Establishment of a New Genus for *Arete borradailei* Coutière, 1903 and *Athanas verrucosus* Banner and Banner, 1960, with Redefinitions of *Arete* Stimpson, 1860 and *Athanas* Leach, 1814 (Crustacea: Decapoda: Alpheidae)

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Arthur Anker and Ming-Shiou Jeng (2007) Establishment of a new genus for *Arete borradailei* Coutière, 1903 and *Athanas verrucosus* Banner and Banner, 1960, with redefinitions of *Arete* Stimpson, 1860 and *Athanas* Leach, 1814 (Crustacea: Decapoda: Alpheidae). *Zoological Studies* **46**(4): xxx-xxx. *Arete borradailei* Coutière, 1903 and *Athanas verrucosus* Banner and Banner, 1960 are transferred to *Rugathanas* gen. nov., based on several unique features on the chelipeds, 3rd pereiopods, antennules, and mouthparts. The establishment of *Rugathanas* enables the redefinition of *Athanas* Leach, 1814 and *Arete* Stimpson, 1860, and a formal revalidation of *Arete*, formerly a synonym of *Athanas*. Two important features, the number of pereiopodal epipods and the number of carpal segments of the 2nd pereiopod, are variable within *Rugathanas* gen. nov., but may be used to distinguish *Athanas* from *Arete*. The distribution ranges of *R.*

borradailei (Coutière, 1903) comb. nov. and *R. verrucosus* (Banner and Banner, 1960) comb. nov. are considerably extended based on recently collected material from the Ryukyu Is., Japan; Kenting, Taiwan; and Norfolk I., off eastern Australia.
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Key words: Alpheidae, New genus, *Athanas*, *Arete*, Indo-Pacific.

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The alpheid shrimp genus *Athanas* Leach, 1814 sensu lato (sensu Banner and Banner 1960 1973, Chace 1988) presently includes over 40 species in the eastern Atlantic and Indo-West Pacific. Most species are small (< 10 mm in total length) and inhabit coral reefs and rocky or muddy-sandy bottoms; some species live in symbiosis (commensalism) with other animals, such as thalassinideans, stomatopods, and echinoderms (Suzuki 1970, Banner and Banner 1973, Gherardi 1991, Froglia and Atkinson 1998, Anker et al. 2001, Hayashi 2002, Marin et al. 2005). *Athanas* species are mainly characterized by the presence of a triangular articulated plate on the 6th abdominal segment, and a well-developed distally acute rostrum. The variously developed orbital teeth, and highly variable chelipeds, often armed with teeth, but without a fossa-tooth mechanism (e.g., Chace 1988) provide evidence that *Athanas sensu lato* is a highly heterogeneous and likely non-monophyletic assemblage.

Banner and Banner (1960) questioned the validity of *Arete* Stimpson, 1860. They considered the features used by Coutière (1899 1903) to distinguish between *Arete* and *Athanas* invalid, e.g., the number of pereiopodal epipods (2 in *Arete* and 3 in *Athanas*) and the number of segments in the carpus of the 2nd pereiopod (4 in *Arete* and 5 in *Athanas*), and formally placed *Arete* in synonymy of *Athanas*. Although several workers (e.g., Holthuis 1993, Hayashi 1995, Nomura et al. 1996) continued to treat *Arete* as a valid genus, without discussing the synonymy proposed by Banner and Banner (1960), the majority of workers accepted this synonymy. However, Banner and Banner (1982) recognized that 2 closely related species originally described as *Arete borradailei* Coutière, 1903 and *Athanas verrucosus* Banner and Banner, 1960 did not fit into either the generic diagnoses of *Arete* nor *Athanas*, and proposed reconsidering the validity of *Arete*, a suggestion they subsequently did not return to.

Both *Are. borradailei* and *Ath. verrucosus* are rarely collected shrimps. The latter species was until now only known from the type locality, Enewetak Atoll, Marshall Is. (Banner and Banner 1960). This is partly due to the small size and cryptic lifestyles of these shrimps, which usually live in crevices of dead and living corals or in porous rocks overgrown with coralline algae. The only efficient method of collecting this type of cryptofauna is to carefully hammer these rocks apart to extract small animals from deep holes and crevices. During the 1st author's (AA) field trip to Kenting National Park, southern Taiwan, 1 specimen of *Ath. verrucosus* was extracted by this method from dead coral rubble, collected from shallow water near the shore. We also examined several specimens of this species from Emily Bay, Norfolk Island, off New South Wales, Australia, and deposited in the Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM). The second author (MSJ) previously collected several specimens of *Are. borradailei* in Kenting. Through the courtesy of Keiichi Nomura (Kushimoto Marine Park Center, Kushimoto, Japan) we were able to study 4 specimens of *Are. borradailei* from the Ryukyu Archipelago. In addition, we examined 2 specimens of *Are. borradailei* from the southwestern Indian Ocean previously reported by Banner and Banner (1983), and numerous specimens of *Athanas* and *Arete* deposited in various museums.

The morphological features of *Are. borradailei* and *Ath. verrucosus* clearly set these 2 species apart from all other species of *Athanas* or *Arete*. Therefore, a new genus, *Rugathanas* gen. nov., is herein established to accommodate these 2 species and formally resurrect *Arete* from synonymy of *Athanas*. *Arete sensu stricto* (*sensu* Stimspon 1860, not *sensu* Coutière 1903) and *Athanas sensu stricto* (*sensu* Coutière 1903, not *sensu* Banner and Banner 1960) are redefined.

MATERIAL AND METHODS

The material used in this study is deposited in the collections of the Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM); the Natural History Museum and Institute, Chiba, Japan (CBM); the Muséum national d'Histoire naturelle, Paris, France (MNHN); the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC); Academia Sinica, Taipei, Taiwan (ASIZ); and the Naturhistorisches Museum in Wien, Vienna, Austria (NHMW).

All drawings were made with the aid of a camera lucida. The carapace length (CL) and total length (TL) were measured in millimeters from the tip of the rostrum to the posterior margin of the carapace and telson, respectively. In cheliped descriptions, the terms equal, subequal, and unequal refer to size, while symmetrical, subsymmetrical, and asymmetrical refer to shape (general shape of the palm, armature of the fingers, etc.). Abbreviations used in the text include: Ar, arthrobranch; Ep, lobe-shaped epipod; Ex, exopod; Ma, mastigobranch (strap-like epipod); Mxp, maxilliped; P, pereiopod; Pd, podobranch; Pl, pleurobranch; r, rudimentary; Se, setobranch; +, present; -, absent.

Taxonomy

Rugathanas gen. nov.

Diagnosis: Body stout. Carapace smooth, not setose. Frontal margin with relatively short, somewhat ascendant rostrum, bearing acute tip, with or without subdistal tooth on ventral margin. Extra-corneal teeth strong, acute, reaching or protruding beyond anterior margin of eyes; supra-corneal teeth usually well developed, acute; infra-corneal teeth reduced or absent. Orbital hoods absent; eyes exposed in dorsal and lateral views. Pterygostomial margin angular, protruding, not acute. Cardiac notch well developed. Second abdominal pleuron greatly expanded in females. Sixth abdominal somite with articulated plate at posteroventral angle; preanal plate rounded. Antennules with minute teeth on distal margin of first segment; ventromesial carina of 1st segment without tooth; lateral flagellum with rudimentary secondary ramus. Antenna with stout basicerite, with or without distolateral tooth; scaphocerite short, broadly oval-shaped. Mandible with palp, incisor process greatly expanded, distally with at least 15 minute teeth. Maxillule with bilobed palp, ventral lobe with 1 seta, dorsal lobe unarmed. Labrum swollen, conspicuously protruding, visible in lateral view. Third maxilliped with penultimate segment as long as wide; ultimate segment with unarmed tip. First pereiopods (chelipeds) sexually dimorphic, carried flexed; coxa unarmed mesially; basis with rudimentary exopod; ischium robust, unarmed mesially; chelae without linea impressa on palm or cavity-tooth system on fingers. Male chelipeds subequal or unequal, subsymmetrical or asymmetrical (with major cheliped situated either on left or right side); ischium armed with spines on dorsal and usually ventral margin; merus swollen, distally depressed; carpus elongated, vase-shaped, excavated ventrally; chela enlarged, oval, compressed, slightly convex mesially, flattened laterally, dorsal and ventral margins rugose; linea impressa absent; fingers unarmed or armed with simple teeth. Female chelipeds equal, symmetrical; ischium usually unarmed or armed with several spines on dorsal margin; merus not or slightly inflated, flattened ventrally; carpus cup-shaped, more or less excavated ventrally; chela varying from oval-shaped to slender, with smooth or rugose margins, fingers unarmed. Carpus of 2nd pereiopod bearing 4 or 5 segments. Third pereiopod with unarmed ischium and merus; carpus with 1 distal spine on ventral margin; propodus with numerous ventral spines; dactylus simple, highly extensible dorsally. Fifth pereiopod with feebly developed propodal brush. Second pleopod with appendix interna and appendix masculina in males, with appendix interna only in females. Telson with 2 pairs of dorsal spines and 2 pairs of posterolateral spines; anal tubercles absent. Gill/exopod formula showing great variation in number of epipods (mastigobranchs/setobranchs), as summarized in following table.

	Mxp1	**Mxp2**	**Mxp3**	**P1**	**P2**	**P3**	**P4**	**P5**
Pl	-	-	-	+	+	+	+	+
Ar	-	-	-	-	-	-	-	-
Pd	-	-	-	-	-	-	-	-
Ep	+	+	-	-	-	-	-	-
Ma	-	-	-/+	-/+	-/+	-	-	-
Se	-	-	-	-/+	-/+	-/+		
Ex	+	+	+	r	r	-	-	-

Type species: *Rugathanas verrucosus* (Banner and Banner, 1960) comb. nov. [*Athanas verrucosus* Banner and Banner 1960: 147]; type locality: Enewetak Atoll, Marshall Is.

Other species included: *Rugathanas borradailei* (Coutière, 1903) comb. nov. [*Arete borradailei* Coutière 1903: 80]; type locality: Hulule Male Atoll, the Maldives.

Etymology: *Rugathanas* is a combination of the Latin adjective *ruga* (rugged, uneven), referring to the characteristic rugosities on the margins of the male chelae, and *Athanas* (a Greek king), referring to its affinity with the genus *Athanas*.

Distribution: Indo-West Pacific from the Red Sea and Madagascar to Japan, Australia, and Samoa.

Remarks: *Rugathanas* may be separated from both *Athanas* and *Arete* by numerous features on the frontal margin of the carapace, antennules, antennae, chelipeds, and mandible. For instance, *Rugathanas* is characterized by the unique shape of the male (and sometimes female) chelipeds. The oval-shaped palm, compressed and flattened laterally and with rugose dorsal and ventral margins, and the vase-shaped, ventrally excavated carpus (Figs. 1a, 2l, m, 3c-e, 4a, 5b, c) are externally the most obvious features separating *Rugathanas* from *Arete* and *Athanas*. The configuration of the frontal margin of the carapace of *Rugathanas* is also characteristic of the genus (Figs. 2a, b, 3a, b, 5a), the most important features being the relatively short, ascendant rostrum, often with a small subdistal tooth on the ventral margin (vs. a long, straight rostrum, without a ventral tooth in *Athanas* and *Arete*); the presence of supra-orbital teeth (absent in all *Arete* and most *Athanas* species, with the notable exceptions of *Ath. djiboutensis* Coutière, 1897 and *Ath. areteformis* Coutière, 1903, cf. Fig. 8b); the absence of infra-corneal teeth (usually absent in *Arete*, but often present in *Athanas*); and the presence of strong extra-corneal teeth reaching or sometimes protruding well beyond the anterior margin of the cornea (vs. usually not reaching far beyond this margin in *Arete* and *Athanas*, but with some exceptions, e.g., *Ath. areteformis*, cf. Fig. 8a).

