

Symbiosis between the Alpheid Shrimp, *Athanas ornithorhynchus* Banner and Banner, 1973 (Crustacea: Decapoda), and the Brittle Star, *Macrophiothrix longipeda* (Lamarck, 1816) (Echinodermata: Ophiuroidea)

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(Accepted February 2, 2005)

Ivan N. Marin, Arthur Anker, Temir A. Britayev, and A. Richard Palmer (2005) Symbiosis between the alpheid shrimp, *Athanas ornithorhynchus* Banner and Banner, 1973 (Crustacea: Decapoda), and the brittle star, *Macrophiothrix longipeda* (Lamarck, 1816) (Echinodermata: Ophiuroidea). *Zoological Studies* 44(2): 234-241. The rarely collected alpheid shrimp, *Athanas ornithorhynchus* Banner and Banner, characterized by a unique platypus bill-shaped dactylus of the minor cheliped, is reported for the first time from Vietnam. Most shrimps were found directly on the arms of large brittle stars, *Macrophiothrix longipeda* (Lamarck), which were dwelling under mud-covered boulders, at depths between 16 and 35 m. The association of the shrimps with the ophiuroids observed in the field, the close attachment of the shrimps to their hosts in aquaria, and the disruptive colour pattern, which renders shrimps cryptic against the arms of their host suggest that *A. ornithorhynchus* lives symbiotically with *Macrophiothrix*, at least locally in Nhatrang Bay, Vietnam. The possible trophic dependence of the shrimps on their hosts remains to be shown. This is the first report of a possibly stable association between an alpheid shrimp and a brittle star. <http://www.sinica.edu.tw/zool/zoolstud/44.2/234.pdf>

Key words: Alpheidae, *Athanas*, Ophiuroidea, symbiosis, Vietnam.

Ophiuroids are among the most common and conspicuous macro-invertebrates in shallow water habitats. Many species live in association with larger invertebrates, such as sponges, corals and other echinoderms (e.g., Baker et al. 2001, Tominaga et al. 2004, Henkel and Pawlik 2005). However, ophiuroids themselves may serve as hosts for many smaller symbiotic animals, including polychaetes, myzostomids, copepods, amphipods, and shrimps (e.g., Barel and Kramers 1977, Bruce 1982, Volbehr and Rachor 1997, Martin and Britayev 1998). The symbiotic associations between brittle stars and caridean shrimps are rather rare and poorly documented (Bruce

1971 1975 1982). Some of the better-known ophiuroid symbionts among the Decapoda are the pontoniine shrimps of the genus *Periclimenes* Costa. For instance, *Periclimenes lanipes* Kemp is associated with the large, gorgonocephalid basket stars (in the ophiuroid order Euryalida), *Euryale purpurea* Mortensen, *Astroboa nuda* (Lyman) and *Astroglymma sculptum* (Döderlein), in the tropical Indo-West Pacific (Bruce 1971 1982, Debelius 2000), while *P. perryae* Chace is associated with the giant basket star, *Astrophyton muricatum* (Lamarck), in the tropical and subtropical Western Atlantic (Chace 1972, Humann and Deloach 2002).

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Within the Alpheidae (snapping shrimps and their relatives), a large and diversified family, members of only three genera are known to be associated with brittle stars. *Arete dorsalis* Stimpson (identification questionable, A. Anker, pers. obs.), normally associated with sea urchins (e.g., Suzuki 1970, Banner and Banner 1973, Bruce 1990a) was found on one occasion to be associated with the brittle star, *Ophiocoma anaglyptica* Ely (Banner and Banner 1973). Several normally free-living species of *Alpheus* and *Metalpheus* have also been reported to be occasional associates of brittle stars: *Alpheus collumianus* Stimpson with *Ophiothrix* (*Keystonia*) sp. and *Placophiothrix* sp. (Banner and Banner 1983), *A. macrochirus* Richters and *A. strenuus* Dana with *Macrophiothrix longipeda* Lamarck (Banner and Banner 1978, 1983), *A. serenei* Tiwari with *Macrophiothrix* sp. (Bruce and Coombes 1997), and *Metalpheus paragracilis* (Coutière) with *Ophiocoma* sp. (Banner and Banner 1983). All these associations are clearly facultative or just accidental. For instance, *A. strenuus* often lives in self-constructed burrows under large intertidal boulders, a microhabitat often shared with other invertebrates, including amphinomid worms, *Eurythoe* sp. (fire worms), and brittle stars. The presence of fire worms may offer protection to both snapping shrimps (Gassel 1994) and brittle stars; this is probably the only reason why the latter animals are often found together.

