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ALPHEID SHRIMPS FROM THE MANGROVES AND MUDFLATS OF SINGAPORE. PART I. GENERA *SALMONEUS*, *ATHANAS* AND *POTAMALPHEOPS*, WITH THE DESCRIPTION OF TWO NEW SPECIES (CRUSTACEA: DECAPODA: CARIDEA)

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***ABSTRACT.* –** Extensive field collections of small alpheid shrimps in Sungei Buloh and Lim Chu Kang mangroves in Singapore, along with the examination of preserved material, yielded two new species and several new records for South-East Asia and Australia. The description of *Salmoneus singaporensis*, new species, is based on a single specimen from Singapore, which differs only slightly from the rarely collected *S. rostratus* Barnard. The latter species is recorded for the first time from Phuket, Thailand. *Potamalpheops johnsoni*, new species, is presently only known from Sungei Buloh, where it occurs syntopically with *P. tigger* Yeo & Ng. The new species can easily be distinguished from *P. tigger* by the presence of a subapical ventral tooth on the rostrum. The latter species is recorded for the first time from northern Australia. The differences in the length and shape of the rostrum and the length of the stylocerite observed in several species of *Potamalpheops* suggest a rather high plasticity of these structures in basal alpheids. *Athanas polymorphus* Kemp and *A. japonicus* Kubo, taxonomically problematic species or species complexes, are recorded for the first time from Singapore. The most remarkable feature of these two species is a pronounced polymorphism in the development of the first chelipeds.

***KEY WORDS.* –** Alpheidae, *Salmoneus*, *Potamalpheops*, *Athanas*, new species, new records, South East Asia, Australia, mangroves, polymorphism, intra-specific variability, species complex.

INTRODUCTION

Despite extensive collection of shrimps in the area of Singapore and the southern Malayan Peninsula, and the publication of two checklists of Caridea and Stenopodidea of Singapore by Johnson (1962, 1976), the alpheid shrimp fauna of Singapore is still poorly known. This is partly due to inadequate sampling, most collecting efforts being concentrated on hand-collecting of larger and more conspicuous intertidal species, and dredging on subtidal soft bottoms. Small species (less than 1 cm in total length), and species confined to particularly cryptic and inaccessible habitats, such as thalassinidean burrows, are not easily captured by using those methods or simply overlooked. An example of such a small inconspicuous alpheid species is *Potamalpheops tigger* described recently from the Sungei Buloh mangrove, together with two other congeneric species (Yeo & Ng, 1997). Because of numerous cryptic species and species complexes among common intertidal species, identification of alpheids can be extremely difficult (Anker, 2001). This fact is highlighted by the level of inaccuracies in Johnson's lists (Johnson, 1962, 1976), which therefore, should be used with some reservation.

The present report deals with three genera, *Salmoneus*, *Athanas*, and *Potamalpheops*, and five species, all confined to soft bottoms and mangrove mudflats. Extensive collections of fresh alpheid material, mainly in Sungei Buloh and Lim Chu Kang mangroves in Singapore, and examination of material in the Zoological Reference Collection, Raffles Museum of Biodiversity Research (National University of Singapore), revealed a further new species in the genus *Potamalpheops* and the first Singapore and South-East Asian records for several other uncommon alpheids. A single specimen of *Salmoneus* collected in 1959 could not be clearly assigned to any known species of this genus, and is also described as new. New figures, synonymy, distribution, remarks on variability, and detailed discussion of taxonomic status, are provided for the other three species.

MATERIALS AND METHODS

Carapace length (CL) is given in mm, and was measured from the tip of the rostrum to the posterior margin. The specimens remain deposited in the following institutions: ZRC – Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of

Singapore; MNHN – Muséum National d'Histoire Naturelle, Paris, France; USNM – National Museum of Natural History, Smithsonian Institution, Washington D.C.; RMNH – Nationaal Natuurhistorisch Museum, Leiden; BPBM – Bernice P. Bishop Museum, Honolulu; NTM – Northern Territory Museum, Darwin; QM – Queensland Museum, Brisbane. Other abbreviations used: Mxp – maxilliped; P – pereiopod; A – abdominal segment.

TAXONOMY

Salmoneus Holthuis, 1955

Salmoneus singaporensis, new species
(Figs. 1, 2, 3a, b)

Salmoneus hilarulus – Johnson, 1962: 49 (part.)(not De Man, 1910).

Material examined. – Holotype - non ovigerous specimen, probably male (CL 8.9 mm), ZRC 1979-4615, with label "*Salmoneus hilarulus* De Man", Tanjong Penuru, Jurong, Singapore, mudflats, coll. Honours, University of Malaya, 24 Jul.1959, id. D. Johnson.

Comparative material. – *Salmoneus rostratus* Barnard, 1962, 1 ovigerous female (CL 6.3 mm), MNHN-Na 13671, Ao Tang Khen, Phuket, Thailand, intertidal, sand-flats, from burrow of *Alpheus* cf. *rapacida*, coll. T. Komai, 24 Oct.1995; 1 non-ovigerous specimen, probably male (CL 6.4 mm), MNHN-Na 4787, Nosy-Bé, Madagascar, intertidal, coll. B. Opic, 07 Sep.1974 id., Banner & Banner (specimen reported in Banner & Banner, 1983).

Description. – Carapace very sparsely setose, with a small, flattened tubercle posterior to rostrum (Fig. 3a). Rostrum very long and slender, reaching almost to midlength of second article of antennular peduncle; inferior margin of rostrum with small, acute, subdistal tooth (Fig. 2c); base of rostrum approximately equal to one third of rostrum length in dorsal view. Extra-corneal teeth well developed, acute. Eyestalks partially visible in dorsal and lateral views, each bearing a small anterior tubercle; corneas somewhat reduced (Figs. 2c, 3a). Pterygostomial angle broadly rounded.

Antennular peduncle robust, second article slightly longer than visible portion of first article, stylocerite acute, slightly exceeding distal margin of first antennular article; mesio-ventral carina with acute tooth; outer flagellum biramous, shorter ramus quite long, well separated from main ramus (Fig. 2c), basal fused portion with four joints. Antenna with basicerite robust, bearing acute ventro-lateral tooth; carpocerite very robust, somewhat elongated, not reaching distal margin of third antennular article; flagellum very robust; scaphocerite blade with anterior margin slightly convex; lateral spine strong, exceeding anterior margin of scaphocerite, but not reaching distal margin of antennular peduncle. Mouthparts not dissected to avoid damage of the unique holotype specimen (usually not species-specific within *Salmoneus*, pers. obs.).

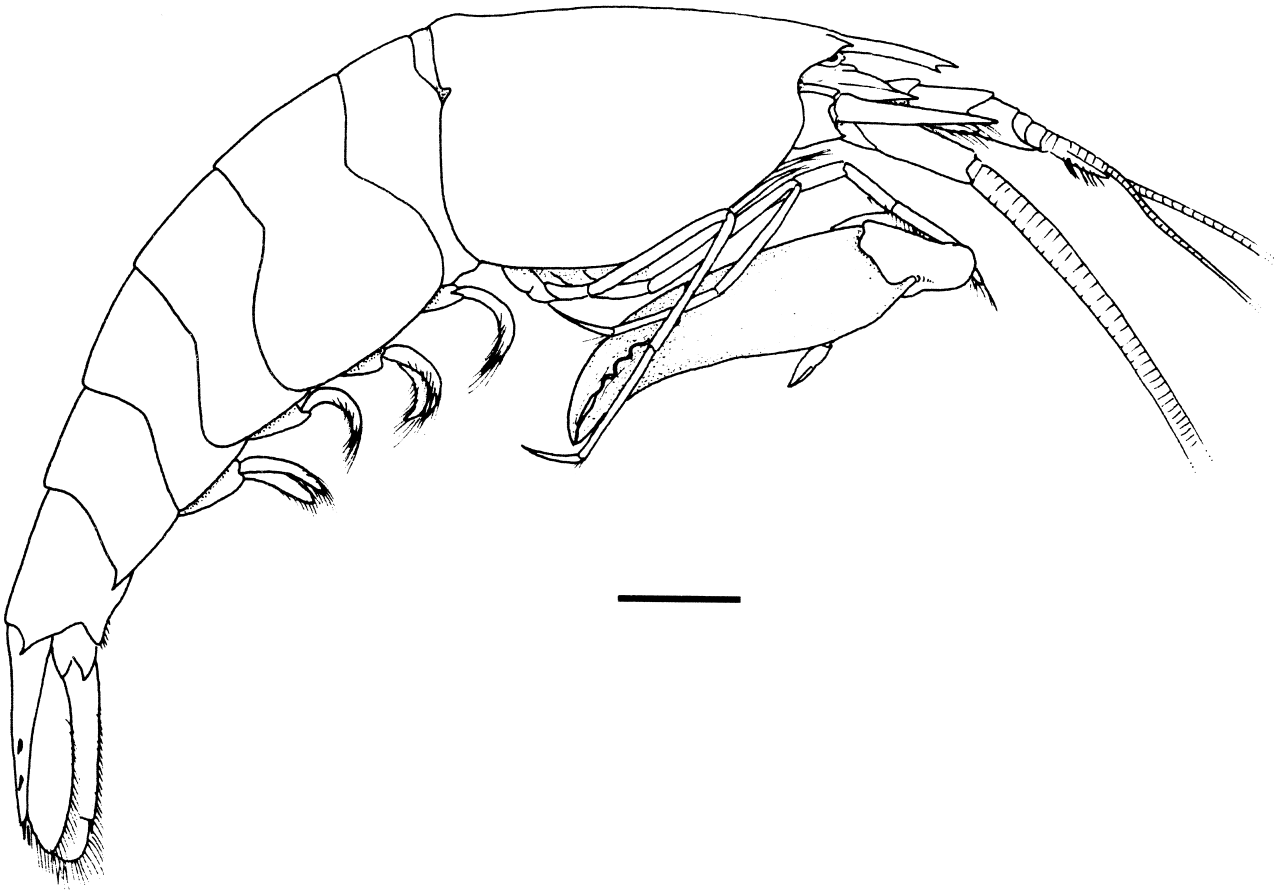

Fig. 1. *Salmoneus singaporensis*, new species, holotype, probably male, habitus. Scale: 1 mm.

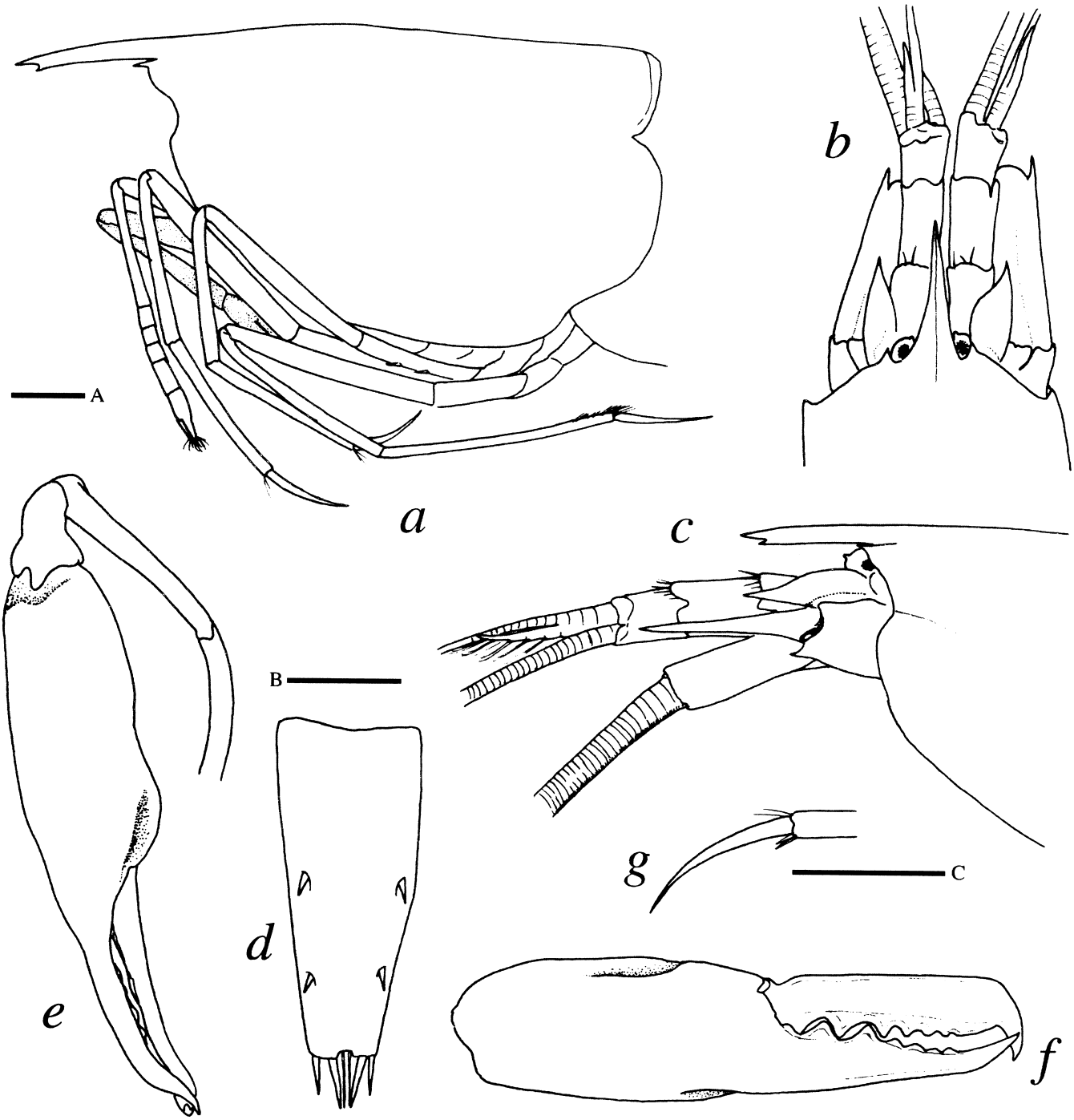

Fig. 2. *Salmoneus singaporensis*, new species, holotype, probably male: a, carapace and first to fifth pereiopods, lateral view; b, frontal region, dorsal view; c, same, lateral view; d, telson; e, major cheliped, ventral view; f, same, chela; g, third pereiopod, dactylus. Scales: A (a), B (b-f) C (g), all scales 1 mm.

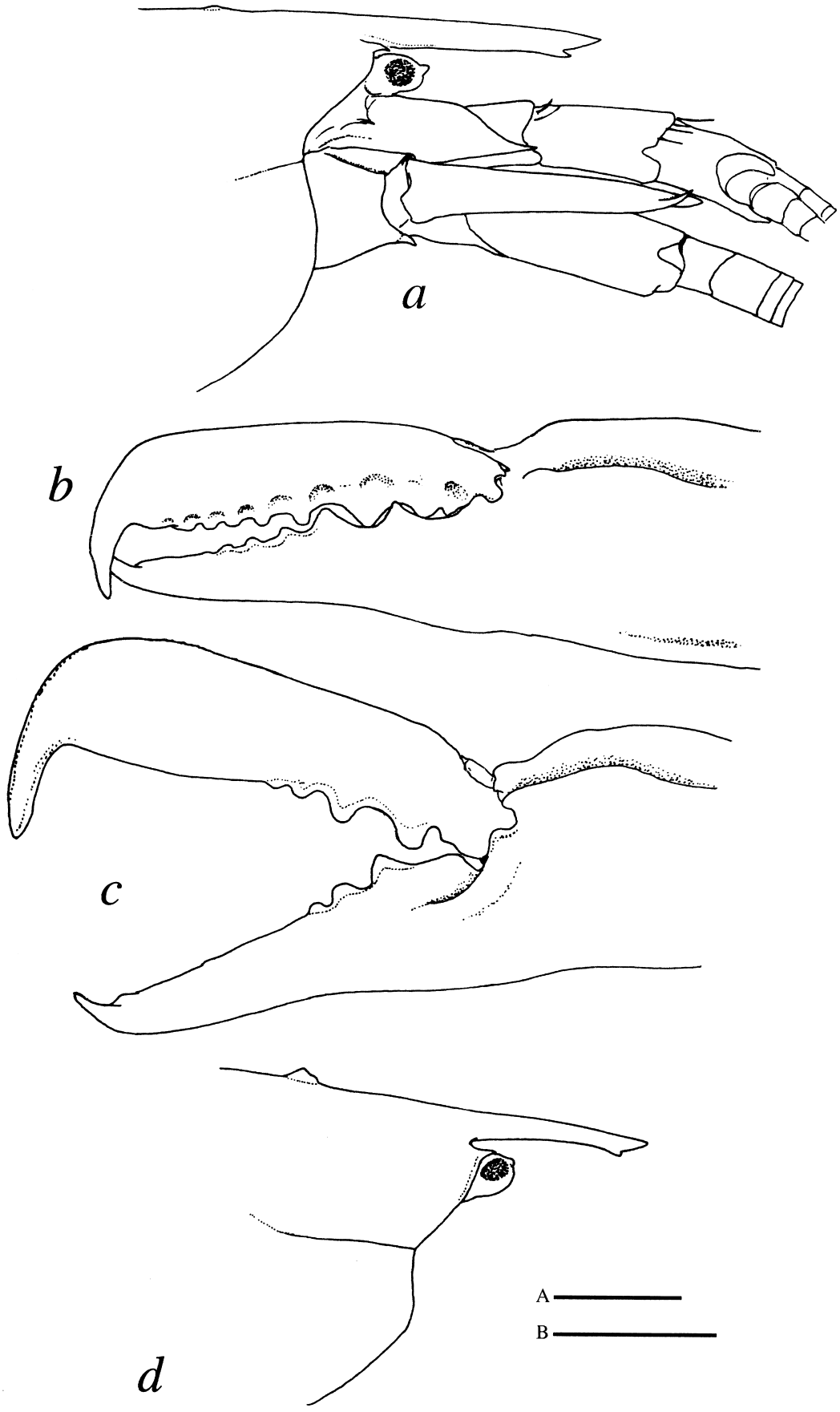

Fig. 3. *Salmoneus singaporensis*, new species, holotype, probably male (a, b) and *Salmoneus rostratus* Barnard, ovigerous female from Phuket, Thailand (c, d): a, c, frontal region, lateral view; b, d, major chela, distal portion of palm and fingers. Scales: A (a, b), B (c, d), both scales 1 mm.

First chelipeds very asymmetrical in shape and unequal in size, both held flexed ventrally. Major cheliped with ischium and merus very slender (Fig. 2e); chela twisted, palm with a deep groove extending from its proximal margin to propodo-dactylar articulation; both fingers, especially dactylus, strongly curved distally (Fig. 2f); both dactylus and pollex armed with rounded or triangular teeth, two most proximal teeth largest and triangular, distal teeth rather small and rounded; distal third of pollex and distal fifth of dactylus without teeth (Fig. 3b). Minor cheliped much shorter than major cheliped, with chela simple and unarmed, carpus, elongated, approximately 6 times as long as wide (Fig. 2a).

