atyoida bisulcata* Randall, 1840:140; gender: feminine].

Atyoidea.—Gibbes, 1850a:25 [erroneous spelling].

Ortmannia Rathbun, 1901:120 [type-species by original designation: *Ortmannia henshawi* Rathbun, 1901:120, footnote (= *Atyoida bisulcata* Randall, 1840:140); gender: feminine].

Alya.—Bouvier, 1904c:136, footnote [erroneous spelling for *Atya* but used only in the combinations *Alya serrata* and *A. bisulcata*].

Pseudatya Roux, 1928:209 [type-species by monotypy: *Pseudatya beauforti* Roux, 1928a:209 (= *Atya pilipes* Newport, 1847:160); gender: feminine].

Vanderbiltia Boone, 1935:159 [type-species by monotypy: *Vanderbiltia rosamondae* Boone, 1935:160 (= *Atya pilipes* Newport, 1847:160; gender: feminine].

DIAGNOSIS.—Body pigmented, eyes well developed; rostrum not strongly compressed laterally, median dorsal carina typically unarmed, ventral keel with 0–4 teeth; anterior margin of carapace armed with antennal spine, pterygostomian margin sharply or bluntly acute; supraorbital spines absent; telson with setigerous posterior margin overreaching posterolateral angles; 3rd maxilliped with uncinate terminal spine; pereopods without exopods; 1st and 2nd pereopods with chelae heteromorphic (with or without palm), fingers tipped with brushes of setae, carpus of both appendages excavate distally, little if at all longer than broad; 3rd pereopod without meral spur in large males; branchial complement consisting of 5 pleurobranchs, 3 arthrobranchs, 1 podobranch, 5 epipods, and 5 mastigobranchs; 1st pleopod of male with endopod tapering sinuously but rather regularly to slender apex; 2nd pleopod of male with appendix masculina subcylindrical, spinose over more than distal half.

RANGE.—Except for the almost certainly erroneous record of *A. serrata* from the Cape Verde Islands by Bate (1888:699) *Atyoida* is known only from the high islands of the Indo-Pacific region: *A. serrata* perhaps being restricted to Madagascar and smaller islands in the tropical western Indian Ocean between 40° and 60° east longitude, *A. pilipes* to eastern Indonesia and the Philippines eastward from about 120° east longitude across the vast expanse of the Pacific Ocean as far as the Marquesas and Gambier islands, and *A. bisulcata* to the Hawaiian islands of Oahu, Maui, and Hawaii.

Key to Species of the Genus *Atyoida*

1. Rostrum bent somewhat ventrad; pterygostomian margin bluntly acute, not spinous; chelae dimorphic, adapted for filter-feeding or sweeping, not for selective picking alone. (Rostrum unarmed or bearing single ventral tooth, less frequently 2 teeth, very rarely 3; fixed teeth on posterior margin of telson inconspicuous.) ..... **A. pilipes**

Rostrum nearly horizontal; pterygostomian margin sharply acute, spinous;

chelae polymorphic, adapted for filter-feeding, sweeping, or selective picking 2

2. Rostrum usually unarmed ventrally; posterior, setigerous margin of telson armed with 2–7 conspicuous fixed teeth ..... **A. bisulcata**

Rostrum with 2–4 ventral teeth; fixed teeth on posterior margin of telson inconspicuous ..... **A. serrata**

Atyoida bisulcata Randall, 1840

FIGURES 1, 2

Atyoida bisulcata Randall, 1840:140, pl. 5: fig. 5 [type-locality: "Sandwich Islands"].—Stimpson, 1860:28.—A. Milne-Edwards, 1864:151.—Ortmann, 1895:407 [part].—Bouvier, 1905:95, 114, 127, 130; 1925:277, 297.—Holthuis, 1955:26, 27.—Smith and Williams, 1982:343–345, 349, 358, 359.

Atyoidea bisulcata.—Gibbes, 1850a:25 [erroneous spelling]; 1850b:196.

Atyoida bisulcata?.—Dana, 1852:540, pl. 34: fig. 1*a–i*.

Atya bisulcata.—Bate, 1888:692, 700, fig. 71, pl. 120.—Thallwitz, 1891b:26.—De Man, 1892:362, 363.—Sharp, 1893:111.—Bouvier, 1904a:447–449; 1904b:378–380; 1904c:137; 1905:98, 100, 107, 127, 130.—Rathbun, 1906:919.—Bouvier, 1909:333.—Calman, 1910:786, 789–791, figs. 1, 3A′, 3A″.—Blaringhem, 1911:192.—Bouvier, 1912b:692, 694:1913a:460; 1918:136.—Bouvier and de Charmoy, 1919:317.—Bouvier, 1925:262, 277, 289, 290, 297–299, 301, 309, 321, 322, 334, 350, 357, figs. 668–671.—Roux, 1925:154.—Edmondson, 1929:5–12, 14, 15, 19–35, figs. 1*e,j–s*, 2*a*–d,r–t, 4*a,d,e–o*, pl. 1A,C; 1930:4–7.—Radir, 1930:351–353.—Edmondson, 1935:17, 18, fig. 6*j,k*; 1936:3, 5, 13, fig. 1.—Woltereck, 1937a:246, 247; 1937b:322–325.—Gurney, 1942:86–88, fig. 20c1.—Roth-Woltereck, 1942:262–264, 268.—Holthuis, 1954:2, 3.—Ullman, 1967:56, 57, 60, 2 figs.—Williams, 1977:412.—Carpenter, 1978:343, 349, 350.—Costa, 1980:697.—Smith and Williams, 1982:343, 344.

Ortmannia henshawi Rathbun, 1901:21, footnote [type-locality: "Kaiwiki, Hilo, Hawaii"]; 1906:919.—Edmondson, 1929:5–15, 19–30, 34, 35, figs. 1*c,d,f–k*, 2*e–q*, 3, 4*b,c*, pl. 1B,D.—Radir, 1930:351–353.—Edmondson, 1935:17.—Woltereck, 1937b:322, 323, 325.—Gurney, 1942:86, 87, fig. 20c2, D1, 2.—Holthuis, 1954:2, 3; 1955:27.—Carpenter, 1978:349.—Costa, 1980:697.—Smith and Williams, 1982:344, 349.

Ortmannia Henshawi.—Bouvier, 1904a:447; 1904b:378, 379; 1905:100, 102, 107, 127–130; 1909:333.—Calman, 1910:789–791, figs. 3B′, B″.—Blaringhem, 1911:192.—Cuénot, 1911:400.—Bouvier, 1911:1821, 1823, 1824; 1912a:920, 922; 1912b:692–694; 1913a:459, 460; 1918:136.—Bouvier and de Charmoy, 1919:317.—Bouvier, 1925:263, 277, 278, 280, 287, 288, 293, 297–299, 321, 322, 333, 345, 349–351, 356–358, figs. 640–644.

Ortmannia, mutation *Henshawi*.—Bouvier, 1904a:448.

Atya bisulcata, *Henshawi* variation.—Bouvier, 1904b:379.

Ortmannia, modification *Henshawi*.—Bouvier, 1904b:379, 380.

Atya bisulcata, mut. *Henshawi*.—Bouvier, 1904c:136; 1905:107.

Atya brevirostris.—Bouvier, 1904c:137 [part].—Seurat, 1934:50, 51 [part]. [Not *A. brevirostris* De man, 1892.]

Ortmannia Henshawi mut. *bisulcata*.—Bouvier, 1905:98, 100, 111, 114, 127, 130.

mutation *bisculcata* of *O. Henshawi*.—Bouvier, 1905:109 [erroneous spelling].

Ortmannia Alluaudi Bouvier, 1905:108, 116 [part].

Atyoida (*Atya*) *bisulcata*.—Bouvier, 1925:303.

Atyoida henshawi.—Roux, 1925:154.

Atya bisculcata.—Edmondson, 1929, fig. 1j,k, 26 [erroneous spelling].

Ortmannia Henshavi.—Woltereck, 1937a:246, 248 [erroneous spelling].—Roth-Woltereck, 1942:262–264, 268, 277.

Ortmannia henssavi.—Woltereck, 1937b:323 [erroneous spelling].

REVIEW OF LITERATURE.—Ten years after Randall (1840) described this genus and species from Hawaiian material collected by Thomas Nuttall, Gibbes (1850a, 1850b) introduced the first of several misspellings of the binomen. Two years later, Dana (1852) tentatively assigned to the species material taken at Oahu by the U.S. Exploring Expedition and was the first of numerous carcinologists to question the propriety of the genus, but Stimpson (1860) and A. Milne-Edwards (1864) continued to recognize it. Bate (1888), however, concurred with Dana's doubts and relegated the species to *Atya*, where it was left by Thallwitz (1891b), De Man (1892), and Sharp (1893). Ortmann (1895) reinstated *Atyoida* because of the nonatyoid chelae in Hawaiian material examined by him, and he mistakenly synonymized *A. tahitensis* with *A. bisulcata*. The *Atya*-like chelae of Randall's type-specimen led Rathbun (1901) to propose a "nom. nov.," *Ortmannia henshawi*, for the form denoted by Ortmann and to treat *Atyoida* as a synonym of *Atya*; inasmuch

as Ortmann's action must be construed as a misidentification rather than the creation of a homonym—if the two forms are considered to represent separate taxa—Rathbun must be deemed to have proposed a new species, instead of a replacement name, and the type-series must include the material examined by her, as well as that mentioned by Ortmann and discussed by her. Bouvier (1904a,b,c) decided that *A. bisulcata* and *O. henshawi* were forms of the same species of *Atya* and he (1904a:449) considered "la mutation *Henshawi*" to be a "forme atavique" representing a species "en voie d'evolution." Rathbun (1906:919) accepted Bouvier's explanation and referred to *O. henshawi* as an "atavic form of *Atya bisulcata.*" Calman (1910) reported that one specimen in a lot of 88 collected by the *Challenger* at Honolulu has three *Atya*-type chelae and the fourth "distinctly of the *Ortmannia*-shape;" he also noted that "Miss Rathbun displaced *Atyoida* on the ground that the surviving type-specimens of Randall's *Atyoida bisulcata*, the type-species of *Atyoida*, have chelae of the *Atya*-type. If, however, *O. henshawi*, the type-species of *Ortmannia*, is only a form of *A. bisulcata*, the two genera are synonymous and the older name should be used." Cuénot (1911) believed that *Ortmannia henshawi* and the "mutation atyienne" *Atya bisulcata* represent a link between the tropical American species of *Ortmannia* (= *Potomirim* Holthuis, 1954) and the American and Indo-Pacific species of the true *Atya.* In his valiant attempt to bring order out of chaos in the extremely difficult family Atyidae, Bouvier (1925) chose ("pour suivre les règles de la nomenclature,") to treat *Ortmannia henshawi* and *Atya bisulcata* separately, the latter albeit as a "mutation atyienne" of the former. By far the most complete coverage of the history, variability, responses to changes in salinity, temperature, light, and pH, as well as regeneration, molting, larval development, associated fauna, and means of dispersal of the species called *Atya bisulcata* (and *Ortmannia henshawi*) is to be found in Edmondson (1929). In a continuation of these studies, Edmondson (1930) experimented with the effects of ultraviolet light on regeneration, Radir (1930) demonstrated hermaphroditism, and Edmondson (1936) determined the effect of X-rays on regeneration. Little attention has been paid to this unusual animal during the past half century, although Ullman (1967) indicated its adaptability to aquarium conditions, and Carpenter (1978) called attention to possible protandry in the species.

PUBLISHED ILLUSTRATIONS.—Accompanying Randall's original description of the species in 1840 is a crude drawing of the third pereopod, showing its slender form in comparison with that of this appendage in the species of *Atya.* Dana (1852), in his atlas (1855), offered a toto illustration and sketches of the mouthparts, chela, and dactyl of the fourth pereopod. Bate (1888) illustrated the entire shrimp in lateral view, the antennule, antenna, mouthparts, and first and fifth pereopods, as well as the zoeal telson. Calman (1910) presented a lateral view of an ovigerous female from the *Challenger* collection and the first and second chelae of both atyoid and ortmannioid forms. Bouvier (1925) showed the anterior end of the animal in lateral view, the rostrum in dorsal view, the preanal spine in ventral and lateral views, the chelipeds, and the dactylar setae of a chela. In the review of the Hawaiian atyids by Edmondson (1929), there are photographs in lateral view of the two forms and of the chelipeds of both, as well as drawings of rostra in lateral view, cheliped variation and setae, pereopod regeneration, and first pleopods. Larval antennules and telson are shown in Edmondson (1935). The same author (1936) depicted the effect of X-rays on cheliped regeneration. Gurney (1942) showed cheliped "mutation." Finally, there are two photographs of the shrimps in an aquarium in Ullman (1967).

DIAGNOSIS.—Rostrum continuing general trend of dorsal surface of carapace in adults, not bent noticeably ventrad, usually unarmed ventrally; pterygostomian angle of carapace sharply acute; telson with 2–7 conspicuous fixed teeth on setigerous posterior margin; chelae polymorphic, adapted for filter-feeding, sweeping, or selective picking.

COLOR NOTES.—A label accompanying the five specimens from a canyon five miles (8 km) east of

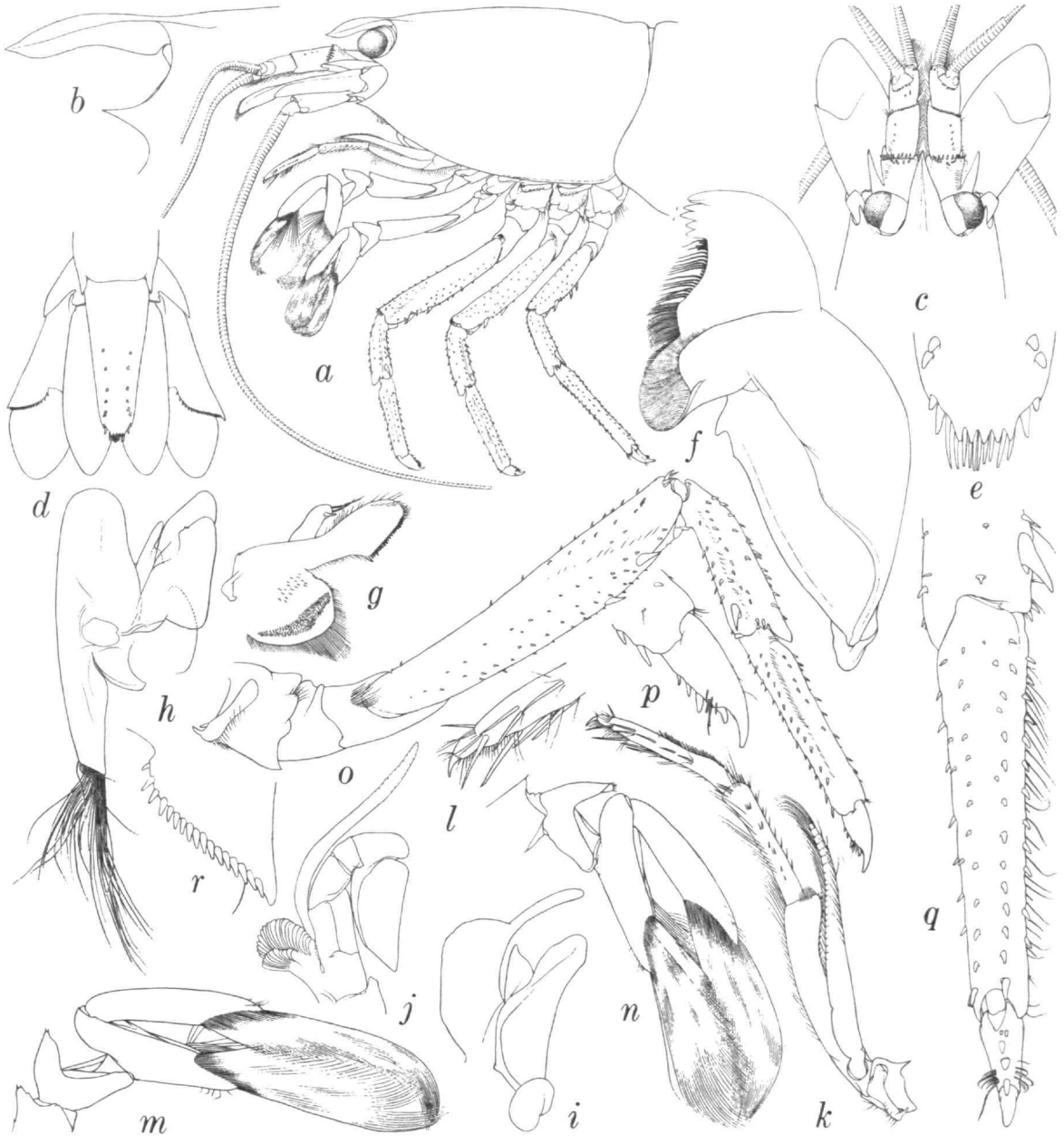

FIGURE 1.—*Atyoida bisulcata* (all from ovigerous female from Pepeekeo, Hawaii, carapace length 8.8 mm): *a*, cephalothorax and appendages, left aspect; *b*, rostrum, left aspect; *c*, anterior carapace and appendages, dorsal aspect; *d*, telson and uropods; *e*, posterior end of telson; *f*, right mandible; *g*, right 1st maxilla; *h*, right 2nd maxilla; *i*, right 1st maxilliped; *j*, right 2nd maxilliped; *k*, left 3rd maxilliped; *l*, same, distal end; *m*, right 1st chela and carpus; *n*, right 2nd chela and carpus; *o*, right 3rd pereopod; *p*, same, dactyl; *q*, same, flexor surfaces of propodus and dactyl; *r*, dieresis of lateral branch of right uropod. (Magnifications: *a*, × 4.3; *c*, *d*, × 5.2; *b*, *g–k*, *m–o*, × 10.8; *e*, *f*, *l*, *p–r*, × 21.5.)

Lahaina, Maui, 12 April 1902, indicates that they were "mottled grayish olive, tinges of red on lateral lappets of carapace." Ullman (1967:60) wrote, "One interesting characteristic of the shrimp not mentioned by Edmondson is the tendency of wild specimens to change color or pattern to match their new environment."

SIZE.—Of the material of this species examined, males have carapace lengths of 6.5 to 10.2 mm, females, 4.7 to 12.7 mm, including ovigerous ones measuring 7.2 to 12.5 mm. The maximum carapace length corresponds with the statement by Edmondson (1929:6): "Full-grown females of both forms may reach 50 mm. in length, being larger than mature males." (See "Life History Notes," p. 9.)

DISTRIBUTION AND SPECIMENS EXAMINED.—*Atyoida bisulcata* is known only from Hawaii, where it has been recorded from the islands of Oahu, Maui, and Hawaii, at altitudes of 5 to at least 540 meters (Edmondson, 1929:6).

Collections have been examined from the following localities. Numbers in parentheses following the specimens listed are measurements, in mm, of postorbital carapace lengths.

MAUI: (1) Lahaina, 3♂ (9.9–10.0), 2 ovig ♀ (11.2, 11.8), U.S. Fish Commission. (2) Stream in canyon 5 miles (8 km) east of Lahaina, 1♀ (12.7), 4 ovig ♀ (11.0–12.5), 12 Apr 1902, U.S. Fish Commission. (3) Iao Valley, 1000 ft (304.8m) elevation, near Wailuku, 1 ovig ♀ (9.5), R.C. McGregor. (4) Nahiku, 1♂ (8.3), 2♀ (4.7, 9.3), 2 ovig ♀ (9.3, 9.9), 9 Feb 1958, N.L.H. Krauss.

HAWAII: (1) Pepeekeo, 10 miles (16.1 km) from Hilo, 1♂ (6.6), 2♀ (8.8, 8.9), 5 ovig ♀ (7.3–9.9), H.W. Henshaw. (2) Kaiwiki, Hilo, 1800 feet (548.6 m) alt, 88♂ (7.0–10.0), 6 ovig ♀ (8.0–11.0), Mar 1900, H.W. Henshaw (including type-series of *Ortmannia henshawi*). (3) Hilo, 1 ovig ♀ (8.3), R.C. Mcgregor.

"Sandwich Is," 2♂ (6.8, 7.7), "Kingsley #411."

VARIATION.—The most unexpected aberration encountered in the material of this species at my disposal is certainly the form of the rostrum displayed by one of the males from Lahaina, Maui (Figure 2*l,m*). The strong lateral rostral teeth in this specimen suggest that the genetic potential to produce a rostrum resembling those characteristic of three well-known species of *Atya* (*A. gabonensis* Giebel, 1875, *A. margaritacea* A. Milne-Edwards, 1864, and *A. scabra* (Leach, 1816)) is present even in a genus in which the rostrum normally tapers to the apex with the merest trace of broadly obtuse angles near midlength. Two of the specimens examined were armed with a distinct tooth on the ventral margin of the rostrum, but none displayed dorsal rostral teeth like those illustrated by Edmondson (1929, fig. 1*o,p*).

On the posterior margin of the telson (Figures 1*e*, 2*e,j,k,n*), the prominent fixed teeth, which are much more distinct in this species than they are in the other two members of the genus, show a regular numerical distribution between 2 and 7, 4 being the commonest number, but 3 and 5 are but little less frequent.

In *A. bisulcata*, as in *A. serrata* (but not *A. pilipes*), the chelae are virtually trimorphic: atyoid (Figure 1*m,n*), presumably used principally for filter-feeding; ortmannioid (Figure 2*h,i*), probably used for both filter-feeding and sweeping the substrate; or caridinoid (Figure 2*a,b*), obviously adapted for selective scraping or picking and not for filter-feeding. Although Edmondson (1929:7) reported that from among more than 2000 specimens 90 percent of the ortmannioid and caridinoid forms were males and a similar proportion of the atyoid forms were females, the limited material at my disposal does not follow this pattern. Of 106 specimens collected by H.W. Henshaw in the vicinity of Hilo, Hawaii, including the type-series of *Ortmannia henshawi*, 39 of 90 males are caridinoid, 44 are ortmannioid, and only 7 are atyoid; 1 of 3 nonovigerous females is ortmannioid, the other 2 atyoid; but 8 of 13 ovigerous females are caridinoid, 1 is ortmannioid, and only the remaining 4 are atyoid. Calman (1910:790) reported finding 1 specimen with 3 atyoid and 1 ortmannioid chelae, and Edmondson (1929:7) mentioned a specimen with 3 ortmannioid and 1 atyoid chelae.

ECOLOGICAL NOTES.—According to Edmondson (1929:6, 11), *A. bisulcata* is most commonly

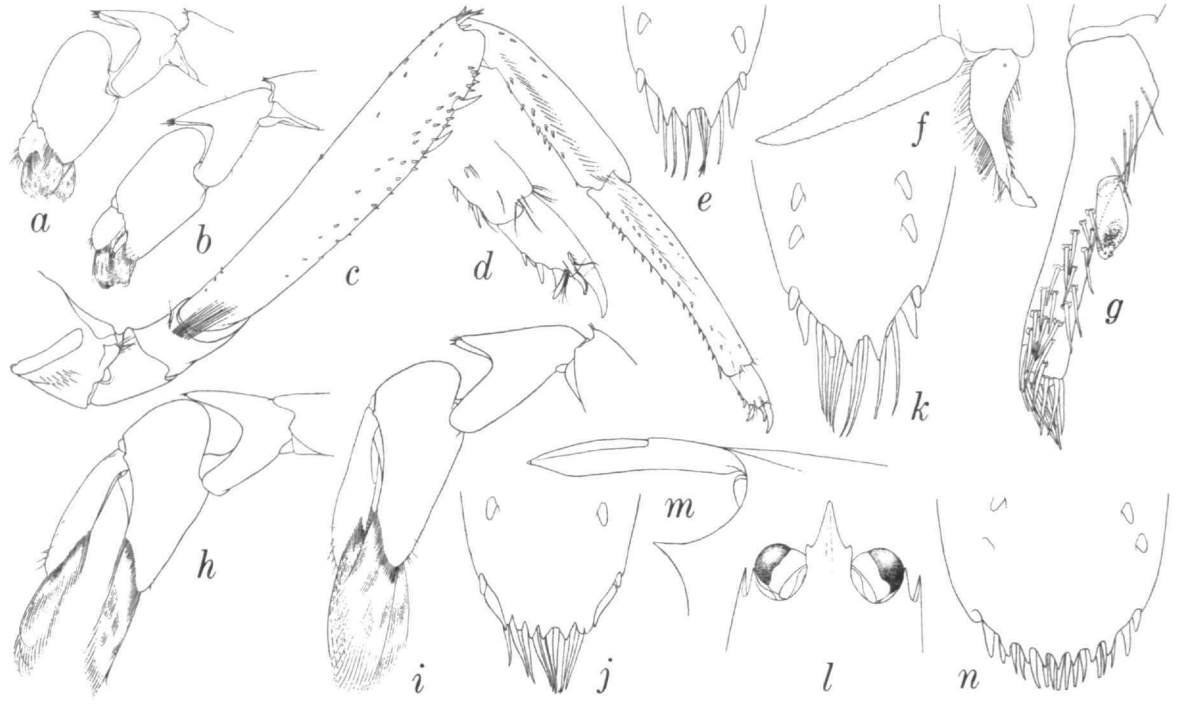

FIGURE 2.—*Atyoida bisulcata* (*a–g*, male syntype of *Ortmannia henshawi*, carapace length 8.3 mm; *h–j*, male syntype of *O. henshawi*, carapace length 9.5 mm; *k*, male syntype of *O. henshawi*, carapace length 9.5 mm; *l*, *m*, male from Lahaina, Maui, carapace length 9.9 mm; *n*, ovigerous female from Lahaina, Maui, carapace length 11.7 mm): *a*, left 1st chela and carpus; *b*, left 2nd chela and carpus; *c*, right 3rd pereopod; *d*, same, dactyl; *e*, posterior end of telson; *f*, exopod and endopod of right 1st pleopod; *g*, right appendix masculina and appendix interna, mesial aspect; *h*, left 1st chela and carpus; *i*, left 2nd chela and carpus; *j*, posterior end of telson; *k*, posterior end of telson; *l*, abnormal rostrum, dorsal aspect; *m*, same, lateral aspect; *n*, posterior end of telson. (Magnifications: *l*, × 5.2; *a–c*, *f*, *h*, *i*, *m*, × 10.8; *d*, *e*, *g*, *j*, *k*, *n*, × 21.5.)

found in cool mountain waters up to altitudes of at least 540 meters and probably higher, but it has also been taken at about 5 meters above sea level. Optimal temperatures seem to range from 20° to 26° C and pH from 8 to 9 (Edmondson). Ullman (1967:60), however, found that the shrimp tolerated a temperature range of 15.5° to 29° C and a pH of 6.5 to 9 with little noticeable change in their activities.

Edmondson (1929:31) reported that *A. bisulcata* is commonly associated with the much larger river shrimp *Macrobrachium grandimanus* (Randall, 1840), gobies that frequent mountain streams, dragonfly nymphs, frogs, and, in lowland areas, top minnows or mosquito fishes. Apparently the only serious threat to the shrimps might be the top minnows, which probably could effectively limit the occurrence of *Atyoida* in coastal regions.

