

TWO NEW SPECIES OF SNAPPING SHRIMPS FROM THE INDO-PACIFIC, WITH REMARKS ON COLOUR PATTERNS AND SIBLING SPECIES IN ALPHEIDAE (CRUSTACEA: CARIDEA)

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ABSTRACT. – *Alpheus tricolor*, and *Alpheus fasqueli*, two morphologically very close, but differently coloured species of snapping shrimps are described and illustrated. Descriptions are based on specimens imported from Indonesia and Sri Lanka. Both new species belong to the *A. edwardsii* group, and can be distinguished from all other species of *Alpheus* by several features of the first and second chelipeds, frontal region, third maxilliped, and most readily by their conspicuous colour patterns. These attractive shrimps are regularly imported from Indonesia and Sri Lanka to Europe and Singapore, sometimes under the name “*Alpheus strenuus*”.

KEY WORDS. – Caridea, Alpheidae, *Alpheus*, cryptospecies, Indonesia, Sri Lanka, aquarium.

INTRODUCTION

Through the courtesy of Dr. Peter K. L. Ng (National University of Singapore) the author received a freshly preserved specimen of an *Alpheus* obtained in one of numerous fish import houses in Singapore. According to fish dealers this specimen was imported from Bali, Indonesia. Prior to the preservation Dr. Ng made a series of colour slides of the living shrimp. Several months later Mr. F. Fasquel (Aquarium du Musée National des Arts d’Afrique et d’Océanie, Paris) obtained another specimen which he kept alive in the aquarium, and of which only a moult has been preserved. This specimen was possibly also imported from Indonesia. Then, in May 2000, two freshly preserved specimens, one of which was in almost perfect condition, and two complete moults, were brought to the Muséum National d’Histoire Naturelle by F. Fasquel. These specimens, obtained in Germany, were imported and with high probability collected in Sri Lanka. Together with the specimens, the author received colour slides of living shrimps from Sri Lanka. Finally, in February 2001, four specimens of the same species were sent to me by Dr. Ng, who obtained them from divers in Sri Lanka, thus confirming the origin of Fasquel’s specimens.

The study of present specimens shows that they belong to two closely related species from the *Alpheus edwardsii* group. The specimens with different colour patterns also

show slight differences in some morphological features (proportions of major chela, shape of scaphocerite, length of stylocerite). Extensive comparisons with related species of *A. edwardsii* group reported from Indonesia (de Man 1911, D.M. & A.H. Banner 1985), the Philippines (A.H. & D.M. Banner 1981, Chace, 1988), the South China Sea (D.M. & A.H. Banner 1978, Liu & Lan 1980, Jeng & Chang 1985), Thailand (A.H. & D.M. Banner 1966), Australia (D.M. & A.H. Banner 1982), Hawaii (Banner, 1953), the Indian Ocean (Coutière 1905, A.H. & D.M. Banner 1983), and the Red Sea (D.M. & A.H. Banner 1981), showed that both species were until now undescribed. They can be readily separated from all other species of *A. edwardsii* group by the shape of the major and minor chelae, and by several other subtle, but nevertheless reliable features. However, these species can be best recognized by their colour patterns, which are very conspicuous and unique not only among *Alpheus* and Alpheidae, but also among all Decapoda.

MATERIAL AND METHODS

Types were deposited in the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore (ZRC), and the Muséum National d’Histoire Naturelle, Paris (MNHN). Abbreviations used in text: CL = carapace length; TL = total length; CHL = Chela length (measured from proximal margin to tip of fixed

finger); Mxp = maxilliped; P = pereopod; WA = western Atlantic; EA = eastern Atlantic; EP = eastern Pacific; IWP = Indo-West Pacific

ORDER DECAPODA LATREILLE, 1803

FAMILY ALPHEIDAE RAFINESQUE, 1815

Alpheus tricolor, new species

(Figs. 1-6)

Material examined. – Holotype, 1 adult female, CL 13.5 mm, ZRC.1999.1488, Bali, Indonesia, by diving, Oct 1999, coll. P. K. L. Ng (obtained from dealers).

Also examined were moults of a young male (CL 9 mm, CHL 10 mm) imported from Sri Lanka, and another specimen, probably a young female (CL 10 mm) imported from Indonesia.

Diagnosis. – Carapace setose; rostrum acute, carinate, reaching to distal margin of first antennular article; orbital hoods unarmed; adrostral furrows shallow, not abruptly delimited. Second antennular article not elongated; stylocerite reaching beyond first article. Basicerite with strong ventro-lateral tooth; carpopocerite stout, slightly exceeding scaphocerite; lamella of scaphocerite not reduced, with anterior margin concave; lateral spine very broad at base. Third maxilliped with epipodial plate bearing numerous thickened setae. First chelipeds with merus bearing strong disto-mesial tooth; chela with superior transverse groove of major chela shallow, proximal shoulder not overhanging groove; inferior groove lacking; longitudinal grooves on each side of palm shallow; ratio palm to dactylus equal to 1.8; plunger short, obliquely truncated; minor chela balaeniceps in both sexes. Second pereopod with first carpal article distinctly longer than second. Third pereopod with ischium armed, merus unarmed, dactylus simple, conical. Telson broad, distally slightly tapering, with 2 pairs of dorsal spines; posterior margin weakly convex, with 2 spines at each angle; dorsal surfaces of telson and uropods very setose.

Description. – Body not especially compressed. Carapace smooth, latero-anteriorly with shallow grooves, dorsally with numerous erect setae; pterygostomial angle rounded; cardiac notch very distinct. Rostrum well developed, acute, slightly descendant; tip reaching to distal margin of first article of antennular peduncle; rostral carina reaching beyond orbital hoods, continued by inconspicuous, flattened ridge to about posterior third of carapace; adrostral furrows, not abruptly delimited; orbital hoods inflated, rounded anteriorly, lacking teeth. Corneas well developed, pigmented; eyes with small anterior processes, visible in lateral view (Fig. 3b).

Antennular peduncles stout; stylocerite with acute tip, overreaching first antennular article; ventral antennular carina well developed, distally with small acute tooth (Fig. 3c); second article not especially elongated, slightly longer than third article; outer flagellum biramous, shorter ramus composed of 3-4 free segments. Antenna with basicerite bearing acute, ventro-lateral tooth; scaphocerite broad, with

well developed lamella, lateral spine strong, thick, very broad at base; anterior margin of lamella slightly convex (Fig. 3e), outer margin slightly concave; carpopocerite slightly exceeding scaphocerite, reaching to distal margin of antennular peduncles.

Mouthparts typical for *Alpheus*. Mandible with 2-jointed palp, incisor process distally bearing approximately 12 teeth; molar process very stout. Maxillula with palp bilobed, inferior lobe bearing 1 slender seta, superior lobe not setose. Maxilla, first and second maxillipeds without specific features. Third maxilliped robust, not expanded; annexed arthrobranch well developed; epipodial plate with acute tip, posterior margin flattened, expanded, densely covered by thickened, distally blunt setae (Fig. 6h); epipod long, slender; exopod slightly exceeding antepenultimate segment of endopod; ultimate segment very setose, distally unarmed.

Major cheliped with merus stout, ventrally flattened, with small spines on mesial margin, distally with strong tooth; superior margin distally with sharp tooth; carpus very short, cup-shaped, without distal teeth; chela about 2.5 times as long as high; palm about 1.8 times longer than dactylus; superior transverse groove shallow; proximal shoulder rounded, not overhanging groove; longitudinal grooves on each lateral side of palm shallow; inferior transverse groove absent; fixed finger with tip curved, sharp; dactylus with sharp tip; plunger short, obliquely truncated, distal surface flattened, with shallow depression; adhesive discs on palm and dactylus small. Minor cheliped with chela slender, about 5 times longer than high, dactylus balaeniceps (lateral ridge of dactylus fringed with setae), not laterally expanded.

Second chelipeds robust, somewhat elongated; ischium relatively short; merus longer than ischium; carpus composed of 5 articles with ratio approximately equal to: 1: 0.6: 0.4: 0.4: 0.6; first carpal article about 3 times longer than broad; chela as long as first carpal article, fixed finger and dactylus with numerous setae, most of them inserted in tufts. Third to fifth pereopods robust; ischium of P3 and P4 each with movable spine; merus and carpus unarmed, without projections; propodus armed with rows of spines as follows: P3: 9 + distal pair, P5: 5 + distal pair; dactylus simple, curved, with subapical portion abruptly narrow (Fig. 5g).

