

12. THE SHRIMPS ASSOCIATED WITH INDO-WEST PACIFIC
ECHINODERMS, WITH THE DESCRIPTION OF A NEW SPECIES IN
THE GENUS *PERICLIMENES* COSTA, 1844 (CRUSTACEA:
PONTONIINAE).

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SUMMARY

At present, fifty one species of shrimp are known to live in association with Indo-West Pacific echinoderms. Of these, only one is a stenopodidean, all others belong to the Caridea, principally to the subfamily Pontoniinae (35 species), with the others in the families Alpheidae (11 species) and the Gnathophyllidae (4 species). The echinoderm hosts may belong to any class but are mainly the Crinoidea (26 species), Echinoidea (18 species) and Asteroidea (18 species), although only a very small number of shrimp species are associated with the latter class. Three ophiuroids, all basket stars, and eight species of holothurians are known to have shrimp associates. The available knowledge of the biology of these associations is outlined.

Keys for the *provisional* identification of these shrimps are provided and one new species, *Periclimenes ruber*, is described and illustrated. The distribution of the shrimps is outlined and the known hosts listed.

INTRODUCTION

The shrimp fauna of the tropical and subtropical Indo-West Pacific region is dominated, in shallow water, by three groups, the Pontoniinae, the Alpheidae and the Hippolytidae. Numerous species of these groups are now known to live in "commensal" association with other marine animals. The details of these associations are very poorly known, and the use of the term "commensal" is, in general, rather misleading as it implies that something is known about the trophic relationships involved. This is rarely the case, and in the vast majority of examples virtually nothing is known about the feeding methods concerned. The use of the term "associates" is probably preferable in the present state of ignorance, especially as it seems probable that a variety of feeding strategies may be involved.

Associations between shrimps and other marine animals are particularly common in the warm tropical waters around coral reefs and are relatively infrequent in colder waters. Only a single example is known from the British Isles, *Typton spongicola* Costa, a pontoniine shrimp that lives in sponges. Little is known of these associations in deep water but they appear to be less frequent. Species of many shrimp families do occur in depths well over 100 fms and some of these probably are "commensals".

SYSTEMATIC ACCOUNT

Keys are provided below for the provisional identification of the known shrimp associates of Indo-West Pacific echinoderms. Where possible these identifications should be based on ovigerous females, and should be checked in detail with the original or later descriptions for confirmation. The keys will not separate related species found on non-echinoderm hosts.

KEY TO THE GENERA OF SHRIMP ASSOCIATED WITH INDO-WEST PACIFIC
ECHINODERMS

1. First two pairs of pereopods with chelae 2
— First three pairs of pereopods chelate *Odontozona*

* Present address: The Darwin Museum, P.O. Box 4646, Darwin, N.T., Australia 5794.

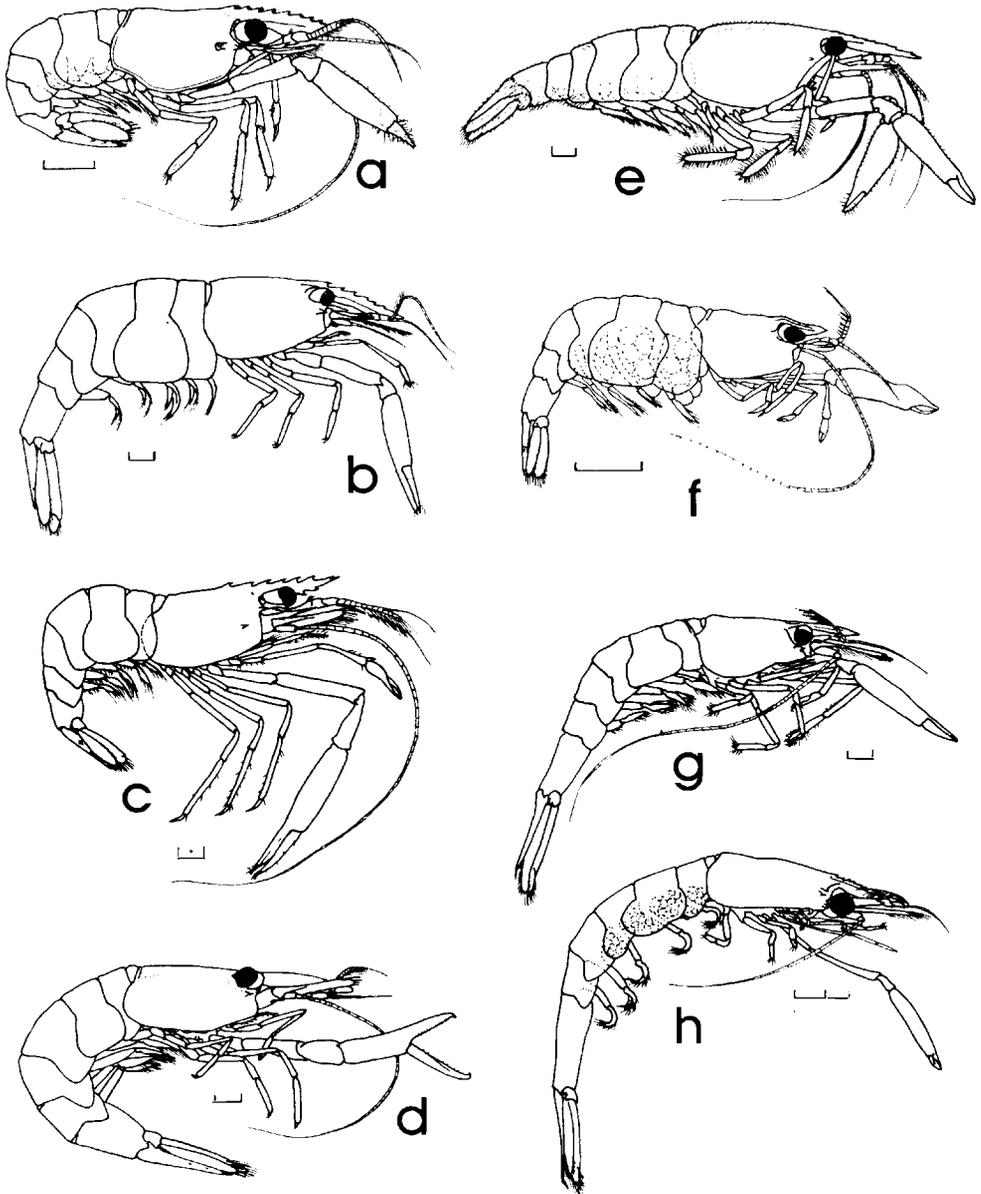


Fig. 1. a. *Allopontonia iaini* Bruce, b. *Araiopontonia odontorhyncha* Fujino & Miyake, c. *Palaemonella pottsii* (Borradaile), d. *Parapontonia nudirostris* Bruce, e. *Periclimenes hirsutus* Bruce, f. *Pontoniopsis comanthi* Borradaile, g. *Stegopontonia commensalis* Nobili, h. *Tuleariocaris zanzibarica* Bruce. Scale = 1 mm.

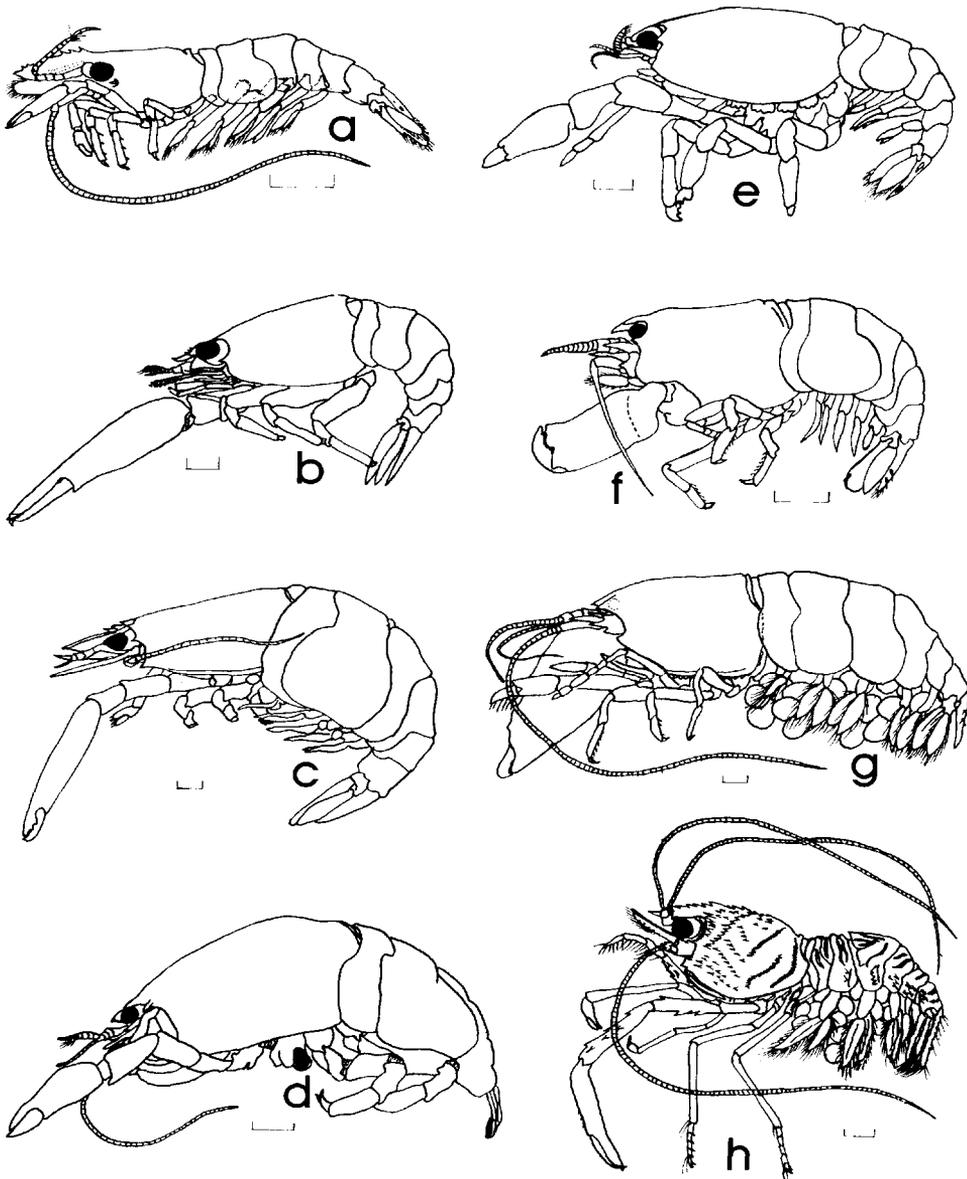


Fig. 2. a. *Zenopontonia noverca* (Kemp), b. *Levicaris mammillata* (Edmondson) (after Fujino & Takeda, 1977), c. *Gnathophylloides robustus* Bruce, d. *Pycnocaris chagoae* Bruce, e. *Conchodytes meleagrinae*, f. *Athanas indicus* (Coutière), g. *Synalpheus fossor* (Paulson), h. *Odontozona* sp. Scale = 1 mm.

