A taxonomic study of six species of *Upogebia* Leach (Crustacea, Decapoda, Thalassinidea) in the collections of the British Museum (Natural History), London

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Synopsis

A recent study of unnamed specimens of *Upogebia* in the collections of the British Museum (Natural History) has enabled me to identify the following six species from among this material: *Upogebia africana* Ortmann, *Upogebia brasiliensis* Holthuis, *Upogebia carinicauda* (Stimpson), *Upogebia darwini* (Miers), *Upogebia issaeffi* (Balss) and *Upogebia spinigera* (Smith). Detailed descriptions are given here of the two species *Upogebia africana* Ortmann and *Upogebia issaeffi* (Balss) as previous accounts are inadequate for comparative studies with other species. The morphological variation of the other four species is described and discussed.

Introduction

The subgeneric division of the genus *Upogebia* into the two subgenera, *Upogebia* (*Upogebia*) Leach and *Upogebia* (*Calliadne*) Strahl, as proposed by de Man (1928) is not used in the present work. De Man assigned the species with a spine on the antero-lateral margin of the carapace, and in which the fixed finger (propodal prolongation) of the cheliped is much shorter than the dactylus to the subgenus *Upogebia*, while he placed species in which the antero-lateral carapace spine is absent and in which the cheliped fixed finger is as long as the dactylus into the subgenus *Calliadne*. Although many species of *Upogebia* can be easily assigned to one or the other subgenus on these above-mentioned features, a few show considerable variation in these respects, for example, in the present study some specimens of *Upogebia brasiliensis* and *Upogebia spinigera* cannot be satisfactorily placed in either subgenus. It has been suggested by Bozic and de Saint Laurent (1972) that before subgeneric partitioning of *Upogebia* can be reconsidered, it will be necessary to examine critically many additional characters, such as branchial formula, mouth appendages, epipods, pereiopods, etc.

The measurements given are carapace lengths (c.l.) measured from the rostral apex to the carapace posterior margin in the mid-line, and the total lengths (t.l.) measured from the rostral apex to the telson posterior margin.

Upogebia africana Ortmann

(Figs 1a–h, 2a–l)

Upogebia africana, Ortmann, 1894 : 22, pl. 2, fig. 4a, b; *Upogebia capensis* Stebbing, 1900 : 45; Stebbing, 1910 : 370; *Upogebia africana* de Man, 1928 : 37, 51; *Upogebia africana* Barnard, 1947 : 380; Barnard, 1950 : 519, 520.

MATERIAL EXAMINED. Port Elizabeth, S. Africa, 1891, 2 ♂♂, c.l. 20 mm, t.l. 57 mm; 2 ♀♀, c.l. 20 mm, 21 mm, t.l. 60 mm, 62 mm.
Port Alfred, S. Africa, 1905, 1 ♂, c.l. 23 mm, t.l. 63 mm.

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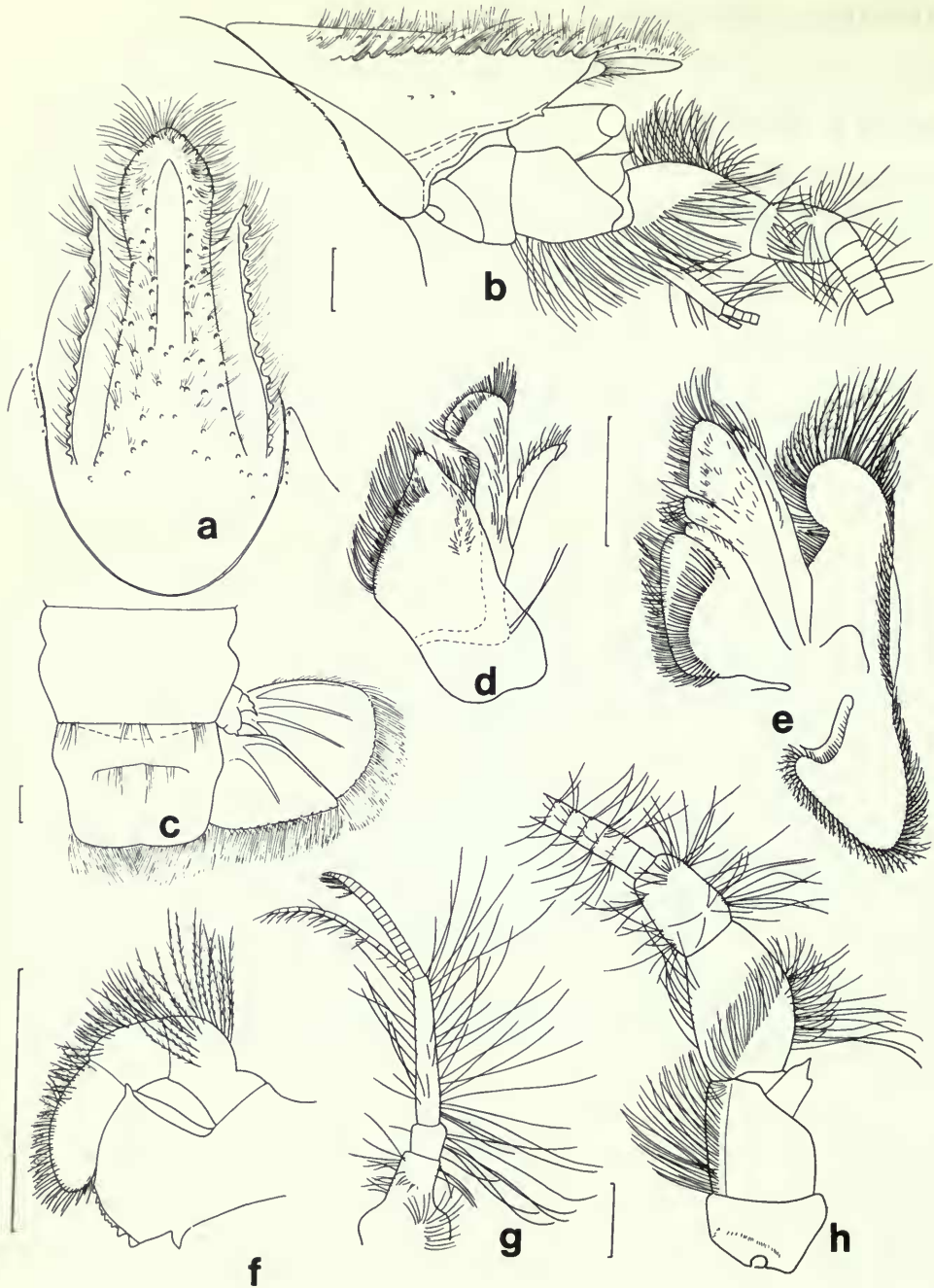
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Fig. 1 *Upogebia africana* Ortmann, ♂, 63 mm t.l., Port Alfred: (a) rostrum, dorsal view; (b) rostrum, lateral view; (c) sixth abdominal segment, telson and uropods; (d) maxillule; (e) maxilla; (f) mandible; (g) antennule; (h) antenna. Scale: 2 mm.
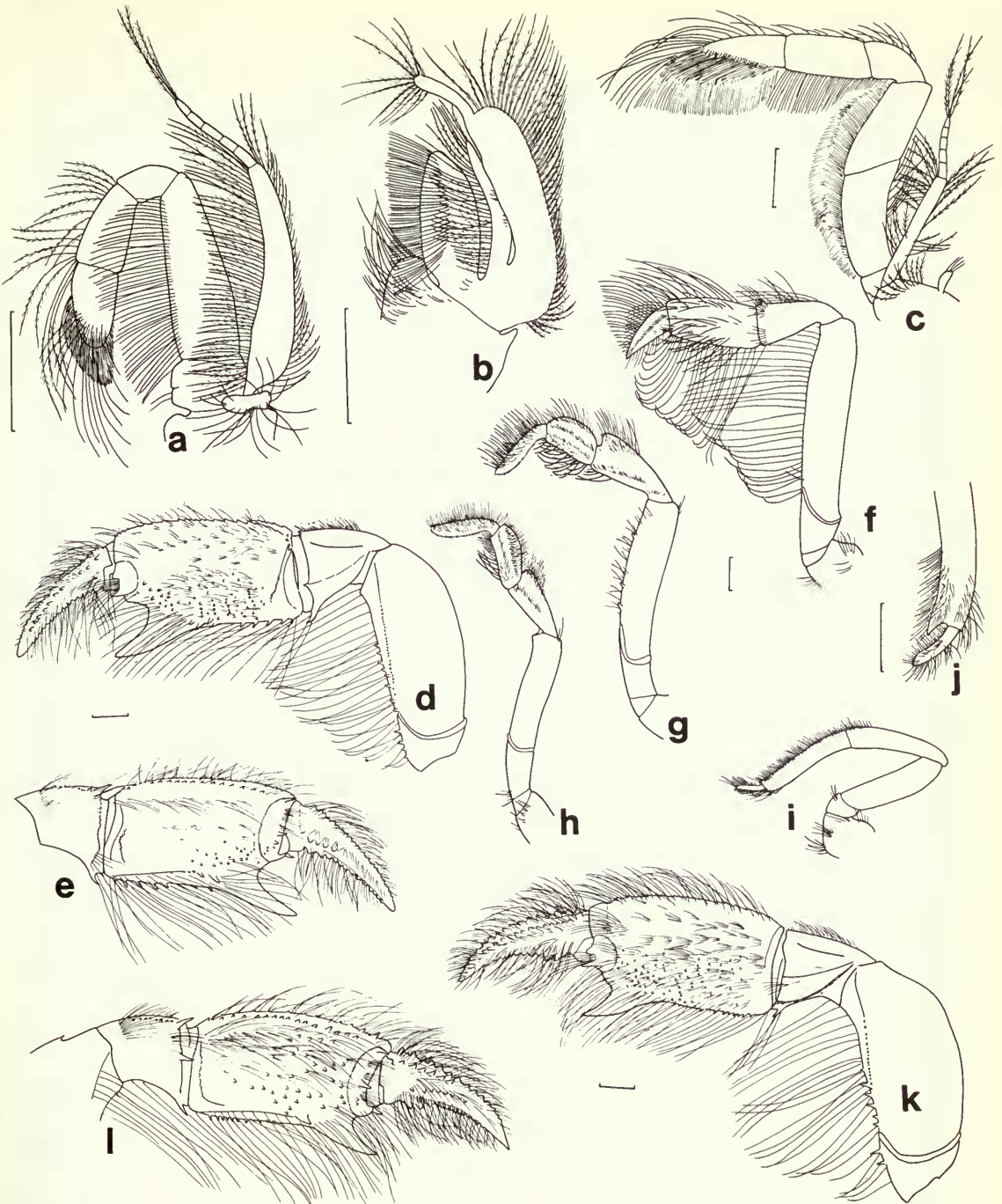
Fig. 2 (a)–(j) *Upogebia africana* Ortmann, ♂, 63 mm t.l., Port Alfred: (a) second maxilliped; (b) first maxilliped; (c) third maxilliped; (d) cheliped, outer lateral view; (e) cheliped, inner lateral view; (f) second pereiopod; (g) third pereiopod; (h) fourth pereiopod; (i) fifth pereiopod; (j) propodus and dactylus of fifth pereiopod enlarged. (k), (l) *Upogebia capensis* (Krauss), ♀, 72 mm t.l., South Africa: cheliped, outer lateral view and inner lateral view respectively. Scale: 2 mm.

DESCRIPTION. *Carapace* broad posteriorly, narrowing anteriorly. Front tridentate (Fig. 1a, b). Rostrum long and conical, setose, projecting far beyond eyes, lower margin unarmed, lateral margins each with five or six acute teeth. Lateral ridges of gastric region with 11–14 teeth, lateral grooves large and divergent posteriorly, a smooth, non-setose medio-dorsal groove anteriorly. Anterior part of gastric region between gastric ridges spinose and setose, posterior quarter unarmed and glabrous. *Linea thalassinica* distinct. Cervical groove deep, lateral part of cervical groove below *linea thalassinica* provided with small denticles in two ♂♂ out of the five specimens.

Telson (Fig. 1c) broader than long, lateral margins slightly convergent distally, postero-lateral angles rounded, posterior margin straight, median groove distinct, median and lateral carinae present but not conspicuous.

Antennule (Fig. 1g) first peduncular segment unarmed, second segment shortest, third segment slender, longer than first and second segments together, flagella simple.

Antenna (Fig. 1h) scaphocerite terminating in a spine, flagellum long and simple.

Mandible (Fig. 1f) with an inner lateral tooth, small teeth on cutting edge and a larger one basally.

Maxillule (Fig. 1d), *maxilla* (Fig. 1e) with normal shape as usually observed in *Upogebia*.

First maxilliped (Fig. 2b), *second maxilliped* (Fig. 2a) and *third maxilliped* (Fig. 2c) each with a small epipod.

Cheliped (Fig. 2d, e) slightly stouter in the male than in the female. Coxa unarmed. Ischium with 1–3 spines on lower margin. Merus with upper margin convex, with two rows of denticles on inner and outer lower margins and 5–7 large teeth proximally. Carpus with one acute spine on distal upper margin followed by a row of 5–7 denticles and another spine on lower margin; outer surface with a longitudinal groove and a smooth ridge ending in a spine, inner surface with 2–3 small denticles on distal margin between the upper and lower spines. Palm with two spinose ridges on upper margin, lower margin of outer surface spinulose proximally, with 1–4 larger spines near the base of fixed finger and another large spine near the base of dactylus; inner surface of palm spinulose distally with one or two spines near the base of fixed finger and two additional spines near the base of dactylus; fixed finger with two denticles on cutting edge in one female specimen, smooth in others. Dactylus with two spinose ridges on upper margin, cutting edge denticulate with two larger teeth near the base, inner surface with a row of 4–5 granules above cutting edge. In the female, the palm and dactylus of cheliped are less spinose than in the male. Only one spinose ridge is conspicuous on upper margin of the palm, spines and spinules are fewer and smaller on both palm and dactylus.

Second pereiopod (Fig. 2f) setose, carpus with a spine on both upper and lower distal margins, other segments unarmed.

Third pereiopod (Fig. 2g) merus with 2–4 spines on lower margin; dactylus elongated, slender, lower margin finely pectinate.

Fourth pereiopod (Fig. 2h) all segments unarmed, dactylus slender with lower margin pectinate.

Fifth pereiopod (Fig. 2i) slender, unarmed and subcheliform; propodus setose with a very small ventro-dorsal process; dactylus small, lower margin pectinate.

Pleopod 1 of the female slender, two-segmented.

Pleopods 2–5 large in both sexes; endopod ovate, exopod larger, elliptical with two blunt carinae on dorsal surface.

Uropod (Fig. 1c) broad, as long as telson; protopod with a spine near the base of endopod; endopod triangular with two longitudinal carinae, exopod rounded with three carinae and a spine on the basal part, posterior margins of both endopod and exopod nearly straight, with many minute spinules.

REMARKS. Balss (1913) and de Man (1927, 1928) considered *U. africana* Ortmann and *U. capensis* (Krauss) as identical species, but Barnard (1950) stated that the two forms appeared to be localized one in the colder water, the other in the warmer water and should be kept separate.

The present specimens have been compared with some material identified as *U. capensis* and deposited in the collections of the British Museum (Natural History). These include 2 ♂♂ from the Natal Coast, 13 mm, 14 mm c.l. and 38 mm, 40 mm t.l. and 1 ♀ from offshore South Africa, 25 mm c.l., 72 mm t.l. The similarities and differences observed are listed in Table 1.

Table 1 Comparison of *U. africana* from Port Alfred and Port Elizabeth with *U. capensis* from Natal Coast and South Africa

	U. africana	*U. capensis*	
	From Port Alfred and Port Elizabeth	From Natal Coast	From S Africa
Denticles on hind margin of cervical groove	present in 2 out of 5 specimens	present, small	present, spiniform
Cheliped ⎰ Coxal spine	absent	absent	present, large
Spine on upper margin of merus	absent	present	present
Large spines on lower outer margin of palm (near fixed finger)	present, 1–4	present, 1	absent
Second pereiopod ⎰ Coxal spine	absent	absent	present
Spine on upper margin of merus	absent	absent	present

The decisive diagnostic character separating the two species (Barnard, 1950) is the presence of coxal spines on legs 1–3 in *U. capensis* and their absence in *U. africana*. In this respect, the material from Natal Coast must be reidentified as *U. africana* while the specimen from South Africa is a true *U. capensis*. Its cheliped is illustrated in Fig. 2k, l.

In addition to the absence of coxal spines on legs 1–3, the material of *U. africana* from Natal Coast and that from Port Alfred and Port Elizabeth all have 1–4 large spines on the lower outer margin of the palm of the cheliped, near the fixed finger and all without a spine on the upper distal margin of the merus of the second pereiopod.

The material of *U. africana* from Port Alfred and Port Elizabeth has no spine on the upper distal margin of the merus of the cheliped, but this spine is present in the specimens of *U. africana* from Natal Coast as well as in that of *U. capensis* from South Africa. It would appear that this variable feature cannot be used in separating the two forms.*

DISTRIBUTION. Port Elizabeth (Ortmann, 1894); Zwartkops River estuary, Algoa Bay (Stebbing, 1900); Gordon's Bay, east side of False Bay (Stebbing, 1910); Somerset Strand and Gordon's Bay, estuary of Breede River (Port Beaufort), Knysna lagoon, Keurbooms river estuary (Plettenberg Bay), Zwartkops estuary, Nahoon river estuary (East London), Port St Johns and Durban Bay (Barnard, 1950); Natal Coast, Port Alfred.

Upogebia brasiliensis Holthuis
(Fig. 3a, b)

Upogebia brasiliensis Holthuis, 1956: 175–181, figs 1, 2; *Upogebia brasiliensis* Gomes Correa, 1968: 97–109.

MATERIAL EXAMINED. Georgetown, British Guiana, 1917, 2 ♂♂, c.l. 7 mm, t.l. 21 mm, 22 mm; 3 ♀♀, c.l. 6–8 mm, t.l. 19–24 mm.

* After the completion of this paper the author had the opportunity to examine some material of *U. capensis* from S.W. Africa (Zool. Mus. Berlin 16130) which was on loan by the Berlin Museum to Dr K. Sakai. The material included 55 specimens of 16–70 mm t.l. in which the following features were observed:
  1. The antenna, both peduncle and flagellum, is more slender than that of *U. africana*.
  2. Coxal spines are present on 1st–3rd pereiopods in all specimens, that of 3rd pereiopod usually small.
  3. Outer surface of cheliped palm with small spinules only but without any large spines.
  4. Merus of 2nd pereiopod with one spine on upper distal margin, except in two specimens.
  The above observations confirm Barnard's view of separating *U. africana* and *U. capensis*.
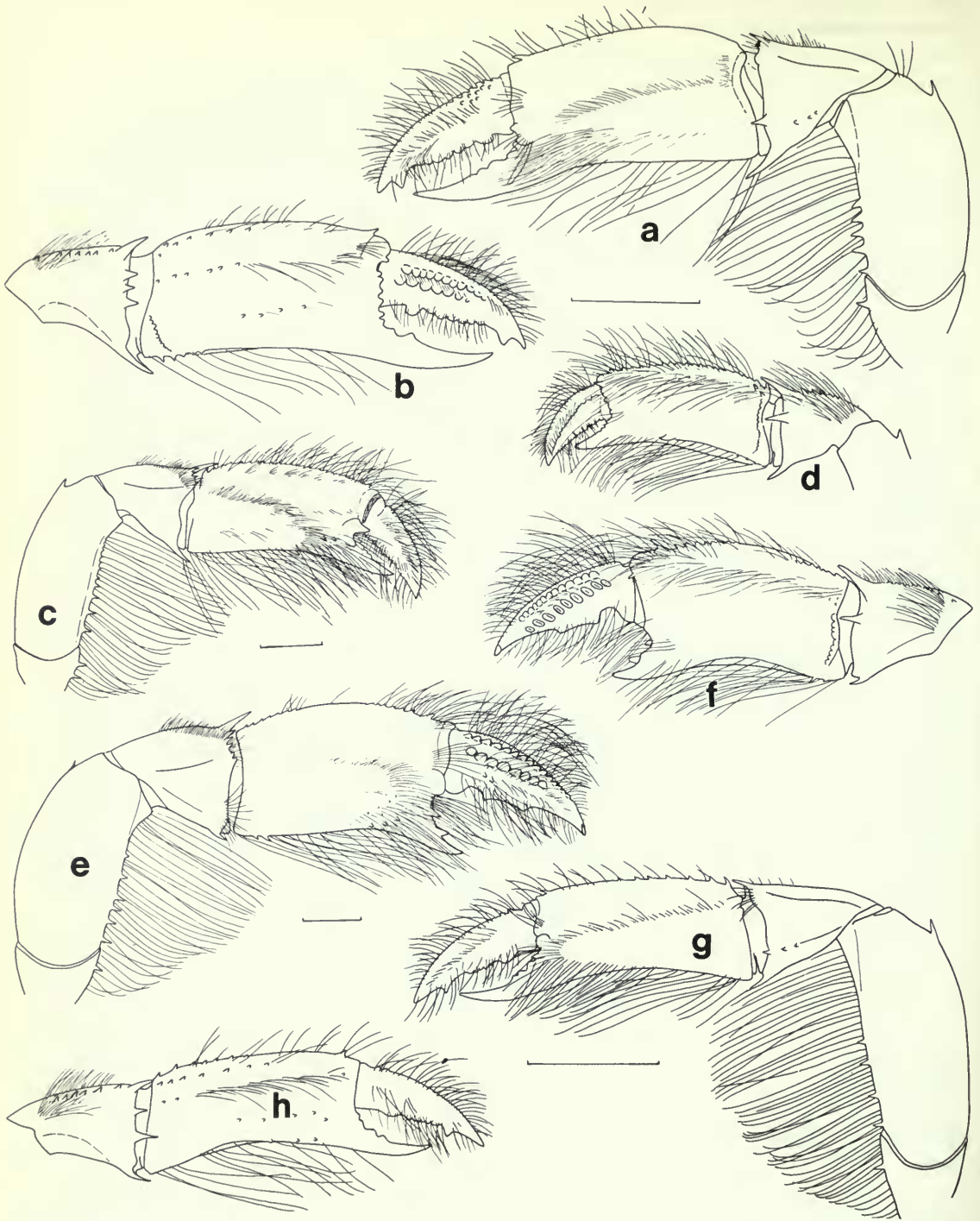
Fig. 3 Cheliped, outer lateral view and inner lateral view respectively: (a), (b) *Upogebia brasiliensis* Holthuis, ♂, 22 mm t.l., Georgetown; (c), (d) *Upogebia carinicauda* (Stimpson), ♀, 39 mm, t.l., Gulf of Siam; (e), (f) *Upogebia issaeffi* (Balss), ♀, 41 mm t.l., Tsur Island; (g), (h) *Upogebia spinigera* (Smith), ♀, 26 mm t.l., West Coast of Central America. Scale: 2 mm.