Members of the genus *Athanas* (sensu stricto, excluding *Arete*), were previously not known to be symbionts of brittle stars, although one species, *A. granti* Coutière, is associated with sea urchins (Banner and Banner 1973), and several others are associated with other marine animals, such as stomatopods (Frogliia and Atkinson 1998, Hayashi 2002), thalassinideans (Anker et al. 2001), and crinoids (Marin and Anker, in prep.). During a field study of the invertebrate biodiversity of Nhatrang Bay, Vietnam, several specimens of the genus *Athanas* were collected from the brittle stars *Macrophiothrix longipeda*. These specimens were identified as *Athanas ornithorhynchus* Banner and Banner, originally described from northwestern Australia (Banner and Banner 1973) and known only from a handful of other localities in the Indo-West Pacific (Bruce 1990b, Nomura et al. 1996, Nomura and Asakura 1998). The biology of this unique species, characterized by a platypus bill-shaped minor chela, was previously unknown. In this study, we report on *A. ornithorhynchus* as a symbiont, perhaps obligate, of the brittle star, *M. longipeda*.

MATERIAL AND METHODS

Dead massive corals were collected by scuba diving at several sites in Nhatrang Bay in Sept.-Nov. 2003. Coral blocks lying on sandy and muddy bottoms were lifted from depths of about 15-35 m, and broken into smaller pieces. The associated fauna was extracted and sorted. Most animals were returned to the laboratory and photographed alive. Live ophiuroids were also photographed in situ. Subsequently, shrimps and their hosts were fixed in a 4% buffered seawater formalin solution for 2-3 days and then preserved in 70% ethanol. Specimens were identified with the help of a light microscope and drawn with the aid of a camera lucida.

RESULTS

In total, six specimens of *A. ornithorhynchus* were collected in Nhatrang Bay, Vietnam: five females in the vicinity of Mung I. (12° 15'01"N, 109° 19'13"E) and one male off Tre I. (12° 10'24"N, 109° 19'40"E). All specimens were found on or closely associated with *Macrophiothrix longipeda*, dwelling in dead corals and mud-covered rocks, at depths of 15-35 m. No shrimps were found on about 20 specimens of *M. longipeda* collected from waters shallower than 15 m.

The largest shrimp measured 8.4 mm in total length from the tip of the rostrum to the posterior margin of the telson. The shrimps were found twice as pairs of adult females (Fig. 2d), and twice as a single female or male individual (Fig. 2c, e, f). In all but one case, they were collected from the arms of brittle stars; in one case, a single female was collected from a deep crevice in the dead coral, from which a brittle star had been extracted a short time beforehand. The shrimps preferred the usually non-exposed parts of the host, and were located mostly on the dorsal or lateral surface of the arms, among strong spines (Fig. 2c-f) and close to the disc. Interestingly, they were never observed on the disc itself. The shrimps would firmly cling to the brittle stars and stay on their hosts even when the latter were taken out of the water. They did not leave their host during the entire observation period in the aquarium (5-6 days). When chased with a pair of forceps, the shrimp quickly moved along the ophiuroid arm, thus avoiding leaving the brittle star and going down onto the substrate, and they did not swim away. No feeding behaviour was observed.

Morphologically, our female specimens (Fig. 1) agree almost perfectly with the type specimens of *A. ornithorhynchus* from Australia (see Banner and Banner 1973) and also with the specimens from Japan (see Hayashi 1995). Similarly Bruce (1990b) noted that his single specimen of *A. ornithorhynchus* from Hong Kong showed no significant difference with the type specimens. However, the single male specimen from Nhatrang Bay remarkably differed from the other specimens in the shape of the chelipeds. Both chelipeds of this male were enlarged, equal in size, and symmetrical in shape, without the typical minor chela bearing flattened, platypus bill-shaped fingers. Surprisingly, this specimen had a well-developed appendix masculina and was ovigerous. In all other morphological features and the colour pattern, this male specimen agrees with the other specimens, and it seems unlikely that the development of the chelipeds is in some way abnormal (e.g., due to unusual regeneration or developmental abnormality). A more-detailed description of *A. ornithorhynchus* specimens from Nhatrang Bay, including a discussion of possible sexual dimorphism in this species, will be provided elsewhere (Marin and Anker, in prep.).

The colour pattern (Fig. 2c-f) perfectly matches the pattern described by Bruce (1990b) and the pattern in the colour photograph published by Bruce (1993). We noted some variations in the width of the red and white bands, and in the coloration of the tail fan, including the telson and the

uropods (Fig. 2d, f). Interestingly, the same individual may have differently coloured uropods (Fig. 2f).

