

QUADRELLA (BRACHYURA: XANTHOIDEA: TRAPEZIIDAE)—REVIEW AND REVISION

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A B S T R A C T

Hexagonalia (Xanthoidea: Trapeziidae), new genus, is described from Styelaeridae in the western Indian Ocean. Descriptions and illustrations are given for two new species of *Quadrella*: *Q. lewinsohni* and *Q. serenei*, and for six previously recognized species: *Q. bispinosa*, *Q. boopsis*, *Q. coronata*, *Q. maculosa*, *Q. nitida*, and *Q. reticulata*. The various synonymies are discussed and a key is provided for their identification.

The species of the nominate subfamily Trapeziinae Miers, 1886, are known as obligate commensals of anthozoans throughout the tropical Indo-Pacific Ocean (Serène, 1984). Scarcity of differentiating features coupled with obscure color patterns have led to perplexing difficulties in determining their taxonomic status (Galil, 1984, in press a, b; Galil and Lewinsohn, 1983, 1984, 1985a, b). Study of extensive trapeziid collections with the purpose of reviewing the genus *Quadrella* revealed the presence of a new genus, *Hexagonalia*, and two new species, *Quadrella lewinsohni* and *Q. serenei*.

MATERIALS

The specimens upon which this study is based are deposited in the following museums: Allan Hancock Foundation, University of Southern California (AH), American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), Bernice P. Bishop Museum (BPBM), National Museum Singapore (NMS), National Science Museum, Tokyo (NSMT), Northern Territory Museum, Darwin (NTM), Muséum National d'Histoire Naturelle, Paris (PM), Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), Natur-Museum Senckenberg, Frankfurt (Senck. M.), University Museum of Zoology, Cambridge (UMZ), National Museum of Natural History, Smithsonian Institution (USNM), Western Australian Museum (WAM).

SYSTEMATICS

Hexagonalia, new genus

Commensal trapeziid crab associated with Styelaeridae (Serène, 1984: 288). Carapace hexagonal, wide, moderately convex. Anterolateral margins of carapace markedly convex, bearing median and epibranchial teeth. Posterolateral margins, longer than anterolateral, sloping diagonally. Thoracic sternum oval, first three sternites forming flattened ogival arch. Last abdominal segment much elongated.

Interorbital margin bilobed, superior orbital angle effaced. Orbita occupying anterolateral angles, orbital margin sinuous. Eye with short calcareous stalk and hemispherical cornea. Lower orbital margin diagonally cut, minutely serrate, not extending to superior orbital angle.

Antennules folding transversely within subfrontal fossets. Basal antennal segments lying within large orbital hiatus. Interantennular septum short. External maxillipeds close-fitting. Exognath of external maxilliped elongated, not quite extending to distal angle of endognath; internal distal margin with rounded tooth, distal margin lacking sulcus. Merus of endognath subquadrate, distal margin medially produced. Internal margins of both ischium and merus fringed with setae. Endognathal palp triarticulate, stocky, setose.

Chelipeds subequal, long. Merus wholly projecting beyond carapace. Carpus

globose. Manus of chela slender, subcylindrical, upper and lower margins carinate. Ambulatory legs long, slender, setose. Double row of triangular teeth on posterior margin of dactyls, curved spines at their distal bases; strong, curved apical tooth; cornute, curved spines distally on anterior surface.

First male pleopod slightly sinuous, tapered, with row of pinnate appendages distally on inner margin.

Type-species. — *Quadrella brucei* Serène, 1973.

Remarks. — Serène (1973: 203) described *Quadrella brucei* and recognized its uniqueness: "Les lobes frontaux à bord antérieur droit et la structure du premier pléopode mâle séparent l'espèce de toutes celles décrites à ce jour," yet he chose to include it in *Quadrella*. On checking the type specimens of the species, deposited in the British Museum, I have found it to bear but a superficial resemblance to the octocorallian-inhabiting genus *Quadrella*. *Hexagonalia* may be distinguished from *Quadrella* by its bilobed frontal margin, presence of orbital hiatus, absence of sulcus at distal margin of exognath of external maxilliped, carinate chela, paired teeth on posterior margin of dactyl, shape of first three thoracic segments and elongate last abdominal segment.

Hexagonalia brucei (Serène, 1973)

Figs. 1 A–E, 2

Quadrella brucei Serène 1973: 202, figs. 3, 8, 17–19, pl. 2a–d, 1984: 288, fig. 192, pl. 41b, c.

Material Examined. — Western Indian Ocean, 4°44'S, 39°24'E, 6 August 1971, 60–80 fms (109–146 m), EAMFRO Manihine, 2 ♂♂ (BMNH 1973:21). Holotype, paratype, det. R. Serène.

Description. — Carapace feebly punctate. Anterolateral margins rounded, bearing prominent, incurved intermediate spine. Epibranchial spine at junction of anterior and posterior lateral margins, incurved, long, acute. Posterolateral margins sloping. Interorbital lobes trapezoid, anterior margins slightly concave, separated by V-shaped emargination. Superior orbital angle narrow, microscopically tuberculate. Postorbital angle acute, projecting outward. Inferior orbital angle developed into conical tooth, tip barely visible beyond frontal margin (Fig. 1A).

Interantennular septum squat, trapezoid. Anterior margin of buccal frame minutely notched medially, arched at termination of efferent canals. Exognath of external maxillipeds columnar, tapering, distal margin slightly concave; small, rounded tooth distally on inner margin. Inner margin of ischium of endognath evenly rounded; merus subquadrate but for triangular protuberance on distal margin (Fig. 1B).

Chelipeds subequal, granulate, with long setae. Ischial anterior margin with 5 spinules; median spine longest. Merus longer than carapace, with eleven curved spines on anterior margin, increasing in size distally. On internal margin of carpus 2 prominent spines. Chela 1.7 carapace length (cl), somewhat laterally compressed. Upper and lower margins distinctly carinate, minutely serrate. Fingers short, inner edge serrate (Fig. 1C). Short spines on posterior margin of ambulatory propodi. Posterior dactylar margin with 8 pairs of triangular teeth having curved, cornute spines basally; large, cornute tooth on dactylar tip; anterior margin with several curved preapical spines; interior surface with 4 short transverse rows of spinules proximally, exterior surface with single transverse row (Fig. 1D).

First male pleopod somewhat flattened, row of slender pinnate appendages distally on inner margin, tip with several long setae (Fig. 2). Last abdominal segment triangular, as long as wide (Fig. 1E).