Second pereiopod slender, carpus five-articulated, with first article longer than all other articles combined, ratio of carpal articles approximately equal to 6.0: 0.9: 0.8: 0.8: 1.5 (Fig. 2a). Third to fifth pereiopods (P3-5) slender, ischium armed with two spines on P3 and P4, unarmed on P5; merus longer than carpus, latter subequal to (P3) or shorter than (P5) propodus; propodus unarmed except small distal spinules on P3 and P4 (Fig. 2g); P5 distally with rows of setae; dactylus simple, elongated, very slender, slightly curved (Figs. 2a, g), 0.35-0.4 length of propodus.

Abdominal segments (A) with postero-ventral angles rounded (A2, A3), angular (A4) or produced in a acute tooth (A5, A6), posterior margin of A6 acutely produced latero-dorsally (Fig. 1); preanal plate acutely produced. Telson rectangular, distally tapering, with two pairs of dorsal spines anterior pair situated approximately on mid-length; posterior margin truncated with a small median incision (Fig. 2d), lateral posterior spines by 1/3 shorter than median spines.

Gill formula typical for *Salmoneus*: pleurobranchs on P1-P5; podobranch absent; arthrobranch on Mxp3; exopods on Mxp1-Mxp3; strap-like epipods (mastigobranchs) on Mxp3 and P1-P4; setobranchs on P1-P5.

Colour. **–** Colour in life not noted.

Habitat. **–** The unique holotype of *S. singaporensis*, new species, was collected at low tide on a mudflat.

Remarks. **–** The genus *Salmoneus* Holthuis, 1955, contains 19 valid and several undescribed species (pers. obs.) that can be divided roughly into two species groups. The first, more homogenous species group includes only four species, all found in the temperate and tropical waters of the eastern Atlantic Ocean from the Mediterranean Sea south to Nigeria. These four species are characterized by the minor cheliped being as long or even longer (although less robust) than the major cheliped (cf. Holthuis, 1951; Fransen, 1992; Dworschak et al., 2000). All other species of *Salmoneus* are characterized by the minor cheliped being much smaller than the major cheliped (with the exception of an undescribed species from northern Australia, pers, obs.). They form a vast heterogenous group, widely distributed in the central and western Atlantic (five species), the eastern Atlantic (one undescribed species in the eastern Mediterranean, G. Grippa, pers. comm.), the eastern tropical Pacific (two species) and the Indo-West Pacific (12 species). Several species, e.g., *S. cavicolus* Felder & Manning, and the type-species, *S. serratidigitus* Coutière (sensu Banner & Banner, 1981) are extremely variable in the shape of the frontal region. Those species could represent several species, and are in need of a thorough revision.

Salmoneus singaporensis, new species, appears to be closest to *S. rostratus* Barnard, a geographically widespread but rarely collected species. *Salmoneus rostratus* is up to present known only from three localities: Nosy-Bé, Madagascar (Barnard, 1962; Banner & Banner, 1983), Hansa Bay, Papua New Guinea (De Grave & Wilkins, 1997) and Phuket, Thailand (present study, new record). The unique specimen of *S. singaporensis*, new species, differs from all specimens of *S. rostratus* personally examined (see comparative material) or illustrated in the literature (Barnard, 1962; De Grave & Wilkins, 1997), by the following features: (1) inconspicuous post-rostral tubercle (cf. Figs. 3a, d); (2) rostrum being less slender and more elongated (cf. Figs. 3a, d); and (3) presence of rounded teeth on the distal half of major chela fingers, especially on the dactylus (cf. Figs. 3b, c). The armature of the major chela is considered to be an important character in the taxonomy of *Salmoneus* species. In view of the quasi-non extant variability in the chela armature among three specimens of *S. rostratus* from geographically very distant localities (see above), the different armature in *S. singaporensis*, new species, along with the feebly developed post-rostral tubercle, justify the erection of a new species. Furthermore *S. singaporensis*, new species, also has a series of shallow, rounded depressions above each tooth of the dactylar cutting edge on the major chela (Fig. 3b); these depressions are not distinct on the chela of Phuket specimens (Fig. 3c).

It is unlikely that the above listed differences between *S. singaporensis*, new species, and *S. rostratus* are examples of intra-specific variation of the latter species, however, more specimens of both species from Singapore and elsewhere are needed to confirm the validity of the new species. Because of the shape of the major chela, the large rounded teeth on the cutting edges of the major cheliped, the presence of a post-rostral tubercle (much less developed in *S. singaporensis*, new species), the very robust antennal flagellum and carpocerite, the small tubercle on the anterior margin of each eyestalk, and the elongated narrow rostrum armed with a second inferior tooth, *S. singaporensis*, new species, and *S. rostratus* occupy a rather isolated position within *Salmoneus*.

Two other species of *Salmoneus* appear relatively distantly related to the new species and to *S. rostratus*. *Salmoneus bruni* Banner & Banner could be the next closest relative of these two species, at least in the shape of the major chela. However, *S. bruni* can be distinguished from *S. singaporensis* new species, by the much shorter rostrum lacking an inferior subdistal tooth and, by the central portion of the cutting edges of the major chela lacking teeth (cf. Banner & Banner, 1966b), as in *S. rostratus*. The description of *Salmoneus tafaongae* was based on a «fragmentary» ovigerous female

collected on «outer portion of fringing reef, shoreward of surf zone, about 1 foot below low water, 3 miles east of Apia, Upolu, Western Samoa» (Banner & Banner, 1966a). This specimen was lacking the major cheliped. No figures were provided, instead Banner & Banner stated that «it was unfortunate that this single specimen was not more nearly intact, and that the small chela and second legs were lost after the initial examination. However, because its form is so distinctive we have decided to describe it as a new species». It was a very unfortunate decision; even if the holotype still exists, which seems unlikely (it is neither in the USNM – pers. obs., nor in the BPBM – L. Eldregde, pers. com.), it would not be very helpful for comparisons with other species.

Several features from the original text description suggest that *S. tafaongae* could be indeed closely related to *S. singaporensis*, new species, especially in having (1) elongated rostrum (three times as long as broad in *S. tafaongae*), with an acute tip and bearing a small tooth; (2) eyes partly exposed dorsally between the extra-corneal teeth and the rostrum, with most of the corneal surface also visible laterally; (3) third to fifth pereiopods elongate and slender, with dactylus simple, slightly curved, seven times as long as broad; and (4) telson with posterior margin bearing a small «trapeziform» median incision. However, *S. singaporensis*, new species, differs from *S. tafaongae* in having shorter stylocerite, which slightly exceeds the first antennular article (in *S. tafaongae* the stylocerite reaches to the end of the second antennular article), the squamous portion of the scaphocerite not exceeding its lateral spine as in *S. tafaongae*, and longer and stouter carpocerite of the antenna, which reaches to the third antennular article in *S. singaporensis*, new species, while it does not reach to the middle of the second article in *S. tafaongae*. Finally, the habitats where the two specimens were collected are quite different: *S. singaporensis*, new species, was collected on mudflats, while *S. tafaongae* was collected on the outer fringing reef.

The type-locality of *S. singaporensis*, new species, Tanjong Penuru, was a mudflat locality on the southern shore of Jurong, Singapore. Unfortunately, it is no longer extant so no further topotypic specimens could be collected in Singapore. The new species is characterized by extremely slender, slightly curved dactyli of third to fifth pereiopods, typical for species adapted for walking on soft bottoms, such as *S. ortmanni* Rankin, a pan-American species found in mangroves, and *S. rostratus* which seems to occur in similar, sandy-muddy habitats (Barnard, 1962; De Grave & Wilkins, 1997). Significantly, the present specimens of *S. rostratus* from Phuket were collected from a burrow of the quite large, goby-associated snapping shrimp *Alpheus* cf. *rapacida* (T. Komai, pers. comm.). Previously, De Grave & Wilkins (1997) reported a possible association of *S. rostratus* with the goby *Mahidolia mystacina* (Valenciennes). Yanagisawa (1978) also reported *M. mystacina* as an associate of *Alpheus* sp. in Japan, and colour slides by R. Kuiter show several species of *Alpheus* (all from *brevirostris* group) sharing its burrow with *M. mystacina* in Indonesia. Thus *S. rostratus* may actually be associated with burrows excavated by larger *Alpheus* species and shared with gobies, such as *M. mystacina*.

Distribution. **–** Known only from the type-locality in Singapore, which is no longer extant (see above).

Potamalpheops Powell, 1979

Potamalpheops tigger Yeo & Ng, 1997
(Figs. 4, 20a, b, 21)

Potamalpheops tigger Yeo & Ng, 1997: 182, figs. 5, 6.

Material examined. **–** Type series of *P. tigger*, ZRC 1996.6-7 (for details see Yeo & Ng, 1997); 1 specimen (sex and CL not noted), ZRC 2000.2158, Sungei Buloh mangrove, Singapore, coll. P3 E, 21 Sep.1992; 2 specimens (sex and CL not noted), ZRC 2000.2159-2160, Sungei Buloh mangrove, Singapore, coll. Y. X. Cai, 29 Jan.2000; 8 specimens (sex and CL not noted), ZRC 2000.2161-2168, Sungei Buloh mangrove, Singapore, in mud under debris and dead wood, coll. A. Anker & Y. Cai, 10. Feb.2000.

Extra-limital material. – 1 female (CL 3.1 mm), NTM Cr-013092, near bridge, Channel Darwin Island, Northern Territory, Australia, 12°3°9’ S, 130°55.4’ E, LWS, Site 3, coll. M. Burke, 14 Jul.1991.

Diagnosis. **–** Carapace glabrous, without grooves; rostrum straight (Figs. 4b, f, h) sometimes slightly descendant towards the tip (Figs. 4a, d), acute, very narrow in some specimens (Fig. 4a), reaching at least to distal third of first article of antennular peduncle, and at most to mid-length of second article (cf. Figs. 4a-c, k), without any trace of a tooth on inferior margin; extra-corneal teeth triangular, acute; eyes exposed in dorsal and lateral views, concealed only proximally, corneas well developed, setae on medio-anterior margin absent; infra-corneal region protruding and rounded; pterygostomial region rounded, without plumose setae; second article of antennular peduncle approximately as long as visible portion of first article; stylocerite acute, reaching far beyond second article of antennular peduncle in most specimens (Fig. 4a), but only to posterior third of second article in some specimens (Fig. 4c); antennular flagellum biramous, fused portion containing usually more than six joints, males with usually more than 15 tufts of aesthetascs, females with few (five to six or even less) aesthetasc groups; lateral spine of scaphocerite exceeding anterior margin, latter slightly convex; tip of third maxilliped with small spines; first chelipeds symmetrical, not sexually dimorphic, not particularly enlarged, held extended or simply folded beneath cephalothorax, carpus cylindrical, with rows of setae on mesial face (Fig. 4i), chela simple, with cutting edges unarmed; carpus of second pereiopod five-articulated, first article longest, slightly longer than fifth; third, fourth and fifth pereiopods with ischium armed with one spine; merus of same appendages armed with two spines; propodus armed with small spines, dactylus slender, slightly curved; appendix masculina with four spines (at least in specimens examined); uropod with diaeresis bearing 17-24 teeth; telson rectangular, narrow, tapering posteriorly, with two pairs of dorsal spines, first pair situated usually just anterior to telson mid-length; posterior margin of telson medially rounded, with two spines,

median spines longer than lateral spines; gill formula as given for genus (Powell, 1979; see also description of new species below).

Colour. – Grey, semi-translucent, with blackish chromatophores forming broad bands on each abdominal segment and carapace (Figs. 20a, b); observed dorsally, some parasagittal or sagittal-oblique areas are lacking chromatophores. Shrimps are apparently able to adapt their colour pattern to the background or to light conditions; this may explain why some specimens appear rather spotted, and not banded, while others present reddish-brown instead of blackish banding (Fig. 21).

Remarks. – *Potamalpheops tigger* was described in detail and illustrated by Yeo & Ng (1997), who noted, but did not figure a large intra-specific variation, especially in the length of the rostrum and the stylocerite. One character on the first chelipeds important for the taxonomy and phylogeny of the genus was not mentioned in the original description. The mesial face of the carpus bears several comb-like rows of setae in *P. tigger*, but also in *P. miyai* Yeo & Ng, *P. amnicus* Yeo & Ng and all other species of the *P. monodi* group, and also in *P. stygicola* (Hobbs)(pers. obs.). The number of the asthetascs on the antennules appears to be sexually dimorphic in *P. tigger* and possibly in other species of *Potamalpheops* (pers. obs.). This specimen represents a considerable range extension of *P. tigger* from Southeast Asia to northern Australia. In light of this new data, the short updated diagnosis of *P. tigger* provided above completes the fuller original description given by Yeo & Ng (1997).

Although the variation in the shape of the rostrum is rather large, it is still considered here as intra-specific. Interestingly, a similar type of rostral variation is observed in two other species of the genus *Potamalpheops* also characterized by the presence of a long rostrum. One of them is the new species described below (cf. Fig. 5); the other is *P. pininsulae* (cf. Bruce & Iliffe, 1992: figs. 48-53). In these two species, the variation affects not only the rostral length and shape (e.g., narrow vs. broad laterally, straight vs. slightly descendant), but also the degree of development of the inferior subapical tooth. The specimen from Channel Island near Darwin, Northern Territory (NTM Cr-013092) has the longest and most slender rostrum among the specimens examined (Fig. 4k); this specimen has furthermore the carpus of the first pereiopods slightly shorter than in the

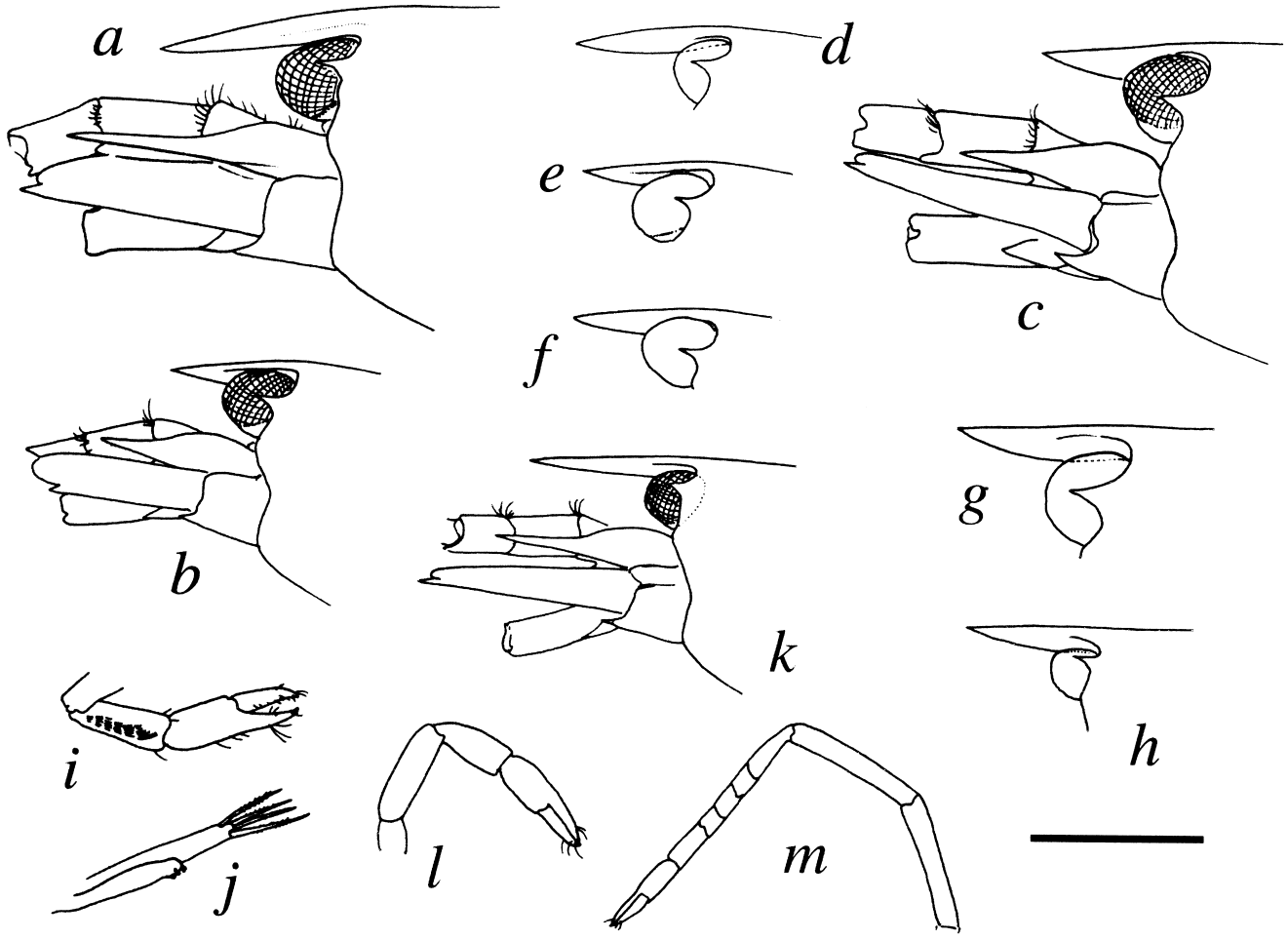

Fig. 4. *Potamalpheops tigger* Yeo & Ng, a-j, series of specimens from Sungei Buloh (ZRC and MNHN): a-c, frontal region of males (a, b) and ovigerous female (c); d-h, variation of rostrum in males (d-f, h) and post-ovigerous female (g); i, first cheliped, carpus and chela, inner view; j, second pleopod, appendix masculina and appendix interna; k-m, female from Darwin (NTM Cr-013092): k, frontal region, lateral view; l, first pereiopod; m, second pereiopod. Scale: 1 mm.

Singapore specimens (cf. Fig. 4l). In all other characters this female agrees well with *P. tigger*.

The length of the stylocerite is more or less constant in other species of *Potamalpheops*. In *P. tigger* there is apparently no correlation between the length of the stylocerite and other important features, e.g., rostrum length, or sex and age of specimens. Therefore, this feature is seen here as undergoing intra-specific variation. However, it would be most interesting to analyze the genetic structure of *Potamalpheops* populations in the Sungei Buloh mangrove, to verify the eventual presence of cryptic species.

***Distribution.* –** Until now, *Potamalpheops tigger* was known only from Sungei Buloh and Lim Chu Kang mangrove swamp forests in Singapore. The female specimen collected on Channel Island near Darwin, Northern Territory, is the first record of this species outside Singapore and represents a range extension of this species from South-East Asia to northern Australia.

