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INVERTEBRATE
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Contributions to the Knowledge of the Alpheid Shrimp
of the Pacific Ocean
Part V. The Indo-Pacific Members of the Genus *Athanas*¹

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THE FOUR PAPERS previously published in this series have dealt with Alpheid shrimp by geographical areas. For this paper, because a major revision of the genus is needed and the shrimps upon which the revision is based come from many different regions of the Pacific, it was considered better to deal with the genus as a whole. Some of the specimens here discussed have been reported in the four previous studies. Those specimens which have not been listed in the previous studies come from three major sources: specimens collected on the Coral Atoll Investigations made by the Pacific Science Board; specimens collected by the senior author travelling in the central Pacific under a grant from Bernice P. Bishop Museum, Honolulu; and specimens collected at Eniwetok and other Marshall Islands, by the senior author and by others under the sponsorship of the Atomic Energy Commission. In this paper, details on collections are not given; these can be found in previous or future papers.

The present study has been supported by National Science Foundation Grant NSF-G-1754. The authors wish to acknowledge their indebtedness to L. B. Holthuis for the use of the bibliography of species of higher crustacea prepared by him; without this help the list of references would have been almost impossible to prepare, especially in Honolulu where the libraries lack many of the older works.

Since the genus *Athanas* was first described by Leach in 1814, some 43 specific and sub-specific names have been applied to the members of this genus, only 7 of which are not known from the Pacific and Indian oceans. The shrimp in this genus are small and inconspicuous; as a result most of the previous workers

had only a few specimens, often broken, upon which to base their description; further, of the Indo-Pacific species, at least 18 have not been reported since their original capture.

The Indo-Pacific genus *Arete*, long accepted as being closely related to *Athanas*, has a somewhat similar history. Since the genus was erected by Stimpson in 1861 for the species *A. dorsalis*, 11 names have been applied to species within the genus, and 4 of these names have been based upon 3 specimens or less.

The specimens available for this study were in some cases collected in large numbers. As will be discussed below, almost all of the species which are so represented show marked variation with size and sex in the form of the large chelae, and several species appear to vary considerably in the form of the rostrum and teeth of the carapace about the eyes. As these are the chief characteristics that have been used in the separation of many of the species, a revision of the two genera is necessary. Unfortunately, the present collections do not contain representatives of enough species to permit a monographic revision, so the purpose of this paper will be to merely initiate such a revision, which other workers from other parts of the Indo-Pacific may elaborate upon and finish.

ANNOTATED BIBLIOGRAPHY OF THE
SPECIES OF *Athanas* AND *Arete*

In the following listing, all species placed in these genera have been listed with reference to the original description and all subsequent Indo-Pacific records. The number of specimens upon which the original description or subsequent redescription were based has been given, wherever possible, together with the localities where the specimens were collected. Most synonyms are indicated in this listing; in the synonymies later in the paper, reference is made back to this listing.

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- Athanas nitescens* (Leach) (described as *Palaeomon nitescens*), 1814. Edinb. Encyc. 7: 401. [Not Indo-Pacific.]
- Athanas edwardsii* Audouin, 1827. Explication sommaire des planches de Crustacés de l'Égypte et de la Syrie, ed. 2, vol. 22, pp. 249–290. Atlas Hist. Nat. vol. 2, Crustacea, pls. 1–13. [Citation taken directly from the bibliography of Holthius. For discussion of date of publication, see Sherborn, C. D., 1897. Proc. Zool. Soc. Lond., pp. 285–288.] [Now *Alpheus edwardsii*.]
- Athanas monoceros* (Heller) (described as *Alpheus monoceros*), 1861. S.B. Akad. Wiss. Wien 44: 274; Red Sea. [Coutière, 1899: 61, 62, makes this a variety of *A. dimorphus* Ortmann 1894, a procedure contrary to the rules of zoological nomenclature.]
- Athanas mascarenicus* Richters, 1880. Beitr. Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164; Mauritius or Seychelles. [Coutière (1896: 381) states that Richters' specimen is too incompletely described or figured; in 1899: 33, he states this is a synonym of *Arete dorsalis* Stimpson; in 1905: 868, he stated he could not identify it with certainty with any known species.]
- Athanas alpheoides* Czerniawsky, 1884. Obshchestvo Ispuitatelei Priroudc pri Imperatorskom Khar'kovskom Universitete (Société des Naturalistes à l'Université Impériale de Kharkow) 13: 26. [Not Indo-Pacific. Coutière (1899: 37) states this is a juvenile.]
- Athanas transitans* Czerniawsky, 1884. Trans. Soc. Univ. Kharkov 13: 25. [Not Indo-Pacific.]
- Athanas transitans longispina* Czerniawsky, 1884. Trans. Soc. Univ. Kharkov 13: 25. [Not Indo-Pacific.]
- Athanas veloculus* Spence Bate, 1888. Challenger Repts. 24: 529, pl. 96, fig. 1. [Not Indo-Pacific.]
- Athanas dimorphus* Ortmann, 1894. Denkschr. Med.-Naturw. Ges. Jena 8: 12, taf. 1, fig. 1; 3 specimens from Dar es Salaam, East Africa.
- Coutière, 1897b. Bull. Mus. Hist. Nat., Paris 3(7): 301. [Here Coutière placed his species *A. dispar* in synonymy.]
- Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 77, fig. 12; Red Sea, New Caledonia. [Drawing of large chela of female.]
- Balss, 1915. Ergebn. Zool. 30: 21; 1 specimen from the Red Sea.
- Tattersall, 1921. J. Linn. Soc. (Zool.) 34: 371, pl. 28, figs. 23, 24; 1 specimen from the Red Sea. [Partial redescription.]
- Gurney, 1924. Zool. Res. Cambridge Exp. Suez Canal, p. 260. [Larval development.]
- Balss, 1927. Trans. Zool. Soc. Lond. 22: 222; 1 female from Dar es Salaam, East Africa. [Record of capture.]
- Gurney, 1927. Trans. Zool. Soc. Lond. 22: 260, fig. 63. [Larval development.]
- Kollmann, 1937. Ann. Fac. Sci. Marseille II, 10: 145, figs. 16–17. [Journal unavailable.]
- Athanas nitescens veloculus* Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 380. [Not Indo-Pacific.]
- Athanas leptocheles* Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 381; 1 specimen from the Red Sea. [Coutière (1897: 233) stated these were females of species renamed *A. dispar*.]
- Athanas leptocheles monoceros* Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 381; 4 specimens from the Red Sea. [Coutière (1896: 381) considered *A. transitans longispina* a synonym of this species.]
- Athanas solenomerus* Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 381; 1 specimen from the Red Sea. [Coutière (1897: 233) stated this was the male of the species he renamed *A. dispar*.]
- Athanas dispar* Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3: 233; several specimens from Djibouti. [Coutière (1897: 301) stated this was a synonym of *A. dimorphus* Ortmann.]
- Athanas dispar monoceros* Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3: 233 (in a footnote). [See *A. monoceros* above and *A. dimorphus monoceros* below.]
- Athanas djiboutensis* Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3: 233; 2 specimens from Djibouti.
- Coutière, 1899. Ann. Sci. Nat. VIII, 9: 62, fig. 4; p. 177, fig. 207. [Discussion of rostrum and chela.]
- Coutière, 1903. Bull. Soc. Philom. Paris

- IX, 5(2): 75; specimens from the Maldive and Laccadive Archipelagoes. [Characteristics and general distribution.]
- Coutière, 1905. *Fauna and Geog. Maldive and Laccadive Archipelagoes* 2(4): 856, fig. 129. [Same as the above.]
- Nobili, 1906. *Ann. Sci. Nat.* IX, 4: 31; 1 specimen from the Red Sea. [Locality only.]
- Nobili, 1907. *Mem. R. Accad. Torino* IIa, 57: 353; 2 specimens from the Tuamotus Archipelago. [Brief remarks.]
- Tattersall, 1921. *J. Linn. Soc. Zool.* 34: 368, pl. 28, fig. 25; 9 specimens from the Sudanese Red Sea. [Description of specimens.]
- de Man, 1922. *Siboga Exped.* 39a¹(5): 21; 1 mutilated specimen from Indonesia. [Description of specimen.]
- Edmondson, 1925. *Bull. Bishop Mus., Honolulu* 27: 9; 1 specimen from Wake Island. [Record of capture.]
- Gordon, 1935. *Ann. Mag. Nat. Hist.* X, 16: 629; Christmas Island, Indian Ocean. [Record of capture.]
- Boone, 1935. *Bull. Vanderbilt (Oceanog.) Mar. Mus.* 6: 119, pl. 31; 2 specimens from Marquesas Islands. [Extensive description.]
- Ramadan, 1936. *Bull. Fac. Sci. Egypt. Univ.* 6: 12; 4 specimens from Ghardaqa, Red Sea. [Remarks on chelae.]
- Kollmann, 1937. *Ann. Fac. Sci. Marseille* II, 10: 145. [Reference not available.]
- Gurney, 1938. *Sci. Rep. Gr. Barrier Reef Exped.* 6: 54, figs. 249–252. [Discussion of larval forms.]
- Armstrong, 1941. *Amer. Mus. Novit.* (1137): 5; 1 female from Samoa. [Record of capture.]
- Barnard, 1946. *Ann. Mag. Nat. Hist.* XI, 13: 388; specimens from Mozambique. [Locality only.]
- Barnard, 1950. *Ann. S. Afr. Mus.* 38: 732–733, figs. 137 c–f; 1 specimen from Mozambique. [Brief description.]
- Chace, 1955. *Proc. U. S. Nat. Mus.* 105(3349): 16; 11 specimens from the Marshall Islands. [Brief remarks.]
- Banner, 1956. *Pacif. Sci.* 10(3): 322; 22 specimens from the Mariana Archipelago. [Brief discussion.]
- Banner, 1957. *Pacif. Sci.* 11(2): 193; 2 specimens from the Marshall Islands. [Record of capture.]
- Athanas sulcatipes* Borradaile, 1898. *Proc. Zool. Soc. Lond.*, p. 1011, pl. 65, fig. 9; 8 specimens from Funafuti. [Coutière (1905: 856) stated this was a synonym of *A. djiboutensis*.]
- Anonymous, 1899. *Mem. Aust. Mus.* 3: 518; specimen from Funafuti. [Record of capture.]
- Athanas ortmanni* Rankin, 1898. *Ann. N. Y. Acad. Sci.* 12(11): 251, pl. 30, fig. 7. [Not Indo-Pacific. Now *Salmoneus ortmanni*.]
- Athanas dimorphus monoceros* (Heller) Coutière, 1899. *Ann. Sci. Nat.* VIII, Zool. 9: 61, 62. [Change of name, see *A. monoceros* Heller, 1861, above.]
- Athanas naifaroensis* Coutière, 1903. *Bull. Soc. Philom. Paris* IX, 5(2): 77, figs. 14–16; 1 specimen from the Maldive Archipelago.
- Coutière, 1905. *Fauna and Geog. Maldive and Laccadive Archipelagoes* 2(4): 859, fig. 131. [Same description as the above.]
- Coutière, 1905. *C. R. Acad. Sci., Paris* 140: 737. [Review of species listed in Maldive and Laccadive Report.]
- de Man, 1922. *Siboga Exped.* 39a¹(5): 16, pl. II; fig. 9; 1 specimen from Indonesia. [Description of specimen.]
- Barnard, 1950. *Ann. S. Afr. Mus.* 38: 731, figs. 136 f–i; 1 specimen from Natal, South Africa. [Brief description.]
- Athanas areteformis* Coutière, 1903. *Bull. Soc. Philom. Paris* IX, 5(2): 79, figs. 17–18; 2 specimens from the Maldive Archipelago.
- Coutière, 1905. *Fauna and Geog. Maldive and Laccadive Archipelagoes* 2(4): 860, fig. 132. [Same description and figures as above.]
- Coutière, 1905. *C. R. Acad. Sci., Paris* 140: 737. [Review of species listed in Maldive and Laccadive Report.]
- Balss, 1915. *Ergebn. Zool.* 30: 21; specimen from the Red Sea. [Locality only.]
- Chace, 1955. *Proc. U. S. Nat. Mus.* 105(3349): 21; 1 specimen from the Marshall Islands. [Locality only.]
- Athanas minikoensis* Coutière, 1903. *Bull. Soc.*