Rugathanas also differs from *Arete* and *Athanas* by the considerably expanded incisor process of the mandible (“psalistome” in Banner and Banner 1960), which is distally furnished with numerous (usually more than 15) minute teeth (Fig. 2g, h). In *Arete* and *Athanas*, the incisor process is not or only slightly expanded, distally bearing 5-12 teeth (A Anker pers. obs.).

One notable exception is again *Ath. areteformis*, in which the incisor process is also expanded and distally bears around 15 teeth (Fig. 8c, d). However, this species has very differently shaped chelipeds (Fig. 8e-j) and plainly belongs to the genus *Athanas* (see below). In species of *Rugathanas*, the labrum is greatly swollen (Fig. 2c), sometimes conspicuously protruding in lateral view (Fig. 3b), apparently to accommodate the expanded incisor process of the mandible. In contrast, the labrum of *Ath. areteformis* is only moderately swollen and not visible in lateral view.

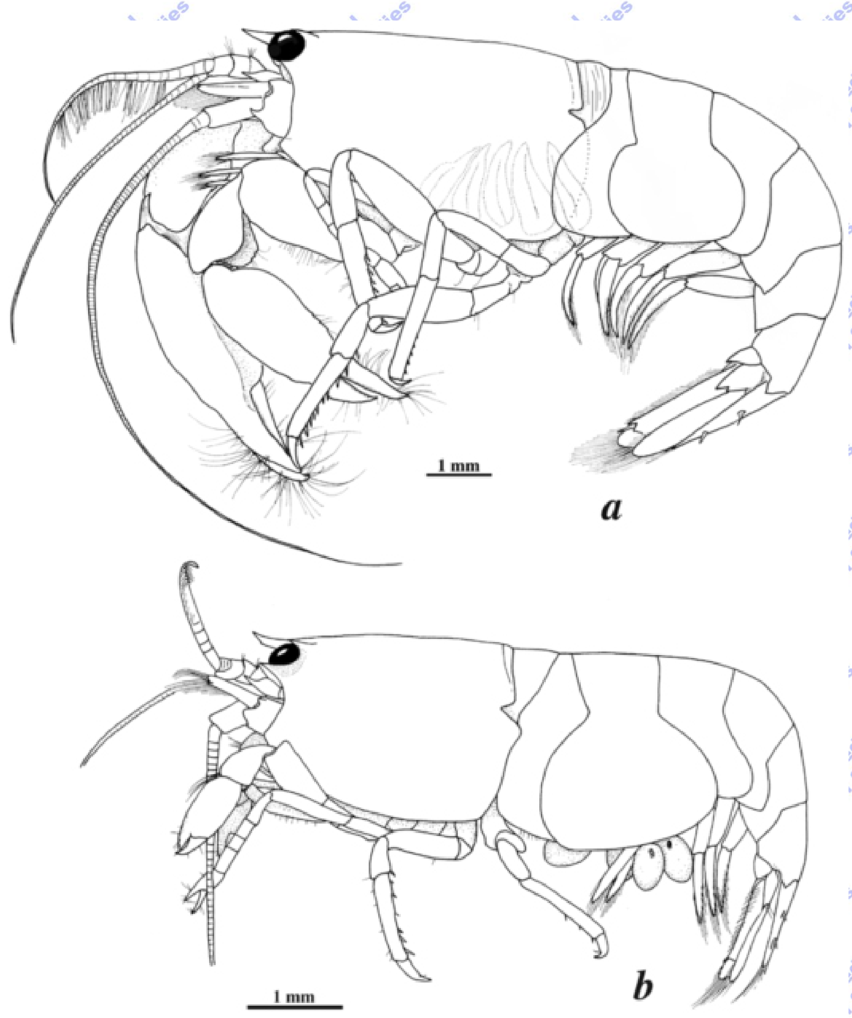

Fig. 1. *Rugathanas borradailei* (Coutière, 1903) comb. nov.: (a) male from Kenting, southern Taiwan (ASM); (b) ovigerous female from the Ryukyu Is., Japan (MNHN).

Other features distinguishing *Rugathanas* from *Arete* and *Athanas* are the stouter and (compared to other antennal parts) larger basicerite (Figs. 2a, 3b); the unarmed ventromesial carina on the 1st antennular segment (Fig. 2d) (vs. armed with strong tooth in all species of *Arete* and *Athanas*, partly visible in Fig. 8a; see also Bruce 1990); the tip of the ultimate segment of the 3rd maxilliped without spines (vs. with spines in all *Arete* and most *Athanas* species); and the dorsally more extensible dactylus of the 3rd-5th pereiopods, which can be placed in an almost perpendicular position to the propodus (Fig. 2p, q). This unusually flexible articulation is strikingly similar to that of the unrelated alpheid genus *Metalpheus* Coutière, 1906, where, however, the dactylus extension is facilitated by a small ventral sclerite (Banner 1959). *Rugathanas* also differs from *Athanas* by the strongly dentate margin of the 1st and 2nd segments of the antennular peduncle (Figs. 3a, 5a) (vs. straight or finely toothed in *Athanas*), and the much shorter penultimate segment of the 3rd maxilliped, which is about as long as wide in *Rugathanas* (Fig. 2k) (vs. distinctly longer than wide in *Athanas*).

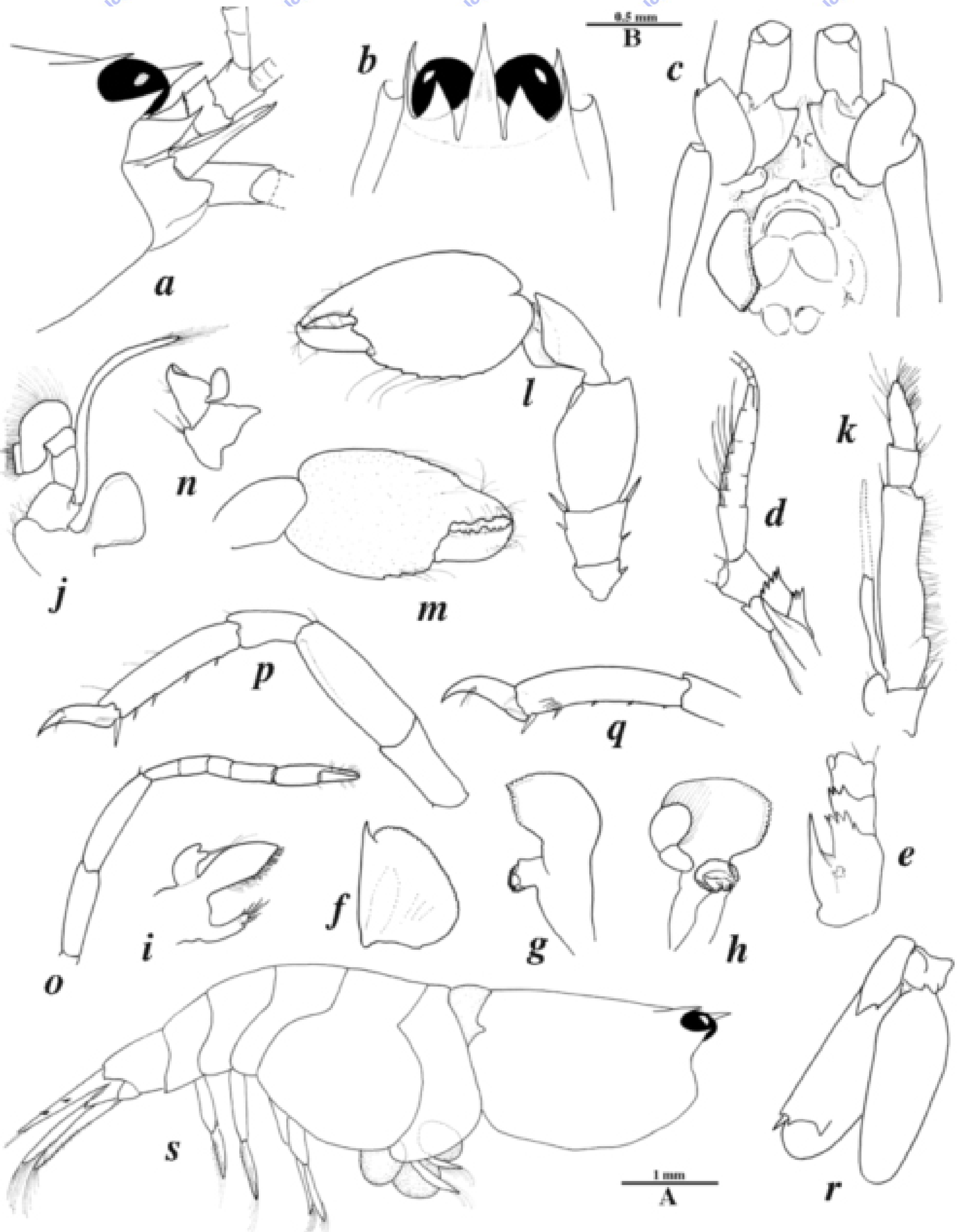

Fig. 2. *Rugathanas borradailei* (Coutière, 1903) comb. nov., ovigerous female (a-k, o-s) and male (l-n) from southwestern Madagascar (MNHN): (a) frontal region, lateral view; (b) frontal margin of carapace, dorsal view; (c) frontal region, ventral view showing bases of antennules and antennae, labrum, and position of mouthparts; (d) antennule, lateral view; (e) same,

peduncle, dorsal view; (f) scaphocerite; (g, h) mandible from 2 different aspects; (i) maxillule; (j) 2nd maxilliped; (k) 3rd maxilliped; (l) left cheliped, lateral view; (m) same, chela, mesial view; (n) same, coxa and basis with exopod; (o) 2nd pereiopod; (p) 3rd pereiopod; (q) 5th pereiopod, distal carpus, propodus, and dactylus; (r) uropod; (s) abdomen and cephalothorax (frontal appendages and pereiopods not drawn). Scales: A (s), B (a-r).