DISCUSSION

Geographic distribution and morphology

The discovery of *A. ornithorhynchus* in Vietnam constitutes the first record of this species for this country and the southern South China Sea. This species was previously known only from several localities in Australia (Banner and Banner 1973, Bruce 1988 1993), southern Japan (Hayashi 1995, Nomura et al. 1996 1998, Nomura and Asakura 1998), and Hong Kong (Bruce 1990b).

Athanas ornithorhynchus is morphologically well defined within the genus *Athanas* by several characters, including the elongated, slender rostrum (Fig. 1a), the biunguiculate dactylus on the third to fifth pereopods, with somewhat variable position of the ventral unguis (Fig. 1e), the strongly asymmetrical female chelipeds (Fig. 1b, c), and the shape of the minor chela, which resembles the bill of a platypus or a duck (Fig. 1c, d). The flattened and broadened dactylus characterizes the second chelipeds of several pontonine shrimps, e.g., *Periclimenes soror* Bruce, associated with sea stars, and *Tuleariocaris zanzibarica* Bruce, associated with sea urchins (Bruce 1982). However, in none of these shrimps does the dactylus

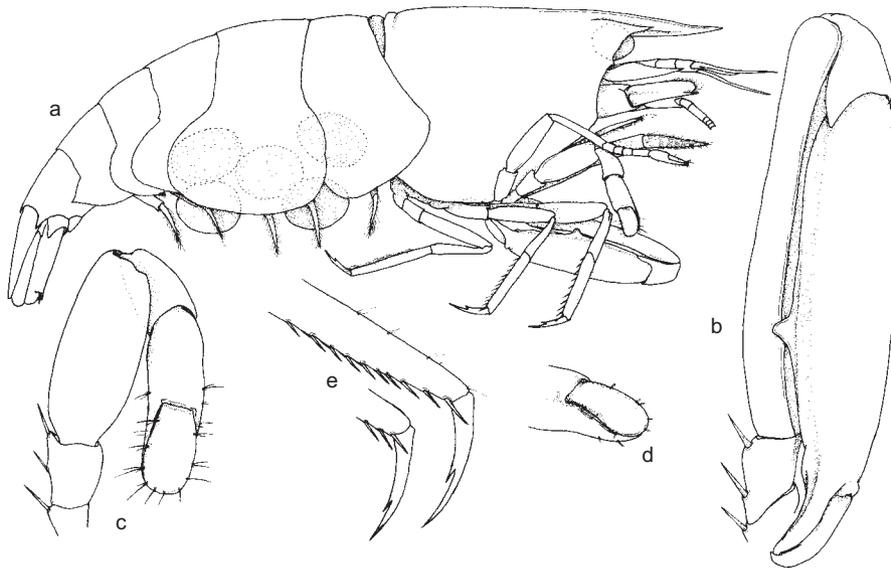


Fig. 1. *Athanas ornithorhynchus*, ovigerous female (CL 3.4 mm) from Nhatrang Bay: a – habitus; b – major cheliped; c – minor cheliped; d – same, dactylus; e – third pereopod, right (upper) and left (lower) dactylus.

lus have the shape of a platypus bill.

The small tubercle on the ventral margin of the palm of the major chela (Fig. 1b) can serve as a locking mechanism, fixing the chela to the merus when the chelipeds are folded. However, this

tubercle is not restricted to *A. ornithorhynchus*, it is also present (either as a single tubercle or a series of tubercles) in several other species of the *Athanas dimorphus* group and several other closely related alpheid genera (A. Anker, pers. obs.).