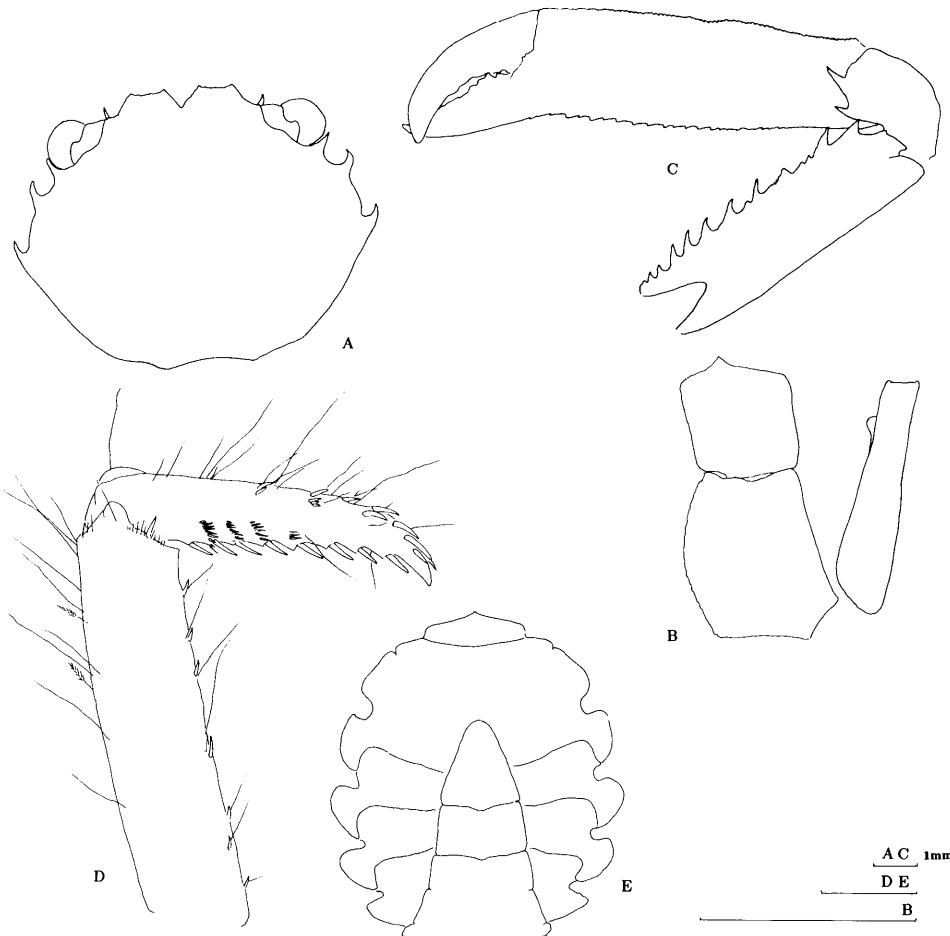


Fig. 1. *Hexagonalia brucei* (Serène). A–E, holotype, male, western Indian Ocean. A, carapace; B, third maxilliped; C, cheliped; D, fourth ambulatory leg, propod and dactyl; E, sternites and abdomen.

Remarks.—*Hexagonalia brucei* was reported from Stylasteridae (Serène, 1984), the first record of commensalism between a trapeziid crab and a hydrozoan.

Quadrella Dana, 1851

Commensal trapeziid crabs, associated with octocorallians (Serène, 1973). Carapace subhexagonal, convex, shagreened, regions of carapace poorly marked. Frontal margin narrower than greatest width of carapace. Epibranchial tooth separating anterior and posterior lateral margins. Thoracic sternum rounded, medially sutured, first 3 sternites forming an arcuate triangle. Last abdominal segment squat, rounded triangle, twice as wide as long (Fig. 3E).

Front, cut into 4 triangular lobes, projecting beyond spiniform or tuberculate supraorbital angle. Orbita, too shallow to conceal eyes, cut out of anterolateral angles of carapace; superior and inferior internal angles meeting so as to exclude antennae. Postorbital tooth acute, directed obliquely outward. Orbital margin crescentic. Inferior internal orbital angle spiniform, incurved, prominent beyond



Fig. 2. *Hexagonalia brucei* (Serène). Holotype. Pinnate appendages on first male pleopod.

frontal margin. Antennae inserted between antennular groove and inferior orbital angle. Crests of endostome, defining efferent canals, well developed. External maxillipeds subrectangular, exognath with uneven U-shaped sulcus at distal end and granulate rounded tooth on internal margin. Ischium of endognath with posterior margin transverse, anterior internal angle produced, inner margin rounded; merus trapezoid, its outer distal angle produced, rounded, inner angle obliquely truncate. Inner margins of both ischium and merus setose.

Chelipeds massive, elongate, subequal in both sexes, dissimilarity more pronounced in adult male. Whole of merus projecting beyond edge of carapace. Manus of chela subcylindrical, somewhat inflated, lower margin carinate. Fingers denticulate, dactyl curved, fitting closely upon immovable finger, curved tips crossing. Ambulatory legs long, slender, decreasing in size posteriorly. Row of triangular teeth, basally spinose, along posterior margin of dactyls; apical tooth cornute; distal curved spines on anterior surface.

First male pleopod distally setose or spinulose.

Type-species.—*Quadrella coronata* Dana, 1852.

Quadrella bispinosa Borradaile, 1902
Fig. 3A-D

Quadrella bispinosa Borradaile, 1902: 266, fig. 58a-c; Barnard, 1950: 819; Guinot, 1967: 275; Serène, 1968: 89, 1973: 198.

Quadrella boopsis—Sakai, 1965: 163, fig. 19a-b, pl. 80, fig. 4 (part); Serène, 1975: 514, figs. 5-12, pl. 2a-f (part); Sakai, 1976: 512, pl. 184, fig. 2 (part); Kensley, 1981: 45; Serène, 1984: 287, fig. 191, pl. 41a.

Quadrella aff. boopsis—Serène, 1973: 202, figs. 2, 14-16.