REMARKS. All specimens agree with the description of the species and with one of the type specimens examined (ovigerous ♀, 29 mm t.l.) except in the following features:

1. The spine on the antero-lateral margin of the carapace is absent in the female from Ecuador.

2. The large subterminal tooth on the cutting edge of the cheliped dactylus is absent in the three females from Georgetown.

3. The cheliped carpus of the male bears a row of six small denticles on its dorsal side, behind the anterior dorsal spine, and on the outer side, another large spine on its anterior margin, between the dorsal and ventral ones.

4. Spines on the lower margin of the cheliped merus are very small in the female from Ecuador.

5. The lower margin of the merus of the third pereiopod is unarmed in one female specimen from Georgetown.

DISTRIBUTION. Brazil (Holthuis, 1956; Gomes Correa, 1968); Georgetown, British Guiana; Esmeraldas, Ecuador.

Upogebia carinicauda (Stimpson)

(Fig. 3c, d)

Gebia carinicauda Stimpson, 1860 : 23; *Gebia barbata* Strahl, 1861 : 1062, figs 7–9; *Gebia carinicauda* Miers, 1884 : 280; *Gebia carinicauda* de Man, 1888 : 256; *Gebia barbata* Ortmann, 1892 : 54, fig. 8; *Gebia barbata* Ortmann, 1894 : 22; *Upogebia (Upogebia) carinicauda* de Man, 1926 : 341–345; de Man, 1928 : 60–65, figs 6, 6a–n; *Upogebia (Upogebia) kempi* Shenoy, 1967 : 777–804, figs 1–12; *Upogebia (Upogebia) kempi* Sankolli, 1972 : 671–682, figs 9, 10.

MATERIAL EXAMINED. Gulf of Siam, 1898, 1 ♀, c.l. 13 mm, t.l. 39 mm.

REMARKS. The present specimen is compared with material of *U. carinicauda* in the BM(NH) with three specimens of *U. carinicauda* of the Siboga Expedition and with two paratype specimens of *U. kempi* Shenoy from Bombay.

Material of *U. carinicauda*
1. Thursday Island, ♀ (BM(NH) Reg. No. 81–31) c.l. 7 mm, t.l. 20 mm
2. Thursday Island, ♂ (BM(NH) Reg. No. 82–7) c.l. 10 mm, t.l. 30 mm
3. Thursday Island, ♀ (BM(NH) Reg. No. 82–7) c.l. 12 mm, t.l. 35 mm
4. Island of Torres Straits, ♀ (BM(NH) Reg. No. 77–12) c.l. 11 mm, t.l. 33 mm
5. Ambon, Siboga Exped. St. 181, ♀, c.l. 6 mm, t.l. 21 mm
6. Ambon, Siboga Exped. St. 181, ♂, c.l. 7 mm, t.l. 23 mm
7. Ambon, Siboga Exped. St. 181, ♀, c.l. 10 mm, t.l. 32 mm

Material of *U. kempi*, two paratypes
8. Bombay, ♀, c.l. 14 mm, t.l. 45 mm
9. Bombay, ovigerous ♀, c.l. 14 mm, t.l. 46 mm

Table 2 lists the main similarities and differences observed.

The present material from the Gulf of Siam agrees very well with specimens of *U. carinicauda* identified by Miers (1884) and also with two specimens of the material from Ambon and is identical to the type specimens of *U. kempi*. With the exception of the female specimen from Ambon of 21 mm t.l., all specimens considered in Table 2 are similar in having: (*a*) four spines on the rostrum; (*b*) an antero-lateral carapace spine; (*c*) a spine on the upper distal margin of the cheliped merus; (*d*) three large spines on the inner anterior margin of the cheliped carpus; (*e*) a large spine on the lower margin of the palm near the fixed finger; and (*f*) a spine on the upper distal margin of the merus of the second pereiopod. The following variations are observed:

1. The rostrum is short in most specimens of total length less than 33 mm. In larger specimens of *U. carinicauda* and *U. kempi*, the rostrum reaches well beyond the eye-stalks.

2. The ovigerous paratype of *U. kempi* has a fairly large tubercle on the antero-lateral margin of the carapace, near the base of the antenna whilst in the other female, a few very small tubercles are present. They are absent in all specimens of *U. carinicauda*.

Table 2   Specimens of *U. carinicauda* and *U. kempi* compared, from various Indo-Pacific localities

	Thursday Isl.	Ambon	Ambon	Thursday Isl.
Specimen number used in text	1	5	6	2
Total length (mm)	20	21	23	30
Length of rostrum	←————about 1·5 times of eye-peduncle————→			about twice that of eye-peduncle
Spines on rostrum	4	4	4	4
Antero-lateral carapace spine	present	absent	present	present
Tubercles on margin of carapace, near antenna	absent	absent	absent	absent
Cheliped				
Spines on ischium	1	absent	1	2
Merus { Spines on upper distal margin	1	absent	1	1
Merus { Spines on lower margin	6	absent	6	20
Carpus { Large spines on inner ant. margin	3	absent	3	3
Carpus { Denticles behind dorsal spine	4, very small	absent	absent	5
Propodus { Row of denticles on upper margin	absent	absent	absent	distal half present
Propodus { Large spine near fixed finger	present	absent	present	present
Propodus { Teeth on fixed finger	4–5	4	3	4
Second pereiopod				
Spine on upper distal margin of merus	present	absent	present	present
Third pereiopod				
Tubercles on lower margin of merus	absent	absent	absent	11–12

U. carinicauda   *U. kempi*

Ambon	Torres Straits	Thursday Isl.	Gulf of Siam	Bombay	Bombay
7	4	3		8	9
32	33	35	39	45	46
←——about 1·5 times that of eye-peduncle——→		←————————about twice that of eye-peduncle————————→			
4	4	4	4	4	4
present	present	present	present	present	present
absent	absent	absent	absent	2–3, very small	1, large
absent	2	2	2	2	2
1	1	1	1	1	1
8	8	10	14	14	18
3	3	3	3	3	3
absent	4	5	6	6	5
absent	present, spines larger distally	present, spines larger distally	present, spines slightly larger distally	present, spines of the same size	present, spines of the same size
present	present	present	present	present	present
4	6	5	6	5	5
present	present	present	present	present	present
absent	6–7	3rd pereiopod missing	3–4	9–10	3rd pereiopod missing

3. Denticles behind the dorsal spine of the cheliped carpus are absent in all specimens from Ambon. In others, they show variation in size which seems to be related to the size of the animals.

4. Denticles on the upper margin of the cheliped palm are absent in one specimen of *U. carinicauda* from Thursday Island and in all specimens from Ambon. When they are present, it would seem that these denticles appear first on the distal part of the palm and then on the proximal part as the animals mature. They are large and apparent in the specimen from the Gulf of Siam and in the paratypes of *U. kempi*.

5. In small specimens, the telson is wider proximally than distally. In larger specimens, it approximates a rectangular shape.

6. Although having four spines on the rostrum, the female specimen from Ambon of 21 mm t.l. is devoid of nearly all other specific characters of *U. carinicauda* and the fixed finger of its cheliped is as long as the dactylus. It is probably an immature specimen, nevertheless its identification as *U. carinicauda* seems to be very uncertain.

DISTRIBUTION. Hongkong (Stimpson, 1860). Luzon (Strahl, 1861). Thursday Island, Torres Straits (Miers, 1884). Elphinstone Island, Mergui Archipelago (de Man, 1888), Samoa Island (Ortmann, 1892). Amboina (Ortmann, 1894; de Man, 1928). Buka, Salomon Islands (de Man, 1926). Anchorage of Labuan Pandan, Lombok; Anchorage off Seba, Savu; Haingsisi, Samau Island, Timor; Taruna-bay, Great-Sangir Island; Dammer; Saleyer-anchorage (de Man, 1928). Bombay, India (Shenoy, 1967; Sankolli, 1972). Gulf of Siam.

Upogebia darwini (Miers)

Gebiopsis Darwinii Miers, 1884 : 281, pl. 32, fig. A; *Gebiopsis intermedia* de Man, 1888 : 256, pl. 16, figs 6–8; *Gebiopsis Darwinii* Henderson, 1893 : 432; *Gebia* (*Gebiopsis*) *intermedia* Ortmann, 1894 : 23; *Gebiopsis intermedia* Zehntner, 1894 : 194; *Gebiopsis intermedia* Lanchester, 1901 : 555; *Upogebia intermedia* Pearson, 1905 : 91; *Upogebia* (*Calliadne*) *Darwinii* Nobili, 1906 : 97; *Upogebia* (*Calliadne*) *Darwinii* Borradaile, 1910 : 262; *Upogebia* (*Calliadne*) *Darwinii* de Man, 1928 : 24, 50, 84–86, figs 12, 12a–f; *Upogebia darwini* Ngoc-Ho, 1977 : 439–464, figs 1–13.

MATERIAL EXAMINED. Singapore, 1899, 1 ♂, c.l. 12 mm, t.l. 34 mm; 2 ovigerous ♀♀, c.l. 11 mm and 11·5 mm, t.l. 31 mm and 34 mm.

REMARKS. The present material agrees with the types of the species with which it has been compared except for some variations in the spinulation of the merus cheliped lower margin. Similarly to the types, the smaller female has 9–10 spines on the merus cheliped lower margin, whilst the male has 19–20 spines and the larger female has up to 28–30 spines on this margin. In the male, those spines are large proximally and decrease in size distally; in both females, they are small.

DISTRIBUTION. Port Darwin (Miers, 1884); Singapore (Miers, 1884, present paper); Elphinstone Island, Mergui Archipelago (de Man, 1888); Rameswaram, Tutticorin, Cheval Par (Henderson, 1893); Amboina (Ortmann 1894, Zehntner 1894, de Man 1928); Pulu Bidan, Penang (Lanchester, 1901); South of Adam's Bridge and Muttuvaratu Paar (Pearson, 1905); Aden, Perim, Obock (Nobili, 1906); Saya de Malha Bank (Borradaile, 1910); Phuket, Thailand (Ngoc-Ho, 1977).

Upogebia issaeffi (Balss)
(Fig. 3e, f; Fig. 4a–i; Fig. 5a–h)

Gebia (*Upogebia*) *issaeffi* Balss, 1913 : 239; Balss, 1914 : 89–90, figs 48–49; *Upogebia* (*Upogebia*) *Issaeffi* de Man 1927 : 27–29; de Man 1928 : 39, 41; *Upogebia issaeffi* Makarov, 1938 : 59–61, figs 19, 20; *Upogebia Issaeffi* Yokoya, 1939 : 278; non *Upogebia* (*Upogebia*) *issaeffi* Sakai, 1968 : 47, fig. 1D.

MATERIAL EXAMINED. Tsur Island (Tsuru Shima or Tsuri Shima, Japan ?), 1892, 7 ♂♂, c.l. 11·5–19·5 mm, t.l. 36–58 mm; 3 ♀♀, c.l. 12–19 mm, t.l. 37–60 mm.

DESCRIPTION. Carapace broad posteriorly, narrowing anteriorly.

Front tridentate. Rostrum (Fig. 4a, b) triangular, setose, projecting far beyond eyes, lower margin unarmed, lateral margins each with four or five acute teeth. Lateral ridges of gastric region with 10–11 teeth, lateral grooves large and slightly divergent posteriorly. Anterior part of gastric region between gastric ridges spinose and setose; middle line and about 1/5 of posterior part of gastric region unarmed and glabrous. *Linea thalassinica* distinct. Cervical groove deep, lateral part below *linea thalassinica* with a few small spinules. Spine on antero-lateral margin of carapace distinct, it is bifid in two specimens.
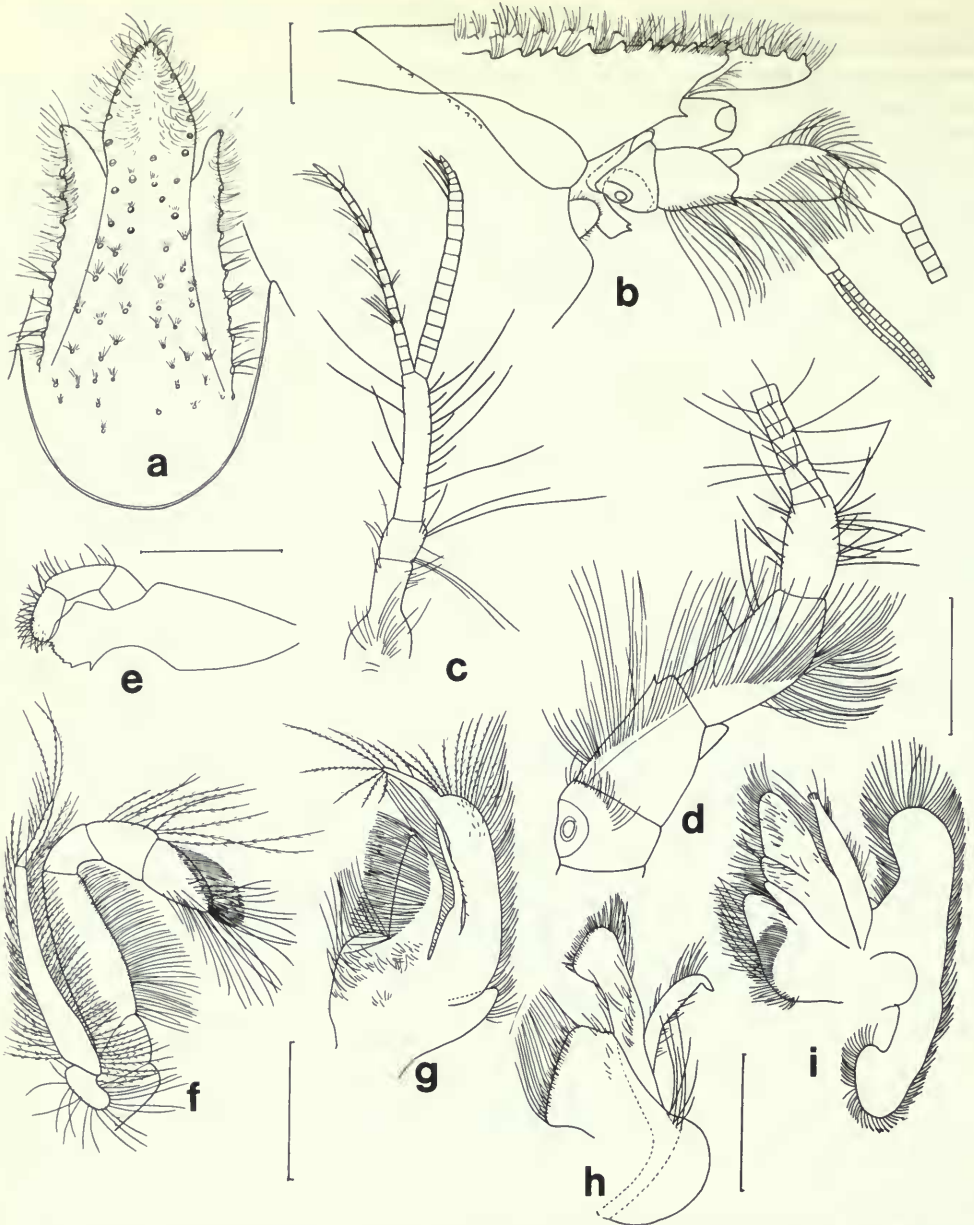
Fig. 4 *Upogebia issaeffi* (Balss), ♂, 51 mm t.l., Tsur Island: (a) rostrum, dorsal view; (b) rostrum, lateral view; (c) antennule; (d) antenna; (e) mandible; (f) second maxilliped; (g) first maxilliped; (h) maxillule; (i) maxilla. Scale: 2 mm.

Telson (Fig. 5h) about as long as sixth abdominal segment and slightly broader than long. Lateral margins a little convergent, postero-lateral angles rounded, posterior margin straight or slightly concave in the middle, median groove distinct but median and lateral carinae unconspicuous.

Antennule (Fig. 4c) first and second peduncular segments of equal length, third segment longer than first and second segments together. Flagella simple.

Antenna (Fig. 4d) second peduncular segment with a spine near distal end of lower margin, scaphocerite rounded without spine, flagellum long.
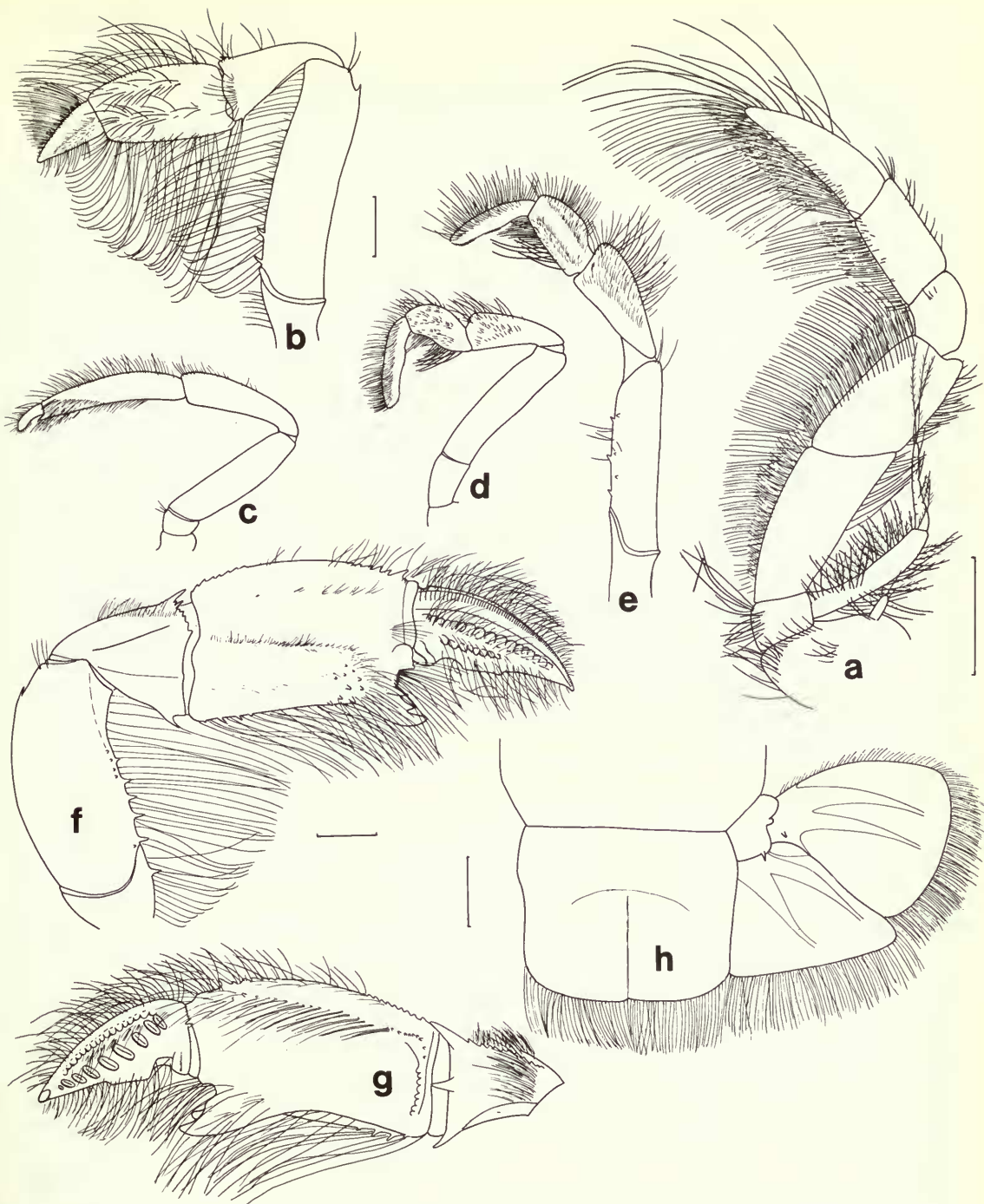
Fig. 5 *Upogebia issaeffi* (Balss), ♂, 51 mm t.l., Tsur Island: (a) third maxilliped; (b) second pereio-pod; (e) third pereiopod; (d) fourth pereiopod; (c) fifth pereiopod; (f) cheliped, outer lateral view; (g) cheliped, inner lateral view; (h) telson and uropods. Scale: 2 mm.

