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A revision of the 'petitthouarsii' species-group of the genus *Periclimenes* Costa, 1844 (Crustacea: Decapoda: Palaemonidae)

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Four *Periclimenes* species are assigned to 2 new genera and 2 new species are described and illustrated. The new genera are closely related, the characters that distinguish these taxa from other pontoniine shrimps are discussed. Both the genera are distributed within the Indo-West Pacific area. A key to the revised '*petitthouarsii*' species-group is provided.

KEYWORDS: Crustacea, Decapoda, Palaemonidae, Pontoniinae, *Periclimenes*, taxonomy, Indo-West Pacific.

Introduction

The pontoniine shrimp genus *Periclimenes* Costa, 1844, inhabits tropical and temperate marine waters of the world. About 150 species have been established up to the present time and these cover a wide range of habits from free-living shrimps to highly specialized associates of various marine invertebrates. As a result, several natural groups of species may be found within this extensive genus. An opportunity arose to examine material of some interesting shrimps related to a group of species, *P. petitthouarsii* (Audouin, 1826), *P. petitthouarsii* var. *spinifera* De Man, 1902, *P. denticulatus* (Nobili, 1906), and *P. sibogae* Holthuis, 1952. New data obtained during this study, including a description of 2 new species, have allowed us to distinguish a group of species from the genus *Periclimenes*, and to establish 2 new genera occupying rather peculiar systematic positions within the palaemonid subfamily Pontoniinae, sharing several characters usually found in shrimps of the subfamily Palaemoninae.

Only restricted synonymies of known species are given in the present paper, a full synonymy has been published by Holthuis (1952). The following abbreviations are used in the text: CL, postorbital length of the carapace; MNHN, Museum national d'Histoire naturelle, Paris; NMNH, National Museum of Natural History, Smithsonian Institution, Washington; NTM, Northern Territory Museum of Arts and Sciences, Darwin; QM, Queensland Museum, Brisbane; RMNH, Nationaal Natuurhistorisch Museum, Leiden; ZMM, Zoological Museum of Moscow State University, Moscow; and ZMA, Zoological Museum, University of Amsterdam, Amsterdam.

New genera

Family Palaemonidae Rafinesque, 1815
Subfamily Pontoniinae Kingsley, 1878

Exoclimenella gen.nov.

Diagnosis. Free-living marine palaemonid shrimps. Body slender, rostrum compressed, longer than postorbital length of carapace, provided with teeth; carapace with epigastric, antennal and hepatic spines, supraorbital spine present or absent; 4th thoracic sternite with median process, 5th sternite with transverse ridge with pair of long acute submedian processes; abdomen slender, pleura of 1st 4 segments broadly rounded; telson elongate narrowing distally into subtriangular posterior border terminating by median process, with 2 pairs of dorsal and 3 pairs of posterior spines; eyes large, cornea globular, small accessory pigment spot present dorsolaterally behind cornea; basal antennular segment with ventromedial spine and distolateral tooth, and with statocyst, stylocerite slender, last 2 segments of antennular peduncle short, upper antennular flagellum biramous with proximal part fused; scaphocerite slender, 4 or more times longer than broad, tapering distally into truncate tip, lateral margin concave with strong distal tooth overreaching end of lamina; mandibles with reduced, 1- or 2-segmented palp, or without palp, brush-like setae present on molar process; exopods present on all maxillipeds, epipods on 1st and 2nd maxillipeds, lateral coxal flange on 3rd maxilliped; 2nd maxilliped with finger-like podobranch, 2 arthrobranchs present on 3rd maxilliped; 1st pereiopods slender, chela with fingers longer than palm, fingers subspatulate laterally and provided with denticulate cutting edges situated medially; 2nd pereiopods strong and dissimilar, major chela without sound-producing fossae on cutting edges; last 3 pereiopods slender, ambulatory dactyli simple; shape of uropods normal.

Type species. *Periclimenes Petitthouarsi* var. *denticulata* Nobili, 1906.

Etymology. Combined from Latin *ex*, out of, and *Periclimenella*, name of the closely related genus.

Gender. Feminine.

Remarks. Two species, *Periclimenes denticulatus* Nobili, 1906, and *P. sibogae* Holthuis, 1952, are assigned to this new genus and 2 new species are described.

Generic distribution. Known from limited localities within the Indo-West Pacific Area including Red Sea, Maldives, **Indonesia**, Marshall Islands, Tuamotu, South China Sea, and Queensland, **Australia**.

Periclimenella gen.nov.

Diagnosis. Free-living marine palaemonid shrimps. Body slender, rostrum compressed, longer than postorbital length of carapace, provided with teeth; carapace with epigastric, antennal and hepatic spines, supraorbital spine present or absent; 4th thoracic sternite with median process, 5th sternite with pair of transverse carinae; abdomen slender, pleura of 1st 4 segments broadly rounded; telson elongate narrowing distally into subtriangular posterior border terminating with median process, with 2 pairs of dorsal and 3 pairs of posterior spines; eyes large, cornea globular, small accessory pigment spot present dorsolaterally behind cornea; basal antennular segment bearing ventromedial tooth and distolateral tooth, with statocyst, stylocerite slender, last 2 segments of antennular peduncle short, upper antennular flagellum biramous with proximal parts fused; scaphocerite slender. 4 × longer than broad, tapering distally into

truncate tip, lateral margin slightly concave with strong distal tooth overreaching end of lamina; mandibles without palp, brush-like setae present on molar process; exopods present on all maxillipeds, epipods on 1st and 2nd maxillipeds, lateral coxal flange on 3rd maxilliped; 2nd maxilliped with finger-like podobranch, one arthrobranch present on 3rd maxilliped; 1st pereiopods slender, chela with fingers longer than palm, fingers subspatulate medially and provided with lateral denticulate cutting edges; 2nd pereiopods strong and dissimilar, major chela with sound-producing fossae on cutting edges; last 3 pereiopods slender, ambulatory dactyli simple; uropods normal.

Type species. *Palaemon Petitthouarsii* Audouin, 1826.

Etymology. The generic name is derived from *Periclimenes* and *Palaemonella*, the names of 2 pontoniine genera related to the new genus.

Remarks. Two species, *Periclimenes petitthouarsii* (Audouin, 1826) and *P. petitthoarsii* var. *spinifera* De Man, 1902, are assigned to this new genus.

Gender. Feminine.

Generic distribution. Indo-West Pacific area.

Generic discussion

The presence of 2 arthrobranchs on the 3rd maxillipeds places *Exoclimenella* gen.nov. closely to the subfamily Palaemoninae, however, the posterior telson armament is typical of pontoniine shrimps. The presence of the mandibular palp in some species and of 2 arthrobranchs on the 3rd maxilliped clearly distinguishes species of the present new genus from their previous genus *Periclimenes*. Those characters, together with the median sternal spine on the 4th thoracic somite, indicate that the new genus belongs to the most primitive genera of the subfamily Pontoniinae. On the other hand, all the species of the genus have specialized cutting edges on the fingers of the 1st pereiopods. Thus, the former data introduce the new genus as intermediate between the palaemonid subfamilies Palaemoninae and Pontoniinae, but the other features place it in the latter subfamily, in a position between the group of lower genera (such as *Palaemonella*, *Vir* and *Eupontonia*) and the large group of highly specialized remaining genera.

Periclimenella gen.nov. is closely related to *Exoclimenella* gen.nov. Both genera have 3 pairs of posterior telson spines which clearly place them in the subfamily Pontoniinae. *Periclimenella* gen. nov. is more advanced lacking the mandibular palp and the upper arthrobranch on the 3rd maxilliped, and differs from *Exoclimenella* gen. nov., as well as from all species of the related genus *Periclimenes*, by the presence of highly specialised sound-producing structures on the major 2nd chela. The presence of the single median process on the 4th thoracic sternite brings both new genera in the relationship with *Palaemonella* and several more primitive species of *Periclimenes*. The latter character, if combined with pectinate cutting edges of spatulate fingers of the 1st pereiopods and simple ambulatory dactyli, distinguishes species of *Periclimenella* gen.nov. from the species with which they were formerly associated in the genus *Periclimenes*. *Periclimenella* gen.nov. may also be easily distinguished from *Exoclimenella* gen.nov. by the medial, instead of lateral, position of the concavity on fingers of the 1st pereiopods, and by the absence of the pair of the long and acute submedian processes on the 5th thoracic sternite.

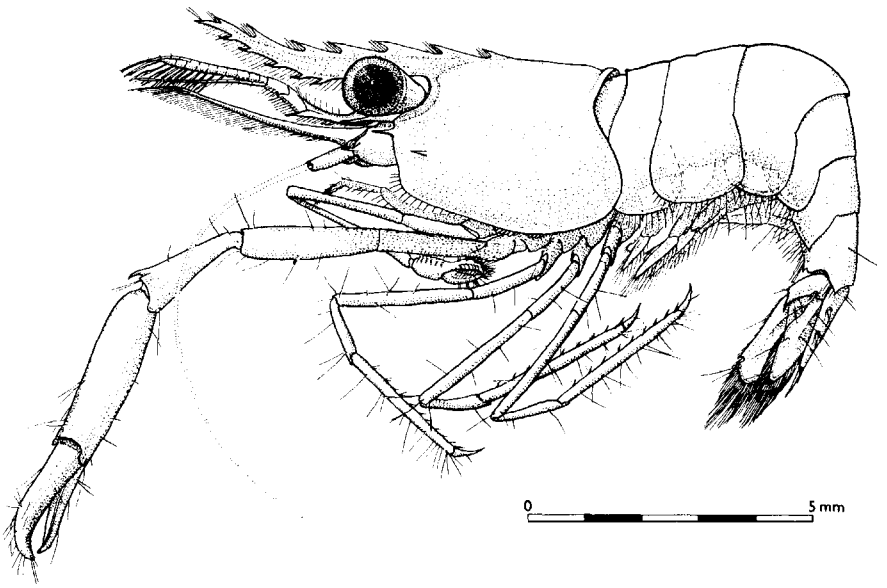

FIG. 1. *Exoclimenella maldivensis*, sp.nov., Holotype, ♂: lateral view. Scale in mm.

New species

Exoclimenella maldivensis, sp.nov.
(Figs 1–5)

Material. R/V *Akademik Petrovskii*, cruise IX, st. 34; Genego Islet, North Nilandu Atoll, Maldive Islands; outer reef-slope, 20 m, SCUBA, coral head of *Seriatopora* sp., coll. ;34(4), 9 March 1980; coll. A. V. Tchesunov; 5 specimens (2 ♂♂ and 3 ♀♀ (2 ovig.)).

St. CA.2; Cartier Reef, Timor Sea, 12°32′S. 123°32′E, depth 18 m, 4 May 1992, coll. J. W. Short; NTM Cr.009566; 6 specimens (3 ♂♂, 2 ovig. ♀♀. 1 juvenile specimen).

St. Ca.23, Cartier Reef, Timor Sea, 12°31′S, 123°32·7′E, depth 12 m, 8 May 1992, coll. J. W. Short; QM W 17692; 1 juvenile specimen.

Description of the male holotype; body generally subcylindrical, moderately slender, smooth (Fig. 1).

Rostrum (Fig. 2A) well developed, slightly sinuate, 1·2–1·3 × longer than CL, far exceeding distal end of antennular peduncle, reaching nearly to end of scaphocerite; dorsal margin with 6 acute teeth, 1st tooth situated behind orbits; ventral margin with 5 acute teeth placed distally, 1st tooth placed below 4th dorsal tooth. Orbits obsolete, lower orbital angle rounded, not produced; epigastric, antennal and hepatic spines present, supraorbital spine absent; antennal spine submarginal, situated immediately below lower orbital angle, hepatic spine placed on lower level and more posteriorly; anteroventral angle of carapace rounded and setose.

Fourth thoracic sternite with long narrow median process (Fig. 2I); 5th with pair of long slender submedian processes placed on broadly rounded transverse ridges, separated by deep fissure (Fig. 2J).

Abdomen (Fig. 1) with posterior dorsal margins of 1st–3rd segments with fine denticulation (most developed on 3rd segment); pleura of 4 anterior segments rounded,

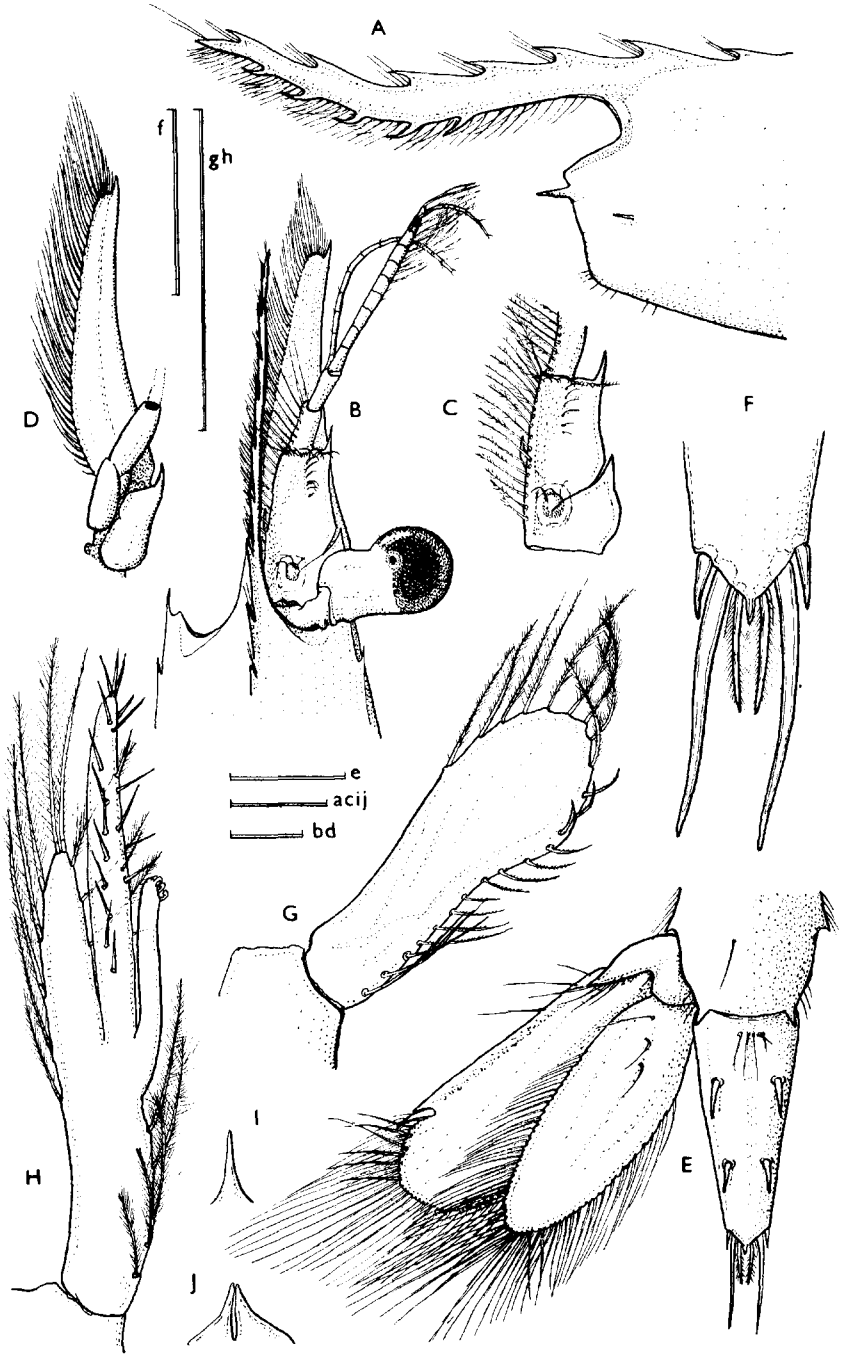

FIG. 2. *Exoclimenella maldivensis*, sp.nov., Holotype, ♂: (A) anterior carapace and rostrum, lateral aspect; (B) anterior part of body, dorsal aspect; (C) basal antennular segment, dorsal aspect; (D) antenna, ventral aspect; (E) posterior abdomen, telson and uropod; (F) posterior telson spines; (G) endopod of male 1st pleopod; (H) endopod of male 2nd pleopod; (I,J) ventral processes of 4th (I) and 5th (J) thoracic sternites. Setulae omitted on (D) and (E). Scales: 1 mm (a–e, i,j), 0·5 mm (f–h).

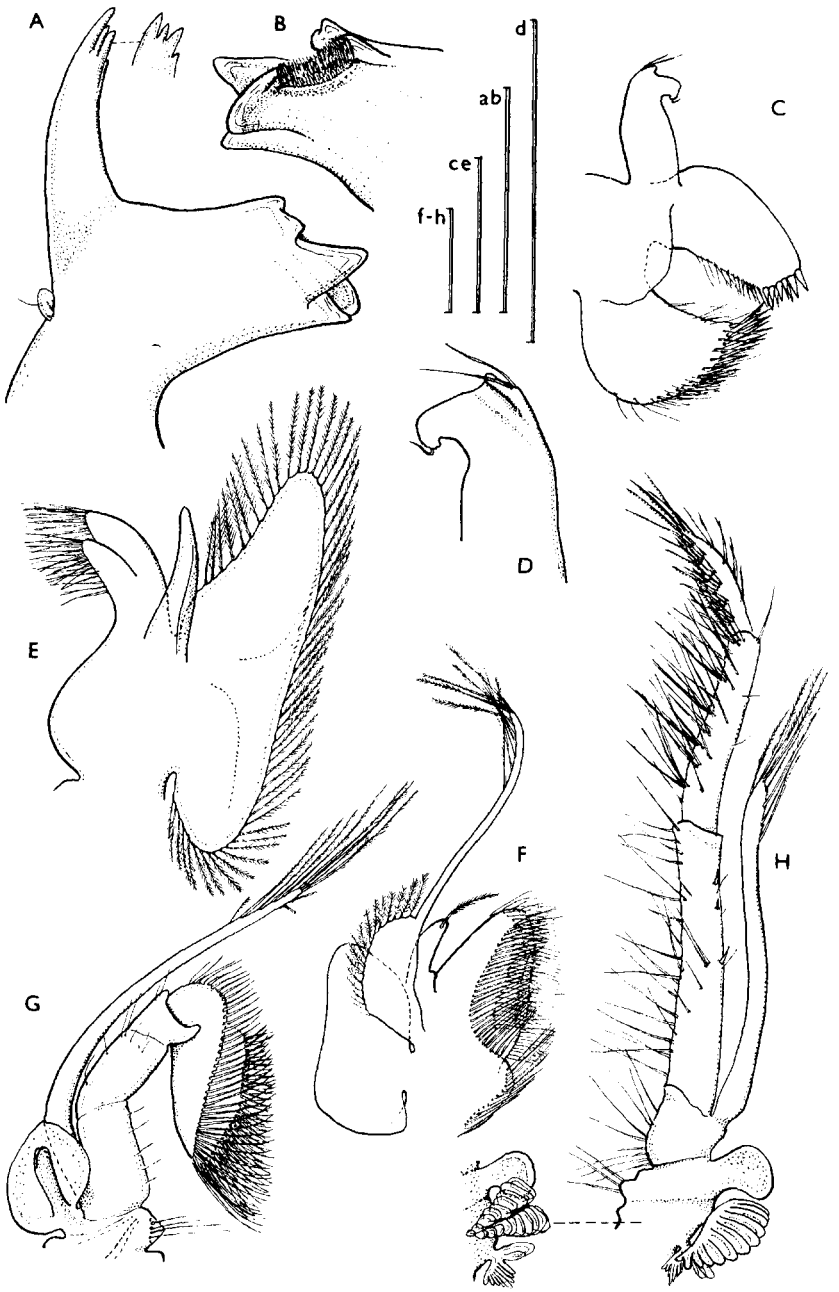

FIG. 3. *Exoclimenella maldivensis*, sp.nov., Maldive Is., paratype, ♂ CL 2·7 mm: (A) mandible; (B) same, molar process; (C) maxillula; (D) same, palp; (E) maxilla; (F) 1st maxilliped; (G) 2nd maxilliped, (H) 3rd maxilliped. Scales: 0·5 mm.

5th segment with acute posterolateral angles, 6th segment with both posterolateral and posteroventral angles acute.