- | | |
|--|-------------------------|
| 2. First pair of pereiopods slender, second more robust | 3 |
| — Second pair of pereiopods slender, first pair more robust | 15 |
| 3. Mandible with incisor process; third maxillipeds with ischio-merus slender, not opposing in midline | 4 |
| — Mandible without incisor process; ischio-merus of third maxilliped broadened, operculate | 13 |
| 4. Mandible with small 2-jointed palp | <i>Palaemonella</i> |
| — Mandible without palp | 5 |
| 5. Rostrum generally dorsally dentate (except in <i>Perichimenes insolitus</i> Bruce) | 6 |
| — Rostrum toothless | 10 |
| 6. Hepatic spine present | 7 |
| — Hepatic spine absent | <i>Araiopontonia</i> |
| 7. Hepatic spine fixed | 8 |
| — Hepatic spine mobile | 9 |
| 8. Third and fifth pereiopods with hoof-shaped ventral process on dactyl | <i>Tuleariocaris</i> |
| — Third and fifth pereiopods without hoof-shaped process on dactyls | <i>Perichimenes</i> |
| 9. First pereiopods with simple chela; protopodite of uropod not with an acute postero-lateral process | <i>Allopontonia</i> |
| — First pereiopod with spatulate chela; protopodite of uropod with an acute postero-lateral process | <i>Zenopontonia</i> |
| 10. Second pereiopods subequal and similar | 11 |
| — Second pereiopods unequal and dissimilar | 12 |
| 11. Hepatic and antennal spines present, epistomal horns present | <i>Parapontonia</i> |
| — Hepatic and antennal spines absent, epistomal horns absent | <i>Conchodytes</i> |
| 12. Hepatic spine present | <i>Stegopontonia</i> |
| — Hepatic spine absent | <i>Pontoniopsis</i> |
| 13. Second maxilliped with carpus and ischio-meral segments greatly elongated | <i>Levicaris</i> |
| — These segments normal | 14 |
| 14. Rostrum with dorsal teeth present | <i>Gnathophylloides</i> |
| — Rostrum without dorsal teeth | <i>Pycnocaris</i> |
| 15. Branchiostegite and pleura greatly broadened, covering pereiopods | <i>Pterocaris</i> * |

**Pterocaris typica* is an unusual shrimp said to possibly occur on echinoderms (Balss, 1957 p. 1414), although the species is known from only a single specimen from Ambon, Indonesia, and Heller's original account makes no mention of any associations (Heller, 1862). Coutière (1899) states that the species may possibly be associated with molluscs or echinoderms, but no further evidence is available. The species is included in this key in case it should prove to be associated with echinoderms, as further specimens of this bizarre shrimp would be of great interest.

- Branchiostegite and pleura normal 16
- 16. Eyes dorsally covered by carapace; second pereopods dissimilar and markedly unequal *Synalpheus*
- Eyes dorsally exposed; second pereopods similar and subequal *Athanas*

KEYS TO AND LISTS OF SPECIES OF SHRIMP ASSOCIATED WITH INDO-WEST PACIFIC

ECHINODERM HOSTS

Family PALAEMONIDAE

Subfamily PONTONINAE

Palaemonella Dana

1. *Palaemonella pottsi* (Borradaile, 1915) (fig. 1c)

Distribution: Type locality, Murray Island, Torres Straits.

Also known from Zanzibar, Kenya, Singapore, Japan, New Caledonia, the Great Barrier Reef and Marshall Islands.

Crinoid hosts: *Comanthina schlegeli* (P. H. Carpenter), *Comanthus bennetti* (J. Müller); *C. parvicirrus* (J. Müller); *C. timorensis* (J. Müller).

Periclimenes Costa

A large genus the members of which are associated with sponges, a wide variety of coelenterates and gastropods, with several free-living predatory species.

A KEY TO CRINOID ASSOCIATED *PERICLIMENES* SPECIES

- 1. Cornea conoidally produced 2
- Cornea globular 4
- 2. Ventral rostral margin with teeth** 3
- Ventral rostral margin without teeth; $R \frac{2-3^{**}}{0}$ *P. ceratophthalmus*
- 3. Chelae of second pereopods subequal; long and slender palm 3.0 times longer than wide and subequal to fingers; $R \frac{6}{1}$ *P. amboinensis*
- Chelae of second pereopods unequal, short and stout, palm 2.5 times longer than wide and double length of fingers; $R \frac{7}{1}$ *P. cornutus*
- 4. Supraorbital spines absent 5
- Supraorbital spines present, $R \frac{5-6}{1-2}$ *P. commensalis*
- 5. Ventral rostral teeth absent 6
- Ventral rostral teeth present 7
- 6. Second pereopods small, subequal, similar; $R \frac{5-6}{0}$ *P. tenuis*
- Second pereopods very unequal, dissimilar; $R \frac{3}{0}$ *P. attenuatus*

**The number of rostral teeth found in various species is indicated in the following keys by the formula $R = \frac{\text{number of dorsal rostral teeth}}{\text{number of ventral rostral teeth}}$.

7. Dactyls of ambulatory pereopods simple 8
 — Dactyls of ambulatory pereopods with distinct accessory spines: $R \frac{8}{2}$
 *P. novaecaledoniae*
8. Propods of ambulatory pereopods without ventral spines 9
 — Propods of ambulatory pereopods with ventral spines 10
9. Dactyl of major second pereopod with distinct lateral flange; $R \frac{10}{3}$
 *P. carinidactylus*
 — Dactyl of major second pereopod without lateral flange; $R \frac{7}{1}$ *P. affinis*
10. Major second pereopod with fingers much less than half palm length, ischium
 much longer than merus; $R \frac{7-8}{1-2}$ *P. ruber* sp. nov
 — Major second pereopod with fingers exceeding half palm length, ischium
 much shorter than merus; $R \frac{6}{1}$ *P. brocketti*

2. *Periclimenes amboinensis* (De Man, 1888)

Distribution: Type locality, Ambon, Indonesia. No subsequent records.

Crinoid host: *Comantheria briareus* (Bell) (new record).

3. *Periclimenes affinis* (Zehntner, 1894)

Distribution: Type locality, Ambon, Indonesia. Also reported from New Caledonia.

Crinoid host: *Comatula cratera* H. L. Clark (new record); *Comanthus* sp.

4. *Periclimenes ceratophthalmus* Borradaile, 1915

Distribution: Type locality, Hulule, Male Atoll, Maldive Islands. Also known from Kenya, Seychelle Islands, Indonesia, Great Barrier Reef and Palau Islands.

Crinoid hosts: *Himerometra robustipinna* (P. H. Carpenter); *Dichrometra afra* A. H. Clark; *Lamprometra klunzingeri* (Hartlaub); *Stephanometra indica* (Smith) (new record); *S. spicata* (P. H. Carpenter).

5. *Periclimenes cornutus* Borradaile, 1915

Distribution: Type locality, Hulule, Male Atoll, Maldive Islands. There have been no subsequent records.

Crinoid host: indet.

6. *Periclimenes commensalis* Borradaile, 1915

Distribution: Type locality, Murray Island, Torres Straits. Also known from Mozambique, Zanzibar, Kenya, Indonesia, Great Barrier Reef, New Caledonia and Palau Islands.

Crinoid hosts: *Capillaster multiradiatus* (Linnaeus); *Comanthina belli* (P. H. Carpenter); *Comanthus bennetti* (J. Müller); *C. parvicirrus* (J. Müller); *C. timorensis* (J. Müller); *Comaster distinctus* (P. H. Carpenter); *Comatella nigra* (P. H. Carpenter) (new record); *Zygometra microdiscus* (Bell); *Heterometra africana* (A. H. Clark); *Himerometra robustipinna* (P. H. Carpenter); *Tropiometra afra* (Hartlaub) (new record).

7. *Periclimenes brocketti* Borradaile, 1915

Distribution: Type locality, North Male Atoll, Maldive Islands. There have been no subsequent reports of this species, which may be synonymous with *P. affinis* (Zehntner).

Crinoid host: indet.

8. *Periclimenes novaecaledoniae* Bruce, 1968

Distribution: Type locality, Ilôt Maître, Noumea, New Caledonia. No further records.

Crinoid host: *Tropiometra afra* (Hartlaub).

9. *Periclimenes carinidactylus* Bruce, 1969

Distribution: Type locality, Bottle and Glass Rocks, Port Jackson, Australia. No further records.

Crinoid host: indet.

10. *Periclimenes tenuis* Bruce, 1969 (fig. 8c)

Distribution: Type locality, Chukwani, Zanzibar. Also known from Eylath, Gulf of Aqaba.

Crinoid hosts: *Heterometra africana* (A. H. Clark); *H. savignyi* (J Müller) *Himerometra robustipinna* (P. H. Carpenter) (new record); *Lamprometra klunzingeri* (Hartlaub); *Decametra chadwicki* (A. H. Clark); *Tropiometra carinata* (Lamarack).