- Philom. Paris IX, 5(2): 76, figs. 9-11; 1 specimen from Laccadive Archipelago, Indian Ocean.
- Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 858, fig. 130. [Same specimens and figures as the above.]
- de Man, 1911. Siboga Exped. 39a¹(2): 149, pl. 2, figs. 5-5h; 2 specimens from Indonesia. [Description and figures.]
- Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 13; 1 specimen from the Red Sea.
- Barnard, 1946. Ann. Mag. Nat. Hist. XI, 13: 388; specimen from Natal, South Africa. [Locality only.]
- Barnard, 1950. Ann. S. Afr. Mus. 38: 731, figs. 137 a-d; 1 specimen from Natal, South Africa. [Partial redescription.]
- Athanas orientalis* Pearson, 1905. Rep. Pearl Fish. Maanar 4(24): 88, pl. 2, fig. 10; 7 specimens from Ceylon.
- Athanas baswelli* Coutière, 1908. Bull. Soc. Philom. Paris IX, 11(5): 2; 1 female from south Adelaide coast, Australia.
- Hale, 1927. Crustacea of South Australia. Vol. 1. P. 47. [Brief remarks, no additional specimens.]
- Athanas granti* Coutière, 1908. Bull. Soc. Philom. Paris IX, 11(5): 192; 5 specimens from south Adelaide coast, Australia.
- Hale, 1927. Crustacea of South Australia. Vol. 1. P. 47. [Brief remarks, no additional specimens.]
- Athanas sibogae* de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 314; 9 specimens from Indonesia.
- de Man, 1911. Siboga Exped. 39a¹(2): 151, pl. 2, figs. 6-6h. [Redescription, same specimens as the above.]
- Athanas tenuipes* de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 316; 1 specimen from Indonesia.
- de Man, 1911. Siboga Exped. 39a¹(2): 157, pl. 3, figs. 8-8c. [Redescription, same specimen as the above.]
- Athanas parvus* de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 315; 1 female from Indonesia.
- de Man, 1911. Siboga Exped. 39a¹(2): 148, pl. 1, figs. 4-4d. [Redescription of same specimen.]
- Tattersall, 1921. J. Linn. Soc. Lond. 34: 372; 3 specimens from the Red Sea. [Brief remarks.]
- de Man, 1922. Siboga Rep. 39a¹(5): 16-18; 1 specimen from Indonesia. [Complete description.]
- Kubo, 1940. Annot. Zool. Jap. 19(2): 99, figs. 1, 2; 1 specimen from Tanabe, Wakayama Prefecture. [Redescription.]
- Miyadi, 1940. Annot. Zool. Jap. 19(2): 143. [Same specimen as reported by Kubo above.]
- Athanas jedanensis* de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 313; 4 specimens from Indonesia.
- de Man, 1911. Siboga Exped. 39a¹(2): 154-156, pl. 2, figs. 7-7f. [Redescription of same specimens.]
- Athanas grimaldii* Coutière, 1911. Bull. Inst. Océanogr. Monaco No. 197, figs. 1-6. [Not Indo-Pacific.]
- Athanas polymorphus* Kemp, 1915. Indian Mus., Mem. 5(3): 289, figs. 31, 32; 27 specimens from Chilka Lake, India.
- Athanas* sp. Stebbing, 1914. Ann. S. Afr. Mus. 15: 88; 1 specimen from Delagoa Bay, Indian Ocean.
- Athanas stebbingi* de Man, 1920. Zoöl. Meded. 5(3): 106; 1 specimen from Indonesia.
- de Man, 1922. Siboga Exped. 39a¹(5): 18, pl. II, III, figs. 10-10f. [Redescription of same specimen.]
- Athanas crosslandi* Tattersall, 1921. J. Linn. Soc. Lond. 34: 372, pl. 27, figs. 13-17; 2 specimens from the Red Sea.
- Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 12; specimen from the Red Sea. [Included in species listing.]
- Athanas gracilis* Boone, 1935. Bull. Vanderbilt Oceanogr. (Mar.) Mus. 6: 122-126, pl. 32; 1 specimen from Raiatea Island, Society Archipelago.
- Athanas japonicus* Kubo, 1936. J. Fish. Inst. Tokyo 31(2): 43, pl. 13; 3 specimens from Japan.
- Athanas oshimai* Yokoya, 1936. Jap. J. Zool. 7: 129, fig. 1; several specimens from Aburatsubo, Japan.

- Athanas erythraeus* Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 13, pl. 1, fig. 1; 1 specimen from Ghardaqa, Red Sea.
- Athanas esakii* Kubo, 1940. J. Fish. Inst. Tokyo 34(1): 93, fig. 13; four specimens from Kusaie, Caroline Islands.
- Athanas lamellifer* Kubo, 1940. Annot. Zool. Jap. 19(2): 102–106; figs. 3–5; 4 specimens from Kominato, Japan.
- Athanas kominatoensis* Kubo, 1942. Zool. Mag. Tokyo 54: 82–84, fig. 2; 5 males from Kominato, Japan.
- Athanas nouvelae* Holthuis, 1951. Atlantide Rep. (2): 104–110, fig. 22. [Not Indo-Pacific.]
- Athanas amazone* Holthuis, 1951. Atlantide Rep. (2): 111, fig. 23. [Not Indo-Pacific.]
- Athanas setoensis* Kubo, 1951. J. Tokyo Coll. Fish. 38(2): 265, figs. 5, 6; 1 specimen from central Japan.
- Athanas marshallensis* Chace, 1955. Proc. U. S. Nat. Mus. 105(3349): 17–20, fig. 8; 22 specimens from the Marshall Islands.
- Banner, 1957. Pacif. Sci. 11(2): 193, fig. 3 a–f; 1 specimen, Marshall Islands.
- Athanas dubius* Banner, 1956. Pacif. Sci. 10(3): 322–325, fig. 2 a–h; 10 specimens from Saipan, Mariana Archipelago.
- Arete dorsalis* Stimpson, 1861. Proc. Acad. Nat. Sci. Philad. 12: 32; found near Hong Kong. [Nec. *A. dorsalis* de Man (1888: 527), see *A. amboinensis*.]
- Coutière, 1896. Bull. Mus. Hist. Nat., Paris 2: 385; 1 specimen from Samoa and 1 from the Indian Ocean. [Brief description.]
- Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3(6): 234; several specimens from Djibouti. [Remarks on ecology.]
- Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 13, figs. 32–34. [States *A. dorsalis pacificus* Coutière is a synonym of *A. dorsalis*.]
- Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 866, figs. 136–137; 1 specimen from Goidu Atoll, Indian Ocean.
- Chilton, 1910. Trans. Proc. N. Z. Inst. 43: 549; 3 specimens from Sunday Island, Kermadec Islands. [Description of specimens.]
- de Man, 1911. Siboga Exped. 39a¹ (2): 167; 2 females from Indonesia. [Description of specimens.]
- Gee, 1925. Lingnaam Agric. Rev. 3: 157; specimens from China. [Record of capture.]
- Gordon, 1935. Ann. Mag. Nat. Hist. X, 16: 629; specimens from Christmas Island, Indian Ocean. [Record of capture.]
- Arete monoceros* Paulson, 1875. Crustacea Mer Rouge. [Paper not available; Coutière, 1899: 27, states this is *Athanas monoceros* (Heller).]
- Arete mascarenicus* (Richters), 1880. (As *Athanas mascarenicus*), Beitr. Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164; Indian Ocean.
- Coutière, 1897. Bull. Mus. Hist. Nat., Paris (7): 301. [Brief remarks.]
- Coutière, 1899. Ann. Sci. Nat. VIII, Zool. 9: 33. [States this is a synonym of *A. dorsalis*.]
- Arete borradalei* Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 80; 1 specimen from the Maldive Archipelago.
- Coutière, 1905. C. R. Acad. Sci., Paris 140: 737. [Listing of specimens in the Maldive Archipelago.]
- Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 861, fig. 133. [Same specimens as in 1903 above.]
- Arete dorsalis pacificus* Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 84, figs. 31–34; found in Hong Kong, has specimens from Samoa, New Caledonia, and Central America. [Coutière (1905: 866) states this is probably *A. dorsalis* Stimpson.]
- Coutière, 1904. Bull. Mus. Hist. Nat., Paris 10(2): 58; several specimens from Marutea, Tuamotus. [Notes on commensalism; in 1905 Coutière names this form *A. maruteensis*.]
- Arete dorsalis indicus* Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 84; several specimens from Djibouti, one from the Maldive Archipelago. [Changed to *A. indicus* by Coutière (1905: 863), see below.]
- Arete maruteensis* Coutière, 1905. Bull. Mus. Hist. Nat., Paris 11(1): 18; 3 examples from

- Marutea commensal with *Heterocentrotus mammillatus*.
- Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 868. [Comparison with *A. dorsalis*.]
- Nobili, 1907. Mem. R. Accad. Torino II, 57: 353; 5 specimens from Marutea, one from Fakarawa, one from Rikitea, French Oceania. [Remarks on commensalism.]
- Arete indicus* Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 863, figs. 134, 135; one specimen from Maldive Archipelago, numerous specimens from Djibouti and 1 from Central America. [See *A. dorsalis indicus* Coutière above.]
- Nobili, 1906. Bull. Sci. Fr. Belg. 20: 24; 1 specimen from the Persian Gulf. [Partial redescription.]
- Balss, 1915. Ergebn. Zool. 30: 21; specimens from the Red Sea. [Locality only.]
- Coutière, 1921. Trans. Linn. Soc. Lond. 17(4): 413; specimens from the Indian Ocean. [Locality only.]
- Arete iphianassa* de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 312; 2 specimens from Indonesia.
- de Man, 1911. Siboga Exped. 39a¹(2): 16, pls. 3, 4, figs. 11–11e. [Same as the above with figures.]
- de Man, 1922. Siboga Exped. 39a¹(5): 22, pl. III, figs. 11–11f; 1 specimen from Indonesia. [Redescription.]
- Banner, 1956. Pacif. Sci. 10(3): 324; 6 examples from the Marianas Islands. [Locality only.]
- Arete maruteensis* Coutière var. *salibabuensis* de Man, 1910. Tijdschr. Ned. Dierk. Ver. II, 11(5): 313; 1 female from Salibabu Island, Indonesia.
- de Man, 1911. Siboga Exped. 39a¹(2): 169, fig. 13 a–c. [Same specimens as the above, with plates.]
- Arete amboinensis* de Man, 1910. Arch. Naturgesch. 76(1): 25, figs. 1–6; 1 example from Amboina.
- Arete intermedius* Yu, 1931. Bull. Mus. Hist. Nat., Paris 3(6): 513, fig. 1; one specimen from Amoy, China.
- Arete ghardaensis* Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 15, pl. 1, fig. 208; 5 specimens from the Red Sea.

Athanas AND *Arete*

According to Coutière's monograph (1899: 322 *et seq.*) the principal differences between *Athanas* and *Arete* lie in the carpus of the second legs, five-jointed in *Athanas* and four-jointed in *Arete*; in the biunguiculation of the dactylus of the third leg in *Arete*, simple in *Athanas*; and in the branchial formula, which contains only six epipodites in *Arete* and seven in *Athanas*. The other differences he cited were mostly differences in proportion, not form. ("Antennules et antennes d'*Athanas*, mais massives et courtes.") With his description of *Athanas areteformis* Coutière felt he had a specimen that showed transition between the two genera. Subsequent description of species by various authors extended the knowledge of differences in form within the two genera, especially in *Athanas*, which, for example, was found to include species with a biunguiculate dactylus.

The two genera have continued to be accepted as separate in spite of the fact that *Athanas areteformis* on one hand and *Arete borradalei* and, later, *Arete ghardaensis*, on the other hand, lie in a position somewhat intermediate between the two genera. They were still separated on the basis of the carpus of the second legs and on the branchial formula.

This is in spite of the fact that in other genera it has been recognized that the branchial formula varies within a genus, for example in *Betaeus* and *Alpheopsis*, and that the number of carpal articles of the second legs may also vary as in *Alpheopsis* and *Synalpheus*. Kemp (1915: 295) in his description of *Athanas polymorphus* reported that in his specimens the number of carpal articles varied from four to five.

In the present study, the branchial formula of *Athanas djiboutensis* was examined in 17 specimens from one locality on Canton Island, Phoenix group. Because the species is small and the branchial formula is difficult to discern, most specimens were examined on both sides. Only two of the specimens had mastigobranchs on the third thoracic appendages and the setobranchs on the fourth, the branchial formula for the genus; on the other 15 specimens the last masti-

gobranch was on the second maxilliped and the last setobranch (at least in those specimens where it was large enough to be seen) was on the third maxilliped. The two specimens with the more complete set did not differ in any other way from the specimens with the reduced branchial formula. Other specimens from Canton and from other localities were spot checked; most were found with the reduced formula, but occasional individuals carried the more complete set. Thus the more common branchial formula in *Athanas djiboutensis* is the same as that for *Arete*.

Athanas verrucosa Banner, described below, is definitely related to the species known as *Arete borradailei* and *Arete ghardaensis* in the form of the rostrum, in the form of the large chela, which is unlike those found in other species of either *Athanas* or *Arete*, and in the general configuration of the body and appendages. In fact, even the specific distinctions between these nominal species is in doubt. However, the second legs of *Arete borradailei* and *Arete ghardaensis* have the four-jointed carpus while *Athanas verrucosa* a five-jointed carpus. It would be unacceptable to place such closely related species in separate genera.