Telson (Fig. 2E) about 1·4 × length of 6th segment, 2·2 × longer than wide anteriorly, sides nearly straight, converging posteriorly; transverse row of setae present

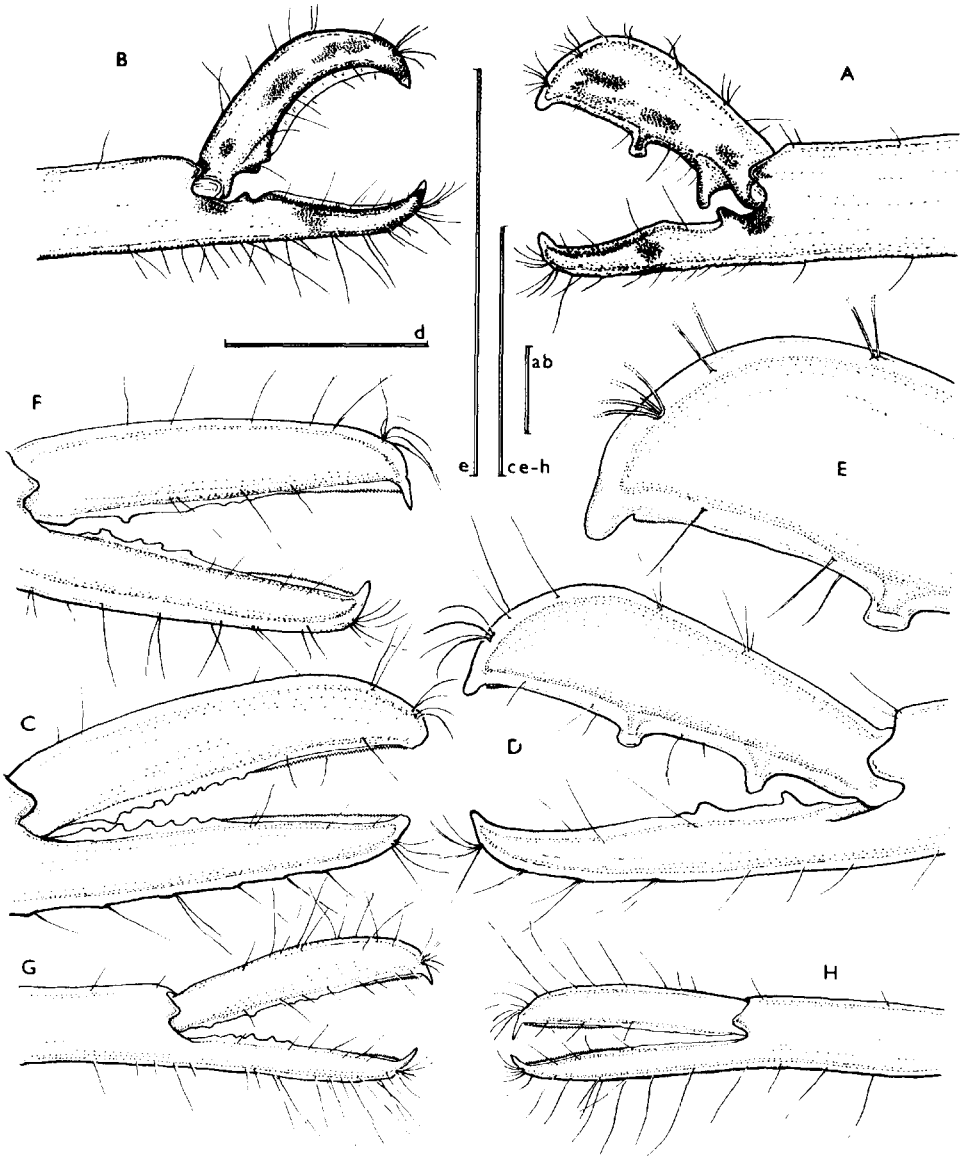

FIG. 5. *Exoclimenella maldivensis*, sp.nov., Timor Sea, NTM Cr. 009566: ♂ CL 3·7 mm (A,B), ovig. ♀ CL 3·6 mm (C–E), ♂ CL 2·7 mm (F); QM W17692: juvenile spm. CL 1·7 mm (G,H). (A,D,E,G) major chela; (B,C,F,H) minor chela. Scales: 1 mm.

on anterior midline of telson; posterior border broadly triangular with acute median process, 0·4 of anterior width; 2 pairs of strong dorsal spines present respectively at 0·3 and 0·6 of telson length, length of spines about 0·17 of telson length; 3 pairs of posterior spines present (Fig. 2F), lateral pair about 0·7 of dorsal spines length, intermediate pair long, about 0·4 of telson length, submedian pair 0·45 of intermediate spines length, bilaterally setulose.

Antennular peduncle (Fig. 2B,C) reaching to 0·7 of length of rostrum; distal margin of proximal segment nearly straight, ventromedial and strong distolateral spines

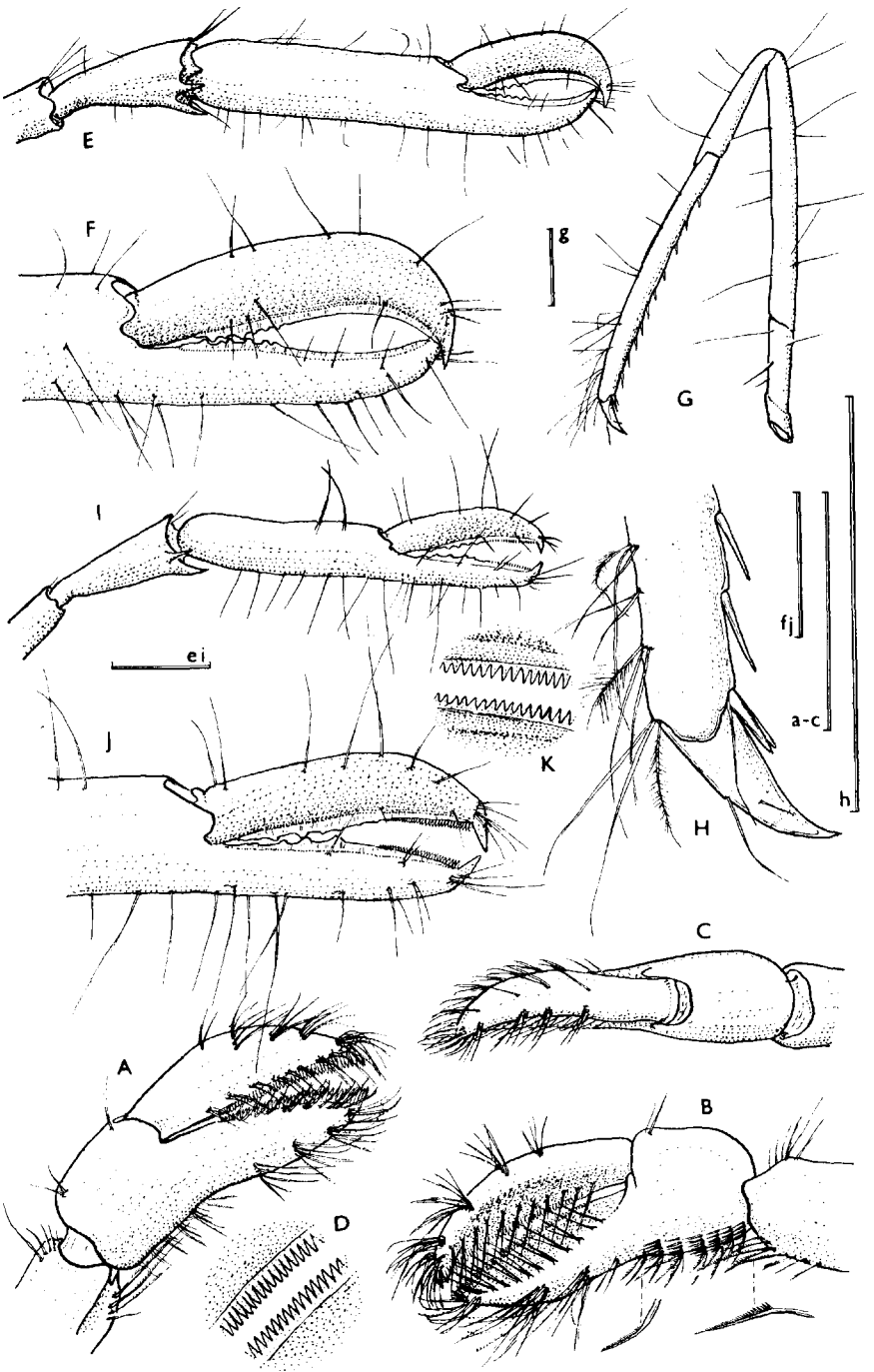

FIG. 4. *Exoclimenella maldivensis*, sp.nov., holotype, ♂ (A–H), allotype, ♀ (I–K): (A) left chela of 1st pereiopod, medial aspect; (B) same, lateral aspect; (C) same, dorsal aspect; (D) same, denticulation of cutting edges; (E) major 2nd chela, inner aspect; (F) same, fingers; (G) 3rd pereiopod; (H) same, distal propodus and dactylus; (I) minor 2nd pereiopod; (J) same, fingers; (K) same, denticulation of cutting edges. Scales: 1 mm.

present, stylocerite reaching half segment length; intermediate and distal segments with combined length about 0·5 of proximal segment length. Upper flagellum biramous with fused part consisting of 8 segments, short free ramus with 2 segments, long free ramus slender and with about 7 segments; about 10 groups of aesthetascs present on upper flagellum. Lower flagellum filiform, with about 12 segments.

Antenna (Fig. 2D) well developed; basicerite with strong lateral tooth, carpocerite short with length about 2·5 of width; flagella lost in specimens studied. Scaphocerite long, narrow, reaching far beyond antennular peduncle, slightly beyond tip of rostrum, about 5 × longer than broad proximally; anterior border rounded, lateral margin concave with strong distal tooth far exceeding anterior margin of scaphocerite.

Eyes (Fig. 2B) large with cornea globular, small accessory pigment spot present on stalk behind cornea; eyestalk slightly depressed, narrower than cornea in lateral aspect.

Mouth-parts as described for male paratype (see below; Fig. 3).

First pereiopod reaching beyond tip of rostrum by chela; chela (Fig. 4A–C) with palm compressed and subquadrate in lateral aspect, about 6 transverse rows of brush setae present ventrolaterally on palm; fingers about 1·6 × palm length, cutting edges finely denticulate and situated medially forming deep cavity on outer (lateral) side of closed chela, distolateral transparent lamina on fingers present (Fig. 4B), rather narrow, not enlarged; chela with groups of specialized setae, palmar brush setae with compressed and slightly enlarged proximal part, distal part curved anteriorly, densely serrulate along anterior margin (Fig. 4B), fingers with transverse rows and terminal patches of long curved serrulate setae on external borders, and with about 11 groups of 2–3 simple straight setae on lateral sites directed over concavity, opposing similar setae of opposite finger; carpus tapering proximally, slightly $< 2 \times$ of chela length, with some long, anteriorly directed distoventral, dorsally setulose setae; merus slightly shorter than carpus; ischium, basis and coxa short, without special structures.

Major chela lost in holotype specimen.

Minor 2nd pereiopod (Fig. 4E) with chela length about 1·8 of CL; fingers occupying distal 0·4 of chela length; fixed finger with upcurved tip; movable finger robust, subcylindrical, about 5 × longer than deep, distal end downcurved, with acute tip; cutting edges of fingers with sharp transparent lamina bearing proximally 5–6 small, bluntly rounded teeth (Fig. 4F); palm subcylindrical, smooth, about 4 × longer than deep; carpus short, about 0·5 of palm length, tapering proximally, distal margin with 2 spines—ventral and medial; merus unarmed, subcylindrical, about 2·8 × longer than carpus; ischium subequal to merus and tapering proximally; basis and coxa without special features.

Ambulatory pereiopods slender. 3rd pereiopod (Fig. 4G) reaching to end of rostrum; dactylus simple, 0·18 of length of propodus, with ventral margin straight, unguis feebly distinguishable from corpus, tip downcurved; propodus about 13 × longer than nearly uniform depth, ventral margin with 10 single spines and pair of distal spines; carpus 0·45 of propodal length, unarmed, about 5 × longer than distal depth; merus as long as propodus and about 10 × longer than deep, uniform, unarmed; ischium, basis and coxa short, without special structures.

Endopod of 1st male pleopod (Fig. 2G) elongate with greatest width distally, narrower proximally; medial border with 14 anteriorly setulose setae decreasing in length from very long proximal to distal setae; 9 plumose setae on distal and distomedial border. Endopod of 2nd male pleopod (Fig. 2H) with 5 plumose setae proximally on medial margin, with 11 plumose setae on distomedial and distal half of lateral margin; well developed appendix masculina far overreaching both narrow appendix interna and

slightly longer endopod; appendix masculina with numerous short slender spines sparsely covering distal 0·8 of length.

Uropod (Fig. 2E) with protopodite bearing strong acute posterolateral lobe; exopod about 2·5 × longer than broad, lateral border straight, with distinct distal tooth and movable spine 2 × longer than lateral tooth; endopod reaching nearly to distal margin of exopod, about 2·5 × longer than wide.

Branchial formula as following:

	Maxillipeds			Pereiopods				
	I	II	III	1	2	3	4	5
Pleurobranchs	–	–	–	1	1	1	1	1
Arthrobranchs	–	–	2	–	–	–	–	–
Podobranchs	–	1	–	–	–	–	–	–
Epipods	1	1	–	–	–	–	–	–
Exopods	1	1	1	–	–	–	–	–

Male paratype. (Maldive Is., CL 3·0 mm). This individual agrees well with the description of the holotype, with the following exceptions: (1) rostrum 1·5 × longer than CL; (2) rostrum with 8 dorsal and 5 ventral teeth. Both the 2nd pereiopods are lost.

Mouth-parts have been examined in this specimen: mandible (Fig. 3A,B) robust, with stout molar process bearing 4 blunt teeth and area of short brush-like setae; incisor process with distal margin possessing 4 teeth, 3 distal teeth larger, with strong distal tooth and smaller 2nd tooth, 3rd tooth nearly as strong as distal tooth, 4th tooth small, inconspicuous, situated more proximally; with small, 1-segmented palp with single subapical seta (Fig. 3A). Maxillula (Fig. 3C) with bilobed palp (Fig. 3D), upper lobe small, with single subapical seta, lower lobe with small uncinate seta; upper lacinia downcurved, with about 8 stout spines distally, with row of setae on lower margin; lower lacinia with broadened setose distal margin. Maxilla (Fig. 3E) with well developed finger-like palp without setae; basal endite bilobed, lobes subequal, setose; coxal endite broadly rounded; scaphognathite with outer margin slightly concave, about 4 × longer than broad. First maxilliped (Fig. 3F) with finger-like palp bearing single plumose terminal seta, not exceeding distal margin of caridean lobe; basal endite produced, well exceeding distal end of palp; coxal endite less developed, broadly rounded; caridean lobe broadly rounded; epipod well developed, tapering distally. Second maxilliped (Fig. 3G) with slender exopod with some plumose setae distally; coxa with triangular medial lobe bearing 5 long setae; epipod broadly ovate with long simple podobranch. Third maxilliped (Fig. 3H) with endopod reaching to distal end of carpocerite; ischiomerus about 5 × longer than broad, with 3 spinules distolaterally and sparsely setose medially; penultimate segment about 0·7 of ischiomeral length, with long setae medially; terminal segment tapering distally, about 0·65 of penultimate segment length, with 6 transverse rows of setae and group of terminal serrulate setae; basis medially rounded bearing 5 long setae; exopod slender, with plumose setae distally; coxa produced into subtriangular medial lobe with 3 setae, lateral flange broadened; 2 arthrobranchs present, lower arthrobranch well developed, consisting of about 11 pairs

of rounded lamellae, upper arthrobranch small, consisting of series of 2 and 8 lamellae (Fig. 3H).

Female allotype. Specimen conforms well with description of holotype. Rostrum length about 1·3 of the postorbital carapace length, 7 dorsal and 5 ventral teeth present. Mandibles with 1-segmented palp. Major 2nd pereiopod missing. Minor 2nd pereiopod (Fig. 4I) detached from the body; general shape similar to that of cheliped in holotype, but more slender; palm subcylindrical; fingers (Fig. 4J) nearly straight and distally compressed, with strongly curved acute tip, and occupying 0·43 of the chela length; cutting edges with sharp narrow transparent lamina bearing several (6 on the dactylus, 4 on the fixed finger) low obtuse teeth on the proximal half of lamina, and row of about 30 acute denticles diminishing posteriorly on distal third, denticulation similar to that of 1st pereiopod chela (compare Fig. 4K and D). Chela sparsely covered with long simple setae, carpus 0·36 of chela length, narrowing proximally, 2 distal (ventral and medial) teeth present; merus unarmed and about 1·5 × longer than carpus, ischium slightly shorter than merus. Walking legs and uropods as in the holotype.

Ovigerous females paratypes. (Maldive Is., CL 3·4 and 3·0 mm). Agree well with allotype. Rostral formula 6–7/4; 1-segmented mandibular palp present, branchial formula as in holotype. Upper lobe of maxillular palp possessing 3 subterminal setae. Larger female with about 100 eggs in an early stage of development, smaller female bearing about 60 ova with eyespots.

Measurement (mm) of the Maldive types:

			Paratypes		
	Holotype ♂	Allotype ♀	♂	Ov.♀	Ov.♀
Postorbital carapace	3·4	2·8	3·0	3·4	3·0
Rostrum	4·6	4·0	4·6	4·5	4·0
Total length	18·0	–	16·0	16·0	–
Telson	2·2	1·8	2·0	2·1	1·9
First pereiopod	8·2	6·9	7·4	7·5	6·8
Major second pereiopod	12·5	–	–	–	–
chela	5·4	–	–	–	–
Minor second pereiopod	–	10·0	–	–	–
Third pereiopod	8·8	6·9	7·8	–	–
Eggs (stage):	–	–	–	(early)	(eyes)
length				0·56	0·64
diameter				0·46	0·53

Types. The Maldive ♂ CL 3·4 mm is designated as the HOLOTYPE, the Maldive non-ovig. ♀ CL 2·8 mm is designated as the ALLOTYPE. The others (♂ CL 3·0 mm, ovig. ♀♀ CL. 3·4 and 3·0 mm), including the Timor Sea specimens (♂♂ CL 3·7, 2·7 and 2·4 mm, ovig. ♀♀ CL 3·6 and 2·8 mm, and the juvenile CL 1·6 mm), are PARATYPES. The Maldive type series is deposited in the Zoological Museum of Moscow State University, Moscow (ZMM No.: 4401—holotype, 4402—allotype, 4403—paratypes), the Timor Sea paratypes are deposited in the Northern Territory Museum of Art and Sciences, Darwin (NTM Cr. 009566—1 ♂, 1 ovig.♀), in the Queensland Museum,

Brisbane (QM W 17692—1 juv.spm), in the Nationaal Natuurhistorisch Museum, Leiden (RMNH D 42626—1 ♂, 1 ovig. ♀), and in the National Museum of Natural History, Smithsonian Institution, Washington (NMNH catalogue number 265045—1 ♂, 1 juv. spm).

Etymology. The name is derived from the Maldive Islands, where the species was first discovered.

Systematic position (see below—Species discussion).

Remarks. The Maldive material studied was in good condition. Unfortunately, all the shrimps lacked the 2nd pereiopods excluding the minor chelipeds of both the holotype male and the allotype. That leg of the latter was found detached from the body but lying in the same tube with the specimen.

The 7 Timor Sea specimens were in perfect condition. All of them agree well with the specimens of the Maldive series and share also all the main morphological features with them: (1) the rostral formula 2 + 6/3–5 (the Maldive types—2 + 5–7/4–5); (2) the median sternal process on the 4th thoracic segment and the pair of elongate subtriangular processes on the 5th segment; (3) the reduced, 1-segmented mandibular palp with a subterminal seta in most specimens (the ovig. female CL 3·6 mm has 2-segmented palps, in the ovig. female CL 2·8 mm the right mandible bears 2-segmented palp while the left mandible has 1-segmented palp); (4) bilamellate podobranch on the epipod of the 2nd maxilliped; (5) 2 arthrobranchs on the 3rd maxilliped, with the upper arthrobranch more reduced; (6) the subspatulate chelae of the 1st pereiopods bearing denticulate cutting edge and distolateral laminae, and with spatulate concavity facing laterally; (7) the endopods of the male 1st and 2nd pleopods as described above (Figs 2G,H).

One of the most interesting features in the new species is the presence of the fine denticulation on the distal part of cutting edges of chelae on the 2nd periopods (Figs 4J,K, 5C–H). Several specimens possess both of the 2nd pereiopods. However, a wide range of variation in the shape of fingers may be observed in these specimens. The fine denticulation of the distal part of cutting edge is not present on the chelae of each specimen, at least in the largest adult male (CL 3·7 mm). In this specimen the minor chela (Fig. 5B) is like that described for the holotype (Figs. 4E,F), and provided with a stout, strongly hooked dactylus, and with a simple transparent lamina along the cutting edges bearing several rounded teeth proximally. The major chela (Fig. 5A) is similar to the minor chela in general shape, but larger, and with a stronger, heavily sclerotized broad and deep dactylus. The dactylus bears 2 teeth on the ventral margin, a narrow, posteriorly directed proximal tooth with acute apex, and a subcylindrical, 'mushroom-like' tooth—narrower near the base and broader in the flat, slightly concave, circular apex. Fixed finger has 1 proximal, anteriorly directed tooth and a simple cutting edge distally.

Two ovigerous females are present in the Timor Sea material. The right chelipeds are missing in both of them, however, the left chelae differ from each other. The largest ovig. female (CL 3·6 mm) possess the 'major-shaped' chela, the smaller ovigerous female has the chela similar to that described as 'minor' for the allotype female (Fig. 4I). It bears a sharp transparent lamina provided with irregular rounded proximal teeth and a series of fine denticulations on the distal part of the fingers, terminating with strong and acute perpendicular tips. A short series of minute denticles is also present distally on the cutting edge of the major chela of the larger female (Fig. 5E). This may indicate a possible reduction of the denticulation during the ontogeny.

The intermediate male (CL 2·7 mm) from the Timor Sea material has the major

chela with the typical major shape, but the minor chela differs from equivalent leg of the large male. It is more slender and possesses the denticulate distal cutting edge. The juvenile (CL 1·7 mm; W 17692) has both chelae similar and subequal, rather slender and with denticulations on distal half of cutting edges.

It is evident that the cutting edge denticulation mentioned above is a feature associated with developmental stages in this species and may also depend on the sex of the specimen. Although additional specimens, especially females with both the 2nd pereiopods, are required for final conclusions concerning this character, we can now state that the feature mentioned is of specific importance although not entirely reliable for the identification of all specimens.

The ovigerous females mentioned above bear eggs in different stages of development. The larger female has numerous eggs at an early stage measuring 1·2 × 0·5 mm, the smaller female bears about 30 ova with eye-spots, 1·15 × 0·45 mm.

Colour. No data are available on the colour pattern of the Maldive specimens. The Timor Sea specimens, freshly preserved in alcohol, and provided with collector's note 'red eye', show the distinct deep carmine-violet coloration distributed as follows: the cutting edges and outer margins on chelae of the 2nd pereiopods; 3 large spots on each side of movable fingers and 1 spot on each side of fixed fingers on those chelae; the palm along the articulation with the dactylus; minute dots at diffused setal bases on the palm, carpus and merus of the 2nd pereiopods; basal segments (proximal ischium, basis, and coxa) of the 2nd to 4th pereiopods; the distal margin of the telson, proximal parts of dorsal and posterior telson spines; the distolateral spine and tooth of the uropodal exopod.

Habitat. The Maldive material was found in a coral colony of *Seriatopora* sp. measuring 30 cm in diameter and situated 20 m deep on an outer reef slope. The coral colony was sparsely covered with red sponges encrusting thin coral branches.

Associated decapod fauna. The coral head where the Maldive specimens were found was also occupied by the following decapod crustaceans: palaemonid shrimps—*Apopontonia falcirostris* Bruce (3 specimens), *Jocaste lucina* (Nobili) (1 specimen), *Periclimenaeus tchesunovi* Ďuriš (1 specimen); alpheid shrimps—*Synalpheus streptodactylus streptodactylus* Coutière (8 specimens), *S. neptunus neptunus* Dana (1 specimen), *S. hastilicrassus* Coutière (10 specimens); 2 galatheids, 2 porcellanid crabs *Polyonyx triunquiculatus* Zehntner, 7 xanthoid crabs *Trapezia coerulea* Rüppel, as well as 12 other xanthoid and 1 majid crabs. The red sponge noted above, rather than the coral, is probably the true host of shrimps of the genera *Apopontonia, Periclimenaeus* and *Synalpheus.*

Distribution. North Nilandu Atoll, Maldive Islands; Cartier Reef, Timor Sea.