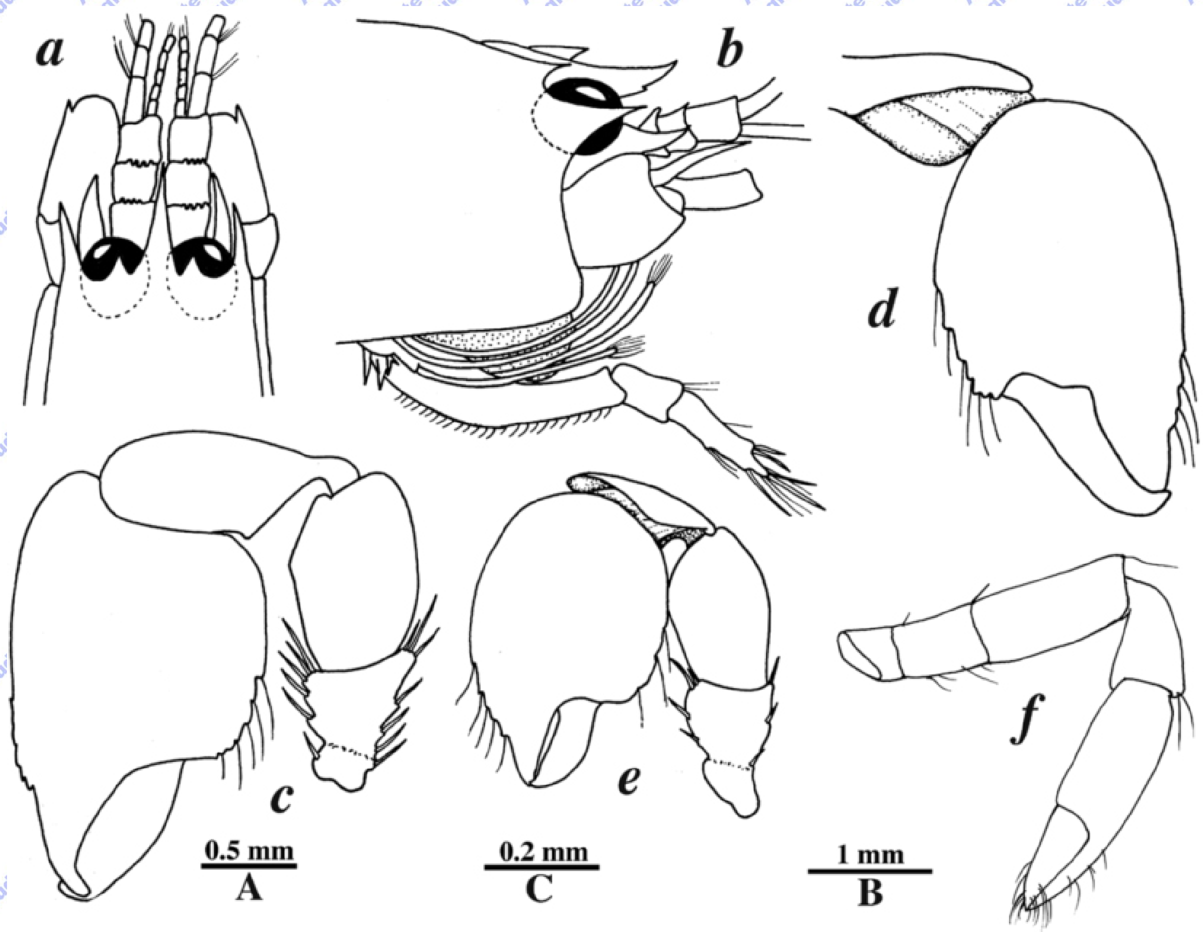

Fig. 3. *Rugathanas borradailei* (Coutière, 1903) comb. nov., male from Samoa reported as *Athanas polynesia* (a-e), and female from Kenting, southern Taiwan (ASM) (f): (a) frontal region; (b) frontal region with protruding labrum and 3rd maxilliped, lateral view; (c) major cheliped, lateral view; (d) same, carpus and chela, mesial view; (e) minor cheliped, mesial view (a-e, adapted from Banner and Banner 1966a). Scales: A (a), B (b-e), C (f).

The number of carpal segments in the 2nd pereiopod varies from 4 in *R. borradailei* (Fig. 2o) to 5 in *R. verrucosus* (Fig. 4a). The strap-like epipods (mastigobranchs) are present on the 3rd maxilliped and 1st and 2nd pereiopods in *R. verrucosus*, but are absent in *R. borradailei*. Although these 2 important characters are variable within *Rugathanas*, they remain valuable for differentiating *Rugathanas* from *Arete sensu stricto* and *Athanas sensu stricto* (see below). Within the Alpheidae, an intrageneric variation in the number of carpal segments is not rare and also occurs in *Synalpheus* Bate, 1888 (4 to 5, see Banner and Banner 1975), *Leptalpheus* Williams, 1965 (4 to 5, see Anker et al. 2006c), *Alpheopsis* Coutière, 1896, and *Prionalpheus* Banner and Banner 1960 (3-5, see Banner and Banner 1971 1973, Bruce 1990b, Martínez-Iglesias and Carvacho 1991). Similarly, intrageneric variation in the number of pereiopodal epipods was also reported in at least 2 other genera, *Alpheopsis* (2-4, see Coutière 1899, Anker et al. 2005) and *Athanas* (see below).

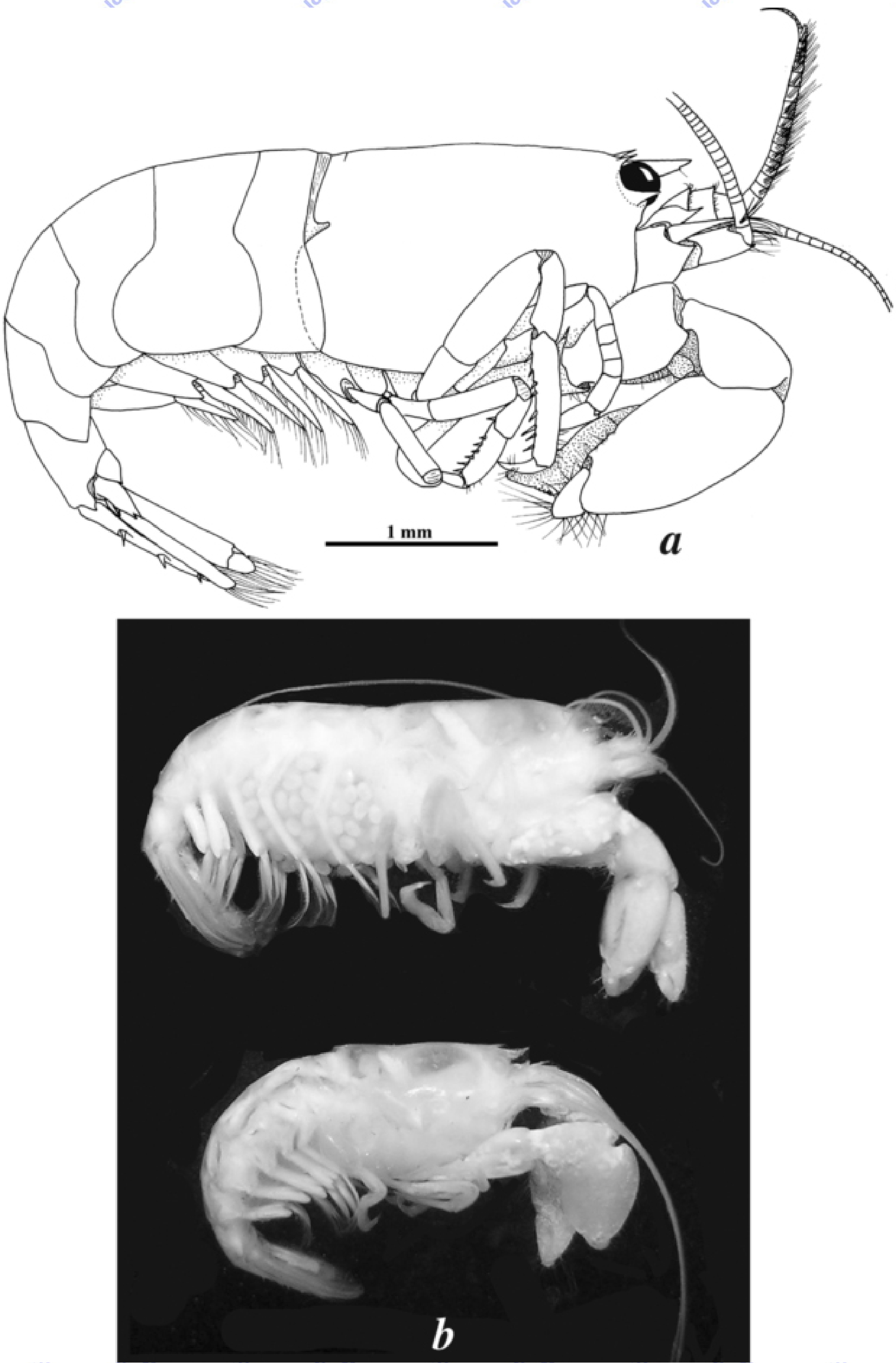

Fig. 4. *Rugathanas verrucosus* (Banner and Banner, 1960) comb. nov.: (a) male from Kenting, southern Taiwan (AS); (b) ovigerous female (above) and male (below) from Norfolk I. (NTM) showing sexual dimorphism in the development of the chelipeds.

Rugathanas, *Athanas* and *Arete* are part of a larger generic complex (athanoid complex); other athanoid genera are *Athanopsis* Coutière, 1896 (5 species), *Pseudathanas* Bruce, 1983 (1 species), *Acanthanas* Anker, Poddoubtchenko and Jeng, 2006 (1 species), and *Aretopsis* De Man, 1910 (1 or 2 species). This complex forms a well-defined monophyletic clade (the clade AP of Anker et al. 2006a) within the family Alpheidae. According to Anker et al. (2006a) *Athanopsis* and *Pseudathanas* are sister genera, as are *Arete* and *Aretopsis*. *Rugathanas* (represented by *R. borradailei*) formed a sister group to *Athanas*. *Athanas* was found to be non-monophyletic; however, first, this genus was not adequately represented in this analysis, and second, the position of *Ath. squillophilus* as a sister to *Athanopsis* and *Pseudathanas* is rather questionable. The recently described *Acanthanas* was not included in Anker et al.'s (2006a) cladogram, but based on its morphological features (see Anker et al. 2006b), this genus appears to form a separate lineage somewhere within the clade *Athanas* – *Rugathanas*.

Key to the genera of the athanoid generic complex and to the species of *Rugathanas*

1a. Rostrum distally rounded -- 2

1b. Rostrum distally acute --- 3

2a. Chelipeds always carried extended, with dactylus in ventral position ------------------- *Aretopsis*

2b. Chelipeds carried flexed (propodus fitting in a deep excavation on merus), dactylus in dorsal or dorsolateral position when chela extended -- *Athanopsis*

3a. Eyestalks with two conspicuously projecting acute spines ---------------------------- *Acanthanas*

3b. Eyestalks without spines --- 4

4a. Diaeresis of uropodal exopod with row of spines ------------------------------------- *Pseudathanas*

4b. Diaeresis of uropodal exopod without spines --- 5

5a. Male chelipeds with oval-rounded chelae, palm with rugose margins, carpus vase-shaped, ventrally excavated; labrum swollen, protruding; mandible with greatly expanded incisor process; supra-orbital teeth present --- *Rugathanas* (6)

5b. Male chelipeds with elongated or oval-shaped chelae, palm with non-rugose margins (sometimes with tubercles), carpus variably shaped; labrum neither swollen nor protruding; incisor process of mandible not or only slightly expanded; supra-orbital teeth present or absent ---------- 7

6a. Strap-like epipods absent; 2nd pereiopod with 4-segmented carpus; male chelipeds asymmetrical; female chelipeds only slightly enlarged ---------------------------------- *R. borradailei*

6b. Strap-like epipods present on Mxp3 and P1-2; 2nd pereiopod with 5-segmented carpus; male chelipeds subsymmetrical; female chelipeds greatly enlarged --------------------------- *R. verrucosus*

7a. Strap-like epipods present on Mxp3 and P1-2; 2nd pereiopod with 4-segmented carpus; cheliped ischium with strong process mesially; supra-orbital teeth absent ----------------------- *Arete*

7b. Strap-like epipods present on Mxp3 and P1-3 (exceptionally on P1-2 or P1-4); 2nd pereiopod with 5-segmented carpus; cheliped ischium without a strong process mesially; supra-orbital teeth absent or present --- *Athanas*

Rugathanas borradailei (Coutière, 1903) comb. nov.