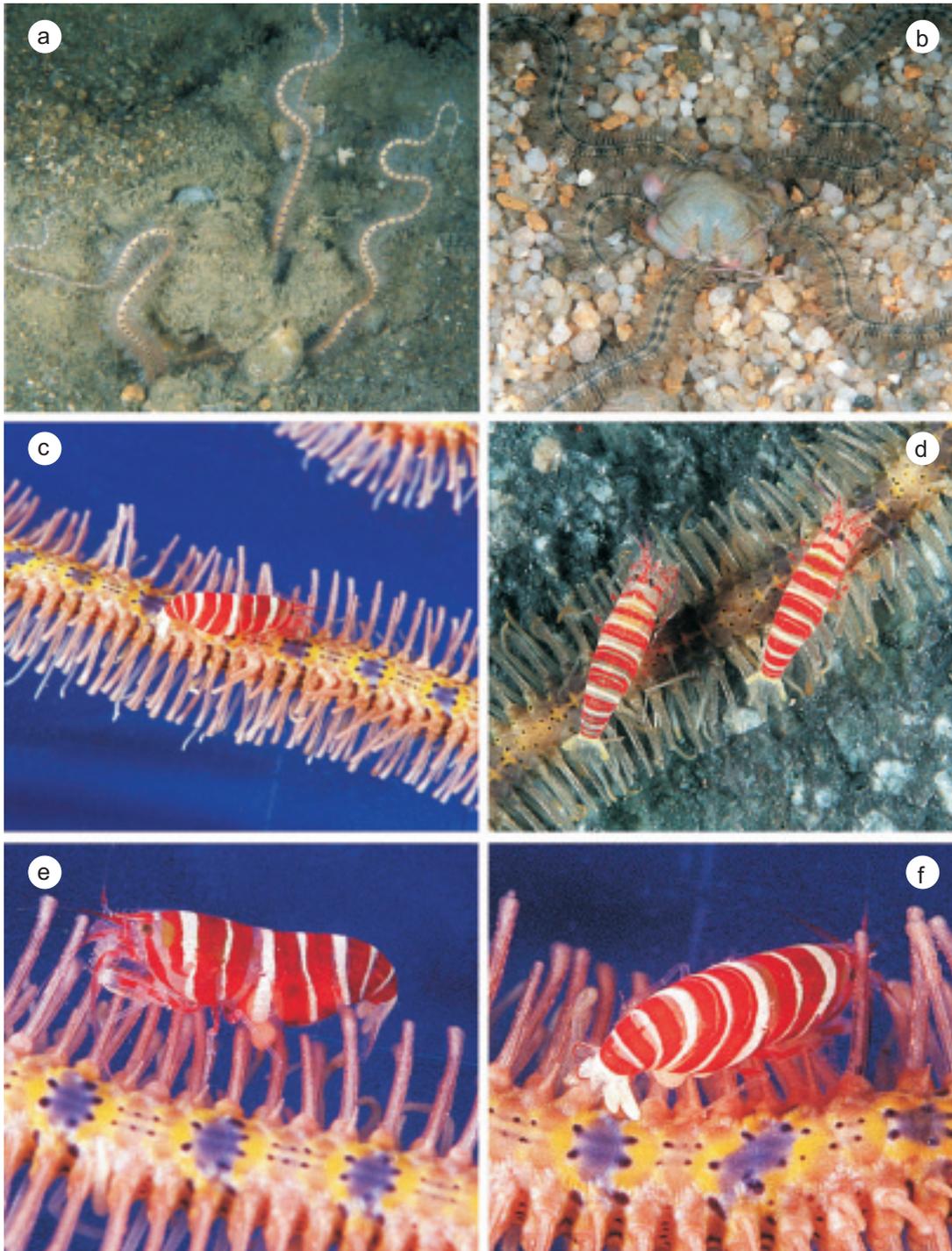


Fig. 2. (a) *Macrophiolithrix longipeda*, feeding, *in situ*, 35 m; (b) *M. longipeda*, colour variation, specimen from 16 m; (c) *Athanas ornithorhynchus*, ovigerous female on *M. longipeda* from 35 m; (d) *A. ornithorhynchus*, 2 females on *M. longipeda* from 16 m; e, f - same as c, different aspects.

Symbiosis and life history

Athanas ornithorhynchus is a rare species previously known only from a few specimens and originally believed to be free-living. The type specimens were "taken from pearl shell growth" and dredged from about 18 m (Banner and Banner 1973). The single Hong Kong specimen was collected from coral rubble by divers (Bruce 1990b). Also, no particular association was noted for the Japanese specimens (K. Nomura, pers. comm.). The specimens reported as *A. ornithorhynchus* from the Great Barrier Reef, associated with the crinoid *Himerometra* sp. (Bruce 1987) most likely belong to a closely related undescribed species (A. Anker, pers. obs., see also below).