Mandible (Fig. 4e) with small teeth on cutting edge and a larger one basally.

Maxillule (Fig. 4h), *maxilla* (Fig. 4i) apparently showing no differences with those of other *Upogebia* species.

First maxilliped (Fig. 4g) with a fairly large and rounded epipod.

Second maxilliped (Fig. 4f), *third maxilliped* (Fig. 5a) each with a small epipod.

Cheliped (Fig. 3e, f; Fig. 5f, g). Ischium with one spine near distal end of lower margin. Merus with one spine near distal end of upper margin, lower margin with a few small tubercles distally and 3–6 acute spines proximally. Upper margin of carpus with a row of 9–10 small tubercles and a large spine at distal end, on the outside of which 2–5 other small spines are present; a spine near distal end of lower margin of carpus and on the inner side, a third spine on distal margin, about halfway between the upper and the lower ones. Upper margin of propodus with a longitudinal ridge provided with small tubercles proximally and distally with 5–7 larger spines, the distal one large and acute; lower margin with two or three blunt spines proximally, with a large, sharp spine and a few tubercles near the base of fixed finger and another rounded spine near the base of dactylus; fixed finger with a large conical tooth. Dactylus setose, upper margin, in male (Fig. 5f, g), with a longitudinal crest bearing on its outer side a row of fine transverse striae; two longitudinal rows of granules on the outer side of dactylus, a row of granules and another row of oblique ridges on the inner side; cutting edge with two obtuse teeth more or less fused together. Dactylus of cheliped of female (Fig. 3e, f) without row of transverse striae on upper margin but with a row of rounded granules; two additional similar rows of granules present, one on the outer side, the other on inner side of dactylus; oblique ridges also present on inner side but much less conspicuous than in the male.

Second pereiopod (Fig. 5b). Merus with one spine near distal end of upper margin and two spines proximally on lower margin; carpus with one spine on distal end of both upper and lower margin; propodus and dactylus very setose but unarmed.

Third pereiopod (Fig. 5e). Merus with three acute teeth and a few small tubercles on lower margin; carpus and propodus setose, flattened and unarmed; dactylus slender, lower margin finely pectinate.

Fourth pereiopod (Fig. 5d). All segments unarmed, carpus and propodus very setose, lower margin of dactylus finely pectinate.

Fifth pereiopod (Fig. 5c). Propodus slender and setose with a small ventro-distal process; dactylus short.

First pleopod, in female, with two elongated segments.

Second to fifth pleopods large in both sexes; endopod rounded, exopod larger, elliptical.

Uropod (Fig. 5h) broad, as long as telson; protopod with a small spine on inner side; endopod triangular, exopod ovate, each with two longitudinal carinae.

REMARKS. Balss (1913) and de Man (1927) considered the stridulating ridge on the dactylus of the cheliped an important feature for separating *U. issaeffi* from other species. However, both authors had probably examined male specimens in which this ridge is clearly present.

Makarov (1938) studying material from Vladivostok observed a sexual difference in the presence or absence of a stridulating ridge on the dactylus of the cheliped, but Sakai (1968) found no such difference in his material of *U. issaeffi* from Japan. Sakai later considered the identification of his material as incorrect (personal communication).

The present material confirms Makarov's view, the stridulating ridge is here present only in the male. As it is absent in the female, this feature can no longer be used as a distinguishing character of the species.

DISTRIBUTION. Vladivostok (Balss, 1913; Makarov, 1938); Onagawa, Miyagi Pref. (Yokoya, 1939); Tsur Island.

Upogebia spinigera (Smith)

(Fig. 3g, h)

Gebia spinigera Smith, 1871 : 92–93; *Gebia longipollex* Streets, 1871 : 242; *Gebia longipollex* Lockington, 1877 : 108; Lockington, 1878 : 300; *Gebia spinigera* Lockington, 1878 : 300; *Gebia spinigera* Pocock,

1890 : 515; *Upogebia* (*Upogebia*) *longipollex* Borradaile, 1903 : 543; *Upogebia* (*Upogebia*) *spinigera* Borradaile, 1903 : 543; *Upogebia* (*Upogebia*) *longipollex* de Man, 1928 : 23, 35, 39, 51; *Upogebia* (*Upogebia*) *spinigera* de Man, 1928 : 29, 39, 45; *Upogebia* (*Upogebia*) *sturgisae* Boone, 1931 : 161, fig. 11; *Upogebia spinigera* Holthuis, 1952 : 1–11, figs 1, 2.

MATERIAL EXAMINED. Rio Tumbler (Rio Tumbes, Peru ?), 1890, 3 ♂♂, c.l. 10–12 mm, t.l. 31–36 mm; 6 ♀♀ (5 ovigerous), c.l. 9–12 mm, t.l. 29–40 mm.
St Lucia, Peru, 1890, 1 ♂, c.l. 11 mm, t.l. 36 mm.
West Coast of Central America, 1875, 1 ♂, c.l. 10 mm, t.l. 31 mm; 2 ♀♀ (1 ovigerous), c.l. 8 mm, 10 mm, t.l. 26 mm, 30 mm.
Esmeraldas, Ecuador, 1925, 2 ♂♂, c.l. 8 mm, 10 mm, t.l. 25 mm, 31 mm; 2 ♀♀ (1 ovigerous), c.l. 10 mm, 12 mm, t.l. 33 mm, 42 mm.

REMARKS. The present material has been compared with the two specimens of *U. spinigera* described by Holthuis (1952). Table 3 lists the main variations observed.

Table 3 Variations in the material of *U. spinigera* from areas of Central and South America

	Material from Colombia	Material from W. coast of Central America	Material from St Lucia, Peru	Material from Rio Tumbler	Material from Esmeraldas, Ecuador
Number of specimens examined	2	3	1	9	4
Spines on hind margin of cervical groove	present, large	present, large	present, small	present, small	present in 2 specimens
Spines on anterior margin of carpus of pereiopod 2	present, large	present in 2 specimens	present, small	present in 4 specimens	present
Spines on upper margin of carpus and merus of pereiopod 2 and 4	present, small and transparent	absent	absent	absent	absent
Spines on lower margin of merus of pereiopod 3	present	present	present	present	present
Spines on lower margin of merus of pereiopod 4	present	present in 2 specimens	absent	absent	absent
Coxal spines on pereiopods 1–3	present	present on pereiopods 2 and 3	absent	present on pereiopod 3	present

1. Spines on the lateral part of the cervical groove, which are apparent in the material from Colombia, are much smaller in the present material and are missing in two specimens (1 ♂, 1 ♀) from Ecuador.

2. The subterminal spine of the cheliped dactylus is large in the present material and usually larger than that of the specimens from Colombia. In some specimens, the cheliped fixed finger is nearly as long as the dactylus. The cheliped of the material from Colombia was illustrated by Holthuis (1952) and that figure seems to represent the inner side of the appendage. The description of the outer side of the cheliped would correspond in fact to the inner side and *vice versa*. The inner and outer side of the left cheliped of the ovigerous female from the West Coast of Central America are here illustrated (Fig. 3g, h).

3. Both the upper and the lower margin of the carpus of the second pereiopod bear a spine distally. These two spines are large in the Colombia specimens but small or absent in the present material.

4. Small and transparent spines are present on the upper margin of the carpus and merus of the third and fourth pereiopods of the Colombia specimens but are absent in the present material. They are not mentioned either in the original description of the species by Smith (1871) and Holthuis (1952) thought they were overlooked by the former author. Since none of the present specimens has got these spines, they may in fact be absent in Smith's material also.

5. Smith (1871), Boone (1931) and Holthuis (1952) mention that the lower margin of the third and fourth pereiopods is armed with spines whilst Streets (1871) states that these segments are unarmed. In the present material, the lower margin of the merus of the third pereiopod is armed in all specimens but in most of them, the same margin of the fourth pereiopod is unarmed.

6. The presence of coxal spines on the 1st–3rd pereiopod is subject to variation among specimens of the present material. Coxal spines are absent from the fourth pereiopod and are present on the fifth pereiopod in all specimens of the present material as well as that from Colombia.

DISTRIBUTION. Gulf of Fonseca, N.W. Nicaragua; Aseredoras Island, W. Nicaragua (Smith, 1871). Isthmus of Panama (Streets, 1871). Fernando Noronha, N.E. Brazil (Pocock, 1890). Patillo Point, Panama (Boone, 1931). Colombia (Holthuis, 1952). Rio Tumbler; St Lucia, Peru; Esmeraldas, Ecuador.

Acknowledgements

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Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 2. *Palaemonetes (Palaemonetes) varians* (Leach, 1814) and morphological variation

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Synopsis

Five larval and selected post larval stages of *Palaemonetes (Palaemonetes) varians* are described from specimens reared in the laboratory. The rate of larval development and the effect of desynchronization of epigenesis and moulting are discussed. Analysis of morphometric and meristic variation showed that normalizing selection may result in a reduction in variation of larval size distribution at metamorphosis. No such reduction in variation of meristic characters was found. A significant increase in variation of the exopodite of the mouthpart maxilla 2 was recorded from the closely related palaemonid *Palaemon (Palaeander) elegans*. The significance of these results is discussed with reference to the life histories of these shrimps.

Introduction

Palaemonetes (Palaemonetes) varians or the ditch shrimp has been the subject of larval development studies for nearly 140 years (see synopsis of larval data, below). The species is reared easily in the laboratory and this explains, to some extent, its popularity. It was cited as an example of poecilogony (Boas, 1889) or larval polymorphism, until Sollaud (1923a) showed that there were, in fact, different species in northern and southern Europe and in North Africa but that co-existence occurred. Heldt (1953) revived the controversy after examining samples of *P. (P.) varians* from Lake Kelbia in Tunis. In different salinities Heldt reported that '. . . ces larves différentes, issues de ces deux sortes d'œufs, aboutissent . . . à des adultes morphologiquement identiques'. It is, however, not difficult to see why the concept of poecilogony has been applied to this species which does, apparently, show considerable phenotypic variation during larval development and metamorphosis.

A species is often characterized solely by genotype and phenotype in discussions on development. Waddington (1953) developed a further concept – the *epigenotype* which he defined as '. . . the system of causal relations by which the newly fertilized zygote . . . becomes realized as the fully developed adult'. He distinguished between normalizing selection in which phenotypes resulting directly from the presence of an abnormal gene were removed from a population, and stabilizing selection which involved the removal of phenotypes disadvantaged by an unstable epigenetic system.

In this context morphometric and meristic data for larval stages of *Palaemonetes (Palaemonetes) varians* were pooled and analysed to see if epigenetic development in shrimps followed the same pattern reported recently in the development of newts (Bell, 1974, 1975), when a decrease in morphological variation was recorded as the animals approached metamorphosis.

Materials and methods

Rearing

Ovigerous *Palaemonetes (Palaemonetes) varians* (Leach) were collected in July 1976 by handnetting from ditches alongside the estuary at Burnham-on-Crouch, Essex, England (grid reference

TQ 943957). Rearing techniques, similar to those reported previously (Fincham, 1977), were used with the following modifications:

1. The constant temperature room was at 22 ± 0.5 °C; 2 °C below the temperature of the water in the ditches where the collections were made.
2. No mass cultures were set up in order to eliminate the problems of identifying later zoeal stages where moulting history was not available. To ensure, however, that adequate material was available for drawing and assessing morphological variation, eight compartmented trays were set up, containing 144 larvae. At each zoeal stage, 10 larvae, their moults, and a further 10 moults from other individuals, were preserved.
3. All trays and equipment were sterilized with boiling water before use to prevent the accumulation of bacteria.

Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1977 : 284.

Analysis of morphometric and meristic variation

Ten moults and larvae were examined at each stage to determine the range of overall size and also of setal numbers on selected appendages. Mean ($\bar{x}$) and standard deviation ($s.d.$) were calculated for each character at the different stages. To test if there was a genuine increase in variation other than an increase expected from animals of greater size, coefficients of variation ($100 \times s.d./\text{mean}$) were calculated.

Palaemonetes (Palaemonetes) varians (Leach, 1814)

Palaemon varians Leach, 1814.
Palaemon variabilis Bouchard-Chantereaux, 1829.
Palaemonetes varians microgenitor Boas, 1889.
Palaemonetes varians occidentalis Sollaud, 1923.
Palaemonetes (Palaemonetes) varians Holthuis, 1949.

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. *Palaemon variabilis*: Du Cane, 1839 (zoeae 1–4, dorsal, lateral views, plankton, British waters); *Palaemonetes varians*: Boas, 1880 (selected appendages of some zoeae, Danish waters); Mayer, 1880 (zoeae 1–4, post larvae, some dorsal, lateral views, appendages, Mediterranean waters); Weldon, 1890 (zoeae 1–3/4, no figures, laboratory reared, British waters); Allen, 1893a, b (development of green gland, shell gland and body cavity in larvae, laboratory reared, British waters); *P. v. microgenitor*: Sollaud, 1914 (egg size, abbreviated development and order of appendage appearance); Sollaud, 1919 (effect of environment on duration of larval life, French waters); Sollaud, 1921 (phototropism before and after metamorphosis); *P. varians*: Gurney, 1923 (breeding period, British waters); *P. v. occidentalis*: Sollaud, 1923a (zoeae 1–5, post larva, French waters); 1923b (larval polymorphism); *P. varians*: Gurney, 1924 (zoeae 1–5, post larvae, plankton and laboratory reared, British waters); Sollaud, 1930 (larval polymorphism); Heldt, 1953 (larval polymorphism); Weygoldt, 1961 (embryology, German waters); Le Roux, 1970 (effect of environment on number of larval stages, French waters).

In the following short descriptions of the key characters of the larval stages, all setal counts have been omitted but these are recorded in Table 1.

DESCRIPTION OF LARVAL STAGES
Key characters are printed in *italic type*.

ZOEA 1 (Fig. 1) 3·8 mm (3·5–4·1 mm)
    Head (Figs 1a, b): *eyes sessile*.
    Carapace (Figs 1a, b): *without spines*, rostrum straight, tapering distally, ventral margin with minute retrorse teeth distally.
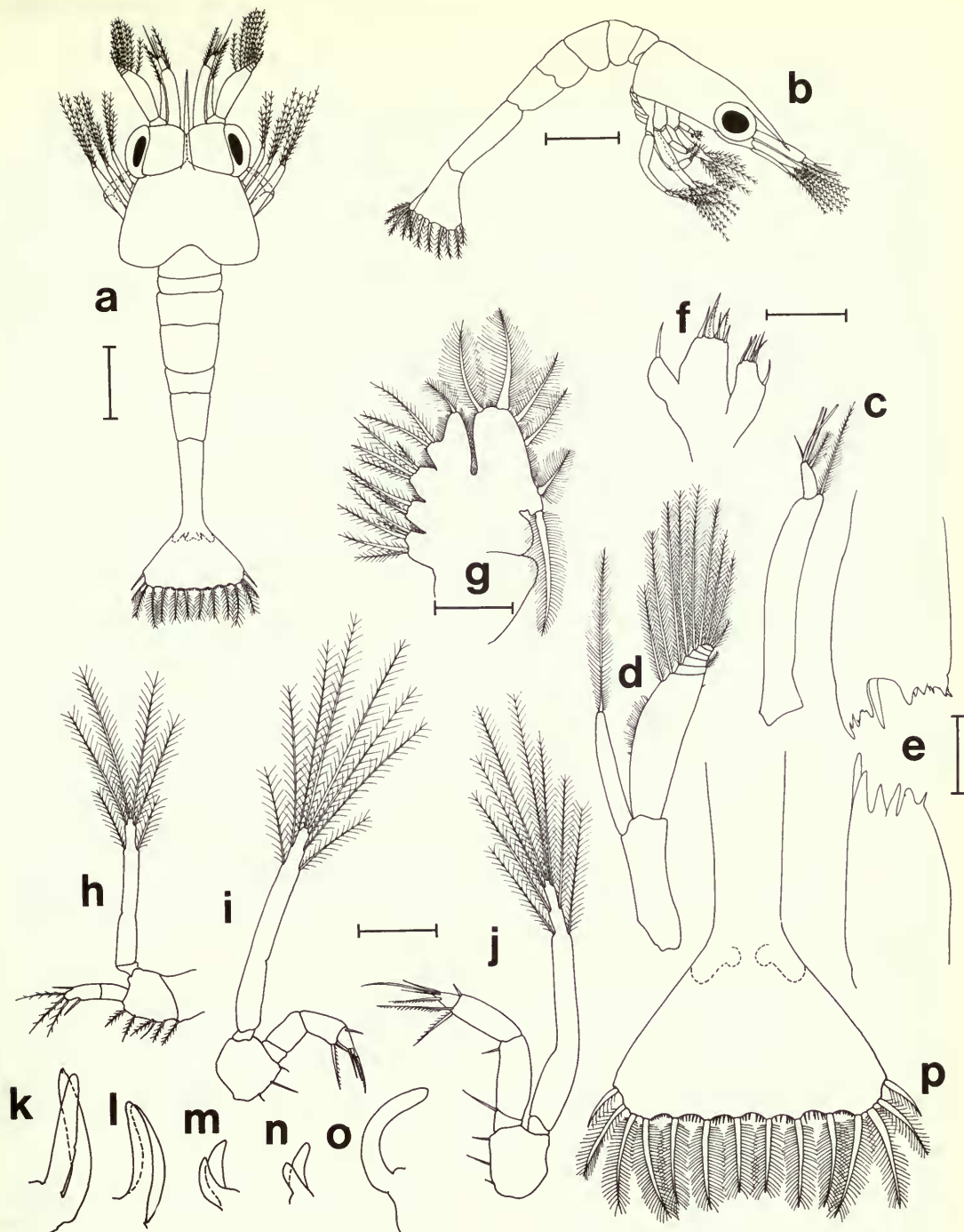
Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; g = 0·1 mm; e, f = 0·05 mm.

Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment with three aesthetascs distally, one wider than the others.*

Antenna 2 (Fig. 1d): exopodite as a broad lamina divided into 5 short segments distally.

Mandibles (Fig. 1e): asymmetrical.

Maxillipeds 1–3 (Figs 1h–j): with natatory exopodites.

Pereiopods 1–4 (Figs 1k–n): *rudimentary, biramous.*

Pereiopod 5 (Fig. 1o): *rudimentary, uniramous.*

Abdomen (Figs 1a, b): somite 6 continuous with telson; pairs of ventral buds on somites 1–5 indicate position of pleopods.

Telson (Fig. 1p): fans out distally, posterior margin bears 7+7 plumose spines, with minute spines between four innermost pairs of spines.

ZOEA 2 (Fig. 2) 4·2 mm (4·0–4·5 mm)

Head (Figs 2a, b): *eyes 'stalked'.*

Carapace (Figs 2a, b): one *dorso-medial* and a pair of supraorbital spines all bent forward with small retrorse teeth ventrally, rostrum without teeth.

Antenna 1 (Fig. 2c): distal segment of peduncle bearing first segment of internal flagellum, external flagellum now with four distal aesthetascs, two wider than others.

Pereiopods 1, 2 (Figs 2k, l): *developed, with natatory exopodites.*

Pereiopods 3, 4 (Figs 2m, n): *rudimentary, biramous.*

Pereiopod 5 (Fig. 2o): *developed, uniramous* (without exopodite).