11. *Periclimenes attenuatus* Bruce, 1971 (fig. 8g)

Distribution: Type locality, Waterhouse Cove, Burukule, Duke of York Islands. No further records.

Crinoid host: indet.

12. *Periclimenes ruber* sp. nov. (figs. 3-5, 8f)

MATERIAL EXAMINED: Holotype (Australian Museum, P.28106), ovigerous female; 2 paratypes (Australian Museum, P.28107 ♂; Rijksmuseum, Leiden, D31955 ♀) ovigerous female and young male, collected by C. T. Liron, Bribie Passage, Pumicestone Channel, Queensland, Australia, in 8 m depth, 23-4-69, from crinoid host: *Zygometa microdiscus* (Bell).

DESCRIPTION: The holotype is a small slenderly built pontonine shrimp with a post-orbital carapace length of 2.5 mm. The second ovigerous female (paratype) has a post-orbital carapace length of 2.4 mm and the male (paratype) of 1.9 mm.

Rostrum well developed, reaching to end of antennular peduncle, horizontal, with moderately deep lamina. Lateral carina feebly developed, dorsal margin with seven or eight small acute, evenly spaced teeth; ventral margin feebly convex with one or two small distal teeth. Dorsal teeth situated over or slightly posterior to posterior orbital margin. Supraorbital and epigastric teeth absent. Orbit obsolete. Inferior orbital angle produced, sub-acute. Antennal spine slender, marginal, situated close below inferior orbital angle. Hepatic spine well developed, robust, below and well behind antennal spine. Antero-lateral angle of carapace slightly produced, rounded. Third abdominal segment slightly produced in midline posterodorsally; sixth segment about 1.8 times the length of fifth, and about 1.8 times longer than deep. Pleura of first three segments broadly rounded, fourth and fifth bluntly produced. Telson about 1.3 times length of sixth abdominal segment, three times longer than wide,

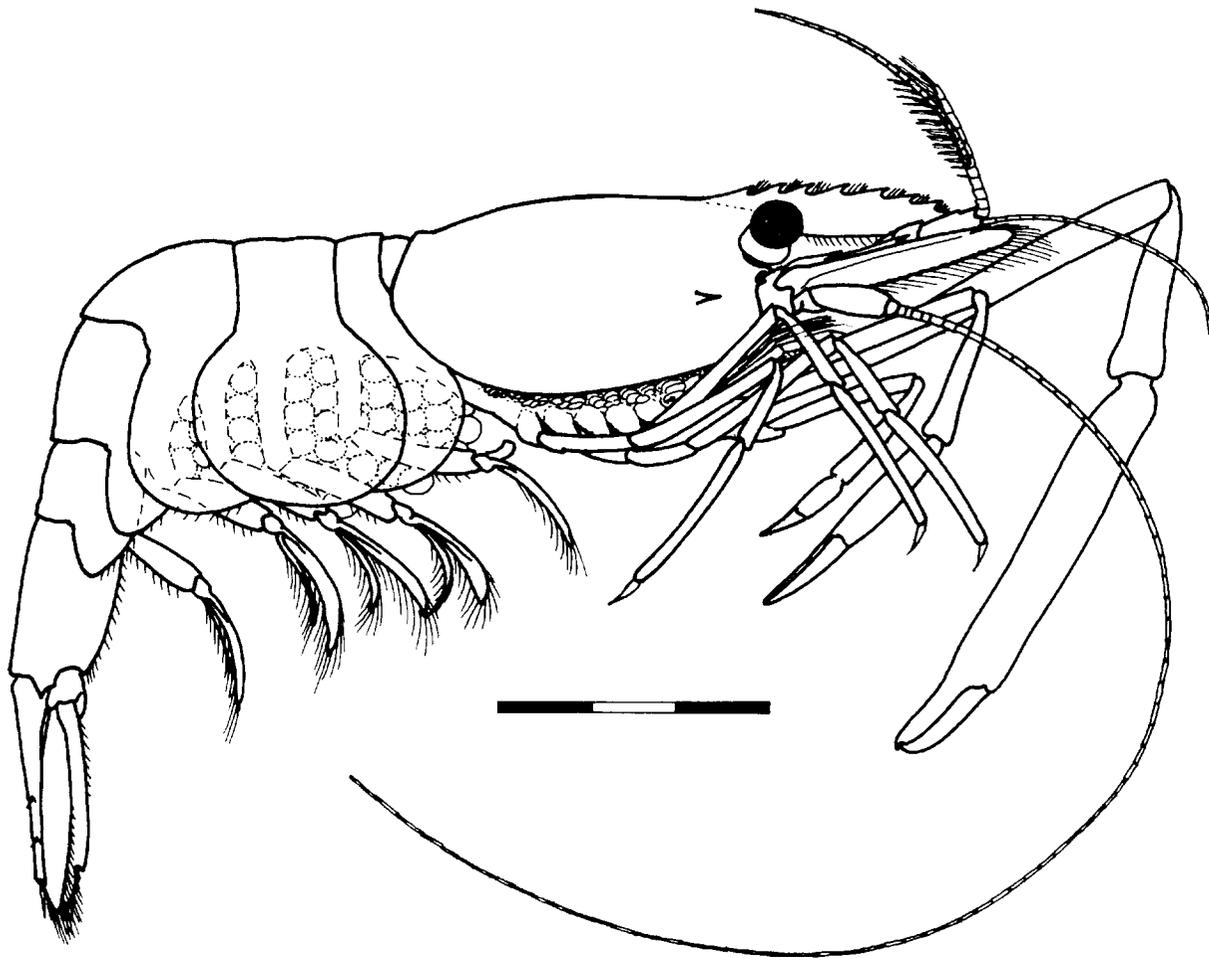


Fig. 3. *Periclimes ruber* sp. nov., holotype, scale = 1 mm.

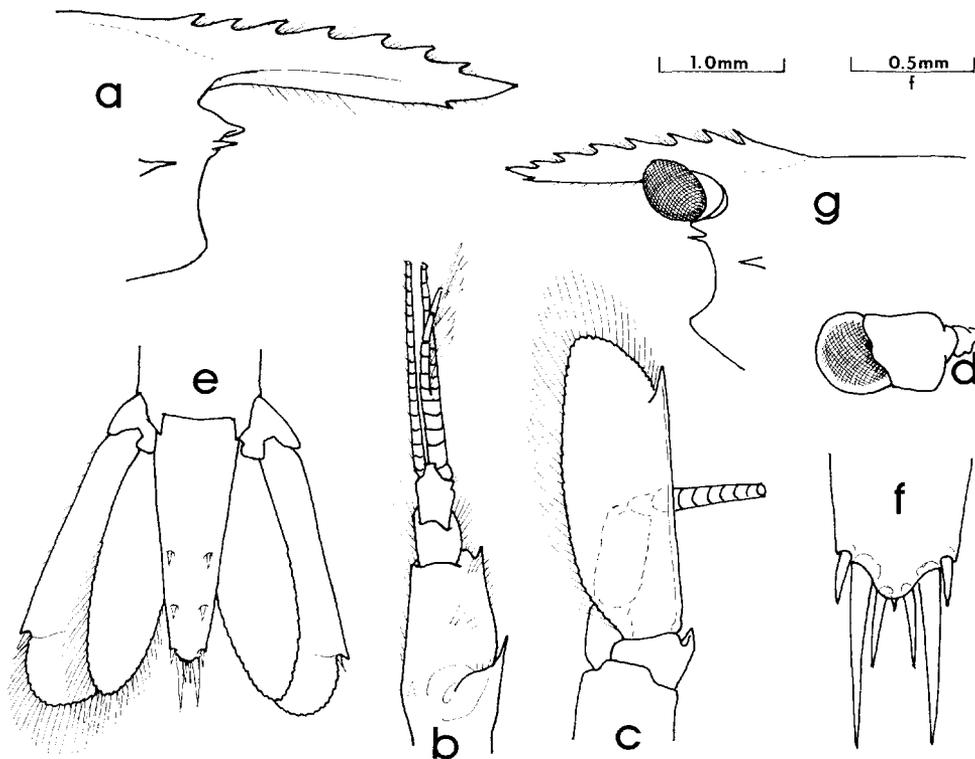


Fig. 4. *Periclimenes ruber* sp. nov., paratype, female. a. anterior carapace and rostrum, b. antennule, c. antenna, d. eye, e. caudal fan, f. posterior telson spines, g. paratype, male, anterior carapace and rostrum.

tapering, with rounded posterior margin with small median point. Two pairs of dorsal spines present at 0.6 and 0.8 of telson length. Three pairs of posterior spines present, intermediate spines twice as long as submedian and three times longer than lateral spines.

Proximal segment of antennular peduncle twice as long as broad, produced disto-laterally with a small lobe and slender lateral tooth. Stylocerite slender, reaching middle of segment length. Slender spine present at one third of the ventral medial border. Intermediate and distal segments short, subequal, together equal to half length of proximal segment. Upper flagellum slender, biramous, with proximal 4-5 segments fused; short ramus with five free segments, longer with about 35. Lower flagellum filiform, about 30 segments. Antenna with basicerite with small lateral tooth; carpocerite short and stout, reaching to middle of scaphocerite. Scaphocerite exceeding rostrum and antennular peduncle, three times longer than broad, well developed distal lobe of lamina extending far beyond strong disto-lateral tooth. Flagellum well developed, slender. Eye with short stout peduncle and large globular cornea. Accessory pigment spot present.

First pereiopod moderately slender, fingers equal to half palm length, simple; palm subcylindrical, 2.3 times longer than deep; carpus slightly longer than chela and slightly shorter than merus. Ischium and basis normal, coxa with a distinct slender setose medial ventral process. Second pereiopods well developed, markedly unequal. In female major chela slender and elongated, palm five times longer than wide, smooth, oval in section, three times length of fingers. Fingers robust, small hooked tips, distal cutting edges entire, proximal cutting edges

with one small blunt tooth on dactyl and two on fixed finger. Carpus about half palm length, unarmed. Merus slender, unarmed, about 1.4 times carpus length, 6.5 times longer than wide, and slightly shorter than the slender ischium. Minor chela much smaller and more slender, chela equal to 0.6 of palm length of major chela; fingers slender, slightly shorter than palm, unarmed, with entire cutting edges. Carpus about 1.2 of palm length, and slightly shorter than merus. Ischium about 1.2 of meral length. In male (paratype), major chela is intermediate between major and minor chelae in female, fingers half palm length, unarmed. Ambulatory pereopods slender; dactyls slender, simple with clearly demarkated slender unguis; propod with ventral border spinulate, with distal groups of spines in pairs. Carpus, merus and ischium normal. Pleopods typical for the genus. Uropods exceed tip of telson; lateral border of exopod straight, with very small distal tooth with much larger mobile spine medially.