Macrophiothrix longipeda (Ophiotrichidae) is a large and fairly common brittle star (with a disc diameter of up to 40 mm and long arms that, when fully extended, may be up to 80 cm long) widely distributed in the Indo-West Pacific (Davie 1998). This species is found mostly on rocky and sandy-rocky shores, close to coral reefs, often under stones and in coral rubble. In Nhatrang Bay, *M. longipeda* was observed from the intertidal zone to about 25-30 m (I. Marin, pers. obs.). *Macrophiothrix longipeda* apparently has several "colour morphs" (Davie 1998, I. Marin, A. Anker, pers. obs.); two are illustrated here (Fig. 2a, b). The brighter colour variation occurred in deeper waters, the darker was found in shallower waters. However, these two distinct colour morphs may actually represent two cryptic species (see also Davie 1998). No other macroanimals were found on *M. longipeda* in Nhatrang Bay, although several symbionts have been recorded from *Macrophiothrix*, including *M. longipeda*, elsewhere. Among these are the parasitic eulimid snail, *Stilapex thielei* (Sturany) (Waren 1981), and polychaete polychaetes, *Hololepidella* spp. (T. Britayev, pers. obs.). *Macrophiothrix longipeda* is also a permanent member of a large complex of animals associated with dead coral galleries (Morton and Morton 1983, Morton 1988).

Three lines of evidence suggest that *A. ornithorhynchus* may have a close, perhaps even obligate, symbiotic association with *M. longipeda*. First, all specimens mentioned here – six in total – were found exclusively on the brittle star, *M. longipeda* (Lamarck), although this might be peculiar to Nhatrang Bay. Second, the behavioural observations revealed that the shrimps preferred to stay on their hosts in the aquarium, even when the host was removed from the water or when the

shrimp was harassed. This suggests that *Macrophiothrix* was more than just a convenient substratum, and it is not impossible that the shrimps may receive some protection (at least from small-sized predators) by hiding beneath the long arm-spines of *Macrophiothrix* (Fig. 2c, d). Third, the distinctive colour pattern of *A. ornithorhynchus* appears to render it cryptic against the background of a *Macrophiothrix* arm. The striking bright red and white bands (Fig. 2c, e) appear to be unique not only within the genus *Athanas* but also within the entire family Alpheidae (A. Anker, pers. obs.). Despite these bright colours, the shrimp remains practically invisible at depths below 15 m (I. Marin, pers. obs.) because of the absorption of red light and because of the disruptive pattern created by the alternating dark and light bands. The pontonine shrimp, *Periclimenes lanipes* Bruce, associated with euryalid basket stars, also has transverse, alternating reddish (or reddish-purple) and whitish bands (Bruce 1971, Debelius 2000, A. Anker, pers. obs.). The hippolytid shrimp, *Hippolyte prideauxiana* Leach (= *H. huntii* (Gosse)), associated with feather stars, *Antedon* spp., in the northeastern Atlantic and the Mediterranean Sea, is another example of this type of coloration (Türkyay and Göthel 1990, Wirtz and Debelius 2003).

The feeding habits of this shrimp remain to be studied. Presently there is no direct evidence (i.e., direct observations) that *A. ornithorhynchus* is also trophically associated with *Macrophiothrix*. The duck-billed tip of the minor chela (Fig. 1c, d) is unique within the Alpheidae, with the exception of a newly discovered, undescribed species of *Athanas* associated with crinoids. That species is closely related to *A. ornithorhynchus*, and has a very similar colour pattern (Bruce 1987, A. Anker, pers. obs.) and platypus bill-shaped fingers on both chelipeds (Marin and Anker, in prep.). 'Spoon-tipped' chelae are present in some herbivorous brachyuran crabs, possibly because pointed tips to the chelae would be ineffective at scraping or for nipping bites from fleshy algae (Warner 1977, Wolcott and O'Connor 1992). For similar reasons, the platypus-billed minor chela of *A. ornithorhynchus* appears particularly well suited for stealing delicate food bundles from its suspension-feeding host. Ophiotrichid brittle stars, which include *Macrophiothrix* spp., feed by extending their arms into the current and capturing fine food particles on both the podia and spines (Warner and Woodley 1982). These particles are then bound with mucus into a bolus that is transported

by podia along the oral groove of the arm towards the mouth (Warner and Woodley 1982). This allows the oral disc to remain in the relative security of a crevice or under a stone (e.g., see Fig. 2a). The shrimps may use their platypus-billed minor chela to grasp and remove these fragile bundles of food particles, a task that would probably be more difficult with conventional alpheid chelae. The aforementioned crinoid-associated new species of *Athanas* which is characterized by both chelipeds bearing this type of fingers, may use them in much the same way, i.e., for stealing small food bundles from its similar suspension-feeding crinoid host. The syllid polychaete, *Branchiosyllis exilis* (Gravier), associated with the brittle star, *Ophiocoma echinata* (Lamarck), in Panama exhibits possibly comparable kleptoparasitic behaviour (Hendler and Meyer 1982), and the abovementioned hippolytid shrimp, *H. prideauxiana*, also completes its diet by feeding on organic particles trapped by the cirri of the crinoid arms (Wirtz and Debelius 2003). Due to the small size of these shrimps, the amount of intercepted food would probably be insignificant to the host. Of course, the shrimps may also feed in the immediate vicinity of the brittle star, simply by picking up small organisms and detritus particles from the bottom or uncovered substrate, but the unique form of the minor chela in two species of *Athanas* respectively associated with an ophiuroid and a crinoid suggests a more-specialized function.