Abdomen (Figs 2a, b): *somite 5 with posterior margin produced into a pair of spines.*

Telson (Fig. 2p): *developing uropods visible beneath exoskeleton;* in central group of small spines, one pair longer than the others.

ZOEA 3 (Fig. 3) 4·6 mm (4·3–4·8 mm)

Carapace (Figs 3a, b): *two dorso-medial spines* and a small frontolateral spine at edge of carapace beneath the eyes, former with retrorse teeth ventrally.

Antenna 1 (Fig. 3c): external flagellum with three distal aesthetascs; conspicuous spine medially and stylocerite forming on proximal external margin of first segment of peduncle.

Antenna 2 (Fig. 3d): exopodite with distal part divided into only three short segments.

Pereiopods 1, 2 (Figs 3k, l): endopodite with internal distal margin of propodus produced slightly forward (will become fixed finger of chela).

Pereiopod 3 (Fig. 3m): *developed, with natatory exopodite.*

Abdomen (Figs 3a, b): *somite six divided from telson by suture.*

Telson (Fig. 3p): narrower, but still broader distally, outer pair of spines on posterior margin considerably reduced: *uropod endopodite with no marginal setae; exopodite with marginal, plumose setae.*

ZOEA 4 (Figs 4, 5) 5·2 mm (4·9–5·5 mm)

Carapace (Figs 4a, b): *three dorso-medial spines* with small retrorse teeth ventrally.

Antenna 2 (Fig. 5b): endopodite with 3-segmented flagellum (usually), as long as scaphocerite, distal part of exopodite divided into two, one or no short segments.

Pereiopods 1, 2 (Figs 5f, g): *endopodite with internal distal margin of propodus* produced forward to over half length of dactylus (excluding terminal setae).

Pereiopod 4 (Fig. 5i): developed with natatory exopodite.

Abdomen (Figs 4b, 5k–o): pleopods on somites 1–5 rudimentary, biramous.

Telson (Fig. 5p): a little broader distally than proximally, posterior margin weakly concave with *5+5 large spines* and with 2 smaller spines on latero-distal margin; *endopodite and exopodite of uropod both with marginal plumose setae.*

ZOEA 5 (Figs 6, 7, 8) 5·8 mm (5·5–6·0 mm)

Carapace (Fig. 6b): *setae in angles of two anterior dorso-medial spines.*

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* In a previous paper (Fincham, 1977) two aesthetascs were recorded distally on the flagellar segment of antenna 1 in zoea 1 of *Palaemon (Palaeander) elegans.* Examination of more material, including specimens from the Marmara Sea, Turkey, indicate that three aesthetascs is the usual number (one wide, two narrow).
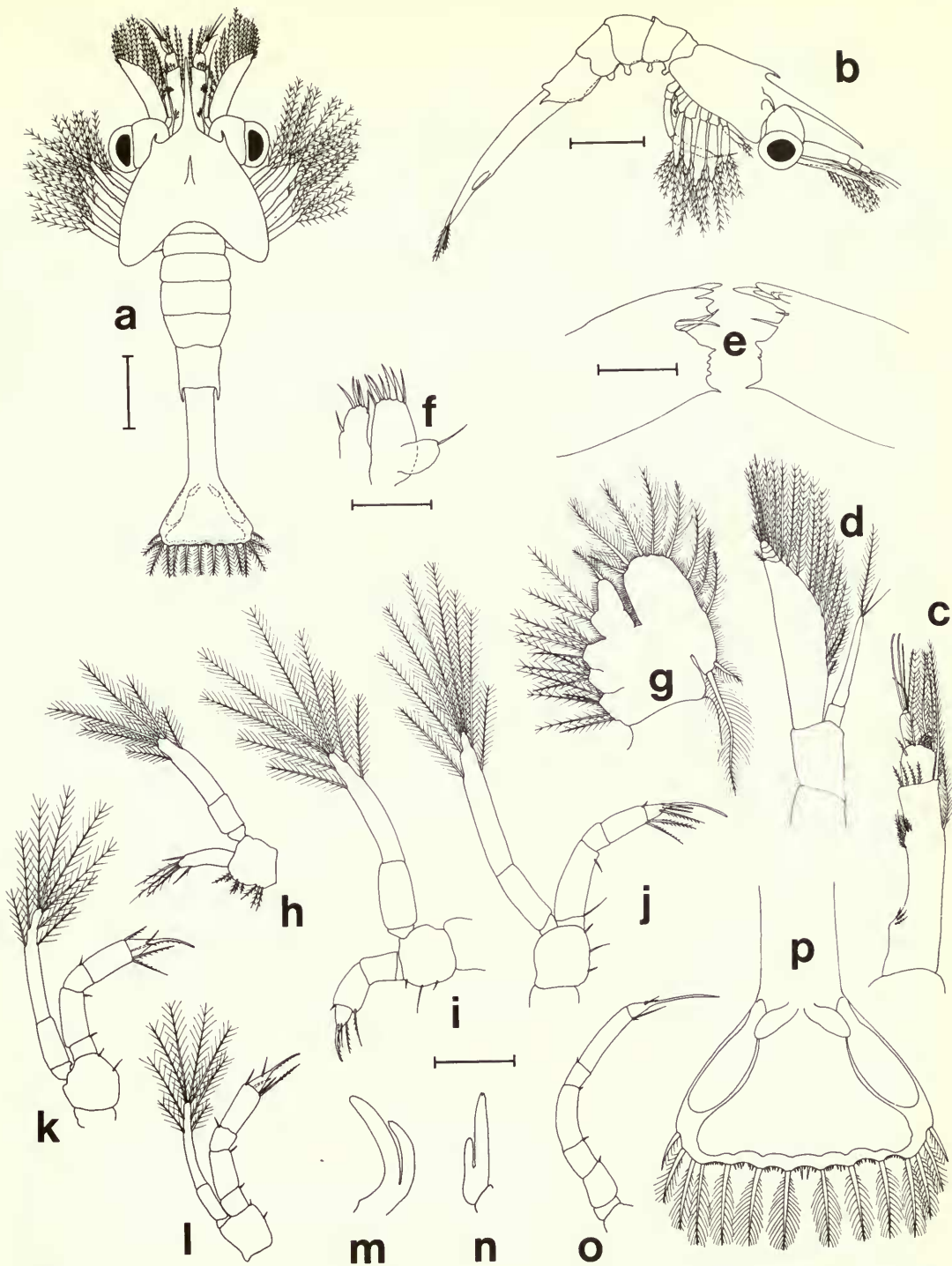
Fig. 2   Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; f, g = 0·1 mm; e = 0·05 mm.

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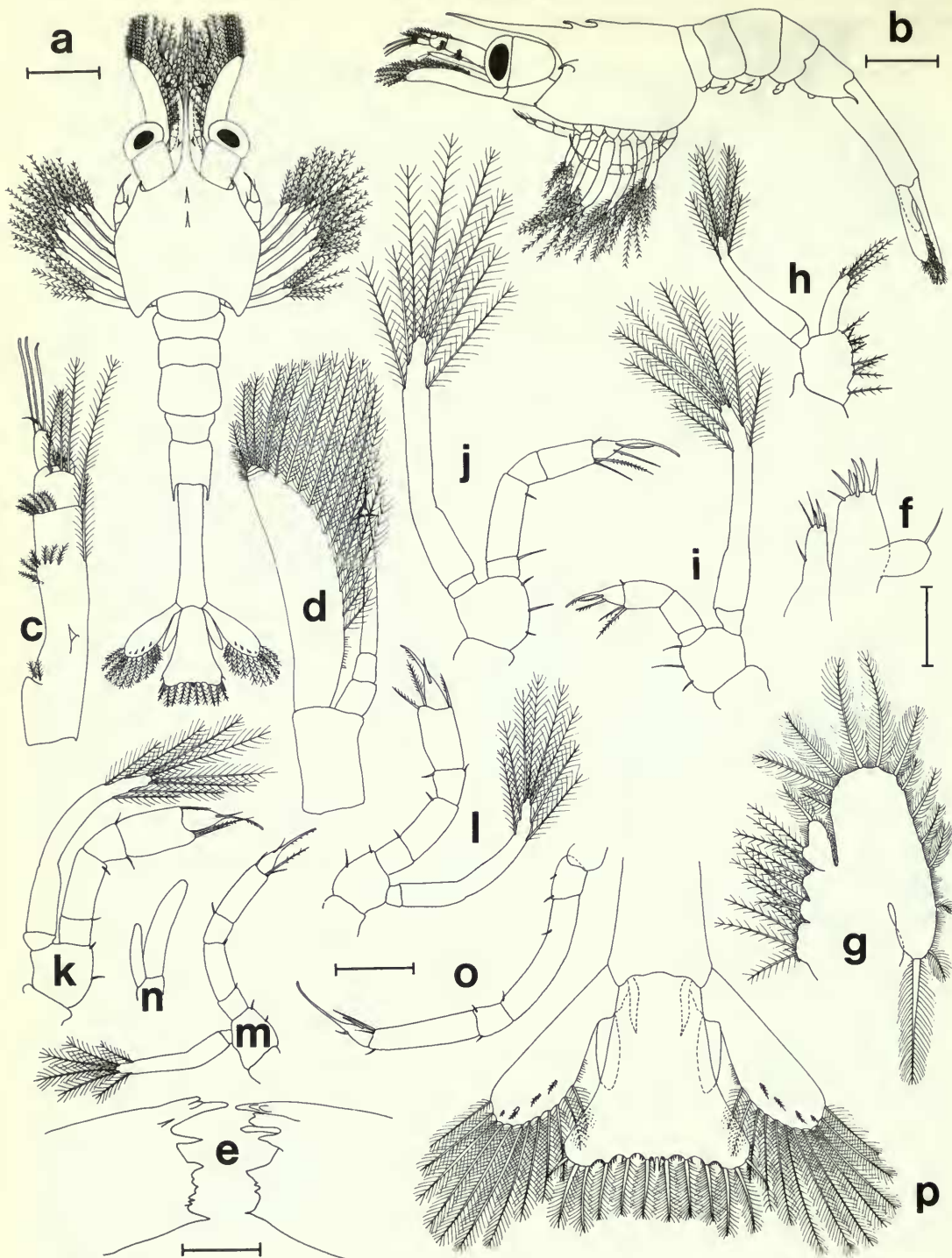
Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; f, g = 0·1 mm; e = 0·05 mm.

Fig. 4 Zoea 4: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b=0·5 mm; c=0·05 mm; d, e=0·1 mm.

Fig. 5 Zoea 4: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) pleopod 1; (l) pleopod 2; (m) pleopod 3; (n) pleopod 4; (o) pleopod 5; (p) telson. Bar scale: a–p = 0·2 mm.

Fig. 6 Zoea 5: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2.
Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.
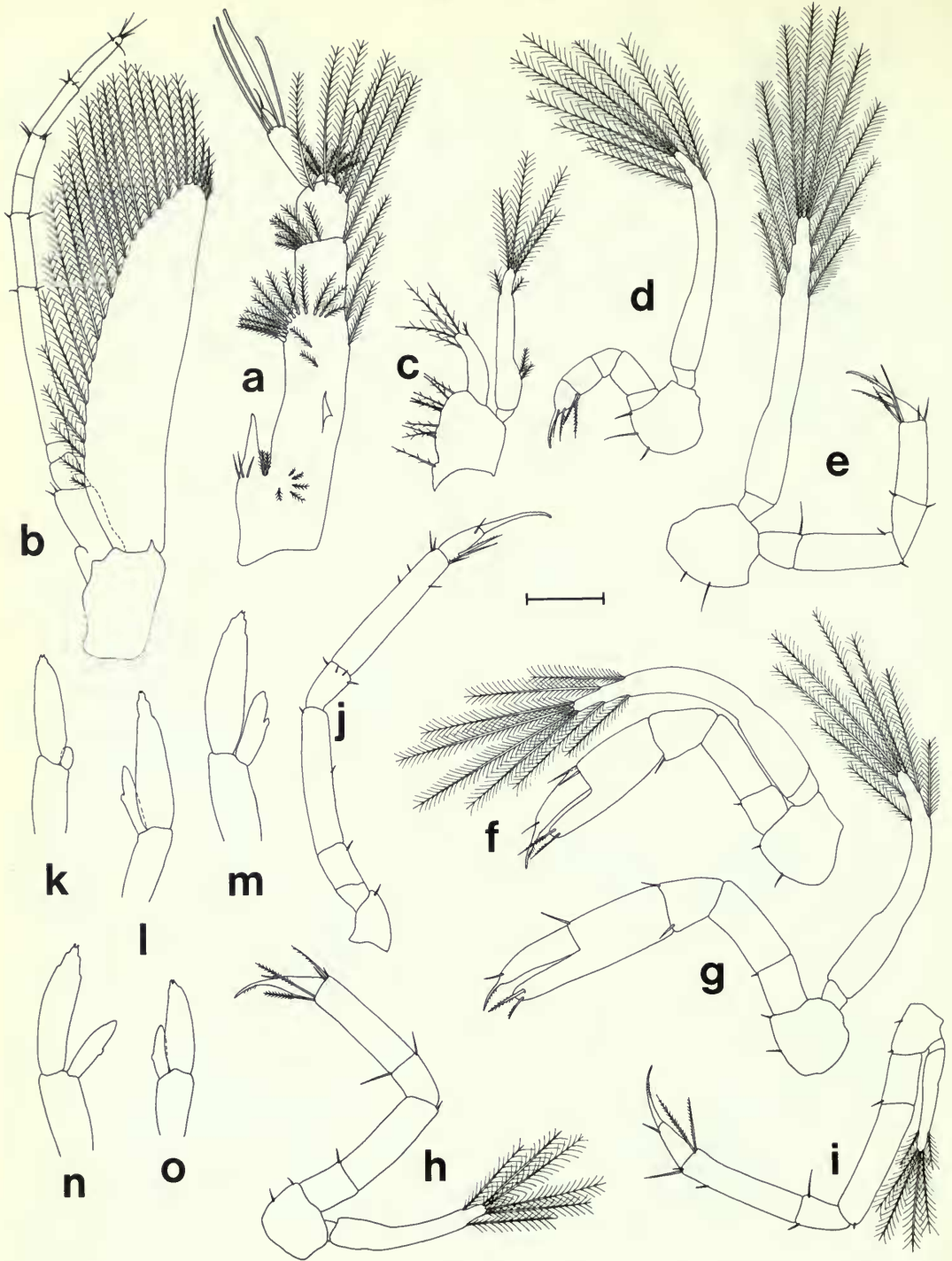
Fig. 7 Zoea 5: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) pleopod 1; (l) pleopod 2; (m) pleopod 3; (n) pleopod 4; (o) pleopod 5. Bar scale: a–o = 0·2 mm.
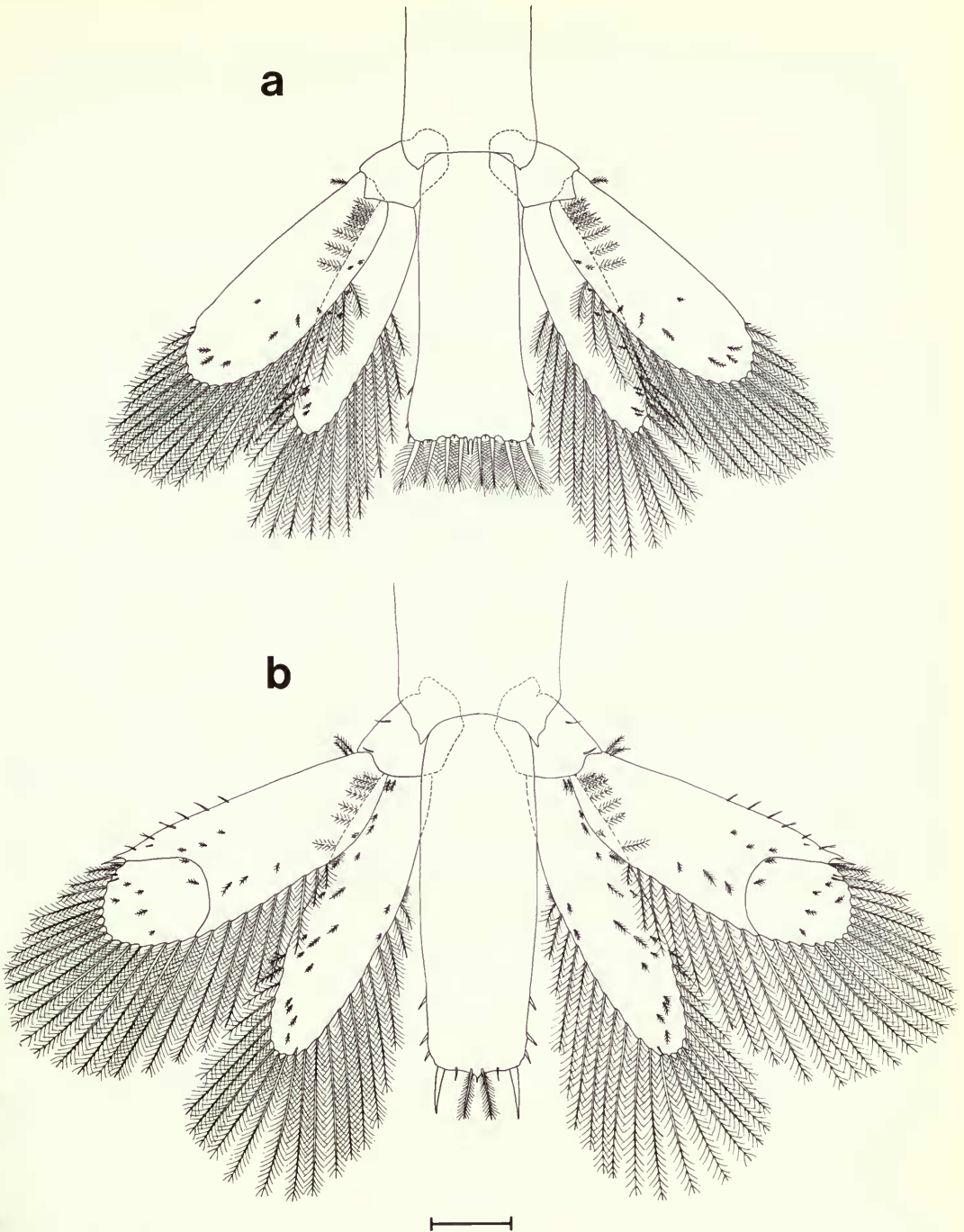
Fig. 8   Zoea 5: (a) telson.   Post larva 1: (b) telson. Bar scale: a, b=0·2 mm.

Antenna (Fig. 7a): circlet of plumose setae developed dorsally on first segment of peduncle, indicating position of statocyst.

Antenna 2 (Fig. 7b): *increase in number of segments of endopodite flagellum, just longer than scaphocerite.*

Pereiopods 1, 2 (Figs 7f, g): *endopodite with immovable finger of propodus produced forward to almost length of dactylus* (excluding terminal setae).

Abdomen (Figs 6a, b, 7k–o): *pleopods with rudimentary setae on margins of exopodite, endopodite of pleopods 2–5 with rudiment of appendix interna* (*stylamblys*).

Telson (Fig. 8a): further narrowing distally, posterior margin still weakly concave with *4 + 4 large spines* and with 3 smaller spines on latero-distal margin.

POST LARVA 1 (Figs 8, 9, 10, 11) 6·4 mm (6·0–7·0 mm)

Carapace (Figs 9a, b): *rostrum with 3–6 dorsal and 1–2 ventral spines, supraorbital spines missing.*

Antenna 1 (Fig. 10a): internal flagellum of 2–4 segments and usually an additional group of 2 aesthetascs distally on first segment of external flagellum.

Antenna 2 (Fig. 10b): endopodite with flagellum multisegmented, more than twice length of scaphocerite.

Mandible (Fig. 9c): *divided into pars incisiva and pars molaris*, lacinia mobilis no longer present.

Maxilliped 2 (Fig. 10d): endopodite with dactylus, propodus and merus flattened, *exopodite shortened and with no setae.*

Maxilliped 3 (Fig. 10e): endopodite dactylus shortened, *exopodite reduced* to less than half length of endopodite, and without setae.

Pereiopods 1, 2 (Figs 10f, g): ischium, merus and carpus lengthened, *exopodite reduced* to about the length of the ischium of endopodite and with no setae.

Pereiopods 3, 4 (Figs 10h, i): endopodite dactylus evenly tapering distally, propodus, carpus and merus lengthened, *exopodite reduced*, extending halfway along ischium of endopodite, setae generally absent but with a few small, plumose setae sometimes present.

Pereipod 5 (Fig. 10j): dactylus evenly tapering distally, other segments of endopodite lengthened.