The distinctions, therefore, between *Athanas* and *Arete* have been entirely lost, and *Arete* must be regarded as a synonym of *Athanas*. Further supporting the combination of the two genera is the fact that species in both genera show parallel variation in the form of the large chela with sex and maturity.

Athanas

REDEFINITION: Alpheidae in which the rostrum is well developed; supra-, extra- and infracorneal spines usually present with varying degrees of development; corneas of eyes exposed anteriorly and largely dorsally and laterally; chelae of the first legs well developed, either carried extended or flexed against an expanded merus, usually asymmetric and sexually dimorphic, always without the cylinder and plunger characteristic of *Alpheus*; carpus of second legs with four or five articles; dactylus of third legs simple or bifid; pleura of sixth abdominal segment articulated; telson without anal tubercles, tip arcuate. Branchial formula variable.

DIAGNOSIS: The exposure of the eyes and the form of the large chela separate this genus from *Alpheus*, *Thunor*, and *Synalpheus*; the articulation of the sixth pleura from *Pterocaris*, *Automate*, *Salmoneus*, *Amphibetaeus*, *Betaeus* (in part), *Batella*, *Metabetaeus*, *Racilius*, and *Pomognathus*. The presence of a rostrum separates the genus from *Betaeus* and *Parabetaeus*, and the exposure of the eyes in dorsal view from *Alpheopsis*, *Neoalpheopsis* and *Athanopsis*. Finally the lack of high dorsal and ventral keel on the rostrum separates this genus from *Aretopsis*.

TYPE SPECIES: *Palaemon nitescens* Leach, 1814.

VARIATION IN FORM

Because previous workers usually had only a few specimens of each nominal species, most were unaware of the variation that might occur. In the present collections the following species are present in great enough numbers to at least tentatively delimit the extent of variation: *A. areteformis* Coutière, *A. parvus* de Man, *A. djiboutensis* Coutière, *A. marshallensis* Chace, *A. rhotionastes* Banner, *A. dorsalis* (Stimpson), and *A. indicus* (Coutière). Of these only one species, *A. djiboutensis*, the most widespread species both ecologically and geographically, seems to show no marked variation except in the branchial formula, as discussed above, and in the chela. In specimens of this species the form of the rostrum, the teeth about the orbits, and the legs are quite constant. The chelae do show changes in proportion with maturity and sex, but these differences are more slight than in other species. The other species all show marked variation. It is the chelae that have the greatest variation. For example, in the two closely related species, *A. marshallensis* and *A. rhotionastes*, the chelae in the females start out as slender appendages where the merus is not expanded, the palm scarcely broader than the merus, the carpus almost as long as the palm; in this condition the fingers are straight and unarmed (Fig. 2). As the individual grows larger the merus expands to accommodate the chela; the palm grows heavy, the fingers develop strong teeth, the carpus either remains the same length, shortening in relation to adjacent articles, or becomes shorter by actual measure-

ment. In the males a comparable but greater differential growth occurs, so that the fully developed male chela is much heavier than that of the female, with a broader merus and palm, a shorter carpus, and with much heavier teeth on the fingers. In *A. dorsalis* it was found that chelae of the smaller males approached the form of the more mature females, and, in one case, the chela of an extremely large female was quite similar to the normal large males (Fig. 5e). This variation was not found to be perfectly correlated with size or maturity; for example, females with a definitely "immature" type of chela were found to be ovigerous, and specimens of the same size from the same locality were found to be of varying development. On all species represented with a sufficient number of specimens this variation was observed, with only *A. djiboutensis* showing it to a more minor extent.

A variation somewhat similar to this was noted by Kemp (1915: 289 *et seq.*) for the males of his species *A. polymorphus*. He had a limited number of specimens and came to the conclusion that breeding activity, not growth, caused the polymorphism. We believe that the evidence given in the following pages indicates that the "polymorphism" must stem primarily from growth. Kemp was also unaware that his variation could be found in other species but he cautioned ". . . it is not unlikely that different forms of the same species have been described under separate names."

More perplexing is the apparent variation in the region of the anterior carapace. In the classification of the species the breadth and length of the rostrum, and the development of supra-, extra- and infracorneal teeth, have been regarded as quite constant and used for specific distinctions. However, in a group of 30 specimens of *A. dorsalis* the tip of the rostrum was found to reach from the end of the first antennular article to the middle of the third antennular article; in the same group of specimens the extracorneal teeth were usually well developed and acute, but in one they were lacking. In *A. areteformis* some specimens carried an infracorneal tooth of varying development, some did not (in three specimens from the same location two are without

teeth, the third with a small infracorneal tooth bilaterally developed).

To the contrary *A. marshallensis*, *A. rbothionastes*, and *A. djiboutensis* all present in some numbers in the collections, are quite uniform in the development of these parts. It would appear that some species are inherently more variable than others, a condition found in members of the genus *Alpheus*.

Finally, in *A. dorsalis* the development of the tooth on the merus of the third legs and the proportions of articles of this leg were also found to vary. Like species in other genera of the family, the telson also varies in its proportions.

These variations will be discussed more fully for each species in the following section.

These variations in parts previously considered to be of taxonomic importance render it difficult to decide upon a valid basis for species differentiation. A possible clue to aid systematists may be found in the ecology of the forms being considered. At least in two pairs of closely related species the most valuable clue is their environment. *A. dorsalis* appears to be usually, if not always, associated with sea urchins of the genus *Heterocentrotus*, while the closely related *A. indicus* with the sea urchins of the genus *Echinometra*; again in the closely related pair, *A. marshallensis* and *A. rbothionastes*, *A. marshallensis* appears to be found only in the silty sandy shorelines of lagoons, associated with *Alpheus strenuus* Dana (whether it is a symbiotic association or a mere ecological association is not known), while *A. rbothionastes* has been found almost exclusively on the coralline ridge of seaward reefs where it is subjected to heavy surf. This type of aid, however, is also questionable, for *A. djiboutensis* is widespread in its environments; most were collected from either the inner zone of outer reefs on islands, especially on the lee side of an island, or from somewhat similar conditions on the lagoon beaches of an atoll; some, however, were collected from near the surf line.

With so much variation, with the extent of this variation apparently inconstant from species to species, and with so many species described on the basis of one or several individuals, it is impossible to decide which species put into the

two genera should be regarded as valid. In the following key we have not combined any species for which we have no specimens. We also do not include the few non-Indo-Pacific species, but we do include those species from the Pacific that are nontropical.

KEY TO THE INDO-PACIFIC SPECIES OF
*Athanas*³

- | | | | | |
|-------|---|---------------------------------|---|------------------------------|
| 1. | Palm of large chela cylindrical or subcylindrical in section; carpus of second legs with five articles.... | 2 | Supracorneal teeth absent..... | 7 |
| | Palm of large chela flattened, definitely higher than broad in section, carpus of second legs with four or five articles..... | 22 | Dactylus of third leg biunguiculate.. | 8 |
| 2(1). | Legs of first pair, when fully developed, carried directed forward; merus short, not excavate..... | 3 | Dactylus of third leg simple..... | 9 |
| | Legs of first pair, when fully developed, with chelae carried folded against an excavate and expanded merus | 6 | 8(7). With infracorneal tooth..... | |
| 3(2). | Supracorneal teeth present..... | | <i>A. parvus</i> de Man | |
| | <i>A. areteformis</i> Coutière ⁴ | | Without infracorneal tooth or projection..... | A. jedanensis de Man |
| | Supracorneal teeth absent..... | 4 | 9(7). Carpus of first leg longer than palm in mature females..... | 10 |
| 4(3). | Dactylus of third legs biunguiculate..... | A. granti Coutière | Carpus of first legs equal in length to palm, or shorter, in mature females | 15 |
| | Dactylus of third legs simple, but may carry an articulated spinule at usual point of biunguiculation.... | 5 | 10(9). Ischium of first legs with strong distal spine..... | A. orientalis Pearson |
| 5(4). | Dactylus of third legs simple; with both extra- and infracorneal teeth | A. crosslandi Tattersall | Ischium of first legs not so armed.... | 11 |
| | Dactylus of third leg carrying an articulated spinule; with only extracorneal teeth (originally described as infracorneal teeth)..... | A. gracilis Boone | 11(10). Palm of chela in female less than 1.5 times length of fingers..... | 12 |
| 6(2). | Supracorneal teeth present..... | | Palm of chela in female 2.0 or more times length of fingers..... | 13 |
| | <i>A. djiboutensis</i> Coutière | | 12(11). Palm of chela in female shorter than fingers; stylocerite reaching to end of third antennular article; dactylus of third legs one-third length of propodus..... | |
| | | | A. setoensis Kubo | |
| | | | Palm in female equal to fingers; stylocerite reaching slightly past end of first antennular article; dactylus of third legs more than half length of propodus..... | |
| | | | A. polymorphus Kemp | |
| | | | 13(11). With extracorneal tooth strong and acute; infracorneal projection almost as long as extracorneal tooth, but rounded..... | |
| | | | A. stebbingi de Man | |
| | | | With only extracorneal tooth (or infracorneal tooth) produced and acute | 14 |
| | | | 14(13). Rostrum reaching to end of second antennular article..... | |
| | | | A. dimorphus Ortmann | |
| | | | Rostrum a little longer than antennular peduncle | |
| | | | A. monoceros (Heller) | |
| | | | 15(9). Infracorneal projection at most slight and rounded..... | 16 |
| | | | Infracorneal projection present and acute | 18 |

³ *Athanas tenuipes* de Man is omitted from the key as the type specimen, the only specimen known, lacked both legs of the first pair. Otherwise, it is characterized by five articles in the carpus of the second legs, the lack of supracorneal teeth, the presence of extra- and infracorneal teeth; its rostrum reaches to the middle of the second antennular article; and third legs and telson of slender and elongate form.

⁴ Those species whose names are in italic are discussed in this paper.

- 16(15). Rostrum reaching to end of antennular peduncle
 *A. lamellifer* Kubo
 Rostrum at most reaching to end of second antennular article, usually shorter17
- 17(16). Palm of chelae 2.5 times length of carpus, or shorter, in mature females.....*A. marshallensis* Chace
 Palm of chelae 3 to 5 times length of carpus in mature females.....
*A. rhotbionastes* Banner
- 18(15). Infracorncal tooth longer than extracorncal tooth19
 Infracorncal tooth shorter than extracorncal tooth20
- 19(18). Dorsal carina extending along anterior half of carapace and rostrum.....*A. japonicus* Kubo
 Anterior carapace without dorsal carina.....*A. esakii* Kubo
- 20(18). Dactylus of large chela of male Strongly curved, "half-moon shaped," much longer than fixed finger.....*A. oshimae* Yokoya
 Dactylus of large chela of male at most slightly curved, not "half-moon shaped," not markedly longer than fixed finger (males unknown in *A. baswelli* below).....21
- 21(20). Carpus and chelae slender in females⁵.....*A. haswelli* Coutière
 Carpus and chelae of females more robust⁵.....*A. minikoensis* Coutière
- 22(1). With well-developed supracorncal teeth 23
 Without trace of supracorncal teeth; carpus of second legs with four articles25
- 23(22). With carpus of second legs with five articles, lower portion of palm of large chela bearing numerous papillae.....
*A. verrucosus* Banner
- With carpus of second legs with four articles; lower portion of palm of large chela without papillae24
- 24(23). Ventral side of rostrum smoothly convex; base of outer flagellum with four articles; propodal spine of uropod simple.....
 *A. borradailei* (Coutière)
 Ventral side of rostrum with an obtuse angle; base of outer antennular flagellum with more than four articles; propodal spine of uropod bifid
*A. ghardaqensis* (Ramadan)
- 25(22). Rostrum reaching to middle or end of third article of antennular peduncle. Usually associated with sea urchins of the genus *Echinometra*.....*A. indicus* (Coutière)
 Rostrum not reaching past middle of second antennular article, usually only to end of first article or shorter26
- 26(25). Telson elongate, 6.5 times as long as posterior margin is broad; posterior margin one-third breadth of base. Symbiotic association, if any, unrecorded.....
 *A. amboinensis* (de Man)
 Telson less than 4 times as long as posterior margin is broad; posterior margin one-fourth to one-fifth breadth of base. Usually associated with sea urchins of the genus *Heterocentrotus*
*A. dorsalis* (Stimpson)

Athanas areteformis Coutière

Athanas nairoensis Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 77, figs. 14-16; [same description and figures in 1905, Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 859, fig. 131 a-c].

Athanas areteformis Coutière, 1903. *Op. cit.* p. 79, figs. 17-19; [same description and figures in 1905, *op. cit.*, p. 860, fig. 132 a-c].

Athanas erythraeus Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 13, pl. 1, fig. 1.

⁵ Coutière's only differentiation between these two species is as follows: "[The cheliped of *A. baswelli*] a la même forme cylindrique et grêle [as *A. dimorphus*] ce qui distingue l'espèce de l'*A. minikoensis* où la pince est beaucoup plus robuste et le carpe court." Bull. Soc. Philom. IX, 11(5): 2, 1908.