***Potamalpheops johnsoni*, new species**

(Figs. 5-7, 20c, d)

Potamalpheops tigger Yeo & Ng, 1997: 182 (part, 1 specimen from ZRC type-series).

***Material examined.* –** Holotype – 1 ovig. female (CL 3.7 mm), ZRC 2000.2172, Sungei Buloh mangrove forest, Singapore, coll. Y. Cai, 29 Jan.2000.

Paratypes – 1 ovig. female (CL 4.2 mm), ZRC 2000.2173, 2 females (CL 3.7 mm and 2.8 mm), ZRC 2000.2178-79, 1 ovig. female (CL 3.4 mm), USNM 1005101, 1 female (CL 3.9 mm), RMNH D 50011, 1 ovig. female (CL 3.7 mm) and 1 post-ovig. female (CL 4.6 mm), MNHN-Na 13755, all same data as for holotype; 1 female (CL 4.4 mm), ZRC 1999.0035, Sungei Buloh mangrove, Singapore, coll. P.K.L. Ng and D. C. J. Yeo, 01 Mar.1998; 1 male (CL 3.1 mm), ZRC 2000.2171, Sungei Buloh mangrove, Singapore, coll. PL E, 10 Oct.1992; 1 female (CL 2.6 mm), ZRC 2003.0088 (from paratype series of *P. tigger*, ZRC 1996.7), Sungei Buloh mangrove, Singapore, 05 Aug.1995, coll. P.K.L. Ng; 1 ovig. female (CL 3.9 mm), 1 male (CL 2.7 mm) and 1 immature specimen (CL not measured), ZRC 2000.2182-84, Sungei Buloh mangrove, Singapore, from mud, under pieces of rotten wood and from water holes at low tide, coll. A. Anker & Y. Cai, 10 Feb.2000; 1 male (CL 2.9 mm) and 1 female, dissected (CL 4.4 mm), MNHN-Na 13720, same data as for ZRC 2000.2182-84.

***Description.* –** Carapace smooth, glabrous, not setose. Rostrum usually exceeding distal margin of first article of antennular peduncle (Figs. 5a,b), laterally compressed, acute, with small subdistal acute tooth on inferior margin (Figs. 5b-j), sometimes with two very small teeth (Figs. 5e, f). Extra-corneal teeth well developed, acute, infra-corneal angle slightly produced anteriorly, rounded. Eyes partially exposed in dorsal and lateral views, cornea large, well pigmented, medio-anterior margin lacking tubercle or long setae. Pterygostomial angle slightly projecting anteriorly, rounded (Fig. 5b), without plumose setae.

Antennular peduncles not elongated, second article slightly longer than first; stylocerite acute, exceeding distal margin of first article (Figs. 5a, 6q); mesio-ventral carina with well developed, acute tooth (Fig. 6q); outer flagellum biramous, with the shorter ramus partly fused to the main ramus (Fig. 6r), aesthetasc tufts scarce, more developed and numerous towards the distal end of the short ramus in females (Fig. 6q), generally more developed and more numerous, extending from the third or fourth joint to the distal end of the short ramus in males (Fig. 6r). Antenna with basicerite bearing acute ventro-lateral tooth; scaphocerite reaching but not exceeding distal margin of antennular peduncles, lateral spine strong, anterior margin convex (Fig. 6o), carpocerite very short, reaching to about 3/5 of scaphocerite.

Mouthparts typical for *Potamalpheops*. Mandible with two-articulated palp; incisor process with six short, triangular teeth. Maxillule, maxilla, first and second maxillipeds as illustrated (Figs. 7c-e), without specific features. Third maxilliped (Fig. 7f) slender; coxa with epipod and lateral plate well developed, latter with some setae (Fig. 7g); tip of ultimate segment with one subdistal spine and one distal spine (Fig. 7h); arthrobranch well developed (Figs. 7f, g).

First chelipeds (Figs. 6a-d) symmetrical, not enlarged; not sexually dimorphic; coxa with strap-like epipod and at least four setobranchial setae; ischium stout; merus much longer than ischium and distinctly longer than carpus; carpus cylindrical, with several (usually six to seven) rows of grooming setae mesially (Figs. 6b, d); chela slightly longer than carpus, fingers clearly shorter than palm (Fig. 6c), distally with numerous tufts of setae; cutting edges unarmed.

Second pereiopod slender, coxa with strap-like epipod and at least four to five setobranchial setae; ischium and merus subqual, slender; carpus five-articulated, ratio of carpal articles equal approximately to (proximal to distal): 4-1-1.2-1-2 (Fig. 6e); chela simple, longer than distal carpal article but much shorter than first carpal article.

Third pereiopod (Fig. 6f) rather slender; coxa with strap-like epipod and four to five setobranchs; ischium armed with one spine, merus armed with 2 spines; carpus unarmed; propodus armed with two or three slender spines on inferior margin and a distal pair of spines (Fig. 6g); dactylus about 0.4 length of propodus, simple, slender, slightly curved (Fig. 6g). Fourth pereiopod very similar to third pereiopod, but with propodus armed with four to five smaller spines (Fig.6 h). Fifth pereiopod with coxa bearing only setobranch, ischium and merus unarmed (at least in female); propodus with several small spines and a well developed brush of grooming setae (Fig. 6i).

Abdominal segments with posterior ventral angles rounded, sixth segment with articulated triangular plate. Uropod with diaeresis finely toothed (around 25 very small teeth in one of the paratypes) on about 2/3 of its length, then abruptly curved and ending (Fig. 6n); lateral spine well developed. Telson elongate, slightly tapering distally, with two pairs of dorsal spines in most specimens (Fig. 6l), exceptionally with three pairs (Fig. 6j); posterior margin of telson medially

convex, with two, rarely three strong postero-lateral spines at each angle (Figs. 6l, k), median spines somewhat longer than lateral spines.

Gill formula typical for genus (Powell, 1979): pleurobranchs on P1-P5; podobranch absent; arthrobranch on Mxp3; exopods on Mxp1-Mxp3; strap-like epipods (mastigobranchs) on Mxp3 and P1-P4; setobranchs on P1-P5.

Largest specimens reaching approximately 4.5 mm CL (12 mm TL).

***Colour.* –** Grey, semi-translucent, large blackish or brownish chromatophores forming broad bands on each abdominal segment and most of the carapace (Figs. 20c, d); first chelipeds, especially chela, and third to fifth pereiopods flecked with small chromatophores. In some individuals the pattern is less distinct, sometimes the banding is diffuse and hardly distinct.

***Habitat.* –** *Potamalpheops johnsoni*, new species, has been collected by hand either washing out the soft mud close to small mangrove pools or under pieces of dead rotten wood. *Potamalpheops tigger* and *P. johnsoni*, new species, may have finely tuned differences in their ecological niches, involving parameters such as intertidal zonation and seasonality, or reproductive patterns. For instance, the eggs in ovigerous females are slightly larger in *P. johnsoni* new species, than in *P. tigger*. Also, *P. johnsoni*, new species, could be either the rarer of the two species or more abundant during a certain season only.

***Remarks.* –** *Potamalpheops johnsoni*, new species, belongs to the *P. monodi* species group, characterized by two spines at each posterior angle of the telson (Yeo & Ng, l997), and by the presence of a well developed row of setae on the mesial side of the carpus of the first pereipods (Fig. 6d). Within the *P. monodi* group, it can be contrasted to species characterized by a well developed, elongate rostrum, and not especially enlarged chelae of the first pereiopods. These are *P.*

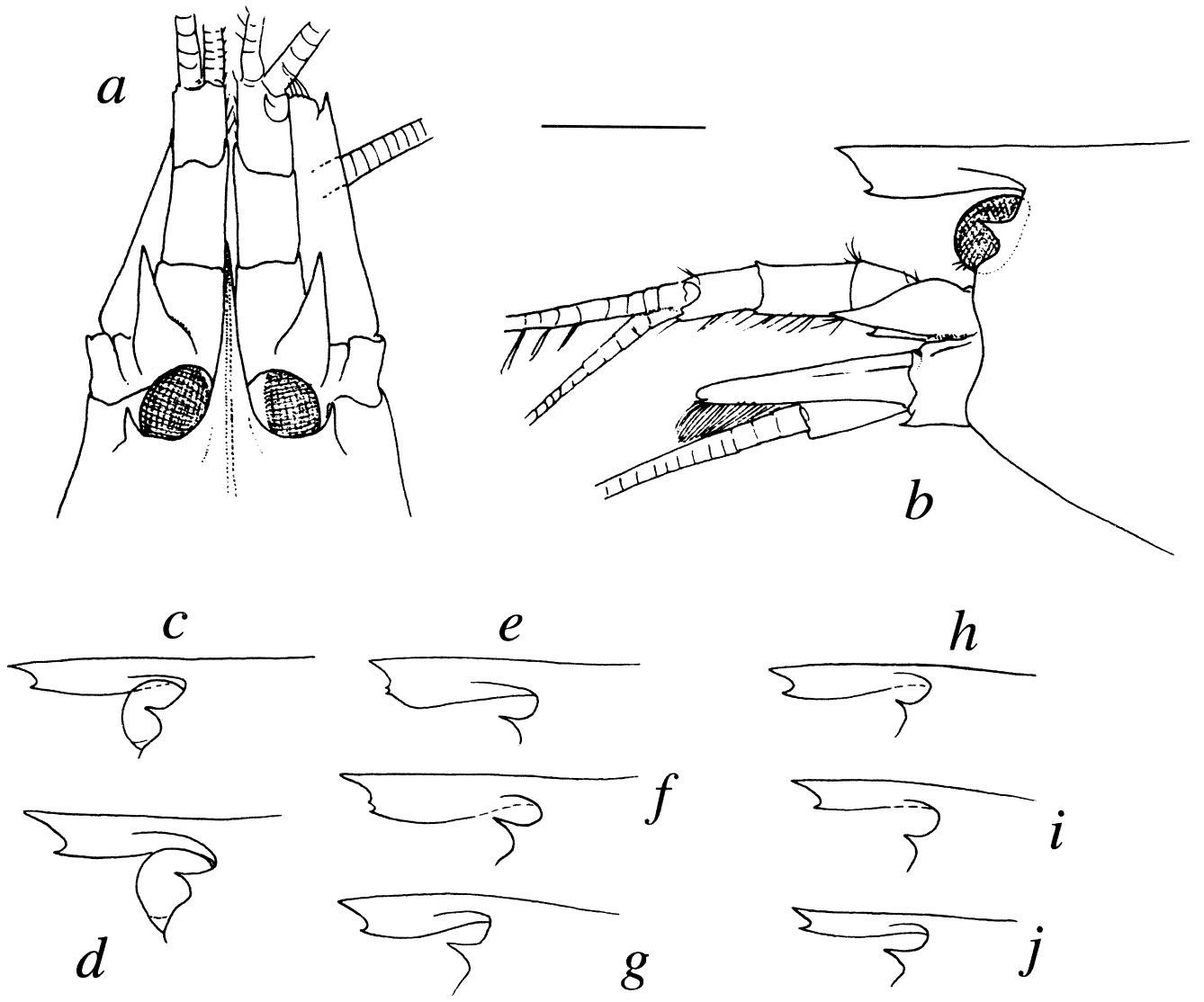

Fig. 5. *Potamalpheops johnsoni*, new species, a, b, paratype, ovigerous female (MNHN-Na 13720), frontal region in dorsal (a) and lateral (b) views; c, holotype, ovigerous female (ZRC 2000.2172), rostrum; d-j, paratype series, males (g-i), female (j), ovigerous females (d-f), variation of rostrum. Scale: 1 mm.

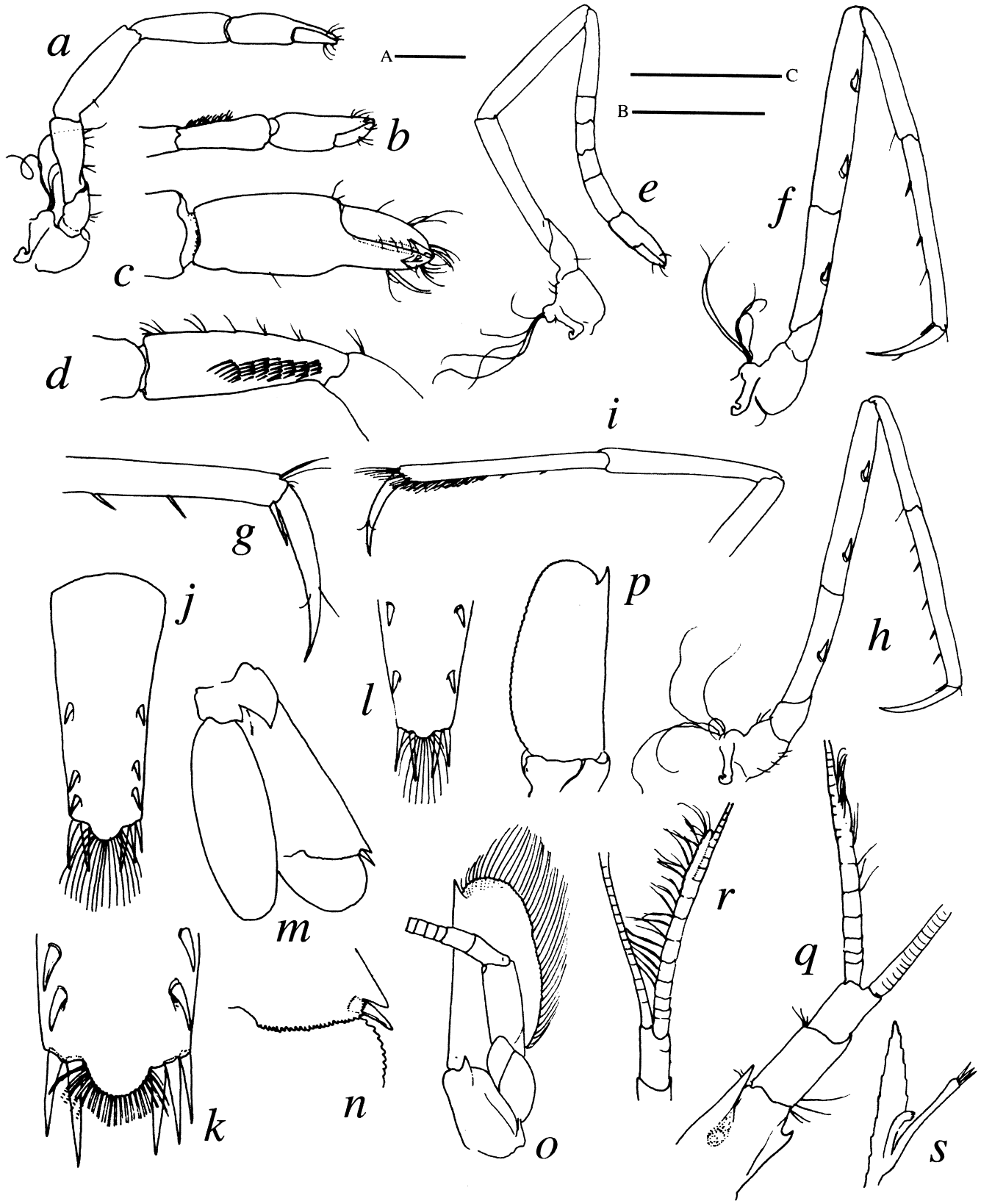

Fig. 6. *Potamalpheops johnsoni*, new species, a-k, paratype, ovigerous female (MNHN-Na 13720): a, first cheliped; b, same, carpus and chela; c, same, chela enlarged; d, same, carpus, mesial view; e, second pereiopod; f, third pereiopod; g, same, distal propodus and dactylus; h, fourth pereiopod; i, fifth pereiopod, distal articles; j, telson; k, same, posterior margin; l, female paratype (ZRC 2000.2173), telson, posterior half; m-q, same paratype as a-k: m, uropod, n, same, detail of diaeresis; o, antenna, ventral aspect; p, same, scaphocerite; q, antennule, ventro-lateral view; r-s, male paratype (from ZRC type series): r, outer antennular flagellum, s, second pleopod, appendix masculina and appendix interna. Scales: A (a, b), B (e, f, h-j, l, m, o, p), C (c, d, g, k, n, q-s), scales A, C, 0.5 mm, scale B, 1 mm.

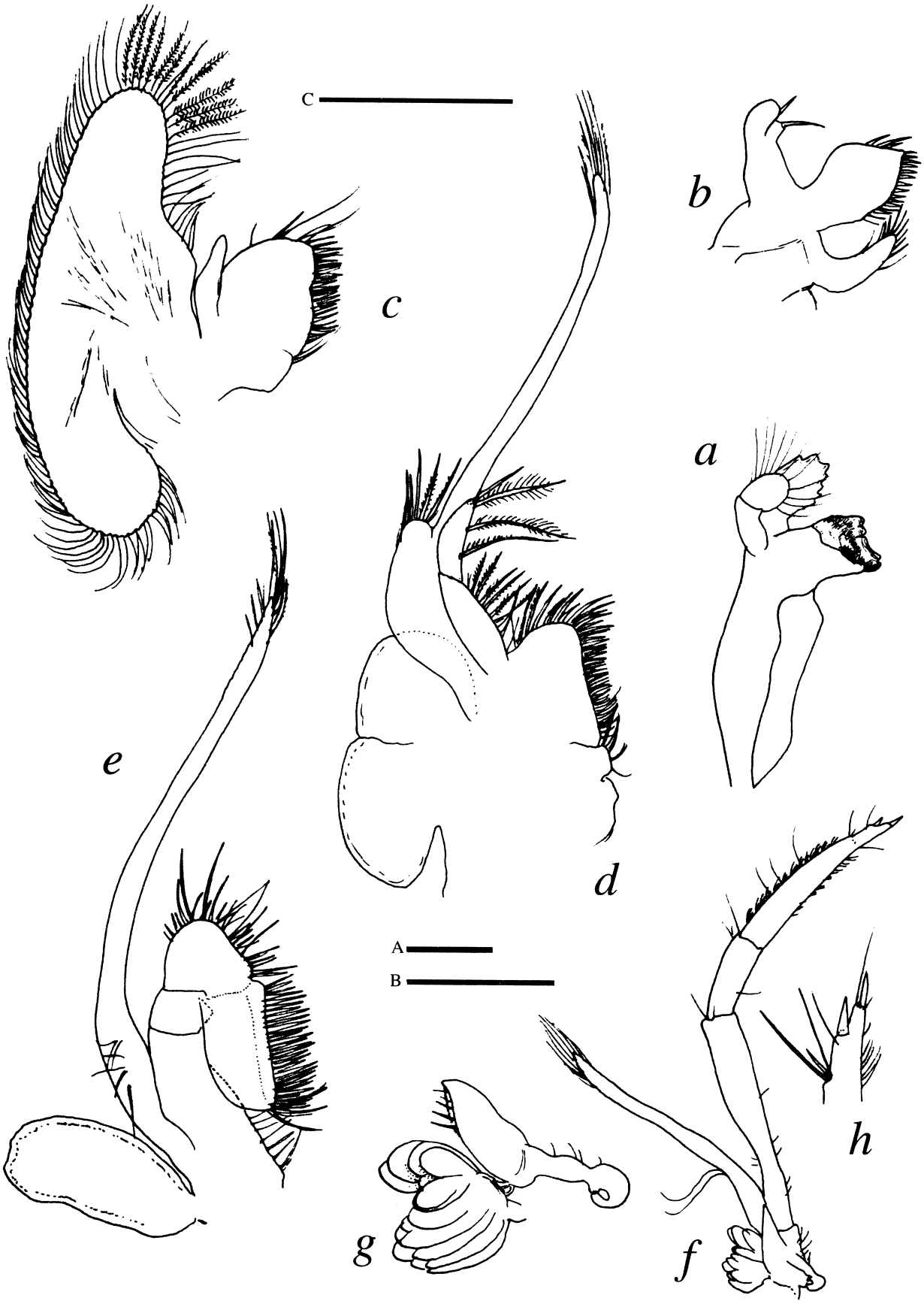

Fig. 7. *Potamalpheops johnsoni*, new species, paratype, ovigerous female (MNHN-Na 13720), a, mandible; b, maxillula; c, maxilla; d, first maxilliped; e, second maxilliped; f, third maxilliped; g, same, base; h, same, apex. Scales: A (f), B (g, h), C (a-e), A, B, 1 mm, C, 0.5 mm.

pininsulue Bruce & Iliffe from the anchialine caves of New Caledonia (Bruce & Iliffe, 1992) and *P. tigger* Yeo & Ng, which occurs in Singapore syntopically with *P. johnsoni*, new species, and is also known from northern Australia (see earlier). *Potamalpheops johnsoni*, new species, can be separated from the slightly larger *P. pininsulae* by the dorsally much less convex carapace (cf. Bruce & Iliffe, 1992: fig.1), the rostrum with the inferior tooth (or teeth) situated more apically (cf. Bruce & Iliffe, 1992: figs. 2, 4), the second and third pereiopods less slender (cf. Bruce & Iliffe, 1992: fig. 23), and the appendix masculina lacking a row of setae on the margin opposed to the endopod, as illustrated by Bruce & Iliffe (1992: fig. 31).