LIFE HISTORY NOTES.—Experiments conducted by Edmondson (1929:28) indicated that proper larval development requires a swift current of water. Zoeae may hatch in noncirculating water, but they rarely develop further, whereas the young in the mysis stage (about 6 mm long) hatch in swift water. These larvae are negatively phototropic and positively rheotropic, and they are able to creep upstream, usually in contact with some surface. Edmondson gave no indica-

tion that a marine environment is necessary for development. Both females with atyoid chelae and those with ortmannioid chelae produce young with ortmannioid chelae, but some of the latter gradually develop atyoid chelae. The rostrum is bent ventrad nearly vertically in young juveniles, subsequently bending upward to a nearly horizontal position.

The somewhat larger size of females and the histological evidence of hermaphroditism reported by Radir (1930) have convinced Carpenter (1978:349) that *A. bisulcata* is protandrous. The unfortunate dearth of females in the available material prevents me from contributing to or contradicting this assumption, except to note that the majority of males in these collections yielded carapace lengths of 8.2 to 9.8 mm, and the far fewer ovigerous females ranged in carapace length from 7.2 to 12.5 mm. This would seem to suggest that females attain a larger size than males, but the data are too sparse to be reliable.

COMMON NAME.—Hawaiian Freshwater Shrimp.

ECONOMIC IMPORTANCE.—None.

REMARKS.—It is unfortunate that interest in this unusual animal seems to have waned during the nearly 50 years since Edmonson experimented with it so extensively. We still do not know whether *A. bisulcata* is protandrous, as believed by Carpenter (1978:349); whether the polymorphism displayed by the chelipeds is sex associated and/or whether it has survival value for a species that lives in mountain streams where food gathering may best be accomplished at different times by filter-feeding, substrate sweeping, or selective scraping and picking; whether the larval stages are abbreviated during torrential conditions, as suggested by Edmonson (1929:16); and how the environmentally correlated modification of color and color pattern is controlled. Few polymorphic animals, as hardy and long-lived as *A. bisulcata*, seem to be so readily available to answer some of these basic biological questions by simple laboratory observations and comparative population analyses.

Atyoida pilipes (Newport, 1847)

FIGURES 3–8

Atya pilipes Newport, 1847:160 [type-locality: "Apia, Upoln, New Zealand" (corrected to "Apia, Upolu, Navigator or Samoan Group" by Dana, 1852:533)].—White, 1847: 74.—A. Milne-Edwards, 1864:150.—Von Martens, 1868:50.—Schmeltz, 1869:x, 135; 1874:79.—Miers, 1876:79; 1880:382.—Filhol, 1885:52; 1886:431, 497.—Ortmann, 1890:466, pl. 36: fig. 8*a*, *b*, *c* [part].—Thallwitz, 1891a:102; 1891b:26, 27.—De Man, 1892:363.—Ortmann, 1895:409.—Schenkel, 1902:501.—Bouvier, 1925: 304, 305.—Roux, 1925:151–154 [part]; 1926a:182, 220; 1928a:208, 209; 1928b:218; 1934:219, 223.—Woltereck, 1937b:323 [part].—Johnson, 1958:179, 180, fig. 6 [part]. —Bayer and Fehlmann, 1960:191.—Holthuis and Rosa, 1965:8 [part].—Holthuis, 1970:92; 1978:29, 30; 1980:69–71 [part]; 1982:609 [part].—Smith and Williams, 1982:344 [part].

Atya.—Dana, 1852:533, footnote.

Atyoida tahitensis Stimpson, 1860:28 [type-locality: "In aquis dulcibus insulae 'Tahiti'"].—A. Milne-Edwards, 1864: 152.—Ortmann, 1895:407.—Bouvier, 1925:269, 272, 294, 297.—Smith and Williams, 1982:349.

Atyoidea bisulcata.—Schmeltz, 1881:15.—Thompson, 1901:21 [erroneous spelling; not *Atyoida bisulcata* Randall, 1840].

Atya tahitensis.—Thallwitz, 1891b:26.—De Man, 1892:363.

Atya brevirostris De Man, 1892:360, 520, pl. 21: figs. 21, 21a–d [type-localities: Flores and Timor].—Weber, 1892:536.—Ortmann, 1894:12; 1895:408, 409.—Nobili, 1900:475, fig. 2.—De Man, 1902:894.—Bouvier, 1904c: 137 [part]; 1905:98, 104, 107.—Bordage, 1908: 1418.—Bouvier, 1925:294, 295.—Roux, 1925:151; 1926a:220.—Seurat, 1934:50, 51 [part].—Woltereck, 1937b:323.—Djajadiredja and Sachlan, 1956:370.—Holthuis, 1965:47; 1978:30.—Smith and Williams, 1982:349.

Atyoida bisulcata.—Ortmann, 1895:407 [part].—Doflein, 1904:407. [Not *Atyoida bisulcata* Randall, 1840.]

Atya bisulcata.—Whitelegge, 1903:8, 12 [not *Atyoida bisulcata* Randall, 1840.]

Atya brevifrons.—Bouvier, 1904a:448; 1904b:380 [lapsus for *A. brevirostris*].

Ortmannia Alluaudi Bouvier, 1905:104–106, figs. 17–19 [part] —Blaringhem, 1911:189, 192–194 [part].—Bouvier, 1925:274 [part].

[?]*Atya brevirostris*.—De Man, 1915:406.

[?]*Atya brevirostris* variety *de-mani*.—De Man, 1915:406.

Atya brevirostris var. *de Mani*.—Bouvier, 1925:294, 295.

Atya spinipes.—Roux, 1928a:209 [lapsus for *A. pilipes*].

Pseudatya beauforti Roux, 1928a:209–213, figs. 1–9 [type-locality: Batjan].—Woltereck, 1937b:324.—Holthuis, 1955: 27.—Johnson, 1961:121.—Smith and Williams, 1982:349.

Atya serrata.—Adamson, 1935:16.—Edmondson, 1935:14–18, figs. 5i, 6g–i,l.—Estampador, 1937:485.—Woltereck,

1937b:322, 323 [part].—Miyake, 1938:107, 111.—Adamson, 1939:36.—Balss, 1957:1530.—Estampador, 1959:19. [Not *Atya serrata* Bate, 1888.]

Ortmannia alluaudi.—Adamson, 1935:16.—Woltereck, 1937b: 322, 323 [part].—Adamson, 1939:36. [Not *O. Alluaudi* Bouvier, 1905.]

Ataya breverostris var. *de mani.*—Blanco, 1935:31 [erroneous spelling].

Vanderbiltia rosamondae Boone, 1935:160, pls. 41, 42 [type-locality: Venus Point Reef, Tahiti, Society Islands].—Holthuis, 1953:113–118, fig. 1; 1955:27.—Smith and Williams, 1982:349.

Vanderbiltia rosamundae.—Holthuis, 1952:22 [erroneous spelling].

Vanderbiltia mirabilis Holthuis, 1953:114 [manuscript name published as a synonym].

Atyoida pilipes.—Smith and Williams, 1982:345, 349, 358, 359 [part].

REVIEW OF LITERATURE.—Fortunately, the original designation of the type-locality of *Atya pilipes* by Newport (1847:160) as "Apia, Upoln, New Zealand" was promptly corrected to "Apia, Upolu, Navigator or Samoan Group" by Dana (1852:533). Stimpson (1860:28) described *Atyoida tahitensis*, which was generally accepted as a distinct species for about 65 years. A. Milne-Edwards (1864:150) considered *Atya pilipes* to be a valid species, but he seems to have been unaware of Dana's correction of the type-locality and cited a third version: "Apia, Upolce, la Nouvelle-Zélande;" he also referred to *Atyoida tahitensis* as a species "presque semblabale à l'*A. bisulcata.*" Schmeltz (1869:152) noted that topotypic material of this species occurred at more than 1000 feet (305 m) above sea level at Upolu. Miers (1876:79) expressed little doubt "that Samoa is the correct locality of the type-specimen" of *Atya pilipes*, a belief that he reiterated four years later (1880:382), but at that time he confused the relationships by remarking that "the types both of *A. spinipes* and of *A. pilipes*, Newport, are small and in bad condition; and it is probable that they are not specifically distinct." Schmeltz (1881) almost certainly misidentified Ponape specimens as "*Atyoidea bisulcata.*" Filhol (1885) listed *Atya pilipes* among New Zealand crustaceans but a year later (1886) he indicated that its presence in New Zealand was doubtful. *Atya brevirostris* was described by De Man (1892) from Flores and Timor. Ortmann (1895) treated *Atya pilipes* as a synonym of *A. spinipes* and *Atyoida tahitensis* as identical with *A. bisulcata*, but he recognized *Atya brevirostris* as distinct. L.B. Holthuis (personal communication) has called my attention to the possibility that the material recorded by Thompson (1901:21) from Ponape may be the same as that listed by Schmeltz (1881:15) in the Godefroy Museum catalog. Doflein (1904:104) similarly identified a single specimen from the Marshall Islands as *Atyoida bisulcata.* Bouvier (1905) and Bordage (1908) synonymized *Atya brevirostris* with *A. serrata.* Bouvier (1925) accepted Mier's statement that *Atya pilipes* is a synonym of *A. spinipes*, and synonymized *Atya brevirostris*, *A. brevirostris* var. *de Mani*, and *Atyoida tahitensis* with *Atya serrata.* Roux (1925, 1926a) synonymized *Atya serrata* and *A. pilipes* and presumably confused material of two species under the latter name. Two years later, Roux (1928a) maintained the same synonymy, reported one male out of 76 specimens with ortmannioid chelae (perhaps the first Indo-Australian specimen found with chelipeds of this form), and described *Pseudatya beauforti* from Batjan. The same author (1934) reported that *Atya pilipes* was much more common than *A. spinipes* at Manus, Admiralty Islands, and that all of the specimens (3 males, 75 females, 108 ovigerous females) bore atyoid chelae. The material from the Marquesas Islands identified as *Atya serrata* and *Ortmannia alluaudi* by Adamson (1935, 1939) must be assignable to *Atyoida pilipes* according to the ranges accepted herein, and Edmondson (1935), Estampador (1937), and Miyake (1938) followed suit with other material beyond the range of *A. serrata.* Boone (1935) created an enigma that defied interpretation for more than 15 years with her inaccurate description of *Vanderbiltia rosamondae* from Tahiti, a species that Holthuis (1953) was able to synonymize with *A. serrata*, the name then used for all material of *Atyoida*, except the Hawaiian *A. bisulcata.* Although Holthuis (1955) synonymized *Pseudatya* with *Atya*, he did not indicate the senior synonym of *P. beauforti*, the type-species of *Pseudatya*, and it

remained for the same author (1980) to include it in the synonymy of *Atya pilipes*. Holthuis and Rosa (1965) indicated the recorded distribution of *Atya pilipes* (including *A. serrata*). Finally, Smith and Williams (1982:349) listed the synonyms of *Atyoida pilipes* (including *Atya serrata*) and its known distribution.

PUBLISHED ILLUSTRATIONS.—The earliest pictures of *Atya pilipes* are probably those offered by Ortmann (1890), consisting of rather crude representations of the rostrum in dorsal and lateral views and of the first pereopod. More detailed illustrations of the anterior end of the animal in dorsal view, the anterior carapace in lateral view, the telson, and the first and third pereopods of *Atya brevirostris* are available in De Man (1892). Nobili (1900) gave stylized sketches of the rostrum in dorsal view, showing the difference between *Atya brevirostris* and the variety *De Mani*. Roux (1928a) provided figures of the rostrum in lateral and dorsal view, of the first, second, third, and fifth pereopods, and of the first and second pleopods, illustrating the juvenile appearance of the species, which he called *Pseudatya beauforti*. The quite inaccurate illustrations that contributed to the confusion about the identity of *Vanderbiltia rosamondae* were published by Boone (1935); they show the carapace and anterior appendages in dorsal and lateral view, the tail fan, the "petasma," the third maxilliped, all 5 pereopods, and the second pleopod. Edmondson (1935) showed the anterior adult carapace and rostrum in lateral view and the larval pereopods, antenna, and telson of the species that he called *Atya serrata*. Substitutions for the incorrect illustrations of the type-specimen of *Vanderbiltia rosamondae*—including the anterior end in lateral view, the rostrum in dorsal view, the telson and right uropod, the antennule and antenna, and the first, second, third, and fifth pereopods—were offered by Holthuis (1953). Finally, Johnson (1958) published a distribution map for *Atya pilipes* (including *A. serrata*).

DIAGNOSIS.—Rostrum usually bent distinctly ventrad, unarmed or with 1 ventral tooth, less frequently with 2, very rarely with more; pterygostomian angle of carapace bluntly acute, not spinous; fixed teeth on posterior margin of telson inconspicuous; chelae dimorphic, adapted for filter-feeding or sweeping, not for selective picking or scraping alone.

COLOR NOTES.—None.

SIZE.—The available material includes males with carapace lengths of 3.0 to 5.8 mm, nonovigerous females, 3.1 to 7.9 mm, and ovigerous females, 4.6 to 8.8 mm. The maximum carapace length corresponds to a total length of about 34 mm. The largest specimens recorded in the literature that seem to be reliably identified with *A. pilipes* are the ovigerous females mentioned by Roux (1928b:218) from Sumba that measured 36 to 38 mm overall, virtually the same as the "1½ inch" cited by Newport (1847) for the holotype. Specimens of 32 to 41 mm from New Guinea were probably accurately identified by De Man (1915:406), but those of 37 to 45 mm recorded from Celebes by Schenkel (1902:500) may be slightly suspect, and certainly the largest specimens (57 to 61 mm) mentioned by Ortmann (1890:467) from "Südsee" and Samoa are probably referable to *Atyopsis spinipes*, a species that Ortmann subsequently (1895:409) treated as a senior synonym of *Atyoida pilipes*. Holthuis (1980:70) indicated total lengths of 20 to 45 mm for *A. pilipes* (including *A. serrata*), presumably accepting the Celebes record of Schenkel (1902:500).

DISTRIBUTION AND SPECIMENS EXAMINED.—The species representing the somewhat variable concept here proposed for *Atyoida pilipes* has been reliably reported from the Philippines and eastern Lesser Sunda Islands at about 120° east longitude eastward through the Pacific high islands, as far north as Rota in the Marianas at about 14° north, as far south as Rapa in the Îles Tubuai at about 27½° south, and as far east as Magareva in the Îles Gambier at about 135° west. It seems to be absent from the Asiatic mainland.

Material has been examined from the following localities. Numbers in parentheses following the specimens listed are measurements, in mm, of postorbital carapace lengths.

FIGURE 3.—*Atyoida pilipes* (all from ovigerous female from Samoa, carapace length 6.8 mm): *a*, cephalothorax and appendages; *b*, rostrum, left aspect; *c*, anterior carapace and appendages, dorsal aspect; *d*, telson and uropods; *e*, posterior end of telson; *f*, left 3rd maxilliped; *g*, same, distal end; *h*, left 1st chela and carpus; *i*, left 2nd chela and carpus; *j*, left 3rd pereopod; *k*, same, dactyl; *l*, same, flexor surfaces of propodus and dactyl; *m*, distal part of lateral branch of right uropod. (Magnifications: *a*, × 5.2; *c*, *d*, *f*, *j*, × 10.8; *b*, *e*, *g–i*, *k–m*, × 21.5.)

PHILIPPINES: (1) Mountain stream back of Romblon, Romblon Island, 1♂ (6.9), 26 Mar 1908, *Albatross* Philippine Expedition. (2) Nonucan River, Mindanao, 18♂ (5.0–5.6), 11♀ (5.8–8.3), 15 ovig ♀ (5.8–8.8), 6 Aug 1909, *Albatross* Philippine Expedition.

CAROLINE ISLANDS: *Arakabesan Island*, *Palau*—(1) Nger Dis, 7°21′00″N, 134°27′00″E, hand collected below Japanese reservoir in riffle area among vegetation, 1 ovig ♀ (6.9), 9 Aug 1976, J. June. *Babelthuap Island*, *Palau*—(2) Stream south of village of Olei, Ngarehelong Peninsula,

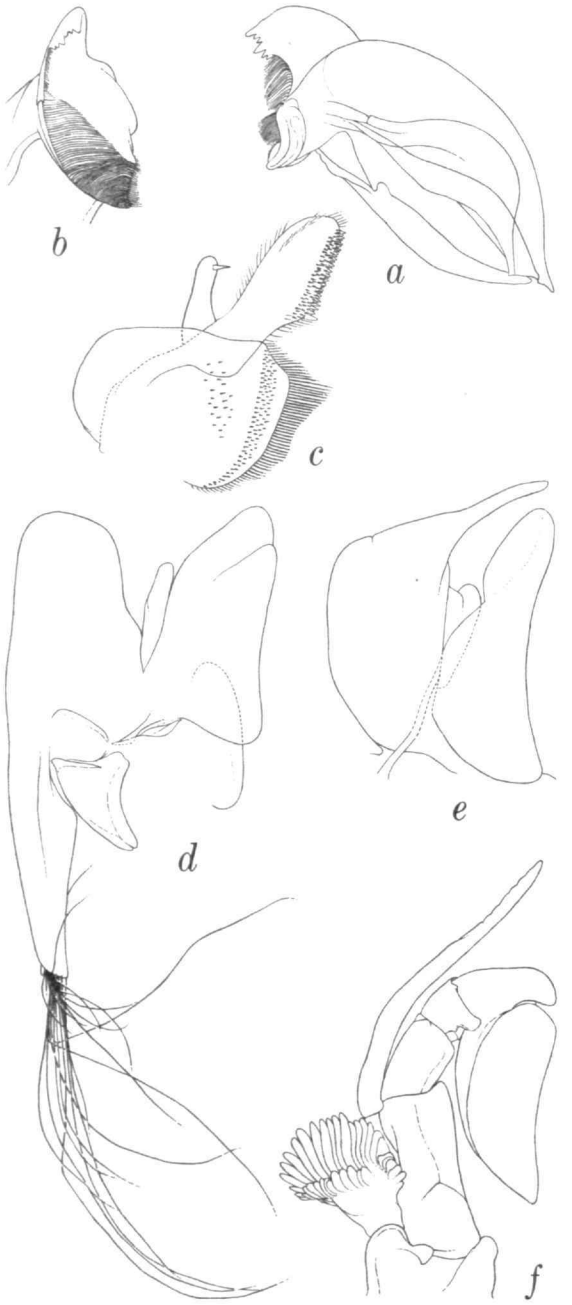

FIGURE 4.—*Atyoida pilipes* (all from female from Samoa, carapace length 7.2 mm): *a*, right mandible; *b*, same, distal aspect; *c*, right 1st maxilla; *d*, right 2nd maxilla; *e*, right 1st maxilliped; *f*, right 2nd maxilliped. (Magnifications: all × 21.5.)

7°42′53″N, 134°37′24″E, water fresh down to last falls, then brackish, yellowish in color, ¼–1½ m/sec current, bottom volcanic rock with potholes, banks rock and mud, overhanging vegetation (liverworts, extensive tree roots), sta 122, 63♂ (3.2–5.0), 37♀ (3.1–6.8), 35 ovig ♀ (5.5–7.4), 13 juv (2.6–2.9), 23 Aug 1955 (1000–1300 hours), liquid rotenone, R.R. Harry, H.A. Fehlmann, F.M. Bayer, Rikrik, Y. Sumang (George Vanderbilt Foundation Expedition). (3) Upper reaches of Hgeremeskang River, Hgiwal municipality, 7°32′50″N, 134°35′47″E, stream 1–3 m wide, current about 1½ m/sec, bottom sand, gravel, rock, banks soil and rock without vegetation, water temperature 26° C, sta 241, 1♂ (4.6), 6 ovig ♀ (6.3–7.6), 18 Oct 1955 (1430–1600 hours), roticide, HAF, YS (GVF). (4) Ilmaw stream, Hgetkip village, Airai municipality, 7°21′37″N, 134°-31′19″E, stream 1–2 m wide, white, slightly turbid water, about 1½ m/sec current, bottom rock, gravel, sand, trailing roots, banks rock and soil without vegetation, water temperature 26° C, sta 250, 30♂ (3.5–5.2), 17♀ (3.3–5.2), 37 ovig ♀ (4.8–7.4), 11 juv (2.5–2.7), 25 Oct 1955 (1430–1700 hours), roticide, HAF, YS (GVF). (5) Iklong stream (tributary to Alsemith River), east of Ngchemliangel village, Aimeliik municipality, 7°31′32″N, 134°29′54″E, stream 1–3 m wide (pools 9–12 m), water white, turbid (heavy rain during night), about 2 m/sec current, bottom gravel, solid rock, many cascades, banks soil and rock without vegetation, water temperature 25° C, sta 268, 1♂ (7.2), 2 ovig ♀ (7.1, 7.4), 1 Nov 1955 (0930–1200 hours), roticide, HAF, YS, Rengiil (GVF). (6) Imengelngal stream (tributary to Alsemith River), northeast of Medorm and Ngchemliangel villages, Aimeliik municipality, 7°27′30″N, 134°30′40″E, slightly brownish and turbid, about 1½ m/sec current, bottom gravel, solid rock, banks soil, solid rock, without vegetation, water temperature 25.5° C, sta 269, 1 ovig ♀ (7.8), 1 Nov 1955 (1300–1515 hours), roticide, HAF, YS, Rengiil (GVF). (7) Arakitaoch stream, strand zone, sta 170, 1♂ (5.4), 31 Oct 1956, A. Fehlmann (GVF). (8) Same, cascade zone, 55♂ (3.9–5.8), 39♀ (3.3–7.9), 102 ovig ♀ (4.8–8.2), 4 Nov 1956, AF (GVF). (9) Same, source region, 4♂

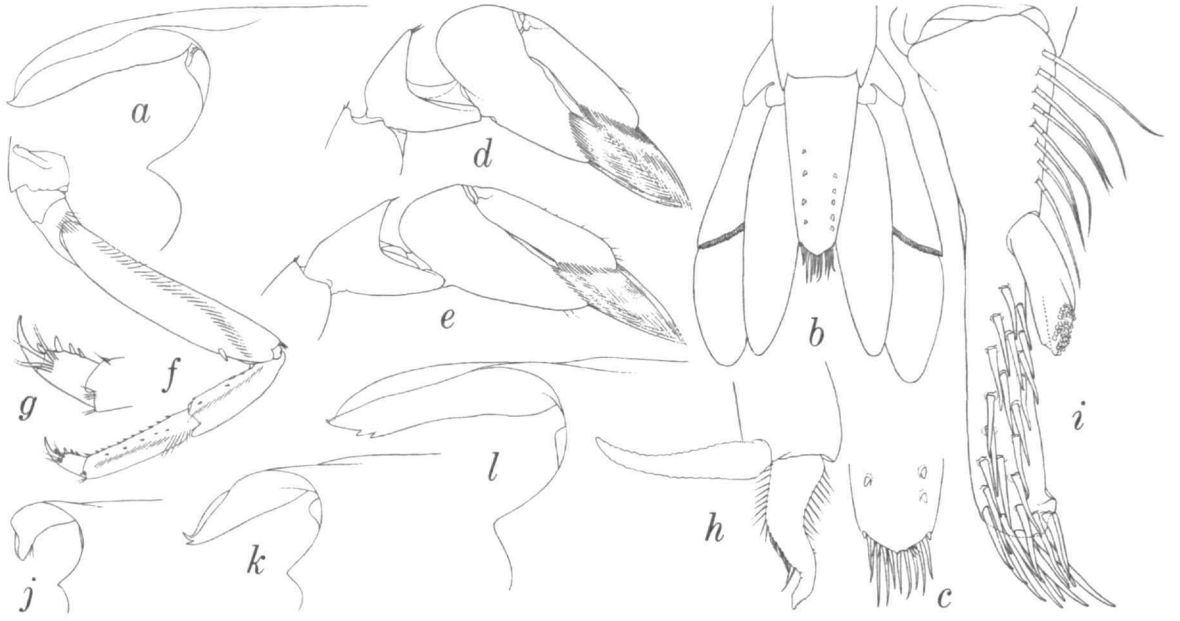

FIGURE 5.—*Atyoida pilipes* (all from Palau specimens; *a–i*, male, carapace length 5.0 mm; *j*, juvenile, carapace length 2.6 mm; *k*, female, carapace length 4.2 mm; *l*, ovigerous female, carapace length 7.0 mm): *a*, rostrum, left aspect; *b*, telson and uropods; *c*, posterior end of telson; *d*, right 1st chela and carpus; *e*, right 2nd chela and carpus; *f*, right 3rd pereopod; *g*, same, dactyl; *h*, exopod and endopod of right 1st pleopod; *i*, right appendix masculina and appendix interna, mesial aspect; *j*, juvenile rostrum; *k*, adolescent rostrum; *l*, variant of adult rostrum. (Magnifications; *b*, *f*, × 10.8; *a*, *c–e*, *g*, *h*, *j–l*, × 21.5; *i*, × 53.8.)

(4.0–5.2), 2♀ (4.0, 5.8), 5 ovig ♀ (4.7–7.0), 5 Nov 1956, AF (GVF). (10) South fork of Arakitaoch River, cascade zone, sta 170-A, 49♂ (2.9–5.6), 85♀ (3.1–7.3), 69 ovig ♀ (4.6–7.7), 1 juv (2.8), 6 Nov 1956, AF (GVF). (11) Same, source zone, 2♂ (3.9, 4.5) 2♀ (6.2, 6.6), 3 ovig ♀ (5.8–6.3), 27 Nov 1956, AF (GVF). (12) Pool in Ghimel River, 1♀ (4.8), 23 Nov 1976, J. June. (13) Cascading waters of Arakitaoch River, 1 ovig ♀ (6.6), 3 Nov 1977, G. Bright. (14) Cascading waters of Metengalakumei River, 2 juv (2.8, 2.8), 17 Nov 1977, GB.

SAMOA ISLANDS: No specific locality, 2♀ (7.3, 7.4), 3 ovig ♀ (6.8–7.5), Rev. J. Whitmee.

SOCIETY ISLANDS: (1) Tahiti, 6 ovig ♀ (7.2–8.4), Apr 1933, Edmondson.

MARQUESAS ISLANDS: No specific locality, 1 ovig ♀ (8.2), 1928, Pere Delmas; 6 ovig ♀ (8.0–8.8), 1930, Pacific Entomological Survey.

VARIATION.—Of 613 specimens with complete rostra from the Palau Islands, 270 have no ventral rostral teeth, 240 have 1, 97 have 2, 5 have 3, and 1 has 4; none have any teeth on the dorsal margin. Of 43 specimens, with rostrum intact, from the Nonucan River, Mindanao, Philippines, 11 have no ventral teeth, 22 have 1, 7 have 2, 2 have 3, and 1 has 4, and 1 specimen has a single dorsal spine near the anterior end of the rostrum.

