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

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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.

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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.
Athanas nitescens (Leach) (described as Palae- nomon nitescens), 1814. Edinb. Encyc. 7: 401. [Not Indo-Pacific.]


Athanas monoceros (Heller) (described as Al- pheus monoceros), 1861. S.B. Akad. Wiss. Wien 44: 274; Red Sea. [Coutiere, 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. [Coutiere (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 Pridroduc pri Imperator- skom Khar’kovskom Universitete (Société des Naturalistes à l’Université Impériale de Kharkow) 13: 26. [Not Indo-Pacific. Coutiere (1899: 37) states this is a juvenile.]


Athanas velocuslus Spence Bate, 1888. Challenger Reps. 24: 529, pl. 96, fig. 1. [Not Indo-Pacific.]


Tattersall, 1921. J. Linn. Soc. (Zool.) 34: 371, pl. 28, figs. 23, 24; 1 specimen from the Red Sea. [Partial redescription.]


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.]


IX, 5 (2): 75; specimens from the Maldive and Laccadive Archipelagoes. [Characteristics and general distribution.]

—— Coutière, 1905. Fauna and Geog. Mal-
dive and Laccadive Archipelagoes 2 (4): 856,
fig. 129. [Same as the above.]

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 speci-
mens.]

—— de Man, 1922. Siboga Exped. 39a (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.]

16: 629; Christmas Island, Indian Ocean.
[Record of capture.]

Mar. Mus. 6: 119, pl. 31; 2 specimens from
Marquesas Islands. [Extensive de-
scription.]

Univ. 6: 12; 4 specimens from Ghardaqa,
Red Sea. [Remarks on chelae.]

seille II, 10: 145. [Reference not available.]

Reef Exped. 6: 54, figs. 249–252. [Discussion of larval forms.]

(1137): 5; 1 female from Samoa. [Record of capture.]

XI, 13: 388; specimens from Mozambique.
[Locality only.]

732–733, figs. 137 e–f; 1 specimen from
Mozambique. [Brief description.]

105(3349): 16; 11 specimens from the Mar-
shall Islands. [Brief remarks.]

22 specimens from the Mariana Archipelago.
[Brief discussion.]

specimens from the Marshall Islands. [Record of capture.]

Soc. Lond., p. 1011, fig. 9; 8 specimens from Funafuti. [Coutière (1905: 856) stated this
was a synonym of _A. djiboutensis_.]

3: 518; specimen from Funafuti. [Record of capture.]

_Athanas ortmanni_ Rankin, 1898. Ann. N. Y.
Acad. Sci. 12(11): 251, pl. 50, fig. 7. [Not
Indo-Pacific, Now _Salmoenus ortmanni_.]

_Athanas dimorphus monoceros_ (Heller) Couti-
ière, 1899. Ann. Sci. Nat. VIII, Zool. 9: 61, 62. [Change of name, see _A. monoceros_ Hel-
ler, 1861, above.]

Philom. Paris IX, 5 (2): 77, figs. 14–16; 1
specimen from the Maldive Archipelago.

—— Coutière, 1905. Fauna and Geog. Mal-
dive and Laccadive Archipelagoes 2 (4): 859,
fig. 131. [Same description as the above.]

140: 737. [Review of species listed in Mal-
dive and Laccadive Report.]

—— de Man, 1922. Siboga Exped. 39a (5):
16, pl. II; fig. 9; 1 specimen from Indonesia.
[Description of specimen.]

731, figs. 136 f–i; 1 specimen from Natal,
South Africa. [Brief description.]

specimens from the Maldive Archipelago.

—— Coutière, 1905. Fauna and Geog. Mal-
dive and Laccadive Archipelagoes 2 (4): 860,
fig. 132. [Same description and figures as
above.]

731, figs. 136 f–i; 1 specimen from Natal,
South Africa. [Brief description.]

732–733, figs. 137 e–f; 1 specimen from
Mozambique. [Brief description.]

—— Balss, 1915. Ergebn. Zool. 30: 21; speci-
men from the Red Sea. [Locality only.]

105(3349): 21; 1 specimen from the Mar-
shall Islands. [Locality only.]


—— Coutière, 1905. Fauna and Geog. Mal-dive and Laccadive Archipelagoes 2(4): 858, fig. 130. [Same specimens and figures as the above.]

—— de Man, 1911. Siboga Exped. 39a 1(2): 149, pl. 2, figs. 5–5h; 2 specimens from Indonesia. [Description and figures.]


—— de Man, 1911. Siboga Exped. 39a 1(2): 151, pl. 2, figs. 6–6h. [Redescription, same specimens as the above.]


—— de Man, 1911. Siboga Exped. 39a 1(2): 157, pl. 3, figs. 8–8c. [Redescription, same specimen as the above.]


—— de Man, 1911. Siboga Exped. 39a 1(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, 1911. Siboga Exped. 39a 1(2): 154–156, pl. 2, figs. 7–7f. [Redescription of same specimens.]