Athanas dubius Banner, 1956. *Pacif. Sci.* 10(3): 323, fig. 2a-h.

DISCUSSION: These four nominal species were all described on the basis of a few specimens, as listed in the introduction: Coutière had two females, one incomplete, for *A. naitaroensis*; one complete male and one incomplete female for *A. areteformis*; Ramadan had one female for *A. erythraeus*; I had nine specimens from Saipan. Since the original description several more specimens have been reported for *A. areteformis* (Chace, 1955: 21; Balss, 1915: 30) and for *A. naitaroensis* (de Man, 1922: 16; Barnard, 1950: 731) and no more specimens have been reported for *A. erythraeus*.

The four species were separated by various characteristics. *A. naitaroensis* differed from *A. areteformis* seemingly only in the presence of infracorneral spines (the chela of the male had never been observed). For his species, Ramadan listed a number of differences that would distinguish it from *A. areteformis*: 1. The visible portion of the first article of the antennular peduncle he stated was considerably longer than the sum of the other two in *A. areteformis* and about equal to the sum in *A. erythraeus*. Apparently this is in error, for Coutière does not state or show such a relationship, and in specimens that are plainly *A. areteformis* the relationship is as it is described for *A. erythraeus*. 2. The lateral corneal spine "is not as well developed" in *A. erythraeus* as in *A. areteformis*. 3. The chela of the female in *A. erythraeus* is like that of the male *A. areteformis* (although Ramadan's plate does not show this condition); the dactyl and fixed finger had low teeth.

A. dubius was distinguished from *A. areteformis* principally by the forms of the male and female chelae with the fingers on the male being slender and straight more like the female *A. areteformis*, and the palm on the female being broader; also the ischium on the male and female carried spines which apparently were lacking in the female *A. areteformis*.

In the present collections there are 25 specimens that can be referred to this complex; unfortunately, many of them are small or incomplete.

These specimens are found to be variable in all characteristics that have been used for the

separation of these species. The rostrum reaches from near the end of the second antennular article to the middle of the third; in some the basal portion has parallel sides, in others the rostrum has an almost uniform taper to the tip. The supracorneral teeth are well developed and acute in some, while in others they are shorter and more rounded, like the condition depicted for *A. dubius*; the cleavage between the base of the rostrum and supracorneral spines also varies in depth and definition. All but five specimens lack the infracorneral tooth; however, on these five the tooth varies from considerably smaller to larger than that depicted for *A. naitaroensis*. In the collection are three specimens from Tonga from the same location, two without teeth and the third carrying a small but definite tooth.

Similar variations can be seen in the length ratios of the antennular articles, and at least within narrow limits, in the development of the lateral spine of the scaphocerite.

In the series many of the specimens lack the chelae. The females all show the type illustrated for *A. naitaroensis* and *A. dubius*. In this appendage the merus varies from 2.5 to 3.3 times as long as broad, with the two sides showing asymmetry and the larger specimens in general with the higher ratios; the length-breadth ratio of the carpus runs from 0.7 to 1.1; the palm, 2.0 to 2.7; the palm varies from 1.3 to 1.8 times the length of the fingers. All specimens have from three to five spines on the ischium. One female of 3.3 mm. carapace length had slight teeth on the dactylus, similar to those described by Ramadan.

Of the males all specimens but one also had a chela as described for *A. dubius* and female of *A. areteformis* with a slender merus, with the length from 1.6 to 3.0 times the breadth; the carpus somewhat elongate, 0.8 to 1.0 times as long as broad; the palm from 1.4 to 2.6 times as long as broad, and the palm 1.4 to 1.8 times the length of the fingers. However, the largest of all males, with a carapace length of 3.2 mm. had the form described for the male *A. areteformis*, with short curved fingers, a heavy cylindrical palm 3.3 times the length of the fingers. This specimen came from the same collection (BE-11) as did two larger females and a small male (carapace length of 2.2 mm.) with a typically

TABLE 1
 VARIATION IN PROPORTIONS IN THE CHELAE OF *Athanas djiboutensis* COUTIÈRE

LOCALITY	SEX	CARAPACE LENGTH	SMALL CHELA					LARGE CHELA						
			Fingers	Palm	Carpus	Merus	Merus l/b	Carpus l/b	Fingers	Palm	Carpus	Merus	Merus l/b	Carpus l/l
			(in proportion to palm)					(in proportion to palm)						
Tahiti	♀	2.7 mm.	0.8	1.0	1.0	1.6	—	—	0.4	1.0	0.2	1.0	—	—
Tahiti	♀	2.7 mm.	1.0	1.0	1.4	2.0	1.6	2.3	0.5	1.0	0.2	1.2	3.0	1.2
Tonga	♀	3.0 mm.	0.8	1.0	1.1	1.8	1.7	2.7	0.4	1.0	0.2	0.9	4.0	1.7
Samoa	♀	3.0 mm.	0.7	1.0	0.9	1.5	2.7	2.0	0.4	1.0	0.2	1.2	5.0	1.6
Canton	♀	3.0 mm.	0.8	1.0	2.0	1.8	4.0	4.0	0.4	1.0	0.2	1.0	2.0	—
Samoa	♀	3.4 mm.	0.8	1.0	1.1	2.0	3.5	2.0	0.4	1.0	0.2	1.0	4.3	1.1
Tonga	♀	3.5 mm.	0.7	1.0	1.2	1.6	3.0	2.5	0.3	1.0	0.2	1.0	4.6	1.4
Tonga	♀	3.6 mm.	—	—	—	—	—	—	0.3	1.0	0.2	1.2	4.1	0.7
Samoa	♂	2.1 mm.	0.8	1.0	0.8	1.4	3.5	2.0	0.4	1.0	0.3	1.0	5.2	1.2
Tahiti	♂	2.2 mm.	0.8	1.0	0.9	1.8	3.0	1.5	0.4	1.0	0.4	1.2	3.0	1.1
Tahiti	♂	2.4 mm.	0.7	1.0	0.3	1.2	—	—	0.3	1.0	0.2	1.1	3.0	1.8
Samoa	♂	2.4 mm.	0.6	1.0	0.9	1.6	2.0	1.6	—	—	—	—	—	—
Samoa	♂	2.4 mm.	0.8	1.0	1.1	1.6	2.6	2.0	0.4	1.0	0.2	1.0	2.5	1.1
Tahiti	♂	2.4 mm.	0.8	1.0	1.0	1.6	1.3	2.5	—	—	—	—	—	—
Fiji	♂	2.5 mm.	—	—	—	—	—	—	0.4	1.0	0.3	1.2	2.2	1.0
Eniwetok	♂	2.7 mm.	0.6	1.0	0.3	1.2	2.5	1.4	0.3	1.0	0.3	1.0	2.2	1.0
Eniwetok	♂	2.7 mm.	0.6	1.0	0.6	1.8	2.6	1.6	0.4	1.0	0.3	1.0	2.1	1.0
Eniwetok	♂	2.8 mm.	0.4	1.0	0.3	1.3	3.8	1.0	0.4	1.0	0.2	1.0	2.4	1.0
Samoa	♂	2.8 mm.	0.5	1.0	0.3	1.4	2.8	1.0	0.4	1.0	0.1	1.0	2.3	1.0
Eniwetok	♂	3.1 mm.	0.4	1.0	0.3	0.9	2.4	1.0	0.2	1.0	0.1	0.8	2.9	1.0
Samoa	♂	3.2 mm.	0.5	1.0	0.2	1.3	2.3	0.9	0.3	1.0	0.3	1.1	2.0	1.5
Samoa	♂	3.4 mm.	0.5	1.0	0.2	1.5	2.6	1.0	0.3	1.0	0.2	0.9	2.1	1.1
Samoa	♂	3.6 mm.	0.6	1.0	0.2	1.3	2.3	1.0	0.3	1.0	0.2	0.9	2.1	0.9
Samoa	♂	3.9 mm.	0.6	1.0	0.3	1.3	2.4	1.4	0.3	1.0	0.2	1.0	2.2	1.2

feminine chela. This variation in the chelae is similar to that of other members of the genus.

With these variations the distinctions between the four nominal species have disappeared. As the original description of *A. areteformis* carries the description and figure of the characteristic chela of the male, we have chosen to retain that name rather than the name *A. naifaroensis*, which would have to be selected were strict page priority to be followed.

DISTRIBUTION: These specimens have been reported from South Africa, the Red Sea, the Maldivic and Laccadive Archipelagoes, and the Marianas. Specimens in the present collections were collected from various places on reef flats and fronts, lagoons, lee and windward reefs at varying depths. There is one specimen for Fiji, four from Tonga, one from British Samoa, four from the Cook Islands, three from the Society Islands, and five specimens from the Marshall Islands.

Athanas djiboutensis Coutière

Athanas djiboutensis Coutière, 1897. Bull. Mus. Hist. Nat., Paris 3 (6):233.

Athanas sulcatipes Borradaile, 1898. Proc. Zool. Soc. Lond., p. 1011, pl. 65, fig. 9.

DISCUSSION: As discussed in the introductory section this widespread and common species is quite constant in its characteristics except for the branchial formula and the growth and sexual differences of the large chela. Some minor differences in length of the rostrum are found, as was discussed for the Saipan specimens (Banner, 1956: 322).

In Table 1 below, the proportions of the male and female chelae are given for specimens taken at random from the collections and arranged according to carapace length. The changes of proportions with sex and growth are clearly shown, and the variation between specimens of nearly the same size does not appear to be from

geographical races, but variation of the type that could be found within a single population.

DISTRIBUTION: This species has been previously reported from the Red Sea, Mozambique, Maldive Archipelago, Christmas Island (Indian Ocean), Indonesia, Great Barrier Reef, Mariana Archipelago, Marshall Islands, Wake Island, Ellice Islands, Samoa, Tuamotus, and the Marquesas. In the present collections specimens are from the Caroline Islands, Marshall Islands, Phoenix Islands, Fiji, Tonga, Samoa, Cook Islands and Tahiti.

Athanas parvus de Man

Fig. 1

Athanas parvus de Man, 1910a. Tijdschr. Ned. Dierk. Ver. II, 11(2): 315. [Additional description and figures in Siboga Exped. 39a¹ (2): 148, fig. 4a-d.]

Athanas parvus de Man, Kubo, 1940b. Annot. Zool. Jap. 19(2): 99, figs. 1, 2. [Additional description.]

Athanas sibogae de Man, 1910a. Tijdschr. Ned. Dierk. Ver. II, 11(2): 314. [Additional description and figures in Siboga Exped. 39a¹ (2): 151, fig. 6a-h.]

DISCUSSION: Unfortunately, none of our eleven specimens are complete. The carapace and the intact appendages agree well with the published descriptions of *Athanas parvus*. There are the usual slight differences in proportions—for example, the merus of the third legs usually runs about 5 times as long as broad instead of 7—but these differences, like those given by Kubo, appear to be of no taxonomic importance.

One male only had a chela intact; it is not known whether this is the larger or smaller, or if they are of symmetrical development. However, as the chela of the male has never been described, it is shown in Figure 1. In it the ischium is rather long and slender; the merus is 3.4 times as long as broad, excavate along the lower margin to accommodate the chela when flexed; the carpus is short and not distally expanded; the palm is slender and tapering, 2.5 times as long as broad, without grooves or ridges; the dactylus has been broken, but the remaining portion of it and the fixed finger are quite straight and bear a series of low, conical teeth. Presumably

this is not the fully mature stage of the chela, and in this condition it resembles the chela described for *A. jedanensis* de Man.

A. parvus was previously placed into the *Nitescens* group of the genus because the chela described for the female, which may be immature, were carried extended; this male shows that its rightful position is in the *Dimorphus* group. With this differentiating character removed only very slight differences can be found between this species and *A. sibogae*. There is a slight difference in the infracorneal tooth, the chelae appear to be different and the lower unguis of the dactylus of the third leg is heavier and make a greater angle to the dactylus in this species than it does in *A. sibogae*. With the great differences in other species, especially in *A. areteformis*, in the development of the orbital teeth, and with the growth and sex differences in the chela in this genus, the first two characteristics cannot be regarded as sufficient for specific separation; the difference in development of the dactyls is so slight that that too cannot be relied upon. The two species later may be found to be distinct, but with the present knowledge of inherent variation within this

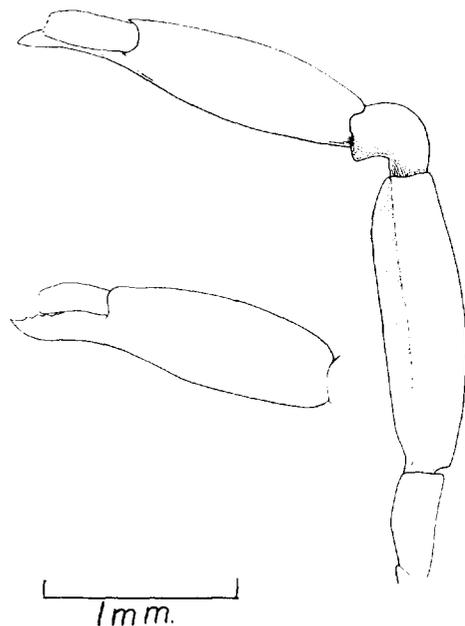


FIG. 1. *Athanas parvus* de Man. Chela of male from Samoa (BBS-10); tip of dactylus lost in specimen.