Analysis of the extensive collections made at different places and times in the Palau Islands (Figures 6, 7) suggest that there is partial protandry in that population and that ortmannioid chelae are prevalent but by no means always present in specimens with an appendix masculina and they are also found in immature females (Figure 8). Among the 44 specimens from the Nonucan River, Mindano, on the other hand, all 18 males are smaller than the smallest female, suggesting complete protandry, and ortmannioid

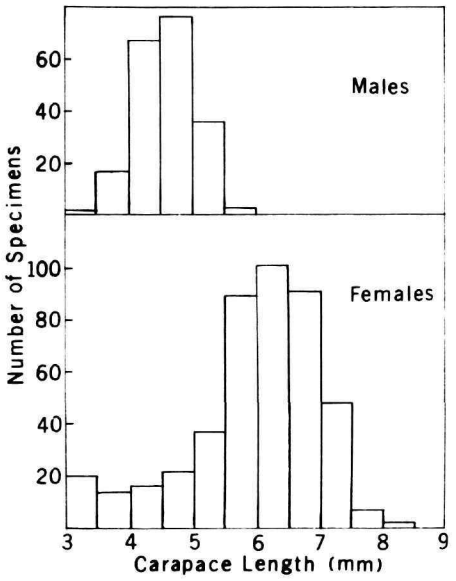

FIGURE 6.—Size distribution of males and females among 647 specimens of *Atyoida pilipes* from the Palau Islands.

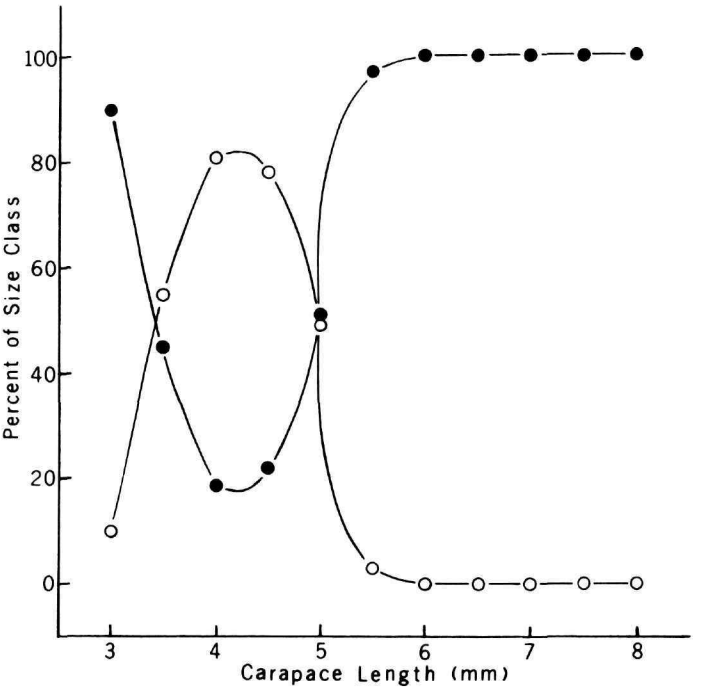

FIGURE 7.—Sex ratios relative to size in 647 specimens of *Atyoida pilipes* from the Palau Islands. Open circles represent males, solid circles females (or juveniles).

chelae are present in all but one of the males, whereas all 26 females have atyoid chelae.

ECOLOGICAL NOTES.—As noted (p. 11), Schmeltz (1869:135) recorded the species from an altitude of more than 1000 feet (305 m) at Upolu, the type-locality. The comprehensive data obtained by the George Vanderbilt Foundation Expedition to Palau in 1955 indicates that the *A. pilipes* populations on Babelthuap Island were found in streams up to 3 meters wide, sometimes with wider pools, flowing at a rate of one-fourth to more than 2 meters per second in cascade zones over a sandy, gravelly, or solid rock bed, between banks of soil and rock, with or without overhanging vegetation; the water varied from white to turbid, and the water temperature at the time of collection varied little, about 25° or 26°C.

LIFE HISTORY NOTES.—None.

COMMON NAMES.—According to Holthuis (1980:70), this and other atyid shrimps are called "Udang grago" in Indonesia, "Apta" and "Yapyap" in Philippine Tagalog and "Daliw daliw" and "Koros" in Philippine Hocaco. The FAO names are "Koras shrimp" in English, "Saltarelle koros" in French, and "Camarón koros" in Spanish.

ECONOMIC IMPORTANCE.—Holthuis (1980:70) notes that, in both the Philippines and Indonesia, this and other atyids are generally sold fresh, but they are sometimes dried and consumed by both humans and other animals, or used for fertilizer.

REMARKS.—The illustrations of this species offered herewith have for the most part been made from Samoan specimens (Figures 3, 4), because Samoa is presumed to be the correct type-locality. As suggested by the slight apparent differences between Philippine and Palauan material, it is quite possible that the integrity of the species as here conceived may be lost when sufficient collections for quantitative analysis become available

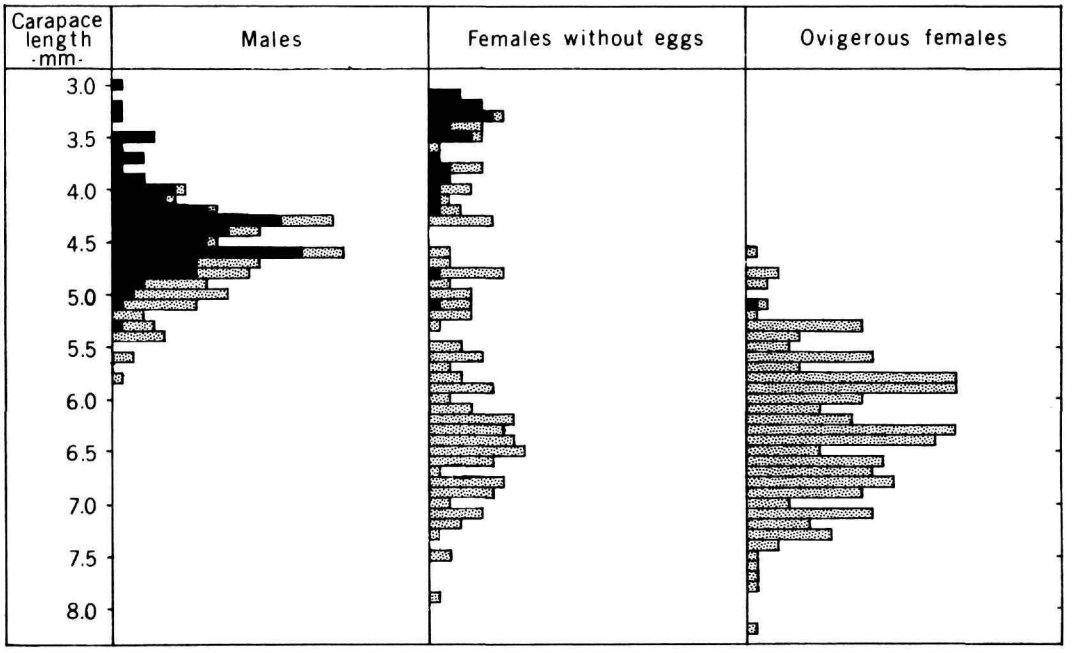

FIGURE 8.—Relationship of chela dimorphism to sex and size in 591 specimens of *Atyoida pilipes* from the Palau Islands. Dark bars represent shrimps with ortmannioid chelae (palm present), light bars indicate shrimps with atyoid chelae (palm virtually absent).

from different parts of the range indicated (p. 12).

Atyoida serrata (Bate, 1888)

FIGURES 9–15

[?]*Atya* (*Atyoida*) sp.—Hilgendorf, 1869:101.—Bouvier, 1925:269, 272, 275, 294, 297.

Atya serrata Bate, 1888:699, pl. 119: fig. 2, 2a [type-locality: "Valley of San Antonio, San Iago, Cape Verde Islands; from a fresh-water stream" (probably erroneous)].—Thallwitz, 1891a:102; 1891b:26, 27.—De Man, 1892:361.—Ortmann, 1895:406, 410.—Bouvier, 1904a:446—449; 1904b:378–380; 1904c:137; 1905:98, 100, 104, 115, 130.—Bordage, 1908:1418, 1419; 1909a:47, 48, 50; 1909b:93, 94, 104–107, figs. 1, 2, 5.—Bouvier, 1909:333.—Calman, 1910:789, 790, 792.—Blaringhem, 1911:189, 192, 194.—Bouvier, 1911:1822, 1824, 1825.—Cuénot, 1911:399, fig. 101.—Bouvier, 1912b:692–694, figs. 4, 6, 7; 1913a:460; 1918:136.—Bouvier and de Charmoy, 1919:317–320.—Bouvier, 1925:269, 271—276, 289, 290, 294–298, 301, 308, 309, 321, 322, 334–344, 351, figs. 611–615, 630–633.—Roux, 1925:151; 1926a:220.—Edmondson, 1929:7–9, 19, 27.—Woltereck, 1937a:246, 247; 1937b:322, 323 [part].—Gurney, 1942:84, 86–88, fig. 20B2.—Roth-Woltereck, 1942:262–264, 268.—Korschelt, 1944:785.—Poisson, 1947:47.—Holthuis, 1951:25; 1954:2; 1965:47.—Carpenter, 1978:343, 349, 350.—Costa, 1980:694.—Smith and Williams, 1982:349.

[?]*Atya brevirostris.*—Coutière, 1900:1267 [part].

Atya serrata, mutation *Alluaudi* Bouvier, 1904a:448, 449 [type-localities: "un torrent de la montagne d'Ambre, à Madagascar . . . Sainte-Marie de Madagascar . . . l'ile Bourbon . . . dans les ravines des montagnes de Salasie et d'Helbour . . . l'ile Maurice"]; 1904c:136; 1905:100, 103.

Atya serrata, modification *Alluaudi.*—Bouvier, 1904b:379, 380.

Atya serrata.—Bouvier, 1904c:136, footnote; 1914:700 [erroneous spelling].

Ortmannia Alluaudi mut. *serrata.*—Bouvier, 1905:98, 100, 105, 111, 115, 127.

Ortmannia Alluaudi Bouvier, 1905:99, 100, 102–104, 108, 127–130, figs. 16–18 [part] [type-localities: Madagascar, Réunion, Mauritius, Marianas].—Bordage, 1908:1419, 1420; 1909a:47.—Bouvier, 1909:333.—Calman, 1910:790.—Blaringhem, 1911:189, 192–194 [part].—Bouvier, 1911:1821–1825.—Cuénot, 1911:399.—Bouvier, 1912a:920, 922; 1912b:692–694, fig. 5; 1913a:460; 1914:699, 700; 1918:135, 136, figs. 5, 6.—Bouvier and de Charmoy, 1919:317, 319, 320.—Bouvier, 1925:263, 272, 274–277,

279, 280, 287, 288, 293–298, 321, 322, 333–345, 349–351, 356–358, figs. 606–611, 616–629, 634–639 [part].—Woltereck, 1937a:246–248.—Roth-Woltereck, 1942:262–264, 277.

mutation *serrata* of *O. Alluaudi*.—Bouvier, 1905:109.

Ortmannia alluaudi.—Bordage, 1909b:93–99, 109, figs. 3, 4.—Blanco, 1935:36.—Woltereck, 1937b: 322, 323 [part].—Gurney, 1942:84, 85, 87, 88, fig. 20B1.—Korschelt, 1944:785.—Holthuis, 1954:2.—Carpenter, 1978:349.—Smith and Williams, 1982:344, 349.

Ortmannia Alluaudi mutation atyienne *serrata*.—Bouvier, 1914:699.

Ortmannia Alluandi.—Colosi, 1919:158 [erroneous spelling].

Ortmannia Alluaudi mutation *serrata*.—Bouvier, 1925:294.

Atya pilipes.—Roux, 1925:151–154 [part].—Woltereck, 1937b:323 [part].—Johnson, 1958:179, 180, fig. 6 [part].—Holthuis, 1965:47.—Holthuis and Rosa, 1965:8 [part].—Costa, 1980:674, 684–688, 694, 695, 697–700, pl. 1a.—Holthuis, 1980:69–71 [part]; 1982:609 [part]. [Not *Atya pilipes* Newport, 1847.]

Atya Alluaudi.—Poisson, 1947:47.

Ortmannia allaudi.—Costa, 1980:697, 699 [erroneous spelling].

Atyoida pilipes.—Smith and Williams, 1982:345, 349, 358, 359 [part].

Atyoida serrata.—Smith and Williams, 1982:359.

REVIEW OF LITERATURE.—If, as seems likely, the seven specimens from a brook on the Seychelles, recorded by Hilgendorf (1869:101) as "*Atya* (*Atyoida*) sp.," belong to the species subsequently named "*Atya serrata*" by Bate (1888:699), some confusion might have been avoided if they had been assigned a new name at that time, thereby diminishing the importance of the documentation associated with Bate's type specimens. Ortmann (1895:406) noted that *Atya serrata* might belong to the genus *Atyoida* but listed it among the "doubtful species." Bouvier (1904a,b,c) correctly determined that *Atya serrata* from Madagascar, Réunion, and Mauritius was polymorphic, and he called the ortmannioid form "la mutation *Alluaudi* de l'*A. serrata*." Later, he (1905) used the combination "*Ortmannia Alluaudi* Bouv. mut. *serrata* Sp. Bate 1888" and mistakenly synonymized *Atya brevirostris* De Man, 1892, with it. The first attempts to rear the young of the two forms of *Atya serrata* were undertaken with difficulty by Bordage (1908); he mentioned zoeal and mysis stages and reported that the ortmannioid form produced young of both forms, whereas the atyoid form begot only atyoid young. The same author (1909a) found that following amputation, chelipeds of the atyoid form regenerated at first in the ortmannioid aspect, gradually becoming more atyoid and assuming the full appearance of the latter after the first molt. Bordage (1909b) summarized his breeding and regeneration experiments. Although these investigations were conducted at Bouvier's request, Bordage deserves credit for persevering over difficult conditions and eventually proving that *Atya serrata* and *Ortmannia Alluaudi* are two forms of the same polymorphic species. Cuénot (1911:399) suggested that the ortmannoid form is a heterozygote and the atyoid form a homozygote, the former yielding a Mendelian 3:1 ratio in the young, while the latter produces only its own kind. In his revisionary work, Bouvier (1925) rather surprisingly treated *Ortmannia Alluaudi* and *Atya serrata* separately but he referred to the former as the "forme maternelle" of the latter. He reported Calman's observation that the smaller of Bate's two specimens is an ortmannioid male and the larger (referred to as "Le type") an atyoid female. Bouvier's belief that the presence of *A. serrata* in the Cape Verde Islands is supported by a Liberian specimen of that species in the Smithsonian USNM collections has been negated by the disclosure by Hobbs and Hart (1982:28) that the Muhlenburg Mission specimen in question is a young male of *Atya africana* Bouvier (1904c). There is little doubt that the specimens identified by Bouvier as *A. serrata* from the Marianas, Tahiti, and Samoa are assignable to *A. pilipes* (which Bouvier synonymized with *A. spinipes*) and that those from the Sandwich Islands may well have been mislabeled, as suggested by Bouvier. Roux (1925) applied the name *Atya pilipes* to the species concept that Bouvier called *A. serrata*. Carpenter (1978:343) believed that the published information indicates that *A. serrata*, like *A. bisulcata*, is protandrous. Finally, Costa (1980) described the ecological relationships of "*Atya pilipes*" in detail and listed the species from Madagascar, the Seychelles, Mauritius, the Comoros, Réunion, and the Andaman and Nicobar islands, without indicating the source of the Andaman and Nicobar records.

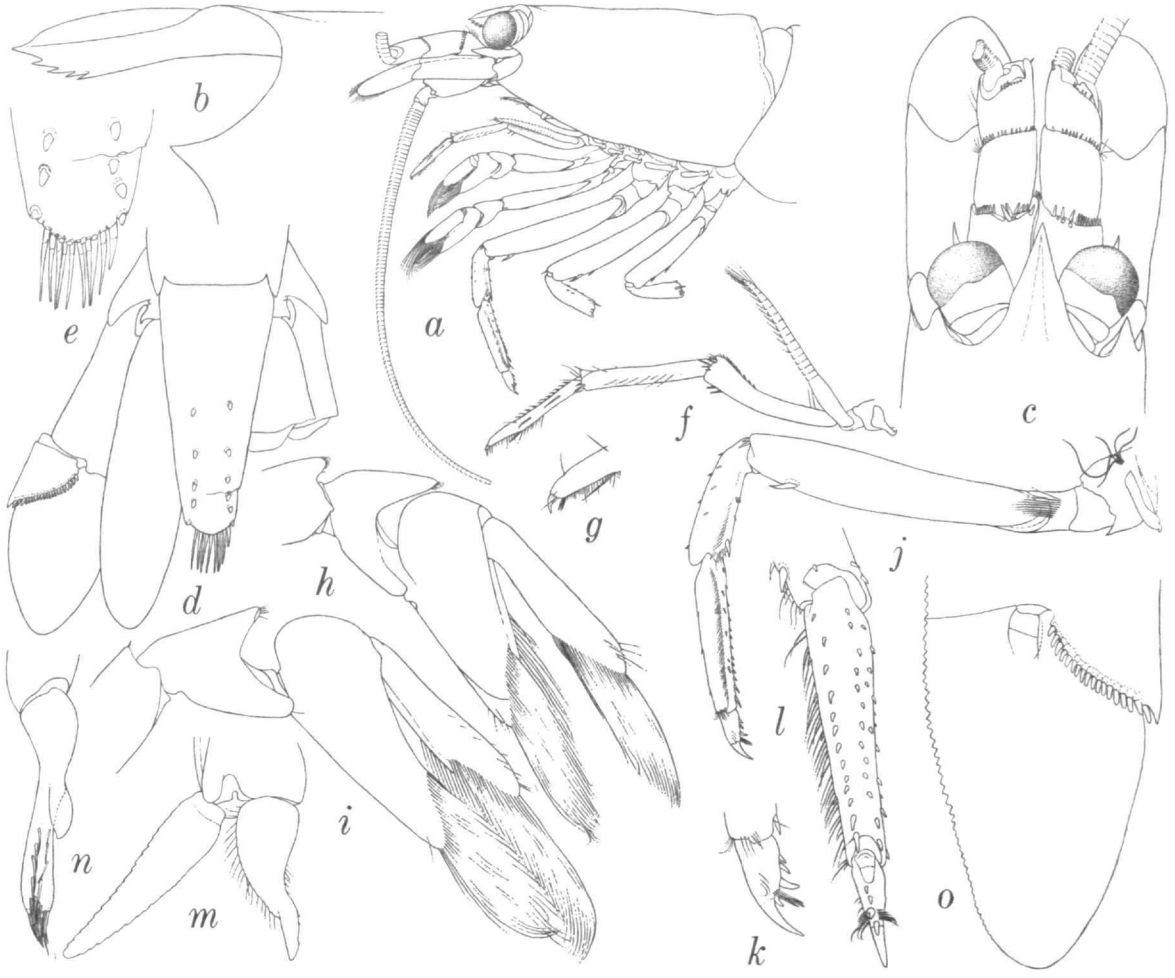

FIGURE 9.—*Atyoida serrata* (all from male syntype of *Atya serrata*, carapace length 6.0 mm): *a*, cephalothorax and appendages, left aspect; *b*, rostrum, left aspect; *c*, anterior carapace and appendages, dorsal aspect; *d*, telson and uropods; *e*, posterior end of telson; *f*, left 3rd maxilliped; *g*, same, distal end; *h*, right 1st chela and carpus; *i*, right 2nd chela and carpus; *j*, left 3rd pereopod; *k*, same, dactyl; *l*, same, flexor surfaces of propodus and dactyl; *m*, exopod and endopod of right 1st pleopod; *n*, right appendix masculina and appendix interna, mesial aspect; *o*, distal part of lateral branch of right uropod. (Magnifications; *a*, × 5.2; *c*, *d*, *f*, *j*, × 10.8; *b*, *e*, *g–i*, *k–o*, × 21.5.)

PUBLISHED ILLUSTRATIONS.—Bate (1888) offered a toto illustration of what must be the female syntype, together with the rostrum in lateral view and the dactyl of the fourth pereopod. Bouvier (1905) published illustrations of the rostrum in dorsal and lateral views, the chelae, the cephalothorax in lateral view, and the dactyls of the third and fifth pereopods of the ortmannioid form that he called "*Ortmannia Alluaudi*." Bordage (1909b) presented a toto illustration in lateral view and illustrated, from the atyoid form, the cephalothorax in lateral view and regenerating chelae and, from the ortmannioid form, the cephalothorax in lateral view, the rostrum in dorsal and lateral views, the chelae, and the dactyls of the third and fifth pereopods. Bouvier

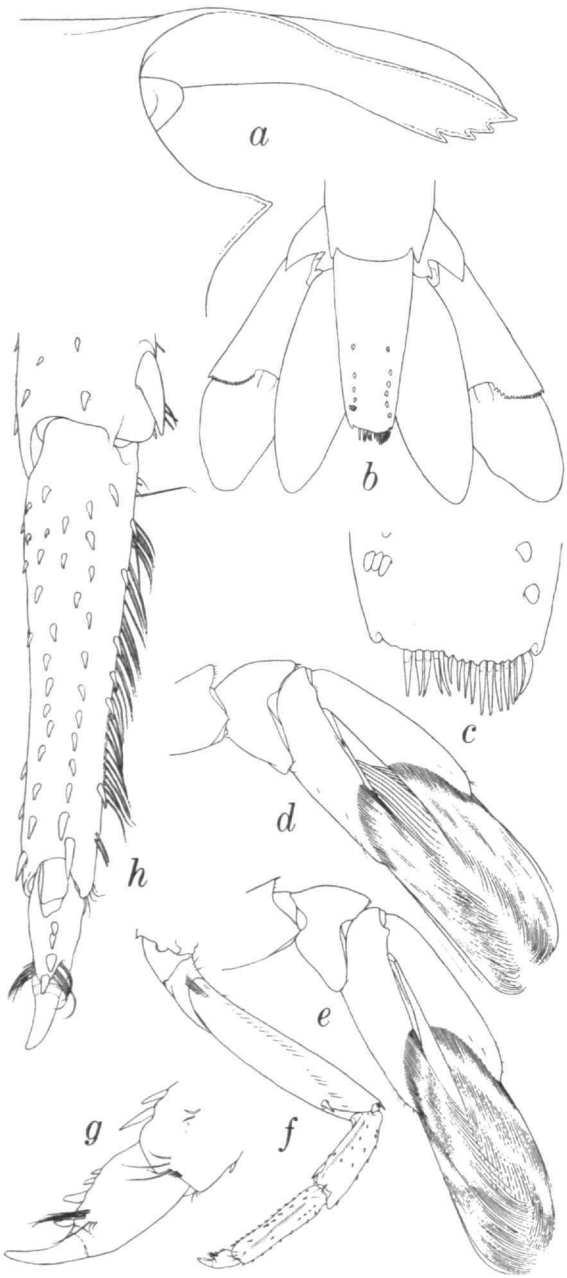

FIGURE 10.—*Atyoida serrata* (all from female syntype of *Atya serrata*, carapace length 10.0 mm): *a*, rostrum, right aspect; *b*, telson and uropods; *c*, posterior end of telson; *d*, right 1st chela and carpus; *e*, right 2nd chela and carpus; *f*, right 3rd pereopod; *g*, same, dactyl; *h*, same, flexor surfaces of propodus and dactyl. (Magnifications: *b*, *f*, × 5.2; *d*, *e*, × 10.8; *a*, *c*, *g*, *h*, × 21.5.)

(1912b) repeated the illustrations of the cephalothorax of the two forms from his 1905 paper, reproduced Bordage's toto drawing from 1909b, and added drawings of the atyoid chela and the tip of a finger with two setae attached. In Bouvier (1918) are illustrations of the chelipeds of both the atyoid and the ortmanniod forms. Bouvier (1925) provided a toto drawing in lateral view and illustrated the cephalothorax in lateral view, the first chela with the tip of a finger and a seta of same, and the dactyl of the fifth pereopod of the atyoid form; he also included a toto illustration of the ortmannioid form in lateral view, together with the cephalothorax in lateral view, a chela, dactyls of the third and fifth pereopods, pleopods, appendix masculina, uropod dieresis, telson, preanal spine in ventral and lateral views of that form, as well as the juvenile rostrum in lateral view and the juvenile chela, dactyl, and telson. Sketches of the atyoid and ortmannioid chelae are included in Gurney (1942). Finally, Costa (1980) offered a photograph of the atyoid form.

DIAGNOSIS.—Rostrum continuing general trend of dorsal surface of carapace in adults, not bent noticeably ventrad, armed ventrally with 2-4 teeth; pterygostomian angle of carapace sharply acute; fixed teeth on posterior margin of telson inconspicuous; chelae polymorphic, adapted for filter-feeding, sweeping or selective picking, or scraping.

SIZE.—Of the eight specimens of this species examined, the four males have carapace lengths of 5.7 to 6.5 mm, the four females, 8.0 to 10.2 mm. The largest male has a total length of about 25 mm, the largest female about 50 mm. Roux (1925:153) recorded males measuring 30–32 mm and a female 44 mm long. The largest specimen mentioned in the literature seems to be the one illustrated "Grandeur naturelle" by Bordage (1909b, fig. 1) that measures about 48 mm.

DISTRIBUTION AND SPECIMENS EXAMINED.—The designation of the Cape Verde Islands as the type-locality of *Atya serrata* is almost certainly in error and no justification is offered for the inclusion of the Andaman and Nicobar Islands in the

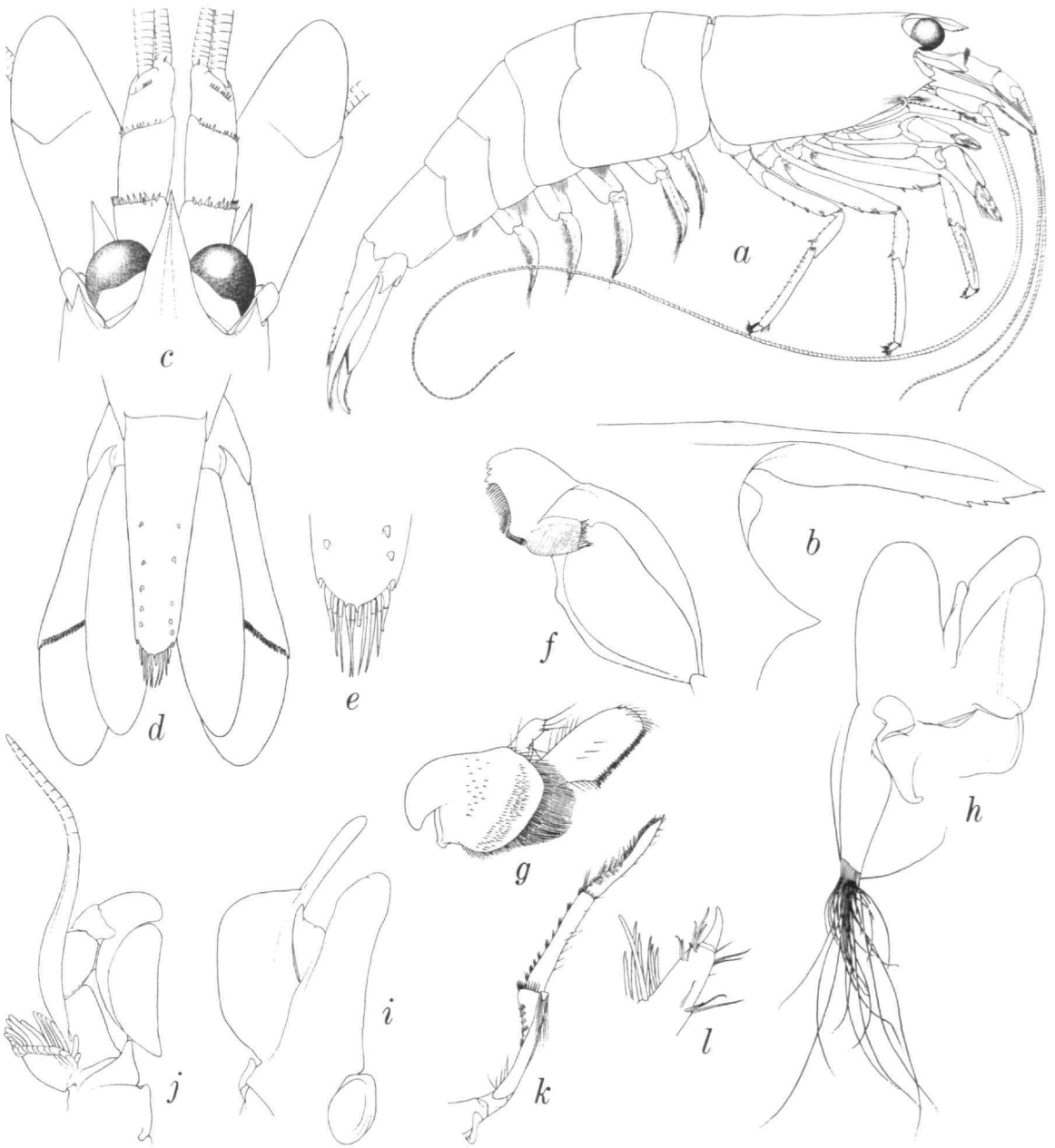

FIGURE 11.—*Atyoida serrata* (all from male from La Réunion, carapace length 5.7 mm): *a*, entire specimen, right aspect; *b*, rostrum, right aspect; *c*, anterior carapace and appendages, dorsal aspect; *d*, telson and uropods; *e*, posterior end of telson; *f*, right mandible; *g*, right 1st maxilla; *h*, right 2nd maxilla; *i*, right 1st maxilliped; *j*, right 2nd maxilliped; *k*, right 3rd maxilliped; *l*, same, distal end. (Magnifications: *a*, × 5.2; *c*, *d*, *k*, × 10.8; *b*, *e–j*, × 21.5; *l*, × 53.8.)