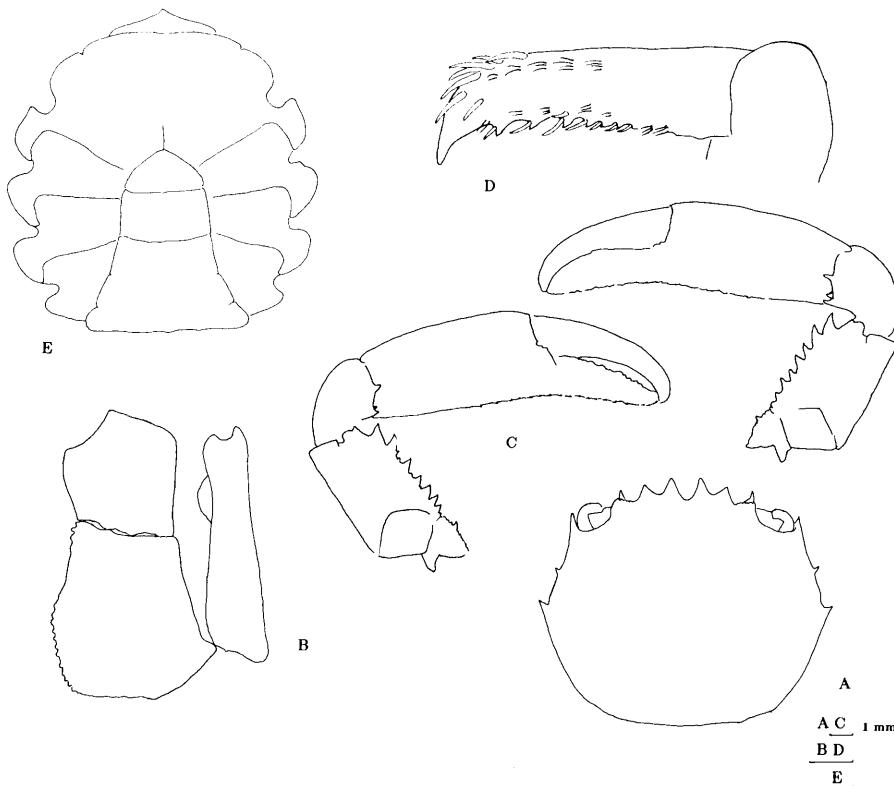


Fig. 3. *Quadrella bispinosa* Borradaile. A-D, holotype, female, Maldives Islands. A, carapace; B, third maxilliped; C, chelipeds; D, fourth ambulatory leg, propod and dactyl. *Quadrella coronata* Dana. E, male, sternites and abdomen.

Material Examined.—Holotype, Addu Atoll, Maldives Islands, 20 June 1900, leg. J. S. Gardiner, 1 ♀, carapace length (cl) 12 mm, carapace width (CW) 14 mm (UMZ).

Description.—Carapace lenticular, minutely shagreened, tubercles larger anteriorly. Frontal margin wide. Anterolateral margins straight, divergent posteriorly. Junction with posterolateral border marked by well-developed epibranchial tooth. Conspicuous acute spine midway between postorbital and epibranchial teeth. Posterolateral borders widely convex (Fig. 3A).

Submedian frontal lobes triangular, their edge finely dentate, separated by deep V-shaped sulcus and from outer lobes by shallower sinus. Outer pair of frontal lobes, not extending as far forward as submedian lobes, directed obliquely outward. Superior angles of orbits tuberculate, tubercles becoming progressively larger laterally. Orbita quadrate, orbital margins minutely tuberculate. Inferior internal orbital tooth visible beyond supraorbital angle, second, smaller tooth closer to frontal margin. Postorbital tooth acute, prominent.

Anterior margin of buccal frame sinuous, medially notched. Anterior margins of efferent canals noticeably raised, rounded. Interantennular septum quadrate. Exognath of external maxilliped nearly columnar, inner margin slightly excavate, bearing flattened, rounded tooth distally. Inner margin of ischium of endognath inflated, proximally tuberculate; anterior distal angle tuberculate, outer margin

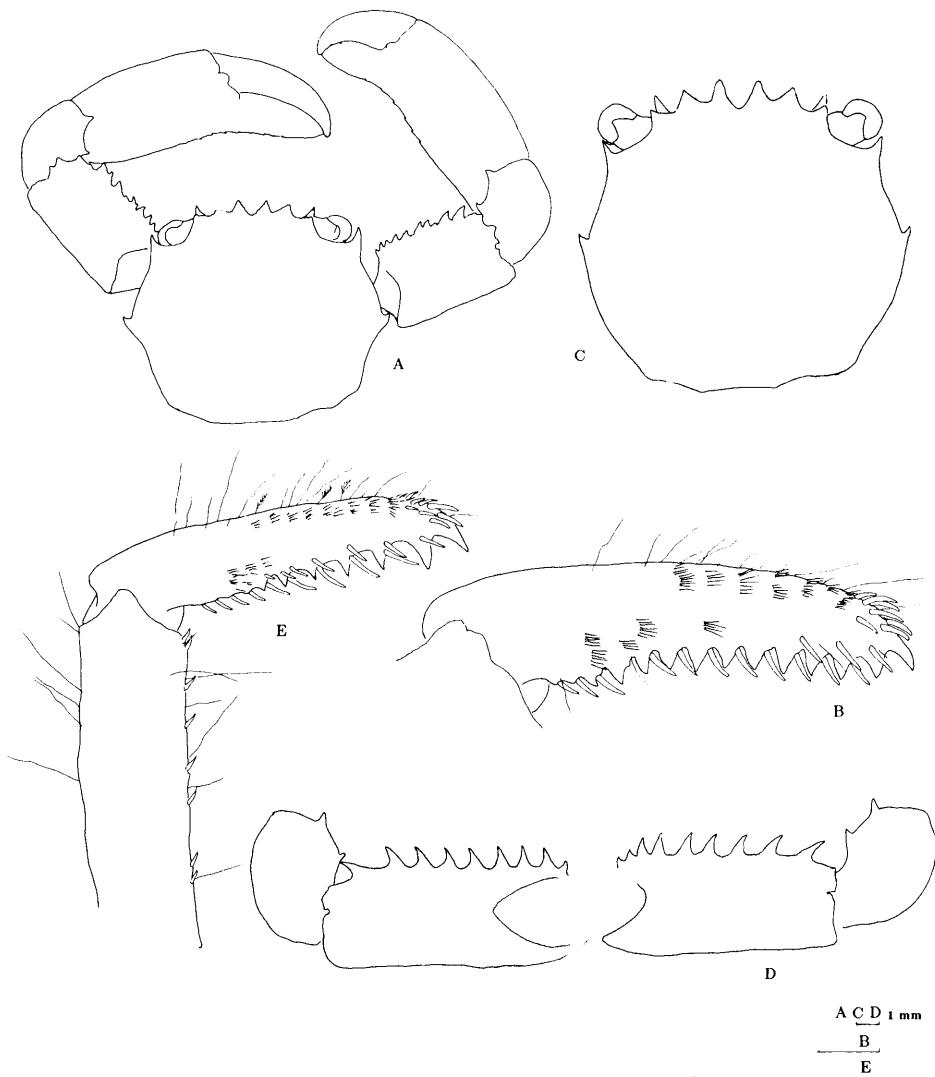


Fig. 4. *Quadrella boopsis* Alcock. A, B, female, Philippine Islands. A, carapace and chelipeds; B, fourth ambulatory leg, dactyl. *Quadrella coronata* Dana. C-E, male, Moluccas Islands. C, carapace; D, chelipeds, merus and carpus; E, fourth ambulatory leg, propod and dactyl.

oblique. Merus subquadrate; inner distal angle obliquely excavate, outer margin straight, inner margin rounded (Fig. 3B).