Abdomen without specific features, surface of each somite bearing conspicuous setae proximal to dorso-posterior margin. Uropodal exopod with strong lateral spine, and well developed, sinuous diarsis; endopod without specific features. Telson broad, tapering distally, with 2 pairs of dorsal spines located in deep depressions; posterior margin slightly rounded, with 2 pairs of lateral spines, inner spines more than length of outer spines; numerous long setae between lateral spines (including a row of superiorly situated, erect setae); latero-inferior margins fringed with short plumose setae; anal tubercles well developed. Branchial formula typical for genus, with 1 arthrobranch on Mxp3 and 5 strap-like epipods on Mxp3 and P1-4.

Coloration. – Carapace mostly yellow-orange, laterally with

three conspicuous, circular or elongated white patches, disposed as illustrated (Fig. 1a, 1b; 2a). Rostrum reddish-orange; orbital hoods translucent; thin red line runs along posterior branchiostegial margin. Antennal and antennular peduncles orange-red, both flagella whitish. Mouthparts mostly colourless, but palp and caridean lobe of Mxp1, and most of Mxp2 reddish. Mxp3 uniformly reddish-orange. Major and minor chelipeds orange-red; merus distally with white patch across outer angle and mesial spine; chelae progressively lighter to almost white on tips of fingers; plunger of dactylus white; medio-superior margin of palm purplish, especially in major cheliped. In younger individuals fingers and distal portion of palm conspicuously white (Fig. 1b). Following pereopods uniformly orange-red. Abdominal segments dorsally yellow-orange, latero-ventrally deep red, with three large and one smaller rounded white patches, disposed as illustrated (Fig. 2a). Pleopods with protopod whitish, rami orange. Tail fan deep red, with broad white band across proximal half; margins of uropods and lateral spine whitish; setae fringing uropods and telson proximally dark red, distally whitish.

Measurements. – Holotype: CL 13.5 mm, TL 36 mm, CHL 16 mm.

Etymology. – Species named after its characteristic colour pattern consisting of three colours: white, red and orange.

Remarks. – As mentioned above I had the possibility of examining two moults of further specimens of *Alpheus tricolor*, new species, which unfortunately could not be preserved for this study. Although much smaller these specimens agree well in most morphological features and in colour pattern with the holotype specimen. Some differences however, are noteworthy. The first moult (corresponding specimen, collected in Sri Lanka was still alive) belongs to a young male (CL 9 mm, CHL 10 mm), and agrees almost perfectly in almost all points with the holotype. As expected, the minor chela of males is clearly balaeniceps in *A. tricolor*, n. sp., as is the case in females. The appendix masculina is slender and short, not extending beyond the appendix interna. The unusual ventral incision present on each second abdominal pleura of the holotype is absent in this and also in following specimen. Thus, this incision could be simply a genetic abnormality of the holotype specimen, or, less probable, be developed only in larger individuals or due to other cause.

The second moult corresponds to a specimen of unknown sex (CL 10 mm), which was imported from Indonesia. The telson of this specimen has only 3 dorsal spines instead of usual 4. The minor chela is not distinctly balaeniceps; the usual longitudinal, slightly oblique ridge is present on lateral sides of the dactylus, but it is not fringed by thickened setae, typical for balaeniceps chela (Fig. 5c). Assuming that the specimen was a young female, the absence of the balaeniceps condition could eventually be explained by its gradual development in females. The colour of the corresponding living specimen is less intense and with more purple on the chelae, but otherwise agrees well with that of holotype.

Biology. – The author could observe the behaviour of the living specimen of *A. tricolor*, new species, in the aquarium. The shrimp spent most of the time in its burrow under a boulder, but came out when pieces of food were distributed. It did not make any attempt to associate with a partner goby (*Amblyeleotris* sp.) also present in the aquarium. The goby obviously preferred to share the burrow with *Alpheus bellulus* Miya & Miyake, 1968, a true partner shrimp.

***Alpheus fasqueli*, new species**
(Figs. 1-6)

Material examined. – Holotype, 1 male, CL 17.5 mm, MNHN 13609, imported from Sri Lanka, coll. F. Fasquel (obtained in Nürnberg, Germany).

Paratypes, 1 male, CL 14.5 mm, MNHN 13610, same data as for holotype; 1 male, CL 15.8 mm, ZRC 2001.1054, off Colombo, Sri Lanka, obtained from divers, Jan.2001, coll. P. K. L. Ng; 2 males, CL 15.0 and 15.3 mm, and 1 female, CL 15.0 mm, ZRC 2001.1055, Trincomalee, Sri Lanka, from aquarium divers, Feb.2001, coll. P. K. L. Ng

Diagnosis. – Carapace slightly setose; rostrum acute, carinate, distinctly exceeding first antennular article; orbital hoods unarmed; adrostral furrows shallow, not abruptly delimited. Second antennular article slightly elongated; stylocerite not exceeding first article. Basicerite with strong ventro-lateral tooth; carpocerite stout, slightly exceeding scaphocerite; lamella of scaphocerite not reduced, lateral spine with slightly broadened base. Third maxilliped with epipodial plate bearing numerous thickened setae. First chelipeds with merus bearing strong disto-mesial tooth; chela with superior transverse groove of major chela shallow, proximal shoulder not overhanging groove; inferior groove lacking; longitudinal grooves on each side of palm shallow; ratio palm / dactylus equal to 1.25; plunger short, obliquely tuncated; minor chela balaeniceps in both sexes. Second pereopod with first carpal article distinctly longer than second. Third pereopod with ischium armed, merus unarmed, dactylus simple, conical. Telson broad, distally slightly tapering, with 2 pairs of dorsal spines; posterior margin weakly convex, with 2 spines at each angle; telson and uropods setose.

Description. – Body not compressed. Carapace smooth, latero-anteriorly with shallow grooves, dorsally with scattered setae; pterygostomial angle rounded; cardiac notch well developed. Rostrum well developed, slightly descendant; tip acute, extending beyond distal margin of first antennular article; rostral carina sharp reaching beyond orbital hoods, continued by slight, flattened ridge to about posterior third of carapace; adrostral furrows deep, not abruptly delimited; orbital hoods inflated, rounded anteriorly, unarmed. Corneas well developed, pigmented; eyes with small anterior processes, visible in lateral view.

Antennular peduncles stout; stylocerite acute, overreaching first antennular article; antennular carina as illustrated (Fig. 3h); second article not especially elongated, only slightly longer than third article; outer flagellum biramous, fused

portion having about 20 segments, shorter ramus composed of 3-4 segments. Antenna with basicerite bearing strong, acute ventro-lateral tooth; scaphocerite broad, with well developed lamella, anterior margin slightly convex, narrower than in *A. tricolor*; outer margin concave; lateral spine strong, less broad at base than in *A. tricolor*; carpoцерite reaching to distal margin of antennular peduncles. Mouthparts as described for *A. tricolor*. Incisor process of mandible with less than 10 blunt teeth. Epipodial plate on coxa of third maxilliped apparently bearing more thickened, blunt setae.

Major cheliped similar to that of *A. tricolor*. Merus slightly crenellated on mesial margin, without teeth, distally with strong mesial tooth and sharp superior tooth; carpus very short; palm of chela about 1.25 times longer than dactylus, with superior transverse groove; proximal shoulder rounded, not overhanging transverse groove; longitudinal groove on each lateral side shallow; inferior transverse groove lacking; fixed finger with tip curved and sharp; plunger of dactylus as described for *A. tricolor*; adhesive discs small. Male minor cheliped balaeniceps, laterally not expanded, tips broken in holotype (Fig. 5i), entire in all male paratypes (Fig. 5j); palm with slightly indicated superior groove; female minor cheliped unknown.

Second chelipeds robust, elongated, left slightly more robust than right; carpus more slender than in *A. tricolor*, first article

almost 5 times longer than broad; ratio of carpal articles approximately equal to 1: 0.55: 0.25: 0.25: 0.40; chela much shorter (about half) than first carpal article, fixed finger and dactylus with numerous dense tufts of strong setae. Third to fifth pereopods similar to those of *A. tricolor*; ischium of P3 and P4 each with small movable spine; merus and carpus unarmed, without projections; propodus of P3 armed with spines (8 + distal pair); dactylus simple, conical, curved, subapically with trace of secondary unguis.

Abdominal segments and caudal fin very similar to *A. tricolor*. Uropodal exopod with moderately developed lateral spine, diarsis well marked, sinuous. Telson broad, tapering distally, with 2 pairs of dorsal spines; posterior margin slightly rounded, with 2 pairs of lateral spines. Branchial formula as described for *A. tricolor*.