TABLE 2
VARIATIONS IN THE CHELAE OF *Athanas marshallensis* CHACE

SEX	CARAPACE LENGTH	LEFT CHELA					RIGHT CHELA						
		Fingers (in proportion to palm)	Palm	Carpus	Merus	Merus l/b	Palm l/b	Fingers (in proportion to palm)	Palm	Carpus	Merus	Merus l/b	Palm l/b
♀	3.1 mm.	0.6	1.0	1.0	1.4	4.0	2.7	0.5	1.0	1.1	1.5	3.7	2.5
♀	3.5 mm.	0.5	1.0	0.8	1.2	3.8	3.0	0.4	1.0	0.6	1.2	3.8	3.6
♀	3.6 mm.	0.5	1.0	1.0	1.4	4.0	3.4	0.4	1.0	0.6	1.2	4.0	3.3
♀	3.7 mm.	0.3	1.0	0.9	1.3	4.5	3.5	0.3	1.0	0.8	1.3	3.8	2.8
♀	4.5 mm.	0.3	1.0	0.4	1.0	3.0	3.0	0.3	1.0	0.6	1.1	3.3	3.7
♀	4.6 mm.	0.4	1.0	0.8	1.4	3.5	3.1	0.3	1.0	0.6	1.2	3.2	3.4
♀	5.2 mm.	0.4	1.0	0.4	1.1	3.3	3.1	0.4	1.0	0.4	0.9	3.0	3.2
♂	4.3 mm.	0.3	1.0	0.2	0.9	3.0	2.7	0.2	1.0	0.2	0.9	2.8	3.0
♂	4.6 mm.	0.2	1.0	0.2	0.9	2.5	3.0	0.2	1.0	0.2	0.9	2.5	3.0
♂	5.3 mm.	0.3	1.0	0.3	1.0	2.7	2.3	0.3	1.0	0.2	0.9	2.5	3.2

genus, it appears wiser to place *A. sibogae* in synonymy.

Indeed, *A. jedanensis* may also be found to be a synonym. In this species the chief distinction, when the differences in the chelae are ruled out, is the absence of the infracorneal spine. If this is variable, as it is in *A. areteformis*, then there is but one species. However, as in this small collection no transitional forms were found, *A. jedanensis* has been retained.

DISTRIBUTION: *A. parvus* has been reported from the type locality, in Indonesia, and from southern Japan; *A. sibogae* only from Indonesia. Specimens in the present collections came from various places on the reef flats in from 1 to 6 feet of water and were largely from dead coral heads. There were seven specimens from Tonga, and four from Samoa.

Athanas marshallensis Chace

Fig. 2

Athanas marshallensis Chace, 1955. Proc. U. S. Nat. Mus. 105(3349): 17-20, fig. 8.

DISCUSSION: All the 11 specimens available were collected in a single narrow habitat at Eniwetok, Marshall Islands, under loose coral boulders resting on a sandy substrate in the intertidal zone where they were collected together with *Alpheus strenuus* Dana, *Salmonens tricristatus* Banner, and *S. sibogae* (de Man). It is noteworthy that in similar habitats in other

archipelagoes producing widespread *A. strenuus* this species was not collected; all specimens known have been collected solely from the northern Marshall Islands.

In this series of specimens the usual changes in form of the chelae with size and sex are found. Table 2 gives the changes in proportion with size of all specimens collected; Figure 2*b-d* shows the changes with growth in the female and the chela of a mature male for contrast. The proportions show that the chelae of the large male are quite symmetrical; it is possible that the chelae of very large females, larger than those represented in the collection, may also become symmetrical.

The differences between this species and *A. rhotbionastes* Banner are discussed under the latter species. This species may prove to be a synonym of *A. esakii* Kubo but at present the two forms appear to be distinct; this is discussed under *A. esakii*.

DISTRIBUTION: As stated above all specimens of this species have been collected from the northern Marshall Islands.

Athanas rhotbionastes sp. nov.

Fig. 3

TYPE SPECIMENS: Holotype, a 12 mm. (4.8 mm. carapace length) ovigerous female; allotype, a male of the same size; paratypes from the same locality, at end of surge channels, edge of reef front, leeward (western) side, Canton

Island, Phoenix group, collected by A. H. Banner 1 March 1954. Additional specimens from Eniwetok, Vitilevu, Tongatabu, Opolu, Tutuila, Aitutake, and Tahiti, all from surf zone on reef fronts except for one specimen from the lagoon at Eniwetok (BE-2); this, however, must have been subject to surge for it came from the base of *Pocillopora meandrina* Verrill, a coral that never lives in still waters.

DESCRIPTION: Rostrum acute with sides of uniform taper or with slight "jog" in lateral margins anterior to eyes; tip reaching to middle of second antennular article; slight carina in anterior half. Supracorneal teeth lacking; extra-corneal teeth acute, reaching almost to end of corneas; infracorneal projection short and rounded; pterygostomial corner rounded. Corneas of eyes concealed in posterior portion and laterally by extra- and infracorneal projections.

Antennular peduncle short and heavy, with first, second and third articles subequal in length, second article as broad as long. Stylocerite long, lanceolate, tip reaching to near end of third antennular article. Scaphocerite broad and long, tip reaching beyond end of antennular peduncle; lateral spine strong, slightly exceeding squamous portion in length. Basicerite unarmed. Carpoperite reaching about to end of antennular peduncle.

Chelae of large female symmetrical. Ischium bearing four strong spines on superior margin. Merus 3.2 times as long as broad, unarmed; superior external and internal surfaces smooth and flat; inferior surface deeply excavate to accommodate propodus, short, 0.2 to 0.3 length of palm (depending upon place measured), normally greatly flexed. Palm subcylindrical, 3.5 times as long as broad, equal in length to merus, tapering slightly towards fingers; dactylus curved, one-quarter as long as palm with irregular, large rounded teeth matching exactly with teeth on fixed finger. Chelae in allotype of same carapace length considerably larger and slightly asymmetrical with the right almost 10 per cent larger than the left; in both male chelae, merus and palm are markedly thicker than those of the female. Armature of fingers poorly developed in smaller chela; on large chela fixed finger bearing single large rounded tooth and smaller tooth proximally, dactylus bearing two teeth in

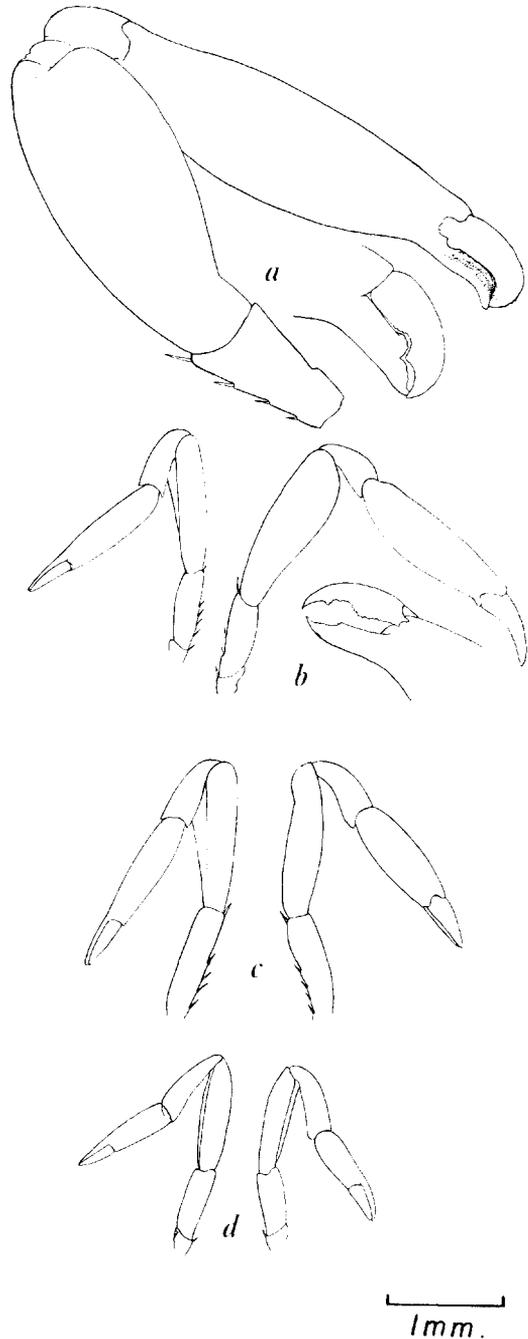


FIG. 2. *Athanas marshallensis* Chace. Chelipeds of various individuals from Eniwetok. a, 4.6 mm. ♂; b, 4.5 mm. ♀; c, 3.7 mm. ♀; d, 3.1 mm. ♀. (All to same scale.)

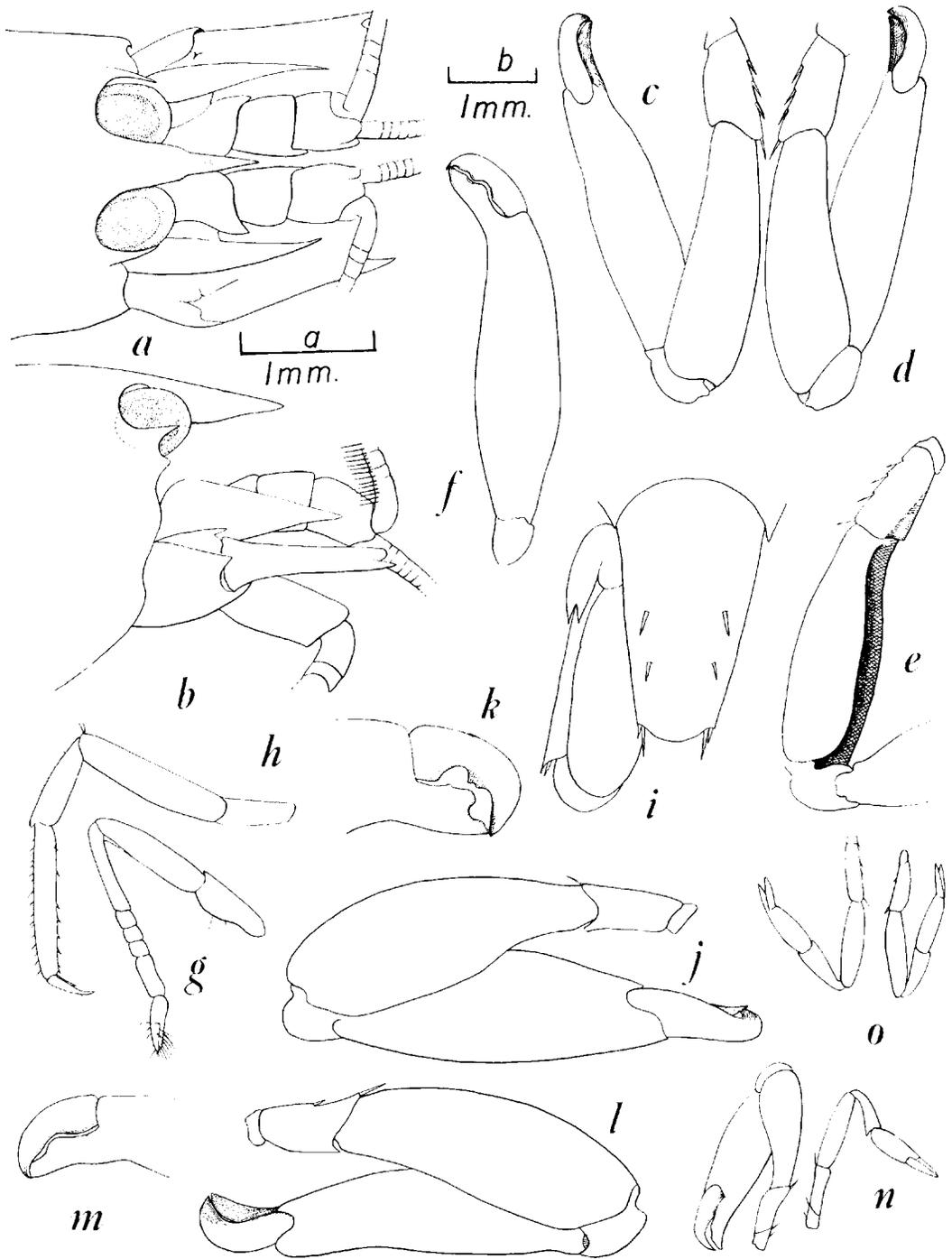


TABLE 3
 VARIATION IN THE CHELIPEDS OF *Athanas rhotbionastes* SP. NOV.