Athanas polymorphus Kemp, 1915. Indian Mus., Mem. 5(3): 289, figs. 31, 32; 27 specimens from Chilka Lake, India.


—— de Man, 1922. Siboga Exped. 39a 1(5): 18, pl. II, III, figs. 10–10f. [Redescription of same specimen.]


Athanas oshimai Yokoya, 1936. Jap. J. Zool. 7: 129, fig. 1; several specimens from Aburatubo, Japan.

**Athanas esakii** Kubo, 1940. J. Fish. Inst. Tokyo 34(1): 93, fig. 13; four specimens from Kusae, Caroline Islands.


**Athanas kominatoensis** Kubo, 1942. Zool. Mag. Tokyo 54: 82-84, fig. 2; 5 males from Kominato, Japan.


**Athanas setoensis** Kubo, 1951. J. Tokyo Coll. Fish. 38(2): 266, figs. 5, 6; 1 specimen from central Japan.


**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. [Remarks on ecology.]


**Arete dorsalis pacificus** Coutière, 1905. Fauna and Geog. Maldives and Laccadive Archipelagoes 2(4): 861, fig. 133. [Same specimens as in 1905 above.]


Marutea commensal with *Heterocentrotus mammillatus*.

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**Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 868.** [Comparison with *A. dorsalis*.]

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**Nobili, 1907. Mem. R. Accad. Torino II, 57: 353; 5 specimens from Marutea, one from Fakarawa, one from Rikitea, French Oceania. [Remarks on commensalism.]

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**Coutière, 1905. Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 863, figs. 134, 135; one specimen from Maldives Archipelago, numerous specimens from Djibouti and 1 from Central America. [See *A. dorsalis indus* Coutière above.]**

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**Bals, 1915. Ergeb. Zool. 30: 21; specimens from the Red Sea. [Locality only.]**

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**Coutière, 1921. Trans. Linn. Soc. Lond. 17(4): 413; specimens from the Indian Ocean. [Locality only.]**

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**de Man, 1911. Biboga Exped. 39a(2): 16, pls. 3, 4, figs. 11-11e. [Same as the above with figures.]**

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**de Man, 1922. Biboga Exped. 39a(5): 22, pl. III, figs. 11-11f; 1 specimen from Indonesia. [Redescription.]**

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**Banner, 1956. Pacif. Sci. 10(3): 324; 6 examples from the Mariana Islands. [Locality only.]**

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**Arete ghardaqensis Ramadan, 1936. Bull. Fac. Sci. Egypt. Univ. 6: 15, pl. 1, fig. 208; 5 specimens from the Red Sea.**

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**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 ghardaqensis*, 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 scutibranchs 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 ghardaqensis 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 ghardaqensis 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, Salmones, Amphibetaeus, Betaeus (in part), Batella, Metabetaeus, Racilius, and Pomonathus. The presence of a rostrum separates the genus from Betaeus and Parabetaeus, and the exposure of the eyes in dorsal view from Aphanopsis, 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. rhitionastes 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. rhitionastes, 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*¹

1. Palm of large chela cylindrical or subcylindrical in section; carpus of second legs with five articles.  2
   Palm of large chela flattened, definitely higher than broad in section; carpus of second legs with four or five articles.  22

2(1). Legs of first pair, when fully developed, carried directed forward; merus short, not excavate.  3
   Legs of first pair, when fully developed, with chelae carried folded against an excavate and expanded merus.  6

3(2). Supracorneal teeth present.  4
   Supracorneal teeth absent.  7

4(3). Dactylus of third legs biunguiculate.  5
   Dactylus of third legs simple.  9

5(4). Dactylus of third legs simple; with both extra- and infracorneal teeth.  8
   Dactylus of third legs carrying an articulated spine; with only extracorneal teeth (originally described as infracorneal teeth).  13

6(2). Supracorneal teeth present.  10
   Supracorneal teeth absent.  11

7(6). Dactylus of third leg biunguiculate.  8
   Dactylus of third leg simple.  9

8(7). With infracorneal tooth.  9
   Without infracorneal tooth or projection.  10

9(7). Carpus of first leg longer than palm in mature females.  10
   Carpus of first legs equal in length to palm, or shorter, in mature females.  15

10(9). Ischium of first legs with strong distal spine.  11
   Ischium of first legs not so armed.  11

11(10). Palm of chela in female less than 1.5 times length of fingers.  12
   Palm of chela in female 2.0 or more times length of fingers.  13

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.  12
   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.  14

13(11). With extracorneal tooth strong and acute; infracorneal projection almost as long as extracorneal tooth, but rounded.  14
   With only extracorneal tooth (or infracorneal tooth) produced and acute.  15

14(13). Rostrum reaching to end of second antennular article.  15
   Rostrum a little longer than antennular peduncle.  16

15(9). Infracorneal projection at most slight and rounded.  16
   Infracorneal projection present and acute.  18

¹ *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.