Pleopod 1 (Fig. 11a): ratio of endopodite to exopodite 1 : 4, *endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.*

Pleopods 2–5 (Figs 11b–e): endopodite over half length of exopodite, both with long, marginal, plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hooks.

Telson (Fig. 8b): *narrow, posterior margin convex with a short, median point, 1 + 1 large spines* and two pairs of setae on the posterior margin, one long and plumose, other simple, also 3 smaller spines on latero-distal margin.

POST LARVA 2 (Fig. 11) 7·2 mm (6·8–7·9 mm)

Maxillipeds, 2, 3: exopodites lengthen and regain marginal, plumose setae.

Pereiopods 1–4: exopodites continue to diminish.

Telson (Fig. 11g): extremely narrow, median point on posterior margin more pronounced.

POST LARVA 5 (Fig. 11)

Antenna 1 (Fig. 11h): development of accessory flagellum on external flagellum.

Antenna 2 (Fig. 11i): morphogenesis of exopodite complete – truncated distally, edges almost parallel.

Discussion

Results of the present study are summarized in Tables 1 and 2. The temporary regression of the exopodites of maxillipeds 2 and 3, in which shortening occurred with loss of marginal plumose setae and also the disappearance of the natatory exopodites of pereiopods 1–4, paralleled exactly the changes at first post larval moult (PL 1) for *Palaemon* (*Palaeander*) *elegans* (Fincham, 1977). The relatively abbreviated development of *Palaemonetes* (*Palaemonetes*) *varians* compared with the 6–9 stages of *Palaemon* (*Palaeander*) *elegans* is accompanied by a change in the sequence of
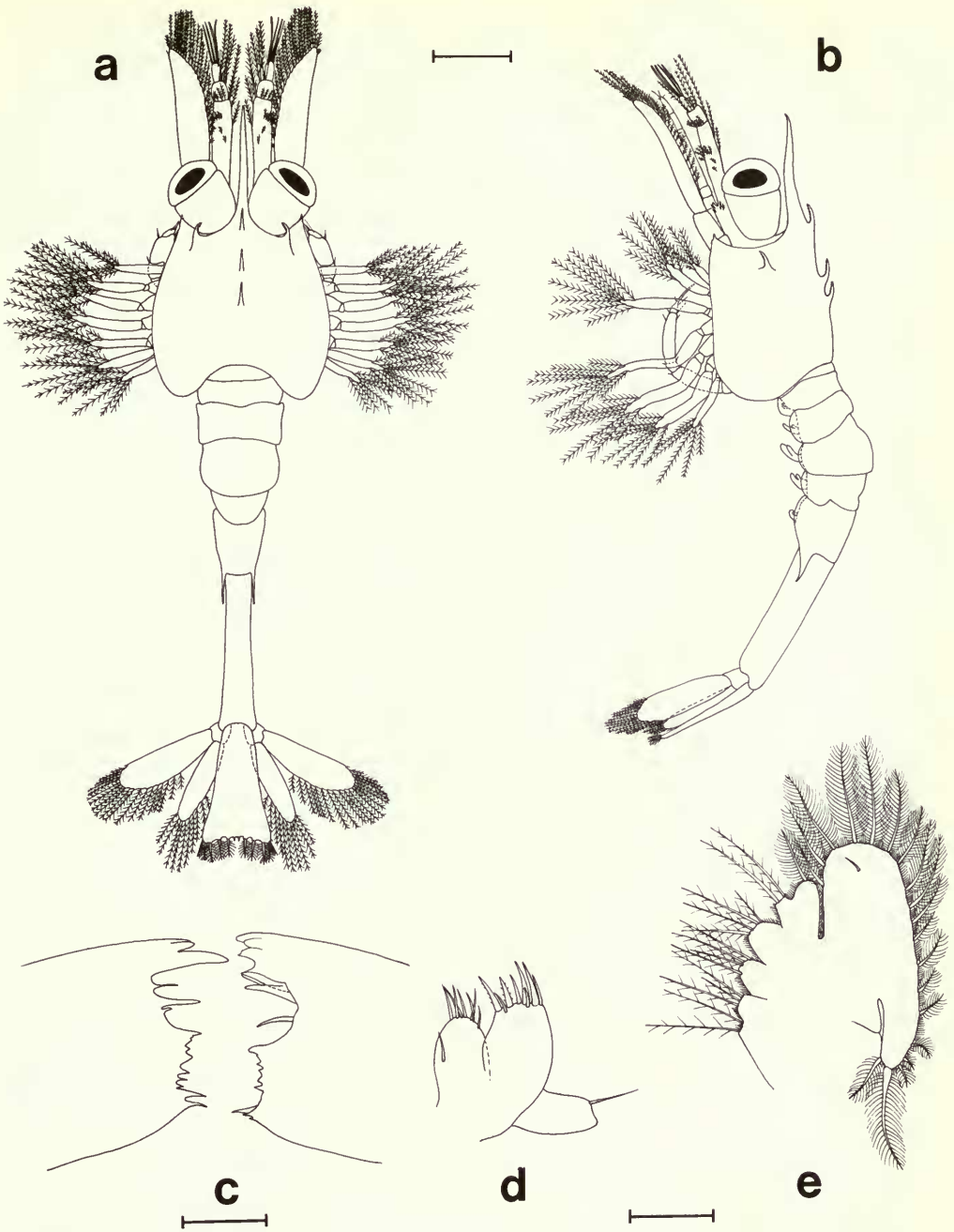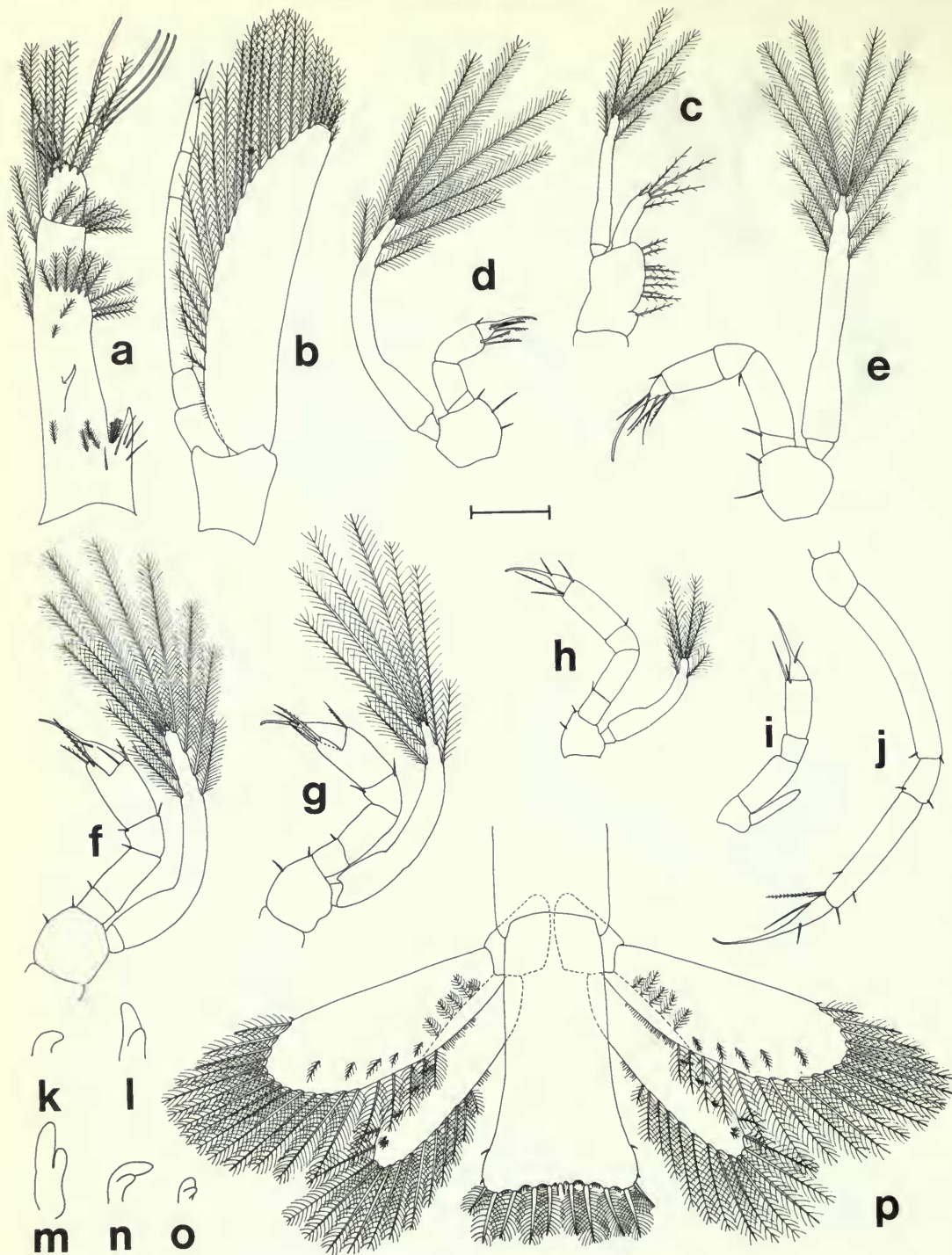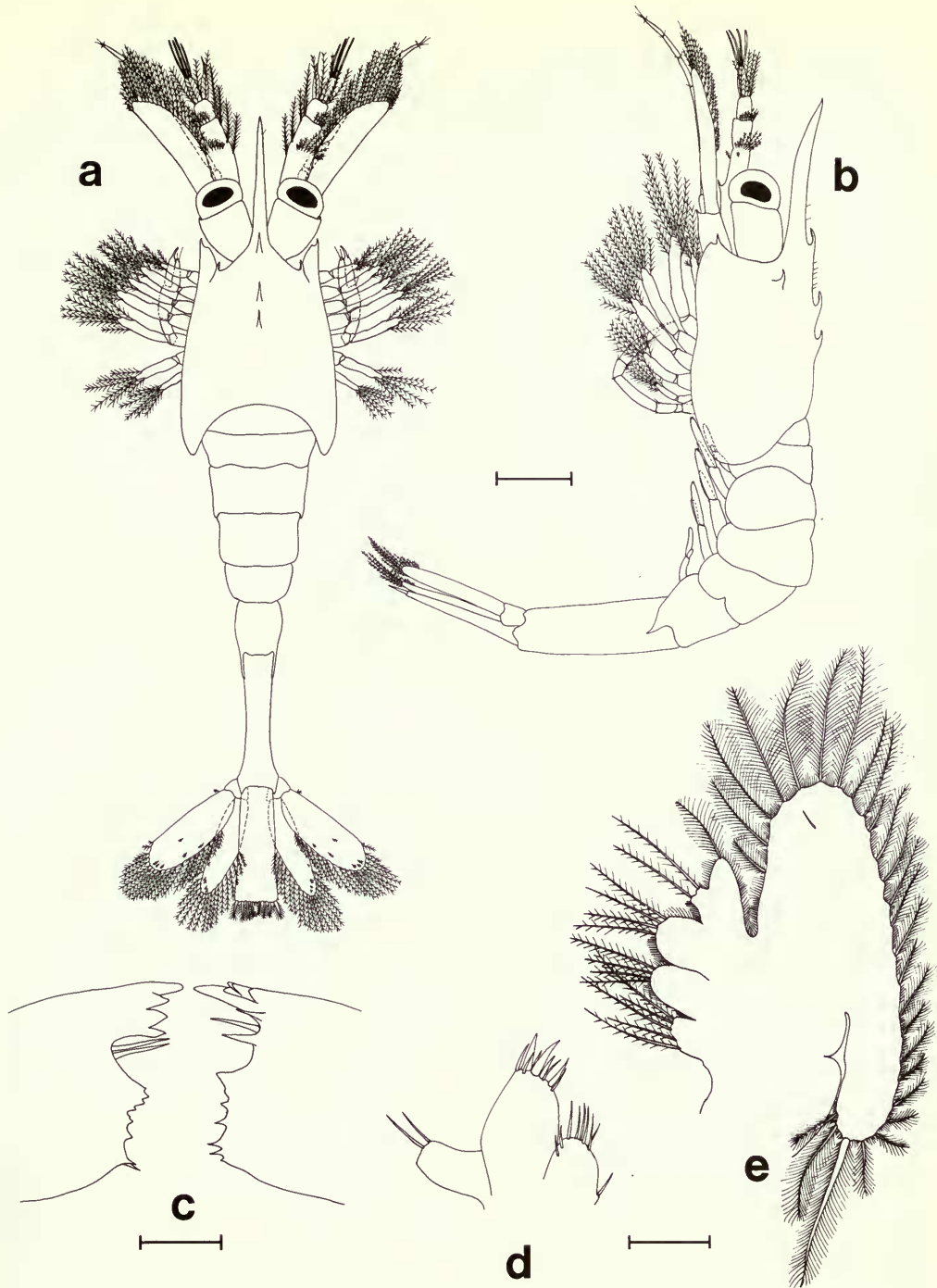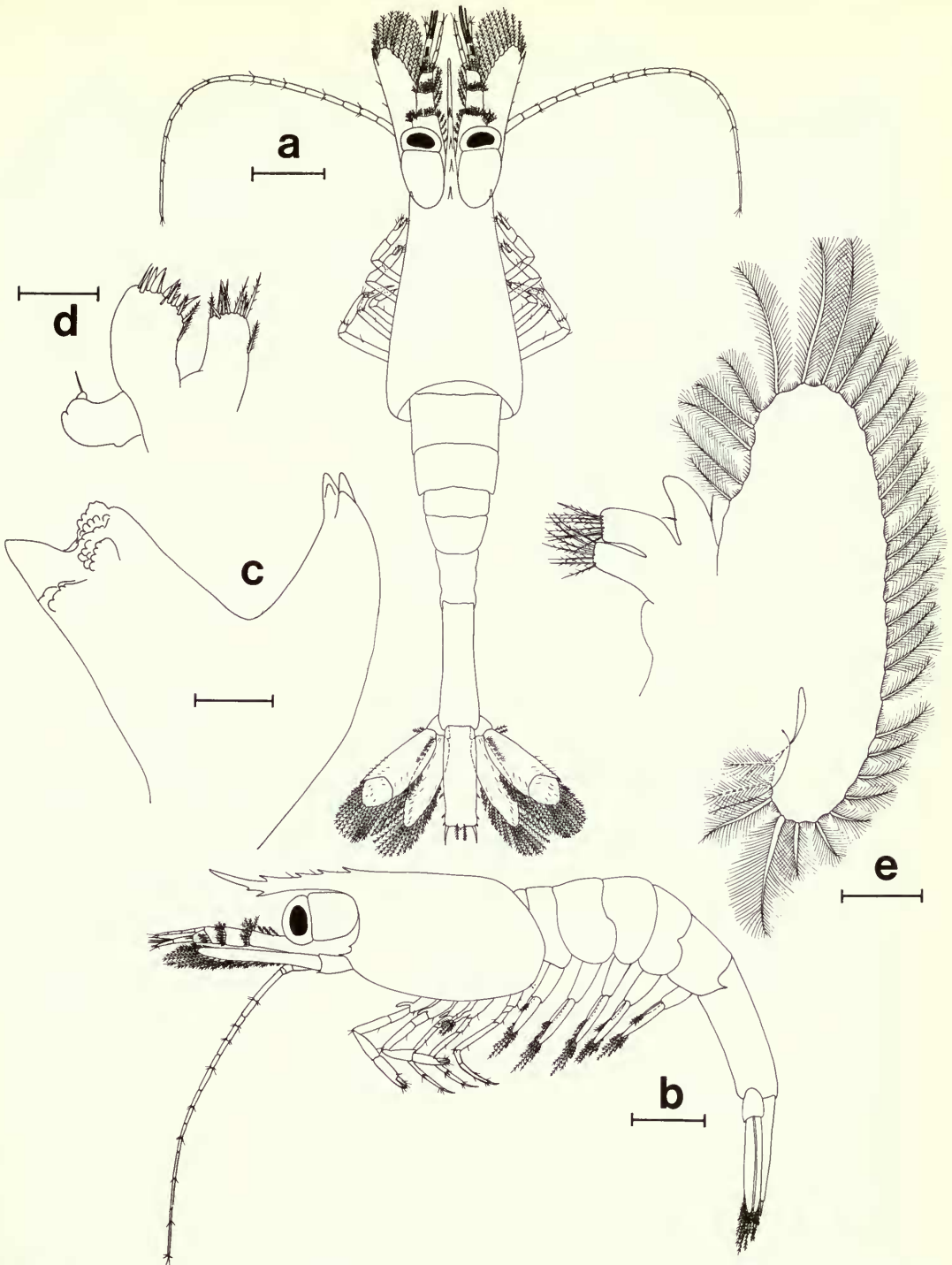
Fig. 9   Post larva 1: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2.
Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.
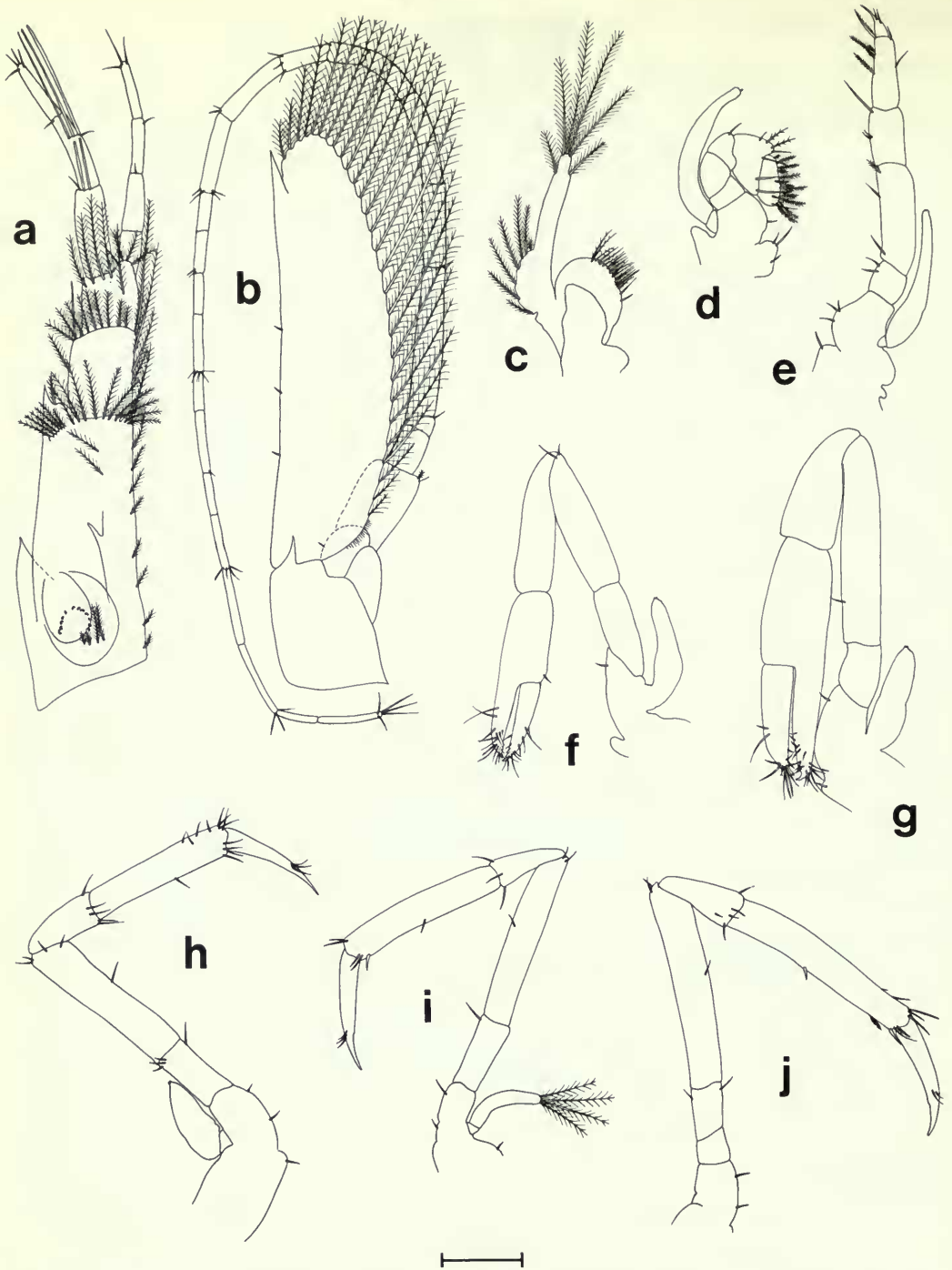
Fig. 10   Post larva 1: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5. Bar scale: a–j = 0·2 mm.
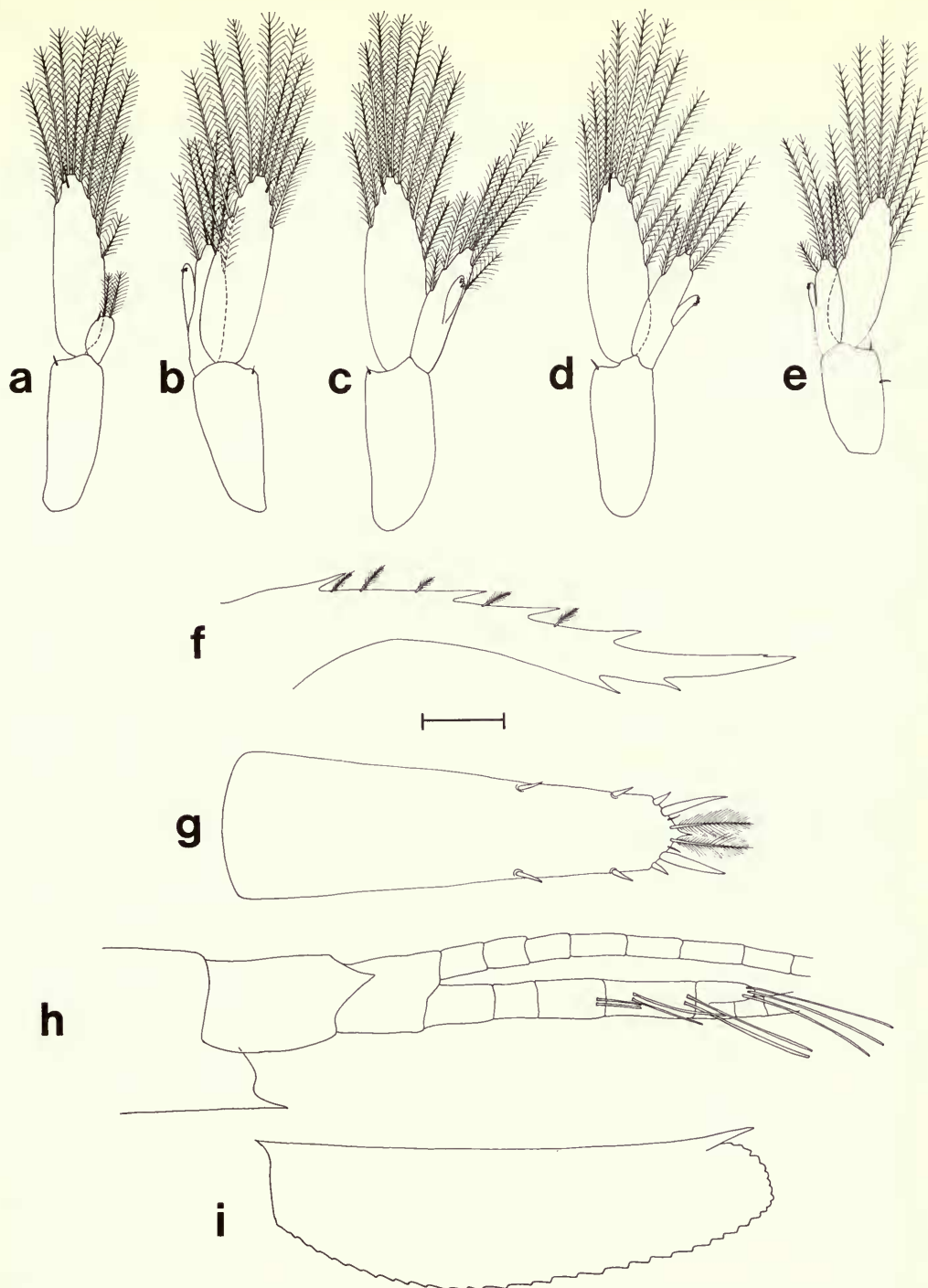
Fig. 11 Post larva 1: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5. Post larva 2: (f) rostrum; (g) telson. Post larva 5: (h) antenna 1 (aesthetascs drawn, setae omitted); (i) antenna 2 (setae omitted.) Bar scale: a–i = 0·2 mm.