FIGURE 12.—*Atyoida serrata* (all from male from La Réunion, carapace length 5.7 mm): *a*, right 1st pereopod; *b*, same, chela; *c*, same, denuded; *d*, same, distal part of long lateral seta; *e*, same, distal part of short mesial seta; *f*, right 2nd pereopod; *g*, same, chela; *h*, same, distal part of long lateral seta; *i*, same, distal part of short mesial seta; *j*, right 3rd pereopod; *k*, same, dactyl; *l*, same, flexor surfaces of propodus and dactyl; *m*, right 4th pereopod; *n*, same, dactyl; *o*, right 5th pereopod; *p*, same, dactyl; *q*, exopod and endopod of right 1st pleopod; *r*, right appendix masculina and appendix interna. (Magnifications: *a*, *f*, *j*, *m*, *o*, × 10.8; *b*, *c*, *g*, *l*, *q*, × 21.5; *k*, *n*, *p*, *r*, × 53.8; *d*, *e*, *h*, *i*, × 223.6.)

range of the species that Costa (1980, table 2) called *Atypa pilipes*. Therefore, the only reliable locality records for *Atyoida serrata* seem to be Madagascar, the Comoro Islands, the Seychelles, Mauritius, and La Réunion.

Collections have been examined from the following localities. Numbers in parentheses following the specimens listed are measurements, in mm, of postorbital carapace lengths.

LA RÉUNION: Rivière Saint-Denis, 3♂ (5.7–6.5) 3♀ (8.0–10.2), Bordage.

The following locality data are probably erroneous:

CAPE VERDE ISLANDS: British Museum (NH) 88–22, San Jago, syntypes of *Atya serrata*, 1♂ (6.0), 1♀ (10.0), *Challenger*.

FIGURE 13.—*Atyoida serrata* (male specimens from La Réunion; *a–d*, carapace length 6.2 mm; *e–j*, carapace length 6.5 mm): *a*, rostrum, right aspect; *b*, posterior end of telson; *c*, right 1st chela and carpus; *d*, right 2nd chela and carpus; *e*, rostrum, right aspect; *f*, posterior end of telson; *g*, right 1st chela and carpus; *h*, same, distal parts of representative setae; *i*, right 2nd chela and carpus; *j*, same, distal parts of representative setae. (Magnifications: *a–g*, *i*, × 21.5; *h*, *j*, × 223.6.)

VARIATION.—The number of ventral rostral teeth varies from 2 to 4 in the 8 available specimens here assigned to *Atyoida serrata*. None of them bears any indication of dorsal teeth.

The teeth on the posterior margin of the telson are much less prominent than those in *A. bisulcata*, but they vary in number from 2 to 7.

As noted by Calman (1910:790) and repeated by Bouvier (1925:276), the smaller type specimen of Bate's species is a male with ortmannioid chelae (Figure 9), while the larger one is a female bearing atyoid chelae (Figure 10). Fortunately, the six specimens from Bordage's Réunion collection, received in exchange from the Muséum national d'Histoire naturelle, Paris, about 1913, were carefully selected to display the variability represented in the material, and they clearly show that the La Réunion population, like that of *A. bisulcata* in Hawaii but unlike that of *A. pilipes*, may bear three quite different kinds of chelae. The male with a carapace length of 6.2 mm and the smallest female, with a corresponding measurement of 8.0 mm, each have the chelae modified for selective picking or scraping (Figures 13*c*,*d* and 15*c*,*g*). The smallest male, with a carapace length of 5.7 mm, has chelae that are apparently designed for either sweeping or filter feeding (Figure 12*a–i*), and the largest male, with

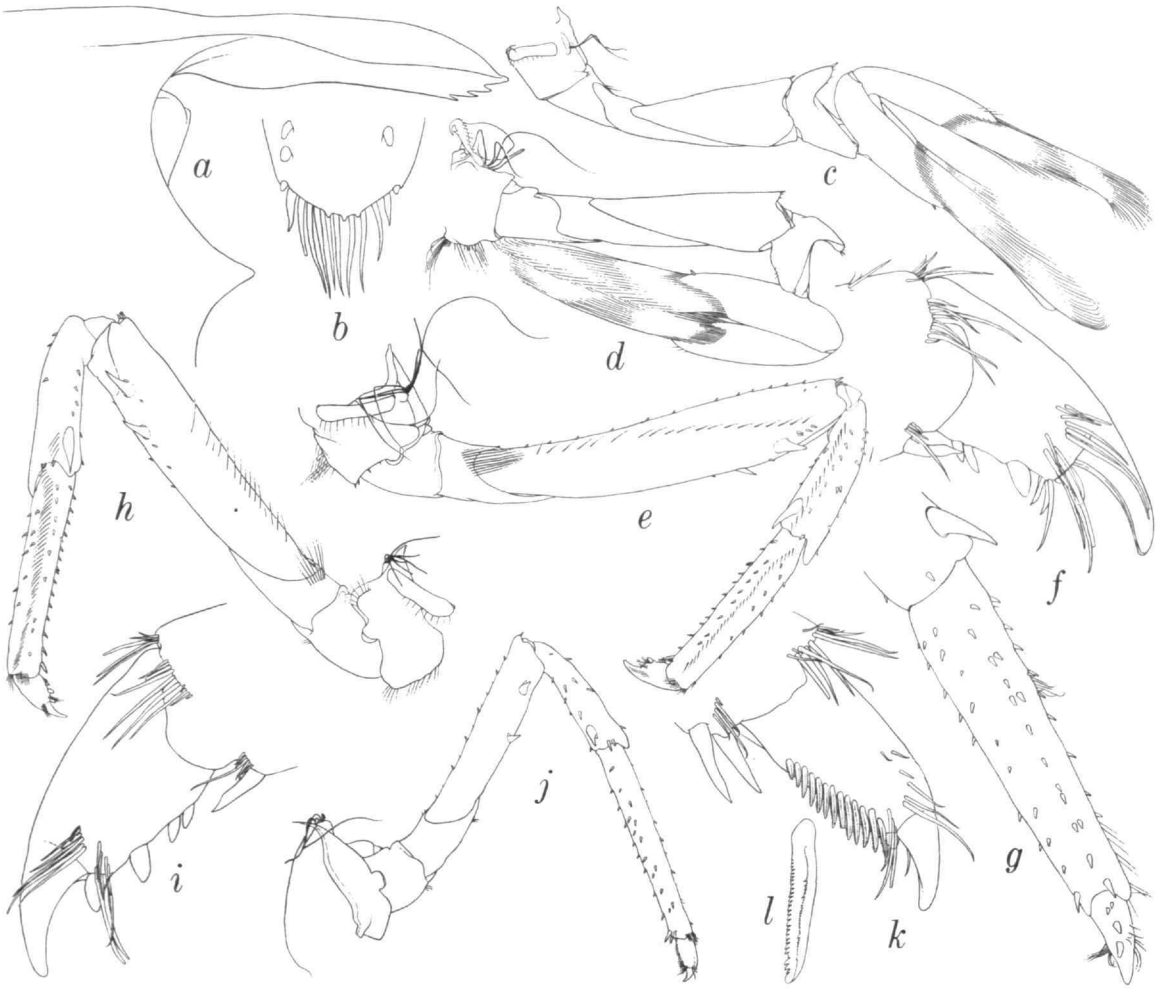

FIGURE 14.—*Atyoida serrata* (all from female from La Réunion, carapace length 8.5 mm): *a*, rostrum, right aspect; *b*, posterior end of telson; *c*, right 1st pereopod; *d*, right 2nd pereopod; *e*, right 3rd pereopod; *f*, same, dactyl; *g*, same, flexor surfaces of propodus and dactyl; *h*, left 4th pereopod; *i*, same, dactyl; *j*, right 5th pereopod; *k*, same, dactyl; *l*, same, spine from flexor margin of dactyl. (Magnifications: *c–e*, *h*, *j*, × 10.8; *a*, *b*, *g*, × 21.5; *f*, *i*, *k*, × 53.8; *l*, × 223.6.)

a carapace length of 6.5 mm (Figure 13*g–j*), and the two larger females, carapace lengths 8.5 and 10.2 mm (Figure 14*c*, *d*), have the chelae seemingly adapted for filter feeding only.

ECOLOGICAL NOTES.—According to Costa (1980:697), "*Atya pilipes*" (= *A. serrata*) is frequently dispersed over the stream bottoms at night and hides during the daytime under rocks and in vegetation that is both centrally situated and occurs along the stream banks. The shrimps frequent streams from one to 20 meters wide, with bottoms of basalt rock and rocks with pebbles and/or, sand, at altitudes from 0.5 to 500 meters, in water 2.5 to 50 cm deep, in currents ranging from 10 cm per second to 1 m per second, at temperatures of 20° to 26° C, and a pH range of 7.0 to 8.4.

LIFE HISTORY NOTES.—Bordage (1908, 1909b)

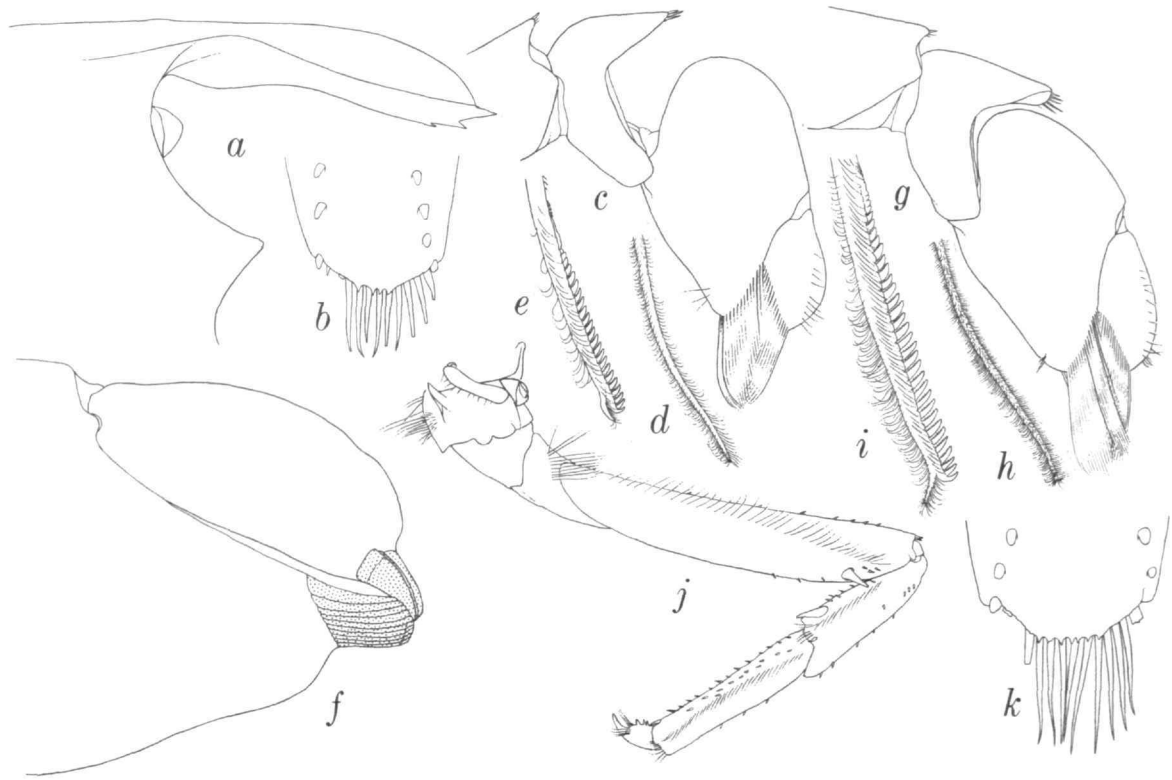

FIGURE 15.—*Atyoida serrata* (female specimens from La Réunion; *a–j*, carapace length 8.0 mm; *k*, carapace length 10.2 mm): *a*, rostrum, right aspect; *b*, posterior end of telson; *c*, right 1st chela and carpus; *d*, same, distal part of long lateral seta; *e*, same, distal part of short mesial seta: *f*, same, denuded fingers; *g*, right 2nd chela and carpus; *h*, same, distal part of long lateral seta; *i*, same, distal part of short mesial seta; *j*, right 3rd pereopod; *k*, posterior end of telson. (Magnifications: *j*, × 10.8; *a–c*, *g*, *k*, × 21.5; *f*, × 53.8; *d*, *e*, *h*, *i*, × 223.6.)

introduced ovigerous females caught in cool mountain streams into masonry basins supplied with running tap water in the warmer coastal region of the island of La Réunion. Although the circulating water was sufficiently cool to maintain the shrimps and their offspring, heavy rains that occurred during part of the experiment led to severe siltation and clogging of the crude filters at the intake and outlet openings of the tanks, resulting in stagnation and warming of the water. Under these somewhat unnatural conditions, zoeal larvae metamorphosed into mysis larvae in about 6 days and into the adult form in 12 days more. Females with ortmannioid chelae produced young with both ortmannioid and atyoid chelae, whereas the young of females with atyoid chelae had only atyoid chelae.

Specimens from Anjouan, Comoro Islands, recorded by Costa (1980), suggested the presence of protandrous development, but the author mentioned only that the kind of hermaphroditism that was found in *Atya bisulcata* probably occurs also in *A. serrata*.

COMMON NAMES.—The only English name currently available for *A. serrata* may be the FAO name "koros shrimp," which is applicable also to the related *A. pilipes* (Holthuis, 1980:70).

ECONOMIC IMPORTANCE.—No information is available on the utilization of these little atyids in the western Indian Ocean.

REMARKS.—There seems to be little doubt that the species described by Bate (1888), ostensibly collected at the Cape Verde Islands during the *Challenger* Expedition, is identical with the one studied by Bordage (1908, 1909a,b) on La Réunion in the western Indian Ocean. As the species has not been reported from numerous subsequent collections from the Cape Verdes, it may be safe to assume that Bate's type specimens were mislabeled. Also, if the species is confined to the tropical western Indian Ocean, as available records would seem to indicate, it is possible that the types were not collected by the *Challenger* at all, for that vessel operated in the Indian Ocean only in the extreme southern part, in the "Roaring Forties."

Possibly the first carcinologist to realize that *Atya pilipes* and *A. serrata* are not synonymous was Johnson (ms:13), who wrote the following after studying the collections in the British Museum (Natural History) in 1958: "Examination of Bate's type specimens shows at once that they cannot belong to the same species as *A. brevirostris* . . . [I]t is clear that *A. serrata* has nothing to do with *A. brevirostris* and cannot be a synonym of *A. pilipes*." Johnson failed, however, to realize that *A. serrata* is a distinct species and—perhaps influenced by the type-locality indicated by Bate—he synonymized it with *Atya occidentalis* Newport, 1847 (= *A. innocous* (Herbst, 1792)).

There is little doubt in my mind that *Atyoida serrata* is clearly distinguishable from *A. pilipes* by the less downturned rostrum, the sharper pterygostomian angle of the carapace, and the polymorphic rather than dimorphic chelae; but firm knowledge of the range limits of *A. serrata* and their relationship to those of *A. pilipes* must await more intensive collecting in what now appears to be a wide gap between the two in the Indian Ocean east of 60° east longitude. Actually, because of the similar polymorphism of the chelae and the nearly horizontal rostrum, *A. serrata* may be more closely related to the Hawaiian endemic, *A. bisulcata*, than it is to *A. pilipes*; it differs from the Hawaiian species most noticeably in the presence of teeth on the ventral margin of the rostrum, which is usually unarmed in *A. bisulcata*, and in the much less conspicuous teeth on the posterior margin of the telson.

Genus *Atyopsis*, new genus

Altya.—Roux, 1971:595 [erroneous spelling].
Atyia.—Roux, 1932:564 [erroneous spelling].
[?] *Ortmania.*—Blanco, 1935:36 [erroneous spelling].

TYPE-SPECIES.—*Atya spinipes* Newport, 1847.

ETYMOLOGY.—The feminine name *Atyopsis* is derived from the name *Atya* and the Greek suffix *-opsis*, having the appearance of, like.

DIAGNOSIS.—Body pigmented, eyes well developed; rostrum not strongly compressed laterally, median dorsal carina typically unarmed, ventral keel with 2–16 teeth; anterior margin of carapace armed with antennal spine, pteygostomian margin sharply acute; supraorbital spines absent; telson with posterolateral angles overreaching setigerous posterior margin; third maxilliped not terminating in single apical spine; pereopods without exopods; 1st and 2nd pereopods with chelae monomorphic (without palm), fingers tipped with brushes of long setae adapted for filter feeding, carpus of both appendages excavate distally, little if at all longer than broad; 3rd pereopod of large males with prominent spur on merus; branchial complement consisting of 5 pleurobranchs, 3 arthrobranchs, 1 podobranch, 5 epipods (reduced posteriorly), no mastigobranchs; 1st pleopod of male with endopod rigid, rhomboidally oval, submarginally spinose; 2nd pleopod of male with appendix masculina subcylindrical, spinose over entire length distal to base of appendix interna.

RANGE.—Like *Atyoida*, *Atyopsis* is known chiefly from the high islands of the Indo-Pacific region, but its occurrence seems to be less extensive longitudinally than that of *Atyoida*, from Sri Lanka to Samoa. It does, however, go as far north as Okinawa in the Ryukyus and, unlike *Atyoida*, it is common on the larger Indonesian islands, as well as on the Asiatic mainland from India to Thailand and the Malay Peninsula.

REMARKS.—Although *Atyopsis* superficially resembles *Atya* more closely than do any of the

other atyid genera, it seems to be distinguished by enough characters to justify its separation from the typical Afro-American species of that genus: telson with posterolateral angles overreaching setigerous posterior margin; epipods reduced on third and fourth pereopods and mastigobranchs lacking on all of them; merus of third pereopod of large males with unique, massive spur near distal end; and endopod of first pleopod of males distinctively rigid and rhomboidally oval, with stout, curved, submarginal spines. Only 2 species are known.

Key to Species of the Genus *Atyopsis*

Rostrum gradually tapering to slender apex, armed ventrally with 7–16 (commonly 10–14) indistinct serrations; endopod of 1st pleopod of male less than 1½ times as long from proximal articulation to base of retinaculate projection as maximum width, not including submarginal spines ..... **A. moluccensis**, new combination

Rostrum rather abruptly narrowing to somewhat broad apex, armed ventrally with 2–6 discrete teeth; endopod of 1st pleopod of male more than 1¾ times as long from proximal articulation to base of retinaculate projection as maximum width, not including submarginal spines ..... **A. spinipes**, new combination.

Atyopsis moluccensis (De Haan, 1849), new combination

FIGURES 16–19

Atya moluccensis De Haan, 1849:186, pl. O [type-locality: Moluccas (indicated on type series label according to information received from L.B. Holthuis)].—Miers, 1880:382, pl. 15: figs. 3, 4.—Thallwitz, 1891b:26.—De Man, 1892: 357, 360–362, 520, pl. 21: fig. 20, 20a–d [part].—Weber, 1892:536.—Ortmann, 1895:407, 408; 1897, pl. 1: fig. 4.—Nobili, 1900:475.—Bouvier, 1904c: 137; 1905:99, 109, 111, 113, fig. 20; 1909:333.—Rathbun, 1910:315, 316.—Bouvier, 1925:294, 299–303, 305, 306, 322, 326, 356, 358, figs. 673–681 [not fig. 672 = *A. robusta*, instead of *A. armata* as indicated].—Roux, 1928a:208.—Edmondson, 1935:16.—Woltereck, 1937b:324 [part].—Suvatti, 1938:47.—Gurney, 1942:87.—Suvatti, 1950: 137.—Djajadiredja and Sachlan, 1956:370.—Smith and Williams, 1982:346.

Atya armata A. Milne-Edwards, 1864:149, 152, pl. 3: figs. 3, 3a [type-locality: "Batavia" (pp. 145, 152), not "les îles Philippines" (p. 149)].—Thallwitz, 1891a:102, 1891b:26, 27, 55, pl. 1: fig. 6.—De Man, 1892:362.—Lanchester, 1900:262; 1901:559.—Bouvier, 1904c:137; 1905:113, fig. 20; 1925:299.—Roux, 1925:150.—Johnson, 1964:28.—Smith and Williams, 1982:346.

[?]*Atya armata*.—Von Martens, 1868:47, 48, 64, pl. 1: fig. 6, 6a.

[?]*Atya bisulcata*.—Hickson, 1889:223, 362 [not *Atyoida bisulcata* Randall].

Atya gustavi Ortmann, 1890:467, pl. 36: fig. 9*a,b,c* [type-locality: "Sumatra, Indrapura-Fluss"].—Thallwitz, 1891b:26, 27.—Weber, 1892:536.—Smith and Williams, 1982:346.

Atya lineolata De Man, 1892:357, footnote [manuscript name attributed to "Kuhl" cited as synonym of *Atya moluccensis*].

[?]*Atya moluccensis*.—Ortmann, 1894:12.—Borradaile, 1899: 405.—Roux, 1925:150.—Blanco, 1935:30.—Tiwari, 1951: 208.—Holthuis, 1978:29.

Atya Gustavi.—Bouvier, 1905:113; 1925:299.

O.[rtmannia] moluccensis.—Bouvier, 1911:1823.

[?]*Altya moluccensis*.—Roux, 1917:595 [erroneous spelling].

Atya gustari.—Roux, 1925:150 [erroneous spelling].

[?]*Atya mollucensis*.—Roxas, 1930:16 [erroneous spelling].

[?]*Atya spinipes*.—Roux, 1932:567.—Johnson, 1957, fig. 5e; 1959:71.—Arudpragasam and Costa, 1962:7, 21–23.—Costa, 1972;128, 133, 134.—Holthuis, 1978:29.—De Silva, 1982:127.

[?]*Atyia spinipes*.—Roux, 1932:564, 574 [erroneous spelling].

Atya spinipes.—Woltereck, 1937b:324 [part].—Johnson, 1958:179, fig. 5 [part]; 1961:120, 144–151, figs. 38–42; 1964:27, 28.—Fernando, 1963:29.—Holthuis and Rosa, 1965:9 [part].—Johnson, 1965:9, 10; 1966:280; 1967:419, 420, 428, 431; 1968:235; 1969:110.—J. E. Bishop, 1973:205, 206.—Holthuis, 1980:71 [part]; 1982:609 [part].—Smith and Williams, 1982:345, 346 [part]. [Not *A. spinipes* Newport, 1847.]

Atya typus.—Mendis and Fernando, 1962:68, 71, fig. 3.

REVIEW OF LITERATURE.—Apart from the name assigned to this species by De Haan (1849:186),

there is no published indication of its place of origin, but L.B. Holthuis has informed me that the type specimens are accompanied by a label bearing the word "Moluccas." A. Milne-Edwards (1864) went to the opposite extreme in redescribing the species under the name *Atya armata* by indicating the type-locality as both "Batavia" and "les îles Philippines;"there is little doubt that the latter was an inadvertent error. From specimens of different sizes available to him from the Philippines, Sunda Islands, and Ceram, Von Martens (1868) suggested that the species described by De Haan and A. Milne-Edwards might be synonymous. On the other hand, Miers (1880) noted differences between adult males of *A. armata* from Java and presumably *A. spinipes* from Samoa, yet he failed to recognize important differences between the type specimens of *A. spinipes* and *A. pilipes*. There is little hope of determining the identity of the material recorded from the northern Celebes by Hickson (1889), but it is hardly the Hawaiian endemic *Atya bisulcata* that he called it. The lateral aspect of the rostrum of the Sumatran specimens named *Atya gustavi* by Ortmann (1890) seems to relate the species more closely to *A. moluccensis* than to any of the other recognized species. Thallwitz (1891b) synonymized *Atya moluccensis* and *A. armata* but retained the junior name for the species. De Man (1892) seems to have had *A. moluccensis* from Java and Sumatra, but at least some of the specimens listed from other localities were probably *A. spinipes*; he (1892:357) also published the manuscript name "*Atya lineolata* Kuhl" for some of the material, but that name was treated as a synonymn of *A. moluccensis*, thereby making it unavailable for subsequent adoption (see "Remarks," p. 35). Ortmann (1895) recognized, with reservations, the distinction between *Atya moluccensis* and *A. spinipes*, indicating that the former inhabited Indonesia and the Philippines, while the latter was known from the Philippines and eastward; he also listed *A. armata*, *A. gustavi*, and *A. dentirostris* as synonyms of *A. moluccensis*. Although Bouvier (1905) recognized both *A. moluccensis* and *A. spinipes* in his key to *Atya*, he (1905:113) indicated in the text that the latter "paraît n'en être qu'une variété." He also noted that *A. armata* is identical with *A. moluccensis* and that the type specimens of the former were indeed collected by "Blecker" at Batavia, the subsequent mention of the Philippines being a lapsus. (L.B. Holthuis has informed me that the person identified as "Blecker" by Bouvier was Pieter Bleeker, the Dutch ichthyologist who wrote extensively on Indonesian fishes.) Bouvier, himself, seemed to display a similar lapsus when he (1905:113) noted that the first pleopods of the male "sont identiques à ceux de l'*A. occidentalis*." In his final remark about *A. moluccensis*, Bouvier (1925:303) recognized that the species that he called by that name is distinguished from all of the other species of *Atya* by the reduction of its epipodial apparatus and by the pronounced projections that form the angles on the posterior margin of the telson. Roux (1928a) corrected a presumed earlier error by relegating *Atya moluccensis* to the synonymy of *A. spinipes*, but Edmondson (1935) considered them to be distinct. The species here presumed to be *A. moluccensis* from Sri Lanka, attaining a length of 7 cm, was called "*Atya typus* Milne Edw." by Mendis and Fernando (1962) but corrected by Fernando (1963). Johnson (1964) noted that immature specimens of "*Atya spinipes*" resemble *Caridina typus*, but the species were never found together in Malaya.