Chelipeds considerably developed, unequal. Anterior margin of ischium crenate, tuberculate, median tubercle prominent. Merus about 0.6 cl, its anterior margin with 8 or 9 curved triangular teeth increasing in size distally. On internal angle of carpus 3 tubercles, 1 proximal, 2 subdistal. Manus subcylindrical, minutely granulate, granules larger on lower margin. Fingers long, their inner margins serrate (Fig. 3C). Inner margin of ambulatory propodi smooth, without spines. Apical dactylar tooth largest, cornute. On posterior margin of dactyl 7 teeth becoming progressively smaller and closer proximally; on interior surface 5 short

rows of spinules anteriorly, 7 rows posteriorly extending to median row of teeth (Fig. 3D).

Distribution.—East Africa, Madagascar, Maldives Islands, Vietnam, Indonesia, Japan.

Remarks.—Borradaile (1902) erected *Quadrella bispinosa* for a single female dredged in the Maldives. The characteristic features—intermediate anterolateral spine, tuberculate supraorbital angle, relatively short, serrulate merus of cheliped—are all apparent in the well-illustrated description.

Quadrella bispinosa was made a synonym of *Q. boopsis* Alcock, 1898, by Sakai (1965). Confusion might have stemmed from Alcock's all too brief description of *Quadrella boopsis* (1898: 227) and Sakai's assertion that the midanterolateral spine is only an abnormality (1965: 163). Illustrations accompanying Sakai's work clearly depict the features of *Q. bispinosa*, i.e., the distinct carapace outline, sloping anterolateral borders, and fourth ambulatory dactyl.

In his first treatment of *Quadrella bispinosa* Serène (1973: 198) was reluctant to adopt Sakai's synonymy: "La ressemblance est frappante si on compare la figure de Borradaile (1902, fig. 58a) pour *bispinosa* avec celle de Sakai (1965, pl. 80, fig. 4) pour *boopsis*." In discussing *Q. boopsis* Serène (1973: 201) wrote: "Je fais une réserve sur l'identité du matériel de Sakai (1965) avec l'espèce d'Alcock." Serène (1973: 202) then described *Q. aff. boopsis* and his accompanying illustration of ambulatory dactyls (fig. 2) places his material without doubt in *Q. bispinosa*. In later works Serène (1975, 1984) accepted Sakai's opinion and synonymized *Q. aff. boopsis* and *Q. bispinosa* with *Q. boopsis*. However, his descriptions and illustrations (1975, figs. 5–12, pl. 2a–e, 1984, fig. 191, pl. 41a) are plainly of *Q. bispinosa*.

Quadrella boopsis Alcock, 1898 Fig. 4A, B

Quadrella boopsis Alcock, 1898: 227; Alcock and Anderson, 1899, pl. 38, fig. 1; Serène, 1973: 201. Not *Quadrella boopsis*—Sakai, 1965: 163, fig. 19, pl. 80, fig. 4; Serène, 1975: 514, figs. 5–12, 1984: 287, fig. 191, pl. 41a.

Material Examined.—Linao Pt., Gulf of Davao, Mindanao, Philippine Islands, 18 May 1908, 23 fms (42 m), Albatross Philippine Expedition D5250, 1 ♀ (USNM).

Description.—Anterolateral margins, constricted behind postorbital angles, convex. Epibranchial spine well developed, procurved. Posterolateral margins slightly concave. Submedian lobes finely serrate, separated by triangular notch. Lateral lobes, less prominent than submedian lobes, separated from latter by skewed, rounded sulcus. Supraorbital angle tuberculate, tubercles increasing in size distally. Inferior inner orbital angle acute, bearing additional minute tubercle anteriorly. Postorbital tooth prominent, acute. Superior orbital margin minutely tuberculate, inferior margin entire (Fig. 4A).

Anterior margin of buccal frame slightly concave, imperceptibly notched medially. Anterior margins of efferent canals arched. Interantennular septum quadrate. Exognath of external maxillipeds nearly columnar, triangular tooth on inner margin. Proximal half of inner margin of ischium of endognath tuberculate; inner distal angle of merus obliquely truncate, lateral margins subparallel.

Chelipeds massive. Three acute tubercles on anterior margin of ischium, median tubercle largest. Merus two-thirds cl and with irregular serration on its anterior margin. Carpus with 3 distinct tubercles, internal posterior tubercle minute. Chela 1.25 cl, inflated, granulate, lower margin serrate. First ambulatory leg 1.25 cl.

Stout spines along posterior edge of propodi. Thirteen (excluding apical spine) evenly spaced triangular teeth on posterior margin of fourth ambulatory dactyl, proximal teeth smallest; spines on interior surface above 3 distalmost teeth; several preapical curved spines on anterior margin. Eight anterior and 5 interior rows of setae on dactyl surface (Fig. 4B).

Distribution.—India, Philippine Islands.

Remarks.—*Quadrella boopsis* was described by Alcock (1898) from a juvenile specimen. Nevertheless the brief description and illustration (Alcock and Anderson, 1899) supply the necessary characters to confirm identification. *Quadrella boopsis* resembles *Q. bispinosa* in its short chelipedal meri; but it lacks the mid-anterolateral spine, its ambulatory propodi are spinose, and the dactyl posterior margin has 13 triangular teeth. In having serrations on the anterior margins of the meri *Q. boopsis* resembles *Q. reticulata*; however, the shorter meri serve to distinguish clearly *Q. boopsis*.

Quadrella coronata Dana, 1852
Figs. 3E, 4C–E

Quadrella coronata Dana, 1852a: 84, 1852b: 266, 1855, pl. 16, fig. 5; Miers, 1886: 163 (footnote); Ortmann, 1897: 210; Alcock, 1898: 266; Borradaile, 1902: 226; Rathbun, 1911: 235; Klunzinger, 1913: 317; Estampador, 1937: 531; Barnard, 1947: 365, 1950: 281, fig. 52e, f; Guinot, 1967: 275; Serène, 1973: 205, figs. 5, 10, 23–26, pl. 4a–d; Serène *et al.*, 1974: 24; Kensley, 1981: 45; Serène and Vadon, 1981: 122; Serène, 1984: 289, fig. 195, pl. 41f.

Trapezia sp.? Miers, 1884: 536 (footnote).

Quadrella coronata var. *granulosa* Borradaile, 1902: 266; Laurie, 1906: 411.

Quadrella boopsis granulosa—Sakai, 1965: 164, fig. 20, pl. 80, fig. 5; Serène, 1968: 89.

Quadrella coronata coronata—Serène 1968: 89.