Coloration. – Carapace bright red, with circular and more elongated, whitish patches, as illustrated (Fig. 1c, 1d; 2b); rostrum red; orbital hoods transparent. Antennal and antennular peduncles reddish, both flagella purplish red. Mxp3 uniformly reddish. Major and minor chelipeds red, merus distally with white patch across outer angle and mesial spine, chelae deep red, proximally lighter, with white tips of fingers and conspicuous white patch on dorsal margin of dactylus, plunger reddish. Following pereopods uniformly red. Abdomen red; pleura ventrally deep to bordeaux-red;

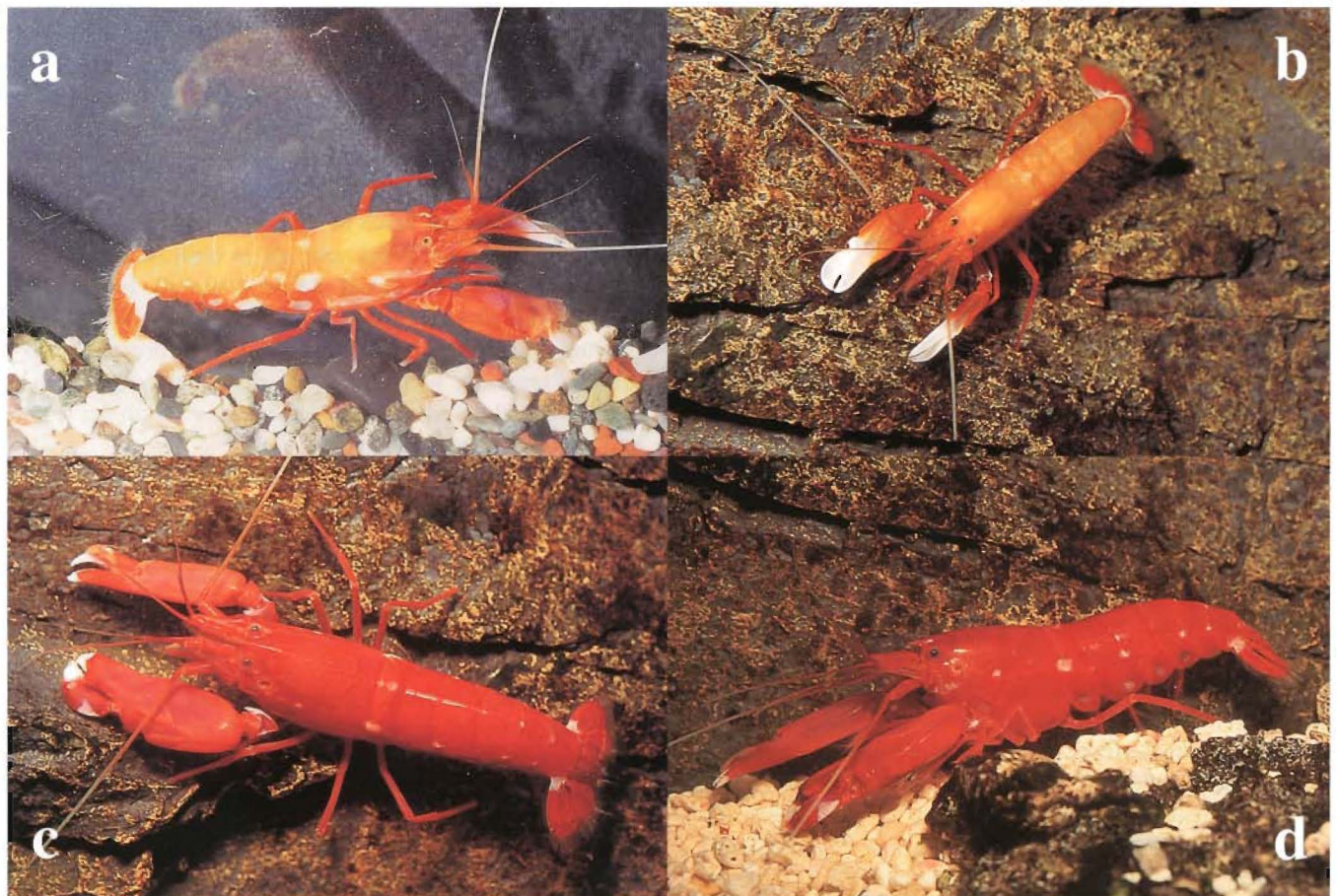


Fig. 1. *Alpheus tricolor*, new species (a, b) and *Alpheus fasqueli*, new species (c, d): a, holotype of *A. tricolor* (ZRC. 1999.1488), photo by P. K. L. Ng; b, younger individual (not preserved); c, d paratype of *A. fasqueli* in dorsal and lateral views (MNHN 13610), photo by F. Fasquel. All photos taken in aquarium.

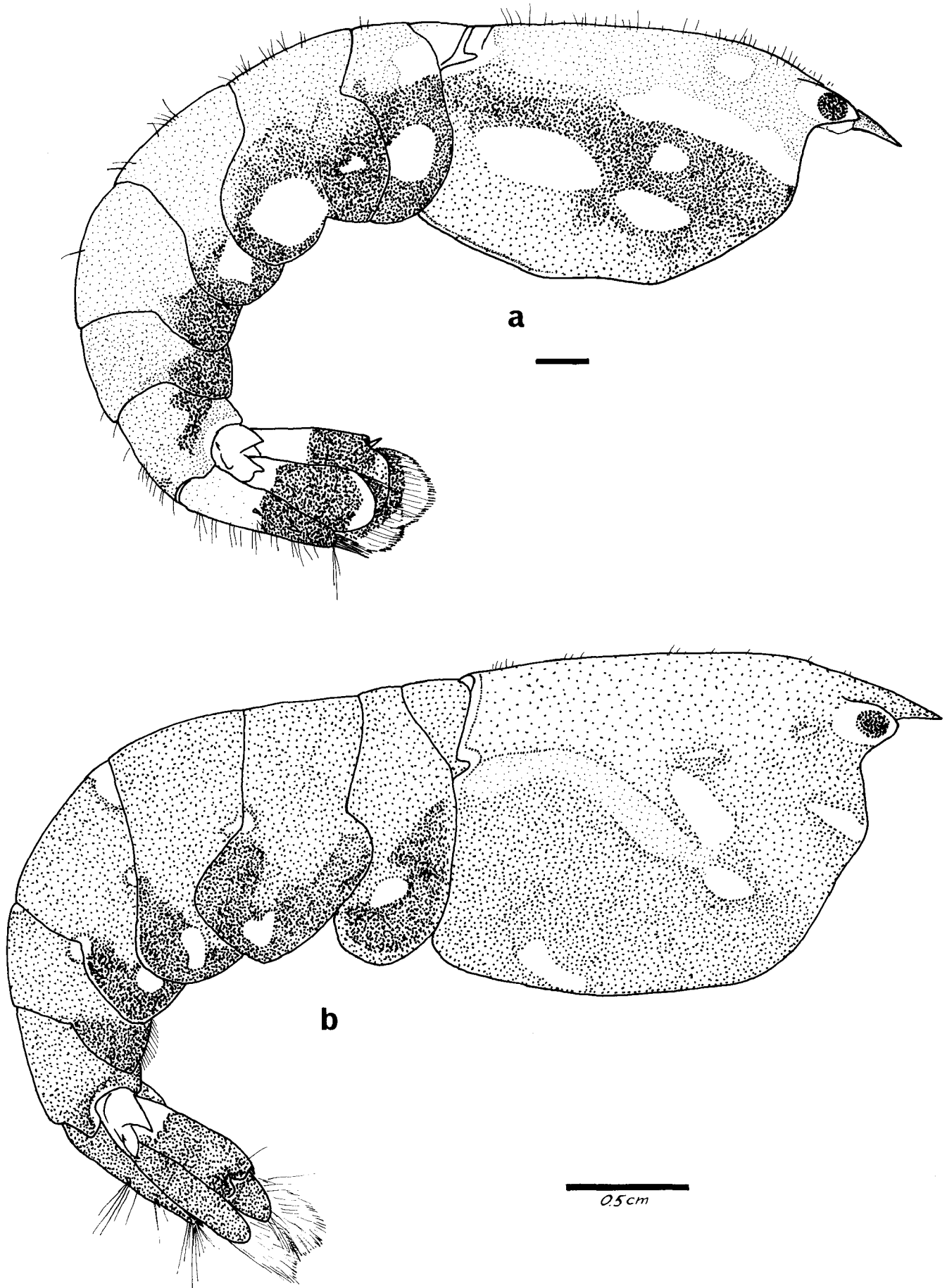


Fig. 2. *Alpheus tricolor*, new species (a) and *Alpheus fasqueli*, new species (b): colour patterns of cephalothorax and abdomen (after freshly preserved holotype specimens). Scale: a - 1 mm, b - 5 mm.