Potamalpheops johnsoni, new species, differs from *P. tigger* by the rostrum bearing a subapical inferior tooth, which is never present or even indicated in *P. tigger* (cf. Fig. 4) and the much shorter stylocerite (cf. Figs. 5b, 4c). The colour patterns also contribute to the separation of these two syntopic species: probably the most consistent difference (though visible only under the dissecting microscope) is the presence of blackish or brownish chromatophores on the third to fifth pereiopods in *P. johnsoni*, new species, and their absence in *P. tigger*.

All other *Potamalpheops* species with non enlarged or "primitive" chelipeds, namely *P. amnicus* Yeo & Ng, *P. miyai* Yeo & Ng, *P. monodi* Sollaud, *P. stygicola* Hobbs, *P. hanleyi* Bruce, an undescribed species of *Potamalpehops* from Palawan (Cai & Anker, in prep.) and a second undescribed species from Nigeria (cf. Powell, 1979, addendum, p. 150), have much shorter rostrums and differ from *P. johnsoni*, new species, in numerous other features (cf. Gordon, 1957; Powell, 1979; Hobbs, 1973, 1983; Bruce, 1991; Yeo & Ng, 1997).

***Distribution.* –** Presently known only from the type locality, Sungei Buloh mangrove in Singapore.

Athanas Leach, 1814

Athanas polymorphus Kemp, 1915
(Figs. 8-13, 20e, f)

Athanas polymorphus Kemp, 1915: 295, figs. 31, 32; Tattersall, 1921: 370; Miya, 1991: 1197; Bruce & Coombes, 1997: 325.
Athanas near *polymorphus* – Banner & Banner, 1966b: 24, fig. 2.

***Material examined.* –** 1 male (CL 5.3 mm)*, 1 male (CL 5.5 mm, dissected)*, 1 male (CL 5.2 mm), 1 juv. male (CL 3.1 mm)*, 1 juv. female (CL 2.6 mm)*, ZRC 2003.0085, Sungei Buloh mangrove, Singapore, at low tide, under dead wood and debris, coll. Y. Cai & A. Anker, 10 Feb.2000; 1 male (CL 4.9 mm)*, 1 female (CL 4.8 mm)*, 1 male (CL 4.1)*, ZRC ZRC 2003.0086, Sungei Buloh mangrove, Singapore, at low tide, in mud under debris, coll. Y. Cai, 28 Feb.2000; 1 female (CL 3.0 mm), MNHN-Na 13688, Lim Chu Kang mangrove, Singapore, in mud under mangrove roots, coll. A. Anker & D. C. J. Yeo, 16 Jan.2002.
* specimens illustrated.

***Description.* –** Specimens from Singapore. Carapace slightly hirsute due to numerous erected setae (Fig. 9a). Rostrum laterally compressed, acute, usually reaching to mid-length of second article of antennular peduncle (Figs. 9a, b); rostral carina feebly marked posterior to eyestalks. Extra-corneal and infra-corneal teeth well developed, acute (Fig. 9a). Eyes exposed in dorsal and lateral views, with large, well pigmented cornea. Pterygostomial angle with a small tooth projecting anteriorly (Fig. 9a); this tooth is slightly larger in some specimens (Fig. 9c).

Antennular peduncles with second article as long as or shorter than first article; stylocerite acute, clearly exceeding distal margin of first article, but not reaching mid-length of second article (Figs. 9 a, d); ventro-mesial carina with acute tooth (Fig. 9d); outer flagellum biramous, fused portion composed of five-seven articles; shorter ramus with several (e.g., four) groups of aesthetascs. Antenna with basicerite bearing acute ventro-lateral tooth; scaphocerite oval and slightly elongate (Fig. 9e), disto-lateral spine strong, exceeding antennular peduncles; carpocerite exceeding 3/4 of scaphocerite.

Mouthparts not species-specific, typical for *Athanas*. Third maxilliped slender (Fig. 9f); tip of ultimate segment with one superior spine and one slender, elongate inferior spine-like seta (Fig. 9g); arthrobranch absent.

First chelipeds highly variable in shape and symmetry. Chelipeds of large adult males subsymmetrical, left and right pereiopods differing only slightly in proportions and armature (Figs. 10, 11); ischium stout, with 1 small dorsal spine; merus elongated, 5-6 times as long as wide at ischio-meral articulation, ventrally excavated, outer margin serrated with teeth, inner margin straight; carpus cup-shaped, distal margin with lobes; palm more or less oval, somewhat twisted, flat on one side, lower margin with a series of small proximal tubercles and a larger tubercle situated approximately on palm mid-length (Figs. 10b, 11a); fingers distally curved (especially dactylus ventrally), about 0.5 times as long as palm; cutting edges of pollex either armed with small serrated teeth – type A (Fig. 10), or armed with a large rectangular tooth bearing serrations distally – type B (Fig. 11); dactylus either finely serrated – type A, or with a rounded tubercle situated basal to the dactylus middle – type B (Fig. 11). Chelipeds of some males asymmetrical in shape but more or less equal in size; larger cheliped of type B (Figs. 13a-c); smaller cheliped different in proportions and shape of chela, especially fingers being longer, more slender, with cutting edges serrated (Figs. 13d-f). First chelipeds of smaller and subadult males usually asymmetrical and unequal – type C (Figs. 12l-n); major cheliped with ischium slender and more elongated than in types A and B; merus with one triangular tooth on outer margin (Figs. 12l, m); carpus cup-shaped, more slender and slightly longer than in types A and B; chela with palm slightly inflated, with (Fig. 12k) or without (Fig. 12m) tubercles on lower margin; fingers only slightly curved and unarmed or finely serrated; minor cheliped of male (Fig. 12n) similar to that of some females (Fig. 12o), with merus and carpus elongated, cylindrical, and chela slender, not inflated. Other males and larger females with chelipeds strongly unequal and asymmetrical; major chelipeds with

shapes and proportions very different from those of males – type D (Figs. 12a-i), fingers either armed, with pollex bearing one large tooth (Fig. 12c), or serrated (Fig. 12 h); minor chelipeds of females as described above, however with carpus distinctly longer (Figs. 12d, e, i). When not used, chelipeds are held folded under cephalothorax with the chela applied against the merus (Figs. 8, 20 f).

Second pereiopod slender; ischium slightly shorter than merus; carpus five-articulated, first article longer than the sum of all other articles; ratio of carpal articles equal to (from proximal to distal): 5.5: 0.9: 0.9: 0.9: 1.8 (Fig. 9h); chela simple, longer than distal carpal article.

Third pereiopod slender (Fig. 9i); ischium armed with two spines; merus and carpus unarmed; propodus with two or three small slender spines one on inferior margin and one distal pair of spines; dactylus about 0.45 length of propodus, simple, slender, gradually curved (Fig. 9i). Fourth pereiopod in most aspects similar to the third pereiopod. Fifth pereiopod with ischium, merus, carpus and propodus unarmed; latter with several rows of grooming setae (Fig. 9j).

Abdominal segments with posterior ventral angles rounded (A1), angular (A3, A4) or pointed (A5); sixth segment (A6) with articulated triangular plate, and posterior angle bluntly producing (Fig. 8). Uropod with diaeresis bearing a pointed tooth proximal to lateral spine, straight from this tooth to inner margin (Fig. 9l). Telson elongated, tapering distally, usually with two pairs of dorsal spines, sometimes with only three spines (Fig. 9m); posterior margin of telson medially convex, with two strong postero-lateral spines at each angle, median spines about 4 times longer than lateral spines.

Gill formula typical for majority of *Athanas* s. str (sensu Anker, in prep.): pleurobranchs on P1-P5; podobranch and arthrobranch absent; exopods on Mxp1-Mxp3; strap-like epipods (mastigobranchs) on Mxp3 and P1- P3; setobranchs on P1-P4.

Largest specimens reaching approximately 5.5 mm CL (13-14 mm TL).

Colour. **–** Ground colour grey-blue or brownish, densely covered with small reddish chromatophores, particularly concentrated on the almost brown dorsal part of the carapace; articulation area between the carapace and the abdomen bluish; carapace dorsally with three whitish to ivory-yellowish, transverse bands, two bands posterior to the rostrum, and one broad band proximal to the posterior margin; branchiostegites with several irregular white patches; rostrum brown; abdominal segments A2-4 and A6 dorsally with a whitish or yellowish, transverse patch, A1 only with a lateral whitish patch, A2, A3 and A5 with small whitish patch proximal to the posterior margin; telson and uropods dark brown, fringing setae whitish; legs semitransparent, with reddish chromatophores; antennular and antennal peduncles brownish, flagella reddish; first pereiopods reddish brown, outer side of the palm whitish with a reddish reticulation; fingers also reddish, tips white (Figs. 20e, f).

Habitat. **–** *Athanas polymorphus* has been collected on mudflats of a brackish lagoon (Kemp, 1915), on mangal flats dominated by *Sonneratia alba* (Miya, 1991), and in rich mangrove forests, in mud, small pools and under rotten pieces of wood and bark (present report). In Singapore, *A. polymorphus* seems to be restricted to mangrove areas such as Sungei Buloh and Lim Chu Kang. However, several

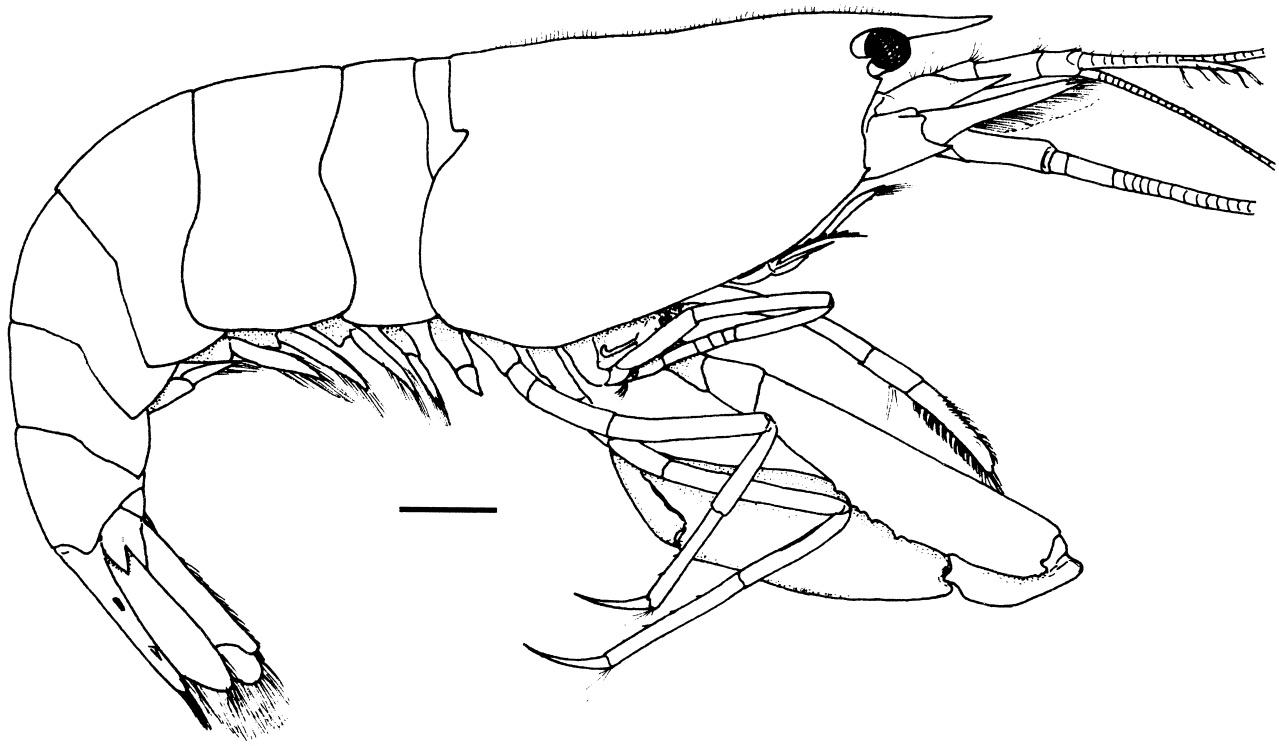

Fig. 8. *Athanas polymorphus* Kemp, male I from Sungei Buloh (ZRC 2003.0085), habitus. Scale: 1 mm.

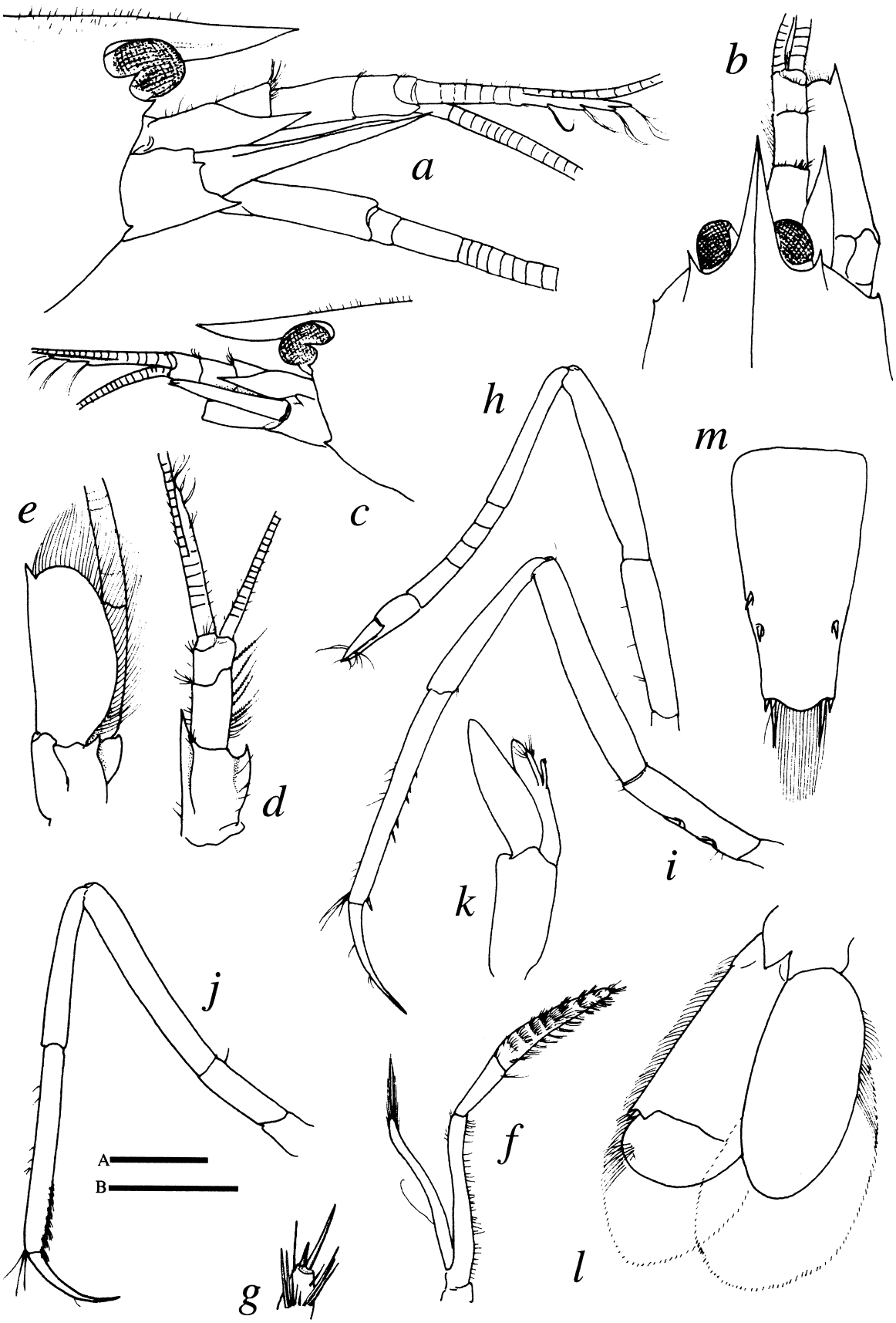

Fig. 9. *Athanas polymorphus* Kemp, a, b, male I from Sungei Buloh (ZRC 2003.0085): a, frontal region, lateral view; b, same, dorsal view; c, smaller male (male II, same lot), frontal region, lateral view; d-m, male I: d, antennule, ventro-lateral aspect; e, antenna, dorsal view of scaphocerite; f, third maxilliped; g, same, apex; i, third pereiopod; j, fifth pereiopod; k, second pleopod; l, uropod; m, telson. Scales: A (b, d-f), B (a, c, h-m), both scales: 1 mm, g, without scale.