LOCALITY	SEX	CARAPACE LENGTH	SMALL CHELA						LARGE CHELA							
			Fingers (in proportion to palm)	Palm	Carpus	Merus	Palm l/b	Carpus l/b	Merus l/b	Fingers (in proportion to palm)	Palm	Carpus	Merus	Palm l/b	Carpus l/b	Merus l/b
Tahiti	♀	2.8 mm.	0.5	1.0	1.6	1.4	2.7	2.5	3.2	0.4	1.0	0.2	0.8	2.7	1.2	2.8
Tahiti	♀	3.2 mm.	0.3	1.0	0.2	1.0	2.6	1.3	2.5	0.4	1.0	0.2	0.8	2.7	1.2	2.5
Tahiti	♀	3.4 mm.	—	—	—	—	—	—	—	0.4	1.0	0.2	1.0	2.8	1.5	2.8
Canton	♀	3.8 mm.	0.3	1.0	0.2	0.8	2.9	1.2	2.8	0.4	1.0	0.2	1.0	3.1	1.4	3.2
Canton	♀	3.9 mm.	0.3	1.0	0.2	0.8	3.0	1.3	3.0	0.3	1.0	0.2	0.9	2.8	1.1	3.6
Eniwetok	♀	4.1 mm.	0.4	1.0	0.2	0.9	2.7	1.4	2.9	0.5	1.0	0.2	0.9	2.6	1.5	2.7
Canton	♀	4.3 mm.	0.4	1.0	0.2	1.0	2.7	1.3	2.7	—	—	—	—	—	—	—
Canton	♀	4.5 mm.	0.4	1.0	0.3	1.1	2.6	1.8	2.8	—	—	—	—	—	—	—
Samoa	♂	2.7 mm.	—	—	—	—	—	—	—	0.4	1.0	0.3	1.1	2.8	1.8	3.2
Tahiti	♂	2.8 mm.	0.3	1.0	0.3	1.0	3.0	1.5	2.7	0.4	1.0	0.2	0.9	2.5	1.0	2.5
Fiji	♂	3.2 mm.	—	—	—	—	—	—	—	0.2	1.0	0.2	0.9	3.0	1.6	2.4
Tonga	♂	3.4 mm.	0.3	1.0	0.2	0.9	2.9	1.6	2.6	0.3	1.0	0.2	0.9	2.6	1.6	2.9
Canton	♂	3.4 mm.	0.4	1.0	0.2	1.0	2.8	1.5	3.3	0.3	1.0	0.2	0.9	2.9	1.3	2.5
Tahiti	♂	3.5 mm.	0.3	1.0	0.1	0.9	3.2	1.6	3.0	—	—	—	—	—	—	—
Tahiti	♂	3.7 mm.	0.3	1.0	0.2	1.1	2.7	1.0	2.9	0.3	1.0	0.2	1.0	3.1	1.2	2.8
Canton	♂	4.2 mm.	—	—	—	—	—	—	—	0.2	1.0	0.2	0.9	3.1	1.0	2.1
Canton	♂	4.3 mm.	0.3	1.0	0.2	1.0	3.0	1.5	2.4	0.3	1.0	0.2	0.9	2.5	0.9	2.4

opposition to large tooth (evidently these are thin and used for cutting as they slide past each other).

Carpal articles of second leg with ratio: 10: 1: 1: 1: 5.

Ischium of third legs unarmed, 0.4 as long as merus; merus unarmed, 5 times as long as broad; superior distal margin of carpus projecting but rounded, carpus 0.5 as long as merus; propodus 0.9 as long as merus, armed with scattered spines along inferior margin; dactylus slender, slightly curved, acute and simple, and 0.3 as long as propodus.

Telson 3.3 times as long as broad distally, twice as broad proximally as distally; lateral margins with uniform taper; tip broadly arcuate; dorsal and terminal spinules normal. Uropods longer than telson, outer uropod armed with tooth and movable spine at articulation.

Color in life not noted.

DISCUSSION: Variation in this series of speci-

mens has been carefully studied to determine if they are distinct from closely related species. The rostrum is always acute, almost always tapering, although there are a few with straight parallel sides in the proximal third to half; the tip reaches from the middle to the end of the second antennular article except for a very small specimen from Samoa, where the tip reaches to the middle of the third antennular article. In many, the rostrum appears more narrow than in the holotype and often has a slight upturn towards the tip when seen in side view. Likewise, with few exceptions, the extra- and infracorneal projections are quite uniform; in the small specimens from Samoa assigned to this species the infracorneal tooth is almost acute; in one from the type locality the extracorneal tooth is bifid on one side and with the infracorneal projection rounded but on the other side in the same specimen the upper tooth is normal and the infracorneal tooth is acute.

FIG. 3. *Athanas rhotbionastes* Banner. Holotype (female) a-i; allotype j-m. a, b. Anterior region; c, d, e, f. chelipeds; f, interior lateral surface of chelae; g, second leg; h, third leg; i, telson; j, k. large cheliped and fingers; l, m. small cheliped and fingers; n, large and small chelae of 2.7 mm. (carapace length) ovigerous female from Tahiti (BD-2); o. same from 3.0 mm. ovigerous female from Eniwetok (BE-4). (Anterior body region and telson, scale a; all other appendages scale b.)

The proportions of the chelipeds are given in Table 3. The 2.7 mm. female from Tahiti with the asymmetrical chela (Fig. 3*n*) is almost certain to belong to this species, for it was collected with larger specimens of the species with normal chelae. There may be some question about the 3.0 mm. female from Eniwetok (Fig. 3*o*) for it was collected alone and its rostrum had been broken. However, as its chelae could represent an earlier stage of development, as it agrees with the species on other characteristics, and as it was collected from the typical habitat of this species, we believe we can safely assume it to belong to *A. rhotbionastes*. The development of ischial spines of the chelipeds appears to be variable.

If these two smallest specimens given in the table do belong to this species, then here again we have the variation on the chelipeds with age and sex that seems to be characteristic of so many species of this genus. The degree of uniformity in the rostrum and corneal spines casts some doubt upon the uniting of species like *A. naifaroensis* and *A. areteformis* (see previous sections).

A. rhotbionastes is closely related, morphologically, to two species, *A. lamellifer* Kubo and *A. marshallensis* Chace. This group of species of the Dimorphus group are characterized by the lack of supracorneal teeth, acute extracorneal teeth, rounded infracorneal teeth, with the palm definitely longer than the carpus in mature females, and with simple dactyli of the third legs. The distinction between this species and *A. lamellifer* is fine and questionable, for the chief differences lie in the length of the rostrum, which exceeds the length of the antennular peduncle in *A. lamellifer* and usually reaches only to the end of the second antennular article in *A. rhotbionastes*, and in the armature of the fingers of the large chela of the male, bearing merely setae in Kubo's species and bearing heavy teeth and setae in this species. The ischium of the cheliped of *A. rhotbionastes* appears consistently longer than that reported by Kubo. The carpus of the cheliped is consistently longer in *A. marshallensis* than in *A. rhotbionastes* in the immature stages and in the fully developed females; there are no obvious differences between the males of the two species.

Possibly better than the morphological differentiation between the three species would be the ecological differences. *A. rhotbionastes* so far as had been collected always occurs in regions of surge or heavy surf on coral reefs, usually on the outermost reef fronts in the coralline ridge and near the end of the surge channels; *A. lamellifer* has been reported only from the colder waters of Tokyo Bay (Tiba Prefecture of Kubo is now transliterated Chika) under stones on a muddy shore, and while there was nothing in the original listing for *A. marshallensis* that would indicate ecology, all specimens I have collected from Eniwetok, the type locality, came from under rocks on a sandy bottom in a somewhat protected cove on the lagoon side of one of the islets.

The specific name is derived from the Greek *rhotbion*, meaning breakers or surf, and *nastes*, meaning inhabitant.

Athanas esakii Kubo

Athanas esakii Kubo, 1940a. J. Fish. Inst. Tokyo 34(1): 93-95, fig. 13*a-p*.

DISCUSSION: This small and obviously immature specimen was collected with numerous and larger specimens of *A. marshallensis* Chace apparently in a single ecological niche. On the basis of ecology, therefore, the separation of the two species is doubtful.

The specimen appears to be distinct from *A. marshallensis* only in the presence of an acute infracorneal tooth, all traces of which are lacking in *A. marshallensis*. While this characteristic does not appear to be reliable in other species of this genus, as in *A. areteformis*, the lack of intergrading specimens would make the placement of *A. marshallensis* in synonymy at this time a questionable step.

The chelae of this specimen are not exactly like either *A. marshallensis* nor *A. esakii*, but sufficiently close to both that the differences could easily be the result of immaturity. In this specimen the chelae have the following proportions:

	Merus	Carpus	Palm	Fingers
Smaller chela	1.5	1.0	1.0	0.6
Larger chela	1.3	0.8	1.0	0.5

Kubo reported that in his female specimen, somewhat larger than this, the chelae were noticeably asymmetrical; in this specimen the chelae were almost the same size.

DISTRIBUTION: Kubo's specimens came from Kusaie in the Caroline Islands while our specimen came from Eniwetok and was found under a boulder in the sand on the lagoon side of an islet.

Athanas verrucosus sp. nov.

Fig. 4

TYPE SPECIMEN: An ovigerous female, carapace length of 3.9 mm., total length of 11 mm., collected from coralline ridge, ocean (windward) reef, Parry Island, Eniwetok, 3 March 1957, by A. H. Banner (station BE-23). Sole specimen known.

DESCRIPTION: Body form usual. Rostrum short, reaching about to end of first antennular article; acute in dorsal view, triangular with straight sides; in lateral view with dorsal margin curved upward towards tip, ventral margin with double curve and bearing small tuft of setae; rostrum and carapace without carina. Supracorneal teeth distinct, acute, reaching almost to end of cornea; extracorneal teeth larger, exceeding length of cornea; infracorneal projection absent. Corneas covered posteriorly by collar between supra- and extracorneal teeth. Pterygostomial corner projecting but rounded.

Antennular peduncle short and heavy, with second article almost twice as long as broad. Superior distal margins of first and second articles each armed with four strong teeth. Stylocerite narrow, with tip reaching to near end of second article. Upper flagellum with only trace of bifurcation. Antennal peduncle also heavy. Basicerite thick, lateral region projecting as a broad tooth, bearing broadly acute tip. Carpo-cerite very heavy, only 1.5 times as long as broad, and 1.3 times broader than thick; tip reaching beyond end of antennular peduncle. Scaphocerite with tip of lateral spine reaching slightly beyond end of antennular peduncle, squamous portion broad and rounded, almost as long as lateral spine. Antennal flagellum reaching posteriorly to end of second abdominal segment.

Mouth parts protruding as those in *A. paragracilis* Coutière and *A. huikau* Banner with in-

flated labrum and with psalidome of mandibles expanded and almost hemispherical; teeth on psalidome small and numerous.

Chelipeds symmetrical except for 10 per cent difference in size. Ischium heavy, 0.7 length of merus, bearing five to six movable spines on inferior, three on superior margin. Merus compressed, triangular in section, with inferior surface flat and less broad than sides; outer face 1.5 times as long as broad at maximum breadth. Carpus 0.8 as long as merus, proximally very thin and narrow, distally greatly expanded to be 0.5 as broad as long; triangular in section; distal margins slightly projecting to cover base of chela. Chela short, 1.8 times length of merus, flattened, with thickness 0.5 of maximum breadth; inner face flattened, outer face convex; suboval area of outer face running from base to articulation of flattened dactylus; area distally delimited on inferior side by rounded shoulder; triangular area of lower distal margin of palm and proximal portion of finger armed by strongly projecting papillae, those best developed longer than broad at base and turned distally; setae arising between bases of papillae; inner face without papillae. Dactylus 0.4 as long as palm, curved, crossing tips with fixed finger, armed with two low rounded teeth fitting exactly with cutting edge of fixed finger.

Second legs markedly shorter than third legs, with length from meral-carpal articulation equal to combined lengths of ischium and merus. First and fifth carpal articles subequal; second, third, fourth articles subequal, each about 0.4 length of first or fifth article; first carpal article proximally narrow, about half width of fifth article.