PUBLISHED ILLUSTRATIONS.—The only figures accompanying the original description by De Haan (1849, pl. O) are good representations of both mandibles, the two maxillae, and the three maxillipeds. The fine toto drawing and dorsal aspect of the rostrum offered by A. Milne-Edwards (1864, pl. 3: figs. 3, 3a) with the description of *Atya armata* caused some subsequent confusion because the figures are numbered from the bottom of the plate upward, leading to the subsequent republication of the illustration of *Atya robusta* as *A. armata*. The natural-size toto drawing and rendition of a cheliped of a juvenile from Ceram by Von Martens (1868, pl. 1) probably represent *Atya armata*, as indicated. Miers (1880) offered good illustrations of the rostra and third pereopods, showing the differences between *Atya moluccensis* and *A. spinipes* that have been generally ignored by more recent workers. The illustrations

FIGURE 16.—*Atyposis moluccensis* (all from male from Ban Kiriwong, peninsular Thailand, carapace length 21.8 mm); *a*, entire specimen, right aspect; *b*, anterior carapace and rostrum, right aspect; *c*, telson and uropods; *d*, posterior end of telson; *e*, 6th abdominal somite and median tubercle on 5th, ventral aspect; *f*, preanal carina, right aspect; *g*, left 3rd pereopod; *h*, same, dactyl; *i*, same, flexor surfaces of propodus and dactyl; *j*, endopod of right 1st pleopod, posterior aspect; *k*, same, anterior aspect; *l*, right appendix masculina and appendix interna, mesial aspect, (Magnifications: *a*, × 1.3; *c*, *e*, *g*, × 2.6; *b*, × 5.2; *f*, *h–l*, × 10.8; *d*, × 21.5.)

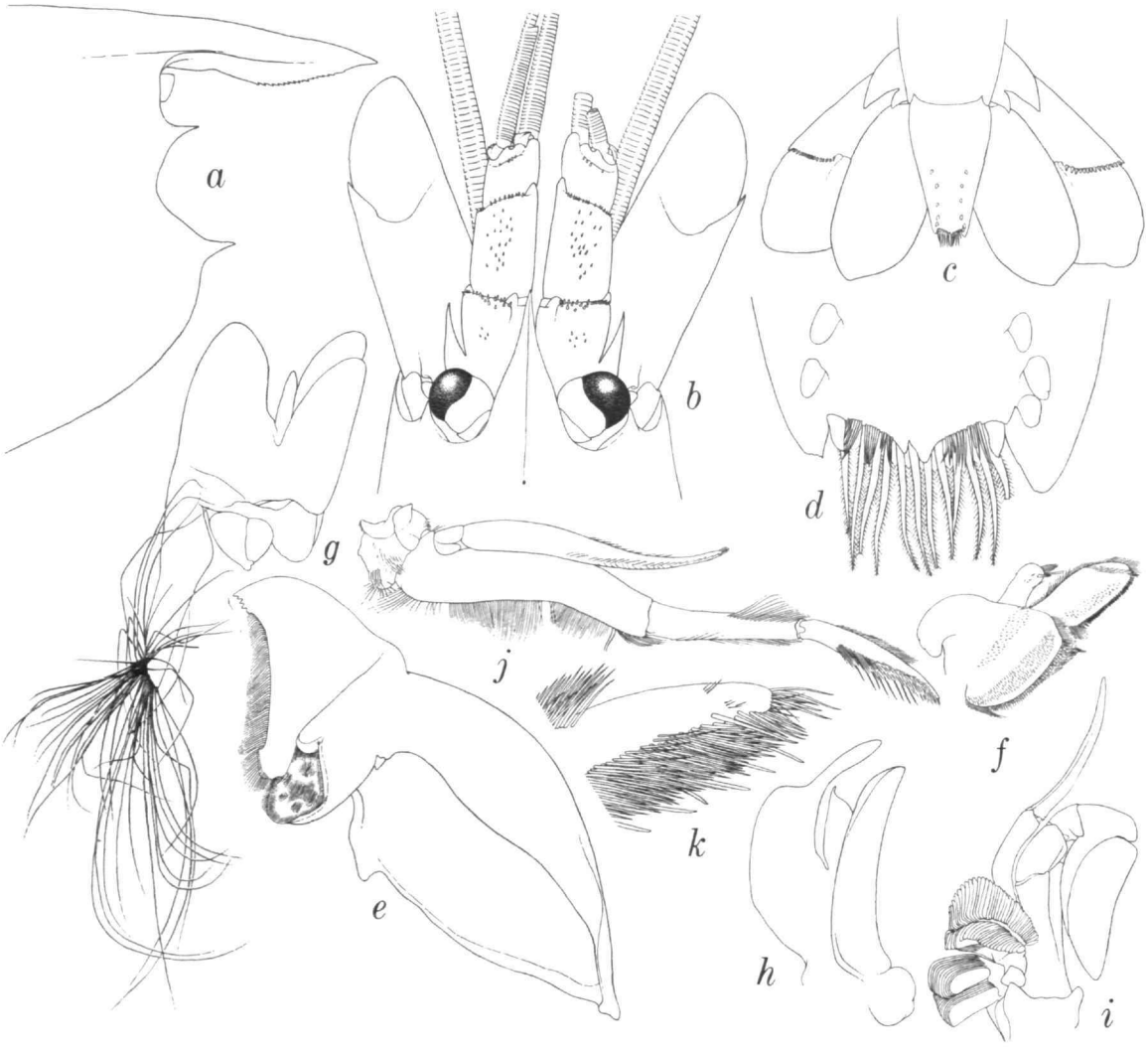

FIGURE 17—*Atyopsis moluccensis* (all from ovigerous female from Bogor, Java, carapace length 20.7 mm): *a*, anterior carapace and rostrum, right aspect; *b*, anterior carapace and appendages, dorsal aspect; *c*, telson and uropods; *d*, posterior end of telson; *e*, right mandible; *f*, right 1st maxilla; *g*, right 2nd maxilla; *h*, right 1st maxilliped; *i*, right 2nd maxilliped; *j*, right 3rd maxilliped; *k*, same, distal end. (Magnifications: *c*, × 2.6; *b*, × 4.3; *a*, *f*–*j*, × 5.2; *e*, × 10.8; *d*, *k*, × 21.5.)

of the rostrum and first pereopod of *Atya gustavi* by Ortmann (1890) are characteristically crude, but the lateral aspect of the rostrum depicts an outline that is consistent with that structure in *A. moluccensis*. Thallwitz (1891b) offered a stylized version of the third pereopod of *Atya armata*, copied from A. Milne-Edwards (1864), for comparison with that appendage in *A. dentirostris* (= *A. spinipes*). De Man (1892) gave good illustrations of the dorsal and lateral aspects of the anterior part of a male, dorsal view of the rostrum of an abnormal female, first peropod of a male, and

FIGURE 18—*Atyopsis moluccensis* (all from ovigerous female from Bogor, Java, carapace length 20.7 mm): *a*, right 1st pereopod; *b*, right 2nd pereopod; *c*, right 3rd pereopod, *d*, same, dactyl; *e*, same, flexor surfaces of propodus and dactyl; *f*, right 4th pereopod; *g*, same, dactyl; *h*, right 5th pereopod; *i*, same, dactyl. (Magnifications: *a–c*, *f*, *h*, × 5.2; *e*, × 10.8; *d*, *g*, *i*, × 21.5.)

third pereopod of a female 78 mm long. Ortmann (1897, pl. 1) reproduced an illustration of the chela of the first pereopod from De Man (1892). Dorsal and lateral aspects of the rostrum of the type specimen of *Atya armata* were included by Bouvier (1905, fig. 20) to illustrate *A. moluccensis*. The toto drawing reproduced by Bouvier (1925) from A. Milne-Edwards (1864, pl. 3) is actually of *A. robusta* (= *A. innocous* (Herbst, 1792)), rather than *A. armata*, as indicated, but the other illustrations in Bouvier's work—anterior end in lateral view, second (called first) maxilliped, dactyls of third and fourth pereopods, endopod of first pleopod, appendix masculina, basal segment of uropod, and posterior margin of telson—evidently are of the species indicated. The outline drawing of "*Atya spinipes*" by Johnson (1957) is only a half-size rendition of the general facies of an adult male of the Malayan form. Johnson (1958) offered a distribution map of *Atya spinipes*, sensu lato, and the same author (1961) presented a natural-size toto drawing in lateral view of an adult male, third pereopods of a large and a small male and female, and graphical representations of the relationship of carapace length to overall length, of merus of third pereopod to overall length, and of merus breadth to overall length. Lastly, Mendis and Fernando (1962) gave an illustration of a 7 cm specimen of what they called "*Atya typus*."

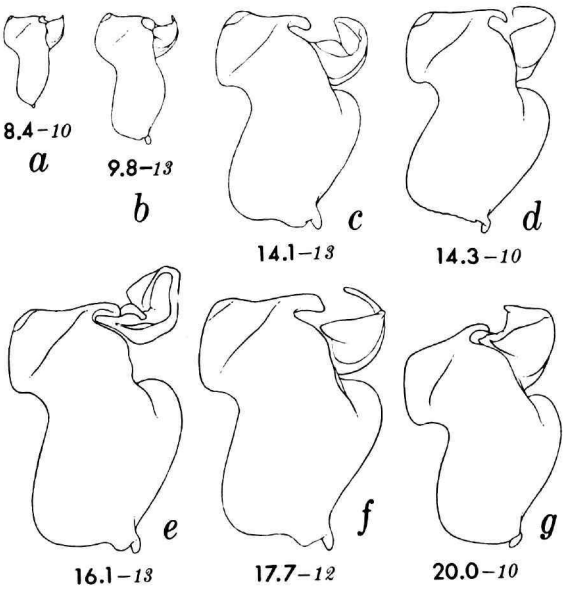

FIGURE 19—*Atyopsis moluccensis*, variation in shape of endopod plate of right 1st pleopod of males from Thailand (*a–f* from Ban Kiriwong, *g* from Khlong Raibon). Left numerals (decimals) indicate carapace lengths of specimens in mm, right numerals (italics) denote number of ventral rostral teeth. (Magnifications: all × 10.8.)

DIAGNOSIS.—Rostrum gradually tapering to slender apex, armed ventrally with 7–16 (commonly 10–14) indistinct serrations; endopod of 1st pleopod of male less than 1.5 times as long, from proximal articulation to base of retinaculate projection, as maximum width, not including marginal spines.

COLOR NOTES.—De Man (1892:360) remarked that *Atya moluccensis* has a moderately broad, pale, dorsal stripe that extends from the rostrum to the telson (see "Remarks," p. 35). Johnson (1959:72) noted that "torrent animals exposed on top of stones almost always have striking disruption patterns which may be remarkably similar in members of very divergent groups. The patterns are effective camouflage to human eyes." The same author (1964:145) wrote that the body form and "the striking, though variable, colour pattern of pale and dark longitudinal stripes serve to identify this prawn at a glance." Specimens from Sri Lanka, according to Arudpragasam and Costa (1962:21), have a body color of light brown or buff, superimposed on which are slightly darker longitudinal stripes that effectively camouflage the shrimps in their usual habitat; larger specimens tend to be a little darker than smaller ones.

SIZE.—The material studied comprises males with carapace lengths of 8.4 to 21.8 mm, non-ovigerous females, 11.2 to 19.7 mm, and ovigerous females, 14.3 and 20.1 mm. The largest specimen has an overall length of about 77 mm. In his unpublished manuscript on the genus *Atya*, Johnson listed a male from Pulau Perak in the northern part of the Strait of Malacca with an overall length of 86 mm (comparable to a carapace length of more than 24 mm), an ovigerous female from southern Malaya with a total length of no

more than 47.5 mm (equivalent to a carapace length of 13.4 mm), and a large female, also ovigerous, from Sarawak, with a length of 79.0 mm (similar to a carapace length of about 22 mm); smaller ovigerous females listed by Johnson (ms) occurred in regions where *Atyopsis spinipes* has also been found, and their identity is therefore uncertain.

DISTRIBUTION AND SPECIMENS EXAMINED.—As indicated below, I have seen specimens of *A. moluccensis* only from Thailand and Java. Records in the literature accompanied by diagnostic evidence, such as the number of ventral teeth on the rostrum, suggest that the species ranges from Sri Lanka in the west (Tiwari, 1951:208, noted that Indian and Andamanese specimens differ somewhat from the Malayan form, but his proposed detailed report on *Atya* seems not to have appeared as yet) through Thailand and Malaya (the only species on the Asiatic mainland according to Johnson, 1961:151) to Sumatra, Java, Bali, Sarawak, Celebes, Moluccas, and perhaps the Philippines. However, *A. spinipes* seems to be common in the Philippines and Moluccas, and both species also appear to occur in Celebes and Sumatra. In their distribution table, Djajadiredja and Sachlan (1956) listed *Atya moluccensis* from Sumatra, Borneo, Java, Sulawesi, and Lesser Sunda Islands, but they indicated that it was not present in the Moluccas.

Material has been examined from the following localities. Numbers in parentheses following the specimens listed are measurements, in mm, of postorbital carapace lengths.

THAILAND: (1) Khlong Raibon, near Muang Krat, southeastern Thailand, 1♂ (20.0), 8♀ (13.7–19.7), Feb 1924, H.M. Smith. (2) Ban Kiriwong, about 26 km west of Nakhon Si Thammarat, peninsular Thailand, 5♂ (14.1–21.8), 10 Jul 1928, HMS. (3) Mae Nam Tadi headwaters at Ban Kiriwong, peninsular Thailand, 2♂ (8.4, 9.8), 1♀ (11.2), 13 Jul 1928, HMS. (4) Waterfall cascade zone, 2.5 km upstream from mouth of Hin Lad stream, south of Aantong village, Ko Samui island, off peninsular Thailand, 9°31′15″N, 99°57′15″E, sta. 58, 2 juv (7.1, 7.2), 16 Nov 1957, R.R. Harry (George Vanderbilt Foundation Expedition).

JAVA: (1) Bogor, 2 ovig ♀ (14.3, 20.7), 1906–1907, T. Barbour.

VARIATION.—Of the 21 specimens from Thailand and Java listed above, 1 each has 7, 9, or 16 ventral rostral teeth, 6 have 10, and 4 have either 11, 12, or 13. The 2 largest males, with carapace lengths of 20.0 and 21.8 mm, have the merus of the third pereopod produced subdistally into a massive projection (Figure 16*g*), but in neither specimen is this tooth as strong as the one illustrated by A. Milne-Edwards (1864, pl. 3: fig. 3) in the type specimen of *Atya armata*; the latter has a carapace length of about 25 mm if that illustration is natural size, as indicated, but which has a total length of only 75 mm according to Bouvier (1905). This projection is much reduced in the smaller males, but it persists as at least an obtuse angle in all 6 males with a carapace length of 14 mm or more. In the 12 females and juveniles in which the merus of the third pereopod is present, it bears 2 spines in 9, 1 in 1, and 3 in 2 specimens. The merus of the fourth pereopod bears 4 spines in 9 specimens, 3 in 7 specimens, and 2 or 3 in 3 specimens. The fifth pereopod bears 2 meral spines in 11 specimens, and 3 in 7 specimens. The dactyl of the third pereopod bears 4 spines on the flexor margin in 11 specimens and 5 spines in 9 specimens. The dactyl of the fourth pereopod bears 4 flexor spines in 6 specimens, 5 in 12 specimens, and 6 in 1. On the fifth pereopod, the dactyl is armed on the flexor margin with 20 to 30 spinules, without any real numerical superiority for any particular count. There are from 14 to 17, usually 15 or 16, spines on the dieresis of the lateral branch of the uropod. Finally, as noted in the "Diagnosis," the endopod of the first pleopod of mature males is about 1.3 or 1.4 times as long as wide, not including the marginal spines (Figures 16*j,k*, 19).

ECOLOGICAL NOTES.—Johnson (1959:71, 72) noted that "*Atya spinipes*" is one of those animals that are adapted for torrent life by a "flattening of the ventral surface combined with a streamlined tent-roof shape to the rest of the body,"

together with "reduction in length and increase in stoutness of appendages." The same author (1961:151) stated that, in Malaya, the species "is normally found clinging to the underside of underwater rock projections in the most torrential portions of the rivers, often in the full force of the current," but "it is apparently absent from the torrent streams of the high mountain country." Arudpragasam and Costa (1962:23) indicated that the population in Sri Lanka is confined to the larger streams and rivers, both in the plains and a little higher up; it frequents the shallower portions of the habitat away from the main current. Competition of "*Atya spinipes*" with *Caridina typus* was discussed by Johnson (1964:27) as a possible explanation of the fact that the 2 species rarely occur together in Malaya, despite their similar habits. In his unpublished manuscript on *Atya*, Johnson wrote (p. 35): "Field observation on *A. spinipes* show that the adults normally occur in the full course of the current of torrential streams and rivers, clinging to the under side of smooth boulders, whilst half-grown and small, mature individuals are found amongst leaves or clinging to vegetation at the edge of such streams."

LIFE HISTORY NOTES.—Johnson (1958:179) remarked that the species called *Atya spinipes* is one of those "freshwater prawns" that "are tolerant of salt water, at least during their young stages." He (1965:10) also listed "*Atya spinipes*" among those "species in which the adult is an inhabitant of freshwaters but the larval stages are passed through in salt water." These comments are probably reflected in Holthuis (1982:609), who reported that "its life history still is incompletely known and the possibility exists that the juveniles live in brackish or salt water."

COMMON NAMES.—The species was called "Torrent Prawn" by Johnson (1957:63). According to Holthuis (1980:71), the official FAO name for *Atya moluccensis*, which that author synonymized with *A. spinipes*, is "Soldier brush shrimp" in English, "Saltarelle soldat" in French, and "Camarón soldado" in Spanish.

ECONOMIC IMPORTANCE.—Johnson (1961:151) noted that "*Atya spinipes*" "is an abundant and well-known species in the Tembeling area [Malaya] and is collected for food by some of the local inhabitants," an observation that was repeated by the same author (1966:280), and referred to again by him (1968:235) as "a very small-scale subsistence fishery in a few areas." Holthuis (1980:71) called the species "of minor importance" to fishery interests.

REMARKS.—The proposal to treat *Atyopsis moluccensis* as a species distinct from *A. spinipes* was prompted originally by the apparently consistent differences in the shape and dentition of the rostrum and the proportions of the endopod of the male first pleopod (Figures 17*a*, 19, 20*b*, 22) in the material available to me from Thailand and Java, as opposed to that from the Philippines, Palaus, and Fijis. The opinion was reinforced by the subsequent discovery that D. S. Johnson, who could hardly be accused of a predilection for "splitting," reached a similar conclusion after examining *Atyopsis* material from Sri Lanka, Malaya, Sumatra, Java, Sarawak, Philippines, Moluccas, New Guinea, Solomons, New Caledonia, Fijis, and Samoa in the collections of the British Museum, the Zoology Museum of Cambridge University, the Rijksmuseum van Natuurlijke Historie in Leiden, and the University of Singapore during a sabbatical leave in 1958. In the still unpublished manuscript based on this research, Johnson wrote (pp. 19, 20):

> I have commented at some length on this species elsewhere (Johnson, 1961). It is very constant in its characters with the exception of those subject to age and sex variation and of the form of the rostrum. There is some geographical variation especially affecting rostral form. Miers (1880) in comparing *A. spinipes* from Samoa with *A. moluccensis* remarks that the rostrum in the former is more rounded distally. Bouvier (1925) comments that the rostral form is highly variable and considers that this character is scarcely sufficient for the separation of the two species. Whilst agreeing with this conclusion I consider that these eastern populations should be placed in a separate subspecies from the western populations. In individuals from Ceylon and Malaysia the rostrum is comparatively long and acutely pointed. In dorsal view it is comparatively narrow and is almost uniformly tapering from base to tip. In individuals from New Guinea, the Solomons, Fiji, and Samoa, the rostrum is shorter and often does not attain the end of the first segment of the antennular peduncle. It is less slender and is blunt-ended. The pronounced dorsal crest often terminates some distance

from the tip, which may be produced into a sharp point. A few individuals from western New Guinea and Goram are somewhat intermediate between these two main types. The eastern representatives of the species also differ from the western in the position of the spiniform projection of the 3rd leg of adult males, which is very slightly more distally situated in the eastern forms. This difference was noted by Miers but was discounted by Bouvier. Though these differences are slight they are sufficient to characterize two subspecies: *A. spinipes spinipes* Newport with a range from New Guinea to Samoa, and *A. spinipes moluccensis* de Haan, ranging from the Moluccas westwards to Ceylon and Travancore.

It may well be that Johnson's decision to treat the two forms as subspecies, based on nearly overlapping rostral and third pereopodal characters is the preferable option; but it seems best to me to avoid subspecific designations unless the material available is sufficient for reliable quantitative analysis. Also, the differences in shape and proportions of the endopod of the first male pleopod in the material before me would seem to offer a more constant character than those associated with the rostrum and third pereopod; it should be borne in mind, however, that I have seen no males of *A. spinipes* with a carapace as long as 14 mm and that two of the males assigned to *A. moluccensis* having a carapace length of less than 14 mm bear a pleopodal endopod that is hardly distinguishable from those of *A. spinipes* of similar size. It would be highly desirable to examine the pleopodal endopod of a specimen like the "old male, 70 millimeters in length [comparable to a carapace length of 20 mm], with 3 teeth on the ventral border of the rostrum [and a third leg with] a large immovable spine on the ventrolateral surface of the merus near the distal end" recorded by Cowles (1951b:148, fig. 1*a*) from a mountain stream near Manila.

There has been none of the difficulty in determining the identity of De Haan's species that there is with that of the type specimen of *Atya spinipes* (see p. 42). I have been kindly informed by L.B. Holthuis (in litt.) that there are two dry types of *Atya moluccensis* in the Rijksmuseum van Natuurlijke Historie in Leiden. "One a male (total length about 80 mm, carapace length without rostrum 22 mm, with rostrum 28 mm). The rostrum carries 11 teeth on the lower margin. And the merus of the third leg has a strong spine like that figured by A. Milne-Edwards for *A. armata*. The second specimen is smaller, it is broken and has most legs missing." This description leaves little doubt that the concept of *A. moluccensis* adopted herein is justified. I am also indebted to Dr. Holthuis for the following note:

As to *Atya lineolata* De Man, 1892, we have here [Rijksmuseum van Natuurlijke Historie, Leiden] an unpublished plate showing a coloured drawing of *A. moluccensis* with a beautifully executed pattern of longitudinal bands of brownish and greenish. Apart from this coloured figure of the animal in lateral view, there is a sketch of the carapace and head in dorsal view, of the tailfan in dorsal view and of the third leg with the large tooth. Over the figures is the indication "Atija (Leach)," below it "Sphyrachela lineolata Nobis. Buitenzorg" and a pencil remark "Waterval Sa . . . , de 3^{e} voet aan het 2^{e} (?) lid van onderen een sterke uitwendige doorn" (Waterfall (name illegible), the 3rd leg with a strong outer spine on the second (?) segment from the base). The figures and watercolour [were] made by A. Maurevert, who from 1821 to 1826 was an artist of Dutch Commission for the study of the natural history of the East Indies, of which Commission H. Kuhl was the leader. However, Kuhl died very early (in September 1821), and his work was continued by others. Very little was ever published on the invertebrates and both *Sphyrachela* and *lineolata* are manuscript names. It is certain that De Haan must have seen this Java material; and one might even wonder whether the type of *Atya moluccensis* is not an incorrectly labelled specimen from Java.

As one last contribution to this study, Dr. Holthuis has informed me that the names "*Atya moluccensis*" and "*A. spinipes*" have apparently been used erroneously for a common Indonesian freshwater crab on at least two occasions. The first usage was by Koningsberger (1911–1915:253, 254, 401) who referred to *Atya moluccensis* as one of the numerous little crabs that burrow into dikes. The second was by Van Weel (1955) who denoted "the tropical freshwater crab, *Atya spinipes* Newport (= *A. moluccensis* de Haan)" as the subject of his study of the glandula media intestini (see editor's footnote in Stanier, Woodhouse, and Griffin, 1968:57).

Atyopsis spinipes (Newport, 1847), new combination

FIGURES 20–22

Atya spinipes Newport, 1847:159 [type-locality: Philippine Islands].—White, 1847:74.—A. Milne-Edwards, 1864:

149.—Miers, 1880:382, pl. 15: figs. 5, 6.—Thallwitz, 1891b:26.—De Man, 1892:363.—Ortmann, 1895:407, 409, 416.—Thompson, 1901:22.—Bouvier, 1905:109, 111; 1909:333.—Cowles, 1915b:150, 151.—Bouvier, 1925:290, 304, 305, 322, 356.—Roux, 1925:150, 151; 1928a:197, 208.—Edmondson, 1935:16.—Woltereck, 1937b:324 [part].—Gurney, 1942:87.—Laird, 1956:68.—Johnson, 1958:179, fig. 5 [part].—Bayer and Fehlmann, 1960:191.—Holthuis and Rosa, 1965:9 [part].—Holthuis, 1970:92; 1980:71 [part]; 1982:609 [part].—Smith and Williams, 1982:345, 346 [part].

Atya armata.—Schmeltz, 1869:x, 135; 1874:79.—Cowles, 1915b:147, 149, 151. [Not *Atya armata* A. Milne-Edwards, 1864.]

Atya pilipes.—Ortmann, 1890:466, pl. 36: fig. 8a,b,c [part].

Atya dentirostris Thallwitz, 1891a:101 [type-locality: "Nord-Celebes"]; 1891b:26, 50, 55, pl. 1: fig. 7a,b,c.—Weber, 1892:536.—De Man, 1902:893, 894.—Bouvier, 1950:113; 1925:299.—Smith and Williams, 1982:346.

Atya moluccensis.—De Man, 1892:357 [part]; 1902:893.—Cowles, 1915a:12, 13, pl. 1: figs. 2, 3; 1915b:149, 151, fig. 1.—De Man, 1915:407, pl. 28: figs. 5–5d.—Roux, 1928b:218.—Woltereck, 1937b:324 [part].—Kubo, 1938: 94–98, figs. 22–24.—Needham, 1938:81, fig. 23.—Yu, 1974:55, fig. 5 ["*Atya molccensis*" in figure legend]. [Not *Atya moluccensis* De Haan, 1849.].

[?]*Atya brevirostris* var. *De Mani* Nobili, 1900:475, fig. 1 [type-locality: "Fiume Sereinu, Isole Mentawei"].

[?]*Atya brevirostris*.—Schenkel, 1902:500, pl. 9: fig.6a–f.