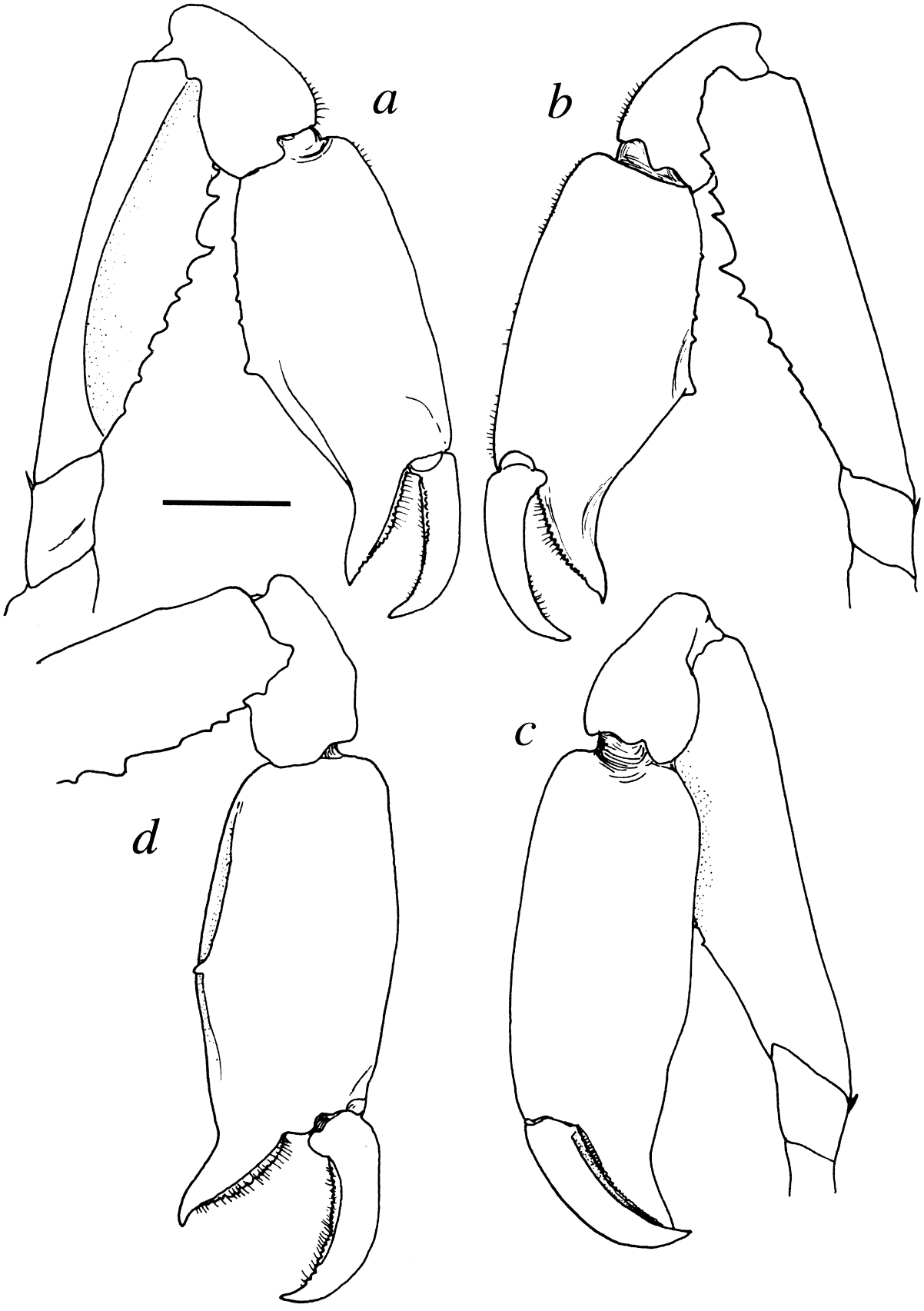

Fig. 10. *Athanas polymorphus* Kemp, male I from Sungei Buloh (ZRC 2003.0085): a, left first cheliped, mesial view; b, same, lateral view; c, right first cheliped, distal merus, carpus and chela, lateral view; d, same, mesial view. Scale: 1 mm.

specimens of "*A.* near *polymorphus*" were collected under rocks on a gravel-sand beach, at Rayong, Gulf of Thailand (Banner & Banner, 1966b).

Remarks. – Kemp (1915) provided a relatively good description of this species, accompanied by some figures. The types of *A. polymorphus* from the Chilka Lake in the State of Orissa, India, were deposited in the Indian Museum in Calcutta (IMC) and are not easily accessible for examination. Because of insufficiency of original figures, rarity of reports of *A. polymorphus*, and increasing number of species in the genus *Athanas*, a redescription of the type material of this species is desirable.

The new material from Singapore agrees rather well with the original description, including the detailed description of the colour pattern. However, some important differences between the type-specimens and the specimens from Singapore do not allow the present description to be considered as a formal redescription of *A. polymorphus*. Some of these differences may be due to inaccuracies in Kemp's illustrations. However, one of the main differences between the two populations concerns the development of the first chelipeds in females. Kemp (1915) noted that from 27 of his Chilka specimens only nine were males, and that only these males exhibited the three "types" I, II and III of the polymorphic first chelipeds (hence the specific name proposed by Kemp). The other 18 specimens of the original type-series of *A. polymorphus* were females, all of which had almost symmetrical and slender first chelipeds, with a small, unarmed chela (cf. Kemp, 1915: fig. 31a). Among the 10 specimens collected in Singapore both males and females present a very pronounced polymorphism in the shape of the first chelipeds. Several types of chelipeds can be recognized in this population: some major chelipeds are apparently typical of males, others are found in both males and females, and the most undeveloped minor chelipeds are found only in a few small and possibly immature females. At least three adult females from Singapore have a robust major cheliped, with an armed chela (cf. Fig. 12), and minor cheliped typical to many species from *A. dimorphus* group, a condition never observed in the 18 females collected from Chilka Lake.

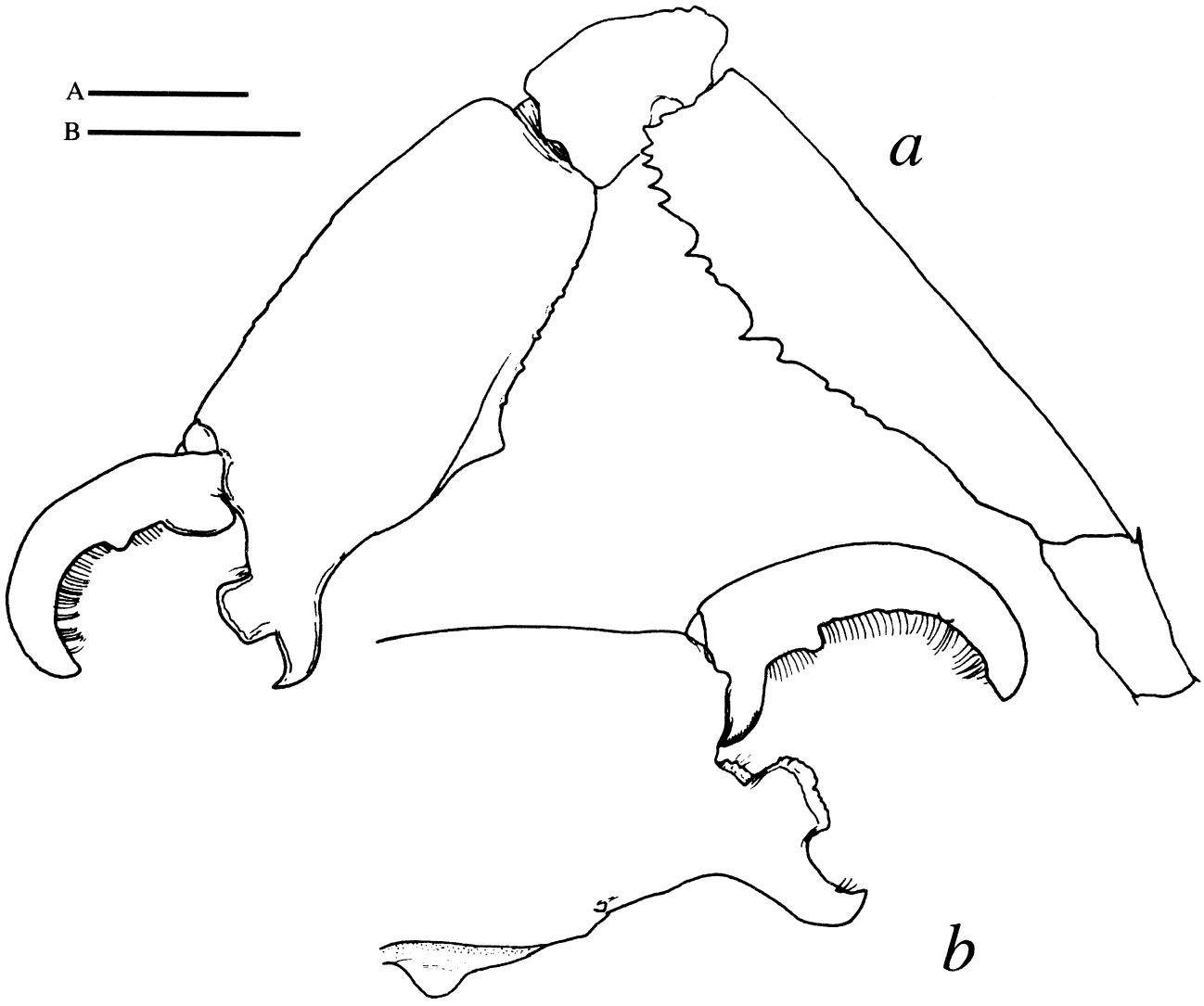

Fig. 11. *Athanas polymorphus* Kemp, male II from Sungei Buloh (ZRC 2003.0085): a, left first cheliped, lateral view; b, same, chela, mesial view, distal palm and fingers. Scales: A (a), B (b), both scales: 1 mm.

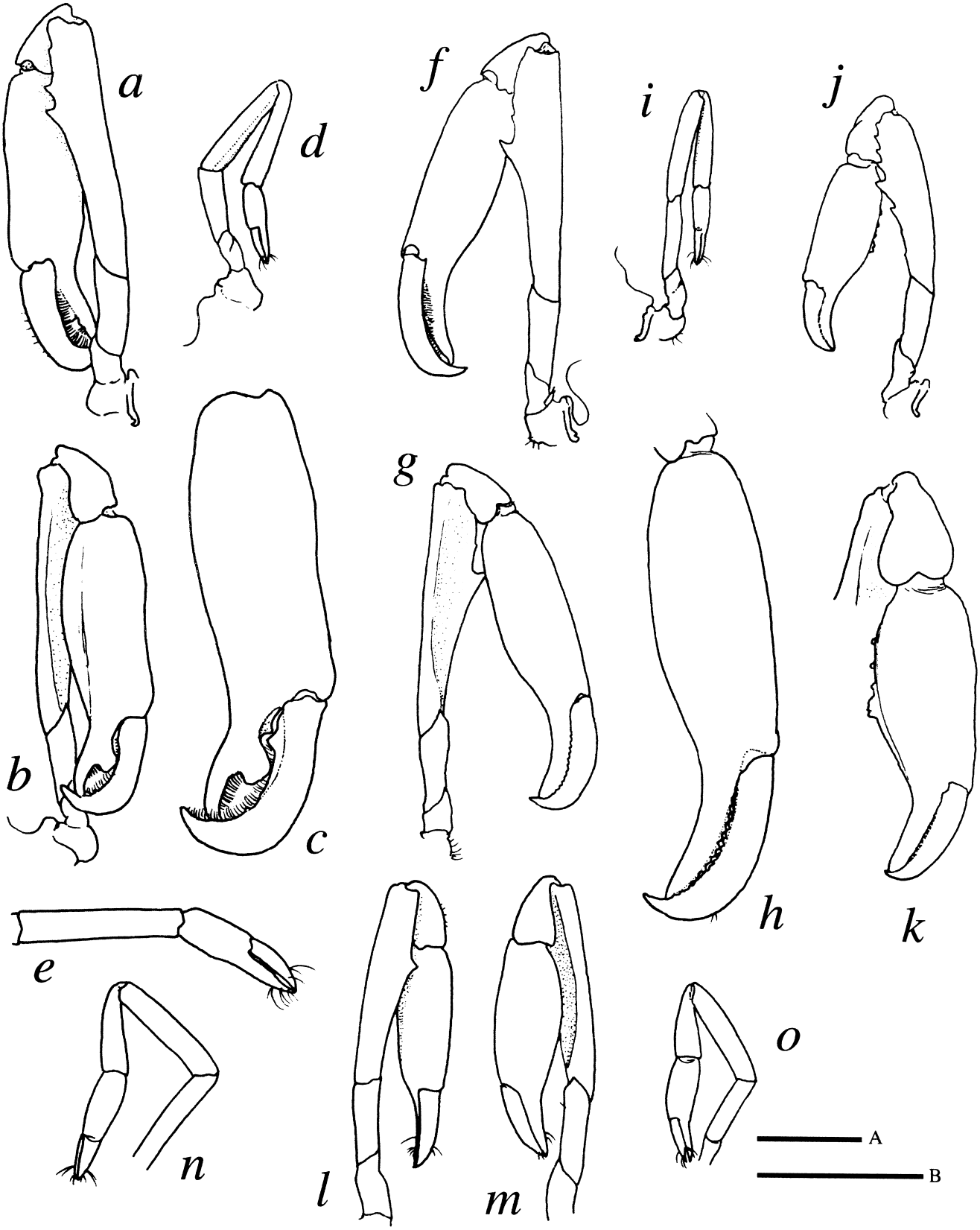

Fig. 12. *Athanas polymorphus* Kemp, first chelipeds of various specimens from Sungei Buloh: a-e, female I (ZRC 2003.0085-86): a, major cheliped; lateral view, b, same, mesial view, c, same, chela; d, minor cheliped; e, same, carpus and chela; f-i, female II (same lot): f, major cheliped; lateral view, g, same, mesial view, h, same, chela; i, minor cheliped; j, k, male III (same lot): j, major cheliped, k, same, carpus and chela; l-n, male IV (same lot): l, major cheliped, lateral view, m, same, mesial view, n, minor cheliped; o, female III (same lot): first cheliped (chelipeds symmetrical). Scales: A (a, b, d, f, g, i, j, l-o), B (c, e, h, k), both scales: 1 mm.

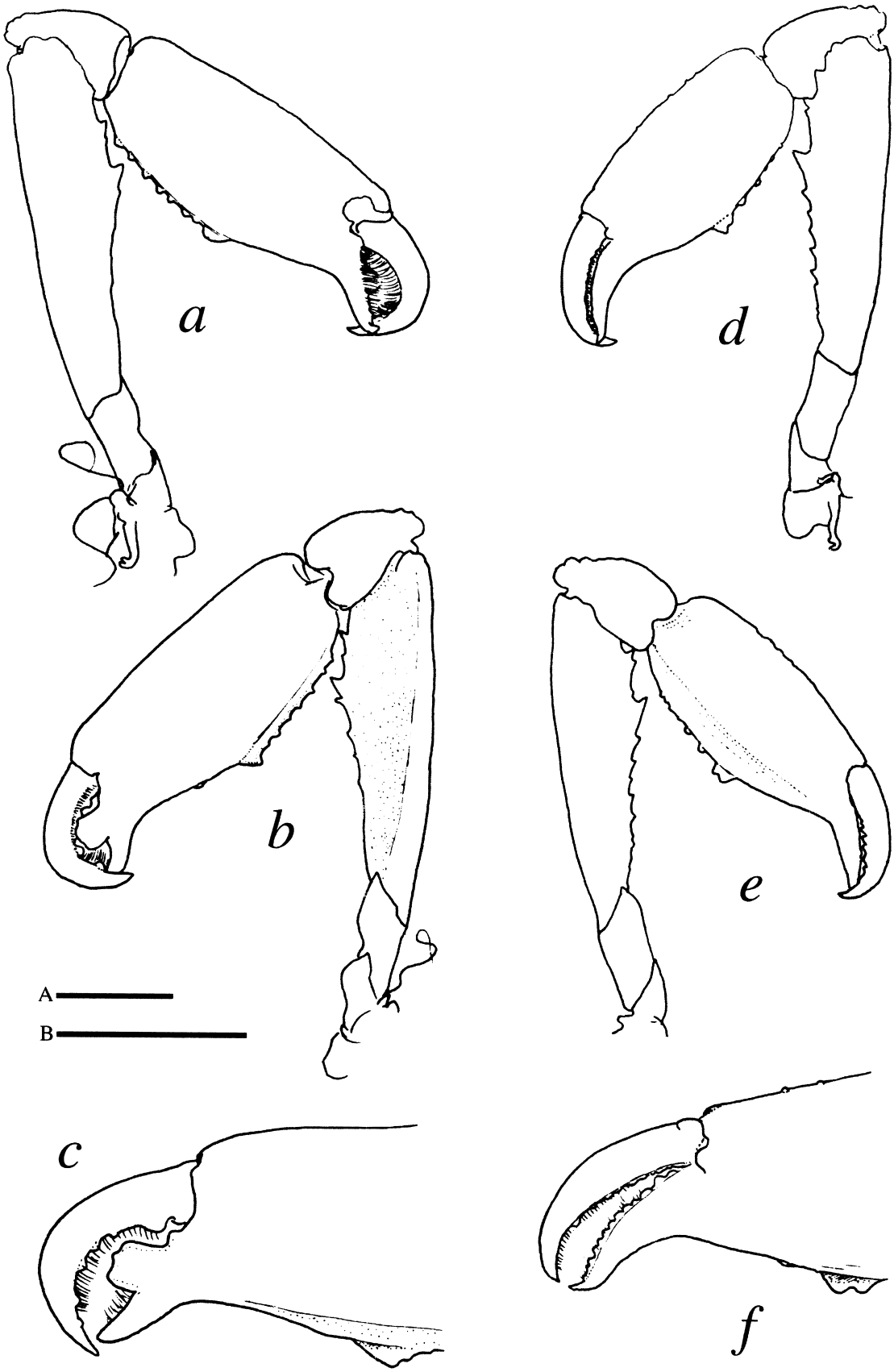

Fig. 13. *Athanas polymorphus* Kemp, first chelipeds of male IV (ZRC 2003.0086) from Sungei Buloh: a, major cheliped, lateral view; b, same, mesial view; c, same, chela, distal palm and fingers; d, minor cheliped, lateral view; e, same, mesial view; f, same, chela, distal palm and fingers. Scales: Scales: A (a, b, d, e), B (c, f), both scales: 1 mm.