Exoclimenella sudanensis sp.nov.
(Figs 6–8)

Periclimenes sibogae—Edwards and Emberton, 1980: 236 (Tab.V, list);—**non** Holthuis, 1952.

Material. Coral reef near Port Sudan, Sudan, Red Sea; in coral head of *Stylophora pistillata* (Esper), August–September 1978, leg. H. Emberton, don. A. J. Edwards, RMNH 37304 [as *Periclimenes sibogae*]; 1 ♂ (HOLOTYPE).

Description. (Male holotype); body generally sub-cylindrical, moderately slender, smooth (Fig. 6).

Rostrum well developed, slightly sinuate, 1·34 × longer than CL, far exceeding end

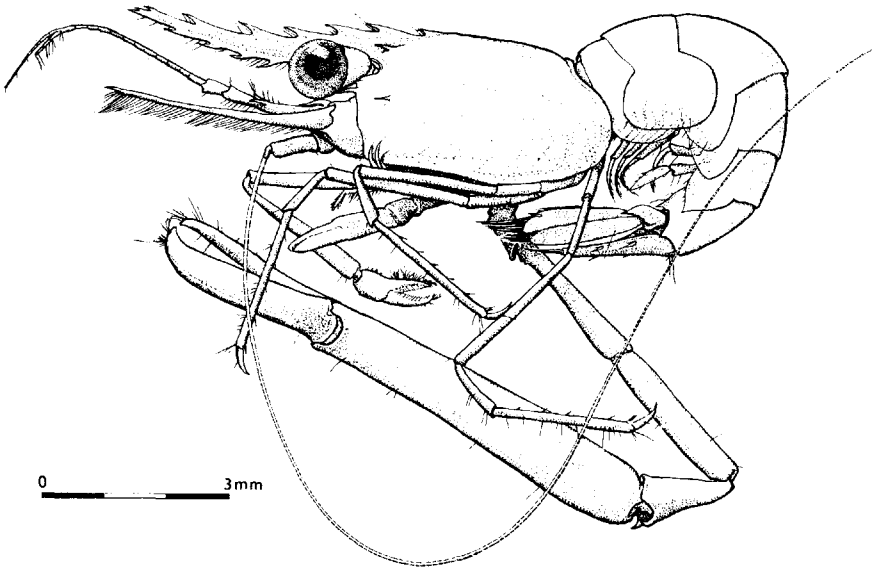

FIG. 6. *Exoclimenella sudanensis* sp.nov., Holotype, ♂. Lateral view. Scale in mm.

of antennular peduncle and reaching nearly to end of scaphocerite; dorsal margin with 7 acute teeth, 1st tooth situated behind orbit; ventral margin with 4 acute teeth placed on distal half. Orbits obsolete, lower orbital angle pointed, not produced; epigastric, supraorbital, antennal and hepatic spines present, last 3 subequal; antennal spine submarginal, situated immediately below lower orbital angle, hepatic spine placed more posteriorly at slightly lower level; anteroventral angle of carapace subrectangular and rounded.

Fourth thoracic sternite with moderately developed narrow median process; 5th sternite with pair of long slender submedian processes placed on broadly rounded transverse ridges, separated by deep notch (Fig. 7C).

Abdomen with posterior dorsal margins of 1st to 3rd segments with fine denticulation (most developed on 3rd segment) (Fig. 7D); pleura of 4 anterior segments rounded, 5th segment with acute posterolateral angles, 6th segment with both posterolateral and posteroventral angles acute; 6th segment about 1·6 of length of 5th segment.

Telson (Fig. 7E) about 1·4 × length of 6th segment and 2·5 × longer than wide anteriorly, sides slightly sinuate, converging posteriorly; transverse row of setae present on anterior midline of telson; posterior border broadly triangular with long acute median process, 0·4 of anterior width; 2 pairs of strong dorsal spines present at 0·3 and 0·6 of telson length respectively, length of spines about 0·13 of telson length; 3 pairs of posterior spines present, lateral pair about 0·7 of dorsal spines length, intermediate pair long, about 0·34 of telson length, submedian pair 0·45 of intermediate spines length, bilaterally setulose.

Antennular peduncle (Fig. 7A) exceeding 0·5 of length of rostrum; basal segment with straight distal margin, distolateral and ventromedial spines present, stylocerite reaching 0·5 segment length; intermediate and distal segments with combined length about 0·45 of basal segment length, distal segment narrower than intermediate segment. Upper flagellum biramous with fused part long and slender, with 12 segments, short

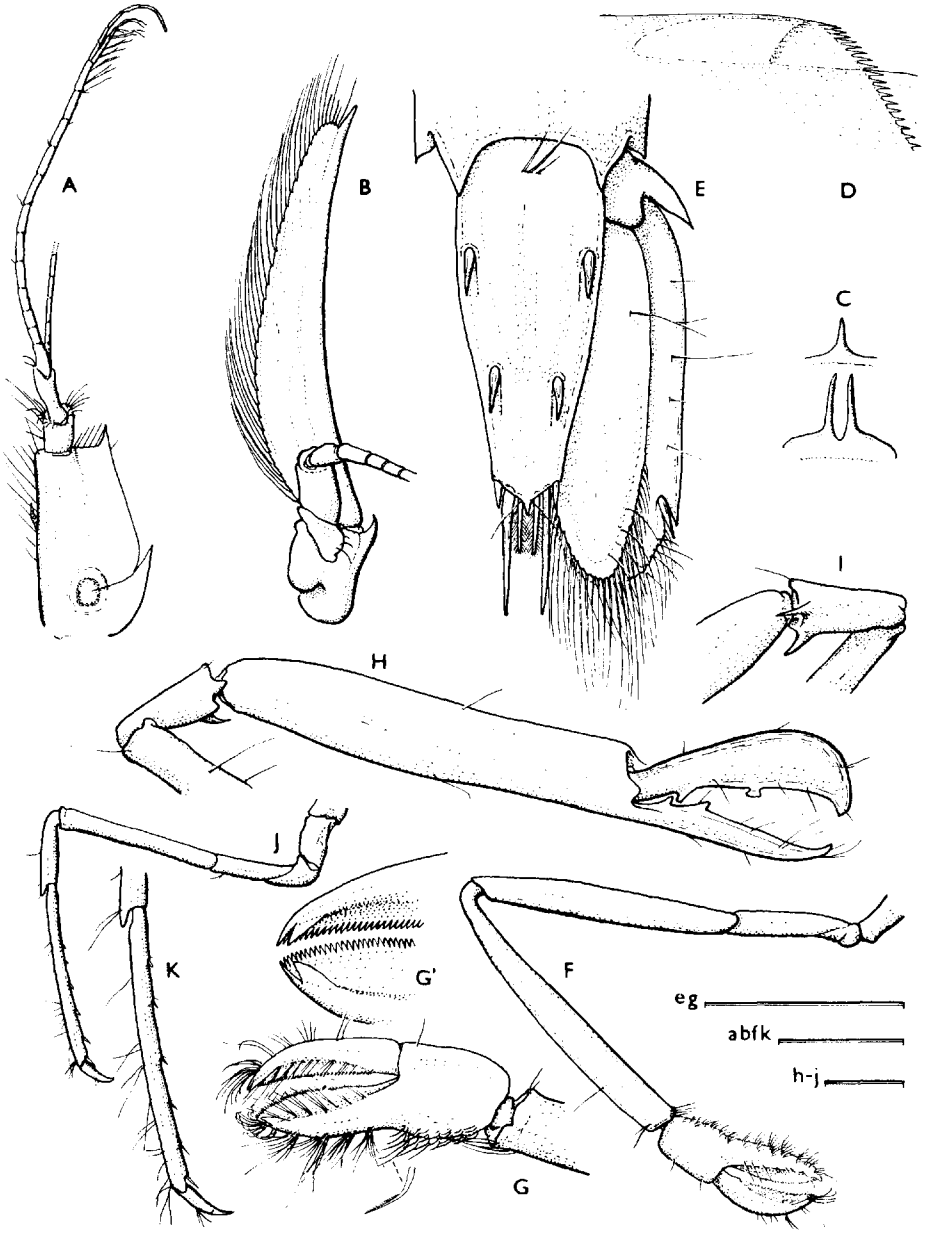

FIG. 7. *Exoclimenella sudanensis* sp.nov., Holotype, ♂: (A) antennule, dorsal aspect; (B) antenna, ventral aspect; (C) thoracic sternites of 4th (above) and 5th (below) segments; (D) dorsal part of posterior margin of 3rd abdominal tergite, antero-lateral aspect; (E) telson and uropod; (F) left 1st pereiopod, lateral aspect; (G) same, left chela, lateral aspect; (G′) same, tips of fingers; (H) major 2nd pereiopod, inner aspect; (I) same, carpus, lateral view; (J) 3rd pereiopod; (K) same, dactylus and propodus. Setulae omitted on (A,B,E). Scales: 1 mm, (G′) unscaled.

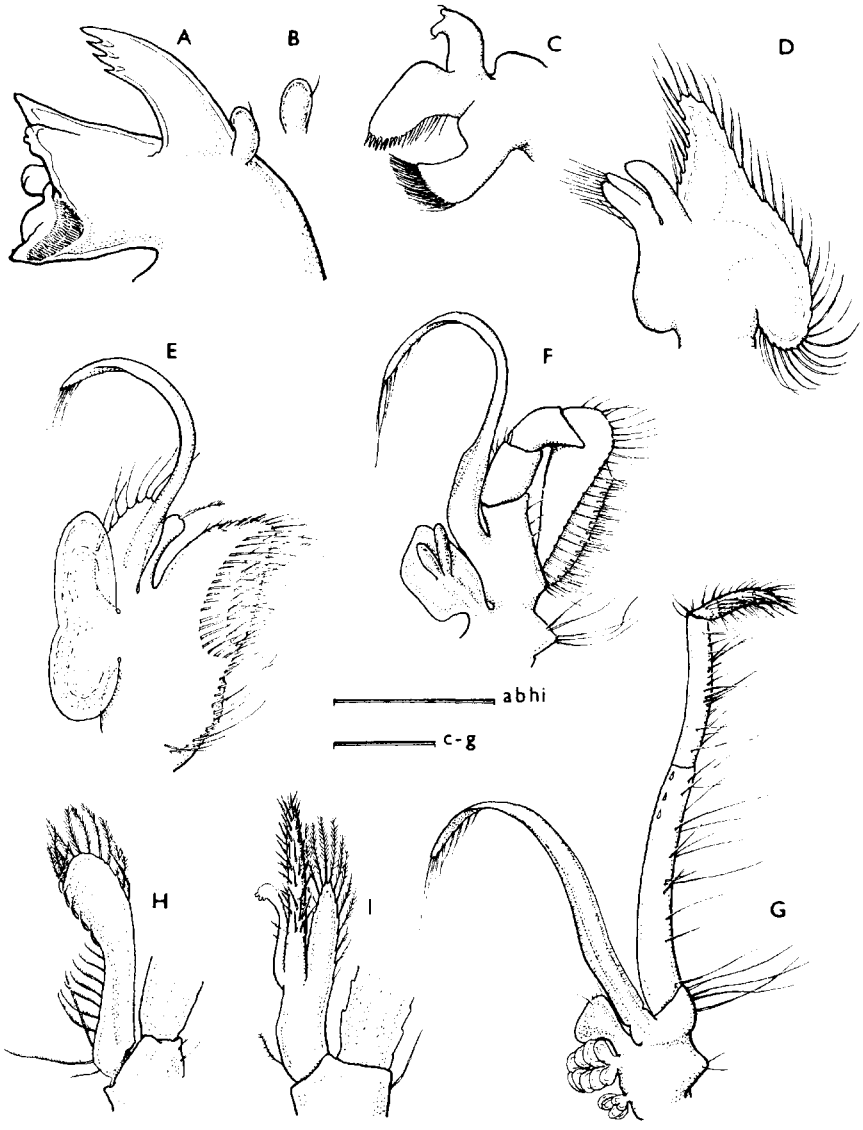

FIG. 8. *Exoclimenella sudanensis* sp.nov., Holotype, ♂: (A) mandible; (B) same, palp, lateral view; (C) maxillula; (D) maxilla; (E) 1st maxilliped; (F) 2nd maxilliped; (G) 3rd maxilliped; (H) endopod of male 1st pleopod; (I) endopod of male 2nd pleopod. Scale: 0·5 mm.

free ramus with 3 segments, long free ramus slender, with about 6 segments; about 7 groups of aesthetascs present on upper flagellum. Lower flagellum filiform, incomplete in specimen studied.

Antenna (Fig. 7B) well developed; basicerite with strong lateral tooth, carpocerite short with length about 2 × width; flagellum filiform, about 5 × carapace length. Scaphocerite long, reaching far beyond antennular peduncle and slightly beyond tip of rostrum, about 5 × longer than broad proximally, narrowing distally; anterior border

rounded, lateral margin concave with strong distal tooth far exceeding anterior margin of scaphocerite.

Eyes large with cornea globular, small accessory pigment spot present dorsally on stalk just behind cornea; eyestalk slightly depressed, narrower than cornea in lateral aspect.

Labrum with vertical carina anteriorly. Mandible (Fig. 8A) robust, molar process stout, with 4 blunt teeth and marginal area of short brush-like setae; incisor process with distal margin oblique, possessing 4 teeth gradually decreasing in size from strong distal tooth to small proximal tooth; palp small, 1-segmented, with single subapical seta (Fig. 8B). Maxillula (Fig. 8C) with bilobed palp, upper lobe small bearing single subapical seta, lower lobe with small uncinate seta; upper lacinia downcurved, with about 10 stout spines distally, with row of setae on lower margin; lower lacinia with broad setose distal margin. Maxilla (Fig. 8D) with well developed finger-like palp without setae; basal endite bilobed, lobes subequal, setose; coxal endite broadly rounded; scaphognathite with outer margin concave, about 5 × longer than broad, anterior lobe narrow, posterior lobe broad. First maxilliped (Fig. 8E) with finger-like palp bearing single plumose terminal seta, reaching to distal margin of caridean lobe; basal endite produced distally, distinctly exceeding distal end of palp; coxal endite less developed, broadly rounded; caridean lobe broader near base, narrower distally, narrow lamina present on medial margin of exopodite opposite distal part of caridean lobe; with well developed, broad, feebly bilobed epipod. Second maxilliped (Fig. 8F) with dactylar and propodal segments of endopod elongate; exopod slender, with some plumose setae distally, proximal 0·33 slightly enlarged; coxa distinctly enlarged into triangular medial lobe with 5 long setae; epipod subqadrate, podobranch fused proximally with epipod, 2 lamellae present distally on podobranch. Third maxilliped (Fig. 8G) with endopod reaching to distal end of carpocerite; ischiomerus about 5 × longer than broad, with 3 spinules distolaterally, sparsely setose medially; penultimate segment about 0·6 of ischiomeral length, slightly narrower, with long setae medially; terminal segment tapering, slightly downcurved distally, about 0·6 of penultimate segment length, with transverse rows of setae and group of terminal spines; basis medially rounded with 5 long setae; exopod slender with plumose setae distally; coxa produced into subtriangular medial lobe, lateral plate broad; 2 arthrobranchs present, lower (distal) arthrobranch well developed consisting of about 9 pairs of rounded lamellae, upper arthrobranch small, consisting of about 7 pairs of lamellae.

First pereiopod (Fig. 7F) exceeding tip of rostrum by chela; chela (Fig. 7G) with palm compressed and slightly longer than deep; about 7 transverse rows of serrulate cleaning setae present ventrolaterally on palm; fingers about 1·4 × palm length, cutting edges finely denticulate and situated medially forming deep cavity on outer side of closed chela, distolateral transparent lamina on fingers present, rather narrow, not enlarged; chela with groups of specialized setae, palmar brush setae with compressed and slightly enlarged proximal part, distal part curved anteriorly, densely setulose along anterior margin (Fig. 7G), fingers with transverse rows and terminal patchs of long curved serrulate setae on external borders, with about 7 groups of 2–3 simple straight setae on lateral sides directed over concavity, opposing similar setae of opposite finger; carpus about 2 × chela length, tapering proximally, with some long, anteriorly directed distoventral, dorsally setulose setae; merus slightly shorter than carpus; ischium, basis and coxa short, without special structures.

Second pereiopods with strong major chela (Fig. 7H). Chela of major pereiopod about 3 × CL, with fingers occupying distal third of chela length; fixed finger narrow,

with upcurved tip and 2 blunt, anteriorly directed teeth on proximal third; dactylus robust, depressed proximally, compressed distally, about 4 × longer than deep, with maximal depth on 0·25 of length from distal end, 2 blunt teeth present on cutting edge, proximal tooth elongate, directed posteriorly, situated at 0·25 of dactylar length, distal tooth angulate, placed at 0·5 length of dactylus, other parts of cutting edge without sharp lamina; palm subcylindrical, smooth, about 5 × longer than deep; carpus short, about 0·26 of palm length, tapering proximally, distal margin with 2 spines—ventral and medial; merus subcylindrical, about 1·8 of carpal length; ischium subequal to merus, tapering proximally; basis and coxa without special features.

Minor chela in early stage of regeneration in specimen studied (Fig. 6).

Ambulatory pereiopods slender. Third pereiopod (Fig. 7J) reaching to end of rostrum; dactylus simple, 0·2 of length of propodus, unguis distinct and downcurved; propodus (Fig. 7K) about 12 × longer than deep, uniform, ventral margin with 5 single spines and pair of distal spines; carpus 0·4 of propodal length, unarmed, about 3·5 × longer than distal width; merus slightly shorter than propodus and about 8 × longer than deep, uniform and unarmed; ischium, basis and coxa short, without special structures.

Endopod of 1st male pleopod (Fig. 8H) elongate with greatest width distally, narrower near middle of length; medial border with 14 shortly setulose setae decreasing in length from very long 2nd proximal seta to about 0·1 seta; 12 plumose setae on distal and distomedial border. Endopod of 2nd male pleopod (Fig. 8I) with single seta proximally on medial margin, and with well developed appendix masculina far overreaching both narrow appendix interna and short endopod; appendix masculina with numerous short strong spines covering distal 0·75 of length.

Uropod (Fig. 7E) with protopodite bearing strong acute posterolateral lobe; exopod about 3 × longer than broad, lateral border straight distally, with strong distal tooth and movable spine 1·3 × longer than lateral tooth; endopod reaching nearly to distal margin of exopod, about 3·8 × longer than wide.

Branchial formula as following:

	Maxillipeds			Pereiopods				
	I	II	III	1	2	3	4	5
Pleurobranchs	–	–	–	1	1	1	1	1
Arthrobranchs	–	–	2	–	–	–	–	–
Podobranchs	–	1	–	–	–	–	–	–
Epipods	1	1	–	–	–	–	–	–
Exopods	1	1	1	–	–	–	–	–

Measurements (mm). Postorbital carapace 3·0; rostrum 4·1; total length about 11·0; telson 1·8; 1st pereiopod 7·0; major 2nd pereiopod 15·0; chela of major 2nd pereiopod 9·0; minor pereiopod (small, regenerating), 3rd pereiopod 6·0.

Types. The only specimen, the male CL 3·0 mm, is designated as HOLOTYPE, and is deposited in the RMNH, Leiden, catalogue number 37304.

Systematic position (see below—Species discussion).

Habitat. The unique specimen was found during examination of the fauna associated with colonies of the branching coral *Stylophora pistillata*. It has been reported (Edwards and Emberton, 1980: Tab. V) as inhabiting a 'reef-flat and deeper water'.

Associated fauna. An extended list of crustaceans found on colonies of *S. pistillata* is given by Edwards and Emberton (1980).

Distribution. Known only from the type locality, Sudan, Red Sea.

Etymology. The name is derived from the type locality, the Sudanese Red Sea.

Species discussion

Exoclimenella sudanensis sp.nov. shows the closest morphological similarity to *E. maldivensis* sp.nov. sharing with it the shape of the 2nd male pleopod with appendix masculina being distictly longer than the endopod and covered with scattered short spines (a), and the presence of 1-segmented mandibular palp (b). *Exoclimenella maldivensis* sp.nov. differs from *E. sudanensis* sp.nov. in the absence of the supraorbital spine and by the presence of the fine denticulation on the 2nd pair of chelae in females and younger males.

Both the new species, as well as *E. denticulata* (Nobili) comb.nov. and *E. sibogae* (Holthuis) comb.nov. (see below), belong to the group of species possessing the pair of long submedian processes on the 5th thoracic sternite (c), 2 arthrobranchs on the 3rd maxillipeds (d), the subspatulate concavity on fingers of the 1st chelae opening laterally (e), and the cutting edges of the major chela without fossae (f). *Exoclimenella sudanensis* sp.nov. differs from all other species of the genus by the presence of supraorbital spines—the feature shared only with *P. spinifera* (De Man) (see below) in the new genus *Periclimenella*.

The shape of the major 2nd chela of *E. sudanensis* sp.nov. is very similar to that of *E. sibogae* (Holthuis, 1952). *Exoclimenella sibogae*, however, differs from the former, not only in the absence of the supraorbital spine, but also in the presence of 3 distal spines on the carpus of the 2nd pereiopods, the upper arthrobranch on the 3rd maxilliped being rudimentary, unilamellate, and the 2nd male pleopod possessing an appendix masculina shorter than the endopod with long simple setae and two terminal serrate spines. *Exoclimenella denticulata* may be distinguished from *E. sudanensis* sp.nov. by the shape of cutting edges of the fingers of the major chela, the accessory meral spines on the 2nd pereiopods, the presence of the hastate setae on 3rd maxillipeds and 2nd pereiopods, and by the shape of the 2nd male pleopod.

New combination

Exoclimenella denticulata (Nobili, 1906), comb.nov.
(Figs 9–11)

Periclimenes Petitthouarsi var. *denticulata* Nobili, 1906: 257; 1907: 358–359.
Periclimenes (Falciger) denticulatus. Borradaile, 1917: 368, 372.