The absence of the typical minor cheliped in the unique male specimen of *A. ornithorhynchus* remains puzzling. This individual must take up its food, at least the larger particles, with the voluminous and relatively rigid chelipeds. Like in all alpheid shrimp, the transport of the food to the mouthparts is assured by the very flexible second pereopods, which end in a minute claw. The second pereopods may also directly take up food (finer particles) from the surface; these appendages are also used for grooming the body and the eggs.

The distal margin of the fingers of the typical platypus-billed minor claw of *A. ornithorhynchus* is furnished with tiny setae or spinules, visible only at the highest magnification on a dissecting microscope. These structures may be used to gently scrape the host surface: this has been shown in a sea urchin-associated pontonine shrimp, *Periclimenes cristimanus* Bruce (P. Ng, pers. comm.). All this shows that there might be several different modes of feeding, some of which might not necessarily be directly host-related. Clearly,

more specimens and especially direct observations of feeding by *A. ornithorhynchus* would be most informative.

Interestingly, most specimens (five of six) of *A. ornithorhynchus* from Nhatrang Bay, the four type specimens from Australia (see Banner and Banner 1973), and also the specimen from Hong Kong (see Bruce 1990b) are females, many of them egg-bearing. The eggs are not numerous (maximum observed, 17) and are fairly large (0.6 x 0.4 mm), which could be an indication of abbreviated development. The single male specimen carried 10 eggs attached to the pleopods; only two of which were fertilized and close to hatching (the eyespots of the future larvae being already visible). The developing eggs were significantly smaller in size and dark yellow; the other eggs were larger, pale white, and obviously not developing, hence non-fertilized (Marin and Anker, in prep.). This observation suggests that *A. ornithorhynchus* displays some form of hermaphroditism. In the closely related genus, *Arete*, at least three species all associated with sea urchins were shown to be protandric hermaphrodites (Suzuki 1970, Nakashima 1987, Gherardi 1991, Gherardi and Calloni 1993), and an indication of a similar phenomenon exists in *Aretopsis amabilis* De Man which is associated with large hermit crabs (Banner and Banner 1968, Nomura 1986). This question also remains open until more evidence becomes available.

Acknowledgments: This study was carried out with the support of the Russian-Vietnamese Tropical Center in Nhatrang City, Republic of Vietnam. The first author (IM) would like to thank Dr. Yuri Y. Dgebuadze (A.N. Severtzov Institute of Problems of Ecology and Evolution of the Russian Academy of Science, Moscow, Russia) for financial support enabling the first author to travel and work on the manuscript with the co-authors at the University of Alberta, Edmonton, Canada. The taxonomic research at the University of Alberta was supported by NSERC operating grant (A7245) to ARP. We also express our gratitude to the directors of the Coastal Department of the Russian-Vietnamese Tropical Center in Nhatrang City, Dr. Victor K. Nezdolij and Nguyen Van Doan, for their assistance in Vietnam, Oleg V. Savinkin for his help in collecting material and providing photographs used in this study, Prof. Roy L. Caldwell (University of California, Berkeley, CA, USA), Paul Humann (Jacksonville, FL, USA) and Helmut Debelius (IKAN, Frankfurt, Germany) for

providing literature, Dr. Dao Tan Ho (Institute of Oceanography, Nhatrang City, Vietnam), for identification of ophiuroids, Keiichi Nomura (Kushimoto Marine Park Center, Arita, Kushimoto, Japan) for providing comparative photographic material, and also to A. Beliaev, A. Zhadan, N. P. U. Vu, N. T. H. Than, N. V. Tuan, and C. V. Bang, who helped with collecting. Three anonymous reviewers improved the quality of the manuscript.