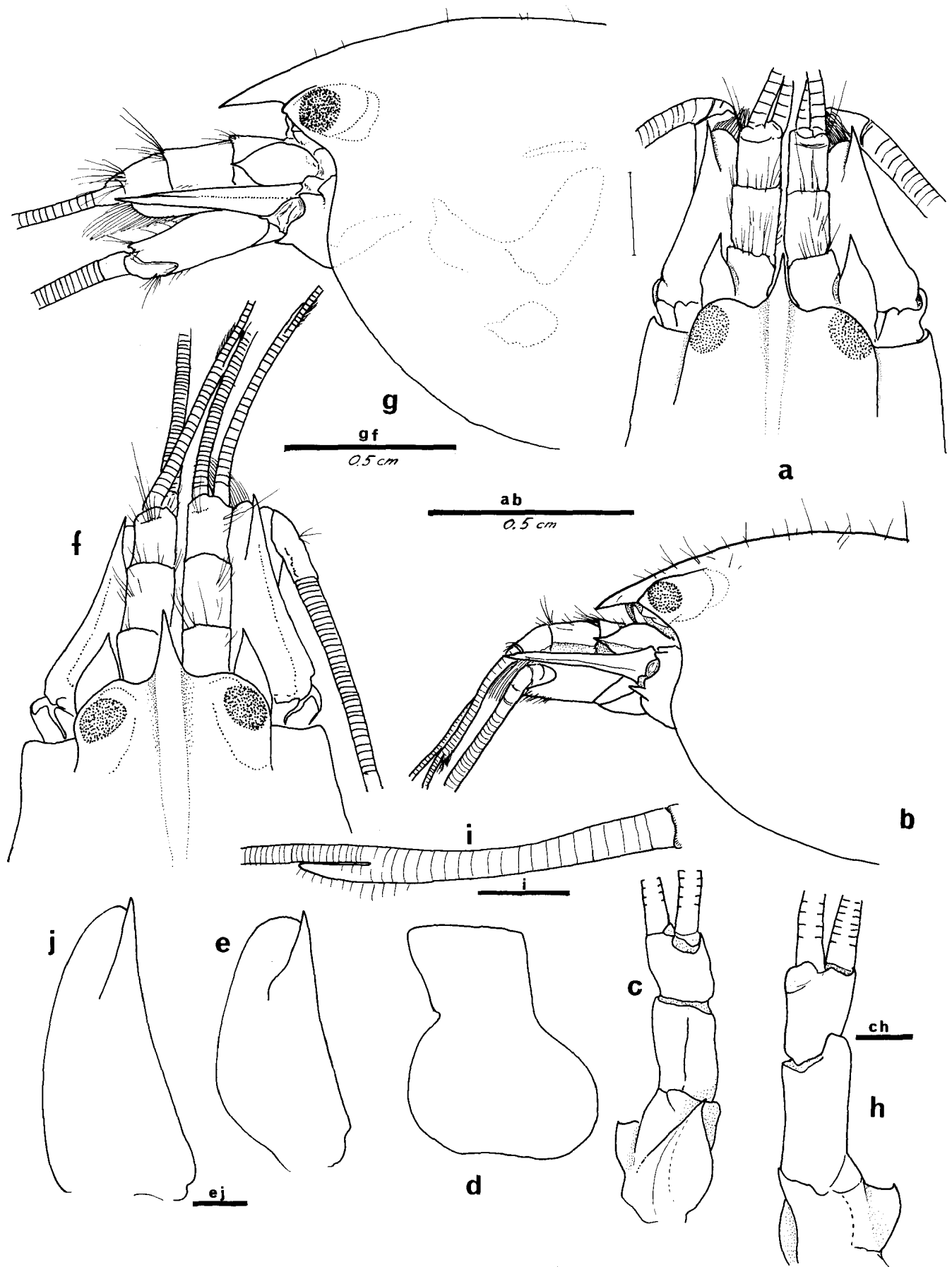


Fig. 3. *Alpheus tricolor*, new species (a-e) and *Alpheus fasqueli*, new species (f-j): a, f, frontal region in dorsal view; b, g, same, in lateral view; c, h, antennule; d, second abdominal pleurite; e, j, scaphocerite, i, flagellum of antennule. a, b and f, g from holotypes, other figures from moults. Scales: c, e, h, i, j - 1 mm; a, b, g, f - 5 mm, d - without scale.

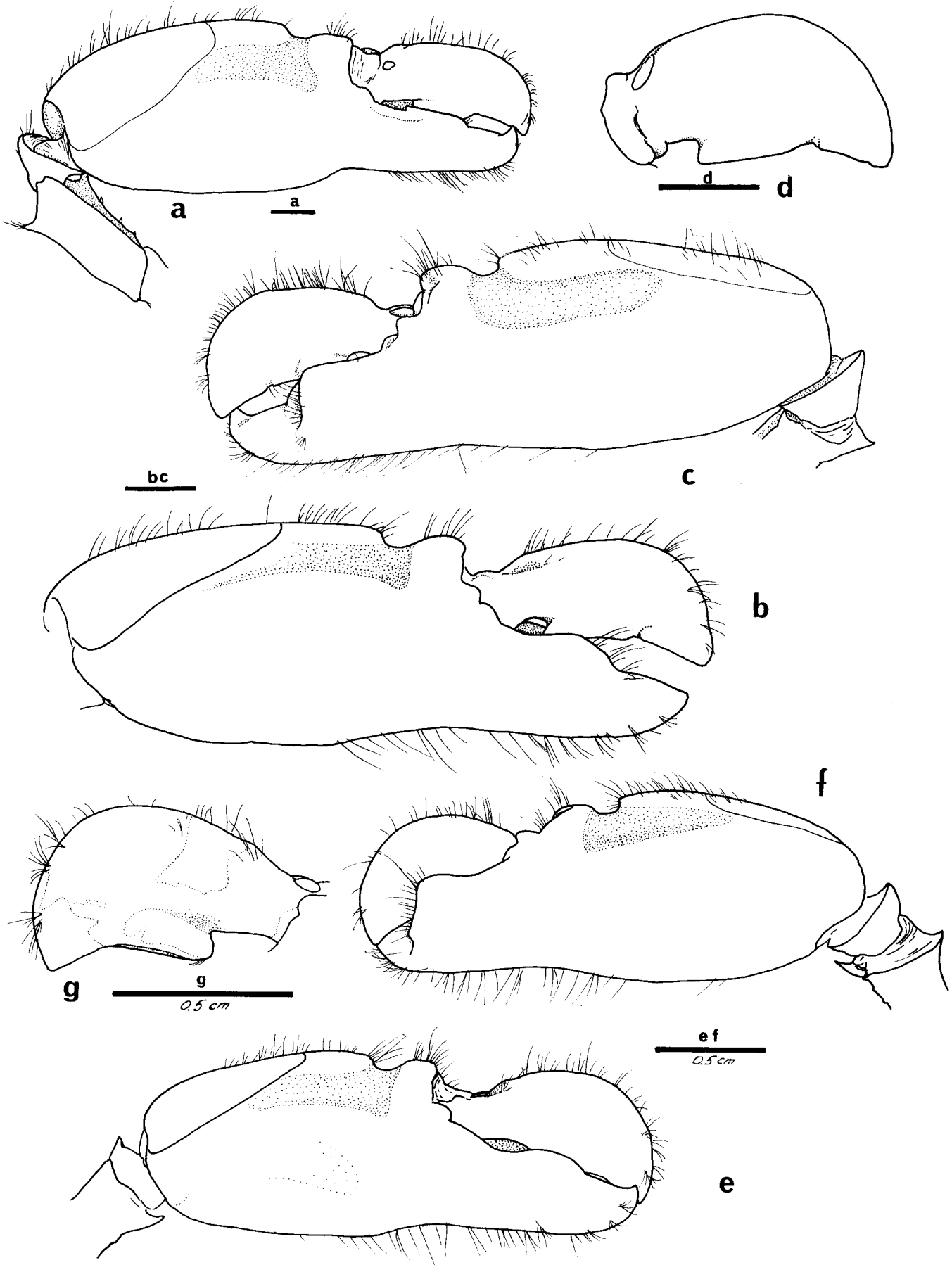


Fig. 4. *Alpheus tricolor*, new species (a-d) and *Alpheus fasqueli*, new species (e-g). Major cheliped (holotypes): a, outer view, b, e, chela, outer view; c, f, chela, inner view; d, g, dactylus. Scales: a, b, c, d - 1 mm; e, f, g - 5 mm.