There are also some other important differences between the Chilka and Singapore specimens. Kemp (1915) reported that his specimens of *A. polymorphus* had either four or five articles in the carpus of the second pereiopod. However, all specimens of *A. polymorphus* from Singapore had five articles in the carpus of the second pereiopod. According to Kemp's drawings, the rostrum is longer and more slender in specimens from the Chilka Lake than in the present specimens from Singapore. Also, in *A. polymorphus* from Chilka the "pterygostomian tooth" arises above the pterygostomial angle (cf. Kemp, 1915: fig. 32a), while in all specimens from Singapore this tooth is actually represented by a small acute anterior projection of the pterygostomial angle itself (Figs. 9a, c). The antennules of *A. polymorphus* seem to be more slender and more elongated, at least according to Kemp's figure 32b, compared to Singapore material (cf. Fig. 9b). The shape of the scaphocerite is also different: it is slightly longer and less broad in *A. polymorphus* (cf. Kemp, 1915: fig. 32c and present Fig. 9e). In larger males, the number of teeth on the lateral margin of the merus of the first chelipeds is approximately 20 in *A. polymorphus* from Chilka, while it never exceeds 10 in specimens from Singapore. Kemp also noted and illustrated the variation in the number of carpal articles in the second pereiopod: some of the Chilka specimens apparently had only four articles instead of the normal five. Seven specimens from Singapore examined especially for this feature all had a normal, five-articulated carpus in the second pereiopod.

The specimens from Singapore appear to be closer to "*A.* near *polymorphus*" collected "under rocks on a gravel-sand beach" in Rayong, Thailand (Banner & Banner, 1966b). The main reasons, for which Banner & Banner (1966b) did not assign the specimens from Rayong unambiguously to Kemp's species are the same as the doubts about the identity of the present specimens from Singapore, namely the presence of strongly asymmetrical chelipeds in both sexes (including a robust major cheliped in females), and the acute pterygostomial tooth arising from the pterygostomial angle itself (not above it), and being much stronger.

It is not clear whether the above mentioned differences are of taxonomic importance or simply reflect an intra-specific, geographical variation. Without having the possibility to examine Kemp's type-series of *A. polymorphus* and Banner's specimens of *A.* near *polymorphus*, the specimens from Singapore are tentatively assigned to *A. polymorphus*, and the species is considered as polymorphic, with a high plasticity of the first chelipeds. Collections on the shores of Chilka Lake, India, the type-locality of *A. polymorphus* (or examination of the type-material at the IMC) and Rayong, Thailand will be necessary to conclude whether *A. polymorphus* is indeed a highly variable species or a species complex. If Kemp's drawings of *A. polymorphus* are correct, a new species must be established for the present specimens from Singapore and possibly those from Rayong, Thailand (*A.* near *polymorphus* in Banner & Banner, 1966b). Similarly, the identity of specimens from northern Australia reported with some doubts as *A. polymorphus* by Bruce & Coombes (1997) remains to be determined.

Athanas polymorphus can be easily distinguished from the majority of other *Athanas* species by the presence of a small acute tooth on the pterygostomial angle. The only other species having an anteriorly produced pterygostomial tooth and a slender, simple dactylus on the third to fifth pereiopods is *A. squillophilus* Hayashi from southern Hokkaido, Japan (Hayashi, 2002). This stomatopod-associated species differs from *A. polymorphus* in having the pterygostomial tooth much more pronounced, the corneas somewhat reduced, and the chelae of the first chelipeds furnished with long and fine filtering setae.

***Distribution.* –** Chilka Lake, Orissa, eastern India (Kemp, 1915); northern Gulf of Thailand (Banner & Banner, 1966b); Singapore (present study); Darwin, Northern Territory, Australia (Bruce & Coombes, 1997).

Athanas japonicus Kubo, 1936
(Figs. 14-19)

Athanas japonicus Kubo, 1936: 43, pl. 13; Miya & Miyake, 1968: 139, figs. 4-6; Nishimura & Suzuki, 1971: 84, pl. 27, fig. 8; Banner & Banner, 1973: 308, fig. 4; Wadley, 1978: 13, figs. 6a-b; Miyake, 1982: 41; Takeda, 1982: 29; Miya, 1995: 283, 287; Hayashi, 1994: 4, figs. 267b-d, 268d, 270g, 271; Bruce & Coombes, 1997: 325; Nomura et al., 1998: 42, fig. 1 H; Nomura & Asakura, 1998: 28.

Athanas lamellifer Kubo, 1940: 102, figs. 3-5; Nakazawa & Miyake, 1957: 776, fig. 2240.

***Material examined.* –** *Athanas* cf. *japonicus* A: 1 male (CL 3.5 mm)* and 1 female (CL 3.3 mm)*, ZRC 2003.0087, belt of muddy sand in front of Lim Chu Kang mangrove, N Singapore, small shallow pool, under debris, low tide, coll. A. Anker, 16 Jan.2002. *Athanas* cf. *japonicus* B: 1 male (CL approx. 3.5 mm)*, ZRC 1979.4.6.15, Ponggol Beach, Singapore, at about LSWT, muddy sand with stones, coll. D. Johnson, 07 Apr.1969, id. D. Johnson as "*Athanas tenuipes* De Man" (J11, 895).

Extra-limital material – *Athanas* cf. *japonicus* C: 2 males (CL 3.4 and 3.7 mm)* QM-W26809, Cooya Beach, Mossman, Queensland, muddy sand at low tide, specimens obtained with yabby pump from burrow of a mud-skipper (Periopthalmidae, possibly *Periphthalmodon* sp.), coll. A. Anker, July 2001.
Athanas cf. *japonicus* D: 1 female (CL 2.9 mm)*, NTM Cr-009968, Channel Island, near Darwin, Northern Territory, Australia, near Bridge, 12°34.9' S, 130°55.4' E, Site 3, LWS, hand collection, coll. M. Burke, 01 Jul.1992.
Athanas japonicus series from Japan: 2 males (CL 3.3 and 3.2 mm), 1 female (CL 4.6 mm), MNHN-Na 13764*, Arita Bay, Kushimoto, Wakayama Pref., intertidal, under rock, coll. K. Nomura, 30 Mar.1994; 2 males (CL 5.1 and 5.2 mm), MNHN-Na 13711, Arita Bay, Kushimoto, Wakayama Pref., intertidal, under rock, coll. K. Nomura, 28 Mar.1997; 2 males (CL 4.1 and 3.9 mm), 1 ovigerous female (CL 4.0 mm), MNHN-Na 13705, Okuda, Chita, Aichi Pref., intertidal, under rock, coll. M. Kasiwara, 08 Sep.1994; 6 males (CL 5.2, 4.7, 4.5, 5.5, 5.0 and 4.3 mm), 1 female (CL 4.7 mm), 1 ovigerous female (CL 4.4 mm), MNHN-Na 13640*, Yamaguchi Bay, Yamaguchi, intertidal, under rock, coll. G. Itani, May.1995; 2 males (CL 4.7 and 5.0 mm) and 1 female (CL 3.1 mm), MNHN-Na 13701, mouth of Hidaka River, Gobou, Wakayama Pref., intertidal, under rock, coll. G. Itani, 27 Sep.1996; 1 male (CL approx. 5.1 mm) and 1 ovig. female (CL 5.4 mm), MNHN-Na

13713, Sasebo, Nagasaki pref., intertidal, under rock, coll. K. Nomura, 23 Jun.2001; 1 specimen (CL not measured), MNHN-Na 13674, Hazama, Tateyama, near Kominato, Chiba Pref., intertidal, under rock, coll. K. Nomura, 15 May.1996; 1 female (CL 4.3 mm), MNHN-Na 13717, Banda, Tateyama, near Kominato, Chiba Pref., intertidal, under rock, coll. K. Nomura, 17 May.1996; 2 males (CL 5.1 and 3.8 mm), 1 ovig. female (CL 4.7 mm), MNHN-Na 13685, Kominato, Chiba Pref., intertidal, under rock, coll. K. Nomura, 24 May.1994; 3 ovig. females (CL 3.9, 4.4 and 5.6 mm), MNHN-Na 13635 (from YMP 1812), Sunabe, Chyatan, Okinawa-jima, intertidal, under rock, coll. K. Nomura, 29 Mar.1998.
* Specimens illustrated.

Description. **–** Specimens from Lim Chu Kang, Singapore (*Athanas* cf. *japonicus* A). Carapace sparsely setose. Rostrum laterally compressed, acute, slightly exceeding distal margin of first article of antennular peduncle (Fig. 14b). Extra-corneal and infra-corneal teeth well developed, acute, supra-corneal teeth absent. Eyestalks largely exposed in dorsal and lateral views; cornea well pigmented, occupying latero-anteror and lateral, but not the most medio-proximal section (Fig. 14a). Pterygostomial angle rounded, not projecting anteriorly, without acute tooth.

Antennular peduncles with second article shorter than first; stylocerite acute, reaching from 1/3 to almost mid-length of second article; ventro-mesial carina with well developed, acute tooth; outer flagellum biramous, fused portion composed of 4 articles. Antenna with basicerite bearing acute ventro-lateral tooth; scaphocerite not exceeding antennular peduncles, oval-shaped, anterior margin broadly convex, lateral spine strong; carpocerite only slightly shorter than scaphocerite, not reaching to distal margin of antennular peduncles.

Mouthparts not species-specific, typical for *Athanas*. Third maxilliped slender; tip of ultimate segment with long setae, without stout spines; arthrobranch absent.

Male first chelipeds very asymmetrical in shape, subequal in size (Figs. 14d, g). Major cheliped (Figs. 14d-f) with ischium short, stout; merus robust, elongated, broadened distally, shallowly excavated on ventral side (Fig. 14e), outer margin armed with eight teeth, two small proximal teeth, followed more distally by two larger teeth, one large triangular tooth situated approximately on mid-length of merus margin, and three medium-sized to small, distal teeth (Fig. 14d); inner margin of merus straight; carpus robust, cup-shaped, distal margin with lobes; palm more or less oval in cross-section, with inner side flattened and forming an angle with ventral side, outer margin of ventral side with three tubercles situated approximately at palm mid-length (Fig. 14e); fingers distally curved, about 0.3 times as long as palm; dactylus irregularly and slightly serrated; pollex armed with a large, rectangular tooth, followed distally by a hiatus (Fig. 14f); outer surface of dactylus and pollex densely covered with fine setae, obscuring direct view of cutting edges. Minor cheliped (Figs. 14g-i) different from major cheliped mainly by shape and armature of chela; ischium and merus similar, latter being more slender compared to that of major cheliped; number and development of teeth on outer margin almost as in major cheliped; carpus similar but slightly shorter; chela very different from that of major cheliped by shape and armature of chela; chela suboval, lower margin of palm with tubercles; fingers long and slender, about 0.7 of palm length, more gradually curved; cutting edges irregularly serrated (Fig. 14i).

Female first chelipeds very asymmetrical in shape and unequal in size. Major cheliped (Figs. 14j-l) robust; ischium elongated (almost twice as long as in male major cheliped); merus slender, shallowly excavated on ventral side, lateral margin with one large triangular tooth situated approximately on mid-length, and several (4-5) smaller teeth situated on distal half; carpus cup-shaped, almost twice as long as carpus in male major cheliped; chela subcylindrical, flattened on one side; lower margin of palm unarmed; fingers slightly less than half length of palm, gradually curved, cutting edges serrated, outer surface of fingers, mostly dactylus, with dense row of fine setae. Minor female cheliped (Figs. 14m, n) slender, much smaller and less robust than major cheliped; ischium elongate subequal to merus, carpus about 0.6 length of merus, elongate, cylindrical; chela simple, slender, fingers about 0.8 length of palm, simple, unarmed, slightly and gradually curved, with some tufts of setae.

Second pereiopod with ischium shorter than merus; carpus five-articulated, first article longest; ratio of carpal articles equal to (from proximal to distal): 5: 1: 1: 1: 2 (Fig. 14o); chela simple, longer than distal carpal article, but shorter than proximal article, fingers with tufts of setae.

Third pereiopod slender, proportions of articles as illustrated (Fig. 14p); ischium armed with two spines; merus and carpus unarmed; propodus unarmed; dactylus about 0.5 length of propodus, simple, slender, gradually curved (Fig. 14p), with a very subtle convexity on ventral margin. Fourth pereiopod similar to third pereiopod. Fifth pereiopod with ischium, merus, carpus and propodus unarmed; latter with several rows of grooming setae.

Abdominal segments with posterior ventral angles rounded (A2), angular (A3-5); sixth segment (A6) with articulated triangular plate. Uropod with diaeresis well developed and straight, lateral spine rather small. Telson broadly oval-rectangular, tapering distally, with two pairs of dorsal spines; posterior margin of telson broad, slightly convex, with two postero-lateral spines at each angle, median spines less than twice as long as lateral spines (Fig. 14c).

Gill formula as in majority of *Athanas* s. str.: pleurobranchs on P1-P5; podobranch and arthrobranch absent; exopods on Mxp1-Mxp3; strap-like epipods (mastigobranchs) on Mxp3 and P1-P3; setobranchs on P1-P4.

Both adult specimens rather small: 3.3 mm and 3.5 mm CL, approximately 9 mm TL.

Colour. **–** Dull reddish, with whitish medio-dorsal stripe; the reddish colour is due to numerous pinkish or red chromatophores dispersed over the whole body except for chelae (few on lateral side), second to fifth pereiopods, flagella of antennule and antenna, and the medio-dorsal longitudinal band.

Habitat. **–** Both specimens from Lim Chu Kang, probably forming a mating pair, were collected on a several meters large belt of dark, muddy sand with various debris (natural

and artificial) lying around or being partly immerged in the mud or sand, only a few metres from some mangrove trees. Both specimens were found in a few centimetres of water remaining in a small depression under a piece of dead wood at low tide. Not a single *Athanas* was collected from the very soft and deep mud occupying large surfaces in this area.

***Remarks.* –** The type of *Athanas japonicus* upon which Kubo's (1936) description and illustrations were based, was an ovigerous female of 10 mm TL from Mitajiri (Yamaguchi Bay), although Kubo stated that two adult males were also collected at the same locality. Only the cheliped of the male was illustrated (cf. Kubo, 1936: pl. XIII, fig. C). The stylocerite of the female type reaches according to Kubo's drawings (cf. Kubo, 1936: pl. XIII, figs. A, G) to only about one third of length of the second article of the antennular peduncle, and the rostrum to the distal margin of the same article. The male cheliped does not have a strong dentition on the outer margin of the merus but bears instead very small and spaced teeth, while the cutting edges of fingers are apparently unarmed. Furthermore, the carpus is half as long as the merus, and about 0.8 times as long as the palm. The infra-corneal teeth are more protruding than the extra-corneal teeth. The posterior margin of the telson is convex only in its median portion (cf. Kubo, 1936: pl. XIII, fig. M). The colour has been described as «deep blue, hence the new Japanese name» (Kubo, 1936). The types of *A. japonicus* were apparently deposited in the Fisheries University in Tokyo (Miya & Miyake, 1968), but could not be located during a recent inspection of the collections of this institution (K. Nomura, pers. com.).

Athanas lamellifer Kubo was separated from *A. japonicus* mainly because of the much longer stylocerite, exceeding the second article of the antennular peduncle, the distinctly shorter carpus of the major cheliped (being only one quarter as long as the merus), and the shorter dactylus of the third pereiopod (cf. Kubo, 1936: pl. XIII, fig. J; 1940: figs. 4G, H). Furthermore, in *A. lamellifer* the infra-corneal teeth are less protruding compared to the extra-corneal teeth, whilst the rostrum is more slender and slightly longer. The posterior margin of the telson is rather broadly convex. The merus of the larger cheliped is only slightly serrated, both in females and males; the cutting edges are also serrated, but without a large tooth on the pollex, at least in Kubo's specimens. The colour of *A. lamellifer* has been described as uniformly deep reddish brown, with a white medio-dorsal band and white tips of uropods and telson (cf. Kubo, 1940: fig. 5).

Athanas ohsimai Yokoya seems to be very close to *A. japonicus*, but can be separated from both *A. japonicus* and *A. lamellifer* by the pollex being much shorter than the dactylus, and also by the pterygostomial angle anteriorly produced, the shorter rostrum and the presence of epipods on the first four pereiopods (Yokoya, 1936; Miya & Miyake, 1968; Hayashi, 1994).

In a major revision of Japanese species of *Athanas*, Miya & Miyake (1968) reported and illustrated an important intra-specific variation in *A. japonicus*, and placed *A. lamellifer* in synonymy with *A. japonicus*. According to Miya & Miyake (1968), the intra-specific variability of *A. japonicus* affects the width and the length of the rostrum, the length of the stylocerite, the development and the armature of chelipeds and the colour pattern. Considerable differences in the length of the stylocerite are rather unusual for Alpheidae, but variations in size, shape and armature of chelipeds, along with sexual dimorphism, occur in several other species of *Athanas*, including *A. polymorphus* Kemp, *A. phyllocheles* Banner & Banner and *A. dimorphus* Ortmann (see Kemp, 1915; D. M. Banner & A. H. Banner, 1973; A. H. Banner & D. M. Banner, 1983; see also above).

A series of specimens of *A. japonicus* from different Japanese localities situated in temperate and subtropical waters, including Yamaguchi Bay (a locality very close to the type-locality), was examined for comparison with the Singapore material. The chelipeds of these specimens are indeed quite different, as are the length of the stylocerite and the development of orbital teeth. The figures of two adult males from Yamaguchi Bay (Figs. 17, 18) and of an adult female from Arita Bay (Fig. 19) show well the differences between Singapore and Japanese specimens, and also within the Japanese material. The length of the rostrum and the stylocerite is obviously different between the male from Yamaguchi and the female from Arita (cf. Figs. 17a, 19a). The chelipeds of these specimens are also quite different from those of the type female described and illustrated by Kubo (1936) and also from the chelipeds illustrated by Miya & Miyake (1968). In large males from Yamaguchi, the lateral margin of the merus is armed with strong teeth, and the pollex bears a large process on the margin opposable to the dactylus (Fig. 17e). Furthermore, the palm of both chelae bears a series of tubercles on the lower margin, absent in the chelae of original male specimens of *A. japonicus* and *A. lamellifer* (cf. Kubo, 1936, 1940). Very small tubercles are also present on the major cheliped in the female from Arita (Fig. 19d). Most larger specimens from the Japanese series have subsymmetrical chelipeds armed with a tooth on the pollex, but some (e.g., one male and one female from Yamaguchi) have asymmetrical chelipeds, with the major cheliped as described above, and the smaller cheliped slender and not enlarged, typical of the females of many species of *dimorphus* group; other specimens have more slender chelipeds, without a tooth on the fixed finger.