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 shorter ................................................. 17

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. rhothionastes Banner

18(15). Infraconal tooth longer than extracornal tooth ................................................................. 19

Infraconal tooth shorter than extracornal tooth .............................................................. 20

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. haswelli below)........ A. borradailei (Coutière)

21(20). Carpus and chelae slender in females\(^a\)........ A. haswelli Coutière

Carpus and chelae of females more robust\(^a\)........ A. minikoensis Coutière

22(1). With well-developed supracornal teeth ................................................................. 23

Without trace of supracornal teeth; carpus of second legs with four articles ........................................... 25

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 papillae ................................................................. 24

24(23). Ventral side of rostrum smoothly convex; base of outer antennular 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 shorter ................................................................. 26

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)

\(^a\) Coutière’s only differentiation between these two species is as follows: “[The cheliped of A. haswelli] 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.
**Arthanas 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. naifaroensis*; one complete male and one incomplete female for *A. areteformis*; Ramadan had one female for *A. erythraeaus*; 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. naifaroensis* (de Man, 1922: 16; Barnard, 1950: 731) and no more specimens have been reported for *A. erythraeaus*.

The four species were separated by various characteristics. *A. naifaroensis* differed from *A. areteformis* seemingly only in the presence of infracorneal 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. erythraeaus*. 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. erythraeaus*. 2. The lateral corneal spine "is not as well developed" in *A. erythraeaus* as in *A. areteformis*. 3. The chela of the female in *A. erythraeaus* 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 supracorneal 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 supracorneal spines also varies in depth and definition. All but five specimens lack the infracorneal tooth; however, on these five the tooth varies from considerably smaller to larger than that depicted for *A. naifaroensis*. 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. naifaroensis* 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
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. arete-formis* 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 Maldives 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


**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, Maldivian 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

![Image](image_url)

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


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

<table>
<thead>
<tr>
<th>SEX</th>
<th>CARAPACE LENGTH</th>
<th>LEFT CHELA</th>
<th>RIGHT CHELA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(in proportion to palm)</td>
<td>Fingers</td>
<td>Palm</td>
</tr>
<tr>
<td>♀</td>
<td>3.1 mm.</td>
<td>0.6</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>3.5 mm.</td>
<td>0.5</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>3.6 mm.</td>
<td>0.5</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>3.7 mm.</td>
<td>0.3</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>4.5 mm.</td>
<td>0.3</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>4.6 mm.</td>
<td>0.4</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>5.2 mm.</td>
<td>0.4</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>4.3 mm.</td>
<td>0.3</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>4.6 mm.</td>
<td>0.2</td>
<td>1.0</td>
</tr>
<tr>
<td>♀</td>
<td>5.3 mm.</td>
<td>0.3</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Athanas marshallensis Chace

Figs. 2


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, Salmonenius tricristatus Banner, and S. sibogae (de Man). It is noteworthy that in similar habitats in other archipelagos 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 2b-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. rhothionastes 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 rhothionastes sp. nov.

Figs. 3

TYPE SPECIMENS: Holotype, a 12 mm. (4.8 mm. carapace length) ovigerous female; allo-type, 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, Viti Levu, 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; extracorneal 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 extracoronal 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. Car pocerite 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 excava 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.)
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: 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 spines 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 specimens 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.

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**Fig. 3. Athanas rhothionastes Banner.** Holotype (female) a-i; allotype j-m. a, b. Anterior region; e, d, e, f. chelipeds; i, interior lateral surface of chelae; g, second leg; h, third leg; t, telson; j, k, large cheliped and fingers; l, m, small cheliped and fingers; n, large and small chela 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. 3n) 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. 3o) 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. rhothionastes*. 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. rhothionastes* 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 infracorneal 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 specific name is derived from the Greek *rhothion,* meaning breakers or surf, and *nastes,* meaning inhabitant.

**Athanas esakii** Kubo


**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:

<table>
<thead>
<tr>
<th></th>
<th>Merus</th>
<th>Carpus</th>
<th>Palm</th>
<th>Fingers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Smaller</td>
<td>1.5</td>
<td>1.0</td>
<td>1.0</td>
<td>0.6</td>
</tr>
<tr>
<td>Larger</td>
<td>1.3</td>
<td>0.8</td>
<td>1.0</td>
<td>0.5</td>
</tr>
</tbody>
</table>
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. Carpopodite 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. para-gracilis* Coutière and *A. haikau* Banner with flattened labrum and with psalistome of mandibles expanded and almost hemispherical, teeth on psalistome 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 metatal-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 unarmmed, 0.5 length of merus. Merus unarmmed, 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 unarmmed. 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 dactylius; *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 pleurobranchs, no arthrobranches, and mastigobranchs extending back to second thoracic leg, setobranchs to third. No anal tubeercles.

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* (Raman, 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 masigobranchs 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)


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

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### *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. komataniensis* 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 leg 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, Ai-tutake, 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


**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 50 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...
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. 6a–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 5b, 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 “coupè 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

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Fig. 6. *Athenas 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 4.05 mm. carapace length; e. male of 4.55 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 specimens were commensal with the sea urchin *Heterocentrotus*.

**REFERENCES**