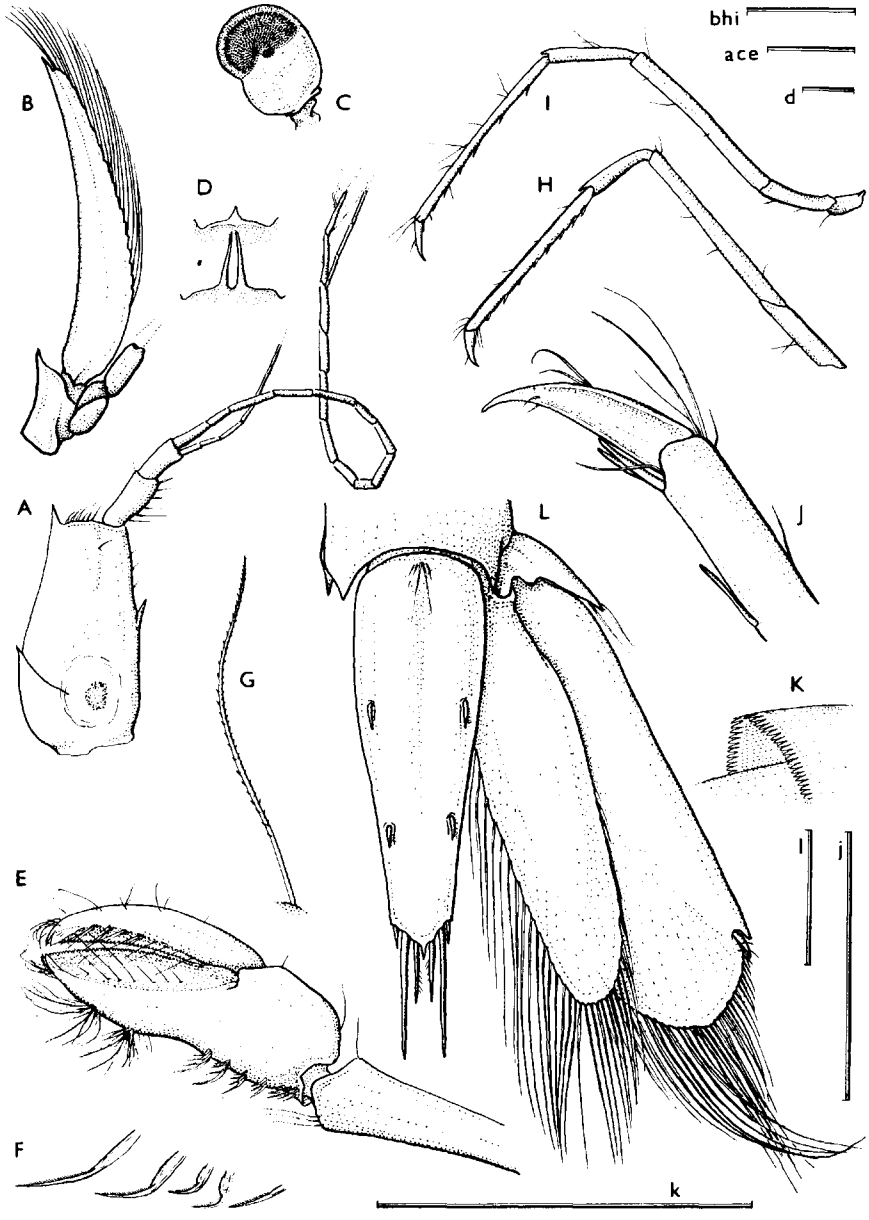

FIG. 9. *Exoclimenella denticulata* (Nobili), Oneroa Island, ♂ CL 2·5 mm: (A) antennule; (B) antenna; (C) eye, dorsal aspect; (D) 4th (above) and 5th (below) thoracic sternites; (E) left chela of 1st pereiopods, lateral aspect; (F) same, brush setae of palm; (G) same, serrate seta of fingers; (H,I) ambulatory pereiopods; (J) dactylus and distal propodus of walking leg; (K) dorsal part of posterior margin of 3rd abdominal tergite, postero-lateral aspect; (L) telson and uropod. Scales: 0·5 mm.

Periclimenes (Ancylocaris) denticulatus. Kemp, 1922: 170, 197.
Periclimenes (Harpilius) denticulatus. Holthuis, 1952: 11.
Palaemonella denticulata. Holthuis, 1953: 55.

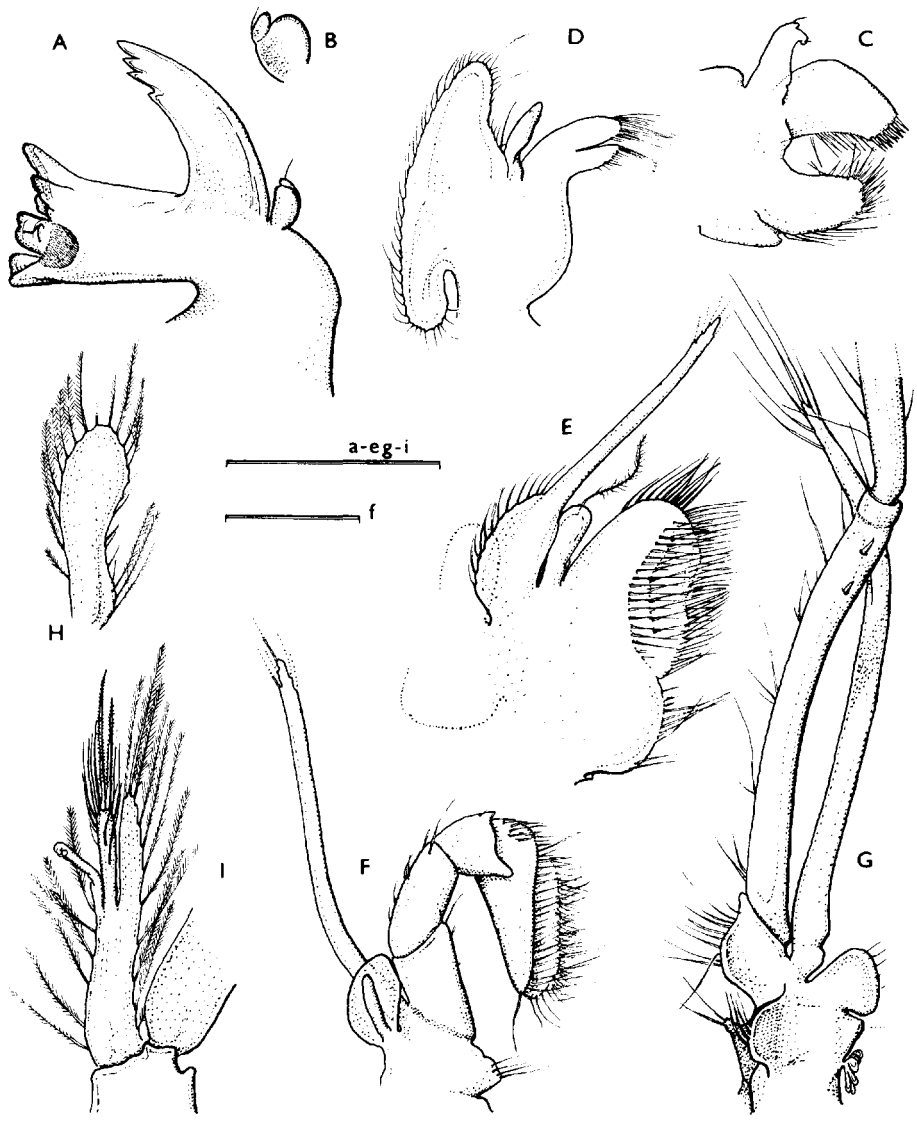

FIG. 10. *Exoclimenella denticulata* (Nobili), Oneroa Island, ♂ CL 2·5 mm: (A) mandible; (B) same, palp, medial view; (C) maxillula; (D) maxilla; (E) 1st maxilliped; (F) 2nd maxilliped; (G) 3rd maxilliped; (H) endopod of male 1st pleopod; (I) endopod of male 2nd pleopod. Scales: 0·5 mm.

Periclimenes denticulatus. Bruce, 1976a: 59; 1990a: 12, 16, 18; 1992b: 59, Figs 12–14; Devaney and Bruce, 1987: 223, 230.

Periclimenes identiculatus. Bruce, 1979: 230–231 [erroneous spelling for *P. denticulatus*].

Material. Oneroa Island, Raroia Atoll, Tuamotu, about 0·75 mile inside lagoon, depth 14 m, sand film over rock pavement and coral patches on bottom, dredge, 9 August 1952, Loc. 2100, coll. J. P. E. Morrison, det. L. B. Holthuis, RMNH Reg.No. 8986 [under generic name *Palaemonella*]; 1 ♂.

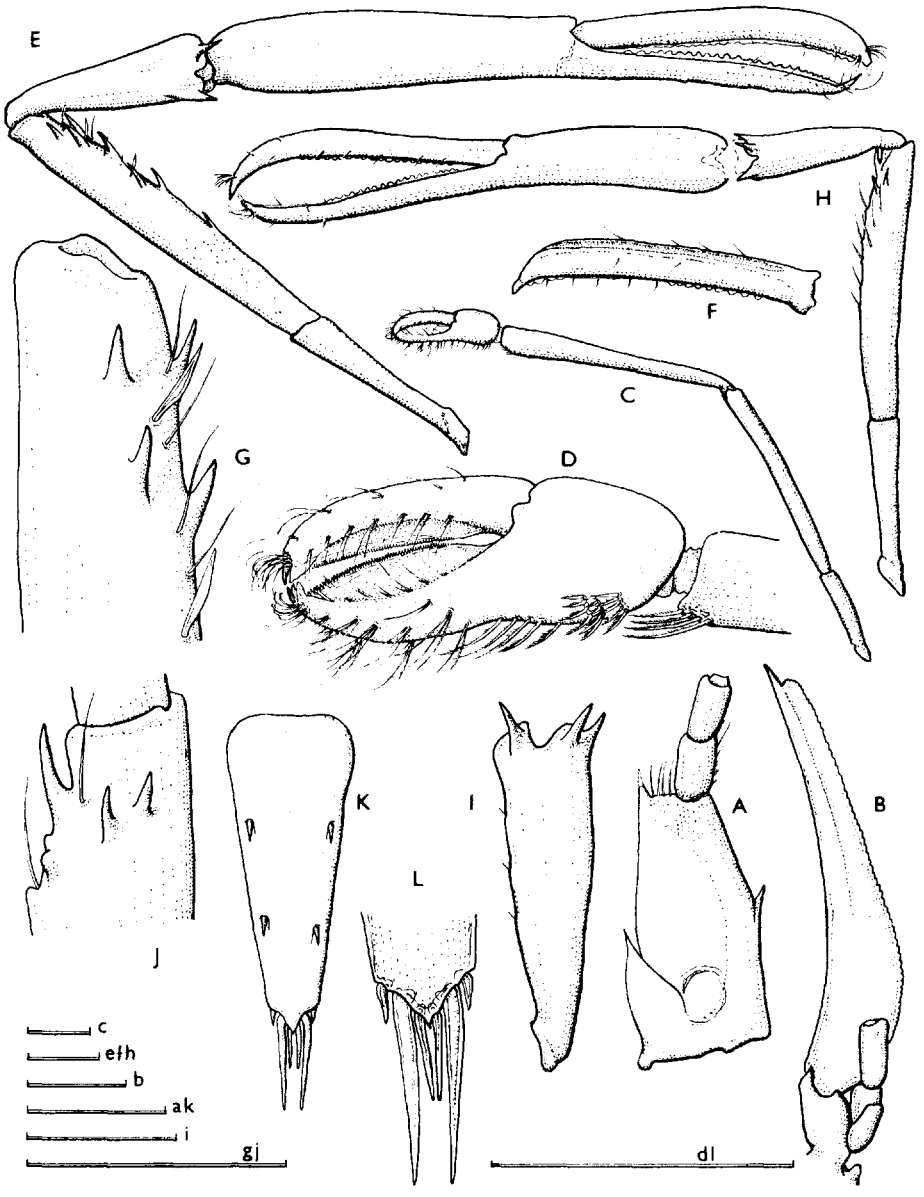

FIG. 11. *Exoclimenella denticulata* (Nobili), Holotype, ♂: (A) antennular peduncle; (B) antenna; (C) left 1st pereiopod, lateral aspect; (D) same, left chela, lateral view; (E) major 2nd pereiopod; (F) same, dactylus; (G) same, distal merus; (H) minor 2nd pereiopod; (I) same, carpus; (J) same, distal merus; (K) telson; (L) same, posterior spines. Scales: 1 mm.

Gatavake, Gambier Islands, coll. L.-G. Seurat; MNHN Na. 1944, 1 ♂ (HOLOTYPE).

Description of the Oneroa Island specimen. Specimen badly damaged, rostrum broken, lacking distal part, both second pereiopods lost.

First dorsal tooth of rostrum situated behind posterior orbital margin; epigastric,

antennal and hepatic spines present; 4th thoracic sternite possessing short median process, pair of processes of 5th sternite long and slender (Fig. 9D).

Fine denticulation present on posterior margin of 3rd abdominal tergite (Fig. 9K); telson (Fig. 9L) about 2·5 × longer than wide with transverse row of setae on anterior midline, and with 2 pairs of small dorsal spines 0·08–0·09 of telson length, situated at 1st and 2nd 3rds of telson length; posterior margin of telson with small acute median process, with 3 pairs of spines, lateral pair 0·75 of dorsal spines length, intermediate pair about 0·35 of telson length, submedian pair feebly setulose, about 0·5 of intermediate spines length.

On one side the antennae and oral parts have been previously dissected and lost. Upper antennular flagellum (Fig. 9A) with unusually long fused part consisting of 14 segments, short free ramus with 2 elongate segments. Antennal basicerite with lateral tooth, carpocerite not reaching distal end of antennular basal segment; scaphocerite long, curved laterally, with distolateral tooth far overreaching lamina (Fig. 9B).

Mandible (Fig. 10A) with small 2-segmented flattened palp (Fig. 10B) with single subterminal seta; incisor process terminated by 3 strong acute teeth and 1 small subterminal tooth, molar process robust, with 4 stout lobes and small field of setae. Maxillula, maxilla, and the 1st maxilliped as figured (Figs 10C,D,E), without special features. Second maxilliped (Fig. 10F) with flattened epipod bearing rudimentary podobranch. Only 1 of 3rd maxillipeds present (Fig. 10G), broken at carpal segment, ischio-merus sparsely setose and with 2 distolateral spinules on dorsal border; coxal segment bearing narrow setose lobe medially and rounded setose longitudinal ridge dorsally; only upper arthrobranch present, consisting of about 6 reduced lamellae (the lower arthrobranch was probably lost during a previous dissection but its position is clearly indicated with a small subtriangular lobe).

First pereiopod slender, fingers about 1·5 of palm length, deeply subspatulate laterally (Fig. 9E), with denticulate medial cutting edges; dactylar tip bearing transparent lamella laterally; patches of setae on external faces of fingers consisting of long serrulate setae (Fig. 9G); ventrolateral face of palm with 7 rows of brush setae (Fig. 9F).

Only 2 ambulatory pereiopods present, both detached from the body; legs similar to each other but slightly unequal in size (Figs 9H,I). Stronger leg (Fig. 9H) with propodus 4·6 × longer than dactylus, (slender leg 5·8 ×), and with ventral margin armed with 8 single spines and 1 pair of distal spines (slender leg 6 + 2 spines). Dactylus simple, with sharp downcurved unguis (Fig. 9J).

First male pleopod (Fig. 10H) with endopod expanded distally and narrower in middle of length, medial margin bearing 3 proximal setulose setae, 5 simple setae in middle part, and 14 plumose setae around distal margin through proximal 4th of lateral margin. Endopod of 2nd male pleopod (Fig. 10 I) with appendices at about 0·6 of the medial margin length, appendix masculina only slightly exceeding appendix interna, not reaching to the tip of the endopod; appendix masculina subcylindrical, about 5·1 × longer than broad, 0·35 of endopod length, apex with pair of stout, finely serrulate spines and about 6 slender simple spines, 3 simple spines placed distomedially, and 2—distoventrally; serrulate terminal spines reaching far beyond simple setae, latter as long as or longer than appendix masculina.

Uropodal rami elongate, exopod exceeding posterior end of endopod (Fig. 9L).

Branchial formula as following:

	Maxillipeds			Pereiopods				
	I	II	III	1	2	3	4	5
Pleurobranchs	–	–	–	1	1	1	1	1
Arthrobranchs	–	–	2	–	–	–	–	–
Podobranchs	–	1	–	–	–	–	–	–
Epipods	1	1	–	–	–	–	–	–
Exopods	1	1	1	–	–	–	–	–

Measurements (lengths; mm). Postorbital carapace 2·5; rostrum (broken); telson 1·5; chela of 1st pereiopod 1·8; second pereiopods (lost); ambulatory pereiopods 2·8.

Colour. No data are available on the colour pattern.

Remarks. The holotype specimen [CL 3·0 mm] of *Periclimenes Petitthouarsi* var. *denticulata* deposited in the Muséum national d'Histoire naturelle was examined by one of the authors (AJB). The specimen (Fig. 11) was in an incomplete and fragmentary condition. The rostrum, all mouthparts, eyes, thoracic sternites, ambulatory pereiopods and uropods were all missing. However, both 2nd pereiopods and 1 1st pereiopod were present. The major second pereiopod had the fingers broken and the minor had the chela separated from the carpus. The body had the thorax detached from the abdomen and the 6th segment detached from the 5th. As Nobili's original description (1906) is extremely brief, it allows us to include remarks on some interesting structures here.

The carapace appears to have had a postrostral carina with one postorbital tooth and an epigastric tooth. Supraorbital spines are lacking. The proximal segment of the antennular peduncle (Fig. 11A) has a short ventromedial tooth. The scaphocerite (Fig. 11B) is formed by narrow, laterally curved lamina terminating with strong distolateral tooth. The fingers of the 1st pereiopod chela (Figs 11C,D) are strongly subspatulate, with the medial cutting edges finely and narrowly denticulate. The spatulation faces the lateral side of the chela, as is indicated by the ventrolateral position of the palmar brush setae (Fig. 11D). The dactyl has a single distal tooth and the fixed finger 2, the former possesses an irregularly dentate transparent lamella laterally, and the latter has an acute lateral process, making the tips of the fingers feebly spatulate. The dactyl of the major 2nd pereiopod (Fig. 11E,F) has a feeble dorsal carina with the dorsolateral surface concave. The cutting edges of both the 2nd pereiopod chelae (Fig. 11E,H) are provided with numerous low blunt teeth diminishing anteriorly. The carpi have 3 strong distal teeth (Fig. 11I). The distoventral parts of the 2nd cheliped meri are armed with several irregularly placed acute teeth (7 on the major, 3 on the minor one), in contrast to the original description: ... 'merus des pattes II avec 4 épines inférieurement' ... (Nobili, 1906: 257); the major 2nd periopod possesses some hastate setae placed distoventrally on the merus amongst the teeth mentioned above (Fig. 11G). Telson (Fig. 11K) of the holotype is similar to that of the Tuamotu specimen, except that the submedian spines are devoid of setulae. These may have been lost through abrasion (Fig. 11L).

It is remarkable that the hastate, or 'fusiform', setae found on the merus of the major

2nd pereiopod are rather unusual, and characteristic for the species. Similar setae have been recently observed (Bruce, 1992b) in a single male specimen of the species from Lizard Island, Queensland. The specimen possessed a single large fusiform seta also on the ischio-meral segment of the 3rd maxilliped. The 2 specimens (♂ CL 2·1 mm; ♀ CL 2·1 mm) reported from Enewetak Atoll, Marshall Islands (Devaney and Bruce, 1987) have also been re-examined by one of us (AJB). They bore 2–3 fusiform setae on their 3rd maxillipeds, the female having both second pereiopods was without such setae on them as was found in the holotype. However, these setae have been noted (Bruce, 1992) as very easily detached. The present specimen from the Tuamotu Islands, lacking both 2nd pereiopods as well as 1 of the 3rd maxillipeds, has also been found without any fusiform setae on the remaining part of the other 3rd maxilliped (Fig. 10G).

The presence of the mandibular palp is also a rather interesting feature. Although five specimens from Raroia Atoll were reported by Holthuis (1953), only 1 of them is now deposited in the Nationaal Natuurhistorisch Museum, Leiden. That specimen bears a small 2-segmented palp with a single subterminal seta. Bruce's specimen (1992) from Lizard Island has been reported with a very small 1-segmented palp with two lateral setae. No previous report is known on the presence or absence of the mandibular palp in *E. denticulata*, although Holthuis' placement (1953) of that species into the genus *Palaemonella* was probably based on the presence of the palp in his material. The mouth-parts of Nobili's type specimen have been lost, so the original condition of that structure cannot be confirmed.

Habitat. Up to the present time, about 13 specimens of *E. denticulata* have been reported in literature. All of them, if the habitat was noted, were found in a lagoon bottom in depths of 13–32 m. Substrata included sand film over rock pavement and coral patches (Holthuis, 1953; present report), *Acropora* head (Holthuis, 1953), coral and lithothamnium rubble (Bruce, 1979), acroporid coral and algae (Devaney and Bruce, 1987), or sand with *Halimeda* (Bruce, 1992). *Exoclimenella denticulata*, like the other species of the genus, seems to be free-living browser, and only incidentaly associated with corals.

Distribution. Type locality: Gatavake, Mangareva Atoll, Gambier Islands. Also known from Arno and Enewetak Atoll, Marshall Islands (Holthuis, 1953; Devaney and Bruce, 1987), Raroia atoll, Tuamotu Island (Holthuis, 1953), the western South China Sea (Bruce, 1979), and from Lizard Island, Queensland, **Australia** (Bruce, 1990a; 1992).

Exoclimenella sibogae (Holthuis, 1952), comb.nov.
(Fig. 12)

Periclimenes sibogae Holthuis, 1952: 12, 73, Figs 28, 29; Bruce, 1976a: 59 [notes].
non *Periclimenes sibogae* Edwards and Emberton, 1980: 236 = *Exoclimenella sudanensis* sp.nov. (see above).