Third legs robust. Ischium unarmed, 0.5 length of merus. Merus unarmed, 0.4 as broad as long. Carpus armed distally on superior margin with rounded tooth, on inferior margin with subterminal movable spine; almost 0.6 as long as merus, slightly more than half as broad as merus. Propodus at most slightly longer than merus, slightly curved, with five inferior and one distal spines; spines leaving middle portion of propodus unarmed. Dactylus curved, acute, simple, bearing tuft of setae. Fourth legs similar but with spines of propodus more continuous in arrangement. Fifth legs with only three inferior spines on propodus; "brush" feebly de-

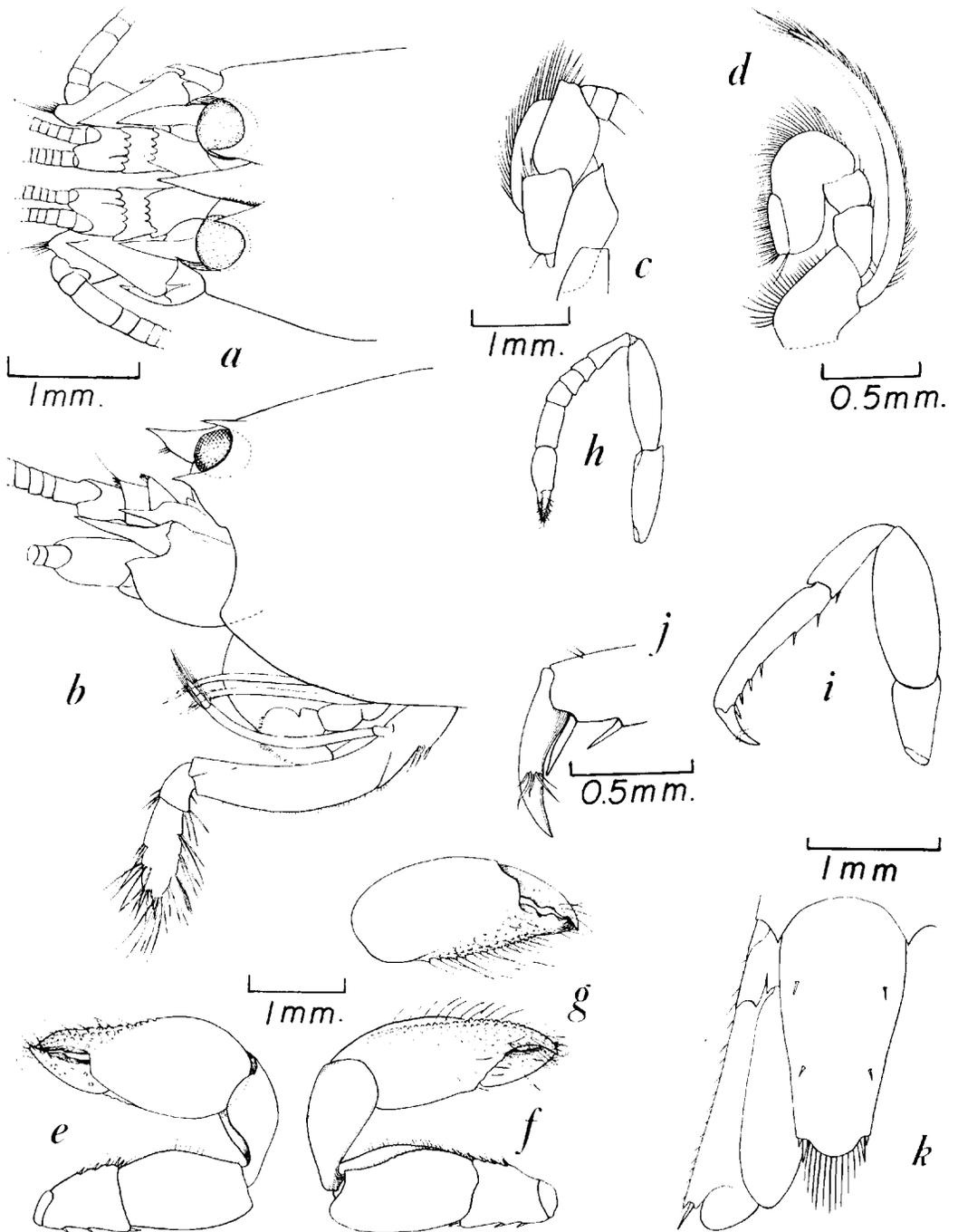


FIG. 4. *Athanas verrucosus* Banner. *a, b*. Anterior body region; *c*. antennal peduncle, inferior aspect, in situ; *d*. second maxilliped; *e*. smaller cheliped, lateral view; *f*. smaller cheliped, medial view; *g*. smaller chela, outer face, viewed flat; *h*. second legs; *i, j*. third leg and dactylus; *k*. telson and uropods.

veloped, with only three rows of light setae found distally.

Abdomen normal except anterior pleura greatly expanded, posterior pleura small; pleura of sixth segment articulated. Telson normal, sides almost straight, tapering, 2.2 times as broad anteriorly as posteriorly, 4 times as long as broad posteriorly; tip extended and rounded. Uropods normal, narrow and long.

Branchial formula including five pleuro-branches, no arthrobranches, and mastigobran-ches extending back to second thoracic leg, seto-branches to third. No anal tubercles.

DISCUSSION: In the old genus *Athanas* this species is closely related to none; in the old genus *Arete*, now united with *Athanas*, this species is most closely related to *A. borradailei* (Coutière, 1903: 9) and *A. ghardaqensis* (Ramadan, 1936: 15). From both of these species it is separated by the five-jointed carpus and the presence of papillae on the palm. The difference in the chelae could be from growth or sexual dimorphism. A point for point comparison reveals other more minor differences. This species differs from *A. ghardaqensis* by a greater number of articulations in the base of the inner flagellum, by the presence of a small tooth on the basicerite, and by longer uropods. From *A. borradailei*, this species is distinguished by: 1. A more sinuate lower margin of the rostrum and a triangular shape (when seen in dorsal view); 2. the presence of serrations on the distal ends of the antennular articles; 3. the presence of many articulations in the antennular flagellum; 4. slight differences in the last article of the external maxilliped; 5. on the chelipeds, the presence of spines on the ischium, and slight differences in the proportions of the merus and carpus in addition to the presence of papillae on the palm; 6. a broader merus of the third legs, being less than 2.5 times as long as broad instead of three times. Also *A. borradailei* is reported to lack all thoracic epipodites, while this species has masigobran-ches on the base of the chela and second legs. Neither Coutière nor Ramadan discussed the mouthparts.

Each of these three species were described on the basis of a single individual. While the differences listed above, especially in the carpus of the second legs, the chelae and the branchial

formulae may be valid for their separation, the three specimens are so similar in general configuration and in the structure of the appendages and rostral front that their specific separation is very doubtful, particularly in view of the variation in other species of this genus. However, with only one specimen of each nominal species, it appears to be safest to leave them as separate species.

The name *verrucosus* refers to the "warty" condition of the palm of the large chela, a character in which this species appears to differ from both related species.

Athanas indicus (Coutière)

Arete dorsalis var. *indicus* Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 85.

Arete indicus Coutière, 1905b. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 863, figs. 134-135.

Arete iphianassa de Man, 1910a. Tijdschr. Ned. Dierk. Ver. II, 11(4): 312; 1911, Siboga Exped. 39a¹(2): 164, pls. 3, 4, fig. 11; 1922, Siboga Exped. 39a⁴(5): 22, pl. 3, fig. 11.

——— Banner, 1956. Pacif. Sci. 10(3): 325.

Arete intermedius Yu, 1931. Bull. Mus. Hist. Nat., Paris II, 3(6): 513-514, fig. 1.

Arete kominatoensis Kubo, 1942. Dobutsugaku Zasshi [Zool. Mag., Tokyo] 54: 82-85, figs. 1, 2.

DISCUSSION: The habitat of 15 of 16 specimens from Aitutake was carefully observed while the collections were made. They came from the inner, but growing, portion of a windward reef, in a pool about six feet deep; every specimen was associated with the boring sea urchin, *Echinometra*, and were found both on the body of the urchin between the spines and within the smooth rounded cavity produced by the urchin. While most of the other specimens were not as carefully observed during their collection, the ones that were noted (as from Eniwetok) were so associated. Evidently, not all individual specimens of *Echinometra* have shrimp in association, for *Echinometra* was frequently encountered while collecting and the shrimp are quite uncommon in the collection.

For the following discussion of variation within the species, it was considered best to

study a single population thereby ruling out differences that might be caused by ecological or geographic races. For this reason the 15 specimens from Aitutake were studied intensively and those from other archipelagoes were used merely as supplements to the study.

Four species closely related to *A. indicus* have been described: *A. iphianassa* de Man, *A. amboinensis* de Man, *A. intermedius* Yu, and *A. kominatoensis* Kubo (all save the last described under the genus *Arete*). Of these, only *A. amboinensis* appears to be distinct; it will be discussed under *A. dorsalis* in the following section.

de Man stated that his species *A. iphianassa* was similar to *A. indicus*, but could be distinguished by the characteristics compared in the accompanying tabulation.

In this series of specimens each of the criteria is either bridged or almost bridged:

1. The length of the extracorneal spines varies both in absolute length and in length relative to the eyes; both described conditions were found in this single series.

2. The basal portion of the outer antennular flagellum is found to vary from four to six articles, with most having four or five articles.

3. The carpocerite is found to vary in the length-breadth relationship from 1:1.5 to 1:2.7; some of this may be due to different rotation of the carpocerite itself.

4. The outer distal margin of the outer uropod may be either straight or curved outward near the tip; all of the males have straight margins, but not all of the females have curved margins.

5. Similar to the condition discussed in the

next section for *A. dorsalis*, the females and the smaller males have straight cutting edges of their large and small chelae; however, the two intact large males have teeth developed, one with a single tooth on the fixed finger, none on the dactylus, the other with two teeth on the fixed finger and one on the dactylus.

6. The proportions of the carpal articles of the second legs are extremely variable, with the first article varying from 1.4 to 3.0 times as long as broad distally; in some, also, the first article is approximately equal in length to the sum of the following carpal articles, in others it is almost twice as long.

7. The spines on the propodus of the third legs vary in number from four to nine, and also in development, with some scarcely more than slight hairs, and others strong and well developed.

Also like *A. dorsalis* the development of the rostrum varies conspicuously. In one specimen the tip reaches beyond the end of the third antennular article, in four it reaches some distance along the third article, in eight it reached somewhere in the length of the second article (most to near the tip of the article) and in one it reaches only to the end of the first article.

The other specimens in the collections available, including those reported from Saipan as *Arete iphianassa* (Banner, 1956: 325), fall within the range of variation reported above with the exception of three fragmentary specimens from Canton Island. These three, unfortunately mostly without legs and with but two chelae among them, all have slightly different

A. iphianassa

1. Extracorneal spines equal in length to the eyes.
2. Four articles on basal portions of outer antennular flagellum.
3. Carpocerite 1.5 times as long as broad.
4. Outer distal margin of outer uropod straight.
5. Various minor proportions of the large chelae, but principally with that of the male bearing 2 teeth on the dactylus and one on fixed finger.
6. Various proportions in second leg, but most conspicuous in the first article of the carpus which is 5 times as long as broad distally.
7. Propodus of third legs bearing 8 to 12 spines.

A. indicus

1. Extracorneal spines slightly longer than the eyes.
2. Six articles in same.
3. Carpocerite 3.0 times as long as broad.
4. Outer distal margin of outer uropod curved outward.
5. Fixed finger of large chela of male bearing 1 tooth, dactylus curved but unarmed.
6. First carpal article 3 times as long as broad distally.
7. Propodus of third legs bearing two to three spines.

rostrums: while its tip reaches to near the end of the second antennular article, well within the range specified above, it was considerably broader and thicker. Possibly more important, however, is the fact that the stylocerite also reaches only to the end of the second antennular article, instead of to the end of the third, a condition found in no other specimens. It may well be that these represent a new species or geographic or ecological subspecies, but with only three specimens, all in very bad condition, it is impossible to decide with certainty.

The other two nominal species also fall well within the range of variation. *A. intermedius* was separated by Yu from *A. indicus* by a slightly longer rostrum, reaching to one-quarter of the length of the third antennular article, and by the presence of 12 spinules on the propodus of the third leg. As shown in the listing above, both of these characteristics are very variable, and the separation of *A. intermedius* seems without basis.

There is more doubt about the combination of *A. kominatoensis* with this species. Unfortunately Kubo did not contrast his species to *Arete*, where it belonged under the old classification (it has only four articles in the carpus of the second leg) but to *Athanas*. By contrasting the description and figures of Kubo with *A. indicus* the three differences are found: 1. The antennular peduncle is 2.2 times as long as broad instead of 3.0 (using the entire visible length of the peduncle divided by the breadth of the second article). 2. Kubo reports and shows a slight dorsal carina extending back to the middle of the carapace, while in *A. indicus* there is no true carina but rather a broad ridge terminating slightly behind the eyes. 3. The inferior margin of the merus of the third legs bears distally a slight tooth while in *A. indicus* it bears a strong tooth. It may be that these are valid criteria, especially the proportions of the antennular peduncle and dorsal carina—the development of the tooth on the third leg has been shown to be variable in the related *A. dorsalis*—and none of the specimens available closely approach the condition described by Kubo. However, in view of the wide variation already reported in this species and in *A. dorsalis* these seem to be questionable characteristics for a specific separation,

yet it may be this form, being found as it is in the waters of southern Japan, is a separate subspecies.