(Figs. 1-3, 6a)

Arete borradailei Coutière 1903: 80, figs. 19-24; Coutière 1905: 861, fig. 133; Jacquotte 1964: 180; Banner and Banner 1966a: 152; Banner and Banner 1983: 73; Chace 1988: 61.

Arete ghardaqensis Ramadan 1936: 15, pl. 1, figs. 2-8.

Athanas ghardaquensis Banner and Banner 1981: 42; Banner and Banner 1983: 73.

Athanas polynesia Banner and Banner 1966a: 152, fig. 7; Banner and Banner 1982: 302, fig. 93; Banner and Banner 1983: 73.

Material examined: CBM-ZC 8469, 1 male (CL 2.6, TL 8.3), Japan, S Ryukyu Arch., Yaeyama Group, Kuro-shima, Nakamoto, dead coral crevices, intertidal, coll. K. Nomura, 24 Sept. 1987 [YMP-672c]; MNHN-Na 15778, 2 ovigerous females (CL 2.5, TL 8.5; CL 2.7, TL 8.5), Japan, S Ryukyu Arch., Yaeyama Group, Kuro-shima, Iko, dead coral crevices, depth 2 m, coll. K. Nomura, 29 Aug. 1986 [YMP-163]; MNHN-Na 15779, 1 ovigerous female (CL 2.8, TL 8.1) Japan, S Ryukyu Arch., Yaeyama Group, Kuro-shima, Urabishi, dead coral crevices, depth 3 m, coll. K. Nomura, 17 July 1999 [YMP-2395]; ASIZ 72761, 1 male (CL 5.3, TL 15.3), 1 female (CL, TL not measured), S Taiwan, Kenting National Park, coll. M.S. Jeng; MNHN-Na 4604, 1 male (CL 2.7, TL 8.8), La Réunion, reef crevices, coll. M. Peyrot-Clausade; MNHN-Na 4610, 1 ovigerous female (CL 2.8, TL 8.8), Toliara (Tuléar), Madagascar, from reef crevices, coll. M. Peyrot-Clausade.

Diagnosis: Male chelipeds enlarged, varying from subequal and subsymmetrical in immature individuals to unequal and asymmetrical in adults; ischium with spines; palm expanded, ventral margin rugose, without papillae; fingers unarmed or with feeble teeth. Female chelipeds feebly enlarged, equal, symmetrical; ischium usually without spines, palm not expanded.

Second pereiopod with 4-segmented carpus. Strap-like epipods (mastigobranchs) absent. For complete description see Banner and Banner (1982 1983).

Size: Small-sized shrimp; largest specimen examined, a male from Taiwan (Fig. 1a), measured 15.3 mm TL; the average TL of Australian specimens (reported as *Ath. polynesia*) being 8 mm (Banner and Banner 1982).

Colour: Semitransparent with greenish or olive tinge and feebly marked yellowish-orange bands on abdomen tail fan and chelae; pale-brown inner organs visible due to transparence; eggs bright green (Fig. 6a).

Habitat: Crevice-dweller on coral reefs; most specimens from western Indian Ocean found in cavities of coral rocks overgrown with coralline algae, in groove and spur system on outer reef edge to 25 m deep; in sections of reef flat and a pinnacle on inner slope; in dead and overgrown coral heads, as well as among branches of living corals, e.g., *Acropora variabilis* (Klunzinger, 1879) and *Stylophora mordax* (Dana, 1846) (Banner and Banner 1983). Jacquotte (1964) found several specimens in boring holes of sea urchin *Stomopneustes variolaris* (Lamarck, 1816). Australian specimens (reported as *Ath. polynesia*) collected from areas covered with encrusting coralline algae in water 2-7 m deep (Banner and Banner 1982).

Distribution: Maldives: Hulule Malé Atoll (type locality of *R. borradailei*) (Coutière 1903 1905); Egypt: Hurghada (type locality of *R. ghardaqensis*) (Ramadan 1936); Gulf of Aqaba (Banner and Banner 1981); Somalia; La Réunion; Mauritius (Banner and Banner 1983); Madagascar (Jacquotte 1964, Banner and Banner 1983); Philippines: Negros I. (Chace 1988); Australia: Lizard I. off Queensland (type locality of *R. polynesia*) (Banner and Banner 1982); Samoa (Banner and Banner 1966a); southern Taiwan: Kenting; southern Japan: Ryukyu Is. (present study).

Remarks: The taxonomic statuses of *Are. ghardaqensis* Ramadan, 1936 and *Ath. polynesia* Banner and Banner, 1966 were reviewed by Banner and Banner (1983), who placed both nominal species in synonymy with *Ath. borradailei* (now *R. borradailei*). Those authors concluded that the chelipeds of *R. borradailei* are variable and sexually dimorphic: slender, symmetrical, with a few or no spines on the ischium in females (Coutière 1905: fig. 135c, Banner and Banner 1982: fig. 93k); and robust, subsymmetrical or asymmetrical, with usually strong spines on ischium in males (Banner and Banner 1966a: fig. 7e-g, 1982: fig. 93c-e). However, other features of *R. borradailei*, such as the development of the orbital teeth, the shape of the rostrum, and the armature of the antennal basicerite, are also variable (Ramadan 1936, Banner and Banner 1983). Therefore, *R. borradailei* cannot be excluded from either being a variable species or a species complex.

Rugathanas verrucosus (Banner and Banner, 1960) comb. nov.

(Figs. 4, 5, 6b)

Athanas verrucosus Banner and Banner 1960: 147, fig. 4; Banner and Banner 1968: 270; Banner and Banner 1983: 75.

Material examined: NTM Cr001663, 2 males (CL 4.5, TL 12.7; CL 2.7, TL 7.4), 1 ovigerous female (CL 5.4, TL 15.0), Point Hunter, Emily Bay, Norfolk I., off New South Wales, Australia, 29°03.8'S 167°57.3'E, depth 0-0.25 m, Sta. HL 84-21, coll. H. Larson, det. A.J. Bruce, 18 Apr. 1984; NTM Cr001663, 2 males (CL 2.3, TL 7.2; CL 4.2, TL 11.8), 4 ovigerous females (smallest, CL 3.8, TL 10.1; largest, CL 4.6, TL 12.3), Point Hunter, Emily Bay, Norfolk I., off New South Wales, Australia, 29°03.8'S 167°57.3'E, depth 0-0.25 m, Sta. HL 84-20, coll. H. Larson, det. A.J. Bruce, 17 Apr. 2004; ASIZ 73699, 1 male, CL 3.4, TL 10.1, S Taiwan, Kenting National Park, from coral rocks, depth 0.5-2 m, coll. A. Anker, 1 Oct. 2004.

Diagnosis: Male chelipeds subequal, subsymmetrical, ischium with spines; palm expanded, ventral margin rugose, distoventral portion of palm, pollex, and proximal portion of dactylus with papillae (i.e., small subacute or rounded tubercles); fingers armed with teeth. Female chelipeds enlarged, slightly less stout than male chelipeds, equal, symmetrical; ischium with spines; palm less expanded than in male, with papillae. Second pereiopod with 5-segmented carpus. Strap-like epipods (mastigobranchs) present on 3rd maxilliped and 1st and 2nd pereiopods. For complete description see Banner and Banner (1960).

Size: Small-sized shrimp; type specimen measuring 3.9 mm CL and 11 mm TL (Banner and Banner 1960); the Kenting male specimen only slightly smaller, at 3.4 mm CL and 10.1 mm TL; the largest examined specimen, an ovigerous female from Norfolk I., at CL 5.4 mm and TL 15.0 mm.

Colour: Semitransparent, with purple-greenish bands on abdomen; fingers of chela with golden-yellow tinge; setae fringing uropods and telson golden-brown (Fig. 6b).

Habitat: In Enewetak, habitat of *R. verrucosus* described as "coralline ridge, ocean (windward) reef" and "coralline ridge, and ends of surge channels, exposed about 0.3 meters above 0.0 tides; ridge dense and hard, very irregular and without the usual smooth algal surface … from superficial burrows, roofed over by calcareous algal sheets" (Banner and Banner 1960 1968); Kenting specimen found in a crevice during process of breaking apart coral rocks and rubble collected in shallow water (0.5-2 m) on a near-shore, exposed reef; Norfolk I. specimens collected on a rocky reef, at depths reaching from low tide mark to 0.25 m.

Distribution: Marshall Is.: Enewetak Atoll (type locality, Banner and Banner 1960 1968); Australia: Norfolk I.; southern Taiwan: Kenting (present study).

Remarks: In *R. verrucosus*, the male chelipeds can be classified as subsymmetrical (Fig. 5b, c), and the female chelipeds are generally only slightly weaker than the male chelipeds (Figs. 3, 5d, e, see also Fig. 3). In contrast to this, in *R. borradailei*, the heterochelate condition (asymmetry) in males (Fig. 3c, e) and the sexual dimorphism (chelipeds significantly larger in males, see Figs. 1a, b, 3c-f) appear to be more pronounced. Ovigerous females of *R. verrucosus* from Norfolk I. carried numerous (several dozen) relatively small-sized eggs. One of the ovigerous females from Norfolk I. had an aberrant number of spines on the telson: 4 dorsal spines + 1 posterolateral spine on 1 side, and 2 dorsal and 2 posterolateral spines (typical condition) on the other side (Fig. 5f).