COLOUR: Uniform dark red over body and appendages, except tips of uropods and telson and a small dorsal spot on the third abdominal segment, which are yellow.

REMARKS: *Periclimenes ruber* is most remarkable for its long slender major second pereiopod, in which the merus far outreaches the distal border of the scaphocerite. It is most closely related to *P. affinis*, which also has markedly unequal second pereiopods, although to a lesser extent, but has the propods of the ambulatory pereiopods without ventral spines. The only other shrimp known to associated with *Zygometra microdiscus* is *P. commensalis*, which can easily be distinguished from *P. ruber* by the presence of distinct supraorbital spines and short, stout, subequal chelae on the second pereiopods.

A KEY TO THE ASTEROID ASSOCIATED *PERICLIMENES* SPECIES

1. Disto-lateral angle of proximal segment of antennular peduncle with a single tooth only, R *P. parasiticus*
 — Disto-lateral angle of proximal segment of antennular peduncle with 2-3 teeth, R *P. soror*

13. *Periclimenes parasiticus* Borradaile, 1898

Distribution: Type locality, Milne Bay, New Guinea. No subsequent records. Probably juvenile specimens of *P. soror*.

Asteroid host: *Linckia* sp.

14. *Periclimenes soror* Nobili, 1904 (figs. 6b-d, 7a, d, 8e).

Distribution: Type locality, Jibouti. Common throughout the whole Indo-West Pacific region and recently found to occur also in the Gulf of Panama.

Asteroid hosts: *Choriaster granulatus* Lütken; *Culcita novaeguineae* Müller & Tröschel; *C. schmideliana* (Retzius); *Pentacaster horridus* (Gray); *P. mammillatus* (Audouin); *P. regulus* (Müller & Tröschel). (New record); *P. tuberculatus* (Müller & Tröschel); *P. hawaiiensis* (Fisher); *Protoreaster lincki* (de Blainville); *P. nodosus* (Linnaeus); *Linckia multifora* (Lamarck); *Acanthaster brevispina* Fisher; *A. planci* (Linnaeus); *Mithrodia clavigera* (Lamarck); *M. bradleyi* Verrill; *Echinaster purpureus* (Gray).

SHRIMP ASSOCIATES OF INDO-WEST PACIFIC ECHINODERMS

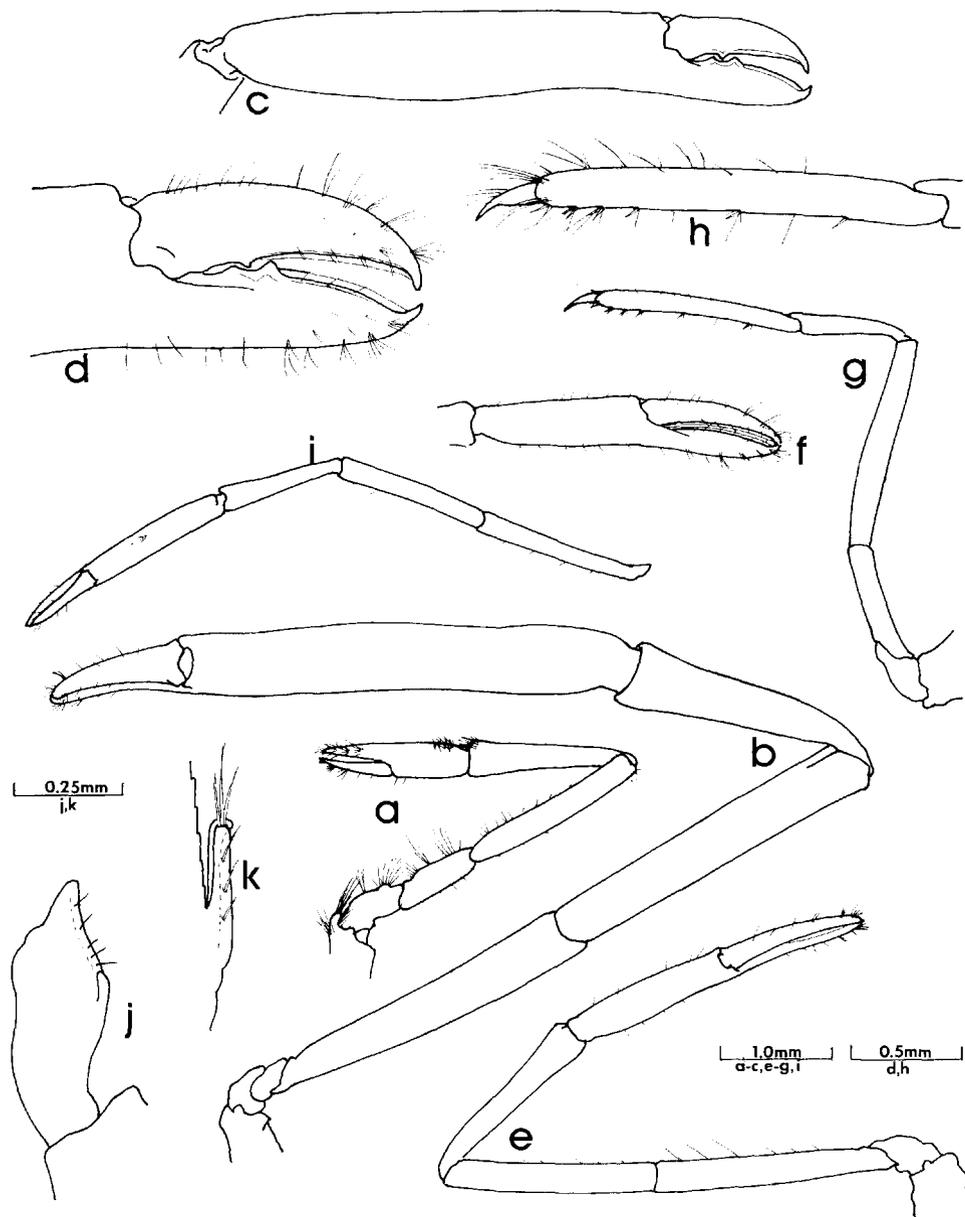


Fig. 5. *Periclimenes ruber* sp. nov., paratype, female. a. first pereiopod, b. major second pereiopod, c. chela of major second pereiopod, d. fingers of major second pereiopod, e. minor second pereiopod, f. chela of minor second pereiopod, g. third pereiopod, h. propod and dactyl of third pereiopod, i. paratype, male, second pereiopod, j. endopod of first pleopod, k. appendix interna and appendix masculina.

OPHIUROID ASSOCIATED *PERICLIMENES* SPECIES15. *Periclimenes lanipes* Kemp, 1922

Distribution: Type locality, Mergui Archipelago. Also recorded from Madagascar, Zanzibar, Kenya, Somalia, New Caledonia and Queensland, Australia.

Ophiuroid hosts: *Euryale purpurea* Mortensen; *Astroboa nuda* (Lyman); *Astroglymma sculpium* (Döderlein).

A KEY TO THE ECHINOID ASSOCIATED *PERICLIMENES* SPECIES

- | | |
|--|------------------------|
| 1. Supraocular teeth (arising from the well-defined orbital margin) present | 2 |
| — Supraocular teeth absent | 4 |
| 2. Rostrum without teeth, $R \frac{0}{0}$ | <i>P. insolitus</i> |
| — Rostrum with small distal dorsal teeth only | 3 |
| 3. Palm of first pereopods sub-equal to fingers, not compressed; fingers subspatulate, dactyl without dorsal carina, $R \frac{3-7}{0}$ | <i>P. zanzibaricus</i> |
| — Palm of first pereopod short, half length of fingers; fingers feebly subspatulate, dactyl with dorsal carina, $R \frac{5}{0}$ | <i>P. cristimanus</i> |
| 4. Merus of ambulatory pereopods with disto-ventral tooth..... | 5 |
| — Merus of ambulatory pereopods unarmed..... | 6 |
| 5. Dactyls of ambulatory pereopods without accessory tooth $R \frac{9-10}{0-1}$ | <i>P. maldivensis</i> |
| — Dactyls of ambulatory pereopods with robust accessory spine, $R \frac{7-8}{1}$ | <i>P. colemani</i> |
| 6. Generally glabrous; ventral rostral teeth present, $R \frac{6}{2}$ | <i>P. hertwigi</i> |
| — Generally hirsute; ventral rostral teeth absent, $R \frac{8}{0}$ | <i>P. hirsutus</i> |

16. *Periclimenes hertwigi* Balss, 1913

Distribution: Type locality, Sagami Bay, Japan. Also recorded from Indonesia and Queensland, Australia.

Echinoid host: *Araeosoma thetidis* (H. L. Clark); *Phormosoma* sp.

17. *Periclimenes cristimanus* Bruce, 1965

Distribution: Type locality, Singapore. Also recorded from Hong Kong and Heron Island, Queensland.

Echinoid hosts: *Diadema setosum* (Leske); *Echinothrix calamaris* (Pallas) (new record).

18. *Periclimenes maldivensis* Bruce, 1969

Distribution: Type locality, Suvadiva Atoll, Maldives. No subsequent records.

Echinoid host: indet.

19. *Periclimenes zanzibaricus* Bruce, 1969

Distribution: Type locality, Fawatu, Zanzibar. Also recorded from Kenya, the Seychelle Islands and Western Australia.

Echinoid hosts: *Centrostephanus tenuispinus* H. L. Clark; *Diadema savignyi*: Michelin; *D. setosum* (Leske); *Echinothrix calamaris* (Pallas).