Material. *Siboga* Expedition, st. 240; Banda anchorage, Indonesia; trawl, dredge and reef exploration; depth 9–36 m; 22 November–1 December 1899; 1 specimen (holotype, ♂ CL 3·0 mm), ZMA De.102 823; det. L. B. Holthuis.

Description. As the original description (Holthuis, 1952) is fully detailed, it is necessary only to emphasise the more interesting features.

Carapace with rostrum provided with 6 dorsal and 2 ventral teeth, 1st dorsal tooth situated well before posterior orbital margin; supraorbital spine absent. Thoracic sternites bearing short median process on 4th segment and pair of long acute submedian

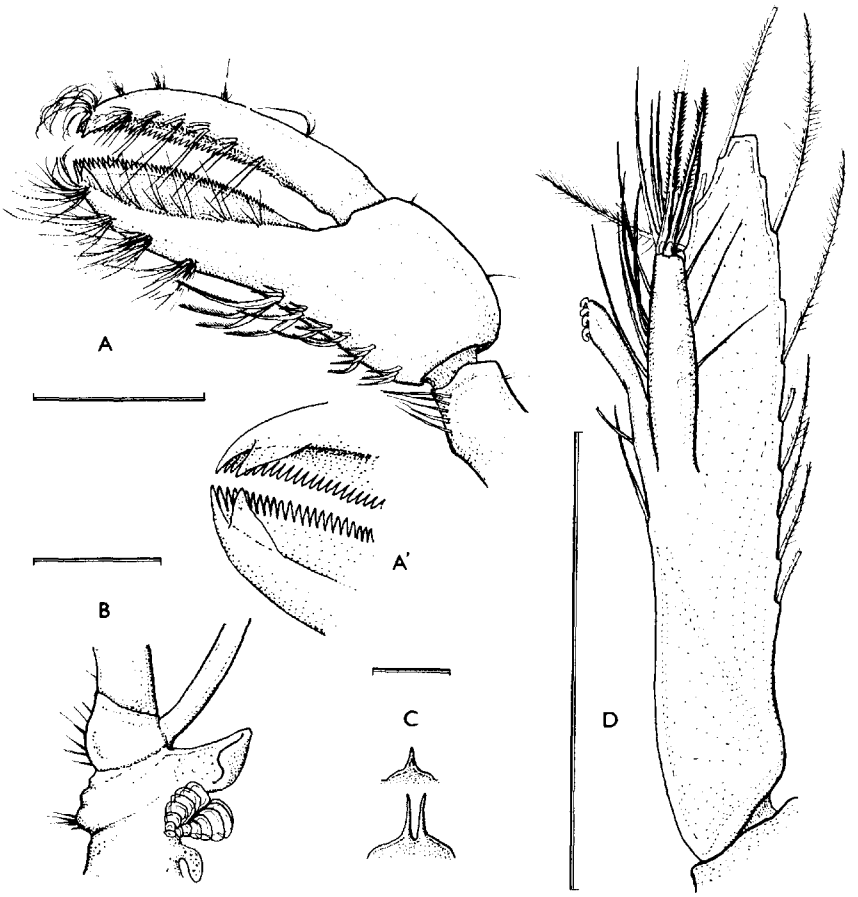

FIG. 12. *Exoclimenella sibogae* (Holthuis), Holotype, ♂: (A) left chela of 1st pereiopods, lateral aspect; (A′) same, tips of fingers; (B) proximal part of 3rd maxilliped; (C) 4th (above) and 5th (below) thoracic sternites; (D) endopod of male 2nd pleopod. Scales: 0·5 mm; (A′) unscaled.

processes situated on transverse ridge on 5th segment (Fig. 12C). Epipod of 2nd maxilliped with simple, unilamellate podobranch, 3rd maxilliped provided with 2 arthrobranchs (Fig. 12B), lower arthrobranch small, well developed, with about 7 pairs of lamellae, upper arthrobranch vestigial, reduced into short inconspicuous process. Fingers of 1st pereiopod (Fig. 12A) subspatulate with cavity open laterally; cutting edges finely pectinate with series of about 50 denticles diminishing proximally; distolateral transparent lamina present on fingers. Second pereiopods with 3 distal teeth on carpus, merus unarmed; cutting edges of major chela with 2 angulate teeth proximally on both dactylus and fixed finger, and with 5 low subtriangular teeth more distally on fixed finger; minor chela with distal cutting edges simple, dactylus with 2 low subtriangular teeth proximally, fixed finger with 6 teeth.

Male pleopods as figured by Holthuis (1952: Figs 29A,B); medial border of endopod of 1st pleopod provided with series of 4 long setulose setae proximally, and with 8 short simple spines distally, 2–3 × shorter than proximal setae, distal end with 10 plumose setae. Endopod of male 2nd pleopod (Fig. 12D) with both appendix interna

and appendix masculina placed at about 0·55 of endopod length, reaching respectively to 0·8 and 0·85 of endopod length; 2 simple setae present on medial border near base of appendix interna, 10 plumose setae situated along distomedial border, following through proximal 3rd of lateral border; appendix masculina subcylindrical, terminated with group of 4 long simple spines, with pair of strong serrate spines, one of latter much longer than terminal simple setae, corpus provided with medial and lateral longitudinal rows with 5 and 3 simple setae respectively.

Remarks. The holotype, the only known specimen of the species, is in a nearly perfect condition. Only 2 walking legs are detached but present, both the mandibles are lost.

The presence of the submedian processes on the 5th thoracic sternites, the presence of the distolateral lamellae and lateral position of the spatulate cavity on the fingers of the 1st pereiopod chela, and the presence of 2 arthrobranchs on the 3rd maxillipeds, as well as the absence of the sound-producing fossae on the fingers and of the single distoventral tooth on the merus of the 2nd pereiopods, allow us to place *E. sibogae*, together with *E. denticulata*, *E. maldivensis* sp.nov. and *E. sudanensis* sp.nov. into a separate genus. The mandibles of the holotype of *E. sibogae* were previously detached from the body and are now missing. Holthuis' statement that the 'oral parts are typical [of *Periclimenes*]' certainly implies that the palp is absent. The absence of the mandibular palp draws *E. sibogae* together with the species of the new genus *Periclimenella*, *P. petithouarsii* and *P. spinifera* (see below). However, *E. sibogae* is closely related to *E. denticulata* sharing also the following features with the latter: 1. Two different groups of medial setae on the endopod of the male 1st pleopod; 2. The endopod of the male 2nd pleopod with a pair of stout serrate terminal spines on the appendix masculina, and with the latter exceeding the appendix interna but distinctly not reaching to the distal end of endopod; 3. The presence of 3 distal spines on the carpus of the 2nd pereiopods. The major chela of *E. sibogae* is very similar to that of *E. sudanensis* sp.nov., with the exception of the presence of 5 small distal teeth in the former which are absent in *E. sudanensis* sp.nov. In addition, the latter differs from *E. sibogae* in the presence of the supraorbital spines on the carapace, the mandibular palp, the more developed upper (proximal) arthrobranch on 3rd maxilliped, and in having 3 instead of 2 distal marginal spines on the carpi of 2nd pereiopods.

Measurements. (In mm). Postorbital carapace 3·0; rostrum 3·7.

Colour. No data are available.

Habitat. Bottom black sand and coral, lithothamnion bank in 18–36 m.

Distribution. Known only from the type locality, Banda Anchorage, Indonesia.

Periclimenella petitthouarsii (Audouin, 1826), comb. nov.
(Figs 13–18)

Without name—Savigny, (? 1812–1825): pl. 10, Fig. 3; 1827: pl. 10, Fig. 3.
Palaemon Petitthouarsii Audouin, 1826: 91; 1827: 276.
Anchistia Petitthouarsii Paul'son, 1875: 114.
Periclimenes Petitthouarsi Borradaile, 1898: 381.
Periclimenes Petitthouarsii Balss, 1915: 25.
Periclimenes (Falciger) petitthouarsi Borradaile, 1917: 366 (key), 369.
Periclimenes (Ancylocaris) petitthouarsi Kemp, 1922: 170 (key), 196.
Periclimenes petitthoursi Ramadan, 1936: 22 [erroneous spelling for *P. petitthouarsi*].
Periclimenes (Harpilius) petitthouarsi Holthuis, 1952: 12, 78 (full synonymy).
Periclimenes (Harpilius) petitthouarsii Holthuis, 1958: 3.

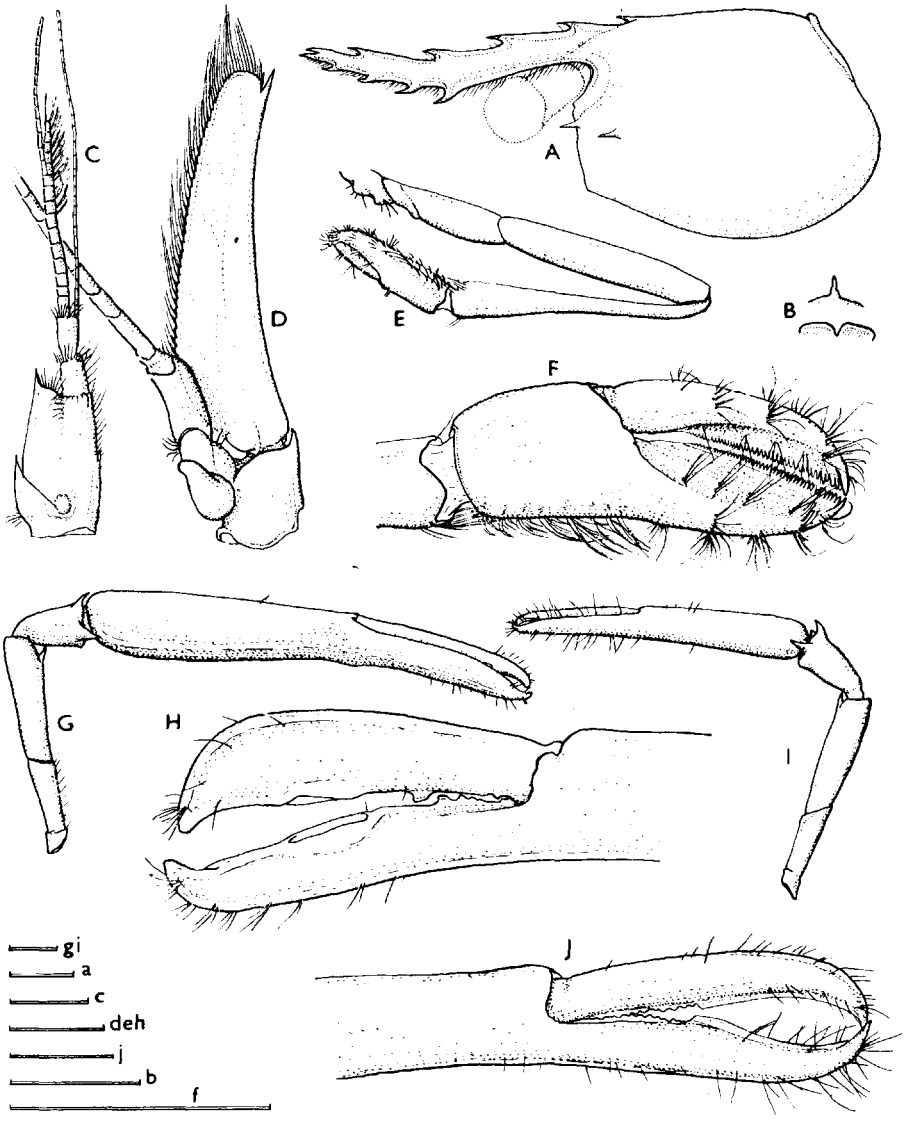

FIG. 13. *Periclimenella petitthouarsii* (Audouin, 1825), Red Sea, ♂ CL 3·4 mm, st. 19[27]: (A) anterior carapace and rostrum; (B) 4th (above) and 5th (below) thoracic sternites; (C) antennule; (D) antenna; (E) 1st pereiopod; (F) same, left chela, medial aspect; (G) major 2nd pereiopod; (H) same, fingers; (I) minor 2nd pereiopod; (J) same, fingers. Scales: 1 mm.

Periclimenes petitthouarsi Bruce, 1971: 2, 4, 7; 1975b: 23, Fig. 2 (colour); 1976a: 41, 59, 62, Figs 2, 11G, 14; 1976c: 6, 63; 1977: 265; 1978: 215, Fig. 5; Bruce and Svoboda, 1983: 37; Edwards and Emberton, 1980: 234–236.

Material. Red Sea (ZMM, det. Z. Ďuriš), R/V *Akademik Petrovskii*, cruise IX-th, st. 19, 19°04′8 N. 42°42′7 E, Sanah-Bor Island, Bight of Asab, southern Red Sea: coll.# 19(9), 12–13 February 1980, 0–2 m, miscellaneous collection, coll. A. V. Tchesunov and V. V. Burakov, 1 ♂; coll.# 19(12), 10 February 1980, lagoon, 0·5–1 m, in

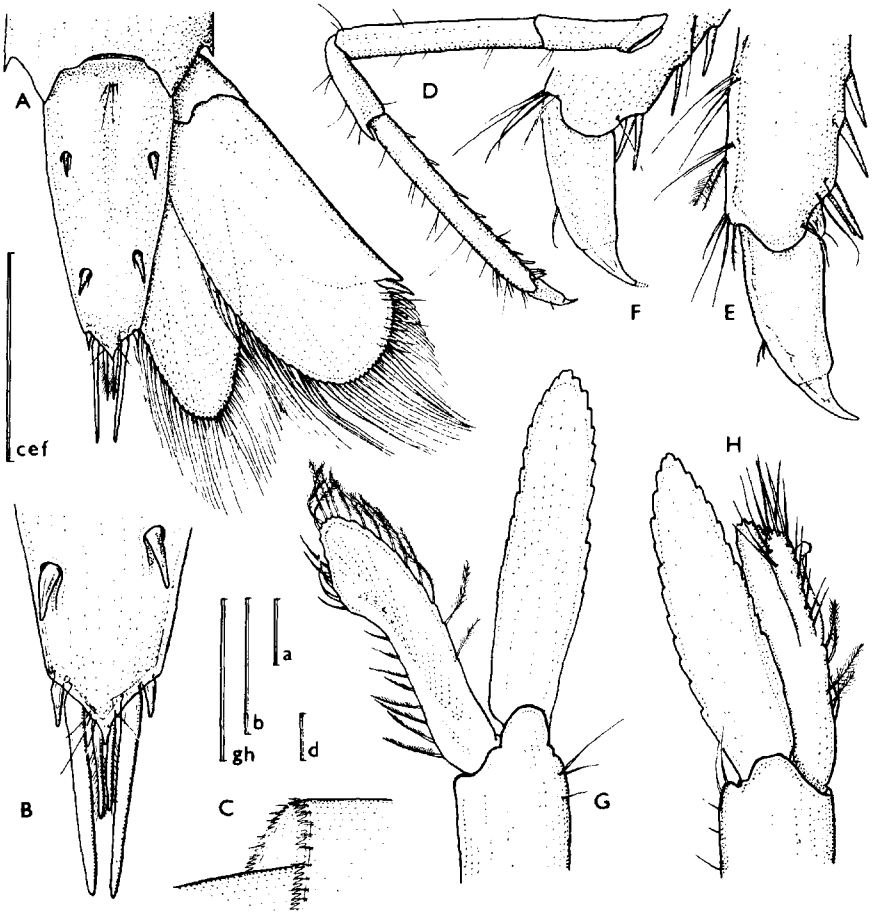

FIG. 14. *Periclimenella petitthouarsii* (Audouin, 1825), Red Sea, ♂ CL 3·4 mm, st. 19[27]: (A) telson and uropod; (B) posterior telson spines; (C) dorsal part of posterior margin of 3rd abdominal tergite, posterolateral aspect; (D) 3rd pereiopod; (E) same, distal propodus and dactylus; (F) dactylus of 5th pereiopod; (G) male 1st pleopod; (H) male 2nd pereiopod. Scales: 0·5 mm.

Stylophora sp. (diam. 25 cm), coll. A. V. Tchesunov, 1 ovig. ♀; coll.# 19(17), 12 February 1980, lagoon, 'zone of green pavements', in *Montipora* sp. (fragments), coll. A. V. Tchesunov, 2 specimens (1 ♂, 1 ♀); coll.# 19(18), 12 February 1980, lagoon, 'zone of microatolls', 0·75 m, in *Montipora* sp. (diam. 30 cm), coll. A. V. Tchesunov, 1 ♀; coll.# 19(19), 13 February 1980, lagoon, 'zone of microatolls and green pavements', in *Montipora* sp. (30 × 20 cm), coll. A. V. Tchesunov, 2 specimens (1 ♂, 1 ♀); coll.# 19(20), 13 February 1980, lagoon, 'zone of microatolls and green pavements', in *Montipora* sp. (diam. 30 cm), coll. A. V. Tchesunov, 6 specimens (2 ♂♂, 4 ♀♀, incl. 1 ovig.); coll.# 19(22), 14 February 1980, reef slope off northern part of island, 2 m, *Stylophora* sp. (diam. 15 cm), coll. A. V. Tchesunov, 2 ♀♀; coll.# 19(27), 11 February 1980, depth 1 m, on dead coral, coll. G. B. Zevina, leg. A. V. Tchesunov, 2 ♂♂; coll.# 19(28), 11 February 1980, depth 1 m, in *Montipora* sp., coll. G. B. Zevina, leg. A. V. Tchesunov, 12 specimens (5 ♂♂, 7 ♀♀); coll.# 19(30), 10

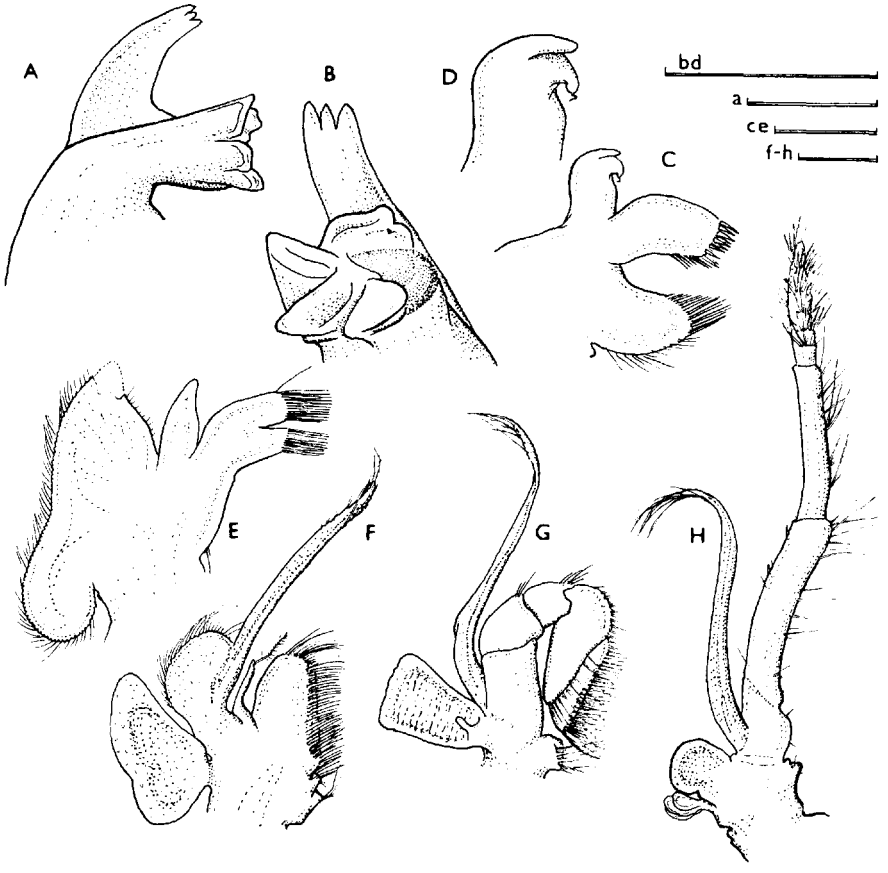

FIG. 15. *Periclimenella petitthouarsii* (Audouin, 1825), Red Sea, ♂ CL 3·4 mm, st. 19[27]: (A) mandible; (B) same, medial aspect; (C) maxillula; (D) same, palp; (E) maxilla; (F) 1st maxilliped; (G) 2nd maxilliped; (H) 3rd maxilliped. Scales: 0·5 mm.

February 1980, depth 1·5 m, on dead corals, coll. G. B. Zevina, leg. A. V. Tchesunov, 3 specimens (2 ♂♂, 1 ♀).

Comoro Islands (NTM, det A. J. Bruce): *Anton Bruun*, st. No. Cr.9, Mounimeri Island, Zaoudzi, Mayotte, Comoro Islands, 23 November 1964, *Seriatopora* sp., coll. A. J. Bruce, NTM Cr.006444, 4 specimens (coll.## 442/7 (♂), 442/18 (♀), 442/20 (ovig. ♀), 442/27 (♂)).