Quadrella granulosa—Serène 1973: 207; Sakai, 1976: 512, pl. 184, fig. 3, fig. 271a, b; Serène, 1984: 289.

Not *Quadrella coronata* var.—Nobili, 1906a: 143, 1906b: 294.

Material Examined.—Providence I., 1882, 19 fms (35 m), HMS *Alert*, leg. R. W. Coppinger (BMNH 1882:24); 4 October 1905, 50 fms (91 m), HMS *Sealark*, leg. J. S. Gardiner, 2 ♂♂, 2 ♀♀ (USNM 41339).—Amirante I., 13 October 1905, 39 fms (71 m), HMS *Sealark*, 4 ♂♂, 3 ♀♀ (UMZ); 32 fms (59 m), HMS *Sealark*, 1 ♂, 1 ♀ (BMNH 1912:2:10:68).—Suvadiva Atoll, Maldives Islands, 30 fms (55 m), off gorgonian, leg. J. S. Gardiner, 1 ♀ (UMZ).—Mahlos Atoll, Maldives Islands, leg. J. S. Gardiner, 1 ♂ (UMZ).—Ceylon, leg. W. A. Herdman, 1 ♂, 2 ♀♀ (BMNH 1907:5:22:272–75).—Wokam, Aru I., Moluccas Islands, 16 June 1970, 38–52 fms (70–95 m), M. King Memorial Expedition, 1 ♂, 1 ♀ (WAM 73-73).—Piru Bay, Ceram I., Moluccas Islands, 1 June 1970, 27–35 fms (49–64 m), M. King Memorial Expedition, 2 ♂♂, 1 ♀ (WAM 74-73); 1 ♀ (WAM 75-73).—Off Port Hedland, Australia, 7 December 1982, on *Acabaria*, *Soela* CSIRO, 1 ♂ (NTM 2729).

Description.—Submedian frontal teeth separated by deep, V-shaped sulcus. Lateral teeth not extending as far forward as submedian pair and separated from latter by shallow, skewed indentation. Superior orbital angle prominent. Post-orbital angle spiniform. Inferior orbital angle conical, acute, projecting almost as far forward as lateral frontal teeth. Anterolateral margins sloping to acute, pro-curved epibranchial spine. Posterolateral margins slightly inflated (Fig. 4C).

Interantennular septum triangulate. Anterior margin of buccal frame sinuous, imperceptibly notched medially. Exognath of external maxilliped columnar, tapering distally, obtuse triangular tooth on distal inner margin. Internal margin of ischium of endognath rounded, prominently tuberculate; lateral margins of merus subparallel.

Anterior margin of ischium of cheliped with single spine. Merus 0.8 cl, its anterior margin with 7–10 curved spines, subequal, but for 1 or 2 proximalmost being distinctly smaller. On interior margin of carpus in juveniles 2 acute spines;

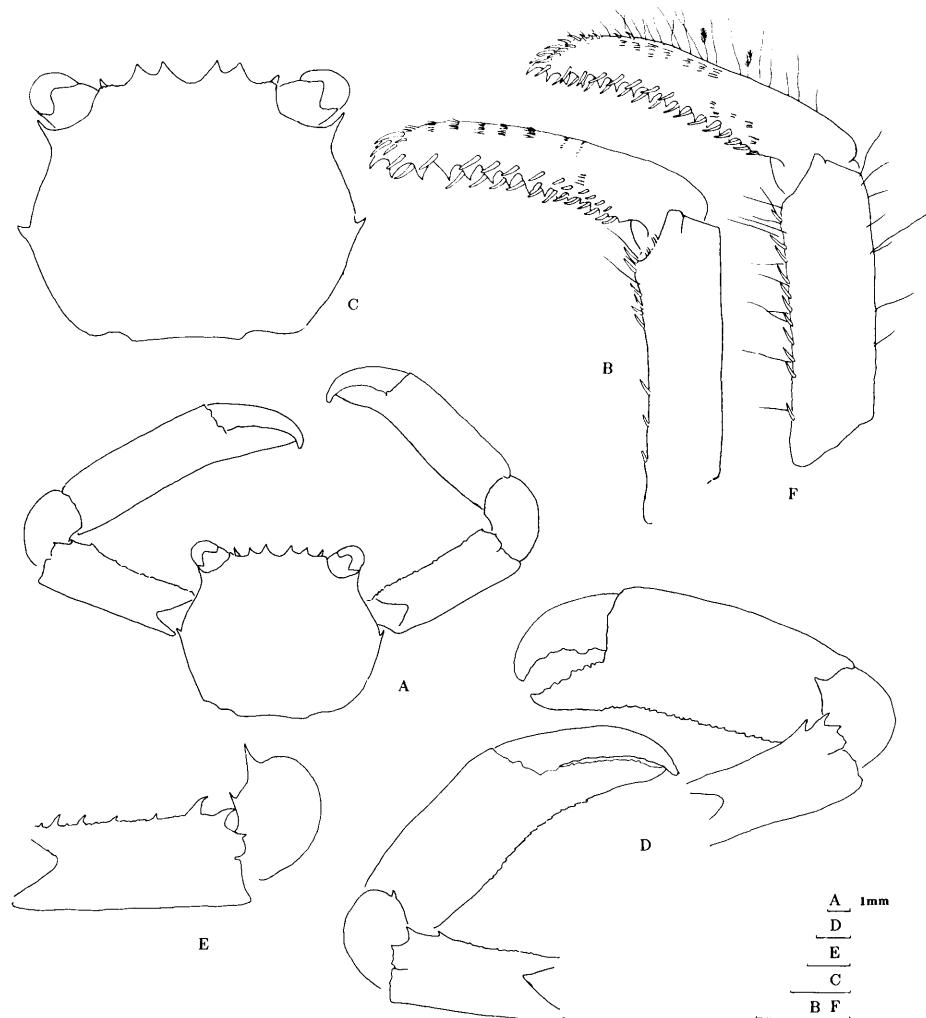


Fig. 5. *Quadrella lewinsohni*, new species. A, B, paratype, female. Nicobar Islands. A, carapace and chelipeds; B, fourth ambulatory leg, propod and dactyl. *Quadrella maculosa* Alcock. C, male, Maldives Islands, carapace; D, male, New Guinea, chelipeds; E, female, Maldives Islands, cheliped, merus and carpus; F, female, Moluccas Islands, fourth ambulatory leg, propod and dactyl.

posterior spine smaller, tuberculate in adults (Fig. 4D). Chela swollen, 1.3 cl, granulate posteriorly.

First ambulatory leg 1.75 times cl. Posterior margin of propodi spinose. On posterior margin of fourth ambulatory dactyl 8 triangular teeth strongly diminishing in size proximally, with 3 proximalmost teeth appearing as tubercles. Six spines on distal internal surface. Apical spine strong, curved. Anterior margin with clusters of small preapical spines. Internal and external surfaces with short, irregular rows of setae (Fig. 4E).