20. *Periclimenes hirsutus* Bruce, 1971 (fig. 1e).

Distribution: Type locality, Nukulau Is., Suva, Fiji. Also known from Zanzibar and the Seychelle Islands.

Echinoid hosts: *Astropyga radiata* (Leske).

21. *Periclimenes insolitus* Bruce, 1974

Distribution: Type locality, Waikiki, Honolulu, Hawaii. No subsequent records.

Echinoid host: *Pseudoboletia indiana* (Michelin).

22. *Periclimenes colemani* Bruce, 1975

Distribution: Type locality, Heron Island, Queensland, Australia. No further records.

Echinoid host: *Asthenosoma intermedium* H. L. Clark.

A KEY TO THE HOLOTHURIAN ASSOCIATED *PERICLIMENES* SPECIES

1. Rostrum with narrow lamina, less than 20 dorsal teeth, ventral rostral teeth present 2
- Rostrum with wide lamina, more than 20 dorsal teeth, ventral rostral teeth absent 3
2. Posterior rostral teeth mobile; chela of first pereopod not spatulate, $R \frac{10-14}{2-3}$
..... *P. hongkongensis*
- Posterior rostral teeth fixed; chela of first pereopod spatulate; $R \frac{9}{1}$
..... *P. pectiniferus*
3. Epigastric spine (situated on the dorsal mid-line of the carapace, posterior to the base of the rostrum) present; disto-lateral angle of proximal segment of antennular peduncle unidentate, dactyls of ambulatory pereopods biunguiculate $R \frac{22}{0}$ *P. rex*
- Epigastric spine absent; disto-lateral angle of proximal segment of antennular peduncle multidentate; dactyls of ambulatory pereopods with accessory spine obsolete, $R \frac{23-30}{0}$ *P. imperator*

23. *Periclimenes rex* Kemp, 1922

Distribution: Type locality, Port Blair, Andaman Islands. Also reported from Madagascar and Mocombique.

Holothuroid hosts: *Thelenota ananas* (Jaeger); *Synapta maculata* (Chamisso & Eysenhardt).

24. *Periclimenes pectiniferus* Holthuis, 1952

Distribution: Type locality, Kabala dua Island, Borneo Bank. Otherwise known only from east of Townsville, Australia.

Holothuroid host: indet.

25. *Periclimentes imperator* Bruce, 1967

Distribution: Type locality, Chumbe Island, Zanzibar. Also recorded from Madagascar, Kenya, Sinai, Seychelle Islands, Comoro Islands, Great Barrier Reef, Palau Islands and Hawaii.

Holothuroid hosts: *Stichopus chloronotus* Brandt; *S. variegatus* Semper; *Bohadschia* sp.; *Thelenota ananas* (Jaeger); *Opheodesoma spectabilis* Fisher; *Synapta maculata* (Chamisso & Eysenhardt).

P. imperator commonly occurs on the nudibranch genus *Hexabranthus*.

26. *Periclimentes hongkongensis* Bruce, 1969

Distribution: Type locality, Rocky Harbour, Hong Kong. No subsequent records.

Holothuroid host: indet.

Allopontonia Bruce27. *Allopontonia iaini* Bruce, 1972 (fig. 1a)

Distribution: Type locality, Zanzibar Harbour. Also reported from Kenya.

Echinoid host: *Salmaciella dussumieri* (L. Agassiz).

Zenopontonia Bruce28. *Zenopontonia noverca* (Kemp, 1922) (fig. 2a)

Distribution: Type locality, New Caledonia. Also reported from Zanzibar and Queensland, Australia.

Asteroid hosts: *Culcita novaeguineae* Müller & Tröschel; *C. schmideliana* (Retzius); *Pentacaster alveolatus* (Perrier); *P. tuberculatus* (Müller & Tröschel); *P. hawaiiensis* (Fisher); *Poraster superbus* (Möbius); *Protoreaster lincki* (de Blainville).

Stegopontonia Nobili, 190629. *Stegopontonia commensalis* Nobili, 1906 (figs. 1g, 6a, 8d)

Distribution: Type locality, Hao, Tuamotu Islands. Also recorded from Kenya, Mauritius and Seychelle Islands, New Caledonia, Great Barrier Reef and Hawaii.

Echinoid hosts: *Diadema savignyi*: Michelin; *D. setosum* (Leske); *D. paucispinum* A. Agassiz; *Diadema* sp.: *Echinothrix calamaris* (Pallas); *E. diadema* (Linnaeus).

Tuleariocaris Hipeau-JacquotteA KEY TO THE ECHINOID ASSOCIATED *TULEARIOCARIS* SPECIES

1. Highly elongated body form, R $\frac{8-10}{1-5}$ *T. zanzibarica*
 —. More robust body form, R $\frac{6-8}{0}$ *T. holthuisi*

30. *Tuleariocaris holthuisi* Hipeau-Jacquotte, 1965

Distribution: Type locality, Tulear, Madagascar. Also reported from Hawaii and Kenya.

Echinoid hosts: *Astropyga radiata* (Leske); *Echinothrix diadema* (Linnaeus); *Stomopneustes variolaris* (Lamarck); *Echinometra mathaei* (de Blainville).

31. *Tuleariocaris zanzibarica* Bruce, 1967 (figs 1h, 7b, 8a-b)

Distribution: Type locality, Mtoni, Zanzibar. Also reported from Madagascar, Kenya, Japan (?) and Bougainville Island.

Echinoid hosts: *Astropyga radiata* (Leske); *Diadema savigny*: Michelin; *D. setosum* (Leske); *Echinothrix calamaris* (Pallas); *E. diadema* (Linnaeus).

Parapontonia Bruce

32. *Parapontonia nudirostris* Bruce, 1968 (fig. 1d)

Distribution: Type locality, Tiare Bay, New Caledonia. Also reported from Queensland, Australia.

Crinoid hosts: *Himerometra robustipinna* (P. H. Carpenter) (new record); *Tropiometra afra* (Hartlaub).

Araiopontonia Fujino & Miyake

33. *Araiopontonia odontorhyncha* Fujino & Miyake, 1970 (fig. 1b)

Distribution: Type locality, Amami Islands, Japan. There have been no subsequent reports.

Crinoid host: indet.

Pontoniopsis Borradaile, 1915

34. *Pontoniopsis comanthi* Borradaile, 1915 (figs 1f, 8h)

Distribution: Type locality, Mabuaig, Torres Strait. Also reported from Zanzibar, Kenya, Gulf of Aqaba, Indonesia, Gilbert and Marianna Is.

Crinoid hosts: *Comanthus timorensis* (J. Müller); *Comatula pectinata* (Linnaeus) (new record); *C. purpurea* (J. Müller) (new record); *Heterometra savignyi* (J. Müller); *Lamprometra klunzingeri* (Hartlaub); *Tropiometra carinata* (Lamarck).

Conchodytes Peters

35. *Conchodytes tridacnae* Peters, 1852 (fig. 2e)

Distribution: Type locality, Ibo, Mocambique. Also known throughout the Indo-West region, from the Red Sea to Hawaii.

Holothuroid host: indet.

C. tridacnae is usually associated with the bivalve genus *Tridacna*.

Family GNATHOPHYLLIDAE

Gnathophylloides SchmittA KEY TO THE ECHINOID ASSOCIATED *GNATHOPHYLLOIDES* SPECIES

1. Rostrum short, scarcely reaching beyond cornea, $R \frac{3-4}{1}$ *G. mineri*
 —. Rostrum long and broad, extending far beyond cornea, $R \frac{2-3}{0}$ *G. robustus*
36. *Gnathophylloides mineri* Schmitt, 1933

Distribution: Type locality, Enserioda, Puerto Rico. Also recorded from Zanzibar, Seychelle Islands, Hawaii, Barbados, Florida, Yucatan, Jamaica, Antigua Island, Tobago cays and Bahia de la Ascension.

Echinoid hosts: *Pseudoboletia indiana* (Michelin); *Tripneustes gratilla* (Linnaeus).

37. *Gnathophylloides robustus* Bruce, 1973 (fig. 2c)

Distribution: Type locality, Point Moore, Geraldton, Western Australia. No further records.

Echinoid host: *Centrostephanus tenuispinus* H. L. Clark.

Levicaris Bruce

38. *Levicaris mammillata* (Edmondson, 1931) (figs 2b, 7e)

Distribution: Type locality, Waikiki, Honolulu, Hawaii. Subsequently recorded only from Japan.

Echinoid host: *Heterocentrotus mammillatus* (Linnaeus).

Pycnocaris Bruce

39. *Pycnocaris chagoae* Bruce, 1972 (fig. 2d)

Distribution: Type locality, East Point, Diego Garcia, Chagos Archipelago. No subsequent records.

Holothuroid host: *Holothuria* (*Semperothuria*) *cinerascens* (Brandt).

Family ALPHEIDAE

AthanasA KEY TO THE ECHINOID ASSOCIATED *ATHANAS* SPECIES (ADAPTED FROM SUZUKI, 1970)

1. Well-developed supra-corneal teeth *A. borradailei*
 —. Without supra-corneal teeth 2
2. With three pairs of epipodites and four pairs of setobranchiae *A. acanthocarpus*
 —. With two pairs of epipodites and three pairs of setobranchiae 3
3. Rostrum proximally broad, triangular in shape. Outer margin of palm of first pereiopod distally angular and sharply pointed at tip *A. dorsalis*
 —. Rostrum lanceolate 4
4. Outer margin of palm of first pereiopod distally angular, sharply pointed at tip. Pterygostomial margin angular *A. indicus*

— Outer margin of palm of first pereopod obtusely angular distally.
 Pterygostomial margin rounded *A. kominatoensis*

40. *Athanas dorsalis* (Stimpson, 1861)

Distribution: Type locality, near Hong Kong. Also widespread in Indian Ocean and Western Pacific Ocean, from East Africa east to the Tuamotu Islands.