Table 1 Larval development and range of morphological variation in *Palaemonetes* (*Palaemonetes*) *varians*

		Zoea/Stage					
		1	2	3	4	5	PL1
Length (mm)	Mean	3·8	4·2	4·6	5·2	5·8	6·4
	Range	(3·5–4·1)	(4·0–4·5)	(4·3–4·8)	(4·9–5·5)	(5·5–6·0)	(6·0–7·0)
Carapace							
No. of dorsal spines		0	1	2	3	3	3–5
No. of ventral rostral spines		0	0	0	0	0	1–2
Supraorbital spines +/−		−	+	+	+	+	−
No. of antero-lateral spines		0	0	1	1	1	2
Rostrum tip – Ventral retrose hooks +/−		+	−	−	−	−	−
Antenna 1							
No. of groups, aesthetascs		1	1	1	1	1	1–2
Stylocerite +/−		−	+/−	+	+	+	+
Statocyst +/−		−	−	−	−	−	+
Medial spine +/−		−	−	+	+	+	+
No. of segments, flagellum – Internal		0	1	1	1	1	2–4
External		1	1	1	1	2	3–4
Accessory flagellum +/−		−	−	−	−	−	−
Antenna 2							
Endopodite – No. of segments		1	2	3	5	7–10	16–28
c.f. Length of scaphocerite		0·50	0·50	0·66–0·75	1·0–1·25	1·50–1·75	2·0+
Exopodite – No. of distal segments		5	4	2	0	0	0
No. of plumose setae		9	16–18	18–21	21–23	23–26	24–32
External spine +/−		−	−	−	−	−	+
Mandible – Lacinia mobilis +/−		+	+	+	+	+	−
Maxilla 1							
No. of endite setae – Coxa		5–6	6	6–7	6–8	8–9	11
Basis		5–6	7	7–8	8–9	9	14
Maxilla 2							
No. of endite setae – Coxa		4–5	4–5	5	5–6	5	2
Basis 1		3	3	3	3–4	4–5	8
Basis 2		4	4	4	4	4–5	7
Endopodite		3–4	3–4	3	3	3–4	0
No. of plumose setae Exopodite		5–6	10–12	12–15	19–21	26–29	29–35
Maxilliped 1							
No. of setae on internal margin – Basis		5	8	9	9	9	19
Exopodite – No. of setae – Lateral (proximal)		0	0	0	0	2	7

pereiopod development. Limb buds were present in zoea 1, and at zoea 2 only pereiopods 3 and 4 were still rudimentary. At zoea 3 pereiopod 3 was fully developed together with a functional natatory exopodite, and at zoea 4 pereiopod 4 was fully formed also. The change to adult-type mandible (Fig. 9c) is made at the moult to PL 1 and is associated with the change in diet necessitated by the major behavioural change from a planktonic to largely benthic existence.

Table 1 *(cont.)*

		Zoea/Stage					
		1	2	3	4	5	PL1
Length (mm)	Mean	3·8	4·2	4·6	5·2	5·8	6·4
	Range	(3·5– 4·1)	(4·0– 4·5)	(4·3– 4·8)	(4·9– 5·5)	(5·5– 6·0)	(6·0– 7·0)
Maxilliped 2							
Endopodite – No. of segments		4	4	4	4	5	5
Exopodite +/−		+	+	+	+	+	+
Setae +/−		+	+	+	+	+	−
Maxilliped 3							
Endopodite – No. of segments		4	5	5	5	5	5
Exopodite +/−		+	+	+	+	+	+
Setae +/−		+	+	+	+	+	−
Pereiopods 1 & 2 +/−		R+	+	+	+	+	+
Biramous +/−		+	+	+	+	+	R+
Endopodite – Propodus fixed finger +/−		−	−	+	+	+	+
Pereiopod 3 +/−		R+	R+	+	+	+	+
Biramous +/−		+	+	+	+	+	R+
Pereiopod 4 +/−		R+	R+	R+	+	+	+
Biramous +/−		+	+	+	+	+	R+
Pereiopod 5 +/−		R+	+	+	+	+	+
Biramous +/−		−	−	−	−	−	−
Abdomen							
Somite 5 – Lateral spines +/−		−	+	+	+	+	+/−
Somite 6 – Continuous with telson +/−		+	+	−	−	−	−
Pleopods +/−		R+	R+	R+	R+	+	+
Fringing setae		−	−	−	−	−	+
Appendix interna 2–5 +/−		−	−	−	−	R+	+
Telson							
Posterior margin concave (−) convex (+)		+/−	+/−	−	−	+/−	+
Spine formula		7+7	7+7	6+6	5+5	4+4	1+1 (PL2:2+2)
Small spines +/−		+	+	+	+	+	−
No. of pairs – Lateral spines		0	0	1	2	3	3 (PL2:2)
Uropods +/−		−	−	+	+	+	+
Long plumose setae – Endopodite				0	10–14	16–18	18–22
Exopodite				11–13	17–20	20–23	21–26

Rate of epigenesis

In order to transform zoea 1 to a miniature adult or juvenile, a definite sequence of morpho-genetic and associated biochemical and physiological development and adaptation has to be completed. If larvae moult 'early', less of the developmental sequence is completed. Epigenesis in Crustacea is a continuous sequential process despite being apparently arrested at morphological

Table 2 Analysis of morphometric variation (a) in overall size in mm and meristic variation in the number of expodite plumose setae of (b) antenna 2, (c) uropod and (d) maxilla 2 during the development to post larva of *Palaemonetes* (*Palaemonetes*) *varians* (n.d. = not developed; see Materials and Methods for statistical abbreviations)

		Stage					
		1	2	3	4	5	PL1
a	$\bar{x}$	3·82	4·24	4·55	5·19	5·77	6·41
	s.d.	0·21	0·18	0·14	0·17	0·18	0·32
	c. of v.	5·49	4·19	3·15	3·20	3·06	5·01
b	$\bar{x}$	9	17·0	19·5	22·3	25·2	27·4
	s.d.	0	0·82	1·08	0·67	0·92	2·37
	c. of v.	0	4·80	5·54	3·03	3·65	8·64
c	$\bar{x}$	n.d.	n.d.	12·2	18·6	21·6	23·7
	s.d.	–	–	0·79	0·97	1·26	1·64
	c. of v.	–	–	6·47	5·19	5·86	6·90
d	$\bar{x}$	5·6	10·6	13·4	19·7	27·5	31·7
	s.d.	0·52	0·70	1·17	0·67	1·35	2·06
	c. of v.	9·22	6·60	8·76	3·43	4·92	6·49

stages during the intermoult period of ecdysis. Moulting and epigenesis become desynchronized after the first few zoeal stages. This results in morphological variation in larvae with similar moulting histories (in terms of the number of moults), but in which epigenesis may have been proceeding at different rates. Also, the longer an intermoult period lasts so the next stage is more advanced. Superimposed on this is normal intraspecific variation including variation within a brood from one female.

The separate control of development and moulting is adaptive in that larvae are able to cope with sub-optimal conditions by slowing epigenetic development while continuing to moult. The animal is constrained physically by the rigid exoskeleton and moulting is essential to permit an increase in size. Epigenesis may be delayed, but moulting continues and may not always be accompanied by an increase in size. This results in so called 'repeat' moults (Rochanaburanon & Williamson, 1976; Fincham, 1977). As moulting uses up energy and increases vulnerability until the exoskeleton hardens after ecdysis, it is reasonable to assume that moulting has functions other than merely allowing an increase in size. It is not clear why moulting does not cease in poor conditions. It has been shown, from analysis of whole larvae, however, that organic substances including proteins and amino acids and inorganic ions such as K^+, Ca^{++}, Mg^{++} rise in concentration during premoult and decrease at postmoult, and the reverse occurs in concentrations for Na^+ and Cl^- (Torres, 1973; Charmantier, 1977). The periodic release into the haemolymph of these molecules and ions may be necessary to make them available for stages in the epigenetic sequence. This leads to the development of the new structures, which in the larval stages is continuous even if, in response to poor external environmental conditions, the rate is slow.

Meristic and morphological variation (Tables 1, 2)

In a study of morphological variation in natural populations of the smooth newt, Bell (1974) found that animals of average length survive in conditions of stress such as the critical period of metamorphosis. As the total length increases, therefore, so variation in this character would be expected to decrease. Waddington (1948) pointed out that development is canalized with a strong tendency for the adult to conform to the morphological norm within prescribed limits. In a later paper Waddington (1953) discussed the inflexibility of the biochemical pathways controlled by the epigenotype during development. These pathways lead inevitably to a similar end result, to a

large extent regardless of unfavourable influences from the genotype or the environment. Bell (1974) stated that '. . . the epigenetic system is so constructed that individuals which are originally quite different tend to become more similar as their development proceeds'.

Both developmental canalization (stabilizing selection) and natural (normalizing) selection have the effect of reducing variation. Bell (1974), however, was able to eliminate the former in accounting for the decrease in variation in the two morphometric characters (standard length and head width) as the larvae approached metamorphosis. This was achieved by keeping laboratory populations of newt larvae in near optimum conditions. Overall survival was better than for equivalent wild populations since external natural selection was less intense in the laboratory, whereas the internal stabilizing selection would have been the same in both wild and laboratory populations. This reduction in variation of larval size distribution was reversed in post-metamorphosis newts and was corroborated by dentition data (Bell, 1975). The obvious advantage of such selective processes is that only typical representatives of the species survive metamorphosis.

The present morphometric results (Table 2) parallel the findings of Bell and show that there is a significant reduction ($P < 0.05$) in variation or normalizing selection of larval size as *Palaemonetes* (*Palaemonetes*) *varians* approached metamorphosis, with a tendency to increase in post-metamorphosis shrimps. All other correlations of meristic characters were not significant and there was no tendency for individuals to become more similar as suggested by Bell (1974). Particular attention was given to the shrimp mouthparts since Bell (1975) found newt dentition data corroborated his morphometric findings. To compare these results of *Palaemonetes* (*Palaemonetes*) *varians*, data (Fincham, 1977) from a closely related palaemonid *Palaemon* (*Palaeander*) *elegans* was analysed to test for changes in variation as metamorphosis approached. In the latter species even morphometric data were not significant. There was, however, a significant *increase* in variation of the plumose setae on the exopodite of mouthpart maxilla 2 in the pre-metamorphosis stages ($P < 0.01$). Clearly there is no simple, general correlation between larval variation and the approach of metamorphosis.

Some similarities in habitat exist between the newt and *Palaemonetes* (*Palaemonetes*) *varians*: both live in shallow ephemeral bodies of water and both showed a reduction in overall length variation. A rigorous selection process may be necessary to ensure survival in this particular habitat. The increase in variation of maxilla 2 in *P.* (*P.*) *elegans* – a genuine increase and not simply a corollary of increased size – presents a totally unexpected reversal of normalizing selection. This shrimp is a common inhabitant of intertidal rockpools and undergoes 6–9 zoeal moults before metamorphosis. The larvae are planktonic and have access to a wide variety of coastal habitats when they become benthic after the final larval stage. There is a degree of uncertainty in making immediate contact with the most suitable rocky coastline and a degree of variation would clearly be advantageous.

Gurney (1924) stated '. . . a knowledge of the larval history is of importance in tracing the systematic relationships of Decapoda . . .'. One of the aims of this present series of papers is to provide detailed descriptions of larval stages to aid identification and to form the basis of a systematic study using numerical methods. For this purpose the extent of larval variation needs to be determined. Gurney (1924) gave details of intermediate post larval stages in which various combinations of late larval and first post larval characters were found. While these were not unknown in the present study, rearing at 22 °C produced a rapid, and in most cases direct, development to PL1 through five larval stages. The delay in the epigenetic process recorded by Gurney was probably a response to environmental stress imposed by the rearing techniques. With regard to larval polymorphism or poecilogony (Boas, 1889; Heldt, 1953) abundant larval variation was recorded in the present study but this did not exceed variability commonly found in larval prawns and shrimps.

Acknowledgement

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A revision of the spider genus *Brettus* (Araneae : Salticidae)

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Introduction

The genus *Brettus* was proposed by Thorell (1895) for the Burmese species *Brettus cingulatus* Thorell. Simon (1900) described four more species (*Brettus martini* from South Africa, *B. albolimbatus* and *B. semifimbriata* from India and *B. adonis* from Sri Lanka) and in 1901 synonymized the genus with *Portia*. Wanless (1978b) revised *Portia* and resurrected *Brettus* in part. *Brettus martini* Simon could not be recognized from the original description and as the type specimen could not be found the name was considered a *nomen dubium*. In the present paper the genus is redefined and its affinities discussed. The four known species (of which one is new) are described and keyed. One species is newly synonymized and three lectotypes designated.

The measurements were made in the manner described by Wanless (1978a).

The known species of *Brettus* are closely related and occur in the Oriental region. They resemble spiders of the genus *Portia*, but are generally smaller in size and lack the abdominal hair tufts. Unfortunately their biology is unknown though it is considered that their behaviour may be similar to that described for some species of *Portia* (Wanless, 1978b), and that specimens may be found living in diplurid or pholcid webs.

Genus *BRETTUS* Thorell

Brettus Thorell, 1895 : 354. Type species *Brettus cingulatus* Thorell, by original designation and monotypy. Simon, 1901 : 402 [=*Portia*] Petrunkevitch, 1928 : 213. Bonnet, 1955 : 915. Wanless, 1978b : 84 [gen. rev.].

DEFINITION. Small to medium spiders ranging from about 3·0 to 8·0 mm in length. Sexes alike; leg fringes present, but abdominal hair tufts apparently lacking; colour patterns composed of setae (easily rubbed). *Carapace*: high, longer than broad; fovea present, behind posterior lateral eyes; sculpturing not marked, cuticle weakly iridescent (under some angles of illumination); in most species, broad marginal bands composed of white setae extend from clypeal region to posterior thoracic margin. *Eyes*: anteriors subcontiguous with apices recurved; posterior median eyes relatively large, nearer to anterior laterals than to posterior laterals; posterior row narrower than anterior row; quadrangle length between 40 and 50 per cent of carapace length. *Clypeus*: moderately high to high, concave. *Chelicerae*: medium to large, more or less vertical; promargin with 3 teeth, retromargin with 3 to 4. *Maxillae*: elongate, usually divergent. *Labium*: subtriangular, about half maxilla length. *Sternum*: elongate scutiform. *Pedicel*: short. *Abdomen*: elongate ovoid; scuta lacking, but four impressed spots usually present; anterior and posterior spinnerets robust, subequal in length, medians slender, relatively short; trachea not examined (insufficient material). *Legs*: long and slender, fringes present on legs I and sometimes II; spines numerous, moderately robust; claws pectinate, tufts present, scopula lacking; legs I–II with minute setae in parallel row on venter of tarsi and metatarsi. *Female palp*: long and slender with terminal claw (difficult to see). *Male palp*: femoral apophyses lacking; tibiae with lateral and ventral apophyses, the former with an associated duct which appears to arise from a flask-like vacuole (Fig. 1E, F). Cymbium modified proximally; embolus very long and slender; conductor apparently lacking; tegulum with peripheral seminal reservoir, a curved furrow (Fig. 1A, B) and a bipartite membraneous apophysis (apparently lacking in *B. adonis*) adjacent to the embolic base; median

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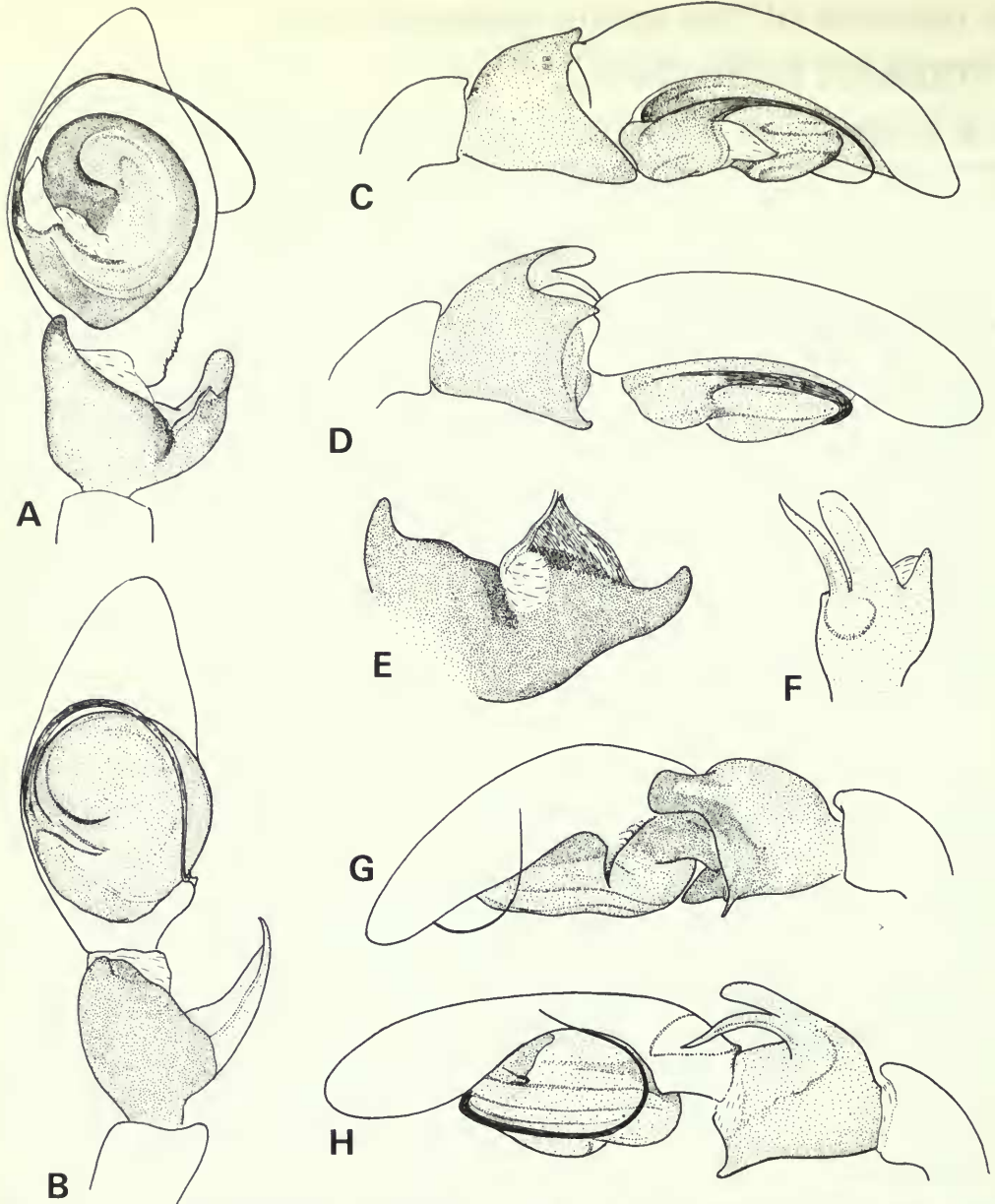
Fig. 1 (A, C, E, G) *Brettus cingulatus* Thorell, holotype ♂: (A) palp, ventral view; (C) palp, mesal view; (E) palpal tibia, posterior view; (G) palp, ectal view. (B, D, F, H) *B. adonis* Simon, ♂: (B) palp, ventral view; (D) palp, mesal view; (F) palpal tibia, dorsolateral view; (H) palp, ectal view.

apophysis lacking. *Epigyne*: relatively simple; openings usually indistinct, leading to elongate ducts which terminate distally as spermathecae.