Description of the Red Sea material. Rostrum (Figs 13A, 16A) distinctly longer than CL, 1·29–1·72 × in males, 1·23–1·60 × in females, rostral dentition mostly 6/4, 5–6/4–5 in males, 5–7/3–5 in females (the only ovigerous female with complete rostrum, 6/5), 1st dorsal tooth situated anteriorly to posterior orbital margin, 1st ventral tooth in middle length of rostrum; epigastric, antennal and hepatic spines present on carapace, supraorbital spines absent, with small acute supraorbital tubercles present in some small immature females (Figs 16A,H). Fourth thoracic sternite with short acute median process, 5th sternite bearing transverse ridge with median notch (Figs 13B,

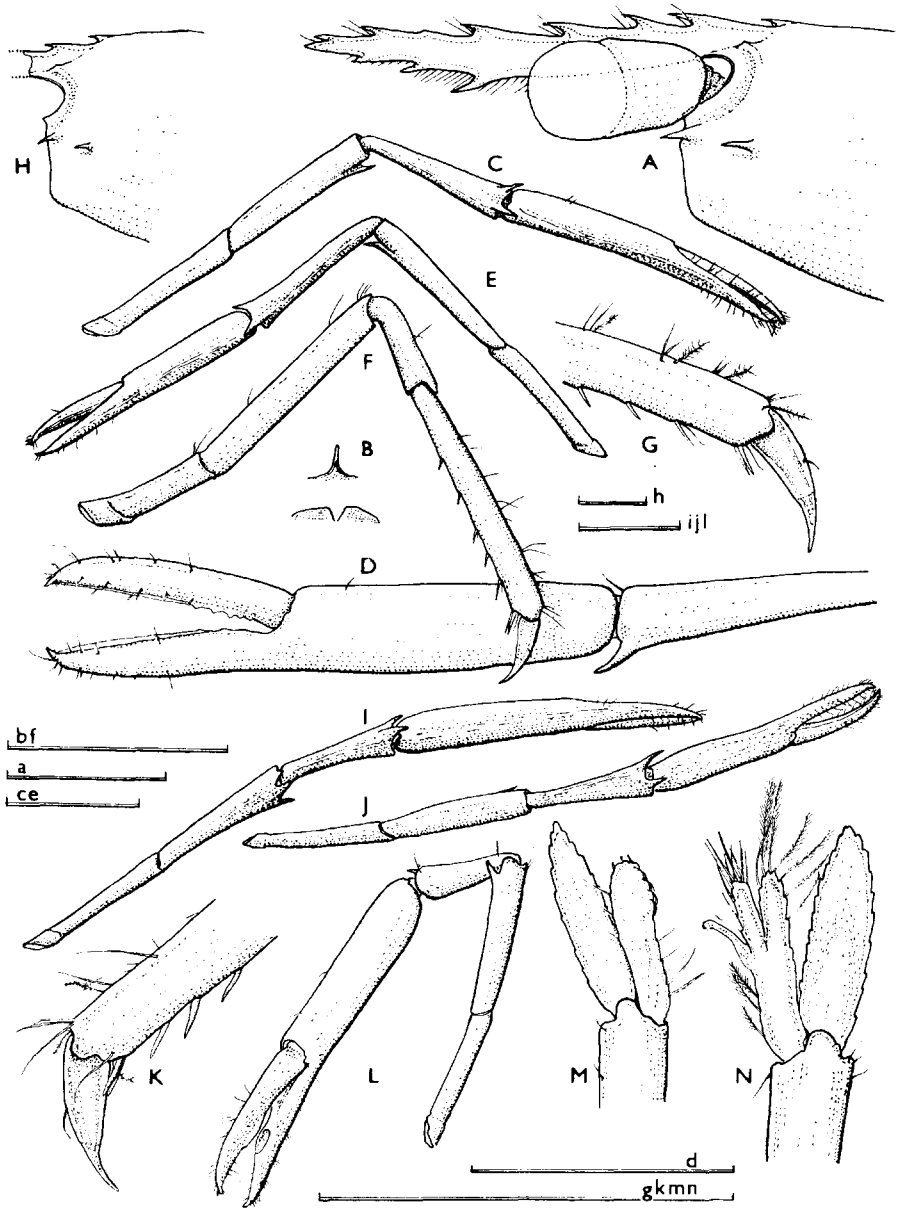

FIG. 16. *Periclimenella petitthouarsii* (Audouin, 1825), Red Sea. (A–G) ♀ CL 1·6 mm, st. 19[28]: (A) anterior carapace, rostrum and eye; (B) 4th (above) and 5th (below) thoracic sternites; (C) major 2nd pereiopod; (D) same, distal carpus and chela, medial view; (E) minor 2nd pereiopod; (F) 3rd pereiopod; (G) distal propodus and dactylus. (H) ♀ CL 2·8 mm, st. 19[12], anterior carapace. (I–K) ♀ CL 1·9 mm, st. 19[28]: (I) major 2nd pereiopod; (J) minor 2nd pereiopod; (K) distal propodus and dactylus of 3rd pereiopod. (L) ♀ CL 2·0 mm, st. 19[18], major 2nd pereiopod. (M,N) ♂ CL 1·8 mm, st. 19[17]: (M) male 1st pleopod; (N) male 2nd pleopod. Scales: 1 mm.

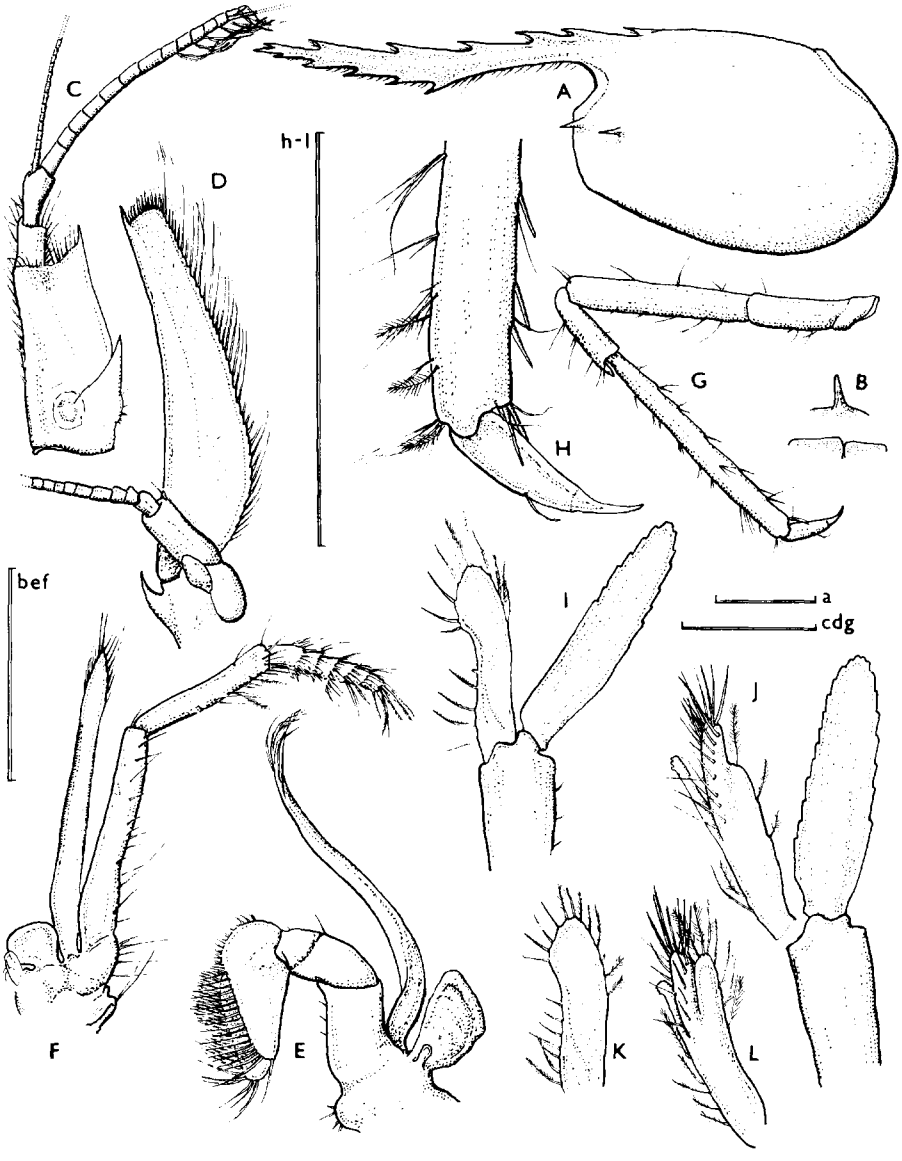

FIG. 17. *Periclimenella petitthouarsii* (Audouin, 1825), Comoro Islands. (A–J) ♂ CL 2·5 mm #442/18: (A) anterior carapace and rostrum; (B) 4th and 5th thoracic sternites; (C) antennule; (D) antenna; (E) 2nd maxilliped; (F) 3rd maxilliped; (G) 3rd pereiopod; (H) same, distal propodus and dactylus; (I) 1st pleopod; (J) 2nd pleopod. (K,L) ♂ CL 2·1 mm #442/7: (K) endopod of 1st pleopod; (L) endopod of 2nd pleopod. Scales: 1 mm.

16B). Third abdominal somite with finely denticulate posterior dorsal margin (Fig. 14C). Telson (Fig. 14A) about 2·2 × longer than broad, with 2 pairs of dorsal spines of about 0·1 of telson length and with transverse row of setae on anterior midline; posterior margin (Fig. 14B) subtriangular with acute median process and 3 pairs of

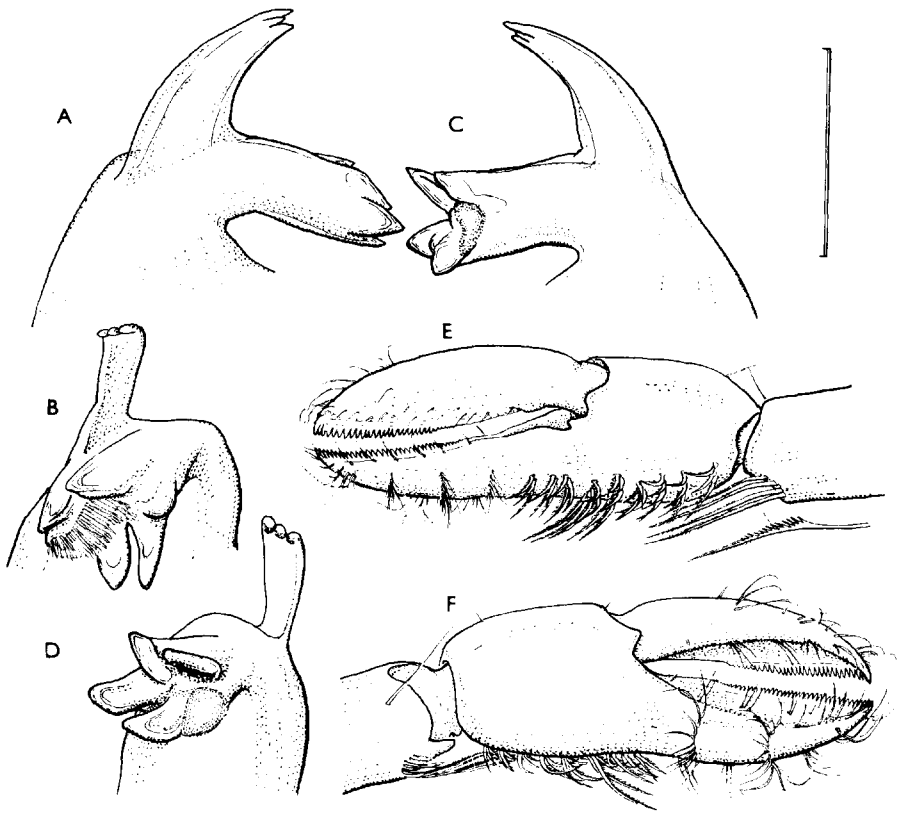

FIG. 18. *Periclimenella petitthouarsii* (Audouin, 1825), ♂ CL 2·5 mm #442/18, Comoro Islands: (A) right mandible; (B) same, medial aspect; (C) left mandible; (D) same, medial aspect; (E) left chela of 1st pereiopods, lateral aspect; (F) same, medial aspect. Scale: 0·5 mm.

spines, lateral pair distinctly shorter than dorsal spines, intermediate pair about 0·36 of telson length, submedian pair longer than half of intermediate spines length and bilaterally feebly setulose.

Basal segment of antennular peduncle (Fig. 13C) 1·6–2·0 × longer than broad and terminating with strong distolateral tooth reaching nearly to end of 2nd peduncular segment; upper flagellum biramous, fused part consisting of 8–10 segments, short free ramus with 5 segments, long free ramus with 10–14 segments, about 13 groups of aesthetascs present; lower flagellum filiform, consisting of about 25 segments. Antennal basicerite (Fig. 13D) provided with distolateral tooth, scaphocerite elongate, with concave lateral margin terminating with strong tooth overreaching distal end of lamina, lamina more than 4 × longer than broad proximally and narrowing distally.

Mandible (Fig. 15A,B) without palp, molar process asymmetrical and provided with 4 strong obtuse teeth and with rounded field of fine setae, incisor process with truncate tip armed with 3 broad teeth; maxillula (Fig. 15C) with bilobed palp, upper lobe without setae, lower lobe with small uncinate seta (Fig. 15D), maxilla and 1st

maxilliped as figured (Fig. 15E,F), 2nd maxilliped (Fig. 15G) with large epipod bearing small reduced podobranch consisting of single process situated near base of epipod; 3rd maxilliped (Fig. 15H) with 2 distolateral spinules on ischiomerus, coxal flange rounded, only 1 reduced arthrobranch present consisting of 3 lamellae and situated close to base of coxal plate.

First pereiopod (Fig. 13E) slender, chela (Fig. 13F) with subspatulate fingers with denticulate cutting edges situated laterally, so that cavity of subspatulate fingers opens on inner site of chela, fingers each with terminal tooth, without additional transparent distolateral lamina; palm with 8 rows of brush setae laterally along ventral margin; carpus 2 × length of chela and 1·25 × longer than merus.

Second pereiopods (Fig. 13G–J) dissimilar and unequal, with fingers slightly shorter than palm; major chela (Fig. 13G,H) possessing sound-producing fossae on cutting edges of fingers, fossae absent on cutting edges of major chela in smallest female CL 1·6 mm (Fig. 16D), small fossa present only on fixed finger in small female CL 1·9 mm (Fig. 16L); palm distinctly longer than carpus, 3·0–3·6 × in males, 2·3–3·06 × in adult females, 1·04–1·45 × in immature specimens (Fig. 16I); carpus with 2 strong teeth on distal margin, merus with strong distoventral tooth. Minor chela (Fig. 13I) with curved fingers terminating with sharp tooth (Fig. 13J), cutting edges provided with numerous low irregular teeth on proximal half, with sharp low longitudinal lamina on distal half; carpus with 2 distal marginal teeth, palm-carpus length ratio 1·4–2·4 in males, 1·4–1·8 in larger females, but only 1·0–1·1 in smallest females (Fig. 16J); distoventral tooth present on merus.

Ambulatory pereiopods subequal to each other, 3rd perciopods (Fig. 14D) slightly stouter than more posterior pairs; dactylus of 3rd perciopod simple, with curved sharp unguis, ventral margin of dactylar corpus distinctly sinuate in adult males (Fig. 14E), with convex distoventral part; ventral dactylar margin of more posterior legs of adult males less sinuate, as well as ambulatory dactyli of smaller males, adult females (Fig. 16K), or immature females (Fig. 16G), more slender with nearly straight ventral margin; propodi of 3rd to 5th pereiopods 3·5–4·5 × longer than dactylus, with 8–5 single ventral spines and pair of distoventral spines; carpus 0·4 of propodal length; merus nearly as long as propodus.

Endopod of male 1st pleopod (Fig. 14G) with series of 8 serrulate medial spines, decreasing in length proximally, and 5 curved serrate spines on distomedial margin, distal and lateral margin with about 14 plumose setae. Male 2nd pleopod (Fig. 14H) bearing subcylindrical appendix masculina with only simple spines—about 6 terminal, 2 distolateral, and 7 lateral setae; appendix masculina slightly longer than appendix interna, not reaching to distal end of endopod; endopod with about 6 plumose setae on proximal part of medial margin, and with series of numerous plumose setae along distomedial and lateral margins. First and 2nd pleopods of smaller male (Cl 1·8 mm) nearly identical to that described above, with exception of less developed setal armature (Fig. 16M,N).

Uropod (Fig. 14A) with ovate exopod with straight lateral margin terminating with strong distolateral tooth and more slender, longer movable spine; both uropodal rami overreaching posterior margin of telson.

Only 2 ovig. females present, female CL 3·3 mm (st. 19(12)) bearing about 40 eggs 0·50 × 0·40 mm in early stage of development, and female CL 2·7 mm (st. 19(20)) with only 10 eggs 0·72 × 0·50 mm with eyespots.

Branchial formula as following:

	Maxillipeds			Pereiopods				
	I	II	III	1	2	3	4	5
Pleurobranchs	–	–	–	1	1	1	1	1
Arthrobranchs	–	–	1	–	–	–	–	–
Podobranchs	–	r	–	–	–	–	–	–
Epipods	1	1	–	–	–	–	–	–
Exopods	1	1	1	–	–	–	–	–

Description of the Comoro material. (Figs 17, 18). Morphologically almost identical with the Red Sea specimens, only more slenderly built.

Rostral formula 6/4–5 in males, 6/3 in ovigerous female; supraorbital spine or tubercle absent (Fig. 17A); 4th thoracic sternite with median process, 5th sternite with ridge divided by deep median notch into pair of transverse plates (Fig. 17B); abdomen and caudal fan similar to above description; basal antennular segment about 1·4 × longer than broad, upper flagellum with fused part consisting of about 12 segments, short free ramus of 2–3 segments, 7–12 groups of aesthetacs present (Fig. 17C); antennal basicerite with strong lateral tooth, scaphocerite elongate with concave lateral margin, with truncate tip overreached by distolateral tooth (Fig. 17D); mandibles without palp, asymmetrical molar processes with distoventral setal fields bearing different arrangement of setae (Figs. 18A-D); epipod of 2nd maxilliped with rudimentary podobranch (Fig. 17E); only 1 (lower) arthrobranch, consisting of 2 rounded lamellae, present on 3rd maxilliped (Fig. 17F); 1st pereiopod chela (Fig. 18E, F) with denticulate cutting edges on subspatulate fingers, concavity opening medially, distolateral lamina of fingers absent; major 2nd chela with fossae on cutting edges, minor chela provided with sharp cutting lamina distally, low teeth proximally; ambulatory pereiopods (Fig. 17G) with slender dactyli (Fig. 17H), propodus of 3rd pereiopod bearing 8 ventral spines (including distal pair); endopod of 1st male pleopod (Fig. 17K) medially with series of 7 proximal serrate spines and 4 simple spines distally, latter followed with about 8 plumose setae distributed along distal half of lateral margin; endopod of male 2nd pleopod (Fig. 17L) with appendix masculina overreaching both endopod and appendix interna, appendix masculina with series of 5–6 medial and anterolateral simple spines and group of about 6 simple terminal spines, endopod with 5 plumose setae on proximal half of medial margin and with series of plumose setae distributed from distomedial margin through to 0·5 of lateral margin. Branchial formula as shown above.

Unusual, aberrant for this species, form of endopod of both 2nd pleopods was found in male CL 2·5 mm (# 442/18) (Fig. 17 I,J): endopods with undeveloped distal part and fused with appendix masculina, latter bearing series of about 8 medial and anterolateral spines, only 2 plumose setae present proximally on medial margin of endopod; medial margin of 1st pleopod with 5 serrate setae proximally and 3 simple setae distally. Dorsal telson armament also incomplete in this specimen, lacking 1 spine from posterior pair.

Ovigerous female CL 2·3 mm with about 20 eggs with eyespots.

Measurements. (Lengths, mm):

	Red Sea			*Comoro Is.*	
Material [st., #]	♂ 19(27)	ovig.♀ 19(12)	juv.♀ 19(28)	♂ 442/18	ovig.♀ 442/20
Postorbital carapace	3·4	3·2	1·9	2·3	2·5
Rostrum	4·5	4·7	2·1	3·8	3·5
Total length	17·0	–	10·7	13·5	13·5
Telson	2·2	–	1·5	1·7	1·7
First pereiopod	9·5	8·3	5·0	6·1	6·3
Major 2nd pereiopod	18·5	14·0	8·5	11·2	10·5
chela	9·6	7·4	3·3	6·7	5·5
palm	5·7	4·6	2·0	3·9	3·1
carpus	1·5	1·5	1·3	1·2	1·2
Minor 2nd pereiopod	12·7	–	7·5	9·2	–
Third pereiopod	8·5	8·0	5·0	5·6	5·4
Eggs (stage)	–	(early)	–	–	(eyes)
length		0·50			0·60
diameter		0·40			0·40

Colour. No data on colour are available for the Comoro specimens. According to the collector's notes, the freshly preserved ovig. female from the Red Sea (coll.# 19(22)) had numerous small red spots distributed on the carapace and the abdomen throughout a yellowish background of the body. Narrow longitudinal red stripes present on eyestalks, similar stripes occured dorsally on the carapace—1 submedian longitudinal pair, and 4 stripes situated obliquely on each side and directed posterolaterally from the level of anterior part of submedian lines. Deeply red coloured branchial lamellae were visible through the semitransparent carapace. Longitudinal lines of similar colour occurred ventraly on the abdomen. Larger red spots were present on ambulatory pereiopods, fingers of 2nd pereiopods were densely covered with minute, deeply red spots. Bruce (1975b: p. 24, fig. 2) has published colour photograph of this species.

Remarks. The special structure on the major chela was one of the features noted by Audouin in his brief original description of this species: 'La figure 3 est encore un palémon, mais beaucoup plus petit que le précédent [= *Palaemon squilla*]: c'est une espèce nouvelle, très remarquable pour la forme de son corps, par le développement de ses yeux et par l'organisation de la main qui terminate la seconde paire de pattes' (Audouin, 1826: 91). It is the figure 3g of pl.10 from the zoological atlas of Savigny (?1812–1825; 1827) that gives the details. Holthuis (personal communication) has kindly clarified for us the confusing dates of these publications. He wrote (letter of 15 February 1990): 'The date of the atlas is not certain. Pl.10 of the Crustacea says 'Dessiné et gravé en 1805–1812', but there is no indication when it was published; it may have

appeared any time between 1812 and 1825. The text prepared by Audouin, after Savigny's ... blindness had [caused him] to discontinue working, was published in 1826.... A second edition of text and plates appeared in 1827'. The dates of Savigny's atlas were also discussed by Sherborn (1897).

Savigny's excellent figures show an animal without any supraorbital spine but possessing the characteristic fossae on the cutting edges of the major chela. The figures agree fairly well with the present specimens of *P. petitthouarsii*, with the exception of the shape of the 3rd maxilliped, as was also commented upon previously by Kossmann (Holthuis, 1952). In our opinion, the lateral margin of the scaphocerite is concave in all species of the genus *Periclimenella*, rather than slightly sinuate as figured by Savigny.

There are some differences between the material studied from the Red Sea and the Comoro Islands. The Comoro adult males are more slenderly built than males from the Red Sea. The most distinct difference is in the male 2nd pleopods which possess the appendix masculina clearly overreaching both the endopod and appendix interna in the Comoro specimens while in the Red Sea males the tip of the endopod exceeds the appendix masculina, and the appendix interna is the shortest process. The last structures strongly resembles those illustrated by Bruce (1978) and those noted by Holthuis (1952) for both *Periclimenes petitthouarsii* and *P. petitthouarsii* var. *spinifera*. The Comoro specimens differ also by having a slender and longer fused part of the upper antennular flagellum bearing 6–7 groups of aesthetascs while in the Red Sea specimens the flagellum is not so uniformly slender but broadening distally and possessing 10–13 groups of long aesthetascs. Cornea of the Red Sea specimens preserved in alcohol are black with a dark transverse band on eyestalks just behind cornea, while light grey in the Comoro shrimps. Unfortunately, no field data are available on the colour of the latter specimens. Both the populations mentioned here may differ also in the live colour pattern. So, additional study is necessary for a final conclusion on the conspecific status of both the collections studied.