DISTRIBUTION: This species has been reported from Djibouti, Maldives and Laccadives, Indonesia, China, and southern Japan. In the present collection we have specimens from Canton, Aitutake, Bora Bora, and the northern Marshall Islands. They were found in heads of dead coral and associated with the boring sea urchin *Echinometra*.

Athanas dorsalis (Stimpson)

Figs. 5, 6

Arete dorsalis Stimpson, 1861. Proc. Acad. Nat. Sci. Philad. 12: 32.

(?) *Athanas mascarinicus* Richters, 1880. Beitr. Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164.

Arete dorsalis var. *pacificus* Coutière, 1903. Bull. Soc. Philom. Paris IX, 5(2): 87, figs. 31–34.

Arete maruteensis Coutière, 1905a. Bull. Mus. Hist. Nat., Paris 11(1): 19, figs. 1–6.

Arete maruteensis var. *salibabuensis* de Man, 1910a. Tijdschr. Ned. Dierk. Ver. II, 11(4): 313; 1911, Siboga Exped. 39a¹(2): 169, pl. 4, fig. 13.

DISCUSSION: To determine the validity of the separation of the three species and subspecies listed above, the specimens in the collection, especially a single collection of about 50 from Namu Island, Marshalls (Station 3167, J. E. P. Morrison), were examined closely. Of these specimens from a single locality, about 30 intact specimens were measured, and the findings confirmed by examination of the specimens from other parts of the Pacific.

Rostrum: In general the form of the rostrum is anteriorly a sharp triangle with an acute tip, while between the eyes the sides approach a parallel condition. In most the tip of the rostrum reaches to the end of the first antennular article or to the first half of the second article; in three specimens it reaches well into the second half of this article, and in one it reaches the beginning of the third article. In most cases it is between 1.6 to 2.1 times as long as broad.

Extracorneal Teeth: In most these are well developed, but to varying degree, and there is

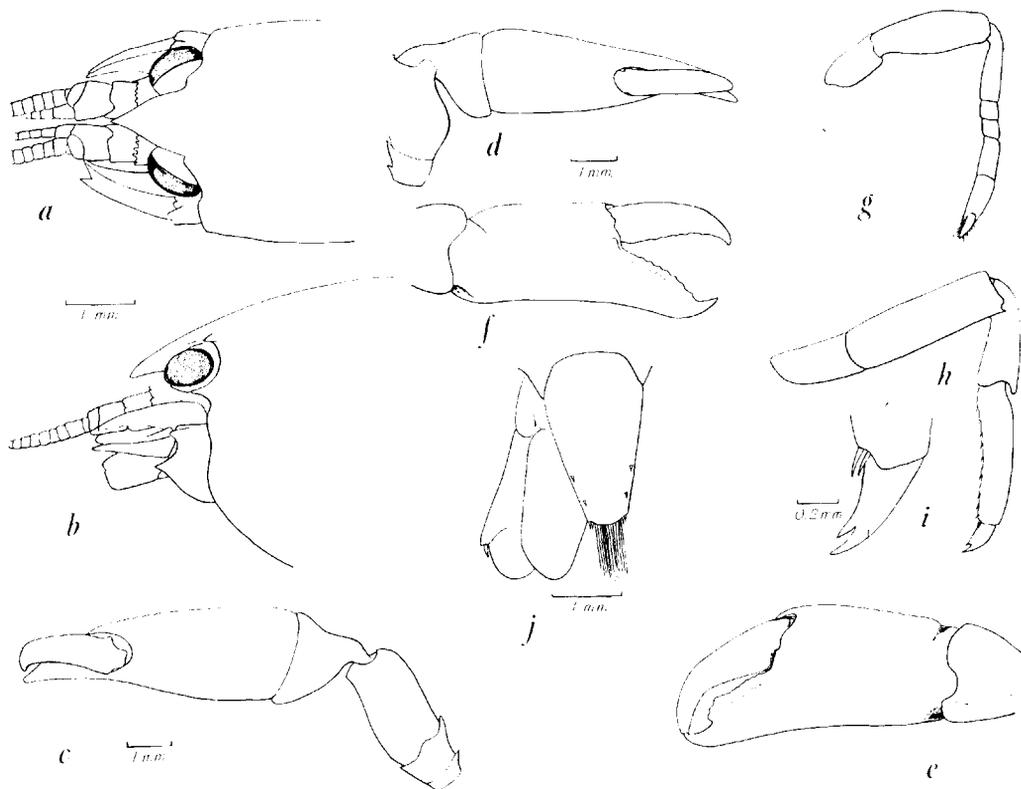


FIG. 5. *Athanas dorsalis* (Stimpson), a 5.5 mm. (carapace length) ovigerous female from Raroia, Tuamotus, Station 1847. *a, b*, Anterior region, dorsal and lateral aspects; *c, d*, large and small chelae, lateral view; *e, f*, same, from lower side; *g*, second leg; *h*, third leg; *i*, third leg, dactylus; *j*, telson and uropod.

a gradual series from those with pronounced teeth to the few with very slight teeth and to the one specimen (from the Tuamotus) without any teeth.

Antennular and Antennal Peduncles: Usually the stylocerite reaches to near the end of the antennular peduncle, the scaphocerite and carpo-cerite exceeding the stylocerite slightly; in no case are the differences in length pronounced, and at times the relationships change.

Large Chela: This appendage is found to exhibit strong growth and sexual differences (see Fig. 6*a-f*), with the young of both sexes showing a more or less uniform taper to the fingers which bear minute serrations on the basal two-thirds and the distal third being smoothly rounded to the curved tip. In adult females there is commonly an outgrowth of an irregular lobe proximal to the distal curve on the larger chela,

while the other chela remains more like that found in the young. In some of the largest males the large chela has developed an exceedingly large tooth on the fixed finger, against which the dactylus closes; however, in other large males and in all smaller males this tooth is variously developed and much smaller. In both sexes the development of the chelae varies considerably between individuals of the same size, and in one very large ovigerous female the tooth of the fixed finger is as fully developed as that of the large male.

Small Chela: In most specimens, male and female, the cutting edge of the finger bears numerous low irregularities which stop abruptly in a tooth that may be obtuse or a right angle. The distal portion is curved. However, in some the irregularities are considerably smoothed, and the final tooth may be low and rounded.

Second Legs: In the merus the length-breadth ratio varies from 1:2.5 to 1:3.7, with most of the specimens bearing the ratio between 1:2.8 to 3.0. Only in a small series the relative lengths of the carpal articles and hand were measured, and these show that the extent of variation is similar to that of the merus.

Third Legs: Three characteristics of the third legs have been carefully observed: the length-breadth ratio of the merus varies from 1:2.5 to 1:3.4, with most of the specimens with the ratio between 1:2.9 to 3.1. The final outer tooth of the inferior margin in no specimen is large and no specimen is lacking, with the maximal development being about that shown in Figure 5*b*, while in the minimal development the tooth is barely visible, and is scarcely more than an obtuse irregularity; it also varies from slightly acute to obtuse. The length-breadth ratio of the propodus exhibits less variation than do the other measured articles, ranging from 1:4.0 to 1:4.6, with most of the specimens grouping around 1:4.5.

Telson: In all of the specimens except three the telson is found to be 3.2 to 4.0 times as long as the posterior margin is broad, with most 3.2 to 3.3 times. In two specimens the telson is only 3.0 times as long as broad, and in one it is 4.2 times as long.

The extent of this variation destroys the validity of the separation of *A. maruteensis* and *A. dorsalis*. Coutière separated his species (which he originally called *A. dorsalis pacificus*) upon the following characteristics: 1. shape of rostrum; 2. traces of extracorneal spines; 3. shape and armature of large and small chelae; 4. relative proportions of the carpal articles and chelae of second legs (for this character it should be noted that in the specimens measured some would be like *A. dorsalis* in two of the relative measurements and like *A. maruteensis* in the third); 5. the length-breadth relation of the articles of the third leg, and the presence of a definite tooth on the merus as opposed to being "coupé à angle droit" in *A. maruteensis*. To these differences de Man adds, in his separation of the subspecies *A. maruteensis salibabuensis* the proportions of the rostrum and merus of the second and third legs. In the group of specimens measured each of the characteristics was found to be

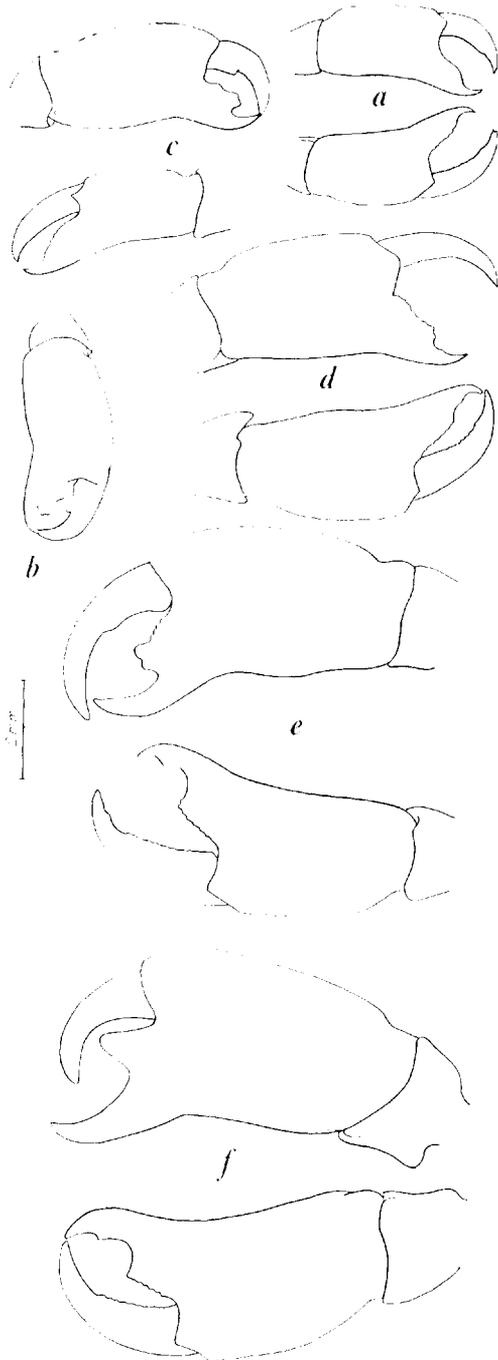


FIG. 6. *Athanas dorsalis* (Stimpson), variations in the development of the chelae. *a*. Male of 3.3 mm. carapace length; *b*. male of 3.5 mm. carapace length; *c*. male of 3.85 mm. carapace length; *d*. male of 4.95 mm. carapace length; *e*. male of 4.95 mm. carapace length; *f*. male of 5.2 mm. carapace length. All drawn to same scale.

variable, with the range of variation not only bridging the supposed differences between the nominal species and subspecies, but also extending beyond any previously reported condition. It is interesting to note that the specimens that agreed best with *A. dorsalis* were those from Raroia, not too far from the type locality of *A. maruteensis*, while the specimens from the Marshalls were more like the description of *A. maruteensis*.

The exact status of *A. mascarinicus* Richters is not known, as the description, without figures, is inadequate. It may be a synonym of this species; it may be the same as, and take priority over *A. indicus* or *A. amboinensis*; it may be regarded as a *nomen dubium*; or it may be a separate and valid species. Unless the type specimen can be redescribed, we feel it is safest to consider it as a synonym of *A. dorsalis*.

On many of these specimens, including the large group from the Marshalls, it was specified that they were collected from large sea urchins of the genus *Heterocentrotus*; however, for some their habitat was specified as "coral" (as was that of Stimpson's original specimen). Whether this indicates that the species normally lives only on sea urchins but may desert them if the urchin is disturbed, as by a collector, or whether it indicates that the species may live either on coral or sea urchins is not known. At least, no significant differences were found between those collected from urchins and those collected from unspecified "coral."

Athanas amboinensis (de Man, 1910b: 25-27, figs. 1-6) is, at least, closely related to *A. dorsalis*, more closely than *A. indicus* (Coutière); it may be found to be a synonym. However, as none of the specimens in the collection approach the proportions of the slender chela and narrow telson given by de Man as specific characteristics, there is no evidence that the two should be combined.

DISTRIBUTION: Stimpson's original specimens came from Hongkong and it has been reported from Djibouti, Indian Ocean, Indonesia, New Caledonia, Kermadec Islands and Samoa. In the present collection we have about 70 specimens, the majority from the Marshall Islands, 2 specimens from Canton Island, 1 from Fiji and 6 from the Tuamotus. At least 50 of the speci-

mens were commensal with the sea urchin *Heterocentrotus*.

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