REFERENCES

- Anker A, MS Jeng, TY Chan. 2001. Two unusual species of Alpheidae (Decapoda: Caridea) associated with upogebiid mudshrimps in the mudflats of Taiwan and Vietnam. *J. Crustacean Biol.* **21**: 1049-1061.
- Baker AN, HES Clark, DG McKnight. 2001. New species of the brittlestar genus *Astrogymnotes* H. L. Clark, 1914, from New Zealand and Japan (Echinodermata: Ophiuroidea). *J. Roy. Soc. N. Z.* **31**: 299-306.
- Banner AH, DM Banner. 1968. Contributions to the knowledge of the alpeid shrimp of the Pacific Ocean, part XII: collections from the Marshall and Caroline Islands. *Micronesica* **4**: 261-294.
- Banner AH, DM Banner. 1983. An annotated checklist of the alpeid shrimp from the Western Indian Ocean. *Trav. Doc. ORSTOM* **158**: 1-164.
- Banner DM, AH Banner. 1973. The alpeid shrimps of Australia, part I: the lower genera. *Rec. Aust. Mus.* **29**: 267-389.
- Banner DM, AH Banner. 1978. Annotated checklist of alpeid and ogyridid shrimp from the Philippine Archipelago and the South China Sea. *Micronesica* **14**: 215-257.
- Barel CDN, PGN Kramers. 1977. A survey of the echinoderm associates of the north-east Atlantic area. *Zool. Verhand Leiden* **156**: 1-159.
- Bruce AJ. 1971. Records of some rare pontoniid shrimps from Australian waters, with remarks upon the mouthparts of some species of the genus *Periclimenes* Costa, 1844. *Zool. Verhand. Leiden* **114**: 1-33.
- Bruce AJ. 1975. Shrimps that live with echinoderms. *Sea Frontiers* **21**: 45-53.
- Bruce AJ. 1982. The shrimps associated with Indo-West Pacific echinoderms, with the description of a new species in the genus *Periclimenes* Costa, 1844. *Aust. Mus. Mem.* **16**: 191-216.
- Bruce AJ. 1987. Has anyone seen this shrimp? *Underwater* **19**: 26.
- Bruce AJ. 1988. The shrimp fauna of a small tropical reef, the East Point Fish Reserve, Darwin. *In* Hanley, JR, HK Larson, MG Michie, eds. Darwin Harbour, Proceedings of the Workshop on Research and Management held in Darwin, 2-3 Sept. 1987. A.N.U.N. Aust. Res. Unit Mangr. Monogr. **4**: 226-245.
- Bruce AJ. 1990a. Redescriptions of five Hong Kong caridean shrimps first described by W. Simpson, 1860. *In* B Morton, ed. Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong: Hong Kong Univ. Press, **2**: 569-610.
- Bruce AJ. 1990b. Additions to the marine shrimp fauna of Hong Kong. *In* B Morton, ed. Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong: Hong Kong Univ. Press, **2**: 611-648.
- Bruce AJ. 1993. Darwin's Harbour Shrimps. *Nat. Territory* **3**: 35-37.
- Bruce AJ, KE Coombes. 1997. An annotated check-list of the caridean shrimps (Crustacea: Decapoda) of Darwin Harbour, with descriptions of three new species of *Periclimenes* (Palaemonidae: Pontoniinae). *In* JR Hanley, et al., eds. The marine flora and fauna of Darwin Harbour, Northern Territory, Australia, pp. 301-337.
- Chace FA Jr. 1972. The shrimps of the Smithsonian-Bredin Caribbean Expedition with a summary of the West Indian shallow water species (Crustacea Decapoda: Natantia). *Smiths. Contr. Zool.* **98**: i-x + 1-179.
- Davie P (ed.). 1998. Wild guide to Moreton Bay. Queensland Museum, Brisbane, 405 pp.
- Debelius H. 2000. Crustacea guide of the world. Frankfurt, Germany: IKAN, 321 pp.
- Froggia C, RJA Atkinson. 1998. Association between *Athanas amazone* (Decapoda: Alpheidae) and *Squilla mantis* (Stomatopoda: Squillidae). *J. Crustacean Biol.* **18**: 529-532.
- Gassel MF. 1994. The behavioural ecology of two sympatric species of snapping shrimps in Hawai'i *Alpheus heeia* and *Alpheus lobidens*. PhD thesis, Univ. of California, Berkeley, CA.
- Gherardi F. 1991. Eco-ethological aspects of the symbiosis between the shrimp *Athanas indicus* (Coutière 1903) and the sea urchin *Echinometra mathaei* (de Blainville 1825). *Trop. Zool.* **4**: 107-128.
- Gherardi F, C Calloni. 1993. Protandrous hermaphroditism in the tropical shrimp *Athanas indicus* (Decapoda: Caridea), a symbiont of sea urchins. *J. Crustacean Biol.* **13**: 675-689.
- Hayashi KI. 1995. Prawns, shrimps and lobsters from Japan (82). Family Alpheidae – Genus *Athanas* (3). *Aquabiology* **17**: 107-110.
- Hayashi KI. 2002. A new species of the genus *Athanas* (Decapoda, Caridea, Alpheidae) living in the burrows of a mantis shrimp. *Crustaceana* **75**: 395-403.
- Hendler G, DL Meyer. 1982. An association of a polychaete, *Branchiosyllis exilis*, with an ophiuroid, *Ophiocoma echinata*, in Panama. *Bull. Mar. Sci.* **32**: 736-744.
- Henkel TO, JR Pawlik. 2005. Habitat use by sponge-dwelling brittlestars. *Mar. Biol.* **146**: 301-313.
- Humann P, N Deloach. 2002. Reef creature identification – Florida, Caribbean, Bahamas. 2nd ed. Jacksonville, FL: New World Publications, 448 pp.
- Marin I, A Anker, in prep. New records and species of Alpheidae (Crustacea, Decapoda) from Vietnam. Part II. Genus *Athanas* Leach, 1814. *Raffles Bull. Zool.*
- Martin D, TA Britayev. 1998. Symbiotic polychaetes. Review of known species. *Oceanogr. Mar. Biol. Annu. Rev.* **36**: 217-340.
- Morton B. 1988. Partnerships in the seas: Hong Kong marine symbioses. Hong Kong: Hong Kong Univ. Press, 124 pp.
- Morton B, J Morton. 1983. The sea shore ecology of Hong Kong. Hong Kong: Hong Kong Univ. Press, 350 pp.
- Nakashima Y. 1987. Reproductive strategies in a partially protandrous shrimp, *Athanas kominatoensis* (Decapoda, Alpheidae): sex change as the best of a bad situation. *J. Ethol.* **2**: 145-159.
- Nomura K. 1986. Description of a shrimp, *Aretopsis amabilis*