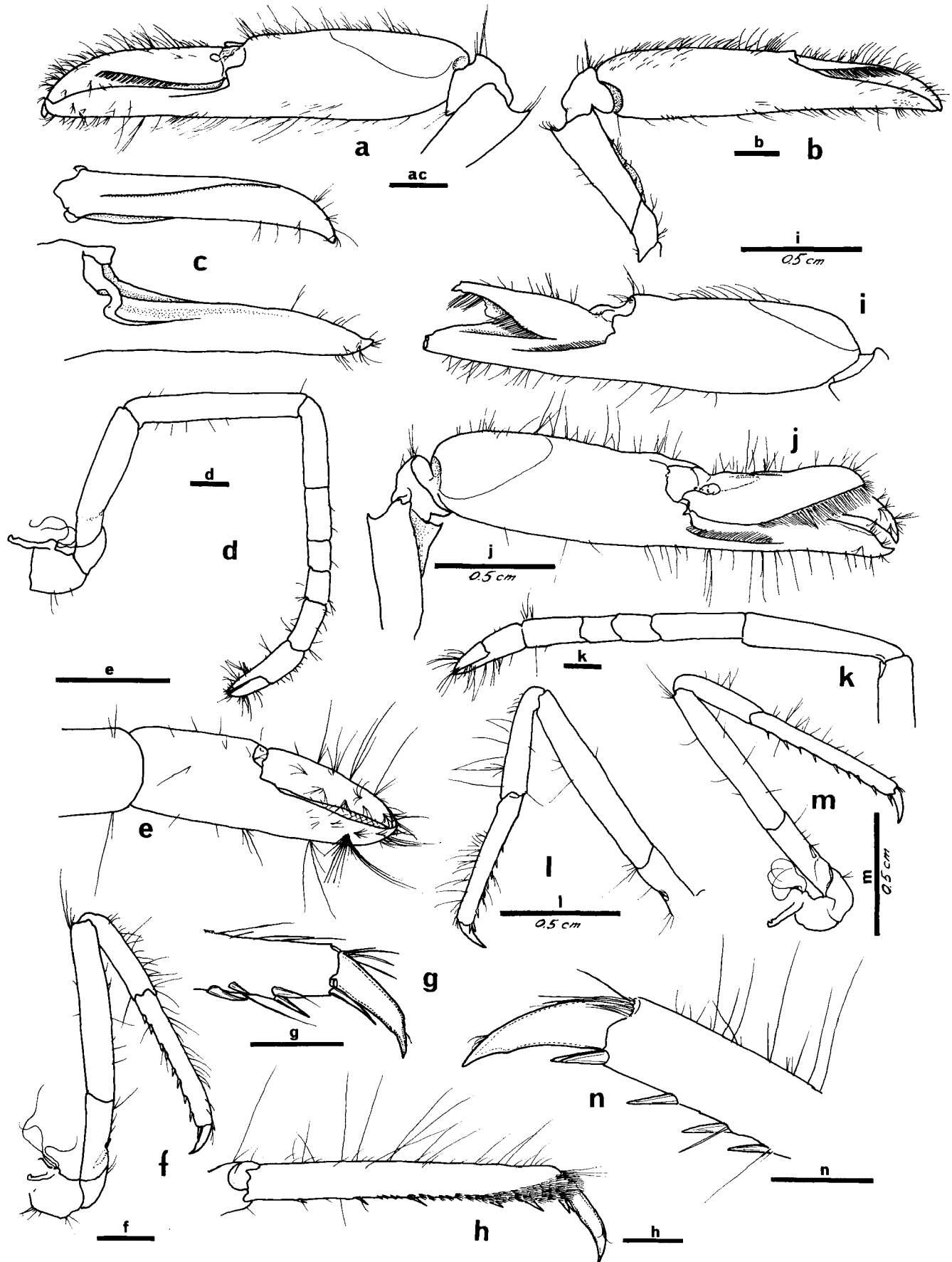


Fig. 5. *Alpheus tricolor*, new species (a-h) and *Alpheus fasqueli*, new species (i-n): a-j small chela, in outer (a, i, j) and inner (b) views, c; details of fixed finger and dactylus; d, second pereiopod; e, same, chela; f, l, m, third pereiopod; g, n, same, dactylus; h, fifth pereiopod, distal propodus and dactylus; k, second pereiopod, carpus and chela. a, b, d-h, i, k, l, n, holotypes; j, m, paratype; c, from moult. All scales – 1 mm, except for i, j, l, m – 0.5 mm.

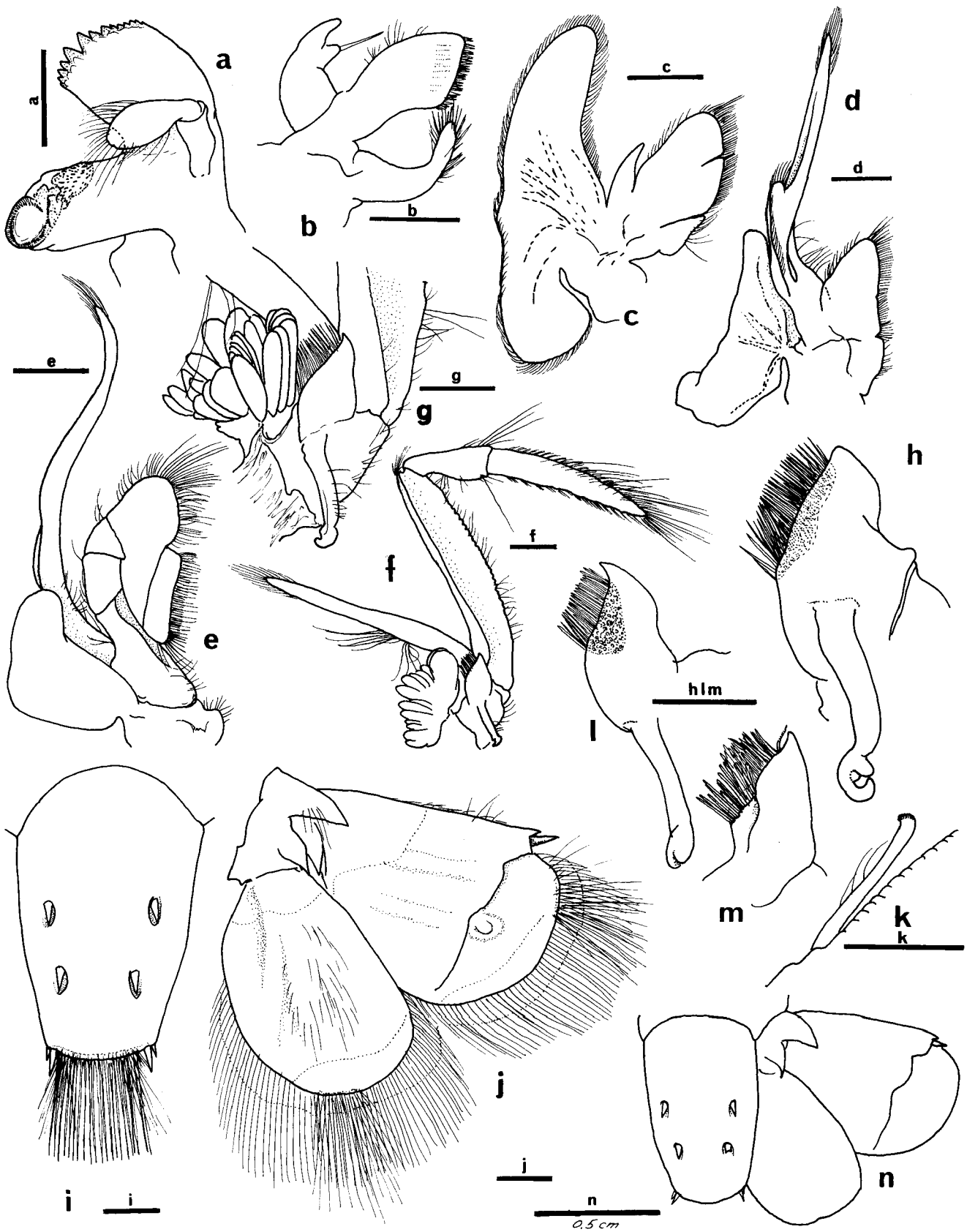


Fig. 6. *Alpheus tricolor*, new species (a-k) and *Alpheus fasqueli*, new species (l-n): a, mandible; b, maxillula; c, maxilla; d, first maxilliped; e, second maxilliped; f, third maxilliped; g, same, coxa and arthrobranch; h, l, m, same, detail of epipodial plate; i, telson; j, uropod; k, appendix interna; n, caudal fan, setae omitted. a-g, i-k, n, holotype; h, l, m, from moult. All scales – 1 mm, except for n – 5 mm.

first four pleura each with medium-sized white patches; fourth and sometimes third segments with white anterio-dorsal patch. Pleopods with protopod whitish and rami red. Uropods red, with white protopod; lateral spine also whitish. Telson entirely red; setae fringing uropods and telson whitish-yellowish.