Male pleopod slightly sinuous, setose, tip incurved.

Distribution.—South Africa, Madagascar, Providence Island, Amirante Island, Seychelles, Maldives Islands, India, Ceylon, Sooloo Sea, Philippines, Aru Archipelago, Ceram Island, South China Sea, Japan, Australia.

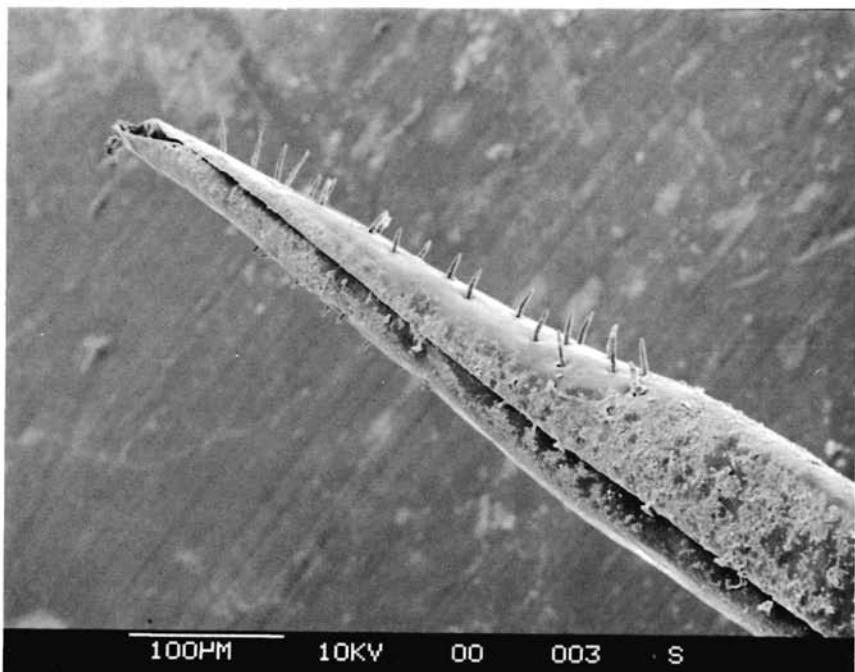


Fig. 6. *Quadrella lewinsohni*, new species. Paratype. First male pleopod, tip.

Remarks.—Dana erected *Quadrella coronata* for specimens found in Sooloo Sea. The characteristic features—regularly spinose merus of cheliped, two-spined carpus, tuberculate supraorbital angle and oblique anterolateral margins—are clearly evident in the well-illustrated description.

Miers (1884) described and placed near *Trapezia* a mutilated specimen from Providence I. that in a later footnote (Miers, 1886) was identified as *Q. coronata*.

Borradaile (1902: 266) described *Q. coronata* var. *granulosa* as having "Carapace broader than long. Chelipeds more or less frosted with granules Fore edge of arm spined," features characteristic of *Q. coronata*. Indeed, on examining specimens from Suvaliva and Mahlos Atolls identified as *Q. coronata* var. *granulosa* by Borradaile I have found them to be *Q. coronata*. Laurie (1906) described *Q. coronata* var. *granulosa* from Herdman's Ceylonese material which I also identified as *Q. coronata*.

Sakai (1965) transferred *Q. granulosa* to *Q. boopsis* even though he recognized that the "Chelipeds are very slender and much longer than [boopsis]. . . . Ambulatory leg very slender and proportionally longer than those of *Q. boopsis*." His drawings, especially that of the fifth dactyl, are beyond doubt of *Q. coronata*.

Initially Serène followed Sakai, but later (Serène, 1973: 207) recognized the similarity of this species to *Q. coronata*: "Contrairement à l'opinion de Sakai (1965), l'espèce est plus voisine de *coronata*, comme le pensait Borradaile (1902), que de *boopsis* La condition figurée par Sakai (1965, text fig. 20b) est presque identique avec celle sur *coronata*." Though he recognized these specimens' affinity with *Q. coronata*, he identified them as *Q. granulosa*.

Nobili's description (1906a: 144) of this material: "La carapace est rayée de grosses lignes rouge-pourpre, irrégulières et confluentes Les dactylopodites ont 12-15 denticules spiniformes," precludes identification with *Q. coronata*.

Quadrella lewinsohni, new species

Figs. 5A, B, 6

Quadrella sp. Monod, 1979: 9, figs. 1–8 (part).*Quadrella cyrenae*—Serène 1975: 510, figs. 3, 4, pl. 1b', e' (part); 1984: 288 (part).

Material Examined.—Tillanchong, Nicobar Islands, leg. I. Eibl-Eibesfeldt, 1 ♂ holotype cl 9.2 mm, cw 10.8 mm; allotype, 1 ♀, cl 11 mm, cw 13.4 mm, same data, paratypes 1 ♂, 5 ♀♀, same data (Senck. M. 9891).

Description.—Carapace wide, globose. Anterolateral margins of carapace constricted behind postorbital spine, swollen posteriorly. Junction with posterolateral margins marked by tooth, well developed, acute in young specimens, tuberculate in adults. Posterolateral margins widely arched. Submedian frontal lobes triangular, separated by wide U-shaped indentation. Lateral lobes slightly less jutting than submedian pair, separated from latter by smaller, oblique sulcus. Supraorbital angle with single small tubercle distally. Postorbital spine directed outwards. Lower orbital margin crescentic, entire. Inner orbital angle developed into acute tooth, projecting almost as far forward as lateral frontal lobes. Eyes protuberant, cornea extending well beyond postorbital angle (Fig. 5A).

Interantennular septum triangulate. Anterior margin of buccal frame sinuous, medially notched; anterior margins of efferent canals medially notched. Exognath of external maxillipeds medially constricted, tapered, rounded tooth on inner margin. Ischium of endognath subrectangular, proximal third of inner margin tuberculate; outer distal angle of merus rounded, inner angle truncate.

Chelipeds massive. Anterior margin of ischium with few blunt tubercles. Merus subcylindrical, granulate, row of tubercles along anterior border, in young specimens tubercles increasing in size and acuteness distally. Inner angle of carpus rounded. Manus subcylindrical, minutely granulate, upper and lower margins rounded. First ambulatory leg about twice as long as carapace. On posterior edge of propodi row of cornute spines. On posterior margin of fourth ambulatory dactyl 15 triangular teeth, successively smaller proximally; row of spines extending internally above serrate posterior margin. On dactylar tip large cornute spine; preapically on anterior margin several curved spines; anterior surface with irregular rows of spinules (Fig. 5B).

First male pleopod straight, tapered, subdistally spinulose (Fig. 6).