[?]*Atya moluccensis*.—Nobili, 1905:480.—Balss, 1914:26.—Roux, 1926a:182, 218, 219.—Edmondson, 1929:27.—Estampador, 1937:485; 1959:18.—Gabriel, 1963:153, fig. 2.—Shokita, 1975:118–120, 126, fig. 1 [map].

[?]*Atya spinipes*.—Nobili, 1907:353.—Roux, 1934:218, 219, 223.—Seurat, 1934:51.—Shokita and Nishijima, 1976:33.

Atya mollucensis.—Cowles, 1915a:12, 13; 1915b:151, fig. 1 [erroneous spelling].

[?]"*Atya gastiva* Ortwann."—Urita, 1921:216 [erroneous spelling of *Atya gustavi* Ortmann].

Atya molluscensis.—McCulloch and McNeill, 1923:57 [erroneous spelling].

[?]*Ortmania* sp.(?).—Blanco, 1935:36, pl. 3: figs. 33–40 [erroneous spelling].

[?]*Atya serrata*.—Blanco, 1935:31, pl. 1: figs. 1–4.

Atya spinifera.—Edmondson, 1935, fig. 5*j,k* [erroneous spelling].

[?]*Ortmannia* sp.—Johnson, 1961:146.

REVIEW OF LITERATURE.—The original description of *Atya spinipes* by Newport (1847) so avoids mention of the characters that are currently of specific or even generic diagnostic importance that it is little wonder that there has been, and still is, confusion about the true identity of the species, even by those who have examined the holotype. A. Milne-Edwards (1864) believed that the species he named *Atya armata* differed from *A. spinipes* (= *Atyopsis spinipes*) in having the third pereopods more spinulose and the major meral spine proximal rather than distal to the minor one; but these differences may be observed in comparing large males and females of the same species (Figures 16*g*, 18*c*). Schmeltz (1869:x) recorded specimens as *Atya armata* from more than 1000 feet (305 m) at Upolu. Miers (1880:382, pl. 15: figs. 3–6) was the first to indicate what may be true differences between *Atya spinipes* (from Samoa) and *A. moluccensis* (= *Atyopsis moluccensis*) (from Java), but he failed to recognize the differences between Newport's type specimens of *Atya spinipes* and *A. pilipes*. It is apparent from the lengths indicated for the specimens, as recorded by Ortmann (1890:467), that at least those from the "Südsee" and some of those from Samoa are probably *A. spinipes* rather than *A. pilipes*. From the size (total length 77 mm, cephalothorax 19 mm) and the presence of only three ventral teeth on the rostrum, the specimens from northern Celebes named "*Atya dentirostris*" by Thallwitz (1891a:101, 102) seem to belong to the concept of *Atyopsis spinipes* postulated here. Nothing in his other description and illustrations, published in the same year (Thallwitz, 1891b:26, pl. 1: fig. 7), refutes this assumption. It would seem, from the small number (3–7) of ventral rostral teeth indicated, that some of the specimens recorded from Sumatra by De Man (1892:359, 360) and those from Celebes, Salajar, Timor, and Flores belong to *Atya spinipes*, rather than to *A. moluccensis*. Ortmann (1895:407–409) followed Miers (1880) in recognizing *Atya moluccensis* and *A. spinipes* and in synonymizing *A. pilipes* with the latter. The total length (53 mm) would suggest that the form described as *Atya brevirostris* var. *De Mani* from Kepulauan Mentawi by Nobili (1900:475) might be *Atyopsis spinipes*. The Halmahera specimens assigned to *Atya moluccensis* by De Man (1902:893) probably represent *Atyopsis spinipes*, as indicated by the few (3–5) ventral rostral teeth. The size (total length 37–45 mm) of the ovigerous females

recorded from Tomohon, Celebes, as *Atya brevirostris* by Schenkel (1902:500) suggests the possibility that they might belong to *Atyopsis spinipes*. The record of *?Atya spinipes* from the Gambier Islands, Tuamotus, by Nobili (1907:353) must be questionable, because only *Atyoida pilipes* is known with reasonable certainty from that area. The two females with three or four ventral rostral teeth recorded from "Sagamibai" as *?Atya moluccensis* by Balss (1914:26) would seem to be identifiable with *Atyopsis spinipes*, but the locality must remain suspect for the time being. There is little doubt that the species called *Atya mollucensis* in his two papers on habits and synonymy by Cowles (1915a, 1915b) are refereable to *Atyopsis spinipes*. The record of "*Atya gastiva* Ortwann" from the Kagoshima Wan region of Kyushu, Japan, by Urita (1921:216) is annoyingly ambiguous. Bouvier (1925:305) believed that the differences between *Atya spinipes* and *Atya moluccensis* (length of the rostrum and position of the spur on the third pereopod of the adult male) were insufficient specific characters, that *Atya spinipes* and *A. pilipes* would eventually be demonstrated to be distinct, and that the former should be adopted as a synonym senior to *Atya moluccensis*. In the species that Roux (1926a:218, 219) called *Atya moluccensis* from Sri Lanka, Burma, Strait of Malacca, and New Caldeonia, the number of ventral rostral teeth varied, usually from 6 to 10, but might be reduced to 2 to 4 in large specimens. The Philippine specimens called *Atya serrata* and *Ortmania* sp. by Blanco (1935:31, 36, pl. 1: figs. 1–4, pl. 3: figs. 33–40) are difficult to identify; the first may be *Atyopsis spinipes*, and the other may be a juvenile of the same species. Edmondson (1935) recognized *Atya spinipes* and *A. moluccensis* as distinct species. Finally, Yu (1974) recorded *Atya spinipes* under the name *Atya moluccensis* from Taiwan.

PUBLISHED ILLUSTRATIONS.—The first illustrations of *Atya spinipes* are the lateral views of the rostrum and of the third pereopod of a large Samoan male furnished by Miers (1880) to show the characters that distinguish the species from *Atya moluccensis*. Those drawings are considerably better than those of the rostrum and first pereopod of *Atya gustavi* offered by Ortmann (1890). Somewhat better than the latter are the dorsal view of the carapace, lateral view of the rostrum, and the third pereopod of *Atya dentirostris* in Thallwitz (1891b). The dorsal view of the rostrum of *Atya brevirostris* var. *De Mani* by Nobili (1900) is so stylized as to be of little interest. Somewhat better is the series of five lateral views of the variable rostrum and the first pereopod of *Atya brevirostris* in Schenkel (1902), that may or may not be referable to *A. spinipes*. Cowles (1915a) presented outline drawings of the first pereopod extended and flexed, a fine toto figure of a female in lateral view (enlarged 50%), the anterior portion of a female in lateral view (enlarged 100%) showing the chelae expanded for filter feeding, and two hairs from the fingers of a cheliped (enlarged much more). The same author (1915b) offered a series of outline drawings of the merus of the third, fourth, and fifth pereopods of five specimens varying in total length from 42 to 70 mm, showing spine modification with growth in Philippine material. De Man (1915) gave excellent illustrations of dorsal views of the anterior portion of the carapace and lateral views of the rostrum of a young male and of an ovigerous female, as well as of partially hooked hairs on the dorsal surface of the carapace. Blanco (1935) offered somewhat stylized drawings of the anterior end in lateral view, both chelipeds, and the posterior margin of the telson of the Philippine species that he called *Atya serrata* and of the rostrum in lateral view, the antennal scale, the antennule, the first pereopod, dactyls of the third and fifth pereopods, the uropodal dieresis, and the posterior margin of the telson of a young Philippine specimen that he called *Ortmania* sp.(?). A lateral view of the rostrum and merus of the third pereopod of a male, probably from the Fijis, and both done in his usual stylized manner, were published by Edmondson (1935). Kubo (1938) gave poor halftones of dorsal and lateral toto photographs and offered outline illustrations of the anterior part of the carapace in lateral view, the telson, the mandible in two aspects, the first, second, third, and fifth pereopods, the first pleopods of the male and

the female, the appendix masculina, and the endopod of the second female pleopod, as well as a distribution map of the species that he called *Atya moluccensis*. Finally, a diagram of the nervous system was included in Gabriel (1963). Most recently, Yu (1974) contributed good line drawings of the entire shrimp in lateral aspect, the carapace in lateral aspect, the telson and uropod, the chela and carpus of the first pereopod, the third pereopod, and the second pleopod in both male and female.

DIAGNOSIS.—Rostrum abruptly terminating in

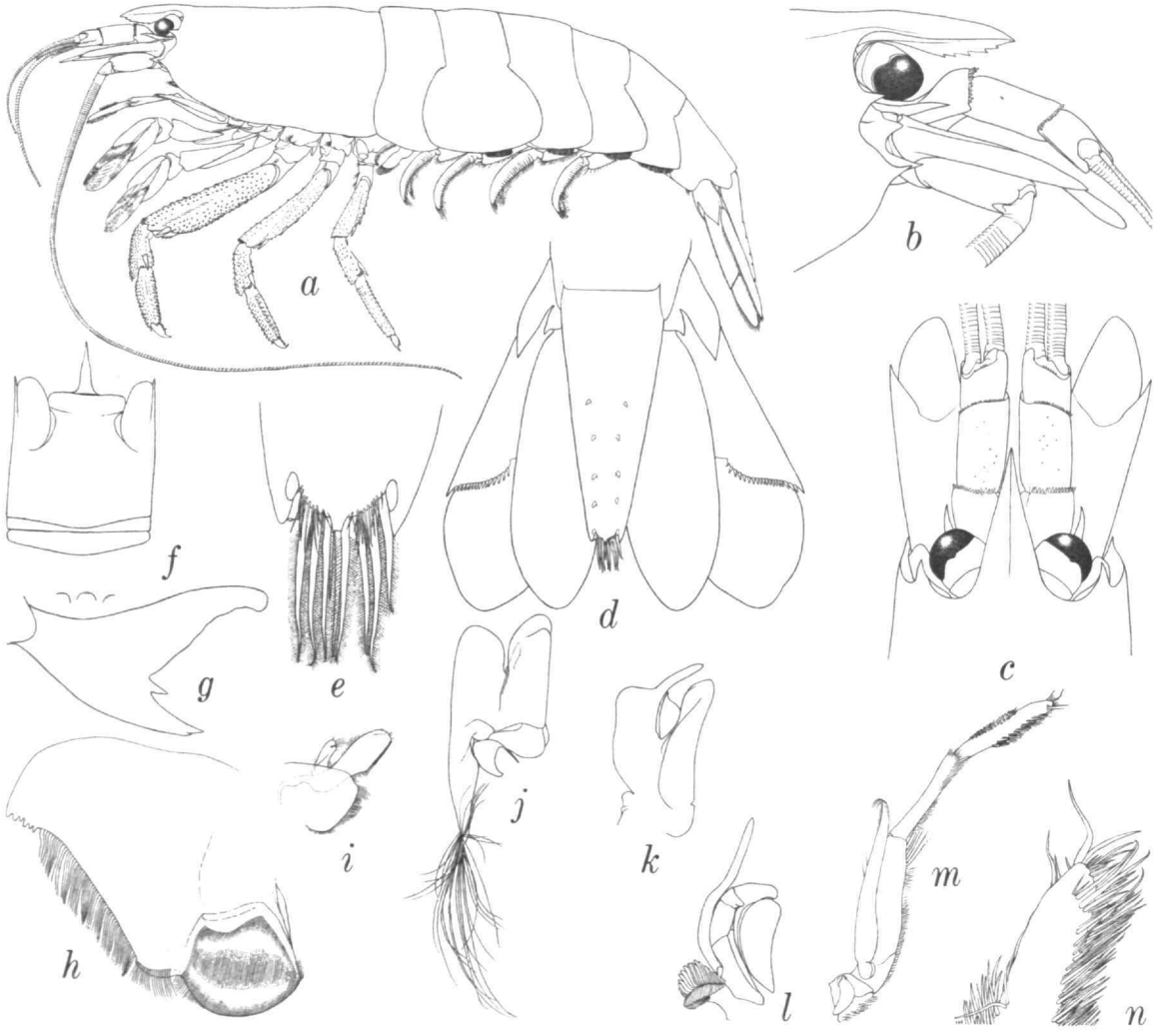

FIGURE 20.—*Atyopsis spinipes* (all from male from "Cabugao" River, Catanduanes Island, Philippines, carapace length 13.8 mm): *a*, entire specimen, left aspect; *b*, anterior carapace and appendages, right aspect; *c*, same, dorsal aspect; *d*, telson and uropods; *e*, posterior end of telson; *f*, 6th abdominal somite and median tubercle on 5th, ventral aspect; *g*, preanal carina, left aspect; *h*, right mandible; *i*, right 1st maxilla; *j*, right 2nd maxilla; *k*, right 1st maxilliped; *l*, right 2nd maxilliped; *m*, right 3rd maxilliped; *n*, same, distal end. (Magnifications: *a*, × 2.1; *b–d*, *f*, *i–m*, × 5.2; *e*, *g*, *h*, *n*, × 21.5.)

comparatively broad apex, armed ventrally with 2–6 discrete teeth; endopod of 1st pleopod of male more than 1¾ times as long from proximal articulation to base of retinaculate projection as maximum width, not including marginal spines.

COLOR NOTES.—Photographs were taken by F. M. Bayer of the larger male and larger female collected by the George Vanderbilt Foundation Expedition in 1955 at station 250 on Babelthuap Island, Palau, and are now in the USNM collections. The color has deteriorated in the transparency, but the color pattern is still clear. The male (carapace length 12.1 mm) had a broad pale streak in the dorsal midline extending from the tip of the rostrum to the end of the telson; anteriorly, the streak was about as wide as the base of the rostrum and it extended posteriorly at this width, broadening slightly on the posterior third of the carapace and reaching as an even slightly broader stripe over the abdomen to the base of the telson, thence tapering a little to coincide finally with the extent of the posterior margin of the telson. Laterally, the carapace was marked with 6 or 7 light longitudinal stripes outlined with dark pigment, the 4 ventral ones broadest and anastomosing near the anterior and posterior margins of the carapace; the abdomen bore about 6 similar stripes anteriorly, merging into 4 on the fifth somite and into 2 on the anterior half of the sixth. The 3 posterior pairs of pereopods were light colored with dark spots on the basis or ischium and near the proximal end of the merus, a band at the distal end of the carpus, 2 bands on the propodus (proximal and distal thirds), and a less distinct band darkening the extreme distal end of the propodus and the proximal end of the dactyl. The female (carapace length 14.7 mm) had a similar middorsal streak that became obscure at its anterior and posterior extremities and was completely obliterated on the gastric region, apparently by the underlying stomach contents. The female was otherwise much darker than the male, the lateral stripes on the carapace and abdomen being much less distinct, and the 3 posterior pairs of pereopods almost uniformly dark colored.

The photograph of a female specimen from the Ryukyu Islands, called *Atya moluccensis* by Kubo (1938, fig. 22), is too poor to permit comparison of the color pattern with that in the Palau specimens, but the lateral stripes seem to be more prominent than they were in the Palau female photographed by Bayer.

SIZE.—The specimens studied include males with carapace lengths of 6.2 to 13.8 mm, nonovigerous females, 5.3 to 14.7 mm, and ovigerous females, 8.1 to 19.6 mm. The largest specimen has an overall length of about 71 mm. Of the specimens listed by Johnson (ms) from localities presumed to fall within the range of *Atya spinipes* (= *Atyopsis spinipes*), the largest male, from Samoa, had an overall length of 65.5 mm (comparable to a carapace length of about 18 mm), a Philippine ovigerous female had a total length of no more than 36.0 mm (equivalent to a carapace length of about 10 mm), and the largest female, also ovigerous and also from the Philippines, had a length of 53.7 (similar to a carapace length of about 15 mm). The largest male that can be positively identified with this species seems to be the "old male, 70 millimeters in length, with 3 teeth on the ventral border of the rostrum" recorded by Cowles (1915b:148) from "a mountain stream near Manila." These measurements might suggest that *Atyopsis spinipes* is a smaller species than *A. moluccensis*, the largest male of the former being little more than 80 percent as long as the maximum length in the latter, and the smallest ovigerous females being only about 60 percent as long in *A. spinipes* as they are in *A. moluccensis*.

DISTRIBUTION AND SPECIMENS EXAMINED.—Specimens available for this study came from the Philippines, Palau, and the Fijis. The most reliable records in the literature suggest that *A. spinipes* ranges from the Philippines and eastern Lesser Sunda Islands at about 120° east longitude northward to Taiwan and as far as Tokuno-shima in the Ryukyus and eastward as far as Samoa. The occurrence of the species in the Sagami Nada region of Japan, reported by Balss (1914), as well as the presence of "*Atya gastiva*" near Kagoshima Wan, recorded by Urita (1921), were not men-

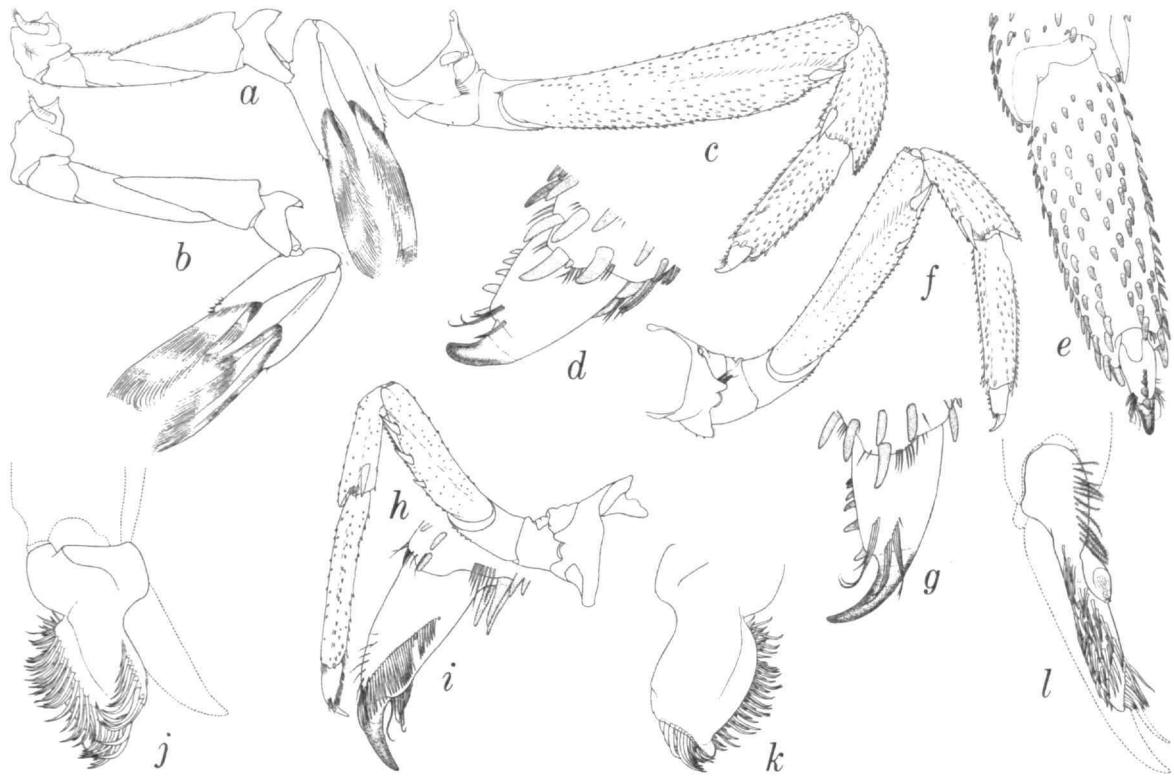

FIGURE 21.—*Atyopsis spinipes* (all from male from "Cabugao" River, Catanduanes Island, Philippines, carapace length 13.8 mm); *a*, right 1st pereopod; *b*; right 2nd pereopod; *c*, right 3rd pereopod; *d*, same, dactyl; *e*, same, flexor surfaces of propodus and dactyl; *f*, right 4th pereopod; *g*; same, dactyl; *h*, left 5th pereopod; *i*, same, dactyl; *j*, endopod of right 1st pleopod, posterior aspect; *k*, same, anterior aspect; *l*, right appendix masculina and appendix interna, mesial aspect. (Magnifications: *a–c*, *f*, *h*, × 5.2; *e*, *j–l*, × 10.8; *d*, *g*, *i*, × 21.5.)

tioned by Kubo (1938), and these records should probably be questioned until they are positively confirmed. Verification is also needed of the Magareva record in Nobili (1907) and Seurat (1934) in order to eliminate the possibility of confusion between *Atyposis spinipes* and *Atyoida pilipes*, which seems to be established on the Gambier island.

Material has been examined from the following localities. Numbers in parentheses following the specimens listed are measurements, in mm, of postorbital carapace lengths.

PHILIPPINES: British Museum (NH) 43-6, no locality, holotype of *Atya spinipes*, 1♀? (~15), Mr. Cumings. No locality, 1 ovig ♀ (19.6), E.A. Mearns. (1) Tayabas River, Luzon, 1♂ (13.5), 25 Feb 1909, *Albatross* Philippines Expedition. (2) "Cabugao" River, Catanduanes Island, 1♂ (13.8), 9 June 1909, *Albatross*. (3) "Varadero Mountain," Mindoro(?), 1♀ (13.4), 23 Jul 1908, *Albatross*. (4) Malaga River, Hinunangan Bay, Leyte, 1♀ (11.2), 4 juv (3.1–4.8), 30 Jul 1909, *Albatross*. (5) Mananga River, Cebu, 1♀ (11.7), 25 Aug 1909, *Albatross*.

CAROLINE ISLANDS: *Babelthuap Island, Palau*—(1) Stream south of village of Olei, Ngarehelong Peninsula, 7°42′53″N, 134°37′24″E, water fresh down to last falls, then brackish, yellowish in color, ¼–1½ m/sec current, bottom volcanic rock with potholes, banks rock and mud, overhanging vegetation (liverworts, extensive tree roots), sta

122, 3♂ (8.0–9.2), 5♀ (4.5–11.0) 4 ovig ♀ (9.6–11.9), 1 juv (2.5), 23 Aug 1955 (1000–1300 hours), liquid rotenone, R.R. Harry, H.A. Fehlmann, F.M. Bayer, Rikrik, Y. Sumang (George Vanderbilt Foundation Expedition). (2) Ilmaw stream, Hgetkip village, Airai municipality, 7°21′37″N, 134°31′19″E, stream 1–2 m wide, white, slightly turbid water, about 1½ m/sec current, bottom rock and soil without vegetation, water temperature 26° C, sta 250, 2♂ (6.2, 12.1), 1♀ (14.7), 1 ovig ♀ (12.4), 25 Oct 1955 (1430–1700 hours), roticide, HAF, YS (GVF). (3) Airisong stream, 2.4–3.2 km north of Hgetkip village, Airai municipality, 7°22′52″N, 134°31′30″E, stream 1–3 m wide, clear, white water, 1½ m/sec current, bottom solid rock, sand, gravel, banks solid rock and soil without vegetation, water temperature 27° C, sta 251, 1♂ (10.5), 26 Oct 1955 (1200–1600 hours), roticide, HAF, YS (GVF). (4) Imengelngal stream (tributary to Alsemith River), northeast of Medorm and Ngchemliangel village, Aimeliik municipality, 7°27′30″N, 134°30′40″E, slightly brownish and turbid, about 1½ m/sec current, bottom gravel, solid rock, banks soil, solid rock, without vegetation, water temperature 25.5° C, sta 269, 1♂ (12.0), 1 Nov 1955 (1300–1515 hours), roticide, HAF, YS, Rengiil (GVF). (5) Arakitaoch stream, strand zone, sta 170, 1 ovig ♀ (11.3), 31 Oct 1956, A. Fehlmann (GVF). (6) Same, cascade zone, 2♂ (8.6, 9.9), 4♀ (7.3–9.0), 1 ovig ♀ (10.3), 4 Nov 1956, AF (GVF). (7) South fork of Arakitaoch River, cascade zone, sta 170-A, 2♂ (8.0, 11.8), 1♀ (11.2), 1 ovig ♀ (8.1), 26 Nov 1956, AF (GVF). (8) Same, source zone, 2♂ (8.3, 10.3), 1♀ (8.5), 27 Nov 1956, AF (GVF). *Koror Island, Palau*—(9) Tibdul stream draining into Iwayama Bay, 7°20′10″N, 134°30′06″E, stream 1–2 m wide, water white, clear, current about 2 m/sec (many falls and cascades), bottom rock and gravel, banks rock, soil, sawgrass, water temperature 26.5° C, sta 216, 1♀ (8.8), 11 Oct 1955 (1500–1800 hours), roticide, HAF, YS.

FIJI ISLANDS: No locality, 1 ovig ♀ (13.3), Aug 1928, H.S. Ladd.

VARIATION.—Of the 47 specimens examined, 44 have the rostrum intact; of these, 5 have 2 ventral rostral teeth, 10 have 3, 15 have 4, 11 have 5, and 3 have 6. Apparently none of the 15 males, ranging in carapace length from 6.2 to 13.8 mm, is large enough to display the spur on the merus of the third pereopod that is characteristic of old *Atyopsis* males. Of all the specimens in which the third pereopod is present, it bears 2 spines in 20 specimens, 3 spines in 12, 4 in 6, and 1 spine in 2 specimens. The merus of the fourth pereopod bears 4 spines in 33 specimens, 3 in 10, 5 in 2, and 2 spines in just 1 specimen. The fifth pereopod bears 3 meral spines in 21 specimens, and 2 in 13 specimens. The dactyl of the third pereopod bears 4 flexor spines in 28 specimens, 5 in 14, and 3 in 6. The dactyl of the fourth pereopod bears 5 flexor spines in 19 specimens, 3 and 4 in 8 specimens, each, and 6 in 2 specimens. In adult specimens, the number of spines on the flexor margin of the dactyl of the fifth pereopod varies from 24 to 34 spinules, without any real numerical superiority for any particular count. There are from 13 to 19, usually 14 to 16, spines on the dieresis of the lateral branch of the uropod. Finally, the endopod of the first pleopod of all but the smallest males varies from 1.7 to 2.2 times as long as wide (not including marginal spines) (Figures 21*j,k*, 22).