Measurements. – Holotype, largest of all available specimens, has CL 17.5 mm, TL 44 mm, and CHL 22 mm.

Etymology. – Named after Frédéric Fasquel (Paris), enthusiastic photographer and collector of shrimps, who obtained numerous rare specimens of alpheid shrimps for the MNHN.

DISCUSSION

Alpheus tricolor, new species, and *A. fasqueli*, new species, appear to be well known to the importers of tropical animals for the marine aquarium in Europe. It is possible, that the shrimps are collected by diving at one or several localities, where they might be relatively common, and then distributed to the dealers all around the world. The two new species are known under several Latin names in the aquarium-oriented literature.

Baensch & Debelius (1992: 498) reported *Alpheus tricolor*, new species under the names «*Alpheus* sp.» and «*Alpheus strenuus*» (not Dana, 1852), and provided two colour photos showing obviously the same species. The species was reported as living with the goby *Amblyeleotris gymnocephala*. This statement is certainly incorrect, since the species shows no particular features of a species having burrowing life style, e.g. the subspatulate dactylus on third to fifth pereopod. Busson (1998: 42), provided a colour photo of *Alpheus tricolor* under «*A. strenuus*», and mentioned that the species is distributed in “Eastern Pacific, frequently encountered in the region of the Hawaiian Islands”. F. Busson (pers. comm.) obtained this apparently erroneous data from the French edition of the above mentioned book by Baensch & Debelius (1992). Finally, *A. fasqueli* was recently illustrated under the name «*Alpheus bisincisus*» (not de Haan, 1849) by Debelius (1998: 272), but the indicated locality «Gubal northern Red Sea» is erroneous, the specimen on the photo was actually imported from Indonesia (H. Debelius, pers. comm.).

The morphology of the major chela clearly indicate that *Alpheus tricolor* and *A. fasqueli* are members of *A. edwardsii* group, but it is closely related neither to *A. strenuus* Dana, 1852, nor to *A. bisincisus* de Haan, 1849. Both species can be distinguished from all the other Indo-Pacific species by the combination of the following characters: superior transverse groove of major chela not overhung by proximal shoulder; inferior transverse groove absent; minor chela balaeniceps in both sexes; frontal region with rostrum reaching at least to distal margin of first antennular article; antennular peduncles with second article weakly elongated; second pereopod robust and elongated; dactylus simple,

conical, with trace of secondary unguis; epipodial plate with dense, blunt setae; plunger of dactylus short, truncated. The conspicuous colour patterns including dark red zones on abdominal segments, containing large white spots, are also diagnostic.

The most important morphological characters of both new species are the absence of inferior saddle on major chela, and the minor chela being balaeniceps-shaped in female. To my knowledge only two species from *A. edwardsii* group have both of these features: *A. balaenodigitus* D.M. & A.H. Banner, 1982, and *A. pareuchirus imitatrix* de Man, 1910. *A. balaenodigitus* differs from both *A. tricolor* and *A. fasqueli* in having a more slender second pereopod, with different ratio of carpal articles (second longer than first), different proportions of major chela, and much more elongated second antennular article. *A. pareuchirus imitatrix* can be separated from *A. tricolor* and *A. fasqueli* by the dactylus of major chela being more elongated, bearing smaller plunger, the proximal shoulder of palm slightly overhanging saddle, and the second pereopod being more slender.

In the absence of minor cheliped, *A. tricolor* and *A. fasqueli* could be confused with *A. spatulatus* A.H. & D.M. Banner, 1968, and *A. proseuchirus* de Man, 1908. The first species is readily distinguished by several features including a spatulate dactylus on third pereopod, sharp tooth on proximal shoulder of palm of major chela, and strong, elongated rostrum. Compared to *A. tricolor* and *A. fasqueli*, *A. proseuchirus* has a very differently shaped major chela (A.H. & D.M. Banner, 1966: 129, fig. 47), while the second pereopods are more slender. *A. leptochiroides* de Man, 1909 seems to be different from *A. tricolor* and *A. fasqueli* in the proportions of the major chela (especially the height), and by the weak inferior groove proximal to the fixed finger.

The numerous setae on the epipodial plate of the third maxilliped (Fig. 6h), present in both new species, are conspicuous, but not unique to *A. tricolor* and *A. fasqueli*. To my knowledge the only other species with similarly developed setae on the epipodial plate is *A. exilis* Kim & Abele, 1988, described on two specimens from Galapagos Islands and Mexico. Without considering the first pereopods, which were lacking in *A. exilis*, this species is different from *A. tricolor* and *A. fasqueli* in having orbital hoods armed with acute teeth, and antennular peduncles elongated.

A. tricolor is morphologically so close to *A. fasqueli*, that the only feature to distinguish them easily is the colour pattern. However, there are also some very slight but apparently constant morphological differences. The rostrum of *A. fasqueli* is slightly longer than that of *A. tricolor*. Also, in *A. fasqueli* the stylocerite is shorter than in *A. tricolor*, while the base of the lateral spine of scaphocerite seems to be much broader in *A. tricolor* than in *A. fasqueli*. The general shape of major chelae is almost identical, but the proportions are slightly different, e. g. the palm is about 1.8 times longer than the dactylus in *A. tricolor*, while the palm is only 1.25 times longer in *A. fasqueli*. The distal portion of the fixed finger is somewhat shorter in *A. fasqueli* than in *A.*

tricolor, and there is also a difference in the shape of the superior margin of the fixed finger, proximally to the articulation with the dactylus. The second pereopod is more slender in *A. fasqueli* than in *A. tricolor*; this is particularly obvious if one compares the ratio length / width of first carpal article, or the ratio chela / first carpal article. Finally, the two new species apparently have different carapace shapes. (Fig. 2)

In the more conventional taxonomy of Alpheidae (D.M. & A.H. Banner 1982, Chace 1988, Miya 1974) these slight differences would be certainly considered as «intraspecific variation». Obviously, the morphology alone is often not sufficient to recognize that two species are involved. Sibling species are species that are difficult or impossible to distinguish based on morphological characters, and are common in all major marine groups and habitats (Knowlton, 1993). «Differences in distribution, behaviour and life history characteristics among sibling species demonstrate that niche diversification is more finely tuned, and interactions among organisms more specific, than most reef ecologists believed previously» (Knowlton & Jackson, 1994). Our strictly morphological species concept has changed, since we receive more and more data on colour patterns, ecology, and genetic, and recently numerous species of *Alpheus*, traditionally considered as widely distributed and variable species, were recognized as species complexes, containing two, three, or even four species.

For example, Hendrix (1971) observed that *Alpheus armillatus* H. Milne-Edwards, 1837, occurred in three different patterns in southern Florida, and that when the shrimps were collected in cohabiting pairs, they both always had the same pattern. Christoffersen & Ramos (1988) also mentioned existence of an unnamed form in Brazil, very closely related to *A. armillatus*, which «constitute the dominant shrimps in the littoral fringe zone along the entire Brazilian coast, including estuarine areas. In the field these shrimps may be immediately separated into two distinct colour patterns of the abdomen ...». An extensive study of numerous specimens from various parts of Brazil could not lead to a clear separation of this form from the typical *A. armillatus*, although some morphological differences were noted.

Hendrix (1971) also suspected that *A. floridanus africanus* Balss, 1916, is a distinct species, sympatric with *A. floridanus floridanus* Kingsley, 1878, but preferred not to change its status, because this would be in conflict with the conclusions reached by Chace (1972). However, today *A. floridanus* is considered to be a species complex, including at least two ecologically different species in the Gulf of Mexico (D. Felder, pers. comm.) and four genetically different species in Panama (N. Knowlton, pers. comm.).

The most interesting examples of the detection of sibling species in Alpheidae, involving colour patterns, remain a series of studies of the species complex *Alpheus armatus* Rathbun, 1901, in the Caribbean Sea (Knowlton & Keller 1983, 1985), and of several other species of *Alpheus* from

Atlantic and Pacific coasts of Panama (Knowlton & Mills, 1992; Knowlton et al., 1993). These studies show that all transisthmian taxa are quite distinct genetically, and those that have been studied are also reproductively isolated. Knowlton & Weigt (1998) concluded that the well known and widely distributed *Alpheus lottinii* Guérin, 1829, symbiont of *Pocillopora* corals, is actually a species complex; this is supported by my personal observations of photographs and colour slides showing different colour patterns, and observations of colour and behaviour by P. Castro (pers. comm.).