Distribution.—Nicobar Islands, Marquesas Islands.

Remarks.—In most aspects *Quadrella lewinsohni* bears resemblance to *Q. serenei*. However, the wider sulcus separating the submedian frontal lobes, the less prominent supraorbital angle, bulging eyes, and the minute tuberculation of the merus of the cheliped clearly distinguish *Q. lewinsohni*.

Monod (1979) described specimens found in the Marquesas Islands. The adult pair resemble *Q. lewinsohni* in the form of the posterior margin of the dactyl, the anterior margin of the merus, and the first male pleopod. A photograph of the frontal margin of Monod's male specimen, kindly provided by Dr. Serène (1975, pl. 1b'), clearly shows the presence of the wide median sulcus mentioned above.

Quadrella maculosa Alcock, 1898

Fig. 5C–F

Quadrella coronata var. *maculosa* Alcock, 1898: 226; Alcock and Anderson, 1899, pl. 38, fig. 2.*Quadrella maculosa*—Rathbun, 1911: 235 (part); Guinot, 1967: 285; Serène, 1968: 89; Garth, 1969: 188; Serène, 1973: 204, figs. 4, 9, 20–22, pl. 3; Serène et al., 1974: 24; Serène, 1975: 513, 1984: 288, fig. 194, pl. 4e.*Quadrella cyrenae* Ward, 1942: 45, pl. 3, figs. 5, 6; Michel, 1964: 30; Guinot, 1967: 275.

Material Examined.—Port Sudan, Red Sea, leg. R. Hartnoll, 1 ♂ (BMNH 1962:9:12:60).—Red Sea, leg. R. Hartnoll, 1 ♂, 2 ♀♀ (BMNH 1962:9:12:57/59).—Amirante I., 11 October 1905, 32 fms (59 m), leg. J. S. Gardiner, Sealark Expedition, 1 ♂ (USNM 41345); 1905, 32 fms (59 m), Sealark Expedition, 1 ♂ (BMNH 1911:9:20:6); 1905, 32 fms (59 m), leg. J. S. Gardiner, Sealark Expedition, 1 ♀ (UMZ).—Maldives Islands, 25 March 1964, 1 ♂, 1 ♀ (AH).—Gulf of Mannar, Ceylon, 1 ♀ (BMNH 1907:5:22: 272).—Golo I., Philippine Islands, 14 February 1908, 22 fms (40 m), Albatross Philippine Expedition, 1 ♂ (USNM 65315).—North of Rowa, Kai I., Moluccas Islands, 11 June 1970, 15–20 fms (27–37 m), M. King Memorial Expedition, 1 ♀ (WAM 78-73).—West of Tg. Derehi, Trangan, Aru I., Moluccas Islands, 19 June 1970, 23–28 fms (42–51 m), M. King Memorial Expedition, 1 ♂, 1 ♀ (WAM 76-73).—Southwest of Tg. Ratoe, Maikoor, Aru I., Moluccas Islands, 18 June 1970, 25–37 fms (46–68 m), M. King Memorial Expedition, 1 ♀ (WAM 77-73).—Northeast of Roemwakon, Aoeri Islands, Geelvink Bay, New Guinea, 21 February 1956, 20–25 fms (37–46 m), 1 ♂ (RMNH).

Description.—Submedian frontal sulcus wide, shallow; lateral indentations asymmetrical. Lateral teeth reaching as far forward as submedian pair. Supraorbital angle minutely tuberculate. Upper orbital margin tuberculate. Postorbital angle spiniform. Infraorbital angle conical, acute, projecting forward almost to lateral teeth. Carapace markedly constricted behind postorbital spines. Anterolateral margins convex. Epibranchial spine prominent, projecting outwards. Postero-lateral margins rounded (Fig. 5C).

Interantennular septum stout, quadrate. Anterior margin of buccal frame concave, medially notched. Exognath of external maxilliped columnar, somewhat constricted distally, rounded tooth at inner margin. Inner margin of ischium of endognath inflated, proximally tuberculate; medial triangular protuberance on distal margin of merus, lateral margins subparallel.

Chelipeds massive. Frontal border of ischium strongly tuberculate, median tubercle larger, spiniform. Merus, little shorter than carapace, strongly granulate, tubercles on anterior margin, spiniform in young, obtuse in adult, distalmost largest, well developed. Carpus rounded, anterior spine on interior margin, prominent posterior spine, in adults appearing as no more than tubercle. Chela 1.5 cl, swollen, tuberculate, tubercles increasing in size posteriorly, giving posterior margin serrate appearance. Serration continuing to finger tips (Fig. 5D). First ambulatory leg more than twice carapace length. On posterior margin of propodi, curved, cornute spines. On posterior margin of fourth ambulatory dactyl 16 triangular teeth, proximally diminishing in size. Internally, 8 distalmost teeth bearing additional spine. Short irregular rows of spinules anteriorly (Fig. 5F).

First male pleopod slightly sinuous, subdistally spinose, proximal spine largest.

Distribution.—Red Sea, Kenya, Madagascar, Amirante Island, Mauritius, Maldives Islands, India, Ceylon, Philippine Islands, Moluccas Islands, New Guinea, Indonesia.

Remarks.—*Quadrella maculosa* differs from *Q. serenei* in its spinose carpus, acute epibranchial spine, proportionally longer ambulatory legs, and number of spines on the interior surface of the dactyl.

Alcock described (1898) and illustrated (Alcock and Anderson, 1899) *Quadrella coronata* var. *maculosa* as having the carapace wider than long, chelipeds minutely granulate, and the anterior border of the arm finely denticulate, with two or three spines at distal end. Rathbun (1911) gave it specific rank, but on examining her material I have found that the ovigerous female collected in Cargados Carajos was misidentified and actually is *Q. serenei*.

Ward (1942: 45) described *Quadrella cyrenae* as having “The anterior margins of the arms . . . with large procurred spines . . . carpus . . . armed with two spines on the inner angle . . . dactyli armed with fine uniform spines . . . on carapace . . . two U-shaped marks, the horns of which are laterally directed.” Wards’s description set subsequent authors puzzling over his identification. Barnard (1950)

regarded it as a variety of *Q. coronata*, probably on account of Ward's reiterated description of the spinose merus. Serène (1973: 205) wrote "L'espèce de Ward est très probablement un synonyme de *maculosa*. l'illustration de Ward (1942, pl. 3, figs. 5, 6) montre que le merus du chélipède de *cyrenae* ne diffère en rien de celui de *maculosa*." Indeed, Ward's photograph agrees in all aspects with Alcock's drawing of *Q. maculosa*. Ward's description probably was of a young specimen; note the comparatively larger eyes, spinose arm, and prominent anterior carpal spine (fig. 4e), all found in young specimens of *Q. maculosa*.