Echinoid hosts: *Centrostephanus tenuispinus* H. L. Clark; *Echinothrix calamaris* (Pallas) (new record); *E. diadema* (Linnaeus); *Stomopneustes variolaris* (Lamarck); *Tripneustes gratilla* (Linnaeus); *Heliocidaris tuberculata* (Lamarck); *H. erythrogramma* (Valenciennes); *Centrostephanus rogersi* (A. Agassiz).

41. *Athanas borradailei* (Coutière, 1903)

Distribution: Type locality, Maldive Islands. No subsequent records.

Echinoid host: *Stomopneustes variolaris* (Lamarck).

42. *Athanas indicus* (Coutiere, 1905) (fig. 2f)

Distribution: Type locality not designated. Widespread throughout the Indian Ocean and western Pacific Ocean.

Echinoid hosts: *Diadema* sp.; *Echinometra mathaei* (de Blainville); *Anthocidaris crassispinia* (A. Agassiz).

43. *Athanas kominatoensis* Kubo, 1942

Distribution: Type locality, Kominato, Japan. Known only from Japanese waters.

Echinoid host: *Anthocidaris crassispinia* (A. Agassiz).

44. *Athanas acanthocarpus* Miya & Miyake, 1968

Distribution: Type locality, Kamiyama-jima, Okinawa Ryu-kyu Islands. Also known from Kenya.

Echinoid host: *Echinometra mathaei* (de Blainville).

Synalpheus Bate, 1888 (fig. 2g)

A KEY TO THE CRINOID ASSOCIATED *SYNALPHEUS* SPECIES (FROM BANNER & BANNER 1975)

- 1. Dactylus of third leg biunguiculate; without orbito-rostral process 2
- Dactylus of third leg triunguiculate; with orbito-rostral process *S. demani*
- 2. Disto-inferior margin of merus of third leg with tooth 3
- Disto-inferior margin of merus of third leg inermous 5
- 3. Dactylus of small chela crescentic, strongly hooked *S. comatularum*
- Dactylus of small chela straight 4
- 4. Fixed finger of large chela bearing strong flat tooth on medial side *S. odontophorus*
- Fixed finger of large chela with medial edge rounded, not projecting *S. stimpsoni*

5. Rostral carina strong and continued almost to posterior end of carapace*S. carinatus*
 — Rostral carina slight and terminating anterior to eye*S. tropidodactylus*

45. *Synalpheus comatularum* (Haswell, 1882)

Distribution: Type locality, Albany Passage, Torres Straits. Numerous records from Australia. Also reported from Ceylon and Singapore.

Crinoid host: *Comanthus timorensis* (J. Müller).

46. *Synalpheus carinatus* (De Man, 1888)

Distribution: Type locality, Ambon, Indonesia. Recorded from Indonesia, Malaysia, Australia and the Caroline, Marshall and Gilbert Islands.

Crinoid hosts: *Comanthina schlegeli* (P. H. Carpenter) (new record); *Comatula purpurea* (J. Müller).

47. *Synalpheus odontophorus* (De Man, 1888)

Distribution: Type localities, Tanahajampeah Island, Kai Islands, and near east coast of Timor. Also known from Sagami Bay, Japan.

Crinoid host: indet.

48. *Synalpheus stimpsoni* (De Man, 1888)

Distribution: Type locality, Ambon, Indonesia. Also known from Singapore, Thailand, Indonesia, Philippines, Japan, Marshall and Gilbert Islands.

Crinoid hosts: *Comanthina schlegeli* (P. H. Carpenter); *Comanthus parvicirrus* (J. Müller); *C. timorensis* (J. Müller); *C. japonicus* (J. Müller); *Comatula purpurea* (J. Müller).

49. *Synalpheus demani* Borradaile, 1900

Distribution: Type locality, Loyalty Islands. Also reported from Red Sea, Indonesia, Philippines, Japan and Marshall Islands.

Crinoid host: *Comanthina schlegeli* (P. H. Carpenter).

50. *Synalpheus tropidodactylus* Banner & Banner, 1975

Distribution: Type locality, off Geraldton, Western Australia. No further records. Association with crinoid is inferred.

Crinoid host: indet.

Family STENOPODIDAE

Odontozona

51. *Odontozona* sp. (fig. 2h)

Specimens of this genus have been found on crinoids off Zanzibar and Ambon, Indonesia.

In the Zanzibar specimens, they closely resemble the host in colour, and were a male and female pair. Another crinoid had a juvenile in association. The Indonesian specimen was also found on a crinoid. A report on these specimens is in preparation.

DISCUSSION

In a study of marine shrimps at Malindi, Kenya, (Bruce, 1976) of the 67 species collected, 57 were known to be 'associates'. Of these, 43.5% were associated with coelenterates, 30% with scleractinian corals, and 6% with echinoderms. A similar study of the pontoniine fauna of the Seychelle Islands (Bruce, 1976) showed 62% were associated with coelenterates and 11% with echinoderms. Although the greatest number of associations at present identified are with coelenterates, a significant proportion are with echinoderms, which rank second in importance above all other phyla as hosts.

The first pontoniine shrimp recorded as an echinoderm associate was *Periclimenes amboinensis* de Man, 1888, found on a crinoid. Subsequently *P. affinis* was reported by Zehntner (1894) from an "*Actinometra*" and Borradaile (1898) reported *P. parasiticus* (which has not been found since) on a black *Linckia*. Nobili (1904) described *P. soror*, a widespread associate of asteroids. Balss, in 1913, reported the first occurrence of a species from deeper water, *P. hertwigi* on an echinoid, *Phormosoma* sp., from 120 m. Borradaile (1915) reported on six species of pontoniine shrimps that had been found in association with crinoids from Torres Straits (*Periclimenes brocketti*, *P. ceratophthalmus*, *P. cornutus*, *P. commensalis*, *Pontoniopsis comanthi* and *Palaemonella pottsii*). The biology of several of these species was also described by Potts (1915), together with the alpheid shrimps *Synalpheus comatularum* and *S. simpsoni*. The early collectors frequently did not identify the hosts in any detail and, as some of the shrimps seem to be naturally uncommon, the identities of some of the hosts are still not known with certainty, e.g. *Periclimenes brocketti* Borradaile. Several shrimp species are still very poorly known, and have not been certainly identified since their original descriptions.

At present about 50 species of shrimp are known to associate with echinoderms in the Indo-West Pacific region. Of these, 34 belong to the Pontoniinae and 11 to the Alpheidae. No hippolytid shrimps are known to associate with echinoderms in this region. The small family of Gnathophyllidae contains four species considered as commensals of echinoderms, and it is possible that all species of this family are associated with echinoderms, either as commensals, or as predators, such as *Hymenocera picta* Dana, *Phyllognathia ceratophthalma* (Balss) and presumably *Phyllognathia simplex* Fujino. The only other shrimp associated with echinoderms is a stenopid, *Odontozona* sp., found on crinoids.

The shrimps of the Pontoniinae are found in association with all classes of the Echinodermata, although they are most numerous in association with the Crinoidea and Echinoidea. The Alpheid shrimps are associated only with echinoids and crinoids and the commensal gnathophyllid shrimps are associated with echinoids and holothurians only. With the exception of the genus *Periclimenes*, all the other shrimp genera are associated with only a single class of host. The genus *Periclimenes* at present includes 11 species associated with crinoids, 7 with echinoids, 2 (? 1 only) associated with asteroids, 2 with holothurians and one with ophiuroids. Of the 7 other pontoniine shrimp genera, 3 are associated with crinoids, 7 with echinoids, 1 with holothurians and 1 with asteroids.

Very little is known about the life of the shrimps associated with echinoderms, or how they affect their host, if they do at all. In several species the normal shrimp population of a host consists of a single male-female pair. Pairs of more than one genus or even several genera, may be present upon a single host. Much depends upon the size of the host animal, larger hosts being found to harbour more associates than the smaller. *Periclimenes imperator* is almost invariably

found in pairs on holothurians, as are the species of *Synalpheus* found in crinoids. This situation probably applies to most of the smaller hosts, but may also depend to a certain extent on the size of the the shrimp commensals. Thus a crinoid, such as *Comanthus timorensis* which may accommodate only a pair of the larger *Palaemonella pottsi* or *Parapontonia nudirostris*, may well also shelter four or five of the smaller *Periclimenes commensalis*. However, the small crinoid associate *Pontoniopsis comanthi* seems only to occur in pairs. Where only a single adult specimen is found on a host, it probably means that the partner was lost in the course of collection. Larger hosts, such as the nocturnal basket stars, often hold a considerable shrimp population — one example of *Astroboa nuda* was host for 56 specimens of *Periclimenes lanipes*. The smallest specimens in these cases are usually post-larval juveniles that have recently settled after their planktonic larval phase. In most shrimp populations the adult females seem to be almost always ovigerous. The ovary is often clearly visible in some of the more transparent species and is usually packed with large ova when the previous batch of eggs is about to hatch. Hatching of the eggs is followed the same night by moulting and the laying of a further batch of ova, so that the females are only very briefly without external eggs. As far as is known at present, all the shrimps have planktonic larvae. The larvae are distributed by the water currents and thus enabled to colonize further hosts. The duration of planktonic life is unknown and wastage of larvae is probably high. Survival will also depend upon locating an appropriate host animal on which to settle. It is probable that once the post-larval shrimps have settled on an appropriate host, they do not voluntarily leave it. The length of life of the adult shrimps remains quite unknown.

Usually each shrimp genus has its own particular niche on the body of the host, as well as its preferred host. *Athanas* species are usually on the oral surface of the test of their host echinoids, if not on the substrate. *Synalpheus* species sit together on the dorsal surface of the disc of their crinoid hosts. Species of *Tuleariocaris* and *Stegopontonia* cling to the spines of their hosts, where *Periclimenes* species are on the aboral surface of the test. *Periclimenes colemani* pairs occupy a bare area on the surface of their host's test, but how these are made is unknown. With many species their favoured station on the host is also unknown, especially in those species that are so cryptically coloured that they are virtually indiscernable when on their host. In some of these the colour pattern does provide a clue. For instance the tips of the caudal fan in *Pontoniopsis comanthi* and *Periclimenes commensalis* may have conspicuous colour spots that exactly match the tips of the crinoid hosts pinnules, suggesting that their niche is on the host's arm, and possibly on a pinnule with the shrimp's head towards the arm.