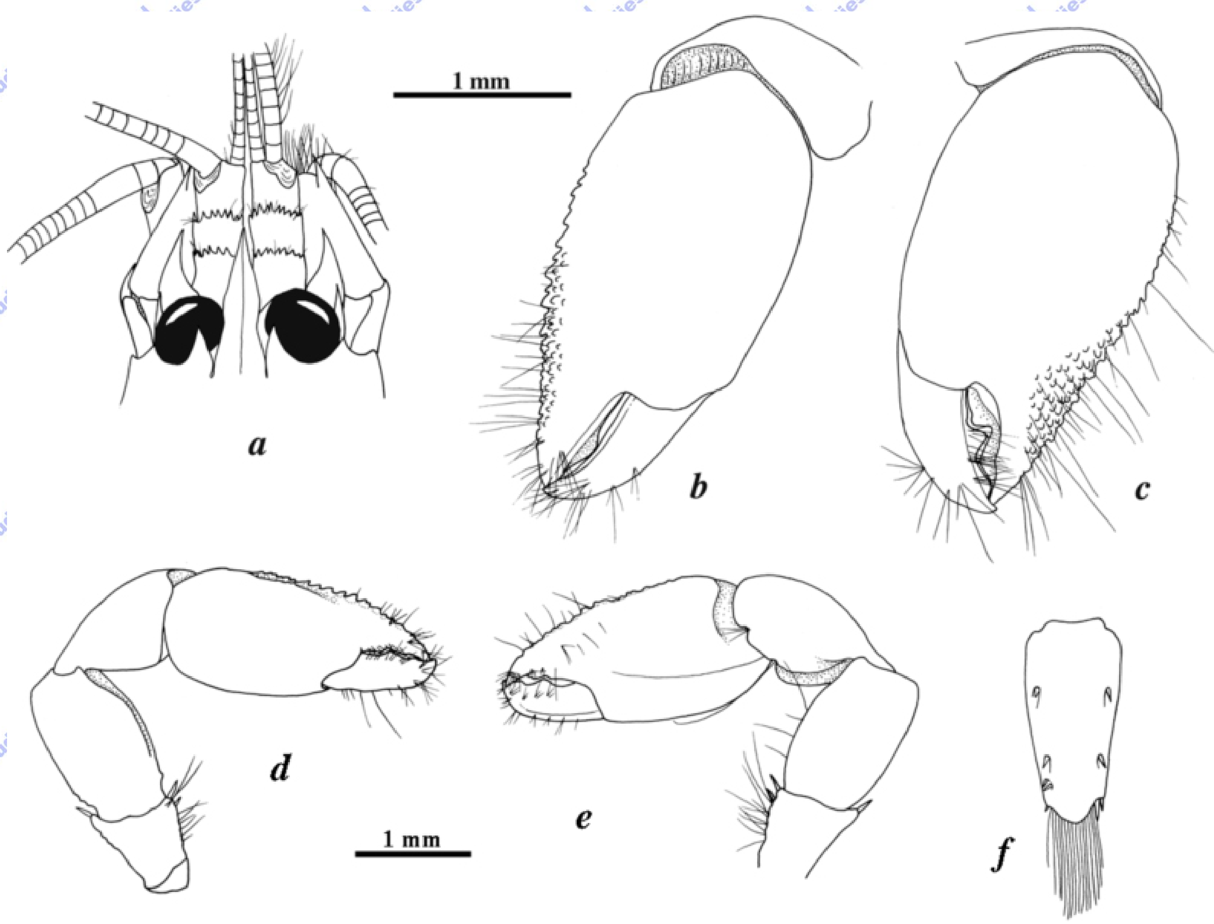

Fig. 5. *Rugathanas verrucosus* (Banner and Banner, 1960) comb. nov., male from Kenting, southern Taiwan (ASM) (a-c); ovigerous female from Norfolk I. (NTM) (d-f); (a) frontal region; (b) male minor chela, lateral view; (c) male major chela, lateral view; (d) female cheliped, lateral view; (e) same, mesial view; (f) abnormal telson.

Arete Stimpson, 1860 *sensu stricto*

Arete Stimpson 1860: 32.

Diagnosis: Body relatively stout. Carapace smooth, not setose. Frontal margin with long, straight rostrum, bearing acute tip, without subdistal tooth on ventral margin. Extra-corneal teeth acute, not protruding beyond anterior margin of eye; supra-corneal teeth absent or feebly developed; infra-corneal teeth absent. Orbital hoods absent; eyes exposed in dorsal and lateral view. Pterygostomial margin usually rounded or angular, sometimes acute. Cardiac notch well developed. Sixth abdominal segment with articulated plate at posteroventral angle; preanal plate acutely produced. Antenules with finely serrated distal margin of 1st segment; ventromesial carina of 1st segment with strong tooth; lateral flagellum with well-developed secondary ramus. Antenna with normal, not particularly stout basicerite, distolateral tooth always present; scaphocerite broadly oval or rounded. Mandible with palp, incisor process slightly expanded, distally with no more than 12 small teeth. Maxillule with bilobed palp, both ventral and dorsal lobes with setae. Labrum not swollen or protruding. Third maxilliped with distally projecting dorsal margin of antepenultimate segment; penultimate segment rectangular, about as long as or slightly longer than wide; ultimate segment with short spines on tip. First pereiopods (chelipeds) feebly sexually dimorphic, equal or subequal, usually subsymmetrical, sometimes asymmetrical (major cheliped situated on either side), stout, carried extended with dactylus in lateral or ventrolateral position; coxa unarmed mesially; ischium usually with strong tooth mesially and with lobes or teeth possessing spines on dorsal margin; basis with rudimentary exopod; merus robust, flattened ventrally; carpus swollen, cup-shaped, embracing proximal portion of palm distally, ventral side somewhat flattened, not deeply excavated; chela smooth, without sculpturing, compressed; palm sometimes with acute distal projection on mesial side proximal to articulation with dactylus, without or with feebly marked linea impressa; fingers armed with teeth, sometimes interrupted by large hiatus, without cavity-tooth system. Carpus of 2nd pereiopod bearing 4 segments. Third pereiopod with ischium unarmed or bearing 1 spine on ventrolateral margin; merus without spines, sometimes with distoventral margin ending in angular or acute projection; carpus unarmed; propodus armed with spines; dactylus stout, biunguiculate. Fifth pereiopod with poorly developed propodal brush (at most 3 rows of setae). Second pleopod with appendix interna and appendix masculina in males and sometimes females. Telson with 2 pairs of dorsal spines and 2 pairs of posterolateral spines; anal tubercles lacking. Gill/exopod formula summarized in following table.

	Mxp1	Mxp2	Mxp3	P1	P2	P3	P4	P5
Pl	-	-	-	+	+	+	+	+
Ar	-	-	-	-	-	-	-	-
Pd	-	-	-	-	-	-	-	-
Ma	-	-	+	+	+	-	-	-
Se	-	-	-	+	+	+		
Ex	+	+	+	r	r	-	-	-

Type species: *Arete dorsalis* Stimpson 1860: 32; type locality: Hong Kong. Synonyms: *Athanas mascarenicus* Richters 1880: 164; *Arete dorsalis pacificus* Coutière 1903: 84; *Arete maruteensis* Coutière 1905: 866; *Arete maruteensis salibabuensis* de Man 1910: 313; ? *Arete kominatoensis* – Suzuki 1970: 2 (not Kubo 1942).

Other species included: Three described and at least 2 undescribed species (K. Nomura, pers. obs.; A. Anker pers. obs.) are included in *Arete*.

Arete acanthocarpus (Miya and Miyake 1968) [*Athanas acanthocarpus* Miya and Miyake 1968: 157]; type locality: Okinawa, Japan.

Arete amboinensis de Man 1910: 25; type locality: Ambon, Indonesia. Specific status needs confirmation.

Arete indicus Coutière 1903: 84; type locality: not designated, type specimens from Djibouti and Hulule Male Atoll, Maldives. Synonyms: *Arete iphianassa* de Man 1910: 312; *Arete intermedius* Yu 1931: 513; ? *Athanas kominatoensis* Kubo 1942: 82 (for synonymy see Banner and Banner 1960 1973, Miya and Miyake 1968).

Arete sp. nov. 1 - *Athanas indicus* – Suzuki 1970: 5 (not Coutière 1903).

Arete sp. nov. 2 - *Athanas dorsalis* – Suzuki 1970: 12 (not Stimpson 1860).

Distribution: Indo-West Pacific: Red Sea, Djibouti, Madagascar, La Réunion, Maldives, Seychelles, Sri Lanka, Japan (including Ryukyu Is.), China, Taiwan, Philippines, Indonesia, Australia (including Lord Howe I.), Micronesia, Melanesia, French Polynesia.

Remarks: *Arete*, as redefined here, may be easily separated from *Rugathanas* by numerous morphological features (see above), and from *Athanas* by the stouter chelipeds (Fig. 7c, e) with large, oval-shaped chelae (vs. slenderer in *Athanas*, Figs. 8e, h, 9); the ischium of the chelipeds often bearing a strong mesial process (Fig. 7d) (unarmed in *Athanas*); the carpus of the 2nd pereiopods bearing 4 segments (Fig. 7h) (vs. mostly 5 in *Athanas*, Fig. 8k); the distoventral margin of the merus of the 3rd pereiopod being angular or subacute (Fig. 7i) (vs. rounded in *Athanas*, Fig. 8l); the dactylus of the 3rd to 5th pereiopods stout (Fig. 7i) (vs. usually slender in *Athanas*, Fig. 8l); the strap-like epipods or mastigobranchs present on 1st and 2nd pereiopods (vs. on 1st to 3rd or 4th pereiopods in *Athanas*); and the preanal plate of the 6th abdominal somite being acutely produced towards the telson (vs. rounded, not produced in *Athanas*). Furthermore, the antepenultimate segment of the 3rd maxilliped usually projects distodorsally in *Arete* (see Bruce 1990a), but not in *Rugathanas* or *Athanas*. The propodal brush on the 5th pereiopod is poorly developed in both *Arete* (cf. Bruce, 1990a) and *Rugathanas* (Fig. 2q), but is well developed in *Athanas* (Fig. 8m).

In *Arete*, both males and females bear enlarged, stout chelipeds, with broadened chelae that are carried extended forward, with the dactylus situated in lateral or ventrolateral position (Fig. 6c, d). The chelipeds of *Athanas* are highly variable in shape (cf. Fig. 6e-h), and may be carried either extended (*Ath. nitescens* (Leach, 1814) species group, cf. Fig. 6e, f), or folded (*Ath. dimorphus* Ortmann, 1894 species group, cf. Fig. 6g, h). The *Ath. nitescens* group may have some affinities with *Arete*, but in none of the species of this group, the chelae are as broad as in *Arete* (compare Figs. 6c, d, 7c-g and Figs. 6e, f, 8e-h, 9), which look like "mini-lobsters" (Fig. 6c, d).