ECOLOGICAL NOTES.—Schmeltz (1869) indicated that the species he called *Atya armata* occurred at an altitude of more than 1000 feet (305 m) at Upolu. Cowles (1915a) noted that *Atyopsis spinipes* (called by him *Atya moluccensis*) is abundant in mountain streams, uncommon in lowland ones. Individuals are so prone to clinging to roots, grasses, etc., in swift water that they will grasp any suitable object, even when removed from the water. In moving water, they spread their chelae in a filter-feeding attitude; in still water, they remain motionless and do not sweep the substrate for food as some atyids do. Cowles (1915a:14) never observed them making burrows of any kind. Shokita and Nishijima (1976) stated that the population on Tokuno-shima, Ryukyus, occurred "in the shallow grass beds of middle streams, where the water flow is relatively rapid." The ecological information gathered by H.A. Fehlmann and other members of the George Vanderbilt Foundation Expeditions to Palau indicates

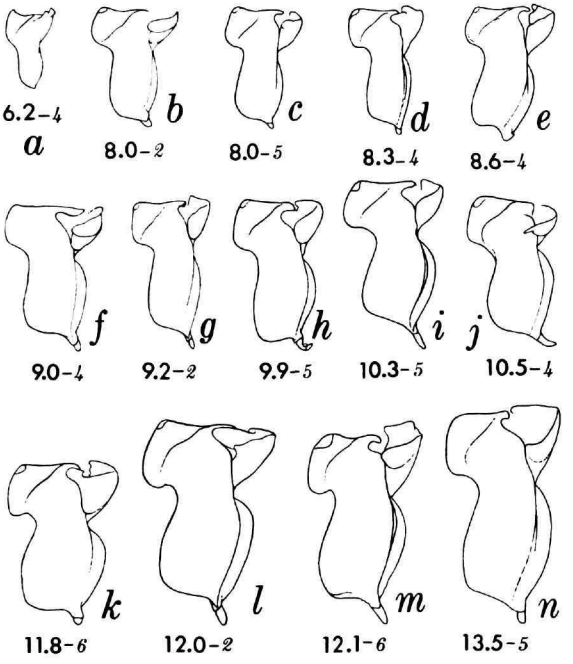

FIGURE 22.—*Atyopsis spinipes*, variation in shape of endopod plate of right 1st pleopod of males from Palau (*a*, *m*, George Vanderbilt Foundation sta 250; *b*, *f*, *g*, GVF sta 122; *c*, *d*, *i*, *k*, GVF sta 170-A; *e*, *h*, GVF sta 170; *j*, GVF sta 251; *l*, GVF sta 269) and Philippines (*n*, Tayabas River, Luzon). Left numerals (decimals) indicate carapace lengths of specimens in mm, right numerals (italics) denote number of ventral rostral teeth.

that *Atyopsis spinipes* frequents streams in those islands that vary in width from 1 to 3 meters, have a current velocity of about ¼ to 2 meters per second over a rock bed sometimes covered with gravel, sand, or mud between banks of rocks and soil, with or without liverworts, tree roots, or other vegetation; the water varied from white to brownish, clear to turbid, and in temperature from 25.5° to 27°C.

LIFE HISTORY NOTES.—None.

COMMON NAMES.—See this section under *Atyopsis moluccensis* (p. 34).

ECONOMIC IMPORTANCE.—Cowles (1915a:11) remarked that Philippine atyids in general, of which the species of *Atyopsis* are the largest, "are of almost no commercial value, although they are sometimes eaten when food is very scarce."

REMARKS.—If, as proposed here, *Atyopsis*, contains more than one species (see "Remarks" under *A. moluccensis*, p.34), the true identity of the unique holotype of *A. spinipes* becomes more important than it would be if the genus were monotypic. Thanks to the kindness of R.W. Ingle of the British Museum (Natural History), I have had the opportunity to examine that specimen, but the resulting conclusions are hardly decisive. Newport's species should be distinguishable from *A. moluccensis* by the form and dentition of the rostrum, the position of the massive spur on the merus of the third pereopod of old males, and the form and proportions of the endopod of the first pleopod in the male. The type specimen of *A. spinipes* is dry and brittle. The posterior portion of the carapace is firmly wedged into the first abdominal somite, making actual size determination difficult; my best estimate is that its postorbital length must be about 15 mm and the total length about 55 mm. The rostrum is broken jaggedly so that its intrinsic shape is indeterminable, and the ventral margin, which bears the diagnostic series of teeth, is almost completely obliterated, thereby eliminating the rostrum as a clue to the identification. Secondly, I believe that the specimen is a female; if true, the other two diagnostic characters could not be ascertained from the specimen no matter what its condition. Under these unfortunate circumstances, it seems best to assume that the specimen from the Philippine collection of "Mr. Cumings" (spelling on specimen label) belongs to the form that seems to be most prevalent in the Phlippines. All 10 of the Philippine specimens in the Smithsonian collections belong to the form here called *Atyopsis spinipes*, as apparently also do those reported by Cowles (1915b:147, 148) "from a mountain stream near Manila" that have 3 to 6 teeth on the ventral margin of the rostrum. Except for the remark by Blanco (1935:30) that the rostra in his 3 specimens from the Dumaguete River, southeastern Negros, are "armed with numerous little teeth on ventral keel" and the fact that Johnson (ms) included the Philippines in the range of *Atya spinipes moluccensis*, there seems to be no indication that the form here assigned to *Atyopsis moluccensis*

occurs in the Philippines. (Johnson mentioned only Newport's type specimen and 6 specimens from a "mountain stream near Mariveles, Manila Bay, Luzon," received from Cowles, as all of the Philippine material seen by him.)

Genus Australatya, new genus

TYPE-SPECIES.—*Atya striolata* McCulloch and McNeill, 1923.

ETYMOLOGY.—The feminine name *Australatya* is derived from the Latin adjective *australis*, southern, used as a prefix to the name *Atya*.

DIAGNOSIS.—Body pigmented, eyes well developed; rostrum not strongly compressed laterally, median dorsal carina unarmed, ventral keel with 4–8 teeth; anterior margin of carapace armed with antennal spine, pterygostomian margin rounded; supraorbital spines absent; telson with setigerous posterior margin overreaching posterolateral angles; 3rd maxilliped with uncinate terminal spine partially concealed by dense setae; pereopods without exopods; 1st and 2nd pereopods with chelae monomorphic, without palm, fingers tipped with brushes of long setae apparently adapted for filter feeding, carpus of both appendages excavate distally, little longer than broad; 3rd pereopod without meral spur in large males; branchial complement consisting of 5 pleurobranchs, 3 arthrobranchs, 1 podobranch, 5 epipods (reduced posteriorly), no mastigobranchs; 1st pleopod of male with endopod tapering to slender apex; 2nd pleopod of male with appendix masculina subcylindrical, spinose on less than distal third of length.

RANGE.—*Australatya* is confined to rivers and streams along the east coast of Australia.

REMARKS.—Although *Australatya* resembles *Atyoida* more closely than it does *Atyopsis* or *Atya*, it seems clear to me that the species originally called *Atya striolata* is excluded from that genus by the broadly rounded pterygostomian margin of the carapace, the reduced epipods on the third and fourth pereopods, the absence of mastigobranchs, the monomorphic chelae apparently adapted primarily for filter feeding, and the elongate appendix masculina spinose on less than the distal third of its length.

Only one species is known.

Australatya striolata (McCulloch and McNeill, 1923), new combination

FIGURES 23, 24

Atya striolata McCulloch and McNeill, 1923:55, pl. 9: figs. 3, 4, pl. 10: fig. 3 [type-locality: Norton's Basin, Nepean River, New South Wales, Australia].—Anderson, 1926:253.—McNeill, 1926:325.—Roux, 1926b:253.—McNeill, 1929:148.—Riek, 1953:111; 1959:252, 254.—J.A. Bishop, 1967:117, 119.—Williams, 1968:145, 146; 1981:1121.—Smith and Williams, 1982:343.

Atyoida striolata.—Smith and Williams, 1982:345, figs. 1–7.

REVIEW OF LITERATURE.—The original description by McCulloch and McNeill (1923) is accompanied by accounts of the type-locality and behavior of the species. Roux (1926b) added a few details and measurements to the initial description, and the editor, Anderson (1926), recorded an additional locality for the species in a footnote to Roux's article. A third locality for the species was mentioned by McNeill (1929). The first Queensland record was published by Riek (1953), who gave a brief description and color notes based on the new material and remarked that the specimens differed slightly from those in the type-series. The same author (1959:254) referred to *Atya striolata* as an atyid "relict element." J.A. Bishop (1967:119) also mentioned that *Atya striolata* might be a "relict species" and recorded specimens as "facultative troglobes" from caves in New South Wales. In his treatise on Australian freshwater invertebrates, Williams (1968:146) offered a key to the Australian atyid genera and made the enigmatic remark that "*Atya striolata* is the only species [of *Atya*] known with any detail but another is recorded in the literature." Finally, Smith and Williams (1982) nearly preempted the purpose of this review by reinstating *Atyoida* for *A. bisulcata*, *A. pilipes*, and *A. striolata*; they fully redescribed the latter from topotypic material, noted that there is little variation throughout the range of the species, demonstrated conclusively that *A. striolata* is a protandrous species, and argued that protandry may have clear adaptive

value by increasing the number of larvae available to attempt the precarious ascent of swift coastal streams.

PUBLISHED ILLUSTRATIONS.—McCulloch and McNeill (1923) gave an excellent toto drawing in lateral view of the holotype, showing the color pattern, but substituting the three posterior pereopods from a smaller paratype of those missing in the holotype; they also depicted the telson in dorsal view and reproduced a photograph of the type-locality. Apparently the only other published illustrations of *Australatya striolata* are those in the extensive series in Smith and Williams (1982), consisting of outline drawings of the holotype in lateral view (lacking four posterior pereopods), the telson in dorsal view, an antennule, antenna, labrum, paragnath, left and right mandibles, both maxillae, two anterior maxillipeds, second pereopod, all five pleopods, and uropod, all from the holotype; the third maxilliped, first pereopod, and third to fifth pereopods of a female paratype; the first and second pleopods of a male topotype; a geographical distribution map for the species; and histograms indicating protandry in two populations of the species. (Several of the illustrations presented herein duplicate those offered by Smith and Williams, but they were prepared before I was aware of the latter contribution, and it seems best to include them for what they may be worth.)

DIAGNOSIS.—Rostrum nearly horizontal, armed ventrally with 4–8 teeth; pterygostomian margin of carapace broadly rounded; telson with single median tooth on posterior margin; chelae monomorphic, adapted for filter feeding; appendix masculina unusually elongate, spinose on less than third of length.

COLOR NOTES.—McCulloch and McNeill (1923:56) offered the following detailed account of the color pattern with the original description of the species.

> Green in life, closely speckled with microscopic blackish-brown dots. A broad, light yellowish, median band extends from the tip of the rostrum to the end of the telson, which is closely speckled and sharply defined by blackish borders. Five narrow longitudinal stripes along each side of the carapace, some of which are more or less interrupted; these are light in colour without darker speckles, and have dark margins. Two similar stripes along each side of the abdomen. Uropods pale green basally, changing to light blue terminally; the outer with a light distal spot with an ill-defined darker border, the inner with a similar but less distinct spot. Antennular peduncles with a light stripe on the upper surface, the remainder green. Limbs and antennae translucent green; pencils of the fingers darker at the bases and tips.

Riek (1953:112) gave the following color description of specimens from Cave Creek near the Queensland-New South Wales border.

> Dull reddish-brown speckled with microscopic black dots. A broad, almost white, median band extending from the rostrum to the telson and sharply defined by a black border of irregular thickness. Five longitudinal stripes along each side of the carapace, somewhat irregular in outline and bordered in black similar to the median dorsal band. Two similar stripes occur along each side of the abdomen.

SIZE.—The 4 males available to me from the type-locality vary in carapace length from 7.8 to 8.7 mm and in total length from 32 to 36 mm. Measurements available from the literature suggest that males range in carapace length from 5.0 to 10.4 mm (total length, 22–43 mm); females with carapace lengths of 7.6 to 13.0 mm (total length, 33–57 mm), with ovigerous specimens as short overall as 30 mm (= carapace length of about 6.8 mm). The species is almost certainly protandrous, as shown by histological studies conducted by Smith and Williams (1982).

DISTRIBUTION AND SPECIMENS EXAMINED.—The species occurs in rivers and streams along the east coast of Australia from Cooktown, northern Queensland, to the Shoalhaven River, New South Wales (Smith and Williams, 1982, fig. 5).

The following lot has been examined. The numbers in parentheses are measurements, in mm, of postorbital carapace lengths.

NEW SOUTH WALES, AUSTRALIA: Norton's Basin, Nepean River, paratypes (?) of *Atya striolata*, 4♂ (7.8–8.7), 23 Nov 1919, A.R. McCulloch.

VARIATION.—Smith and Williams (1982:355) compiled data on 33 proportional attributes of 20 male, 24 female, and 2 juvenile topotypes, as well as of material from 18 other populations, and concluded that "the species is remarkably uniform over its whole known range," except that

FIGURE 23.—*Australatya striolata* (all from male paratype(?) from Norton's Basin, Nepean River, New South Wales, carapace length 8.7 mm): *a*, entire specimen, left aspect; *b*, anterior carapace and rostrum, left aspect; *c*, anterior carapace and appendages, dorsal aspect; *d*, telson and uropods; *e*, posterior end of telson; *f*, right mandible; *g*, right 1st maxilla; *h*, right 2nd maxilla; *i*, right 1st maxilliped; *j*, right 2nd maxilliped; *k*, right 3rd maxilliped; *l*, same, distal end. (Magnifications: *a*, × 2.6; *c*, *d*, × 5.2; *b*, *g–k*, × 10.8; *e*, *f*, × 21.5; *l*, × 53.8.)

specimens from far northern Queensland are slightly more pubescent, especially on the antennular peduncle, including the stylocerite, and on the basis, epipod, and ischium of each pereopod; the northernmost specimens also tend to have the rostrum proportionately shorter and the carpi of the 2 anterior pereopods more deeply excavate. The rostra in the series of topotypes were armed with 4 to 8 ventral teeth.

ECOLOGICAL NOTES.—McCulloch and McNeill (1923:57) indicated that "these shrimps appear to occur only in running water and in rock localities where there are stones for them to hide under. They apparently dislike any but clear water." No specimens could be found in pools in which the water had ceased to flow, even though drought conditions resulted in minimal flow throughout the River at the time the collections

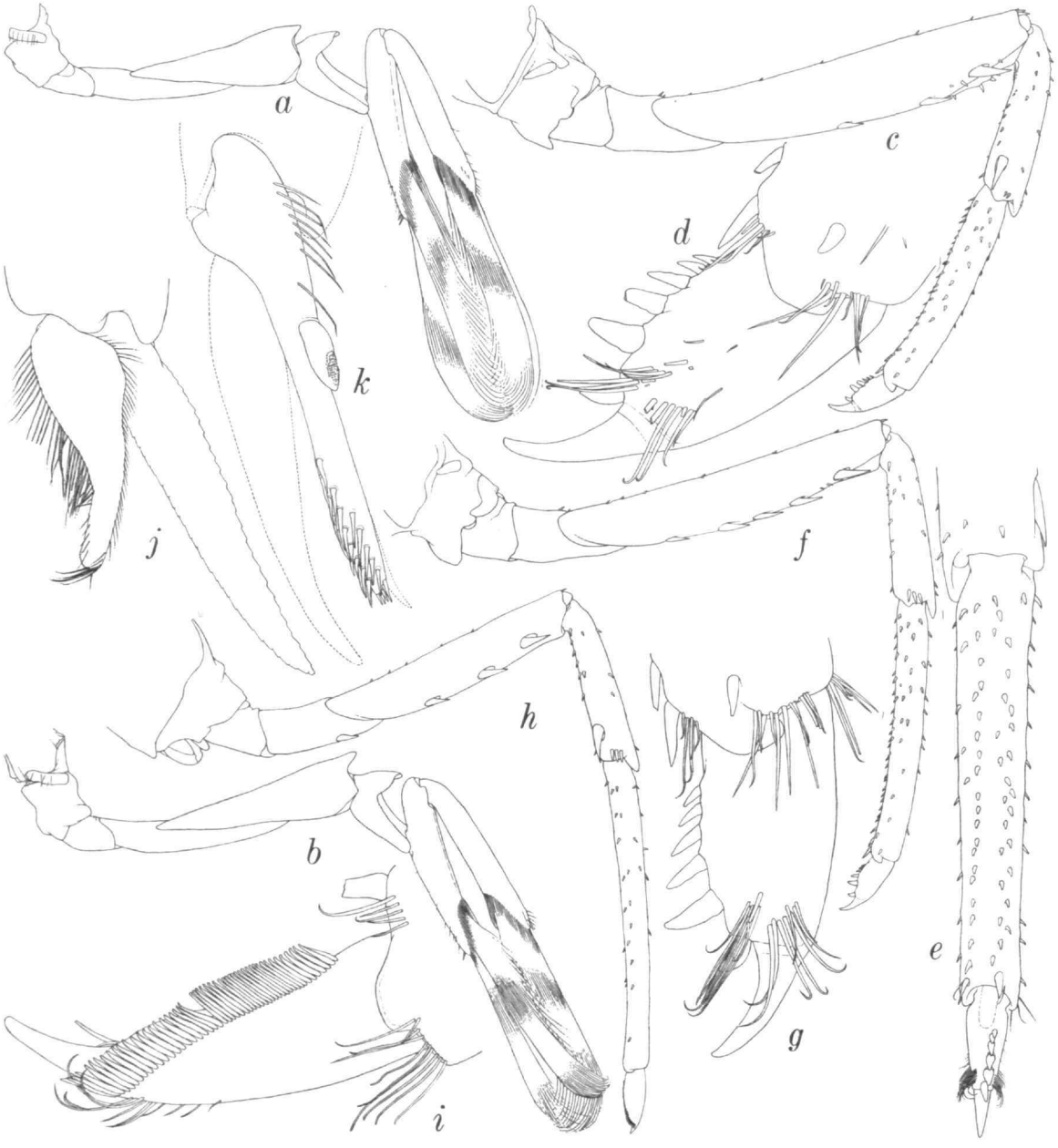

FIGURE 24.—*Australatya striolata* (all from male paratype(?) from Norton's Basin, Nepean River, New South Wales, carapace length 8.7 mm): *a*, right 1st pereopod; *b*, right 2nd pereopod; *c*, right third pereopod; *d*, same, dactyl; *e*, same, flexor surfaces of propodus and dactyl; *f*, right 4th pereopod (carpus abnormal, lacking single large spine); *g*, same, dactyl; *h*, right 5th pereopod; *i*, same, dactyl; *j*, endopod and exopod of right 1st pleopod, posterior aspect; *k*, right appendix masculina and appendix interna, mesial aspect. (Magnifications: *a–c*, *f*, *h*, × 10.8; *e*, *j*, *k*, × 21.5; *d*, *g*, *i*, × 53.8.)

were made. These authors (1923:57) noted that the shrimps "readily left a shallow dish of water by crawling over its sides, a habit which is evidently associated with their migration from one pool to another when drought conditions cut off the supply of running water." The shrimps "run freely in an upright position over the flat surface of a table, and if thrown on their sides, will speedily regain their normal position." According to Riek (1953:113), specimens from Cave Creek, Upper Nerang River, southern Queensland, were found only at the overflow of a pool below a small fall; search for them elsewhere in the stream was fruitless. J.A. Bishop (1967:119) reported *Atya striolata* living as a facultative troglobite in Gloucester Caves, New South Wales.

LIFE HISTORY NOTES.—None. Smith and Williams (1982:359) postulated that *Atyoida striolata* may have a life cycle that involves "a downstream migration of ovigerous females, the release of large numbers of larvae in estuaries of other marine situations, an upstream migration of sexually immature shrimps, followed by a sexual change from mature male to mature female. Such a life-cycle would explain the occurrence of this atyid in habitats whose rapid flow pre-empts any larval survival *in situ*."

COMMON NAMES.—None.

ECONOMIC IMPORTANCE.—None.

Literature Cited

Adamson, A.M.

1935. Non-marine Invertebrate Fauna of the Marquesas (Exclusive of Insects). *Bernice P. Bishop Museum Occasional Papers*, 11(10): 39 pages.

1939. Review of the Fauna of the Marquesas Islands and Discussion of Its Origin. *Bernice P. Bishop Museum Bulletin*, 159: 93 pages, 2 figures.

Anderson, C., editor

1926. Footnote 22. *In* J. Roux, An Account of Australian Atyidae. *Records of the Australian Museum*, 15(3): 253.

Arudpragasam, K.D., and H.H. Costa

1962. Atyidae of Ceylon—I. *Crustaceana*, 4(1):7–24, 5 figures.

Balss, H.

1914. Ostasiatische Decapoden, II: Die Natantia und Reptantia. *In* F. Doflein, editor, Beiträge zur Naturgeschichte Ostasiens. *Abhandlungen der Mathematisch-Physikalischen Klasse der Koniglichen Bayerischen Akademie der Wissenschaften zu München*, supplement 2 (10):1–101, figures 1–50, plate 1.

Bate, C.S.

1888. Report on the Crustacea Macrura Collected by H.M.S. *Challenger* during the Years 1873–76. *Report on the Scientific Results of the Voyage of H.M.S.* Challenger *during the Years 1873–76, Zoology*, 24: xc + 942 pages, figures 1–76, plates 1–157.

Bayer, F.M., and H.A. Fehlmann

1960. The Discovery of a Freshwater Opisthobranchiate Mollusk *Acochlidium amboinense* Strubell, in the Palau Islands. *Proceedings of the Biological Society of Washington*, 73:183–194, figures 1–3.

Bishop, J.A.

1967. The Zoogeography of the Australian Freshwater Decapod Crustacea. *In* A.H. Weatherly, editor, *Australian Inland Waters and Their Fauna*, pages 107–122, 6 figures. Canberra: Australian National University Press.

Bishop, J.E.

1973. Limnology of a Small Malayan River Sungai Gombak. *Monographiae Biologicae*, 22: iv + 485 pages, figures 1–67, plates 1–15.

Blanco, G.J.

1935. The Atyidae of the Philippine Islands. *Philippine Journal of Science*, 56(1):29–39, plates 1–3.

Blaringhem, L.

1911. Les transformations brusques des etres vivants. *In* G. Le Bon, *Bibliothèque de philosophie scientifique*, 353 pages, 49 figures. Paris: E. Flammarion.

Boone, L.

1935. Crustacea: Anomura, Macrura, Euphausiacea, Isopoda, Amphipoda and Echinodermata: Asteroidea and Echinoidea. *In* Scientific Results of the World Cruise of the Yacht "Alva," 1931, William K. Vanderbilt, Commanding. *Bulletin of the Vanderbilt Marine Museum*, 6: 264 pages, 13 figures, 96 plates.

Bordage, E.

1908. Recherches expérimentales sur les mutations évolutives de certains Crustacés de la famille des Atyidés. *Comptes Rendus Hebdomadaires des Séances de l'Academie des Sciences* (Paris), 147:1418–1420, figures 1, 2.

1909a. Sur la régénération hypotypique des chelipèdes chez *Atya serrata* Sp. Bate. *Comptes Rendu Hebdomadaires des Séances de l'Academie des Sciences* (Paris), 148:47–50.

1909b. Mutation et régénération hypotypique chez certains Atyidés. *Bulletin Scientifique de la France et de la Belgique*, series 7, 43(1):93–112, figure 1–7.

Borradaile, L.A.

1899. On the Stomatopoda and Macrura Brought by Dr. Willey from the South Seas. *In* A. Willey, *Zoological Results Based on the Material from New Britain, New Guinea, Loyalty Islands and Elsewhere, Collected during the Years 1895, 1896, and 1897*, 4:395–498, plates 36–39.

Bouvier, E.-L.

1904a. Sur le genre *Ortmannia* Rathb. et les mutations de certains Atyidés. *Comptes Rendus Hebdomadaires des Séances de l'Academie des Sciences* (Paris), 138:446–449.

1904b. On the Genus *Ortmannia*, Rathbn., and the Mutations of Certain Atyids. *Annals and Magazine of Natural History*, series 7, 13:377–381. [Translated from Bouvier, 1904a.]

1904c. Crevettes de la famille des Atyidés: Espèces qui font partie des collections du Muséum d'histoire naturelle. *Bulletin du Muséum National d'Histoire Naturelle* (Paris), 10:129–138.

1905. Observations nouvelles sur les crevettes de la famille des Atyidés. *Bulletin Scientifique de la France et de la Belgique*, 39:57–134, figures 1–26.

1909. Les crevettes d'eau douce de la famille des Atyidés qui se trouvent dans l'île de Cuba. *Bulletin du Muséum National d'Histoire Naturelle* (Paris), 15(6):329–336.

1911. Nouvelles observations sur les mutations évolu-

tives. *Comptes Rendus Hebdomadaires des Séances de l'Academie des Sciences*, 152:1820–1825.

1912a. Sur la classification du genre *Caridina* et les variation extraordinaires d'une espèce de ce genre, la *Caridina brevirostris* Stimpson. *Comptes Rendus des Séances de l'Academie des Sciences* (Paris), 154:915–922.

1912b. La variabilité des êtres et l'évolution, II: Mutations et évolution des Atyidés. *Revue Générale des Sciences Pures et Appliquées*, 23:690–695, figures 1–7.

1913a. Les Caridines des Seychelles. *In* The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the Leadership of Mr. J. Stanley Gardiner, 4(28). *The Transactions of the Linnean Society of London*, series 2 (Zoology), 15(4):447–472, plates 27–29.

1913b. Sur la classification des crevettes de la famille des Atyidés (Crust.). *Bulletin de la Société Entomologique de France*, 1913(8):177–182.

1914. Sur la faune carcinologique de l'île Maurice. *Comptes Rendus des Séances de l'Academie des Sciences* (Paris), 159:698–705.

1918. *La vie psychique des Insectes*. 300 pages, 16 figures. Paris: Ernest Flammarion.

1925. Recherches sur la morphologie, les variations, la distribution géographique des crevettes de la famille des Atyidés. *Encyclopédie Entomologique*, series A, 4: 370 pages, 716 figures.

Bouvier, E.-L., and d'E. de Charmoy

1919. Mutation d'une Caridine en Ortmannie et observations générales sur les mutations évolutives des crevettes d'eau douce de la famille des Atyidés. *Comptes Rendus des Séances de l'Academie des Sciences* (Paris), 169:317–321.

Calman, W.T.

1906. Report on the Macrurous Crustacea. *In* Zoological Results of the Third Tanganyika Expedition, Conducted by Dr. W.A. Cunnington, 1904–1905. *Proceedings of the Zoological Society of London*, 1906 (1):187–206, plates 11–14.

1910. The Researchers of Bouvier and Bordage on Mutations in Crustacea of the Family Atyidae. *The Quarterly Journal of Microscopical Science*, 55(4):785–797, figures 1–4.

Carpenter, A.

1978. Protandry in the Freshwater Shrimp, *Paratya curvirostris* (Heller, 1862) (Decapoda: Atyidae), with a Review of the Phenomenon and Its Significance in the Decapoda. *Journal of the Royal Society of New Zealand*, 3(4):343–358, 7 figures.

Colosi, G.

1919. Mutazionismo sperimentale. *Rassegna delle Scienze Biologiche*, 1:158, 159.

Costa, H.H.

1972. Results of the Austrian-Ceylonese Hydrobiological Mission 1970 of the 1st Zoological Institute of the University of Vienna (Austria) and the Department of Zoology of the Vidyalankara University of Ceylon, Kelaniya, Part V: Decapoda Caridea. *Bulletin of the Fisheries Research Station, Sri Lanka (Ceylon)*, 23(1–2):127–135, 5 figures.

1980. Results of the Austrian Hydrobiological Mission, 1974, to the Seychelles-, Comores- and Mascarene-Archipelagos, Part III: The Ecology and the Distribution of Decapoda Caridea in the Indian Ocean Islands of Seychelles, Mauritius, Comores & Reunion. *Annalen des Naturhistorischen Museums in Wien*, 83:673–700, 1 figure, 1 plate.

Coutière, H.

1900. Sur quelques Macroures des eaux douces de Madagascar. *Comptes Rendus des Séances de l'Academie des Sciences* (Paris), 130:1266–1268.

Cowles, R.P.

1915a. The Habits of Some Tropical Crustacea, II. *The Philippine Journal of Science*, 10(1):11–17, figures 1, 2, plates 1–3.