Virtually nothing is known about the food materials utilized by the shrimps that feed *in situ* on the host, rather than on the substrate. Stomach contents examined have shown no identifiable material. The mouth-parts of the shrimps show a considerable range of variation, upon which much of their taxonomy, at generic level, is based. This suggests some specialization in feeding or the food materials utilized. In the Pontoninae, all the echinoderm associates retain well developed exopods on the three pairs of maxillipeds. This contrasts with several of the genera associated with coelenterates in which the exopods of the second and third maxillipeds are lost. In most species the exopods are only moderately developed, for example *Periclimenes soror* (fig. 7a,d), *P. commensalis*, but in others, e.g. *Stegopontonia* (fig. 6a) and *Tuleariocaris* (fig. 7b), they are strongly developed and resemble those of the pontonine *Coralliocaris* (fig. 7c). In the latter genus they are capable of beating rapidly and forming a vortical current converging on the oral region. Such a current may enable these genera to feed on planktonic organisms. Their normal situation on the spines of *Diadema* or *Echinothrix* would ensure that they were in a position to utilize the passing currents. One of the most remarkable specializations found is in *Levicaris mammillata*, which occurs on *Heterocentrotus mammillatus*. In this species the second maxilliped (fig. 7e), usually a most conservative appendage in carideans, has the carpus and merus greatly elongated. The appearance of the modified appendage strongly suggests that the pair are used for scraping the host's spines and drawing foodstuffs towards the shrimp's mouth.

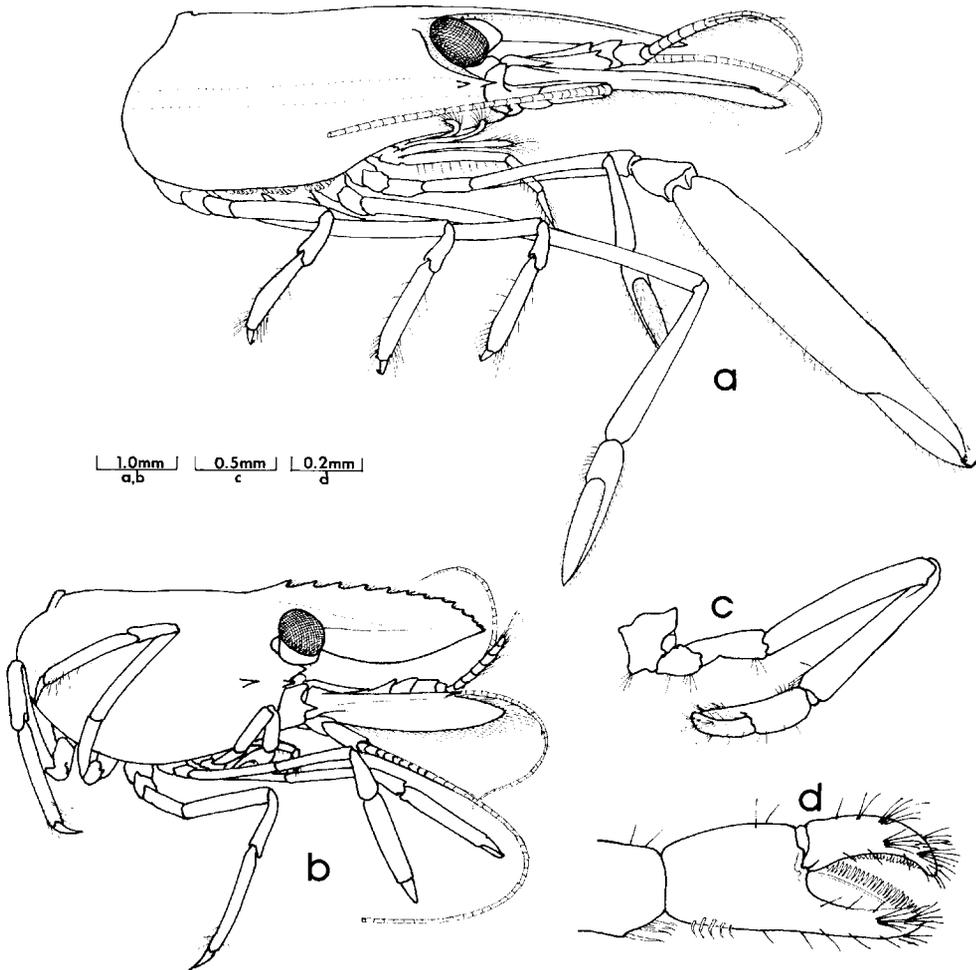


Fig. 6. a. *Stegopontonia commensalis* Nobili, cephalothorax and appendages, b. *Periclimenes soror* Nobili, cephalothorax and appendages, c. *idem*, first pereiopod, d. *idem*, chela of first pereiopod.

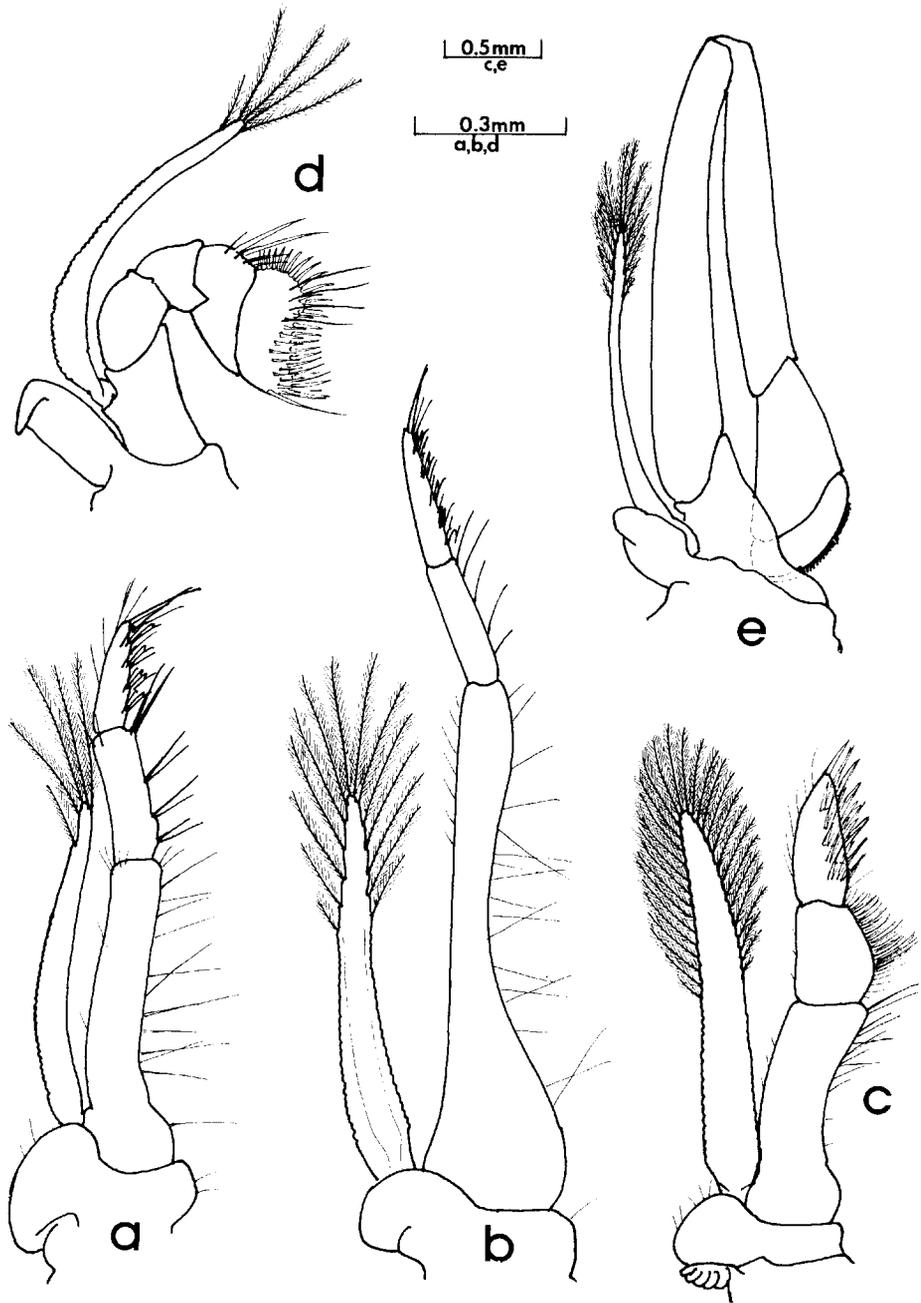


Fig. 7. Third maxillipeds. **a.** *Periclimeses soror* Nobili, **b.** *Tuleariocaris zanzibarica* Bruce, **c.** *Coralliocaris viridis* Bruce; Second maxillipeds, **d.** *Periclimeses soror* Nobili, **e.** *Levicaris mammillata* (Edmondson).

In some species of pontoniine shrimps, such as *Tuleariocaris* spp. the incisor process is greatly reduced. This suggests a diet of soft material in which no cutting up is required. In all the gnathophyllid shrimps, both commensal and free-living, which are closely related to the pontoniines, the incisor produced is completely lacking. Several of the commensal gnathophyllid shrimps have broad opercular ischio-meral segments in the third maxillipeds. Similar maxillipeds also occur in the free-living predatory *Gnathophyllum americanum*, which has been observed using these outer maxillipeds to browse on the extended papulae on the dorsal surface of asteroids. These opercular maxillipeds may have a similar browsing function in the "commensal" species of gnathophyllid shrimps. The first pair of pereopods are an essential part of the feeding mechanism in pontoniine and gnathophyllid shrimps. In several of the echinoderm associated species the chelae of these appendages have strongly subspatulate fingers (*Periclimenes imperator*, *P. lanipes*) and in some (*P. soror*, *P. pectiniferus*) the cutting edges of these fingers are distinctly denticulate (fig. 6c-d). The reduced incisor process of the mandible and the spatulate chelae of the first pereopods may be related to a diet of mucus, or mucus and entrapped particles, which may well also form the basis of a common theme running through a wide spectrum of commensal associations.