AFFINITIES. Wanless (1978b) suggested that on behavioural and anatomical grounds *Portia*, *Brettus*, *Cocalus* and several other genera with large posterior median eyes could be related to lyssomanid spiders and that *Brettus* may form a link between *Portia* in the Salticidae and *Asemonea* in the Lyssomanidae. Unfortunately the link cannot be satisfactorily demonstrated from the known species of *Brettus* which are evidently closer to *Portia* than to *Asemonea*. Preliminary

observations on male *Asemonea* have shown that the palps are generally very complex and that some males (e.g. *A. tenuipes* O.P.-C.) apparently have ducts associated with the femoral apophyses. The presence of these ducts may indicate a distant relationship with *Brettus*, but their significance cannot be evaluated at the present time.

DIAGNOSIS. *Brettus* is distinguished from *Portia* by the very long embolus and the apophysal duct on the tibiae in males, and the long fertilization ducts in females. A fuller diagnosis cannot be given until other related genera have been revised.

List of species in the genus *Brettus* Thorell, 1895

Brettus adonis Simon, 1900
B. albolimbatus Simon, 1900
B. anchorum sp. n.
B. cingulatus Thorell, 1895

Key to speices of *Brettus*

1 Males –   2
– Females   3
2 Retrolateral tibial apophysis not bifurcate, ectal margin of cymbium with pointed spur (Fig. 1G)
   (Burma)   .   .   .   .   *cingulatus* Thorell (p. 185)
– Retrolateral tibial apophysis bifurcate, ectal margin of cymbium lacking pointed spur (Fig. 1H)
   (Sri Lanka)   .   .   .   .   *adonis* Simon (p. 186)
3 Distal margin of epigynal plate clearly projecting beyond epigastric fold (Fig. 3A) (Sri Lanka)
                                                                          adonis Simon (p. 186)
– Distal margin of epigynal plate not projecting beyond epigastric fold   4
4 Spermathecae extending laterally (Figs 3B; 4C, D) (India)   .   .   *anchorum* sp. n. (p. 188)
– Spermathecae extending anteriorly (Figs 3C, D; 4A, B) (India)   .   .   *albolimbatus* Simon (p. 188)

Brettus cingulatus Thorell
(Figs 1A, C, E, G; 2A, B)

Brettus cingulatus Thorell, 1895 : 355, ♂. Holotype ♂, Burma, Tharrawaddy (NR, Stockholm, no. 1605) [Examined]. Wanless, 1978*b* : 83.
Portia cingulata: Simon, 1901 : 402. Reimoser, 1925 : 90. Roewer, 1954 : 934. Bonnet, 1958 : 3766. Prószyński, 1971 : 461.

DIAGNOSIS. The male of *B. cingulatus* is readily distinguished from that of *Brettus adonis* by the pointed spur on the ectal margin of the cymbium (Fig. 1G).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 2A, B): orange-brown with paler eye region and a wide marginal band composed of recumbent, silky white hairs from clypeus to posterior thoracic margin. *Eyes*: with black surrounds except AM; anteriors fringed by whitish hairs. *Clypeus*: densely clothed in silky white hairs. *Chelicerae*: orange-brown; thinly covered in fine light brown hairs; promargin with 3 teeth, retromargin with 4. *Maxillae and labium*: pale orange-brown tinged with grey. *Sternum*: light orange-brown with poorly defined reddish orange margins; sparsely clothed in dull white hairs. *Abdomen*: rubbed; light yellow-orange tinged with black; pattern indistinct. *Legs*: anteriors dark orange-brown, posteriors lighter; brown ventral fringes present on femora, patellae and tibiae of legs I and II; spines numerous, moderately robust. *Palp* (Fig. 1A, C, E, G).
   Dimensions (mm): total length 5·6; carapace length 2·56, breadth 2·2, height 1·48; abdomen length 2·88; eyes anterior row 1·44, middle row 1·08, posterior row 1·28; quadrangle length 1·08. *Ratios*: AM : AL : PM : PL : 12·5 : 6·5 : 5 : 6; AL–PM–PL : 6·5–9.

DISTRIBUTION. Burma.

MATERIAL EXAMINED. Holotype ♂, data given in synonymy.

Brettus adonis Simon comb. rev.
(Figs 1B, D, F, H; 2D, E; 3A)

Brettus adonis Simon, 1900 : 32, ♀, LECTOTYPE ♀ (here designated) Sri Lanka, Galle (MNHN, Paris, no. 20416) [Examined].
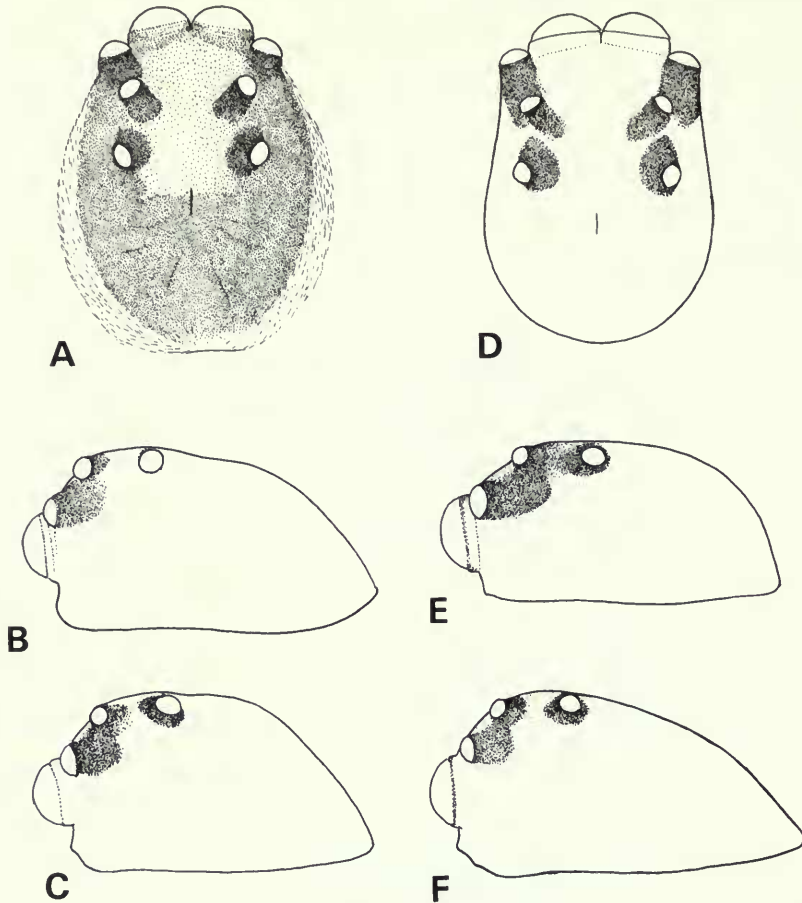*Portia adonis* (Simon): Simon, 1901 : 402. Roewer, 1954 : 934. Bonnet, 1958 : 3766. Prószyński, 1971 : 461.

Fig. 2 (A, B) *Brettus cingulatus* Thorell, holotype ♂: (A) carapace, dorsal view; (B) carapace, lateral view. *B. albolimbatus* Simon, lectotype ♀: (C) carapace, lateral view. (D, E) *B. adonis* Simon, ♂: (D) carapace, dorsal view; (E) carapace, lateral view. *B. anchorum* sp. n. holotype ♀: (F) carapace, lateral view.

The vial labelled '20416 Port Adonis [sic] E. S. Galle type' contains one male and one female. The female is considered to be the type specimen and is designated lectotype. The male, which appears to be conspecific, is described below.

DIAGNOSIS. *B. adonis* is distinguished from *Brettus cingulatus* by the absence of a pointed spur on the ectal margin of the cymbium in males (Fig. 1H), and the posterior projection of the epigynal plate in females (Fig. 3A).

MALE FROM GALLE, SRI LANKA. *Carapace* (Fig. 2D, E): light orange with yellow-orange eye region; very sparsely clothed in minute iridescent setae (mostly rubbed). *Eyes*: with black surrounds except AM; anteriors fringed by pale yellow hairs. *Clypeus*: fringed by short silky white hairs. *Chelicerae*: yellow with faint sooty markings; fringed proximally with transverse band of silky

white hairs; teeth not examined. *Maxillae and labium*: yellow tinged with grey. *Sternum*: yellow, glossy. *Abdomen*: yellow with faint blackish mottling; very sparsely clothed in minute iridescent setae. *Legs*: legs I orange to pale orange, lightly tinged with black; remaining legs pale yellow; legs I densely fringed by stiff orange-brown hairs on venter and dorsum of tibiae, venter of patellae and distal venter of femora. Spines moderately robust and numerous. *Palp* (Fig. 1B, D, F, H).

Dimensions (mm): total length 3·16; carapace length 1·65, breadth 1·28, height 0·92; abdomen length 1·44; eyes anterior row 1·08, middle row 0·84, posterior row 0·92; quadrangle length 0·80. *Ratios*: AM : AL : PM : PL : 9·5 : 4·5 : 3·5 : 4; AL–PM–PL : 5–6·5.
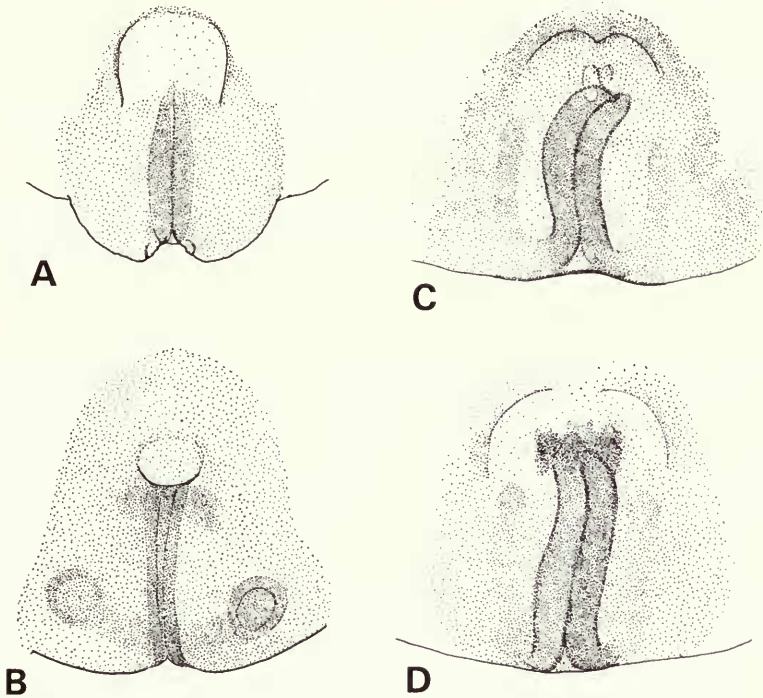

Fig. 3 *Brettus adonis* Simon, lectotype ♀: (A) epigyne. *B. anchorum* sp. n. holotype ♀: (B) epigyne. (C, D) *B. albolimbatus* Simon, lectotype ♀: (C) epigyne; paralectotype ♀: (D) epigyne.

FEMALE LECTOTYPE. Body form and colour similar to ♂. *Carapace*: as in ♂, but irregularly clothed with recumbent white hairs, iridescent under some angles of illumination, apparently forming a wide marginal band from clypeus to posterior thoracic margin. *Eyes*: more or less as in ♂. *Clypeus*: thinly clothed in fine whitish hairs. *Maxillae and labium*: as in ♂. *Sternum*: as in ♂. *Abdomen*: pale yellow with a greyish tip and markings forming an ill-defined ventral band from spinnerets to epigyne. *Legs*: similar to ♂ but dorsal fringes on legs I lacking and with patellae and ventral tibial fringes composed of long white hairs proximally. *Palps*: long and slender, whitish yellow with white hairs. *Epigyne* (Fig. 3A): vulva not examined.

Dimensions (mm): total length 4·6; carapace length 1·96, breadth 1·56, height 1·04; abdomen length 2·52; eyes anterior row 1·27, middle row 0·98, posterior row 1·12; quadrangle length 0·96. *Ratios*: AM : AL : PM : PL : 11·5 : 6 : 4 : 5; AL–PM–PL : 6–8.

DISTRIBUTION. Sri Lanka.

MATERIAL EXAMINED. Lectotype ♀, data given in synonymy. SRI LANKA: Galle, 1 ♂ in the same vial as the lectotype.

Brettus albolimbatus Simon comb. rev.
(Figs 2C; 3C, D; 4A, B)

Brettus albolimbatus Simon, 1900 : 31, ♀. LECTOTYPE ♀ (here designated) India, Trichinopoly (MNHN, Paris, no. 17534) [Examined].

Portia albolimbata (Simon): Simon, 1901 : 402. Roewer, 1954 : 934. Bonnet, 1958 : 3766. Prószyński, 1971 : 461. Wanless, 1978b : 85.

Brettus semifimbriatus Simon, 1900 : 31, ♀. LECTOTYPE ♀ (here designated) India, Trichinopoly (MNHN, Paris, no. 18918) [Examined]. **Syn. n.**

Portia semifimbriata (Simon): Simon, 1901 : 401, 402. Strand, 1912 : 148. Roewer, 1954 : 934. Bonnet, 1958 : 3767. Wanless, 1978b : 85.

Portia foveata Strand, 1912 : 148. [Published as a synonym of *P. semifimbriata* (Simon).]

The vial labelled '17534 Port. Scultzi Karch [sic] (albolimbata E. S. type) Natal C.M.' contains one female which is conspecific with the lectotype of *Brettus semifimbriatus* Simon. In view of this conspecificity and the reference to 'albolimbata E. S. type' on the label, the locality and collector data, i.e. Natal, C[h]. M[artin], is probably erroneus and the specimen is considered to be the type of *B. albolimbata*.

DIAGNOSIS. *B. albolimbatus*, known only from the female, is distinguished from other females of *Brettus* by the S-shaped fertilization ducts and the anteriorly extended spermathecae (Figs 3C, D; 4A, B).

MALE. Unknown.

FEMALE LECTOTYPE. *Carapace* (Fig. 2C): light orange-brown with yellow-orange eye region and faint sooty marking radiating from fovea; shiny and weakly iridescent under some angles of illumination; from AL to posterior thoracic margin a broad white marginal band composed of recumbent white hairs. *Eyes*: with black surrounds except AM; anteriors fringed by whitish hairs. *Clypeus*: thinly covered in white hairs. *Chelicerae*: pale orange-brown with sooty markings; sparsely clothed in long fine pale orange hairs; pro- and retromargins with 3 teeth. *Maxillae and labium*: light orange-brown tinged with grey. *Sternum*: light orange-brown, shiny; thinly clothed in fine light orange hairs. *Abdomen*: whitish yellow tipped with grey, with greyish markings dorsally and subparallel bands from epigyne to spinnerets; irregularly clothed in white and orange-brown hairs (rubbed). *Legs*: pale yellow to orange-brown with ventral brown fringes on tibiae I, patellae I and femora I; similar fringes on legs II, but less dense; spines numerous, moderately robust. *Palp*: white with yellowish tips. *Epigyne* (Fig. 3C).

Dimensions (mm): total length 5·04; carapace length 2·4, breadth 2·0, height 1·4; abdomen length 2·76; eyes anterior row 1·44, middle row 1·14, posterior row 1·26; quadrangle length 0·98. *Ratios*: AM : AL : PM : PL : 12·5 : 6 : 5 : 5·5; AL–PM–PL : 7–9.

VARIATION. Females vary from 5·04 to 7·2 mm total length, 2·4 to 2·9 mm carapace length (three specimens). The appearance of the epigynal fertilization ducts is evidently variable (Fig. 3C, D).

DISTRIBUTION. India.

MATERIAL EXAMINED. Lectotype females, data given in synonymy. INDIA: Madras, Trichinopoly, 1 ♀ paralectotype in the same vial as the lectotype of *B. semifimbriatus* (no. 18918).

Brettus anchorum sp. n.
(Figs 3B; 4C, D)

DIAGNOSIS. *B. anchorum*, known only from the female is separated from other females of *Brettus* by the laterally extended spermathecae (Figs 3B; 4C, D).

MALE. Unknown.

FEMALE HOLOTYPE. *Carapace* (Fig. 2F): pale orange with yellowish eye region and broad marginal bands of recumbent white hairs from AM to posterior thoracic margin. *Eyes*: with black surrounds

except AM; anteriors fringed by white hairs. *Clypeus*: thinly clothed in whitish hairs. *Chelicerae*: pale orange with long fine white hairs; promargin with 3 teeth, retromargin with 4. *Maxillae and labium*: pale orange tinged with grey. *Sternum*: light yellow, shiny. *Abdomen*: whitish yellow. *Legs*: whitish yellow to orange; tibiae I, patellae I and distal half of femora I ventrally fringed by stiff orange-brown hairs. *Palp*: light yellow. *Epigyne* (Figs 3B; 4C, D).

Dimensions (mm): total length 7·82; carapace length 2·72, breadth 2·36, height 1·48; abdomen length 4·7; eyes anterior row 1·4, middle row 1·08, posterior row 1·26; quadrangle length 1·12. *Ratios*: AM : AL : PM : PL : 13 : 6 : 5 : 6; AL–PM–PL : 7–9·5.
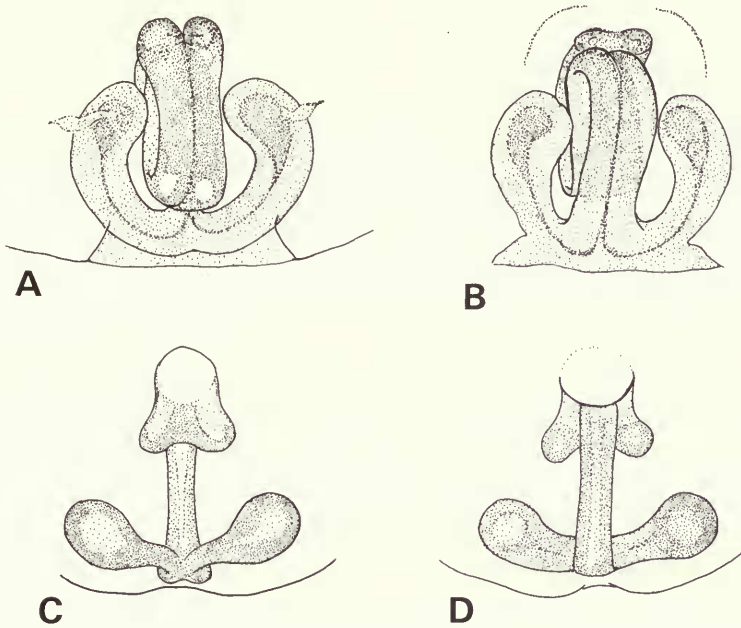

Fig. 4   (A, B) *Brettus albolimbatus* Simon, paralectotype ♀: (A) vulva, ventral view; (B) vulva, dorsal view. (C, D) *B. anchorum* sp. n. holotype ♀: (C) vulva, ventral view; (D) vulva, dorsal view.