As none of the chelipeds illustrated by Miya & Miyake (1968) or examined personally on present specimens from Japan were identical to the chelipeds of *Athanas* cf. *japonicus* from Lim Chu Kang mangrove in Singapore, it is quite possible that the latter belong to an undescribed species within what appears to be the *A. japonicus* complex. The most obvious difference between the specimens of *A.* cf. *japonicus* from Lim Chu Kang and other specimens of the *A. japonicus* complex is the very robust merus of both chelipeds, armed with very strong serrated teeth on the lateral margin. However, Hayashi (1994) illustrated the first chelipeds of a male from Japan, which are quite similar to those of *A.* cf. *japonicus* from Lim Chu Kang. Until the true status of Kubo's *A. japonicus* is determined, the taxonomic status of *A.* cf. *japonicus* from Singapore will remain unclear.

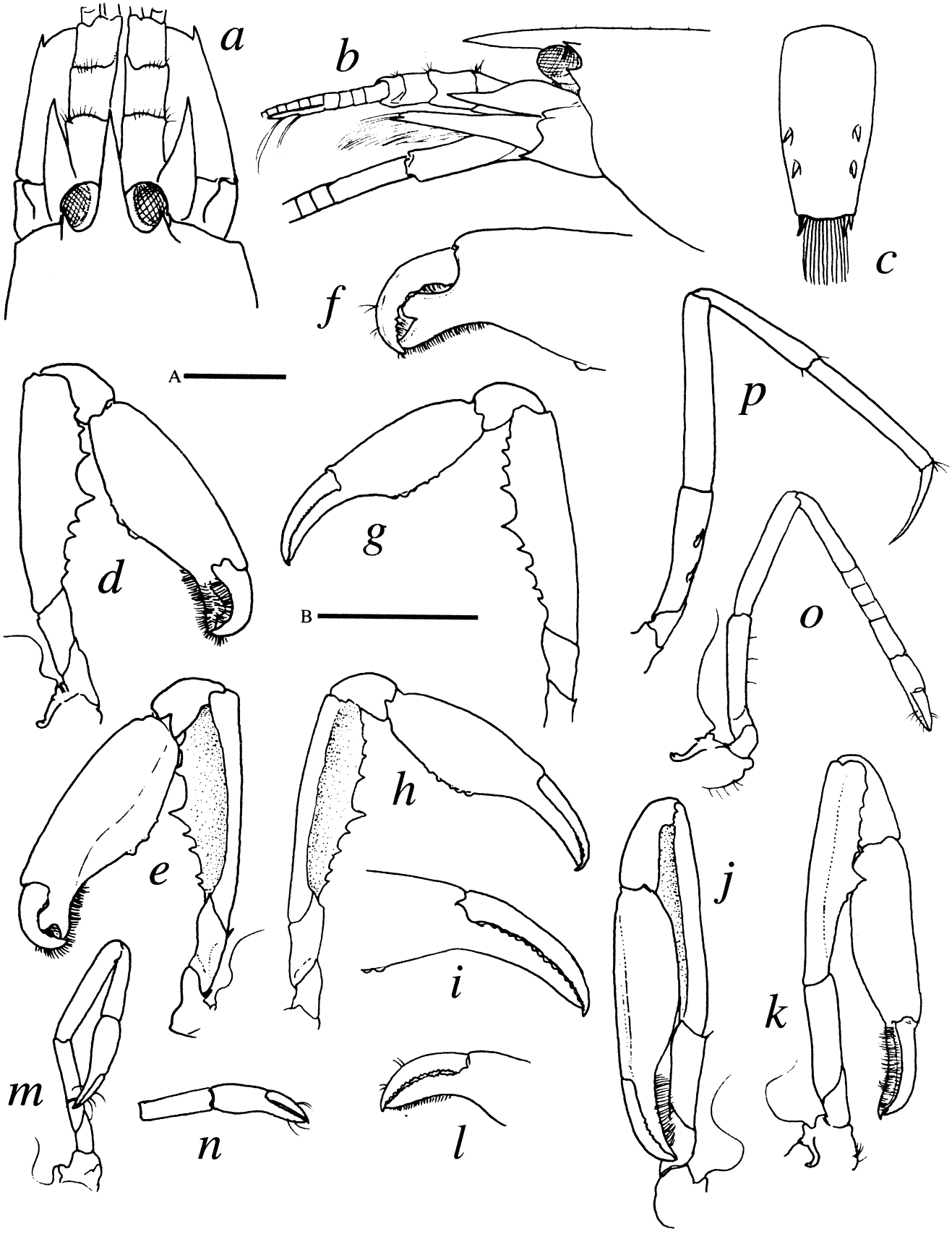

Fig. 14. *Athanas* cf. *japonicus* Kubo, male (a-i, o, p) and female (j-n) from Lim Chu Kang, Singapore (ZRC 2003.0087): a, frontal region, dorsal view; b, same, lateral view; c, telson; d-n, first cheliped: d, male major cheliped, lateral view; e, same, mesial view; f, same, chela, distal palm and fingers; g, male minor cheliped, lateral view; h, same, mesial view; i, same, chela, distal palm and fingers; j, female major cheliped, mesial view; k, same, lateral view; l, same, chela, distal palm and fingers; m, female minor cheliped; n, same, carpus and chela; o, second pereiopod; p, third pereiopod. Scales: A (d, e, g, h), B (a-c, f, i-p), both scales: 1 mm.

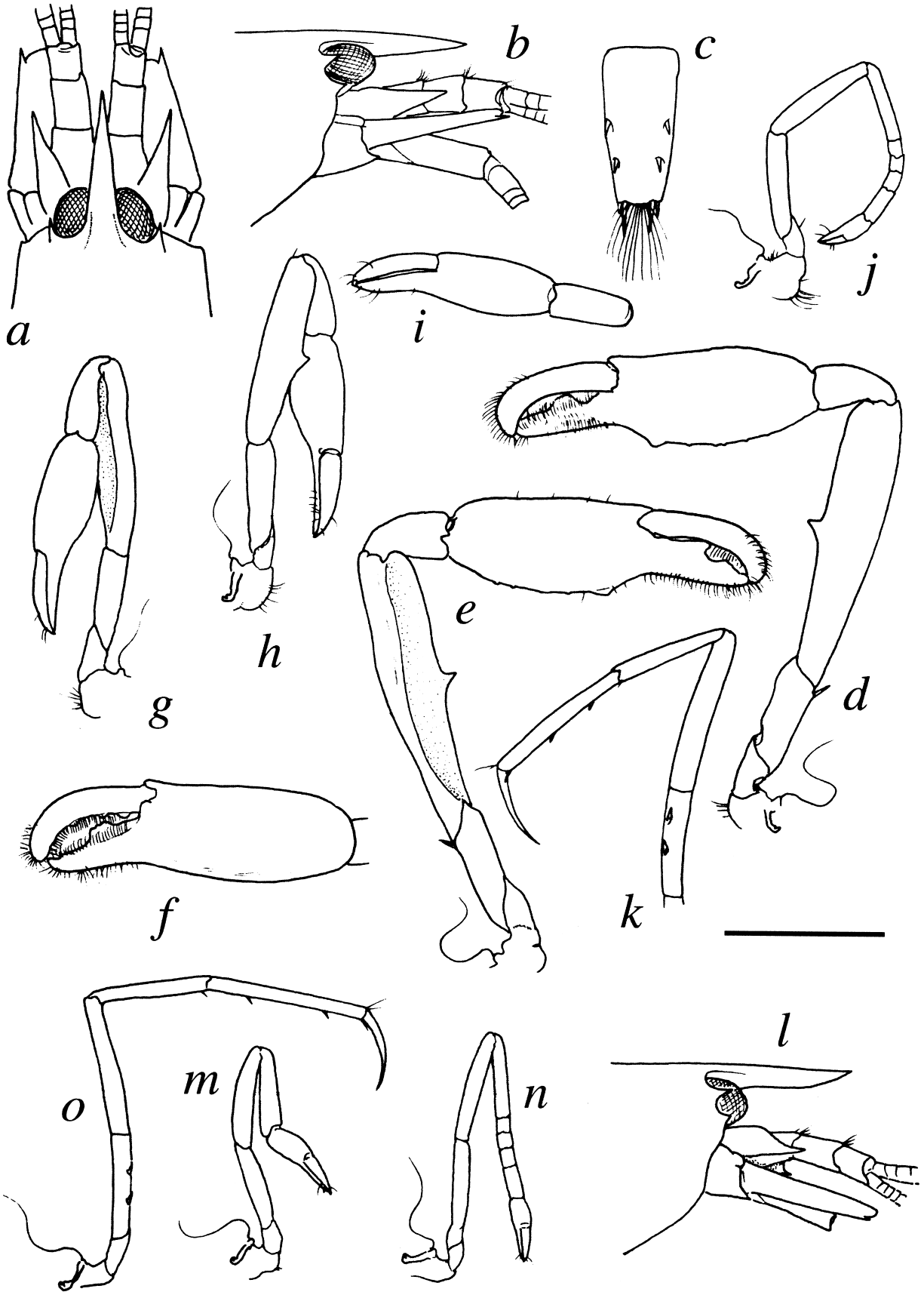

Fig. 15. *Athanas* cf. *japonicus* Kubo, male from Cooya Beach, Mossmann, Queensland (QM-W26809): a, frontal region, dorsal view; b, same, lateral view; c, telson; d-i, first cheliped: d, major cheliped, lateral view; e, same, mesial view; f, same, chela; g, minor cheliped, mesial view; h, same, lateral view; i, same, carpus and chela; j, second pereiopod; k, third pereiopod. *A.* cf. *japonicus*, female from Channel Island, Darwin (NTM Cr009968): l, frontal region, lateral view; m, first cheliped (chelipeds symmetrical); n, second pereiopod; o, third pereiopod. Scale: 1 mm.

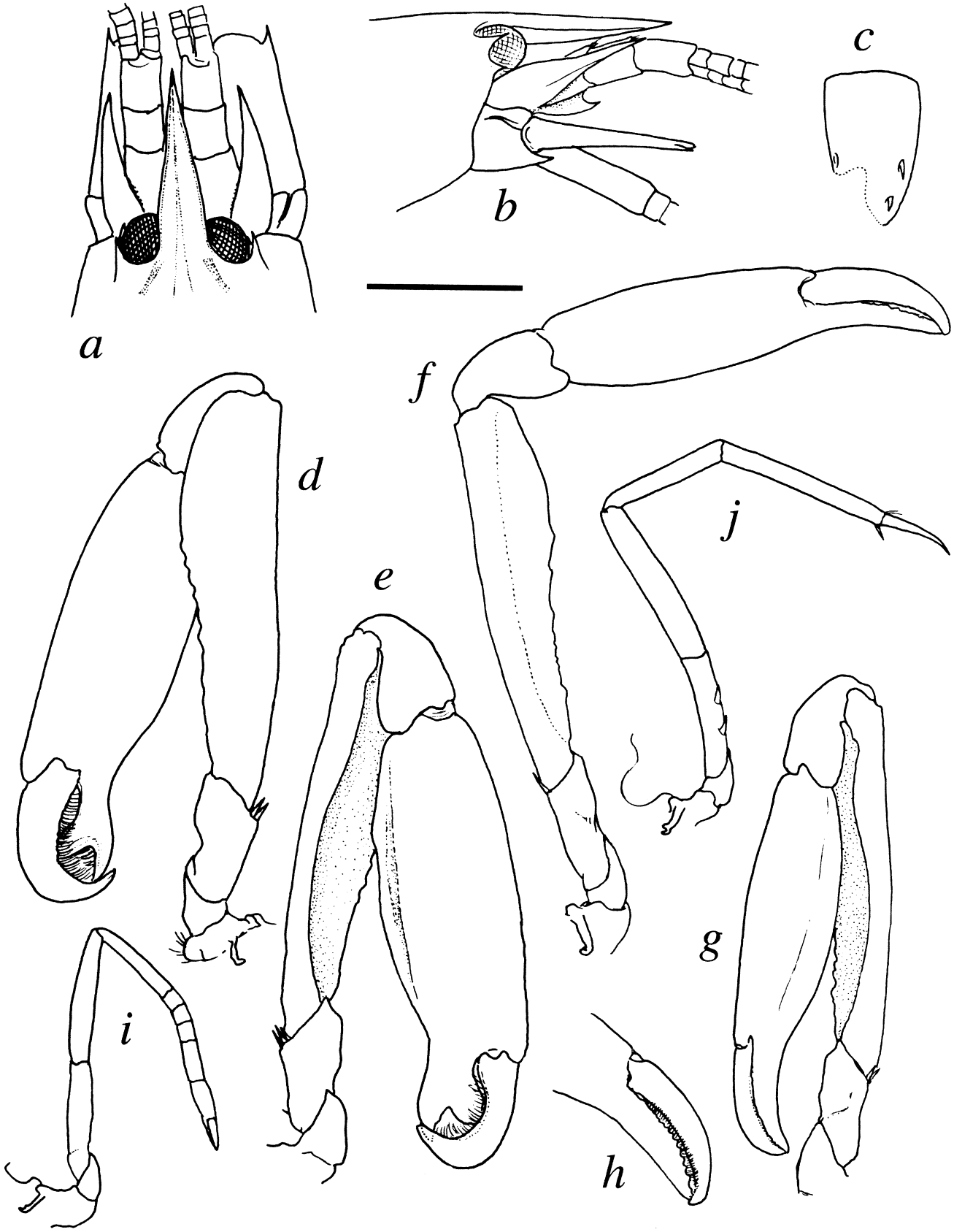

Fig. 16. *Athanas* cf. *japonicus* Kubo, male from Ponggol beach, Singapore (ZRC 1979.4.6.15): a, frontal region, dorsal view; b, same, lateral view; c, telson (damaged); d-h, first cheliped: d, major cheliped, lateral view; e, same, mesial view; f, minor cheliped, lateral view; g, same, mesial view; h, same, chela fingers; i, second pereiopod; j, third pereiopod. Scale: 1 mm.

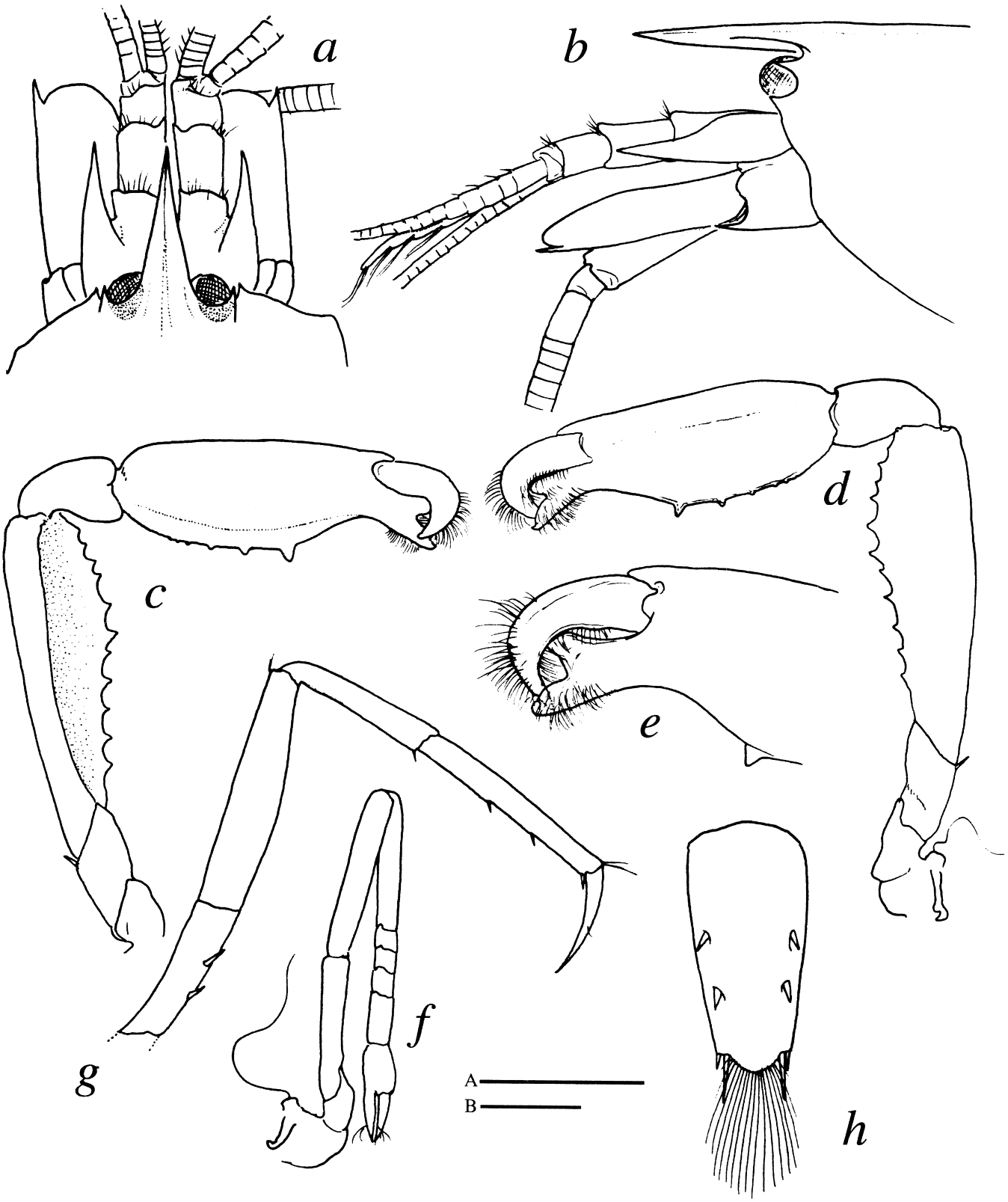

Fig. 17. *Athanas japonicus* Kubo, male from Yamaguchi, Japan (MNHN-Na 13640): a, frontal region, dorsal view; b, same, lateral view; c, (major?) first cheliped, mesial view; d, same, lateral view; e, same, chela, distal palm and fingers; f, second pereiopod; g, third pereiopod; h, telson. Scales: A (c, d), B (a, b, e-h), both scales: 1 mm.