Further evidence of close adaptation of these shrimps to their hosts is shown by the dactyls of the ambulatory pereopods, with which they cling to the host's surface (fig. 8). These present a wide range of variations, from simple unornamented forms such as *Palaemonella pottsi*, or *Periclimenes ruber* (fig. 8f) to those with distal accessory spines, *P. soror* (fig. 8e) and *Pontoniopsis comanthi* (fig. 8h), or more elaborate forms, *Stegopontonia commensalis* (fig. 8d) or *Tuleariocaris zanzibarica* (fig. 8b) which has a hoof-like ventral process on the third and fifth pereopods (fig. 8a).

Details have been provided of the range of echinoderms at present known to act as hosts for Indo-West Pacific shrimps. At present 71 host species have been recognised, but undoubtedly many more remain to be identified. Crinoids and echinoids are particularly well represented, and are hosts for a wide variety of shrimps. The asteroids are hosts for only a few pontoniine shrimps and a few holothurians are utilized by a few pontoniine or gnathophyllid shrimps. Ophiuroids are particularly poorly represented as hosts and only the basket stars have attracted a single species of shrimp commensal, *Periclimenes lanipes*. Part of the explanation of this paucity of association lies in the lack of cover offered by the host. Crinoids and echinoids offer well concealed niches that are not provided by most holothurians and many asteroids. Probably also the ventral surface of these mobile animals is too closely in contact with the substrate to provide a suitable living space for animals as large as shrimps. However, some of these can be quite small, being adult at 1 cm total length, and other factors must also be involved. This is also supported by the lack of shrimp commensals on a variety of echinoids and crinoids that would appear to be suitable as hosts. As yet no shrimps have been found in association with cidarid urchins or with stalked crinoids. Most ophiuroids are probably too small and without sufficient ornamentation to provide a safe niche for commensals.

Where commensal shrimps do live in an exposed situation they usually show the closest resemblance in colour pattern to their host. A good example is *Pycnocaris chagoae* on the holothurian *H. cinerascens*, and also *Periclimenes soror* on *Acanthaster*, in its red and white colour form. In many species the shrimp colour pattern and range of variation is not well known. In several, such as *Gnathophyllodes mineri* on *Tripneustes* spp., it may be consistent throughout the whole range of distribution from Kenya to Hawaii and also the Caribbean region. Other species, such as *Periclimenes commensalis*, show a wide range of variations in colouration, each appropriate to its wide range of host species. Some species show two colour forms. *Periclimenes soror* when found on *Culcita*, *Protoreaster* or *Pentaceraster* is usually a deep purple red. When found on *Acanthaster* it is usually a bright red with a conspicuous white dorsal stripe, clearly of

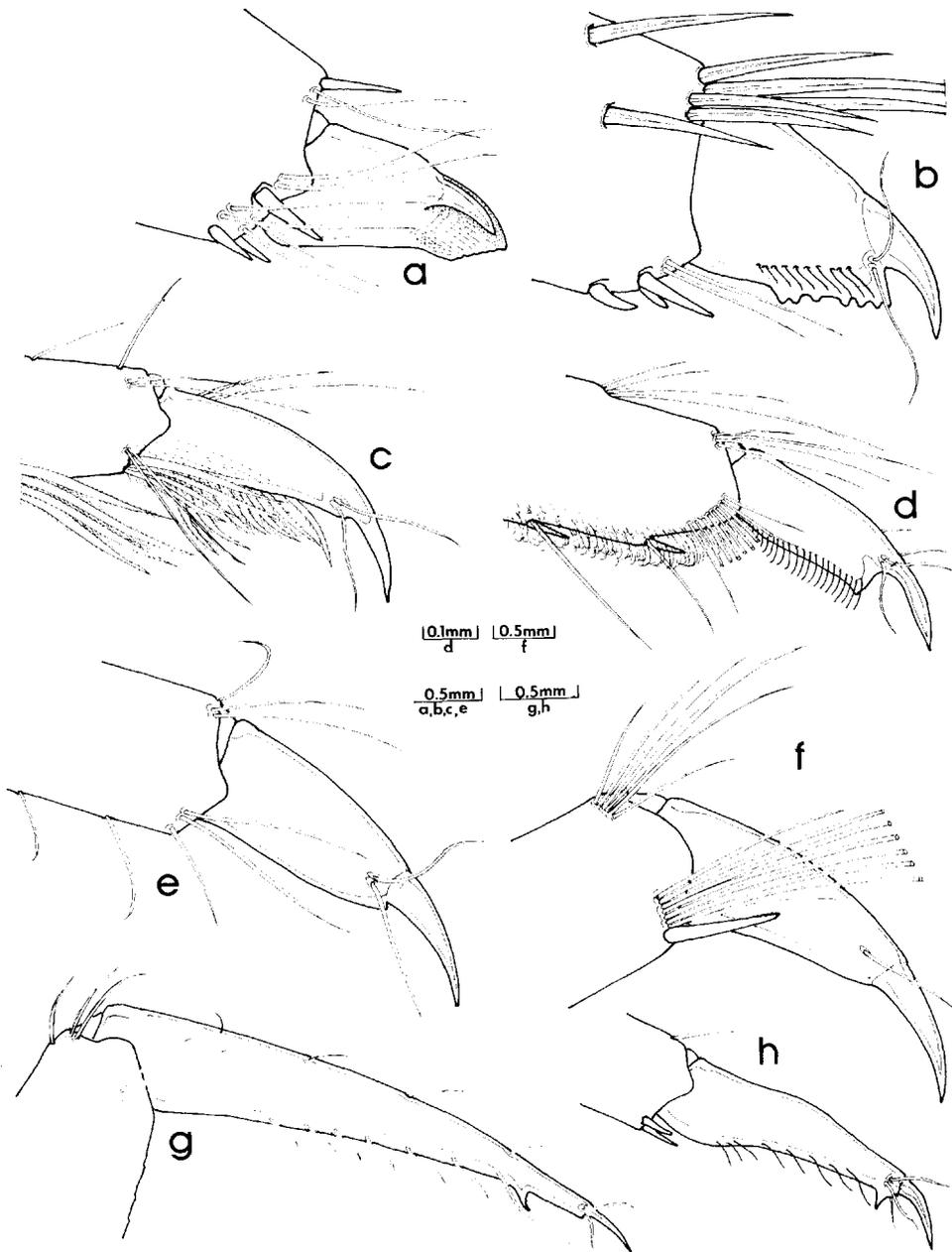


Fig. 8. Dactyls of ambulatory pereiopods. a. *Tuleariocaris zanzibarica* Bruce, third pereiopod, b. idem, fourth pereiopod, c. *Periclimenes tenuis* Bruce, third pereiopod, d. *Stegopontonia commensalis* Nobili, third pereiopod, e. *Periclimenes soror* Nobili, third pereiopod, f. *Periclimenes ruber* sp. nov., third pereiopod, g. *Periclimenes attenuatus* Bruce, third pereiopod, h. *Pontoniopsis comanthi* Borradaile, third pereiopod.

cryptic value on that host. Occasionally specimens of a particular pattern are found on the "wrong" host, and it may be that this species actually consists of two closely related species that do not show any discernable morphological differences when preserved. In contrast, *Periclimenes imperator*, also with a striking red and white colour pattern, that is very constant throughout its range from the Red Sea to Hawaii, often contrasts conspicuously with its dull coloured holothurian hosts, *Stichopus* and *Bohadschia* spp. The colour pattern is apparently genetically fixed and appropriate to that of the normal host, the red and white nudibranchs of the genus *Hexabranhus*, on which the shrimps are most inconspicuous. This species is one of the few known examples of a shrimp that lives in association with hosts of two different phyla. On the nudibranchs the shrimps nestle amongst the host's gills and are quite difficult to see. Most of the shrimps found on *Diadema* or *Echinothrix* are a dark blue-black colour, often with a fine longitudinal white line. *Athanas indicus* from *Echinothrix* is almost a uniform black colour. *Periclimenes colemani*, found in *Asthenosoma intermedium*, also closely matches its hosts colour pattern, being white with large red spots. In deeper water, *Periclimenes hertwigi* is red, with white tips to the chelae of the second pereopods and the telson. All show a clear resemblance to their host animals. Some of the species found on crinoids also enhance their cryptic colour patterns by having large parts of their bodies completely transparent. The dorsal and ventral surfaces of the body are pigmented, so that the shrimp is distinctly visible when viewed from above, but the tissues between are transparent, so that the shrimp is much less easily seen when viewed laterally. This form of colouration is found in *Palaemonella pottsi*, *Periclimenes commensalis* and *P. tenuis*.

Most of the associations mentioned above are from the shallow waters. *Periclimenes hertwigi*, found on *Phormosoma* and *Asthenosoma* in depths of up to 300 m, is the only example known to occur in deeper water as yet. However, a number of pontonine shrimps are known to occur in deeper water, and some of these species may be associated with echinoderms. *Periclimenes curvirostris* Kubo, from 310 m off Japan, seems to be a particularly likely example, in view of its close resemblance to *P. lanipes*.

One of the strangest associations concerns the pontonine shrimp *Conchodytes tridacnae*, which has been found in the cloaca of holothurians (Chopra, 1935). This shrimp is normally found in the branchial cavities of giant clams of the genus *Tridacna*. It is another of the rare cases of a commensal being found in association with hosts of different phyla.

Undoubtedly many more shrimp-echinoderm associations remain to be identified and much more needs to be known about the "commensal" relationships involved. The frequency of these associations on coral reefs and in tropical waters generally is one important component in making a major contribution to the high species diversity of these regions. Careful collections by scuba divers can provide the most useful information of these associations in shallow waters as the catches in grab, dredge or trawl hauls are usually inextricably mixed up so that the links between host and commensal are obliterated. Photography from submersibles has not shown much evidence of commensal shrimps in deeper water, but identification of cryptic species under these circumstances on their host is generally impossible. Precise collections from submersibles may provide more information.

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