Two other studies demonstrated the presence of sibling species among coral reef species of *Alpheus* in the Indo-Pacific region (Bruce 1987, 1999). *Alpheus bannerorum* Bruce, 1987 is most readily distinguished from *A. parvirostris* Dana, 1852 by four conspicuous ocellus-like spots on the abdominal segments. Morphological differences between these two species are very subtle. *Alpheus soror* Bruce, 1999, a strikingly coloured species now quite popular in the aquarium trade (Fasquel, pers. comm.), is very close to *Alpheus gracilipes* Stimpson, 1860, whose range is presently thought to include a vast area from the Red Sea to the Hawaiian Islands. The type-locality of *A. gracilipes* is Tahiti. However, further studies will probably show that more than two species are involved in this cryptospecies complex, and that these species might have much more restricted ranges. For example the colour slides by P. K. L. Ng of a specimen from Hawaii (now in the ZRC) show a brownish-mottled pattern, with two large, dark ocellus-spots on the abdomen, lacking in the specimen of *A. gracilipes* from Darwin, Australia (Bruce, 1999). Some specimens from Taiwan and the Ryukyu Islands (colour slides by M.S. Jeng; Kamezaki et al. 1988) have a completely different, greenish-blue reticulated pattern, without ocellus-spots. Obviously, some of these specimens represent undescribed, sibling species closely related to *A. gracilipes*.

At present, the definition and the status of some of the most common and widely distributed *Alpheus* species, such as *A. lobidens* De Haan, 1849, *A. edwardsii* Audouin, 1827, and *A. malabaricus* Fabricius, 1798, remain uncertain. Each of these species occurs in the Indo-Pacific region in several different patterns (pers. obs.), and some of these patterns appear to correspond to the morphologically described species placed later in synonymy by various workers, mostly by Banner & Banner. This is the case of *A. crassimanus* Heller, 1865 and *A. inopinatus* Holthuis & Gottlieb, 1958, both presently treated as synonyms of *A. lobidens*; *A. audouini* Coutière, 1905, placed in synonymy of *A. edwardsii*; *A. dolichodactylus* Ortmann, 1890, *A. mackayi* Banner, 1959 and *A. mazatlanicus* Wicksten, 1983, considered to be synonyms of *A. malabaricus*. Field collections on the rocky shore of the Labrador Beach in Singapore showed that two slightly different colour patterns without intermediates exist for *A. lobidens* and *A. edwardsii*, and that at least *A. audouini* and *A. inopinatus* might be valid species.

The colour photo of *A. architectus* de Man, 1897 from the

Table 1. Problematic species and cryptospecies complexes in Alpheidae

| SPECIES | STATUS | REFERENCES |
|--|--|--|
| Alpheus macrocheles group | | |
| <i>A. collumianus</i> | status of subspecies | — |
| <i>A. cylindricus</i> | status of EP, WA and EA forms | Knowlton et al. 1993 |
| <i>A. hailstonei</i> . | status of subspecies | pers. obs |
| Alpheus sulcatus group | | |
| <i>A. architectus</i> – <i>A. bullatus</i> | species complex (2 spp.) | pers. obs. |
| <i>A. armatus</i> – <i>A. immaculatus</i> – <i>A. roquensis</i> – <i>A. polystictus</i> | species complex (4 spp.)* | Knowlton & Keller 1985 |
| <i>A. canaliculatus</i> | 2 spp. involved | Ahyong, pers. comm Knowlton et al. 1993 |
| <i>A. formosus</i> – <i>A. panamensis</i> | status of EP and WA forms | Knowlton & Mills, 1992 |
| <i>A. gracilis</i> | probably species complex | — |
| <i>A. lottini</i> | species complex (3-4 spp.) | Knowlton & Weigt 1998 pers. obs. |
| <i>A. malleator</i> | status of EP, WA and EA forms | — |
| <i>A. normanni</i> – <i>A. packardii</i> | status of EP and WA forms status of | Kim & Abele, 1988 |
| <i>A. socialis</i> | « varieties » | Hale, 1927 D.M. & A.H. Banner, 1982 |
| <i>A. splendidus</i> | probably species complex | — |
| <i>A. sulcatus</i> – <i>A. macrochirus</i> | status of IWP, EA and EP forms | Crosnier & Forest 1966 Miya, 1981 |
| <i>A. villosus</i> | status of N and S Australian form | D.M. & A.H. Banner 1982 |
| <i>A. websteri</i> – <i>A. fagei</i> – <i>A. arenensis</i> | status of EP, WA and EA forms | Crosnier & Forest, 1966 |
| Alpheus diadema group | | |
| <i>A. bidens</i> – <i>A. praedator</i> | 2 distinct species | Bruce (pers. comm.) |
| <i>A. diadema</i> | 2 colour morphs (? 2 spp.) | pers. obs. |
| <i>A. gracilipes</i> – <i>A. soror</i> | species complex (4 spp.) | Bruce, 1999; pers. obs |
| <i>A. paracrinitus</i> – <i>A. bengalensis</i> — | species complex (4-5 spp.) | Knowlton et al. 1993 |
| <i>A. rostratus</i> | status of <i>A. bengalensis</i> | Knowlton & Mills, 1992 Holthuis 1958 |
| Alpheus crinitus group | | |
| <i>A. alcyone</i> – <i>A. aculeipes</i> | 2 colour patterns (? 2 spp.) | pers. obs. |
| <i>A. amirantei</i> | status of <i>A. aculeipes</i> | — |
| <i>A. cristulifrons</i> | status of subspecies <i>sizou</i> status of EP and WA forms | — Knowlton et al. 1993 Knowlton & Mills 1992 |
| <i>A. longecarinatus</i> | status of subsp. <i>bucephaloides</i> | — |
| <i>A. styliceps</i> – <i>A. eulimene</i> | specific status | — |
| <i>A. spongiarum</i> – <i>A. paraculeipes</i> | specific status | — |
| Alpheus obesomanus group | | |
| <i>A. obesomanus</i> – <i>A. lutini</i> | status of <i>lutini</i> | — |
| <i>A. simus</i> – <i>A. saxidomus</i> | | Knowlton et al. 1993 |
| Alpheus brevirostris group | | |
| <i>A. bellulus</i> | species complex (3 spp.) | pers. obs. |
| <i>A. brevirostris</i> | taxonomical status | Miya in Bruce, 1994 |
| <i>A. digitalis</i> | status of <i>A. distinguendus</i> 2 cryptospecies in Japan 2 cryptospecies in Thailand | Miya in Bruce 1994 Hayashi (pers. comm.) pers. obs. |
| <i>A. djeddensis</i> – <i>A. djiboutensis</i> | species complex (4-5 spp.) | pers. obs. |
| <i>A. fenneri</i> | possibly 2 spp. involved | pers. obs. |
| <i>A. floridanus</i> | species complex (4 spp.) | Hendrix 1971 Knowlton (pers. comm.) Felder (pers. comm.) Miya in Bruce 1994 |
| <i>A. heterocarpus</i> – <i>A. homochirus</i> | status questionable | pers. obs. |
| <i>A. macroskeles</i> | several cryptospecies ? | pers. obs. |
| <i>A. miyakei</i> | incomplete (invalid ?) species description | Bruce, 1994 |
| <i>A. nonalter</i> | possibly 2 spp. involved | pers. obs. |
| <i>A. rapacida</i> | species complex | pers. obs. |
| <i>A. rapax</i> | species complex | pers. obs. |
| <i>Alpheus</i> spp. <i>brevirostris</i> group | 3 invalid names species complexes | Karplus 1987 |
| <i>A.</i> « <i>rubromaculatus</i> » | 2 sibling spp. | pers. obs. |
| <i>A.</i> « <i>ochrostriatus</i> » | 2-3 sibling spp. | pers. obs. |
| <i>A.</i> « <i>purpurilenticularis</i> » | undescribed species | Karplus, 1987 |
| <i>Alpheus</i> sp. « <i>Kochi</i> » | ? undescribed species | Anker, 2000 |