DISTRIBUTION. India.

MATERIAL EXAMINED. Holotype ♀, India, Madras, Nilghiri Hills (*Sir George Hampson*) (BMNH. Reg. No. 1977.12.21.1).

Acknowledgements

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Notes on the osteology of the Arab horse with reference to a skeleton collected in Egypt by Sir Flinders Petrie

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Synopsis

A horse skeleton from Egypt donated by Sir Flinders Petrie to the British Museum (Natural History) and previously assumed to be ancient has been shown by radiocarbon dating to be only about three to four hundred years old. As a result of this, the skeleton has acquired an altogether different importance as a rare source of comparative material relevant to the history and development of the Arab horse. Comparative measurements of the skeletons of two modern Arab horses show that these closely resemble the Petrie horse. Other valuable osteological material collected by Petrie is briefly discussed.

Introduction

Amongst the material in the osteology collections of the Mammal Section at the British Museum (Natural History) is the skeleton of a horse donated by Sir Flinders Petrie, probably at the beginning of this century. There is no documentation with the skeleton to give its historical age, date of collection or provenance beyond the fact of its having come from Egypt. The skeleton has recently been registered in the Museum's computer catalogue of archaeological animal remains as ARC 1977 5101.

The earliest evidence for the domestic horse in Ancient Egypt is at present the single skeleton from the Middle Kingdom fortress of Buhen in northern Sudan, dated historically to *circa* 1675 B.C. (Clutton-Brock, 1974), and there are in fact very few remains of horses even from later periods in Egypt. For this reason and because the Petrie skeleton is remarkably complete, except for the cranial region which is unfortunately fragmentary, we were anxious to establish its date and locality. The age could be determined by radiocarbon dating, but the locality has proved more elusive.

There appears to be no mention of the horse skeleton in any publication by Petrie, and we have examined all the relevant manuscripts and other records held by the Egypt Exploration Society and in the Petrie Museum of the Department of Egyptology at University College London. The documents in the Petrie Museum have been recently catalogued by Mrs Barbara Adams (1975, pp. 108–111) and include photocopies of original journals held at the Griffith Institute, Ashmolean Museum, Oxford, the other main repository of the Petrie archives. Unfortunately, we found no reference to the horse skeleton although there were several useful references to other animal remains held at the British Museum (Natural History).

Despite the absence of records we considered it justifiable to proceed with the radiocarbon dating in the hope that it would shed light on the early history of the horse in Egypt. To our initial dismay this date came out at only 328 radiocarbon years before the present, that is to the early seventeenth century A.D.

It took a little time to overcome our surprise at this result, and to become reconciled to the fact that we were no longer dealing with a specimen from Ancient Egypt, but we then realized that the skeleton has considerable intrinsic value. This is we believe the only well-dated skeleton

Fig. 1   The Arab mare Ajjam with Lady Wentworth. (Photo: Special Press.)

of a horse that comes from the North African region, at a period when horses were beginning to undergo intensive improvement in Britain by cross-breeding with stock imported from the East. To anyone interested in the history of the Arab horse this skeleton should therefore be of value as comparative material, for it was in about A.D. 1689 that the first of the famous Arabs, Byerley Turk, arrived in England. As far as is known, there are no extant remains of the original imported Arab horses so we have not been able to make direct metrical comparisons with contemporary skeletons. However, detailed measurements have been recorded of the Petrie horse and compared with two Arab skeletons from the modern collections of the British Museum (Natural History) (Tables 1 and 2). One of these skeletons, No. 37.1.26.9, is of Ajjam, an Arab mare that died in 1937. Ajjam was owned by Lady Wentworth, who as is well known, was the daughter of Lady Anne Blunt, and had a world-famous stud of imported Arab stock at Crabbet Park in Sussex (Fig. 1).

We cannot be certain, of course, that the skeleton of the horse collected by Petrie in Egypt was of Arab breed, but it can be seen from the measurements that the bones bear a close resemblance to the two modern Arab skeletons.

Osteological description

The skeleton of the seventeenth century A.D. horse that was presented to the British Museum (Natural History) by Sir Flinders Petrie, was from an aged animal that was certainly more than 20 years old at the time of death, and may have been more than 30 years. The age was assessed

from the state of wear on the upper left corner and intermediate incisors (I^2 and I^3), these being the only incisor teeth present.

The skull and upper jaws of the horse only remain as comminuted fragments, but there is enough of the diastema region of the left maxilla and premaxilla to indicate that no canine tooth was present. There is therefore a high probability that the animal was female and this assertion is supported by the shape and proportions of the pelvic bones. The post-cranial bones are almost all present and are well enough preserved to enable measurements to be taken on each bone from either the left or right side of the skeleton. These measurements which were taken according to the method of von den Driesch (1976), are given in Table 1, whilst the dimensions of the lower cheek teeth are given separately in Table 2. Although most of the bones were complete, their condition was fragile so it was decided to impregnate them with polyvinyl acetate (PVA emulsion) to conserve them. This was carried out on the whole skeleton with the exception of the left humerus, some ribs and the right ulna which was destroyed for the radiocarbon determination.

When choosing modern comparative material to be measured against the Petrie horse we decided to take the skeleton of the Arab mare Ajjam (BM(NH) No. 37.1.26.9), although its skull was not available for measurement, and it was immediately apparent that the bones of the two specimens were very similar in their proportions. In addition an Arab stallion, Little Joker (BM(NH) No. H.40, presented by the Bombay Veterinary College in 1911), was selected for measurement and in this specimen the skull is complete so its gross dimensions are included in Table 1. The skull of the Petrie horse is unfortunately too fragmentary to allow any valid measurements to be recorded from it, but the mandible is complete except for the incisor region, so this may be compared with the mandible of the stallion, Little Joker. It can be seen that the lower teeth of the Petrie mare are considerably smaller than those of the stallion, but this is at least partly due to the greater age of the mare when it died and consequently the heavier wear on its cheek teeth. Although these teeth are much worn they are healthy and show no unevenness from biting on a bit.

The Petrie skeleton is from a large horse; it stood more than 15 hands (1509 mm) at the withers when it was alive (Table 1) and this is high, especially for a mare. The bones show that the animal was fine-limbed, and although it is not possible to tell the breed from an examination of the skeleton the proportions are close to those of the modern Arab mare and stallion that were taken as comparative material. The slenderness index of the metacarpal (Table 1) indicates that the Petrie mare was slightly more stockily built than the mare Ajjam, but only marginally more so than the stallion Little Joker, and in overall height she was taller than the stallion.

The numbers of vertebrae in the Petrie skeleton and the two comparative skeletons are as follows:

	Petrie mare	Ajjam	Little Joker
Cervical	7	7	7
Thoracic	18	18	17
Lumbar	5 (estimated)	5	6

The fifth lumbar vertebra is missing in the Petrie skeleton but it is evident from examination of the articular surfaces of the fourth lumbar and the sacrum that this mare only had five lumbar vertebrae. Stecher (1962) carried out a numerical survey of the numbers of vertebrae in the spines of modern horses, and he provided authoritative support for the contention of horsemen that the purebred Arab horse is 'short-coupled', that is, compared to other races of horses, it has a reduced number of vertebrae. Stecher found that the more usual number of six lumbar vertebrae was often reduced to five in Arab horses, and that if six lumbars were present then the thoracic vertebrae were reduced from the more usual 18 to 17. The two skeletons of Ajjam and Little Joker provide examples of these two alternative numberings, whilst that of the Petrie mare is consistent with the usual number found in the Arab breed.

In both Ajjam and Little Joker the two posterior lumbar vertebrae are fully ankylosed, indicating that both these horses were ridden extensively before they were fully mature. Although the Petrie mare was an aged animal when it died, there is no sign of ankylosis or other pathological condition in the spine which appears to be perfectly healthy. The rest of the skeleton of the Petrie

Table 1   Measurements of the Petrie horse skeleton together with those from male and female modern Arab horse skeletons. All measurements are in mm. Figures in brackets are estimates

	Designation as in von den Driesch (1976)	Petrie horse 77.5101 ♀	Ajjam 37.1.26.9 ♀	Little Joker H.40 ♂
Skull				
Basal length	3	–	–	482·0
Condylobasal length	2	–	–	510·0
Brow width (max.)	41	–	–	192·3
Breadth of cranium	38	–	–	99·0
Max. width occ. condyles	34	–	–	87·9
Max. A-P diameter of orbit	31	–	–	57·7
Max. D-V diameter of orbit	32	–	–	55·2
Mandible				
Length	1	–	–	386·2
Width of condyle	–	47·5	–	53·9
Depth of ramus between M_2–M_3	–	–	–	80·0
Height of vertical ramus	19	220·0	–	216·3
Atlas				
Max. width	GB	(140·3)	142·0	151·0
Axis				
Max. width of articular surface (ant.)	BFcr	86·1	87·6	91·5
Min. width of vertebra	SBV	43·6	48·5	52·7
Scapula				
Min. width of neck	SLC	67·3	66·7	66·1
Length of glenoid cavity	LG	58·0	62·0	64·0
Width of glenoid cavity	BG	44·0	51·2	49·4
Length of glenoid cavity + coronoid process	GLP	97·1	95·8	97·8
Height	HS	350·0	352·0	328·0
Humerus				
Length	GL	(310·0)	314·0	304·0
Lateral length	GLl	(310·0)	314·0	304·0
Distal width	BT	77·4	81·2	83·0
Radius				
Length	GL	358·0	368·0	351·0
Lateral length	GLl	351·0	350·0	337·0
Proximal width	BFp	76·3	80·4	81·4
Distal width	BFd	64·8	67·1	68·8
Min. width of shaft	SD	39·0	40·4	39·0
Ulna				
Length of head	LO	83·8	82·0	81·5
Width of articular surface	BPC	43·6	47·9	48·7
Metacarpal				
Length	GL	242·1	251·5	240·0
Lateral length	GLl	240·0	247·0	236·6
Proximal width	Bp	49·6	53·5	54·2
Distal width	Bd	53·1	50·3	53·7
Min. width of shaft	SD	33·9	32·3	32·3

Table 1 *(cont.)*

	Designation as in von den Driesch (1976)	Petrie horse 77.5101 ♀	Ajjam 37.1.26.9 ♀	Little Joker H.40 ♂
Pelvis				
Max. length of innominate bone	GL	(405·0)	445·0	410·0
Length of acetabulum	LAR	62·4	67·6	66·9
Femur				
Length	GL	(420·0)	436·0	411·0
Lateral length	GLl	(420·0)	436·0	411·0
Proximal width	Bp	(116·0)	127·2	126·9
Distal width	Bd	–	97·4	98·9
Min. width of shaft	SD	41·2	41·8	38·8
Tibia				
Length	GL	389·0	390·0	368·0
Lateral length	GLl	360·0	355·0	335·0
Proximal width	Bp	96·4	101·8	102·6
Distal width	Bd	76·3	76·7	80·2
Min. width of shaft	SD	41·9	40·7	40·1
Talus				
Length	GH	62·7	62·6	64·0
Greatest width	GB	62·3	65·7	65·0
Calcaneum				
Max. length	GL	118·0	118·7	114·7
Phalanx I Fore				
Length	GL	93·9	93·2	90·4
Proximal width	Bp	56·3	54·6	58·0
Proximal depth	Dp	38·4	37·4	37·3
Distal width	Bd	46·3	46·4	49·6
Min. width of shaft	SD	34·2	34·3	35·0
Phalanx I Hind				
Length	GL	90·5	88·3	88·9
Proximal width	Bp	56·0	56·6	57·2
Proximal depth	Dp	41·6	40·2	40·4
Distal width	Bd	42·2	45·2	46·0
Min. width of shaft	SD	32·2	33·4	33·4
Phalanx II Fore				
Length	GL	49·4	44·5	49·0
Proximal width	Bp	54·2	52·9	54·5
Proximal depth	Dp	32·1	31·3	32·4
Phalanx II Hind				
Length	GL	51·4	46·9	50·0
Proximal width	Bp	53·6	52·5	54·9
Proximal depth	Dp	34·2	32·6	33·3

Table 1   *(cont.)*

	Designation as in von den Driesch (1976)	Petrie horse 77.5101 ♀	Ajjam 37.1.26.9 ♀	Little Joker H.40 ♂
Phalanx III Fore				
Length	GL	(60·9)	67·5	74·8
Width	GB	(83·7)	74·1	79·3
Height in region of extensor process	HP	(41·7)	47·8	36·6
Phalanx III Hind				
Length	GL	68·9	62·9	66·1
Width	GB	72·8	71·0	75·3
Height in region of extensor process	HP	47·7	45·8	38·0
Metatarsal				
Length	GL	288·3	300·0	288·5
Lateral length	GLl	285·4	295·0	282·3
Proximal width	Bp	53·5	55·3	55·0
Distal width	Dp	50·3	51·0	53·7
Min. width of shaft	SD	31·2	30·6	28·8
Sacrum				
Max. width of wings	GB	230·7	226·0	200·0
Length of body of sacrum without first caudal vertebra	PL	206·4	194·2	179·0
Slenderness index of metacarpal				
Min. width of shaft × 100/length	–	14·00	12·84	13·45
Estimate of withers height: *Humerus*				
Lateral length × 4·87	–	1509·7	1529·2	1480·5
Metacarpal				
Lateral length × 6·41	–	1538·4	1583·3	1516·6

Note: In Britain the withers height of living horses is usually measured by 'hands'. One hand = 101·6 mm.

mare is also healthy with the exception of the extensive exostoses on the mandible, described in the appendix below (see also Figs 2 and 3). Moreover, the hoof cores and anterior phalanges show no signs of the animal having been ridden or driven over hard ground, as is usual in aged horses that have been kept in primitive conditions and overworked.

As we have not been able to discover, up to now, how this mare came to be buried nor why it was later excavated by Sir Flinders Petrie and brought to England we can only speculate on its origins, but at least the healthy condition of the spine and limb bones does indicate that it was unlikely to have been a common beast of burden. One further small piece of evidence on its demise is provided by the tufa-like matrix that surrounded the fragments of skull. This is almost entirely composed of the casts of great numbers of fly larvae and pupae which have been identified by Mr K. G. V. Smith of the Department of Entomology, British Museum (Natural History) as belonging to *Chrysomya albiceps* (Wiedemann). This fly is found all over Africa and is a common feeder on carrion which means that the head of the mare must have been exposed to the open air, shortly after death, for long enough to become a breeding ground for flies that were later sealed in with sand or silt.

Table 2   Measurements of the lower teeth of the Petrie horse compared with the modern Arab male, H.40

	Designation as in von den Driesch (1976)	Petrie horse 77.5101 ♀	Little Joker H.40 ♂
Lower teeth			
Length of cheek teeth row	6a	160·0	162·2
Length of premolar row	8a	76·5	86·6
Length of molar row	7a	77·7	78·3
Length P_2	L	(28·0)	33·8
Width P_2	B	17·2	18·6
Length P_3	L	24·8	27·5
Width P_3	B	16·3	22·2
Length P_4	L	24·3	25·9
Width P_4	B	17·2	20·8
Length M_1	L	22·7	24·0
Width M_1	B	18·1	19·1
Length M_2	L	24·3	24·3
Width M_2	B	16·5	16·6
Length M_3	L	32·0	31.0
Width M_3	B	13·3	15·3

Dating

As mentioned above the right ulna of the horse was sacrificed to provide a sample for radio-carbon dating. The most reliable part of bone for radiocarbon dating purposes is collagen, the protein constituent, as dates on whole bones almost invariably prove to be too young. For this reason the olecranon process of the right ulna was first completely demineralized with dilute hydrochloric acid. A quantity of well-preserved, uncontaminated collagen was obtained which was converted chemically to benzene for measurement of ^{14}C activity by the liquid scintillation counting method. From this measurement the following date was obtained:

BM-1357. 328 ± 52 bp (ad 1622)

This result is expressed in radiocarbon years before A.D. 1950 on the basis of the 5570 year half-life, the normal mode of reporting dates at present. Thus the bp/ad notation indicates that this date has not been corrected for the known differences between radiocarbon and calendar years. These differences are not large in the period in which the date falls but the true calendar date to which it is approximately equivalent will be some 80 years earlier, that is about A.D. 1540. This corrected date has in turn an estimated error of about ± 75 years at the level of one standard deviation.

Discussion

Although we do not know the reasons for the recovery of the skeleton of the horse or whether or not Petrie believed that it was ancient, it is not altogether surprising that he apparently kept no record. By comparison with the splendour and interest of the objects that Petrie uncovered in the

Fig. 2   Lingual side of left mandibular ramus of the Petrie horse showing extent of exostosis.
(Photo: Royal Veterinary College.)

Fig. 3   Petrie horse. Detailed view of exostosis on ramus. (Photo: Royal Veterinary College.)

course of his excavations and of which he often wrote eloquently in his journals, the animal remains must have seemed commonplace and, though in many instances worthy of retention, unworthy of special note. Similarly, the important botanical materials that Petrie found, some of which are also in the collections of the British Museum (Natural History), appear to have received scant mention in his records. It is perhaps difficult to comprehend this today, with the present emphasis on reconstruction of the environment and economy of earlier human populations from exactly this kind of evidence rather than from the more material remains. Such a commentary takes no account of course of the scale of Petrie's work, its pioneer character, the huge and important collections that he made and distributed to museums in many parts of the world, and the immense volume of material that he published over a long life of ceaseless work. He was in fact one of the principal founders of modern archaeology. Fortunately he did record some of the skeletal material he found as exemplified by the following passage from *Gizeh and Rifeh* (Petrie, 1907):

> In the cemetery some tombs full of animals' skeletons were found. All the skulls in good state were preserved, and sent to the British Museum (Natural History). Mr. Oldfield Thomas has kindly given the following report upon them: "The skulls form a wonderfully fine set, which will no doubt prove of great value when some one arises with time and taste to work out such things in detail. I never saw so fine a series before. There are 192 cats' skulls, mostly *Felis ocreata*, but no doubt some are *F. chaus*. They are, however, a wonderfully varying lot, and would require much work for every one to be certainly and exactly determined. One might believe that the Ancient Egyptians had as many different kinds as we have now. Also 7 mongoose skulls (*Mungos ichneumon*), 3 wild-dog (*Canis lupaster*), and 1 fox (*Vulpes famelica*)."

The series of 192 cats' skulls was later described by Morrison-Scott (1952) but the rest of the collections presented by Petrie to the British Museum (Natural History) remain to be studied. Although much of this material lacks documentation we are optimistic that further information may yet come to light. We intend to subject more specimens to radiocarbon dating in the belief that this will yield interesting results and contribute to our knowledge of the history of domesticated animals in Egypt. Petrie died in 1942, a decade before the advent of radiocarbon dating but doubtless its application to material he collected would have greatly interested and gratified him. The continuing need to retain excavated skeletal material for possible future investigation cannot be overstressed. In the present instance, the precise dating of the horse skeleton has endowed it with a scientific value which Sir Flinders Petrie would have been the first to applaud.

Appendix

Pathological examination of the mandible of the Petrie horse

A region of prominent exostosis on the left mandibular ramus of the horse (Figs 2 and 3) was kindly examined for us by Dr E. C. Appleby of the Pathology Department, Royal Veterinary College, London, who reported as follows:

> Part of the mineralized material forming a plaque on the mandibular surface near the base of the cheek teeth was removed and decalcified for histological examination. This revealed a trabecular structure suggestive of new, superficial bone growth possibly overlying a lesion deeper in the bone. The exostosis appears to have been inflammatory in origin and may have been the result of an abscess at the base of a tooth or perhaps due to traumatic or other injury to the periosteum. Somewhat similar, but much smaller, deposits elsewhere on the mandible were not examined histologically. The condition had evidently been established for some weeks. Bone changes of this kind are not uncommon in horses although usually associated with chronic degenerative diseases of the joints rather than present in the facial region. Lesions on the mandible of horses can occur as part of a generalized skeletal change associated with space-occupying lesions in the chest (acropachia) but, as stated in the main text above, in this case all the other surviving bones of the horse were healthy in appearance.

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