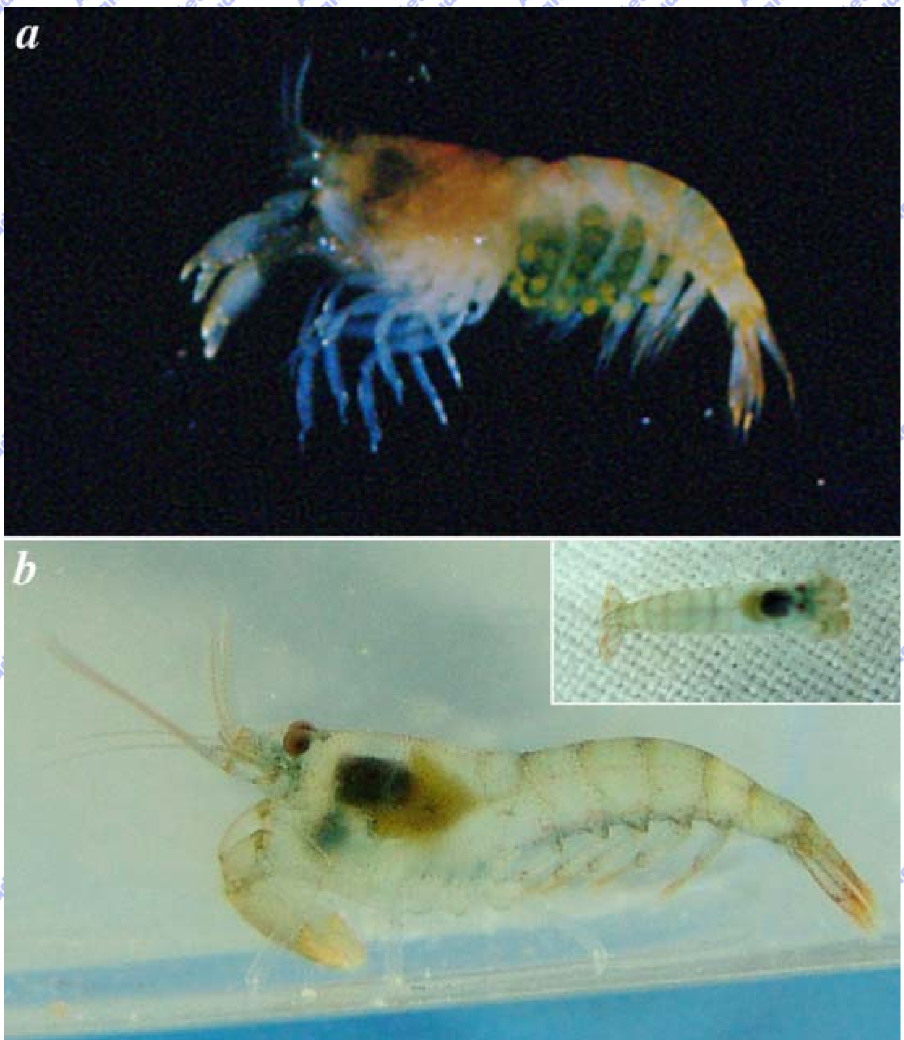

Fig. 6. Habitus of some species of *Rugathanas* gen. nov. (a, b), *Arete* Stimpson, 1860 (c, d), and *Athanas* Leach, 1814 (e-h): (a) *Rugathanas borradailei* (Coutière, 1903) comb. nov., ovigerous female from Kenting, southern Taiwan; (b) *Rugathanas verrucosus* (Banner and

Banner, 1960) comb. nov., male from Kenting, southern Taiwan; (c) *Arete* cf. *dorsalis* Stimpson, 1860, specimen from southern Japan; (d) *Arete* cf. *dorsalis*, shrimp in situ among spines of a sea urchin, Lord Howe I., off eastern Australia; (e) *Athanas areteformis* Coutière, 1903 (*Ath. nitescens* group), male from southern Japan; (f) *Athanas nitescens* (Leach, 1814) (*Ath. nitescens* group), male from Banyuls-sur-Mer, Mediterranean coast of France; (g) *Athanas japonicus* Kubo, 1936 (*Ath. dimorphus* group), ovigerous female from southern Japan; (h) *Athanas amazone* Holthuis, 1951 (*Ath. dimorphus* group), male from Banyuls-sur-Mer, Mediterranean coast of France (photograph credits: a, M.-S. Jeng; b, A. Anker; c, e, g, M. Itoh; d, N. Coleman; f, h, P. Lecomte leg. P. Noël).

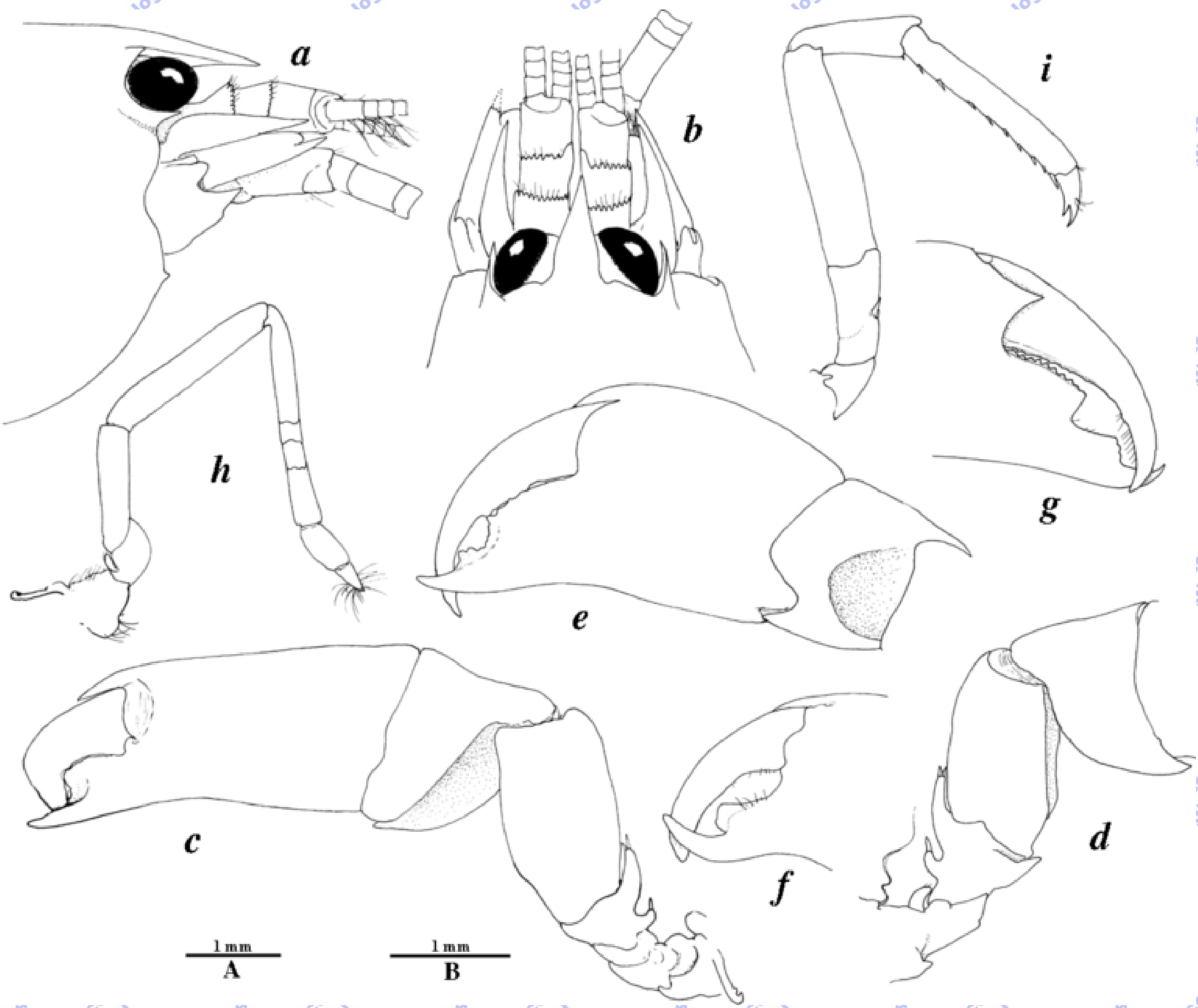

Fig. 7. *Arete* cf. *indicus* Coutière, 1903, 2 males from Sesoko Beach, Okinawa (ZRC) (a-f, h, i) and male from Sri Lanka (NHMW) (g): (a) - frontal region, lateral view; (b) same, dorsal view;

(c) left cheliped, lateral view; (d) same, coxa to carpus, mesial view; (e) same, chela and carpus, lateral view; (f) fingers of chela of a different specimen, lateral view; (g) fingers of chela of a different specimen, mesial view; (h) 2nd pereiopod; (i) 3rd pereiopod. Scales: A (a-f, h, i), B (g).

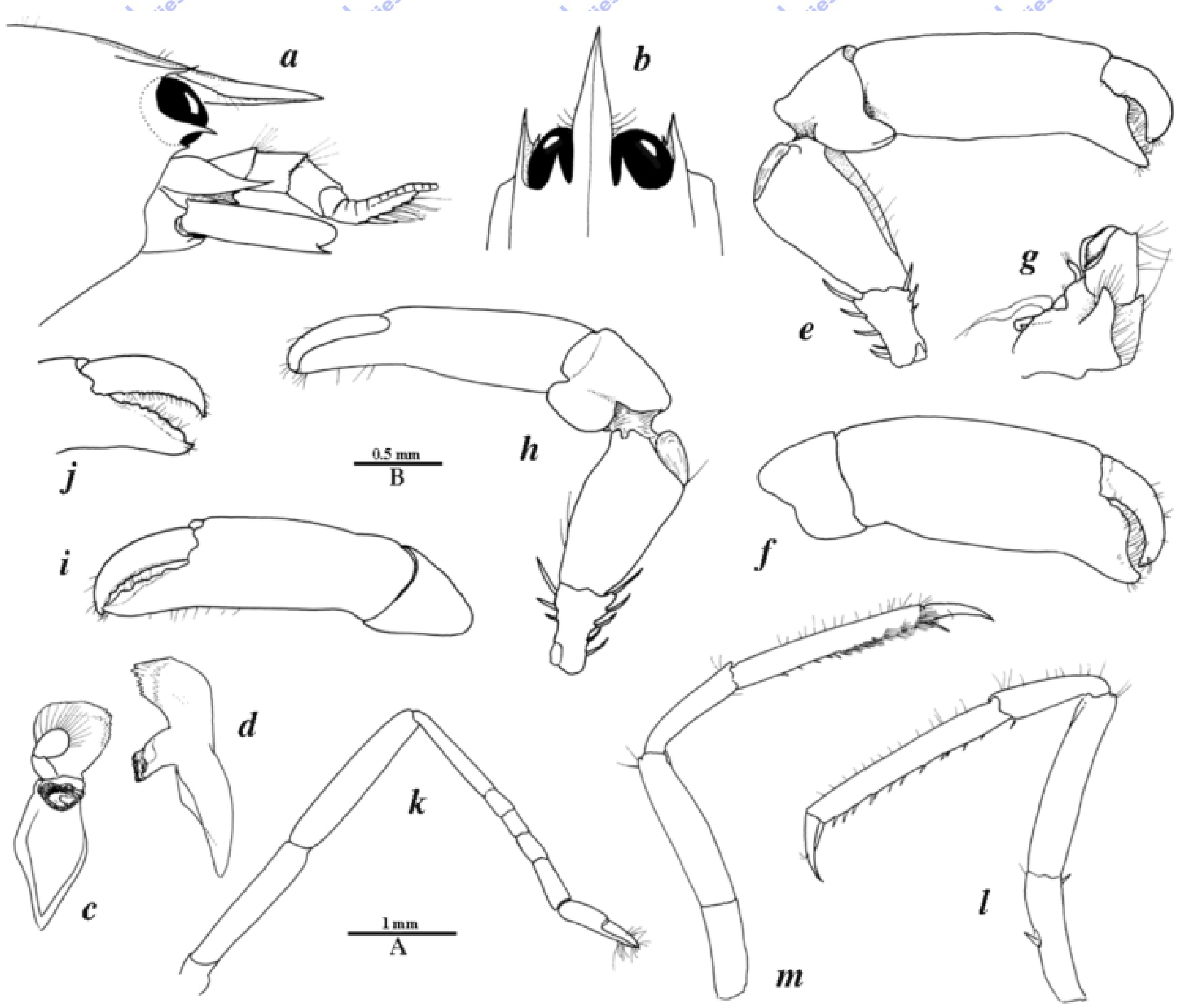

Fig. 8. *Athanas areteformis* Coutière, 1903, male from Papua New Guinea (MNHN): (a) frontal region, lateral view; (b) frontal margin of carapace, dorsal view; (c, d) mandible from 2 different aspects; (e) left (major) cheliped, mesial view; (f) same, chela and carpus, mesial view; (g) same, coxa and basis with exopod; (h) right (minor) cheliped, mesial view; (i) same, chela and carpus, mesial view; (j) same, lateral view; (k) 2nd pereiopod; (l) 3rd pereiopod; (m) 5th pereiopod. Scales: A (a, b, e, f, h-m), B (c, d, g).