Table 1. continue

| SPECIES | STATUS | REFERENCES |
|--|---|--|
| <i>Alpheus edwardsii</i> group | | |
| <i>A. armillatus</i> | species complex (3 spp. incl. or not <i>A. angulatus</i> , <i>A. verrilli</i> etc.) | Hendrix, 1971 McClure (pers. comm.) Christoffersen & Ramos, 1988 |
| <i>A. bouvieri</i> | possibly species complex | — |
| <i>A. edwardsii</i> – <i>A. audouini</i> | 2 or more spp. involved | pers. obs. |
| <i>A. euphrosyne</i> | ? species complex | — |
| <i>A. heterochaelis</i> – <i>A. estuariensis</i> | ? 3rd sibling sp. in this complex | pers. obs. |
| <i>A. lobidens</i> – <i>A. inopinatus</i> – <i>A. lobidens polynesica</i> | species complex (3 or more spp. involved) | Lewinsohn & Galil, 1982 pers. obs. |
| <i>A. malabaricus</i> – <i>A. mazatlanicus</i> – <i>A. dolichodactylus</i> – <i>A. mackayi</i> <i>A. microrhynchus</i> | species complex | pers. obs. |
| <i>A. nuttingi</i> – <i>A. canalis</i> | possibly 2 or more spp. involved 2 or more species involved status of EP and WA forms | pers. obs. Bruce (pers. comm.) Knowlton et al., 1992 Knowlton & Mills, 1992 |
| <i>A. pacificus</i> | several colour « morphs », probably species complex | pers. obs. |
| <i>A. richardsoni</i> | ? species complex | Bruce (pers. comm.) |
| <i>A. parvirostris</i> – <i>A. bannerorum</i> | species complex (2 spp.)* | Bruce, 1987 |
| <i>A. strenuus</i> | status of subspecies <i>A. cremnus</i> | — |
| <i>A. tricolor</i> – <i>A. fasqueli</i> | 2 cryptospecies* | present study |
| <i>Alpheopsis</i> | | |
| <i>A. aequalis</i> | species complex, status of var. <i>truncatus</i> and <i>A. consobrinus</i> | pers. obs. Armstrong, 1941 |
| <i>A. trigonus</i> | species complex (2 spp) | Anker (in study) Rodriguez, 1986 |
| <i>A. trispinosus</i> | status of <i>A. africanus</i> , <i>A. garricki</i> | Chace, 1988 |
| <i>A. yaldwyni</i> | ? 2 species | pers. obs. |
| <i>Arete</i> | | |
| <i>A. dorsalis</i> | variety of hosts, possibly species complex | D.M. & A.H. Banner, 1973 Bruce, 1990 |
| <i>A. dorsalis</i> sensu Suzuki | possibly undescribed species | Bruce, 1990 |
| <i>A. indicus</i> – <i>A. kominatoensis</i> | 2 distinct species | Bruce 1989, 1990 |
| <i>Arctopsis</i> | | |
| <i>A. amabilis</i> | possibly species complex | — |
| <i>A. manazuruensis</i> | specific status to be confirmed | Chace, 1988 |
| <i>Athanas</i> | | |
| <i>A. amazone</i> | strong morphological variation | pers. obs. |
| <i>A. dimorphus</i> | ? species complex | — |
| <i>A. nitescens</i> | status of var. <i>laevirhynchus</i> and <i>A. veloculus</i> | Holthuis & Gottlieb, 1958 pers. obs. |
| <i>A. sibogae</i> – <i>A. parvus</i> | ? distinct species | — |
| <i>Automate</i> | | |
| <i>A. dolichognatha</i> – <i>A. gardineri</i> – <i>A. kingsleyi</i> – <i>A. talismani</i> | species complex (3-4 spp.) | Anker (in study) |
| <i>A. evermanni</i> | possibly 2 species | Anker (in study) |
| <i>Batella</i> | | |
| <i>B. parvimanus</i> | 2 closely related, undescribed species | — |
| <i>Betaeus</i> | | |
| <i>B. granulimanus</i> – <i>B. pingi</i> – <i>B. levifrons</i> | status of <i>B. pingi</i> and <i>B. levifrons</i> | pers. obs. |
| <i>Leptalpheus</i> | | |
| <i>L. forceps</i> | 2 closely related species | pers. obs. |
| <i>L. mexicanus</i> | status of Colombian populations | Felder (pers. comm) |
| <i>Leptalpheus</i> spp. | several closely related spp. | pers. obs. |
| <i>Metabetaeus</i> | | |
| <i>Metabetaeus</i> spp. | status of Madagascar and Indonesian populations | — |
| <i>Metalpheus</i> | | |
| <i>M. paragracilis</i> – <i>M. rostratipes</i> | ? pantropical species or species complexes | — |
| <i>Parabetaeus</i> | | |
| <i>P. culliereti</i> | intraspecific variability | Nomura & Anker (in study) |
| <i>P. euryone</i> | ? species complex | pers. obs. |

Table 1. continue

| SPECIES | STATUS | REFERENCES |
|--|--|--|
| Potamalpheops | | |
| <i>P. tigger</i> | 2 species different in colour pattern and morphology | Anker (in study) |
| Salmoneus | | |
| <i>S. cavicolus</i> | 2 species involved | Anker (in study) |
| <i>S. serratidigitus</i> – <i>S. latirostris</i> | probably 2 distinct species | Coutière 1899 |
| <i>S. tricristatus</i> | probably 2 species involved. | Miya 1972 Anker (in study) |
| Synalpheus (selected) | | |
| <i>S. digueti</i> | possibly species complex | pers. obs. |
| <i>S. tumidomanus</i> | species complex | pers. obs. |
| <i>Synalpheus</i> spp. <i>gambarelloides</i> group | status of subsp. <i>africanus</i> and <i>congoensis</i> cryptospecies complexes | Crosnier & Forest 1966 Duffy 1996, 1998 Rios & Duffy, 1999 |
| Vexillipar | | |
| <i>V. repandum</i> | ? 2 species | pers. obs. |

Ryukyus published by Kamezaki et al. (1988) shows a differently coloured shrimp than the photo of *A. architectus* from the eastern Africa, printed on the frontispiece of A.H. & D.M. Banner (1983). The latter belongs probably to *A. bullatus* Barnard, 1955, which was placed in synonymy under *A. architectus* by D.M. & A.H. Banner (1982). *A. sulcatus* Kingsley, 1878 is another problematic taxon in the *sulcatus* group. The present taxonomic status of the Indo-West Pacific, the eastern Atlantic and the eastern Pacific forms, all placed in one widely distributed species *A. sulcatus*, is far to be satisfying. Crosnier & Forest (1966) treated the Indo-West Pacific *A. macrochirus* Richters, 1880 as a species slightly different from the West African *A. sulcatus*. These authors published figures of major chela of *A. macrochirus* and *A. sulcatus* showing clear differences in the shape and the proportions. Kingsley's original types of *A. sulcatus* from Panama are lost. Kim & Abele (1988) published figures of what they believe to be *A. sulcatus*. The major chela of this specimen is clearly different from the chela of both West African *A. sulcatus* and Indo-West Pacific *A. macrochirus*. If we accept that Kim & Abele's specimens (collected in the Gulf of California south to Galapagos) correspond most likely to the true *A. sulcatus*, then, the Indo-West Pacific form should be assigned to *A. macrochirus*, while a new name should be found for the West African form.

Many problems exist also among the Indo-Pacific members of the *A. brevirostris* group, to which belongs the above mentioned *A. floridanus*. This group contain about 40 morphologically similar species (Bruce, 1994). The taxonomic status of several species, such as *A. digitalis* De Haan, 1849 (= *A. distinguendus* de Man, 1909) and *A. brevirostris* (Olivier, 1811) (Miya, in Bruce, 1994) is still not clear. Especially problematical are the numerous goby-associated species: *A. djeddensis* Coutière, 1897, *A. djiboutensis* de Man, 1909, *A. bellulus* Miya & Miyake, 1969, *A. rapax* Fabricius, 1798, *A. rapacida* de Man, 1909, and several others unnamed or named but formally undescribed species (Karplus et al., 1981); therefore, more taxonomical studies in this group are necessary to elucidate all these

problems. However, revisions of these *Alpheus* complexes encounter numerous obstacles. The major obstacles are the lack of large samples of specimens, the absence of data on colour patterns and ecology in many descriptions, and the lack of important details in the older descriptions, which therefore become applicable to several closely related species. It should also be noted that similar species complexes exist in other alpheid genera, such as *Alpheopsis*, *Salmoneus* (pers. obs.), *Arete* (Bruce, 1990), *Potamalpheops* (pers. obs.) and *Synalpheus* (Duffy, 1996). Table I gives an non-exhaustive account of some « problematical » alpheid species, on which, it is hoped, future workers will focus. This table also lists already resolved complexes (marked with an *). It is true that the colour patterns, ignored by many of previous workers, will continue to have an important part in the identification of sibling species. However, other techniques, such as molecular genetics (Knowlton & Weigt, 1998), behavioural ecology - mating studies, host specificity (Knowlton & Keller, 1982; Knowlton et al., 1993) are also expected to be very useful in this regard.

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