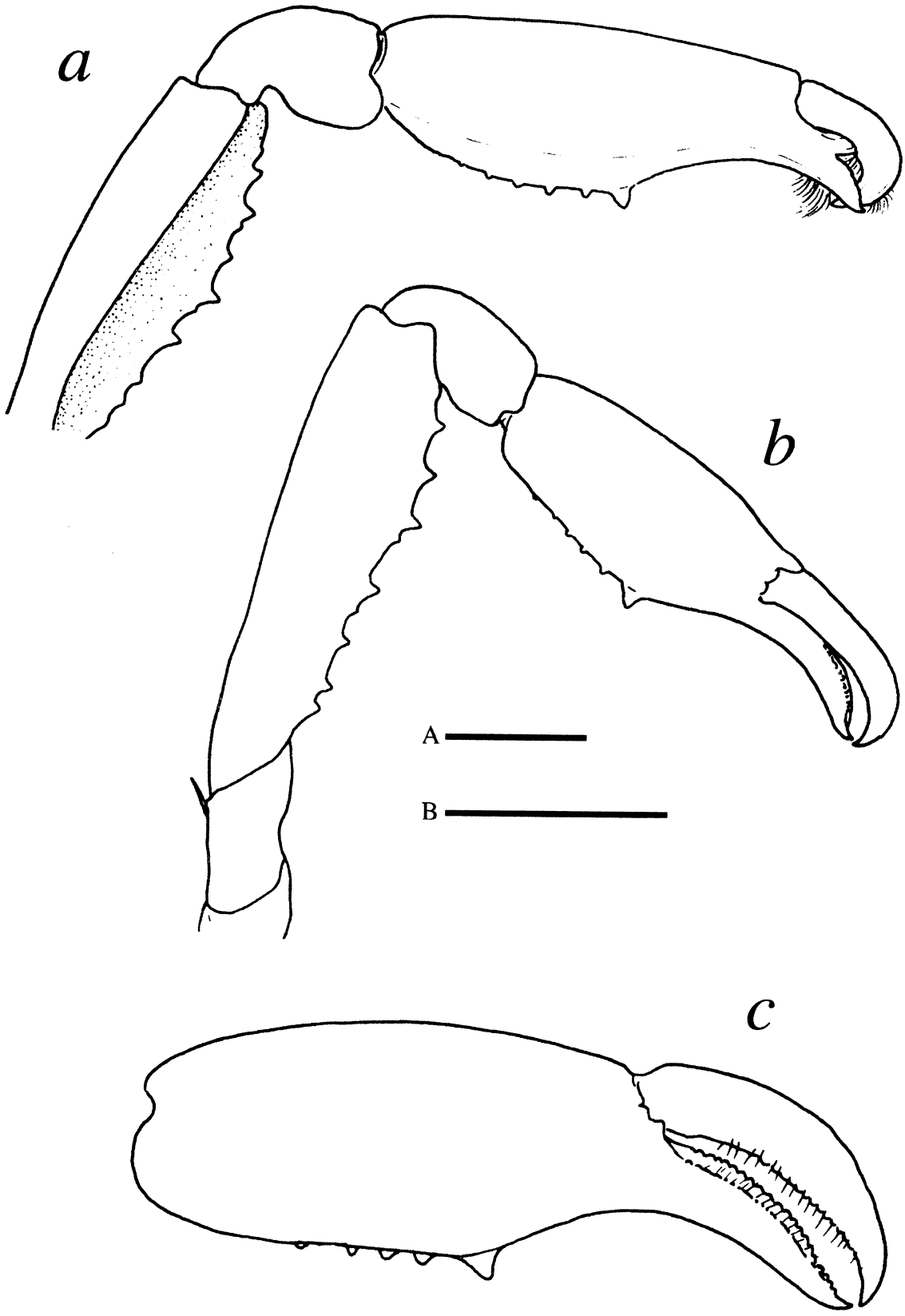

Fig. 18. *Athanas japonicus* Kubo, male from Yamaguchi (MNHN-Na 13640) first chelipeds: a, major cheliped, ventro-lateral view; b, minor cheliped, lateral view; c, same, chela. Scales: A (a, b), B (c), both scales: 1 mm.

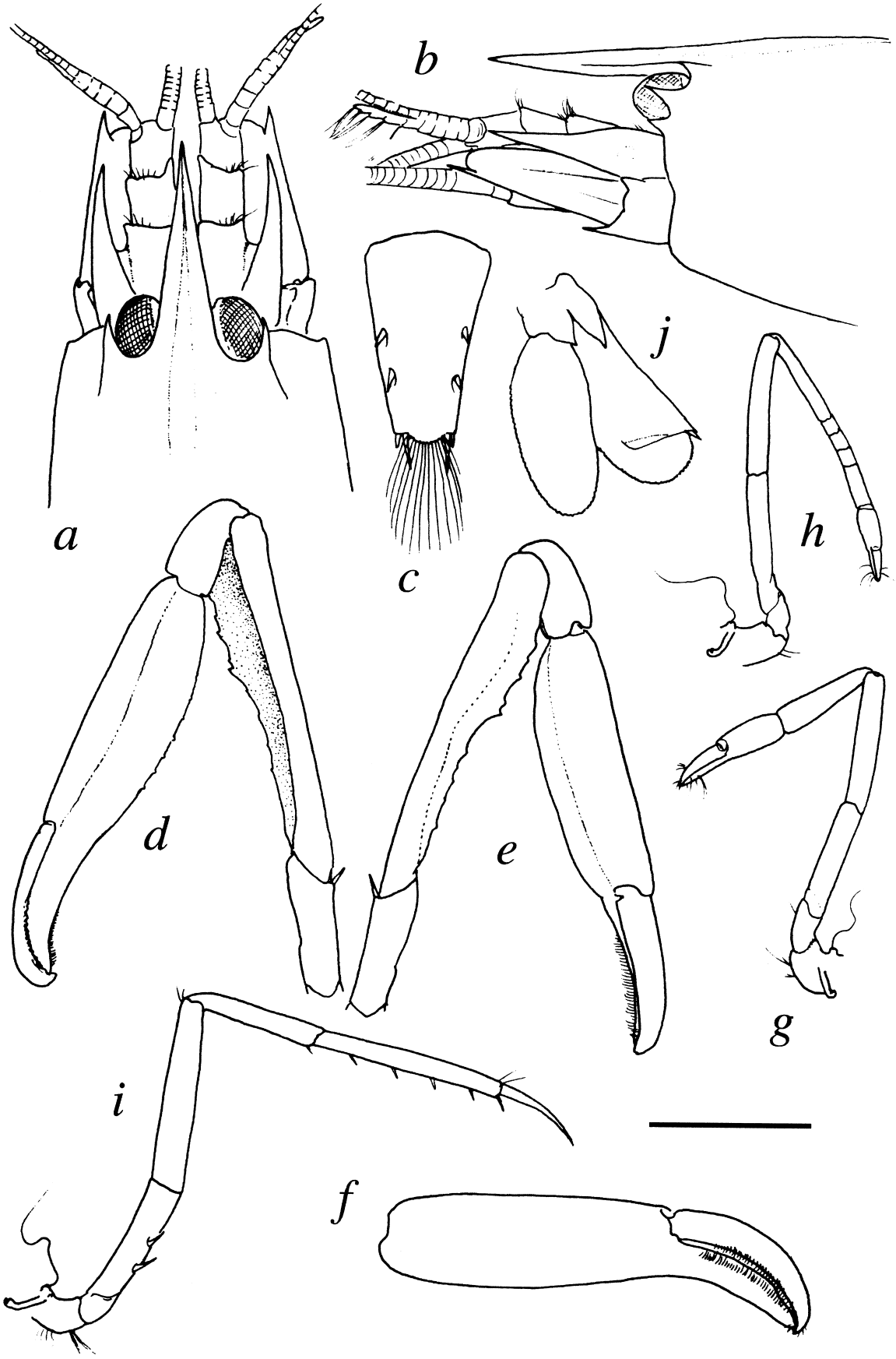

Fig. 19. *Athanas japonicus* Kubo, female from Arita (MNHN-Na 13764): a, frontal region, dorsal view; b, same, lateral view; c, telson; d-g, first chelipeds: d, major cheliped, mesial view; e, same, lateral view; f, same, chela; g, minor cheliped; h, second pereiopod; i, third pereiopod; j, uropod. Scale: 1 mm.

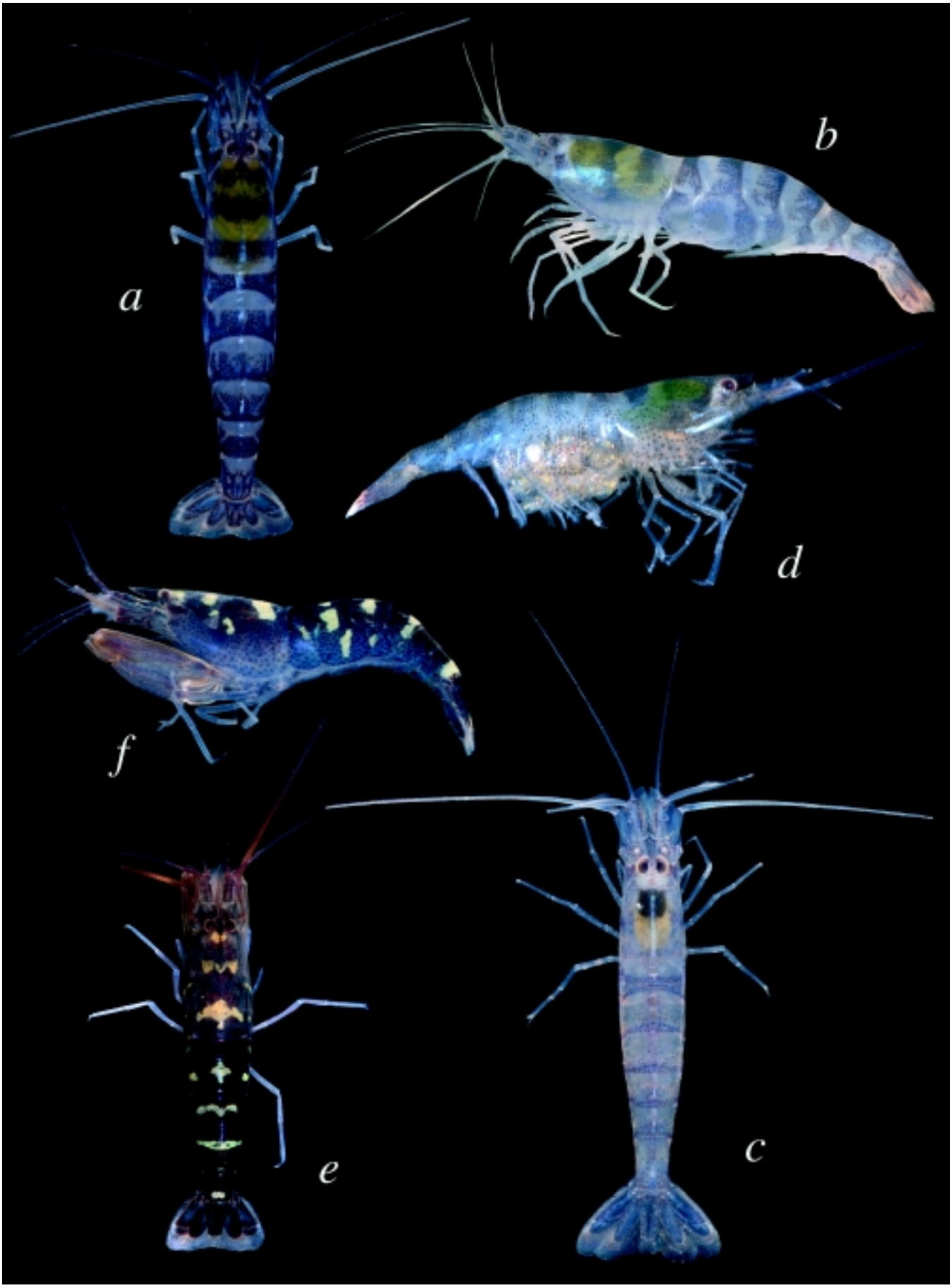

Fig. 20. Colour patterns of some Alpheidae from Sungei Buloh, Singapore: a, b, *Potamalpheops tigger* Yeo & Ng; c, d, *Potamalpheops johnsoni*, new species; e, f, *Athanas polymorphus* Kemp. All more or less to scale.

The only literature records of *A. japonicus* outside of Japan are from Australia: Darwin, Northern Territory (Banner & Banner, 1973; Bruce & Coombes, 1997) and Moreton Bay, Queensland (Wadley, 1978). Banner & Banner's (1973) female specimen from Darwin is closer to *A. lamellifer* in the confirmation of orbital teeth and in all cheliped features, and similar to *A. japonicus* only in the length of the stylocerite. The ischium of the third pereiopod of the specimen from northern Australia bears only one spine instead of two, as in *A. japonicus* from Japan (Fig.17g, not mentioned for the type) and *A. lamellifer* (cf. Kubo, 1940: fig. 4G). An immature female recently collected near Darwin (Figs. 15l-o) is referable to the *A. japonicus* complex, mainly because of the very slender dactylus of the third pereiopod. This female bears two perfectly symmetrical chelipeds, which are very similar to the minor chelipeds of many other *Athanas* species (Fig. 15m).

Wadley (1978) listed *A. japonicus* in the key to the epibenthic shrimps of Moreton Bay, and provided two superficial figures of the anterior carapace. More recently, two male specimens of *A.* cf. *japonicus* were collected by the author with the aid of a yabby pump from a burrow of a mud-skipper (Periopthalmidae) near Mossman, North Queensland (Figs. 15a-k). In several features (length of the stylocerite, length of the carpus in the minor first cheliped, dactylus of the third pereiopod) these specimens are similar to the type of *A. japonicus*, however, there are also some important differences to both Japanese and Singapore material (compare Figs. 15, 17, 19).

Fig. 21. Variation of colour pattern in *Potamalpheops tigger* Yeo & Ng: a, specimen with rusty reddish pattern; b, young specimen with black spotted pattern (compare with Fig 20, a, b).

The specimen from Ponggol Beach, Singapore (ZRC 1979.4.6.15) was collected and initially identified by D. Johnson as *Athanas tenuipes* De Man. However, this record remained unpublished. *Athanas tenuipes* was described by De Man (1910) upon a specimen lacking first pereiopods, and has not been reported since the original description. After having examined De Man's original description and figures (De Man, 1911, 1915) the conclusion was reached that the Ponggol specimen is different from *A. tenuipes* sensu De Man, and instead, presents several features of the *A. japonicus* complex. This specimen (Fig. 16) is here tentatively assigned to the *A. japonicus* complex. The rostrum of *A.* cf. *japonicus* from Ponggol is significantly longer than in *A. tenuipes* (cf. De Man, 1915: pl. III, fig. 8), whilst the telson, although heavily damaged, is much broader (cf. De Man, 1915: fig. 8b). The dactylus of the walking legs in *A.* cf. *japonicus* from Ponggol is less slender than in *A. tenuipes* (cf. De Man, 1915: fig. 8d), and the ischium of the third pereiopod bears two spines instead of one as in *A. tenuipes*. Also, the stylocerite is much longer and the infra-corneal tooth much more developed in the Ponggol specimen compared to *A. tenuipes*; these features however are considered to be variable within the *A. japonicus* complex. Furthermore, *A. tenuipes* is apparently a species from deeper water (the type has been dredged from 72 m), while the specimen from Ponggol has been collected intertidally, possibly in the same type of habitat as *A. japonicus*. Notably, *A.* cf. *japonicus* from Ponggol seems to differ from specimens of *A.* cf. *japonicus* from Lim Chu Kang and Mossman (compare Fig. 16 with Figs. 15 and 17, respectively), and also from the Japanese specimens of *A. japonicus*, especially in the more excavated merus of the first chelipeds (Fig. 16d).

In conclusion, the morphological variability shown here suggests that several species may be involved in what is believed to be *A. japonicus*. Examinations of morphology, colour patterns and morphometry of numerous specimens from Japan and elsewhere, and designation of a neotype of *A. japonicus* from the type-locality (or geographically close locality) in Japan will be necessary to resolve this complex.

DISCUSSION

All three alpheid genera, *Salmoneus*, *Potamalpheops* and *Athanas*, have several representatives in shallow mudflat or sandflat habitats. For example, from around dozen known species of *Potamalpheops*, more than half are found in mangroves, mudflats or brackish peat swamps (*P. tigger* Yeo & Ng, *P. miyai* Yeo & Ng, *P. johnsoni*, new species, *P. darwiniensis* Bruce and *P. hanleyi* Bruce, *P. pylorus* Powell and *P. monodi* Sollaud). These species are physiologically adapted to the fluctuations of salinity and temperature, and *P. tigger* and *P. johnsoni*, new species, are able to crawl outside the water (Yeo & Ng, 1997; pers. obs.). The typical mudflat and sandflat species of *Salmoneus* and *Athanas* are characterized by a very slender sickle-shaped dactylus on the walking legs (third

to fifth pereiopods), enabling the shrimps to walk easily on soft substrates. Remarkably, numerous species of *Salmoneus* and *Athanas* speciliazed to soft substrates seem to be associated with burrows of other crustaceans, such as thalassinideans, stomatopods or larger alpheids (see Froglia & Atkinson, 1998; Felder & Manning, 1986; Dworschak et al. 2000; Anker et al., 2001; Hayashi, 2002), and some species, e.g., *A. squillophilus* Hayashi and *A. dentirostris* Anker, Jeng & Chan) developed particularly dense brushes or rows of setae on the major or both first chelipeds, probably serving as a filtering apparatus.

The intra-specific variation observed in several species of *Potamalpheops* affects mostly the shape (e.g., slenderness, presence of a subapical tooth) and the length of the rostrum and the length of the stylocerite. The morphological variation within *Athanas* is more problematic and more pronounced, especially in *A. polymorphus* and *A. japonicus*. The taxonomic identity of these two species remains not fully established. The specimens from Singapore, reported here under *A. polymorphus* and *A.* cf. *japonicus* (specimens from Lim Chu Kang and Ponggol), could belong to new species for they are clearly different from the respective types, at least according to Kemp's (1915) and Kubo's (1936) original descriptions and illustrations.

The remarkable polymorphism of the first chelipeds observed in *A. polymorphus* and *A. japonicus* is perhaps related to the social environment of the shrimps (e.g., hierarchy, dominance, reproduction). Similar cheliped polymorphism exists in several other species of *Athanas*, including *A. dimorphus* (Banner & Banner, 1973), *A. phyllocheles* (Banner & Banner, 1983), *A. amazone* (Holthuis, 1951; Crosnier & Forest, 1973; Anker, 2001), and in the genera *Arete* (Suzuki, 1970; Gherardi, 1991) and *Aretopsis* (Bruce, 1969), which are closely related to *Athanas*.

The presence of *A. polymorphus*, *A.* cf. *japonicus* and *P. tigger* in Singapore and in the Darwin area suggests that these two localities could share a very similar mangrove-mudflat shrimp community. The finding of new species in the relatively well studied Sungei Buloh mangrove situated in the huge urban area of Singapore shows that more efforts should be made towards collecting smaller shrimps (less than 1 cm TL) in sandy-muddy shallow water habitats (mangroves, mudflats), and particularly in investigating burrows of larger sediment-burrowing invertebrates (e.g., thalassinideans, stomatopods, echiuran and polychaete worms).

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