1915b. Are *Atya spinipes* Newport and *Atya armata* Milne Edwards Synonyms for *Atya moluccensis* De Haan? *The Philippine Journal of Science*, 10(2):147–153, figure 1.

Cuénot, L.

1911. *La genèse des espèces animales*. iii + 496 pages, 123 figures. Paris: Ancienne Librairie Germer Baillière et Cie.

Dana, J.D.

1852. Crustacea, Part 1. In *United States Exploring Expedition during the Years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes, U.S.N.*, 13:1–685. Atlas (1855): 27 pages 96 plates. Philadelphia.

De Haan, W.

1833–1850. Crustacea. *In* P.F. von Siebold, *Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit*. i–xvii, ix–xvi, 1–243, [244], i–xxxi, plates A–J, L–Q, 1–55, circ. fl. tab. 2. Lugduni-Batavorum [Leiden].

De Man, J.G.

1892. Decapoden des Indischen Archipels. *In* Max Weber, *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien*, 2:265–527, plates 15–29.

1902. Die von Herrn Professor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden. *In* Kükenthal, Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 25 (3):467–929, plates 19–27.

1915. Macrura. *In* Zur Fauna von Nord-Neuguinea, nach den Sammlungen von Dr. P.N. van Kampen und K. Gjellerup in den Jahren 1910–1911. *Zoologische Jahrbucher Abteilung für Systematik, Geographie*

und Biologie der Tiere, 38(6):385–458, plates 27–29.

De Silva, K.H.G.M.

1982. Studies on Atyidae (Decapoda, Caridea) of Sri Lanka, I: On a New Species, a New Subspecies, and Two Species New to Sri Lanka. *Crustaceana*, 43(2):127–141, 5 figures.

Djajadiredja, R.R., and M. Sachlan

1956. Shrimp and Prawn Fisheries in Indonesia with Special Reference to the Kroya District. *Indo-Pacific Fisheries Council Proceedings*, 6:366–377, 5 figures.

Doflein, F.

1904. Krebse. *In* P. Schnee, Die Landfauna der Marschall-Inseln nebst einigen Bemerkungen zur Fauna der Insel Nauru, I. *Zoologische Jahrbücher Abtheilung für Systematik, Geographie und Biologie der Thiere*, 20(4):406, 407.

Edmondson, C.H.

1929. Hawaiian Atyidae. *Bernice P. Bishop Museum Bulletin*, 66: 36 pages, figures 1–4, plate 1.

1930. Effect of Ultraviolet Rays in Regeneration of Chelipeds. *Bernice P. Bishop Museum Occasional Papers*, 9(7): 7 pages, 1 figure.

1935. Atyidae of Southern Polynesia. *Bernice P. Bishop Museum Occasional Papers*, 11(3): 19 pages, 6 figures.

1936. Effect of X-rays on Regeneration of Chelipeds of *Atya bisulcata*. *Bernice P. Bishop Museum Occasional Papers*, 11(16): 15 pages, 1 figure, 1 plate.

Estampador, E.P.

1937. A Check List of Philippine Crustacean Decapods. *The Philippine Journal of Science*, 62(4):465–559.

1959. Revised Check List of Philippine Crustacean Decapods. *Natural and Applied Science Bulletin*, 17:1–127.

Fernando, C.H.

1963. A Guide to the Freshwater Fauna of Ceylon. Supplement 1. *Fisheries Research Station, Department of Fisheries, Bulletin*, 16:29–38, figures 1–10, 1–13.

Filhol, H.

1885. Considérations relative à la faune des Crustacés de la Nouvelle-Zélande. *Bibliothèque de l'École des Haut Études, Section des Sciences Naturelles*, 30(2):60 pages.

1886. Crustacés. *In* Recherches zoologiques, botaniques et géologiques faites a l'île Campbell et en Nouvelle-Zélande, 1: Zoologie, Chapter VII. *Recueil de mémoires, rapports et documents relatifs a l'observation du passage de Vénus sur le soleil du 9 Decembre 1874, Commission du passage de Vénus, Académie des sciences* (Paris), 3(2):349–510, plates 38–55.

Fryer, G.

1977. Studies on the Functional Morphology and Ecology of the Atyid Prawns of Dominica. *Philosophical Transactions of the Royal Society of London, B: Biological Sciences*, 277(952):57–128, figures 1–121.

Gabriel, R.C.

1963. Studies on Cephalization of the Central Nervous System in Some Malacostracans and Its Possible Phylogenetic Significance. *Natural and Applied Science Bulletin*, 18:151–165, 4 figures.

Gibbes, L.R.

1850a. Catalogue of the Crustacea in the Cabinet of the Academy of Natural Sciences of Philadelphia, August 20th, 1847, with Notes on the Most Remarkable. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 5:22–28.

1850b. On the Carcinological Collections of the United States, and an Enumeration of Species Contained in Them, with Notes on the Most Remarkable, and Descriptions of New Species. In *Proceedings of Third Meeting of American Association for Advancement of Science, Held at Charleston, S.C., March, 1850*, pages 167–201. Charleston: Corporation of Charleston.

Giebel, C.G.

1875. *Atya gabonensis*, neuer Krebs aus Gabon. *Zeitschrift für die gesammten Naturwissenschaften*, 45:52–55.

Gurney, R.

1942. Larvae of Decapod Crustacea. *The Ray Society*, 129: viii + 306 pages, 122 figures.

Haan, W. de. *See* De Haan

Herbst, J.F.W.

1791–1796. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten*, 2: viii + 266 pages, plates 22–46. Berlin: Gottlieb August Lange.

Hickson, S.J.

1889. *A Naturalist in North Celebes: A Narrative of Travels in Minahassa, the Sangir and Talaut Islands, with Notices of the Fauna, Flora, and Ethnology of the Districts Visited.* xv + 392 pages, 35 figures. London: John Murray.

Hilgendorf, F.

1869. Crustaceen. *In* Baron Carl Claus von der Decken, *Reisen in Ost-Afrika in den Jahren 1859–1865*, 3(1):67–116, 147, plates 1–6.

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

1982. The Shrimp Genus *Atya* (Decapoda: Atyidae). *Smithsonian Contributions to Zoology*, 364: 143 pages, 53 figures.

Holthuis, L.B.

1951. The Caridean Crustacea of Tropical West Africa. *Atlantide Report*, 2:7–187, figures 1–34.

1952. The Decapoda of the Siboga Expedition, Part XI: The Palaemonidae Collected by the *Siboga* and *Snellius* Expeditions with Remarks on Other Species, II: Subfamily Pontoniinae. In *Siboga-Expeditie*, $39a^{10}$: 254 pages, 110 figures.

1953. On the Type Specimen of *Vanderbiltia rosamondae* Boone (Crustacea Decapoda Macrura). *Zoologische Mededelingen Uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden*, 32(12):113–118, figure 1.

1954. On a Collection of Decapod Crustacea from the Republic of El Salvador (Central America). *Zool-*

ogische Verhandelingen Uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden, 23: 43 pages, 15 figures, 2 plates.

1955. The Recent Genera of the Caridean and Stenopodidean Shrimps (Class Crustacea, Order Decapoda, Supersection Natantia) with Keys for Their Determination. *Zoologische Verhandelingen Uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden*, 26: 157 pages, figures A, B, 1–105.

1965. The Atyidae of Madagascar. *Memoires du Museum National d'Histoire Naturelle*, series A (Zoologie), 33(1): 48 pages, 17 figures.

1970. Études hydrobiologiques en Nouvelle-Calédonie (Mission 1965 du Premier Institut de Zoologie de l'Université de Vienne), IX: The Freshwater Shrimps (Crustacea, Decapoda, Natantia) of New Caledonia. *Cahiers O.R.S.T.O.M., Serie Hydrobiologique*, 3(2):87–108, 4 figures.

1978. A Collection of Decapod Crustacea from Sumba, Lesser Sunda Islands, Indonesia. *Zoologische Verhandelingen Uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden*, 162: 55 pages, 14 figures, 1 plate.

1980. Shrimps and Prawns of the World: An Annotated Catalogue of Species of Interest to Fisheries. *FAO Fisheries Synopsis*, 125(1): xvii + 271 pages. [Volume 1 of FAO Species Catalogue.]

1982. Freshwater Crustacea Decapoda of New Guinea. *Monographiae Biologicae*, 42:603–619, figures 1–5.

Holthuis, L.B., and H. Rosa, Jr.

1965. List of Species of Shrimps and Prawns of Economic Value. *FAO Fisheries Technical Paper*, 52: iii + 21 pages.

Hunte, W.

1978. The Distribution of Freshwater Shrimps (Atyidae and Palaemonidae) in Jamaica. *Zoological Journal of the Linnean Society of London*, 64(2):135–150, 7 figures.

Johnson, D.S.

1957. A Survey of Malayan Freshwater Life. *Malayan Nature Journal*, 12:57–65, figures 1–6.

1958. Some Aspects of the Distribution of Freshwater Organisms in the Indo-Pacific Area, and Their Relevance to the Validity of the Concept of an Oriental Region in Zoogeography. In *Proceedings of the Centenary and Bicentenary Congress of Biology, University of Malaya (Singapore), 1958*, pages 170–181, 9 figures.

1959. Some Aspects of Morphological Adaptation to Water Flow in Malayan Freshwater Animals. In *Proceedings of the XVth International Congress of Zoology, London, 1958*, pages 70–72.

1961. Notes on the Freshwater Crustacea of Malaya, I: The Atyidae. *Bulletin of the Raffles Museum, State of Singapore*, 26:120–153, 42 figures.

1962. A Synopsis of the Decapoda Caridea and Stenopodidea of Singapore, with Notes on Their Distribution and a Key to the Genera of Caridea Occurring in Malayan Waters. *Bulletin of the National Museum, State of Singapore*, 30:44–79, plate 2.

1964. Distributional and Other Notes on Some Fresh-Water Prawns (Atyidae and Palaemonidae) Mainly from the Indo-West Pacific Region. *Bulletin of the National Museum Singapore*, 32:5–30, figures 1–5.

1965. A Review of the Brackish Water Prawns of Malaya. *Bulletin of the National Museum Singapore*, 33(2):7–11.

1966. Edible Crustaceans. *The Malayan Nature Journal*, 19:275–282.

1967. Some Factors Influencing the Distribution of Freshwater Prawns in Malaya. In *Proceedings of the Symposium on Crustacea Held at Ernakulam from January 12 to 15 1965*, 1:418–433, figures 1–3. [Symposium Series 2, Marine Biological Association of India.]

1968. Biology of Potentially Valuable Fresh-Water Prawns with Special Reference to the Riceland Prawn *Cryphiops* (*Macrobrachium*) *lanchesteri* (de Man). *In* M.N. Mistakidis, editor, Proceedings of the World Scientific Conference on the Biology and Culture of Shrimps and Prawns, volume II: Review, Regional Summary and Experience Papers, E/2. *FAO Fisheries Reports*, 57(2):233–241.

1969. Non-Penaeid Prawns of Inland Waters, Including Brackish Waters, in Western Malaysia and Singapore. *In* B.C. Stone, editor, *Natural Resources in Malaysia and Singapore: Proceedings of the Second Symposium on Scientific and Technological Research in Malaysia and Singapore (1967), Kuala Lumpur, University of Malaya*, pages 109–113.

Ms. Notes on the Genus *Atya* (Crustacea: Decapoda: Family Atyidae). 53 pages, 5 figures. [Undated manuscript; copies available in the British Museum (Natural History); Rijksmuseum van Natuurlijke Historie, Leiden; and Smithsonian Institution.]

Koningsberger, J.C.

1911–1915. *Java zoologisch en biologisch.* 663 pages. Buitenzorg: G. Kolff & Co. Batavia.

Korschelt, E.

1944. Ontogenie der Decapoden. In *H.G. Bronn's Klassen und Ordnungen des Tierreichs*, 5(part 1, book 7, number 6):671–861, figures 741–841.

Kubo, I.

1938. On the Japanese Atyid Shrimps. *Journal of the Imperial Fisheries Institute*, 33(1):67–100, figures 1–24.

Laird, M.

1956. Studies of Mosquitoes and Freshwater Ecology in the South Pacific. *Royal Society of New Zealand Bulletin*, 6:1–213, figures 1–3, plates 1–11.

Lanchester, W.F.
1900. On Some Malacostracous Crustaceans from Malaysia in the Collection of the Sarawak Museum. *Annals and Magazine of Natural History*, series 6, 6:249–265, plate 12.
1901. On the Crustacea Collected during the "Skeat" Expedition to the Malay Peninsula, Together with a Note on the Genus *Actaeopsis*, Part I: Brachyura, Stomatopoda, and Macrura. *Proceedings of the Zoological Society of London*, 1901:534–574, plates 33, 34.

Leach, W.E.
1815. A Tabular View of the External Characters of Four Classes of Animals, Which Linné Arranged under Insecta, with the Distribution of the Genera Composing Three of These Classes into Orders, &c. and Descriptions of Several New Genera and Species. *Transactions of the Linnean Society of London*, 11:306–400.
1816. *Atya.* In *Encyclopaedia Britannica*, supplement to the fourth, fifth, and sixth editions, 1(1):421, plate 21. Edinburgh: Archibald Constable and Company. [Reprinted 1824.]

Man, J.G. de. *See* De Man

Martens, E. von. *See* Von Martens

McCulloch, A.R., and F.A. McNeill
1923. Notes on Australian Decapoda. *Records of the Australian Museum*, 14(1):49–59, figures 1, 2, plates 9–11.

McNeill, F.A.
1926. Prawns and Shrimps. *In* A. Wilberforce Jose and J. Carter, *The Australian Encyclopaedia*, 2:324–326, figures 1–3.
1929. Studies in Australian Carcinology, No. 3. *Records of the Australian Museum*, 17(3):144–156, figures 1–4, plates 35–37.

Mendis, A.S., and C.H. Fernando
1962. A Guide to the Freshwater Fauna of Ceylon. *Fisheries Research Station, Department of Fisheries, Bulletin*, 12: 160 pages, 301 figures.

Miers, E.J.
1876. *Catalogue of the Stalk- and Sessile-eyed Crustacea of New Zealand*, xii + 136 pages, plates 1–3. London.
1880. Crustacea Anomura and Macrura (except Penaeidea): On a Collection of Crustacea from the Malaysian Region, Part III. *Annals and Magazine of Natural History*, series 5, 5:370–384, plates 14, 15.

Milne-Edwards, A.
1864. Revision des Crustacés macroures de la famille des Atyoidées. *Annales de la Société Entomologique de France*, series 4, 4:145–152, plate 3.

Miyake, S.
1938. Notes on Decapod Crustaceans Collected by Prof. Teiso Esaki from Micronesia. *Annotationes Zoologicae Japonenses*, 17(2):107–112, figure 1.

Needham, A.E.
1938. The Crustacea: Some Adaptations. *Irish Naturalist's Journal*, 7:74–84, figures 1–25.

Newport, G.
1847. Note on the Genus *Atya* of Leach, with Descriptions of Four Apparently New Species, in the Cabinets of the British Museum. *Annals and Magazine of Natural History*, 19:158–160, plate 8: figure 1.

Nobili, G.
1900. Decapodi e Stomatopodi Indo-Malesi. *Annali del Museo Civico di Storia Naturale di Genova*, series 2a, 20(40):473–523, figures 1–4.
1905. Decapodi e Isopodi della Nuova Guinea Tedesca Raccolti dal Sign. L. Biro. *Annales Musei Nationalis Hungarici*, 3:480–507, plates 12, 13.
1907. Ricerche sui Crostacei della Polinesia: Decapodi Stomatopodi, Anisopodi e Isopodi. *Memoria della Reale Accademia delle Scienze di Torino*, series 2, 57:351–430, plates 1–3.

Ortmann, A.
1890. Die Unterordnung Natantia Boas: Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berucksichtigung der von Herrn Dr. Döderlein bei Japan und bei dem Liu-Kiu-Inseln gesammelten und z. Z. im Strassburger Museum aufbewahrten Formen, I. Theil, *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, 5:437–542, plates 36, 37.
1894. Crustaceen. *In* R. Semon, Zoologische Forschungreisen in Australien und dem malayischen Archipel, V. *Denkschriften Medizinisch-Naturwissenschaftliche Gesellschaft zu Jena*, 8:3–80, plates 1–3.
1895. A Study of the Systematic and Geographical Distribution of the Decapod Family Atyidae Kingsley. *Proceedings of the Academy of Natural Sciences of Philadelphia*, [46] (1894):397–416.
1897. Os Camorões da agua doce da America do Sul. *Revista do Museu Paulista*, 2:173–216, plate 1.

Poisson, H.
1947. Les Crustacés alimentaires de Madagascar: Étude zoologique et économique. *Cahiers Section d'Océanographie Appliquée, Société des Amis du Parc Botanique et Zoologique de Tananarive*, 4:1–74, plates 1–8.

Radir, P.L.
1930. An Interpretation of the Taxonomic Status of *Atya bisulcata*, Randall, and *Ortmannia henshawi*, Rathbun. *Annals and Magazine of Natural History*, series 10, 5:351–354, plate 13.

Randall, J.W.
1840. Catalogue of the Crustacea Brought by Thomas Nuttall and J.K. Townsend, from the West Coast of North America and the Sandwich Islands, with Descriptions of Such Species As Are Apparently New, among Which Are Included Several Species

of Different Localities, Previously Existing in the Collection of the Academy. *Journal of the Academy of Natural Sciences of Philadelphia*, 8:106–147, plates 3–7.

Rathbun, M.J.

1901. The Brachyura and Macrura of Porto Rico. *United States Fish Commission Bulletin for 1900*, 20(2):1–127, 129*–137* [index]; 24 figures, 2 plates. [Preprint (*) published 1901. Bulletin for 1900 published 1902.]

1906. The Brachyura and Macrura of the Hawaiian Islands. *Bulletin of the United States Fish Commission (1903)*, 23(3):827–930 [reprint with index pages i–viii], figures 1–79, plates 1–24.

1910. Decapod Crustaceans Collected in Dutch East India and Elsewhere by Mr. Thomas Barbour in 1906–1907. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 52(16):305–317, plates 1–6.

Riek, E.F.

1953. The Australian Freshwater Prawns of the Family Atyidae. *Records of the Australian Museum*, 23:111–121, figures 1–11.

1959. The Australian Freshwater Crustacea. *In* A. Keast, R.L. Crocker, and C.S. Christian, editors, *Biogeography and Ecology in Australia*, 14:246–258. The Hague: Dr. W. Junk. [*Monographiae Biologicae*, volume 8.]

Roth-Woltereck, E.

1942. Untersuchungen an Atyiden (Decapoda) von Belgisch Kongo, mit besonderer Berücksichtigung der Rassen- und Artbildungsfrage. *Revue de Zoologie et de Botanique Africaines*, 38:229–312, figures 1–18.

Roux, J.

1917. Crustacés. *In* C.E.A. Wichmann, expédition de 1903. *Nova Guinea, résultats de l'expédition scientifique néderlandaise à la Nouvelle-Guinée*, (Zoologie), livre 6:589–621, plates 27, 28.

1925. Über einige Süsswasserdekapoden (Atyidae) des Berliner Zoologischen Museums. *Zoologische Anzeiger*, 62:145–154.

1926a. Crustacés décapodes d'eau douce de la Nouvelle-Calédonie. *In* F. Sarasin and J. Roux, editors, *Nova Caledonia, Zoologie*, 4(2):181–240, 56 figures. Munich: C.W. Kreidel's Verlag.

1926b. An Account of Australian Atyidae. *Records of the Australian Museum*, 15(3):237–254.

1928a. Notes carcinologiques de l'Archipel indo-australien, I: Décapodes macroures d'eau douce de l'Archipel indo-australian. *Treubia*, 10(203):197–216, 9 figures.

1928b. Notes carcinologiques de l'Archipel indo-australien, II: Crustacés décapodes d'eau douce provenant de l'île de Soemba. *Treubia*, 10(2–3):216–222.

1932. Süsswassermacruren der Deutschen Limnologischen Sunda-Expedition. *Archiv für Hydrobiologie*, supplement 11(Tropische Binnengewasser), 3(67): 563–574, 1 figure.

1934. Notes de carcinologie mélanésienne, I: Décapodes d'eau douce de l'Archipel Bismarck et des Iles de l'Amirauté. *Revue Suisse de Zoologie*, 41(11):217–229, figures 1–10.

Roxas, H.A.

1930. *The Puerto Galera Marine Biological Laboratory of the University of the Philippines (A Report to the President of the University, Together with a Check-list of Animals of the Puerto Galera Region)*, 24 pages, 4 plates. Manila: University of the Phillipines.

Schenkel, E.

1902. Beitrag zur Kenntnis der Dekapodenfauna von Celebes. *Verhandlungen Naturforschende Gesellschaft in Basel*, 13:485–585, plates 7–13.

Schmeltz, J.D.E.

1869. *Museum Godeffroy Catalog*, 4: xliv + 141 pages.

1874. *Museum Godefroy Catalog*, 5: xxxvi + 215 pages.

1881. Museum Godefroy, Hamburg, Catalog VIII. *Zoologische Anzeiger*, 4(supplement 91):1–18.

Seurat, L.G.

1934. La faune et le peuplement de la Polynésie française: Contribution à l'étude du peuplement zoologique et botanique des îles du Pacifique. *Mémoires de Société de Biogéographie* (Paris), 4:41–74.

Sharp, B.

1893. Catalogue of the Crustaceans in the Museum of the Academy of Natural Sciences of Philadelphia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1893:104–127.

Shokita, S.

1975. The Distribution and Speciation of the Inland Water Shrimps and Prawns from the Ryukyu Islands, I. *Bulletin of Science & Engineering Division, University of the Ryukyus (Mathematics & Natural Sciences)*, 18:115–136, figures 1–6.

Shokita, S., and S. Nishijima

1976. Faunal List of Inland-Water Malacostraca of Amami Group, the Ryukyu Islands. *Ecological Studies of Nature Conservation of the Ryukyu Islands*, 2:31–38, figure 1.

Silva, K.H.G.M. de. *See* De Silva

Smith, M.J., and W.D. Williams

1982. Taxonomic Revision of Australian Species of *Atyoida* Randall (Crustacea: Decapoda: Atyidae), with Remarks on the Taxonomy of the Genera *Atyoida* and *Atya* Leach. *Australian Journal of Marine and Freshwater Research*, 33(2):343–361, figures 1–7.

Smith, S.I.

1871. List of the Crustacea Collected by J.A. McNiel in Central America. *Report of the Peabody Academy of Science*, 1869:87–98.

Stanier, J.E., M.A. Woodhouse, and R.L. Griffin
1968. The Fine Structure of the Hepatopancreas of *Carcinus maenas* (L.) (Decapoda Brachyura). *Crustaceana*, 14(1):56–66, plates 1–10.

Stimpson, W.
1860. Crustacea Macrura: Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septemtrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit, pars VIII. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1960(January):22–47.

Suvatti, C.
1938. *A Check-List of Aquatic Fauna in Siam (Excluding Fishes)*. 116 + 8 unnumbered pages. Bangkok: Bureau of Fisheries.
1950. *Fauna of Thailand*. iv + 1100 pages. Bangkok: Department of Fisheries.

Thallwitz, J.
1891a. Über einige neue indo-pacifische Crustaceen. *Zoologischer Anzeiger*, 14(359):96–103.
1891b. Decapoden-Studien, inbesondere basirt auf A.B. Meyer's Sammlungen im Ostindischen Archipel, nebst einer Aufzählung der Decapoden und Stomatopoden des Dresdener Museums. *Abhandlungen und Berichte des Königlichen Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden*, 1890/91(3):1–56, 1 plate.

Thompson, D'A.W.
1901. *A Catalogue of Crustacea and of Pycnogonida Contained in the Museum of University College, Dundee*. 56 pages. Dundee. [Printed for the Museum.]

Tiwari, K.K.
1951. Occurrence of the Genus *Atya* Leach (Crustacea: Decapoda: Atyidae) in the Indian Mainland. *Current Science*, 20(8):208.

Ullman, H.L.
1967. Hawaiian Freshwater Shrimp. *Tropical Fish Hobbyist*, 16(2):56, 57, 60, 2 figures.

Urita, T.
1921. Species and Distribution of Natantia Found in Kagoshima Bay. *Zoological Magazine, Tokyo*, 33: 214–220, 1 map.

Van Weel, P.B.
1955. Processes of Secretion, Restitution, and Resorption in Gland of Mid-gut (Glandula Media Intestini) of *Atya spinipes* Newport (Decapoda-Brachyura [sic]). *Physiological Zoölogy*, 28:40–54, figures 1–10.

Villalobos F., A.
1960. Un nuevo genero de *Atyidae* (Crustacea, Decapoda), procedente de la Isla de Cocos. *Anales del Instituto de Biología, Universidad Nacional Autonoma de México*, 30(1–2):331–347, 25 figures.

Von Martens, E.
1868. Ueber einige ostasiatische Süsswasserthiere. *Archiv für Naturgeschichte*, 34(1):1–64, plate 1.

Weber, M.
1892. Die Süsswasser-Crustaceen des Indischen Archipels, nebst Bemerkungen über die Süsswasser-Fauna in allgemeinem. *In* M. Weber, *Zoologische Ergebnisse einer Reise in Niederlandisch Ost-Indien*, 2:528–571, figures 1–22, plate 30.

Weel, P.B. van. *See* Van Weel

White, A.
1847. *List of the Specimens of Crustacea in the Collection of the British Museum*. viii + 143 pages. London: Edward Newman.

Whitelegge, T.
1903. The Crustacea and Echinodermata. *In* R. Etheridge, Jr., editor, Notes on the Zoology of Paanopa or Ocean Island and Nauru or Pleasant Island, Gilbert Group. *Records of the Australian Museum*, 5(1):8–13.

Williams, W.D.
1968. *Australian Freshwater Life: The Invertebrates of Australian Inland Waters*. ix + 262 pages, 94 figures. Melbourne: Sun Books Pty Ltd.
1977. Some Aspects of the Ecology of *Paratya australiensis* (Crustacea: Decapoda: Atyidae). *Australian Journal of Marine and Freshwater Research*, 28(4):403–415, figures 1–5.
1981. The Crustacea of Australian Inland Waters. *In* A. Keast, editor, *Ecological Biogeography of Australia*, 2(part 4, no. 39):1101–1138, figures 1–10. The Hague: W. Junk.

Woltereck, E.
1937a. Systematisch-variationsanalytische Untersuchungen über die Rassen- und Artbildung bei Süsswassergarneelen aus der Gattung *Caridina* (Decapoda, Atyidae). *International Revue der Gesamten Hydrobiologie und Hydrographie*, 34(3/5):208–262, figures 1–6, plates 2–7, diagrams a–e.
1937b. Zur Systematik und geographischen Verbreitung der Caridinen. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, 34(3/5):294–330, figures 1–14.

Yu, H.-P.
1974. On the Atyid Shrimps (Crustacea, Decapoda, Atyidae) from Taiwan. *Aquiculture* (Taiwan), 2(2):49–58, figures 1–5.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

Copy must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information; **abstract** page with author, title, series, etc., following the established format; table of **contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

First page of text should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or ". . . Jones (1910:122)." If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume(number):pagination: "10(2):5–9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

Legends for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

Illustrations must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustration should appear on the art rather than in the legend.

Some points of style: Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

Arrange and paginate sequentially every sheet of manuscript in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when manuscript is submitted.