Periclimenella petitthouarsii is closely related to *P. spinifera* (De Man, 1902), the only other species of the new genus. The presence or absence of the supraorbital spines easily distinguishes the species from each other. Although the supraorbital spines are well developed also in juvenile specimens of *P. spinifera* (Bruce, 1976b), the fact that some of the smallest specimens of *P. petitthouarsii* reported here (juv. ♀ ♀ CL 1·6 and 2·7 mm, coll.# 19(28)) possess distinct supraorbital tubercles or even minute spines (Fig. 16A,H) may present a special importance which clearly indicates a close phylogenetic relationship, although all other specimens lack any trace of such structure. Similarly, the sound-producing fossae are well developed and distinct in all the specimens studied, with the exception of the smallest female (CL 1·6 mm) in which fingers of the major 2nd pereiopod are simple (Fig. 16D), and of the young female (CL 1·9 mm, both coll.# 19(28)) with a small fossa developed only on the fixed finger. Thus, individual differences may also be observed during ontogeny in features of a specific importance.

Distribution. The previous distribution reports reviewed by Holthuis (1952) showed this species to be restricted to the Red Sea and the Persian Gulf. The species is now known also from the Gulf of Aden, **Tanzania**, **Kenya**, **Comoro Islands**, and north-east of **Madagascar** (Bruce, 1977). In the rest of the Indo-West Pacific Area it is replaced by the closely related species, *P. spinifera* (De Man, 1902).

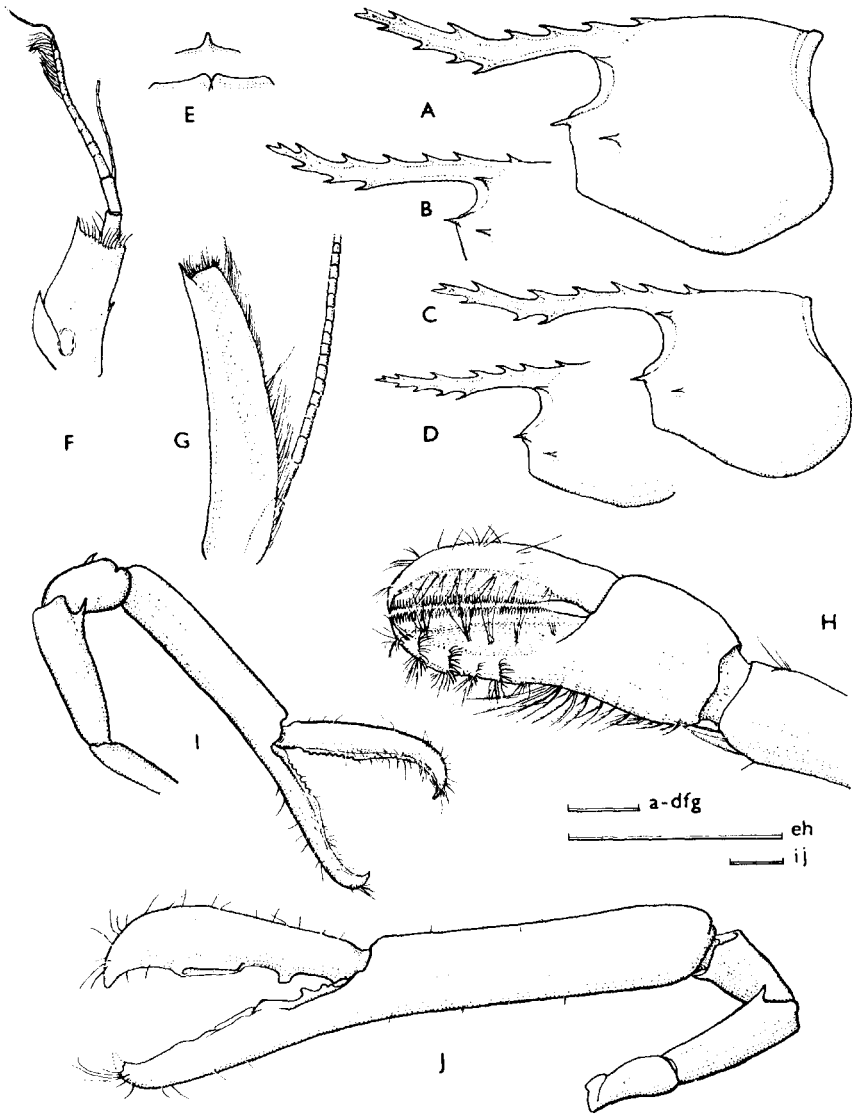

FIG. 19. *Periclimenella spinifera* (De Man), Oxley Island, Australia: (A–D) carapace and rostrum: (A) ovig. ♀ CL 3·8 mm, (B) non-ovig. ♀ CL 2·5 mm, (C) ♂ CL 3·6 mm, (D) ♂ CL 3·2 mm; (E–J) ♂ CL 3·6 mm: (E) 4th and 5th thoracic sternites; (F) antennule; (G) antenna; (H) right chela of 1st pereiopods, medial aspect; (I) minor 2nd pereiopod; (J) major 2nd pereiopod. Scales: 1 mm.

Periclimenella spinifera (De Man, 1902), comb. nov.
(Figs 19–20)

Periclimenes petitthouarsii var. *spinifera* De Man, 1902: 824.
Periclimenes (Falciger) spiniferus Borradaile, 1917: 324, 366 [key], 369, pl.52 Fig.1.
Periclimenes (Ancylocaris) spiniferus Kemp, 1922: 170 [key], 195; 1925: 322.
Periclimenes (Harpilius) spiniferus Holthuis, 1952: 12, 76, Fig. 30 [full synonymy]; 1953: 55; Sastry, 1981: 20 [list], 25, Fig. 4.
Periclimense spiniferus Johnson, 1963: 288 [erroneous spelling for *Periclimenes*].

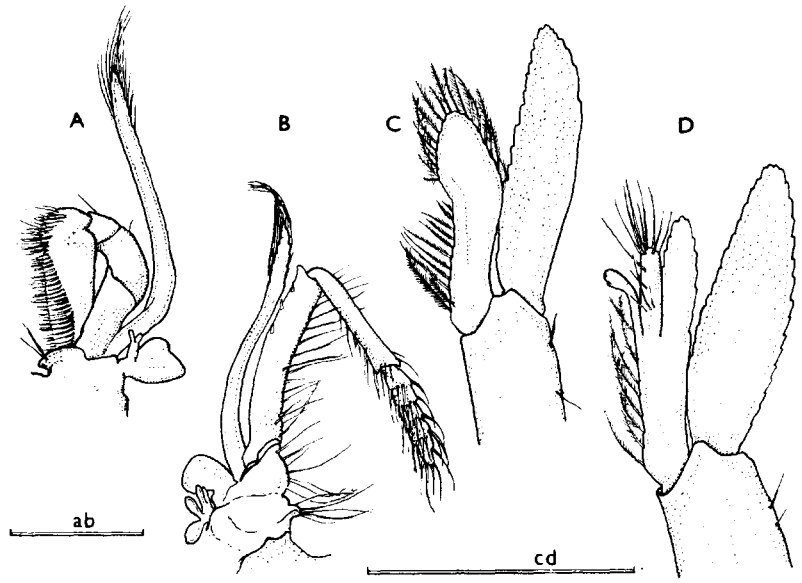

FIG. 20. *Periclimenella spinifera* (De Man), Oxley Island, Australia, ♂ CL 3·6 mm: (A) 2nd maxilliped; (B) 3rd maxilliped; (C) ♂ 1st pleopod; (D) ♂ 2nd pleopod. Scales: 1 mm (a,b), 0·5 mm (c,d).

Periclimenes spiniferus Patton, 1966: 271 [notes]; McNeill, 1968: 7, 23; Bruce, 1971: 2, 7; 1972a: 67; 1972b: 400, 401; 1974: 438, 440; 1976a: 59, 62, 71; 1976b: 92, 95, 143, 145, Figs 5–6; 1979: 229; 1981a: 20; 1981b: 79; 1983a: 210; 1983b: 43; 1983c: 165; 1983d: 886; 1984: 145; 1987b: 229, 238 [key]; 1990a: 17, 19: Devaney and Bruce, 1987: 223, 231.

Material. Oxley Is., Northern Territory, **Australia**, st. NY-9, 11°59·5'S, 135°48·8'E, depth LWS, coral reef, edge of reef-flat, 20 October 1982, coll. and det. A. J. Bruce [under generic name *Periclimenes*], NTM Cr.003155; 7 specimens (3♂ ♂, 4♀ ♀ (incl. 3 ovig.)).

Description. Rostrum (Figs 19A–D) distinctly longer than CL, 1·42–1·61 × in males, 1·36–1·47 × in females, slightly more sinuate in ovigerous females (Fig. 19A) than in males or young specimens (Figs 19B–D); rostral dentition 6/4, in single non-ovig. female 6/3; 1st dorsal tooth situated anteriorly to posterior orbital margin, 1st ventral tooth in middle length of rostrum; epigastric, supraorbital, antennal and hepatic spines present on carapace. Fourth thoracic sternite with short acute median process, 5th sternite bearing transverse ridge with median notch (Fig. 19E). Third abdominal somite with finely denticulate posterior dorsal margin. Telson about 2·4 × longer than broad, with 2 pairs of dorsal spines of about 0·1 of telson length and with transverse row of setae on anterior midline; posterior margin subtriangular with acute median process and with 3 pairs of spines, lateral pair distinctly shorter than dorsal spines, intermediate pair about 0·35 of telson length, submedian pair longer than 0·5 of intermediate spine length and bilaterally feebly setulose.

Basal segment of antennular peduncle (Fig. 19F) about 1·8 × longer than broad, strong distolateral tooth reaching nearly to middle of 2nd peduncular segment length; upper flagellum biramous, fused part consisting of 10–12 segments, short free ramus with 2–3 segments, long free ramus with about 12 segments, about 20 groups of aesthetascs present; lower flagellum filiform, longer than upper flagellum, with about

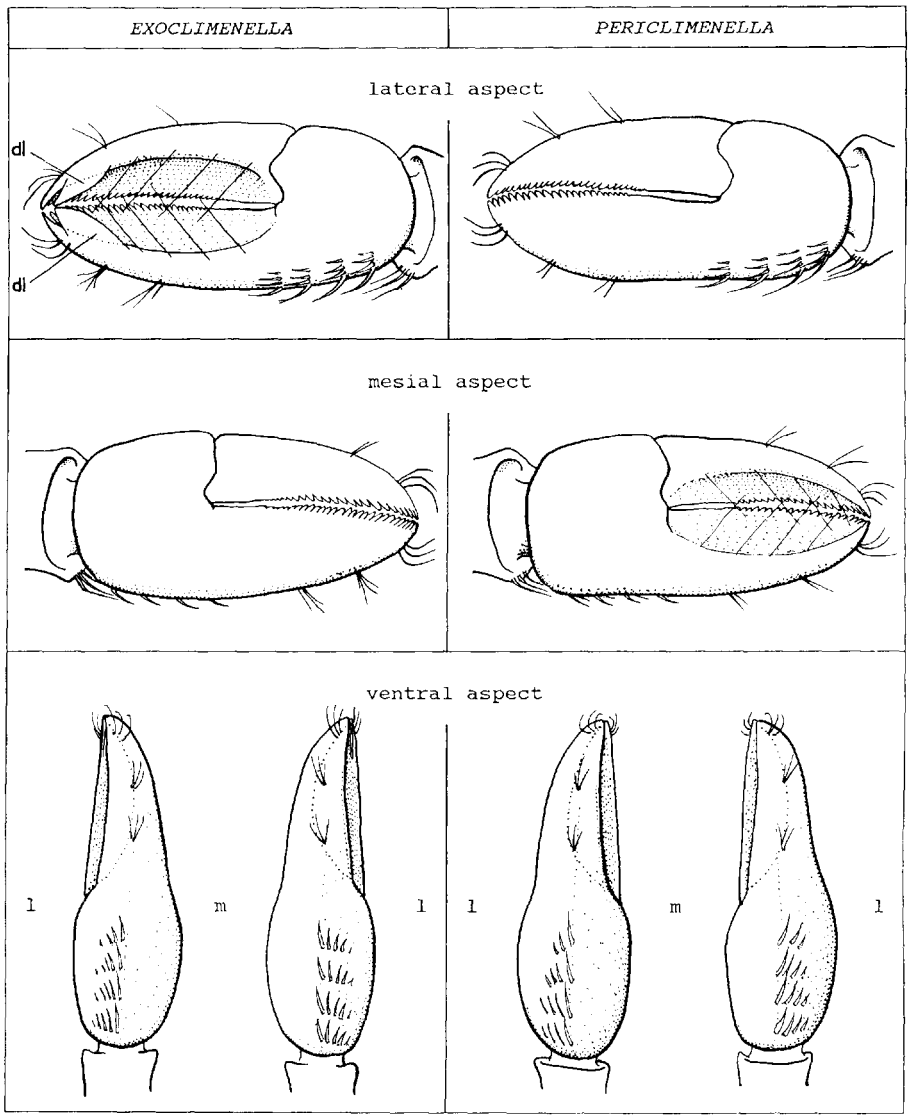

FIG. 21. Diagrammatic comparison of chelae of 1st pereiopods of *Periclimenella* and *Exoclimenella* showing the orientation of the finger concavities. The lateral and medial aspect of the left chelae is drawn, the ventral aspect figures pairs of chelae. (dl) distolateral lamina; (l,m) lateral and medial sides.

30 segments. Antennal basicerite with distolateral tooth, scaphocerite (Fig. 19G)elongate, with concave lateral margin terminating with strong tooth overreaching truncate tip of lamina, lamina more than 4 × longer than proximal width, narrowing distally; carpocerite reaching to distal end of basal antennular segment; antennal flagellum about 1·5 × longer than total body length.

Mandible without palp; 2nd maxilliped (Fig. 20A) with epipod with small reduced podobranch bearing 2 lamellae and situated near base of epipod; 3rd maxilliped (Fig. 20B) with 3 distolateral spinules on ischiomerus, coxal flange rounded, with single reduced arthrobranch consisting of 4 lamellae and situated near base of coxal plate.

First pereiopod slender, chela (Fig. 19H) with subspatulate fingers with denticulate cutting edges situated laterally, concavity of subspatulate fingers opening medially of chela, both fingers with terminal tooth but without additional transparent distolateral lamina; palm bearing about 9 rows of brush setae laterally along ventral margin; carpus 2 × as long as chela in adults, in juveniles, 1·5 × longer than chela, merus slightly shorter than carpus.

Second pereiopods dissimilar and unequal; major chela (Fig. 19J) possessing sound-producing fossae on cutting edges of fingers; palm 1·3–1·5 longer than fingers; carpus bearing 2 strong teeth on distal margin, carpus very short, palm:carpus ratio 3·9 and 4·1 × in adult males (CL 3·2 and 3·6 mm respectively), 1·9 × in young male (CL 1·9 mm), 2·6, 3·1 and 3·6 × in ovig. females (CL 3·2, 3·8 and 3·8 mm respectively) and 1·7 × in immature female (CL 2·6 mm); merus with strong distoventral tooth. Minor chela (Fig. 19I) with curved fingers terminating with acute hooked tip, cutting edges provided with numerous low irregular teeth on proximal 0·4 of length and with sharp low longitudinal lamina on distal part; carpus with 2 distal marginal teeth, palm:carpus lengths ratio 2·5–2·6 in adult males, 1·4 in young male, 1·6–1·9 in ovig. females, 1·4 in immature female; distoventral tooth present on merus.

Dactylus of 3rd pereiopod simple, stout, with curved sharp unguis; propodus about 4 × longer than dactylus, with 9–10 ventral spines (including distal pair); carpus 0·4 of propodal length, merus nearly as long as propodus.

Endopod of male 1st pleopod (Fig. 20C) with series of 11 serrate medial spines decreasing in length proximally, distomedial and distolateral margin with about 18 plumose setae. Male 2nd pleopod (Fig. 20D) bearing subcylindrical appendix masculina provided with only simple spines—about 8 terminal and 5 ventral; appendix masculina slightly longer than appendix interna but distinctly shorter than distal end of endopod; endopod with 8 plumose setae on proximal part of medial margin, with series of numerous plumose setae along distomedial and 0·5 of lateral margins.

Uropod with ovate exopod with subtriangular distolateral tooth and more slender, longer movable spine; both uropodal rami reaching beyond distal end of telson.

Branchial formula as in *P. petitthouarsii* (see above).

Three ovigerous females present (CL 3·2–4·3 mm), each bearing numerous eggs in early stage of development.

Measurements. (lengths in mm):

				Ovig.			
	♂	♂	♂	♀	♀	♀	♀
Postorbital carapace	1·9	3·2	3·6	4·3	4·0	3·2	2·5
Rostrum	2·4	5·0	5·8	5·4	5·5	–	3·6
Total length	8·5	13·7	14·3	16·4	16·0	12·6	11·4
Telson	1·6	2·3	2·8	2·5	2·4	2·1	1·9
First pereiopod	4·9	8·3	9·6	9·6	9·5	8·2	6·6
Major 2nd pereiopod	7·0	17·8	20·5	14·4	15·3	13·4	9·4
chela	3·6	10·5	12·2	6·8	8·2	5·9	4·5
palm	2·2	6·4	7·2	4·2	4·9	3·6	2·6
carpus	1·1	1·65	2·0	1·7	1·6	1·4	1·5

Measurements. (lengths in mm): —*Continued*

				Ovig.			
	♂	♂	♂	♀	♀	♀	♀
Minor 2nd pereiopod	6·8	14·4	16·0	11·9	14·5	9·8	7·8
Third pereiopod	4·9	8·5	9·4	8·7	9·6	8·0	6·0
Eggs (stage)	–	–	–		(early)		–
length				0·55	0·51	0·49	
diameter				0·45	0·44	0·42	

Colour. No data are available on the present specimens. Kemp (1922) in his detailed description of the colour reported: '... a ring of black pigment on the upper part of cornea. Adult males, when living, are for the most part semitransparent with minute red and white dots. On the anterior part of carapace (sometimes on the posterior part also) there are oblique or transverse bands of white dots, broadly outlined with deep carmine or black and the eyestalks are striped with the same colour. The distal ends of the merus, carpus, and palm of the peraeopods are suffused with orange or orange red and beyond this suffusion a white patch is frequently found. The fingers are spotted with black and often have a blue tinge. The other legs are finely dotted with red or reddish-brown and with white. At the distal ends of the telson and each uropod there is a white spot and the setae of the uropods are sometimes dark blue at the base ...' (Kemp, 1922: 195–196). The rings of black pigment on upper cornea have been reported also by Holthuis (1952) and Bruce (1976b), and are also present in our specimens.

Remarks. Wide variation has been reported in literature on the rostral dentition. Kemp (1922) stated the rostral formula is 6–7(9)/3–4(2–5). Bruce (1976b) described a juvenile specimen with 5 dorsal teeth and one ventral tooth. The present specimens are quite typical in this aspect, possessing 6 dorsal and 4 (3 in one case) ventral teeth.

Periclimenella spinifera is closely related to *P. petitthouarsii*, and the only constant feature distinguishing it from the latter is the presence of the supraorbital spines. Those structures are, however, well developed also in the smallest specimens.

Dr F. A. Chace, Jr, and Professor L. B. Holthuis turned our attention to the following nomenclatural aspect. Holthuis (personal communication, letter of 3 March 1993) commented that: 'One minor advantage of *Periclimenella* is that the original spelling of De Man's (sub)specific name '*spinifera*' can again be used. De Man (1902) used the feminine ending *-era* probably while he considered it a variety and the latin word varietas is feminine. Of course since the name was in the masculine genus *Periclimenes* he should have treated it as a masculine adjective '*spinifer*'. Later authors ... made the mistake of changing *spinifera* to *spiniferus* instead of *spinifer* ... Now of course this is no longer of importance as *spinifera* can be used correctly'.

Habitat. *Periclimenella spinifera* has been observed on living scleractinian corals of the genera *Acropora*, *Montipora*, *Pavona*, *Pocillopora*, *Porites*, and *Seriatopora* (Holthuis, 1953; Bruce, 1971, 1972a,b, 1976b, 1981a), or a hydroid *Millepora tenera* (Bruce, 1981b). Sastry (1981) has reported this species from a crinoid host, but this association is most probably accidental. The shrimp is also frequently found in dead corals, or in pools of reef-flat devoid of corals (Bruce, 1974; 1976b; 1981a), and is considered to be a free-living browser (Bruce, 1972a; 1976a; 1981a).

Distribution. Holthuis (1952) reviewing literature and his own data showed the following distribution: eastern **Madagascar**, **Seychelles**, Maldive and Chagos Archipelagoes, Gulf of Manaar, Andaman and Nicobar Islands, Java Sea, Ternate, Amboina, Papua, Great Barrier Reef, Samoa, Tahiti, Wake Island. Subsequently, the following records were reported: Seychelles (Bruce, 1971; 1976b), Réunion (Bruce, 1983d), Maldive Islands (Bruce, 1974), Burma (Sastry, 1981), Singapore (Johnson, 1963), South China Sea (Bruce, 1979), Moluccas (Bruce, 1983d), Ryukyu Islands (Nomura *et al.*, 1988), Mariana and Marshall Islands (Holthuis, 1953; Devaney and Bruce, 1987), Northern Territory, Australia (Bruce, 1983b; 1987b), Great Barrier Reef, Australia (Patton, 1966; McNeill, 1968; Bruce, 1981a; 1983a; 1987b), Fiji (Bruce, 1972a; 1981b).