- De Man (Decapoda Alpheidae) from Kushimoto, the Kii Peninsula, with some remarks on the genus *Aretopsis* from Japan. *Nanki Seibutsu* **28**: 7-10. (in Japanese)
- Nomura K, A Asakura. 1998. The alpheid shrimps (Decapoda: Alpheidae) collected from Kushimoto on the Pacific coast of central Japan, and their spatial distributions, zoogeographical affinities, social structures, and life styles. *Nankiseibutsu* **40**: 25-34. (in Japanese)
- Nomura K, K Hagiwara, H Ikeda. 1998. The alpheid shrimps (Decapoda: Alpheidae) recorded from Kanagawa Prefecture, on the Pacific coast of Central Honshu, Japan. *Kanagawa Prefect. Natl. Hist. Data* **19**: 39-48. (in Japanese)
- Nomura K, S Nagai, A Asakura, T Komai. 1996. A preliminary list of shallow water decapod Crustacea in the Kerama Group, the Ryukyu Archipelago. *Bull. Biogeogr. Soc. Jap.* **51**: 7-21.
- Suzuki H. 1970. Taxonomic review of four alpheid shrimps belonging to the genus *Athanas*, with reference to their sexual phenomena. *Sci. Rep. Yokohama Natl. Univ. Sect. II*, **17**: 1-37.
- Tominaga H, S Nakamura, M Komatsu. 2004. Reproduction and development of the conspicuously dimorphic brittle star *Ophiodaphne formata* (Ophiuroidea). *Biol. Bull.* **206**: 25-34.
- Türkay M, H Göthel. 1990. Garnelen als Untermieter der Haarsterne. *Nat. Mus.* **120**: 401-404.
- Volbehr U, E Rachor. 1997. The association between the caprellid *Pariambus typicus* Krøyer (Crustacea, Amphipoda) and ophiuroids. *Hydrobiologia* **355**: 71-76.
- Warén A. 1981. Revision of the genera *Apicalia* Adams and *Stilapex* Iredale and description of two new genera (Mollusca, Prosobranchia, Eulimidae). *Zoologica Scripta* **10**: 133-154.
- Warner GF. 1977. The biology of crabs. London: Paul Elek (Scientific Books), 201 pp.
- Warner GF, JD Woodley. 1982. Food and feeding mechanisms: Ophiuroida. In M Jangoux, JM Lawrence, eds. *Echinoderm Nutrition*. Rotterdam: Balkema, pp. 161-181.
- Wirtz PH, H Debelius. 2003. *Niedere Tiere – Mittelmeer und Atlantik*. Hamburg, Germany: Jahr Verlag, 305 pp.
- Wolcott DL, NJ O'Connor. 1992. Herbivory in crabs: adaptations and ecological considerations. *Am. Zool.* **32**: 370-381.