All *Arete* species are characterized by a 4-segmented carpus in the 2nd pereiopod and the presence of strap-like epipods on the 1st and 2nd pereiopods. In the vast majority of *Athanas* spp., the carpus of the 2nd pereiopod is composed of 5 segments (A. Anker pers. obs.). Kemp's (1915) reported specimens of *Ath. polymorphus* Kemp, 1915 from Chilka Lake (India) that had either 4 or 5 segments, but in 7 examined specimens of *Ath. polymorphus* from Singapore, the carpus had 5 segments (Anker 2003). In *Ath. squillophilus* Hayashi, 2002, the number of carpal segments varies from 5 to 6 (Hayashi 2002). One of us (AA) also examined a specimen of *Ath. dimorphus* with 6 instead of the typical 5 carpal segments. In most species of *Athanas*, the strap-like epipods are present on the 1st-3rd pereiopods, although *Ath. ohsimai* Yokoya, 1936 appears to have a complete epipod set, i.e., in this species, the strap-like epipods are present on the 1st-4th pereiopods (Yokoya 1936). Banner and Banner (1960) reported an infraspecific variation in the number of pereiopodal epipods in a population of *Ath. djiboutensis* Coutière, 1897, with most specimens having epipods on the 1st and 2nd pereiopods, and only some on the 1st-3rd pereiopods.

Despite all the aforementioned exceptions, the combination of the cheliped features (e.g., chelae broad, oval-shaped in *Arete*, more or less elongated in *Athanas*); the number of carpal segments in the 2nd pereiopod (4 in *Arete*, 5 in *Athanas*, exceptionally 4 or 6); and the number of pereiopodal epipods (on P1 and P2 in *Arete*, on P1-3 in *Athanas*, exceptionally on P1 and P2 or P1-4) enables *Arete* to be distinguished from *Athanas*.

Arete is also ecologically distinct from *Rugathanas* and *Athanas*. All *Arete* species are obligate symbionts of sea urchins (Fig. 6d), mostly species of *Echinometra*, *Anthocidaris*, *Heterocentrotus*, *Heliocidaris*, *Echinothrix*, *Tripneustes*, and *Centrostephanus* (Suzuki 1970, Banner and Banner 1973), and at least 2 species exhibit protandric hermaphroditism (Suzuki 1970, Gherardi and Calloni 1993), which explains the presence of an appendix masculina in some ovigerous specimens. Within *Athanas*, only *Ath. granti* Coutière, 1908 occasionally associates with sea urchins of the genus *Centrostephanus* (Banner and Banner 1973). Remarkably, this species shows some resemblance to *Arete*, but differs in many other respects and clearly belongs to *Athanas* (see below). Protandric hermaphroditism has yet to be documented in *Athanas*, although it is suspected in *Ath. ornithorhynchus* Banner and Banner, 1973, a remarkable species associated with brittle stars (Marin et al. 2005).

As already mentioned, *Arete* requires revision at the species level. The taxonomic status of de Man's "*Arete maruteensis salibabuensis*" placed in synonymy of *Are. dorsalis*, as well as the taxonomic statuses of *Are. iphianassa*, *Are. intermedius*, and *Are. kominatoensis* (originally described as "*Ath. kominatoensis*"), placed in synonymy with *Are. indicus* (Banner and Banner 1973), should be reconsidered. All these forms should be contrasted to 2 species misidentified as *Are. indicus* and *Are. dorsalis* by Suzuki (1970), and which probably represent undescribed species (K. Nomura, pers. comm.). Therefore, many of the previous identifications of *Arete* species (e.g., Banner and Banner 1960 1973, Miya and Miyake 1968, Suzuki 1970, Bruce 1989 1990a), including Bruce's (1990a) redescription of *Are. dorsalis*, are questionable. As such a key to the genus *Arete* is considered premature.

Athanas Leach, 1814 sensu stricto

Athanas Leach 1814: 401.

Diagnosis: Body usually slender. Carapace usually smooth, sometimes setose. Frontal margin with long, straight, slightly ascendant, or descendant rostrum, with acute tip, without subdistal tooth on ventral margin, rarely with teeth on dorsal margin. Extra-corneal teeth present, acute, sometimes protruding beyond anterior margin of eye; supra- and infra-corneal teeth absent or present. Orbital hoods absent; eyes exposed in dorsal and lateral views.

Pterygostomial margin usually rounded, rarely sharply protruding or with small acute tooth. Cardiac notch well developed. Sixth abdominal segment with articulated plate at posteroventral angle; preanal plate rounded. Antennules with straight, not serrated distal margin of 1st segment; ventromesial carina of 1st segment with strong tooth; lateral flagellum with well-developed secondary ramus. Antenna with normal, not particularly stout basicerite, distolateral tooth present; scaphocerite variably oval to subrectangular, usually more or less elongated. Mandible with palp, incisor process usually not expanded, distally with 5-8 medium-sized teeth, rarely expanded, with 12-15 minute teeth. Maxillule with bilobed palp, both ventral and dorsal lobes with setae. Labrum not swollen or protruding. Third maxilliped without distal tooth on dorsal margin of antepenultimate segment; penultimate segment elongated, distinctly longer than wide; ultimate segment often with spines on tip. First pereiopods (chelipeds) highly variable in shape, size, and degree of asymmetry, often sexually dimorphic or polymorphic, carried folded or extended with dactylus in lateral position; coxa usually with apressed subtriangular tooth mesially; basis with rudimentary exopod; ischium unarmed mesially, usually with spines on dorsal and ventral margins; chelae without linea impressa on palm and without fossa-plunger on fingers. Male chelipeds usually enlarged and/or elongated, equal, subequal, or unequal, symmetrical, subsymmetrical, or asymmetrical (with major cheliped situated either on left or right side); ischium sometimes with lobes furnished with spines on dorsal margin; merus usually stout, depressed or excavated ventrally; carpus elongated or cup-shaped, sometimes flattened ventrally; chela highly variable, usually conspicuously swollen or elongated, sometimes with tubercles along ventral margin; fingers usually armed with teeth. Female chelipeds variable from slightly elongated to greatly enlarged, equal, subequal, or unequal, symmetrical, subsymmetrical, or asymmetrical (with major cheliped situated on left or right side); merus variable, slender to stout, flattened or excavated ventrally; carpus elongated or cup-shaped, sometimes flattened ventrally; chelae variable from slender to oval or elongated, sometimes with tubercles along ventral margin; fingers unarmed or armed with teeth. Carpus of 2nd pereiopod bearing 5 segments, exceptionally 4 or 6. Third pereiopod with ischium unarmed or bearing 1 spine on ventrolateral margin; merus unarmed, distoventral margin never acute or angular; carpus unarmed; propodus usually with ventral spines or slender spinules, rarely unarmed; dactylus more or less slender, simple or biunguiculate. Fifth pereiopod with well-developed propodal brush. Second pleopod with appendix interna and appendix masculina in males, appendix interna in females, exceptionally with appendix masculina in ovigerous specimens. Telson with 2 pairs of dorsal spines and 2 pairs of posterolateral spines; anal tubercles absent. Gill formula with somewhat variable number of epipods, as summarized in following table (untypical condition indicated in parentheses).

	Mxp1	**Mxp2**	**Mxp3**	**P1**	**P2**	**P3**	**P4**	**P5**
Pl	-	-	-	+	+	+	+	+
Ar	-	-	-	-	-	-	-	-
Pd	-	-	-	-	-	-	-	-
Ma	-	-	+	+	+	+(-)	-(+)	-
Se	-	-	-	+	+	+	+(-)	-(+)
Ex	+	+	+	r	r	-	-	-

Type species: *Athanas nitescens* Leach, 1814 [*Palaemon nitescens* Leach 1814: 401]; type locality: England. Most important synonyms: *Palaemon laevirhincus* Risso 1816: 108; *Athanas* var. *laevirhincus* (Risso, 1816) Holthuis and Gottlieb 1958: 32; *Arete diocletiana* Heller 1862: 404; *Athanas transitans* Czerniawsky 1884: 25; *Athanas nitescens* var. *suchumicae* Czerniawsky 1884: 24; *Athanas nitescens* forma *rotundicauda* Czerniawsky 1884: 24; *Athanas transitans* var. *longispina* Czerniawsky 1884: 25; *Athanas transitans* var. *pontica*

Czerniawsky 1884: 26; *Athanas veloculus* Bate 1888: 529. The taxonomic statuses of *Ath. laevirhincus* and *Ath. veloculus* requires confirmation (see below).

Other species included: *Athanas* includes all the remaining species described mostly under the generic name *Athanas*.

Athanas amazone Holthuis 1951: 111; type locality: Nigeria.

Athanas anatidactylus Anker and Marin 2007: 163; type locality: Vietnam.

Athanas areteformis Coutière 1903: 79; type locality: Hulule Male Atoll, Maldives. Synonyms: *Athanas naifaroensis* Coutière 1903: 77; *Athanas erythraeus* Ramadan 1936: 13; *Athanas dubius* Banner 1956: 322 (see Banner and Banner 1973). The taxonomic statuses of *Ath. naifaroensis*, *Ath. erythraeus* and *Ath. dubius* require confirmation.

Athanas crosslandi Tattersall 1921: 372; type locality: Khor Dongonab, Red Sea.

Athanas dentirostris Anker, Jeng and Chan 2001: 1049; type locality: Haiphong, Vietnam.

Athanas dimorphus Ortmann 1894: 12; type locality: Dar es Salaam, Tanzania. Synonyms: *Alpheus monoceros* (Heller 1862: 274, *nomen dubium*); *Athanas setoensis* Kubo 1951: 265; *Athanas dimorphus seedang* Banner and Banner 1966b: 28 (see Banner and Banner 1960 1973). The taxonomic statuses of *Ath. setoensis* and *Ath. dimorphus seedang* require confirmation.

Athanas djiboutensis Coutière 1897: 233; type locality: Djibouti. Synonym: *Athanas sulcatipes* Borradaile 1898: 1011 (see Banner and Banner 1960 1973).

Athanas esakii Kubo 1940: 93; type locality: “Kusaie”, possibly Kosrae, Caroline Is.