As noted above, this widespread species is known from the whole Indo-West Pacific area excluding the northwestern Indian Ocean and the Red Sea where it is replaced by *P. petitthouarsii.*

Discussion

Although, as a rule, there are no problems over where to place an individual shrimp genus, the features distinguishing the palaemonid subfamilies are not at all clear. Borradaile (1917), followed by Kemp (1922), defined 4 subfamilies within the family Pontoniidae: Desmocaridinae Borradaile, Pontoniinae Kingsley, Typhlocaridinae Annandale and Kemp, and Palaemoninae Kingsley. In his revision of shrimp genera, Holthuis (1955), including the genus *Desmocaris* Sollaud in the subfamily Palaemoninae, has mentioned only 3 subfamilies. Burukovsky (1974), following Holthuis' previous (1952) point of view, has raised the Desmocarididae to family rank, but made the Euryrhynchinae Holthuis a subfamily of Palaemonidae, together with 3 remaining subfamilies. Lately Bruce (1986) has incorporated the family Gnathophyllidae Dana into Palaemonidae, and synonymized it with the pontoniine shrimps resulting in the subfamily Gnathophyllinae (however, the previous name Pontoniinae is now preferred), together with the reestablishment of the subfamilies Hymenocerinae and Anchistioidinae. In addition to these revisions, Chace (1992) now proposes 6 families—Anchistioididae, Desmocarididae, Gnathophyllidae, Hymenoceridae, Typhlocarididae and Palaemonidae, with his typhlocaridid family containing the subfamilies Typhlocaridinae and Euryrhynchinae, and with the Palaemonidae also having 2 subfamilies—Palaemoninae and Pontoniinae. Finally, Bruce (1993) places all Chace's taxa named above at the subfamily level within the family Palaemonidae, and adds a newly established, 9th, subfamily, Kakaducaridinae.

All these authors, excluding Chace (1992), have mentioned the presence of the pleurobranch (or 1 or 2 arthrobranchs (Bruce, 1993)) on the 3rd thoracic somite as most important for distinguishing the subfamily Palaemoninae from Pontoniinae. Recently

large specimens of palaemonine shrimp *Macrobrachium* have been examined by us and it appeared that the 3rd maxilliped has 2, an upper (dorsal) and a lower (ventral), arthrobranchs, but no pleurobranch. Patwardhan (1937), in his detailed study of *M. malcolmsonii*, Abele and Felgenhauer (1986: Fig. 7A) in *Macrobrachium* sp., and Bruce, (1992a) in *M. handschini* also report 2 arthrobranchs. We suggest that Borradaile (1917) and Kemp (1922) called the large gill a pleurobranch and most authors just followed their example. As has been recently shown by Bruce (1990b: 576, and Fig. 6), in some palaemonids that 'pleurobranch' may be reduced, smaller than the 'arthrobranch'. Such gill mórphology is very similar to the one observed here in species of *Exoclimenella* gen.nov. which possess a pair of arthrobranchs on the 3rd maxillipeds.

In the Pontoniinae, at most 1 small or vestigial arthrobranch may be present, but it is lacking in the great majority of pontoniine genera. In this regard, the newly established genus *Exoclimenella* gen.nov. occupies rather special taxonomic position—possessing a typical pontoniine condition of telson spines, but with the presence of 2 arthrobranchs on the 3rd maxillipeds, suggesting a generic affinity with the subfamily Palaemoninae.

All species of the new genera *Periclimenella* and *Exoclimenella* possess a small, but functional, 1- or bilamellate podobranch on the 2nd maxilliped. This feature is widely distributed within Palaemoninae, but is not referred for the majority of pontoniine shrimps.

Borradaile (1917) reviewed several features considered near to the ancestral type in the Pontoniinae. *Exoclimenella* species also shows wide variation in these features. The presence of the mandibular palp in 3 species relates the genus to the Palaemoninae, as well as to less specialized pontoniine genera *Palaemonella*, *Vir*, and *Eupontonia*. In recent years, however, and in some palaemonid species particularly, this feature has become a character of rather dubious taxonomic value. So often, particularly with the rarer species, knowledge of the palp is based only on the dissection of a single example. In *Palaemon debilis*, for example, Chace (1972) has shown that the palp can be present or absent, or the number of segments can vary from 1 to 3. Carvacho (1977) has reported specimens of *Leander tenuicornis* possessing 2- or 3-segmented palps. Fujino and Miyake (1968) have similarly shown that the number may vary considerably also between left and right in several species of *Palaemon*. They state, 'As far as the number of the mandibular palp [segments] is concerned, it seems advisable not to regard it as important subgeneric character between *Palaemon* and *Palaeander*' (p. 199). Bruce (1989) has also concluded that the presence or absence of the mandibular palp, by itself, does seem to be an inadequate character on which to separate palaemonid genera, unless additional characters can be called into evidence to support generic separation. The newly established genus *Exoclimenella* shows such a situation; 3 species possess a reduced, 1- or 2-segmented mandibular palp, and the 4th species, as well as the both species of *Periclimenella* gen.nov., lacks the palp. A small variation in the palp segmentation is observed also in *E. maldivensis*. More extensive collections of the species need to be examined to assess the true taxonomic value of the palp within the new genus. The presence of a mandibular palp appears to be a plesiomorphic character.

The presence of the supraorbital spine was also mentioned by Borradaile (1917) as a primitive feature. Two species of the 2 new genera retain the character, *P. spinifera* and *E. sudanensis* sp.nov., sharing it with some species of pontoniine genus *Palaemonella*, Dana (Bruce, 1970; 1975a).

Borradaile (1917) also commented on the 'comb arrangement' on the fingers of the 1st chela in *E. denticulata*, and compared it with similar structures in many primitive

oplophorid shrimps and penaeid prawns. Pasiphaeid and bresiliid shrimps also possess such structures on chelae. The denticulate cutting edge on the fingers of the 1st chelae is present in all known species of *Periclimenella* gen.nov. and *Exoclimenella* gen.nov. In 2 of them, *E. denticulata* and *E. maldivensis* sp.nov., a similar arrangement has been found also on 2nd pereiopods. Regarding the latter, such structure have recently been described also in some highly specialized commensal shrimps of the genera *Periclimenaeus* Borradaile (Bruce, 1980; Ďuriš, 1990), and *Periclimenoides* Bruce (Bruce, 1990c). In *E. maldivensis* the denticulation is reduced during the ontogeny and absent in largest males. These developments could well be of convergent origin in different genera and are useful for taxonomy mainly at species level where their presence or absence is consistent.

Thoracic sternal armament is also of some importance, in our opinion. Most authors have omitted any reference to this character for most palaemonid and other shrimps. The presence of a finger-like median process on the 4th thoracic sternite, extending ventrally between the bases and coxae of the 1st pereiopods, are not confined only to *Periclimenella* gen.nov. and *Exoclimenella* gen.nov., and is interpreted as a plesiomorphic character as a similar process is also conspicuous in less specialized pontoniine genus *Palaemonella* (Bruce, 1970), or in the '*grandis*' group of species of the genus *Periclimenes* (Bruce, 1987a). The process is also present in some free living palaemonid genera such as *Palaemon* and *Macrobrachium* although absent in *Leander* and *Leandrites*, but is generally absent from most commensal pontoniine species (Bruce, 1987a).

Together with the presence of the plesiomorphic characters mentioned above, the wide range of their reduction, commented above, is observed most conspicuously within species of *Exoclimenella* gen.nov.. Moreover, in some cases, *Exoclimenella* gen.nov. also possesses some specialized structures, such as the subspatulate 1st chelae. This is rare within pontoniine shrimps, and, together with the denticulation of the cutting edges, is interpreted as a feature adaptive for a free-living browsing habit (Bruce, 1976a). Some pontoniine species, for example *Periclimenes soror*, *P. imperator*, and *Zenopontonia noverca*, also have subspatulate chelae on 1st pereiopods, with pectinate cutting edges. However, the pereiopods are short and stout, not elongate and slender, as in the new genera described above. These species are commensal shrimps, not free-living browsers.

The sound-producing mechanism, found in *P. petitthouarsii* figured in detail by Bruce (1976a: Fig. 14) and *P. spinifera*, is rather different from that in other shrimps capable of producing a snapping noise, particularly *Coralliocaris* (Bruce, 1976a: fig. 13), or *Alpheus* and *Synalpheus*. In *Periclimenella* gen.nov. the fingers of the major chela are provided with opposing pits on the cutting edges. Their sudden closure produces a sharp snap, as has been reported by Bruce (1976a) who has also described sound producing capabilities of those and other pontoniine and alpheid shrimps. It also is remarkable that all species of the related genus *Exoclimenella* gen.nov., with the exception of *E. denticulata*, possess a very special swollen tooth with flat, or slightly concave, lower surface on the dactylar cutting edge of the major chela just at the same place where species of *Periclimenella* gen.nov. have the sound-producing fossa.

A fine denticulation observed on the posterior dorsal margin of the 3rd abdominal segment (Figs 7D, 9K, 14C), a structure not reported in earlier literature, is not a character unique to the pair of genera described in this paper. Several available palaemonine and pontoniine species have been examined in this aspect. Although the posterior dorsal margin of the 3rd abdominal segment is provided with fine but entire

transparent lamina in most of examined pontoniine genera (*Apopontonia*, *Coralliocaris*, *Fennera*, *Harpiliopsis*, *Ischnopontonoia*, *Jocaste*), deep and narrow incisions make the margin more or less irregularly divided in several species (*Conchodytes meleagrinae*, *Palaemonella rotumana*, *Vir orientalis*, *Pontonides unciger*), or is fairly regularly arranged with fine trapezoidal denticles (*Thaumastocaris streptopus*). Slender elongate denticles are present in the pontoniine species *Periclimenes nilandensis*. Well developed denticles similar to those of *Periclimenella* gen.nov. and *Exoclimenella* gen.nov. have also been observed in the Mediterranean shrimp *Palaemon elegans*. In that species, less developed denticulation were seen also on margins of other abdominal segments. The taxonomic status of the marginal denticulation on the abdominal tergites will be the object of a separate study.

Another feature largely omitted so far from descriptions but perhaps should be noted in future reports is a group of setae situated dorsally on the anterior part of the telson. In his review of 2 Australian species of the genus *Palaemonetes*, Bray (1970) has stated (p. 83): 'There is, however, a character that links *P. atrinubes* with *P. australis* and clearly distinguishes them from other Australian species: this character is the absence of a transverse row of small setae on the anterior midline of the telson. The setae are small and not obvious unless closely examined. They were not mentioned by Yaldwyn (1954) in his description of *Palaemon affinis* but are shown in his drawing of the telson ...'. Bruce (1992b) has illustrated them in his *Periclimenes lacertae* in lateral view but omitted them from the dorsal view. Groups of such setae have also been observed in species of *Periclimenella* gen.nov. and *Exoclimenella* gen.nov. during the present study (Figs 1, 2E, 6, 7E, 9L, 14A).

In conclusion, we can state that the *Periclimenella–Exoclimenella* generic pair provide a distinctive set of plesiomorphic as well as synapomorphic characters. The plesiomorphic features, including the conservative branchial condition, show an affinity with the subfamily Palaemoninae, or, at least, with less specialized pontoniine genera. The presence of some advanced structures may place the genus *Periclimenella* gen.nov. in the subfamily Pontoniinae, close to the specialized commensal genera. Thus, it is possible that the new generic pair could occupy an independent position intermediate between Palaemoninae and Pontoniinae.

However, the other feature frequently used to distinguish the 2 subfamilies is a number of telson spines. In his recent revision of Caridea, Chace (1992) omits a discussion of the branchial condition and distinguishes the Palaemoninae from the Pontoniinae only on the basis of the posterior margin of the telson having 2 pairs of spines instead of 3. On this basis, *Exoclimenella* gen.nov., as well as *Periclimenella* gen.nov., stay safely in the Pontoniinae, rather than in the Palaemoninae.

Although the species of *Periclimenella* gen.nov. and *Exoclimenella* gen.nov. represent a compact group in regard to their general morphology, a wide range of variation and differences are observed within the 2 genera, including characters of higher taxonomic importance in other shrimp groups (see above). The species of *Exoclimenella* gen.nov. keep most of the ancestral characters discussed above. Only the species of this genus possess the mandibular palp, although variation in the reduction of this structure may also be observed. *Exoclimenella denticulata* beares 2-segmented palp, in *E. maldivensis* sp.nov. this number varies from 1 to 2, while in *E. sudanensis* sp.nov. the palp consists only of 1 segment, and in *E. sibogae* it completely is absent. It is also absent in *Periclimenella* gen.nov. The long finger-like median process on the 4th thoracic sternite is also present only in the genus *Exoclimenella* gen.nov., excepting

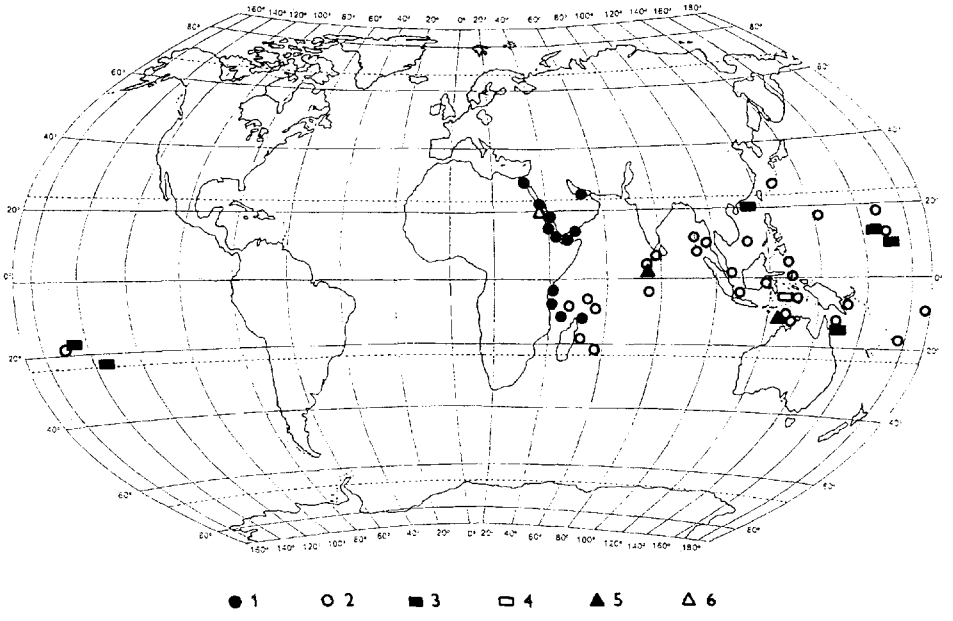

FIG. 22. Distribution of species of the genera *Periclimenella* and *Exoclimenella*. (1) *P. petitthouarsii*, (2) *P. spinifera*, (3) *E. denticulata*, (4) *E. sibogae*, (5) *E. maldivensis* sp.nov., (6) *E. sudanensis* sp.nov.

E. denticulata where it is short, as in the genus *Periclimenella* gen.nov. The presence of a pair of long finger-like processes on the 5th thoracic somite, however, readily distinguishes the former genus from the latter.

However, the most peculiar difference between the 2 genera is in the position of the concavity on the subspatulate 1st chela, not reported in the literature until now. In the species of the *Periclimenella* gen.nov., the concavity faces medially, while in the species of the genus *Exoclimenella* gen.nov. the concavity faces laterally (Fig. 21). This aspect could not be interpreted as a result of a rotation of the palm or a result of a side change of detached appendages as the chelae were examined still attached, extended anteriorly in a standardized position, with the dactylus uppermost. Moreover, the lateral surface of the chela is also clearly indicated by the presence of the transverse rows of cleaning setae invariably situated laterally on the proximal ventral margin of the palm (Fig. 21, ventral aspect). Thus, in all species of *Exoclimenella* gen.nov. the setae are present at the same side of the chela together with the concavity while in the species of *Periclimenella* gen.nov. the setae have been found at the opposite side, on the ventrolateral face of the palm, although the concavity was at the inner side. Finally, the additional distolateral transparent lamina is also present on the fingers of the 1st pereiopod chelae of *Exoclimenella* gen.nov. species, but absent in the species of the other genus. These unusual and probably unique differences in the spatial orientation of these organs, important as indicators of distinctive feeding habits, may be the result of the phylogenetic changes caused by significant changes in feeding behaviour. *In situ* behavioural observations on the shrimps are necessary for final clarification of this aspect.

Regarding the phylogeny between the new generic pair, *Exoclimenella* gen. nov. seems to be less divergent from the ancestral form while *Periclimenella* gen.nov. is represented by more specialized forms. The species of the latter genus, *P. petitthouarsii* and *P. spinifera*, are the only ones possessing the sound-producing fossae on the major 2nd chela, and lacking also the mandibular palps, the small proximal arthrobranch on the 3rd maxilliped, and the pair of processes on the 5th thoracic sternite. Moreover, this genus is widely distributed throughout the entire Indo-West Pacific rea and representatives of its 2 species are among the most common shrimps sampled in this region. Both the species are very similar to each other, and the only character readily distinguishing them is the presence or absence of the supraorbital spines on the carapace. It is evident that *Periclimenella* gen.nov. has developed from *Exoclimenella* gen.nov. It seems likely that any evolutionary factor, for example an appearance of the new orientation of the concavity of the fingers of the 1st chela, provides the species of *Periclimenella* gen.nov. with an important functional advantage resulting in their high population abundance and wide biogeographic distribution. The close morphological similarity of both its species and small intraspecific differences noted in this between the Red Sea and Comoro populations of *P. petitthouarsii*, suggest that the time of the evolutionary changes has been relatively recent and insufficient for further specific or intraspecific divergences to occur within this modern genus.

On the other hand, the less specialized genus *Exoclimenella* is now represented by 4 apparently rare species known at present only from a small number of specimens, in most cases from a unique specimen or from the type locality only. Therefore, their known distributions are very restricted and isolated. It seems they represent an older, recessive evolutionary branch possibly restricted in several relict populations, and replaced now by more successful species of *Periclimenella* gen.nov.

The genus *Exoclimenella* gen.nov. is less compact and two pairs of species may be compared. The second male pleopods of *E. sibogae* and *E. denticulata* have the appendix masculina short, intermediate in length between the appendix interna and the endopod tip, and covered with long simple distal spines with a pair of strong serrate spines. The 1st male pleopod has the medial spines divided into 2 series of several long and plumose basal setae, and of numerous short curved but simple distal spines. *E. sudanensis* sp.nov. and *E. maldivensis* sp.nov. have the appendix masculina of the 2nd male pleopod long, far exceeding both the appendix interna and the endopod, and covered with uniformly short simple spines. The basal series of serrate spines on the 1st male pleopod gradually diminish distally and occupies 0·5 the length of the medial margin, the distal series consists of curved setae. Apart from such groupings, there are also important differences between the species of *Exoclimenella* gen.nov. in the presence or absence of supraorbital spines, in the reduction of mandibular palps and of the upper (proximal) arthrobranch on 3rd maxillipeds, in the length of sternal processes, in the shape of the cutting edge on the fingers of the 2nd chelae, or in number of meral spines on second pereiopods. This suggests a greater evolutionary age of the genus *Periclimenella* gen.nov., resulting in deeper morphological divergences between species.

Summarizing the data discussed here, we can assume that the possible ancestral form agreed with the generic diagnosis of *Exoclimenella* gen.nov. (see above). It shared the supraorbital spine and the 2-lamellate podobranch on the 2nd maxilliped with 2

recent species, *E. sudanensis* sp.nov., and with *P. spinifera*, indicating a possible evolutionary branch leading from *Exoclimenella* gen.nov. to the modern genus *Periclimenella* gen.nov. Two-segmented mandibular palp, an irregular number of the meral spines on the 2nd pereiopod, a unique character in the Palaemonidae, and the denticulate cutting edge on the major chela, places *E. denticulata* closely to the hypothetical ancester, while *E. sibogae*, lacking the mandibular palp and bearing the most reduced, vestigial upper (proximal) arthrobranch on the 3rd maxilliped somite, seems to represent the most specialized species within the genus but represents an independent branch sharing the shape of male second pleopods with *E. denticulata*. Two remaining species occupy intermediate positions within the genus, with *E. maldivensis* sp.nov. related more closely to *E. denticulata*, and with *E. sudanensis* sp.nov. more to *E. sibogae*.

Key to the determination of genera and species of *Periclimenella* gen.nov. and *Exoclimenella* gen.nov.

1 Mandibular palp absent, maxillular palp non-setose; 1 arthrobranch present on 3rd maxilliped; transverse ridge on 5th thoracic sternite without any processes (Figs 13B, 16B, 17B, 19E); 1st pereiopods with subspatulate concavity situated on medial aspect of chela, fingers without distal lamina (Figs 13F, 18F, 19H); merus of 2nd pereiopods with single distoventral tooth (Figs 13G,I, 19I,J); major chela with sound-producing fossae on opposite cutting edges of fingers (Figs 13H, 16L, 19J). . . . . genus *Periclimenella* gen.nov. 2

– Mandibular palp reduced (Figs 3A, 8A,B, 10A,B) but present (excl. *E. sibogae*); 2 arthrobranchs present on 3rd maxilliped (Figs 3H, 8G, 12B), proximal (upper) arthrobranch reduced; 5th thoracic sternite with transverse ridge bearing pair of long, slender acute submedian processes (Figs 2J, 7C, 9D, 12C); 1st pereiopod with subspatulate concavity placed on lateral side of chela (Figs 1, 6, 21), fingers with transparent distolateral lamina (Figs 4B, 7G, 9E, 11D, 12A); merus of 2nd pereiopods unarmed (Figs 1, 4E, 6, 7H,I) or with several acute teeth (Figs 11E,G,H,J); major 2nd chela without sound-producing fossae on cutting edges of fingers. . . . . genus *Exoclimenella* gen.nov. 3

2 Supraorbital spine absent (Fig. 13A) . . . . . *P. petitthouarsii* (Audouin)

– Supraorbital spine present (Figs 19A–D) . . . . . *P. spinifera* (De Man)

3 Supraorbital spine present (Fig. 6) . . . . . *E. sudanensis* sp.nov.

– Supraorbital spine absent 4

4 Carpus of 2nd pereiopods with 2 distal teeth (Figs 4E,I) . *E. maldivensis* sp.nov.

– Carpus of 2nd pereiopods with 3 distal teeth (Figs 11H,I) 5

5 Merus of 2nd pereiopods with group of several distoventral spines (Figs 11E,G,H,J) . . . . . *E. denticulata* (Nobili)

– Merus of 2nd pereiopods unarmed . . . . . *E. sibogae* (Holthuis)

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