Athanas gracilipes Banner and Banner 1978: 234; type locality: South China Sea.

Athanas gracilis Boone 1935: 122; type locality: Raiataea, Society Is.

Athanas granti Coutière 1908: 192; type locality: Adelaide, South Australia.

Athanas grimaldii Coutière 1911: 1; type locality: not designated, type specimens from Biscaya Gulf, France and Cape Verde Is.

Athanas haswelli Coutière 1908: 192 (amended from the original spelling *Ath. hasswelli* by Banner and Banner 1973); type locality: Adelaide, South Australia.

Athanas hongkongensis Bruce 1990b: 624; type locality: Hong Kong.

Athanas japonicus Kubo 1936: 43; type locality: Yamaguchi, Japan. Synonyms: *Athanas lamellifer* Kubo 1940: 102 (see Miya and Miyake 1968). The taxonomic status of *Ath. lamellifer* needs clarification.

Athanas jedanensis de Man 1910: 313; type locality: Pulau Djedan, eastern Indonesia.

Athanas locincertus Banner and Banner 1973: 311; type locality: "Panchoran Buoy", possibly in western Australia.

Athanas marshallensis Chace 1955: 17; type locality: Marshall Is.

Athanas minikoensis Coutière 1903: 76; type locality: Minikoy Atoll, Laccadives.

Athanas naga Banner and Banner 1966b: 26; type locality: Gulf of Siam, off Thailand.

Athanas nouvelae Holthuis 1951: 104; type locality: Cape Verde Is.

Athanas ohsimai Yokoya 1936: 129; type locality: Sagami Bay, Japan.

Athanas orientalis Pearson 1905: 88; type locality: Gulf of Manaar, Sri Lanka.

Athanas ornithorhynchus Banner and Banner 1973: 319; type locality: not designated, type specimens from Northern Territory and Western Australia.

Athanas parvus de Man 1910: 315; type locality: Timor, Indonesia. Synonym: *Athanas sibogae* de Man 1910: 314 (see Banner and Banner 1973, Chace 1988).

Athanas phyllocheles Banner and Banner 1983: 152; type locality: off La Réunion.

Athanas polymorphus Kemp 1915: 295; type locality: Chilka Lake, eastern India.

Athanas rhothionastes Banner and Banner 1960: 142; type locality: Canton, Phoenix Is.

Athanas squillophilus Hayashi 2002: 396; type locality: southern Hokkaido, Japan.

Athanas stebbingi de Man 1920: 106; type locality: Pulau Bawean, Indonesia.

Athanas tenuipes de Man 1910: 316; type locality: Sulawesi, Indonesia.

Athanas sp. nov. 1 aff. *dimorphus* (A. Anker pers. obs.), Pulau Bintan, Indonesia.

Athanas sp. nov. 2 aff. *parvus* (A. Anker pers. obs.), Vietnam.

Athanas sp. nov. 3 aff. *amazone* (A. Anker pers. obs.), Ivory Coast.

Athanas sp. nov. 4 aff. *phyllocheles* (A. Anker pers. obs.), New South Wales, Australia.

Distribution: Indo-West Pacific from the Red Sea to southern Africa, Australia, French Polynesia, and Japan; eastern Atlantic from southern Norway and Ireland to southeastern Africa, including the Mediterranean and Black Seas (absent from central and western Atlantic and eastern and north-central Pacific).

Remarks: *Athanas*, as redefined here, differs from *Rugathanas* and *Arete* in several morphological features (see descriptions of *Rugathanas* and *Arete* above). The presence of a subtriangular projection on the mesial face of the cheliped coxa, a previously unconsidered feature, may turn out to be a further diagnostic feature of *Athanas*. This projection was present in all 12 personally examined species of *Athanas* (A. Anker pers. obs.), including *A. dimorphus*, *A. nitescens*, and *A. areteformis* (Fig. 8g), but is absent from all species of *Arete* and *Rugathanas*.

With over 30 species, *Athanas* remains a relatively heterogeneous genus. It was subdivided into 2 informal species groups by Coutière (1899), the *Ath. nitescens* group (chelipeds carried extended) and the *Ath. dimorphus* group (chelipeds carried folded). The *Ath. nitescens* group appears to be relatively homogenous, except for the somewhat aberrant *Ath. areteformis* and *Ath. granti*. However, these 2 species clearly belong to the *Ath. nitescens* group based on the features of the chelipeds (see below). The *Ath. dimorphus* group is much more heterogeneous and may be further subdivided into several smaller groups mainly defined by the features of the chelipeds, frontal teeth, and walking legs (A. Anker pers. obs.). However, the complex intrageneric structure of *Athanas* is beyond the scope of this study and will be examined elsewhere.

The placement of *Ath. areteformis* within the *Ath. nitescens* group is based mainly on the features of the male chelipeds. The shape of the frontal margin of the carapace (Fig. 8a, b) and the expanded incisor process of the mandible (Fig. 8c, d) of this species are superficially similar to those of *Rugathanas*, but the chelipeds (Fig. 8e-j), in particular the stout major chela (Fig. 8f), greatly differ from the chelipeds of *Rugathanas*, and more closely resemble those of *Ath. grimaldi* or *Are. indicus* (Fig. 7). The specific name *Ath. areteformis* (resembling *Arete*) given by Coutière (1903) refers to the general resemblance of the chelipeds of this species to the chelipeds of *Arete*. Banner and Banner (1960) misinterpreted this as Coutière's doubts about the distinction between *Arete* and *Athanas*. Despite some similarities with *Rugathanas* and *Arete*, *Ath. areteformis* plainly belongs to the genus *Athanas*, as redefined above, because of the general shape of the chelipeds, the non-extensible dactylus of the 3rd-5th pereiopods, the well-developed row of setae on the propodus of the 5th pereiopod, as well as the presence of 3 strap-like epipods on the pereiopods (P1-3).

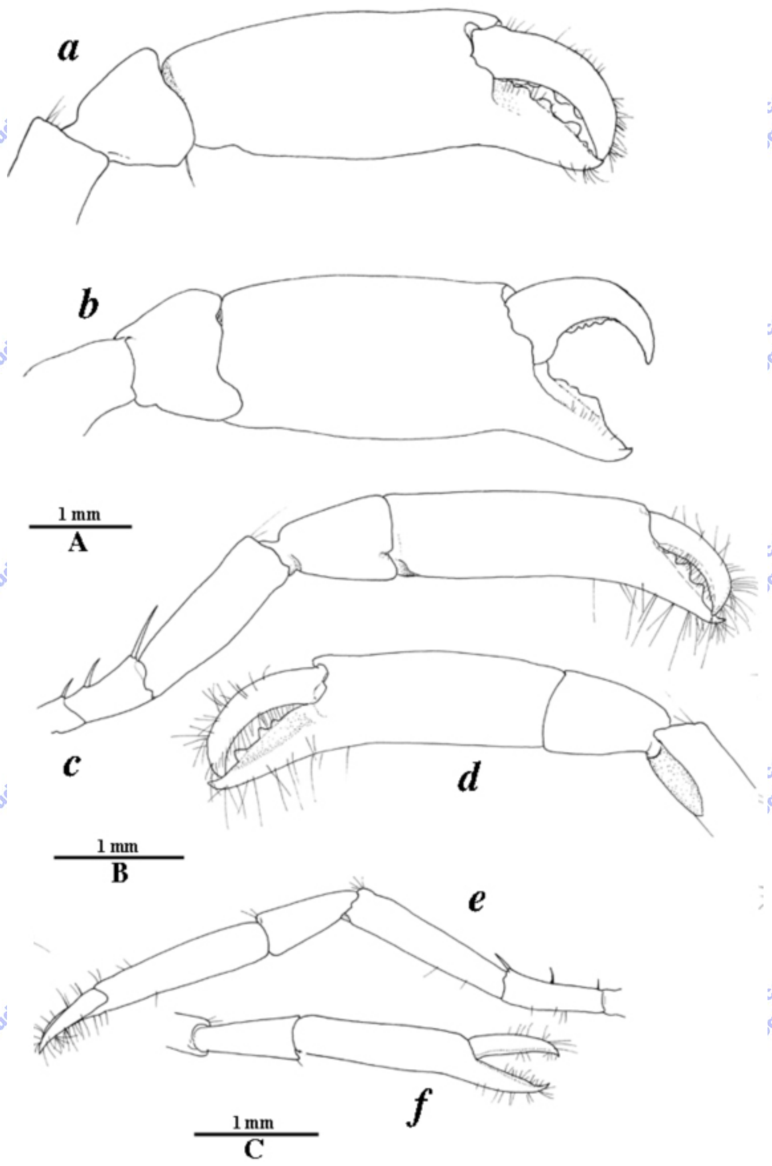

Fig. 9. Chelipeds of 3 species from the *Athanas nitescens* group: (a) *Athanas grimaldii* Coutière, 1911, male from Senegal (MNHN), major cheliped, carpus, and chela, mesial view; (b) *Athanas granti* Coutière, 1908 from southern Australia, type (MNHN), major cheliped, carpus, and chela, mesial view; (c-f) *Athanas* cf. *nitescens* (Leach, 1814) from Senegal (MNHN), (c) male cheliped, lateral view; (d) same, chela and carpus, mesial view; (e) female cheliped, lateral view; (f) same, chela and carpus. Scales: A (a), B (b), C (c-f).

Another species that shows some morphological and ecological resemblance to *Arete* is *Ath. granti*. This species also has a robust major cheliped (Fig. 9b), stout biunguiculate dactylus on the 3rd-5th pereiopods, and is furthermore, facultatively associated with the sea urchin *Centrostephanus rodgersii* (Agassiz, 1863) (Banner and Banner 1973). However, the shape of the frontal margin; the marked asymmetry of the chelipeds (the minor cheliped being much slenderer, see Banner and Banner 1973); the 5-segmented carpus of the 2nd pereiopod; the number of pereiopodal epipods; and the absence of tooth on the mesial face on the cheliped ischium, all indicate that *Ath. granti* is indeed a member of *Athanas*. Furthermore, in none of the species of the *Ath. nitescens* group, including *Ath. nitescens* (Fig. 9c, d), *Ath. grimaldii* (Fig. 9a), *Ath. aretefromis* (Fig. 8f), and *Ath. granti* (Fig. 9b), does the palm of the chela reach the same broadness as in *Arete* (Fig. 7). Banner and Banner (1973) reported the presence of a median flap on the 5th abdominal sternite in *Ath. granti* and *Are.* sp. cf. *dorsalis*. Interestingly, this flap was absent from the closely related *Are.* sp. cf. *indicus* (both *Are. dorsalis* and *Are. indicus* were probably misidentified by Banner and Banner (1973), see above). The function of this odd flap is unknown; it may have evolved independently in some *Arete* species and in *Ath. granti*, and perhaps plays a role in the symbiosis with the sea urchins. On the other hand, it is also possible that the *Arete* clade evolved from ancestors within *Athanas*, in which case the latter genus would be paraphyletic and require further splitting. The absence of a phylogeny of the *Athanas* complex (based on molecular and/or morphological characters) and the morphological complexity of *Athanas* make further conclusions impossible.

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Figure legends