Quadrella nitida Smith, 1869

Fig. 7A–C

Quadrella nitida Smith, 1869: 288; Lockington, 1876: 105; Milne Edwards, 1881: 344; Rathbun, 1898: 590, 1910: 586, 617, 1930: 561, pl. 229; Crane, 1937: 74; Garth, 1946: 494, pl. 80, fig. 6. *Quadrella coronata*—Ortmann, 1897: 210 (part); Klunzinger, 1913: 317 (part); Estampador, 1937: 531 (part).

Material Examined.—Mexico: Gorda Banks, Gulf of California, 22–23 April 1936, Tempelton Crocker Zaca Expedition, 6 ♂♂, 4 ♀♀ (AMNH 13677); Arena Bank, Gulf of California, 20 April 1936, Tempelton Crocker Zaca Expedition, 1 ♂ (AMNH 13678); Arena Bank, 30 April–1 May 1936, Tempelton Crocker Zaca Expedition, 6 ♂♂, 8 ♀♀ (AMNH 13683).

Description.—Carapace lenticular, globose. Lateral lobes far less prominent than submedian pair. Submedian lobes separated from each other by deep U-shaped sulcus, and from lateral lobes by shallow, skewed indentation. Supraorbital angle minutely granulate. Orbita subquadrate, oblique. Postorbital angle acute. Inferior orbital angle triangular. Anterolateral margins convex. Epibranchial spine acute in juveniles, blunt tubercle in adults. Posterior lateral margins rounded (Fig. 7A).

Interantennular septum slender. Anterior margin of buccal frame sinuous, medially notched. Anterior margin of efferent canals arched, notched. Exognath of external maxilliped tapering distally, rounded tooth at distal inner margin. Ischium of endognath subrectangular, inner margin convex. Merus subquadrate, inner distal angle excavate.

Anterior margin of ischium minutely tuberculate. Merus short, less than carapace length, anterior margin invested with slender, curved spines. Anterior internal margin of carpus with acute spine in juveniles, blunt in adults. Manus 1.4 cl, swollen, minutely granulate (Fig. 7B). First ambulatory leg 1.4 cl. Posterior margin of propodi smooth, lacking spines. Posterior margin of fourth ambulatory dactyl bearing 4 triangular teeth, diminishing in size proximally. Basally on inner surface, each tooth with stout spine. Tip of dactyl with large curved, cornute tooth, proximal part with several smaller spines. On anterior margin of dactyl several irregular rows of pinnate spinules; medially on interior surface 5 rows of pinnate spinules (Fig. 7C).

First male pleopod tapered, markedly sinuous, sparsely setose distally.

Distribution.—Mexico, Panama, Galapagos Islands.

Remarks.—*Quadrella nitida* ranges from the Gulf of California to Panama and the Galapagos Islands. Its geographical isolation contributed, no doubt, to its singular taxonomic position. Ortmann (1897) followed by Klunzinger (1913) synonymized *Q. nitida* with *Q. coronata*, probably on account of their spinate chelipeds. Rathbun (1898: 50) recognized *Q. nitida* as a distinct species: "*Q. nitida* has only one carpal spine instead of the two in *coronata*. The sinuses separating the median from the next pair of frontal teeth are more shallow than represented in Dana's figure and the lateral margins are much more convex." *Quadrella nitida*

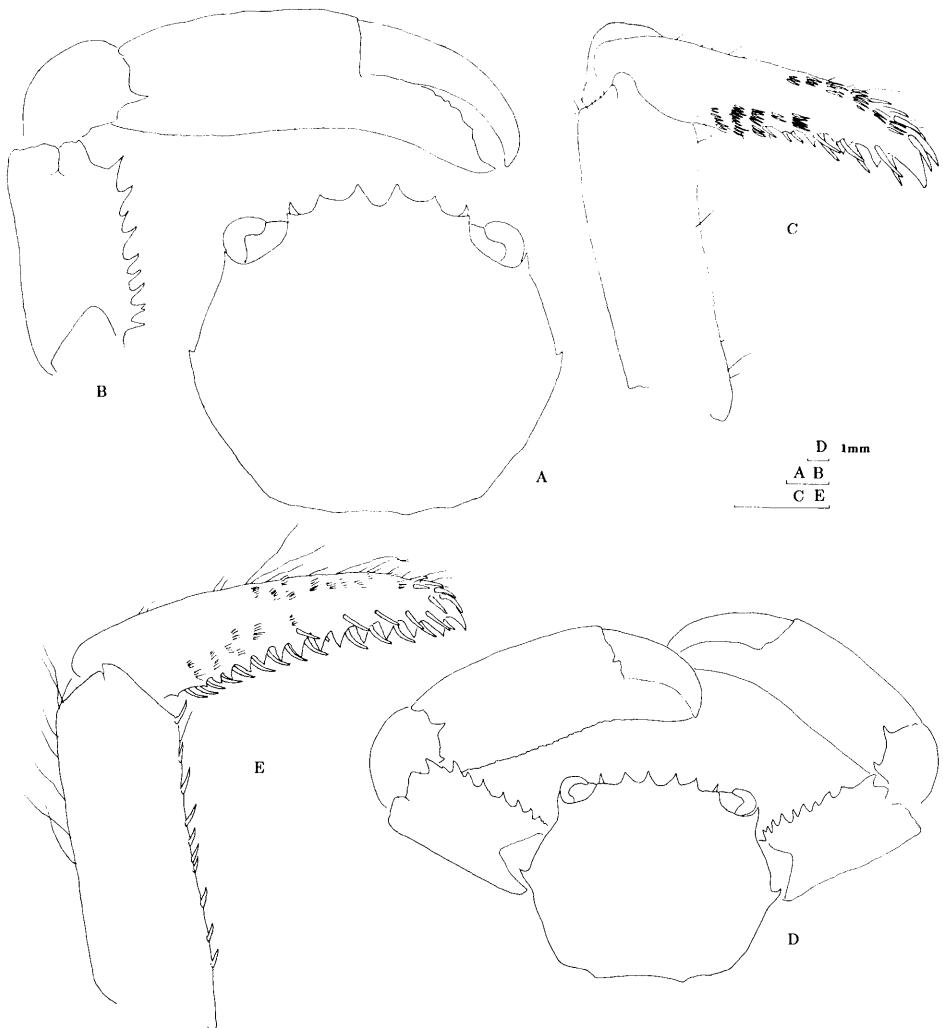


Fig. 7. *Quadrella nitida* Smith. A–C, male, Arena Bank. A, carapace; B, cheliped; C, fourth ambulatory leg, propod and dactyl. *Quadrella reticulata* Alcock. D, E, male, South China Sea. D, carapace and chelipeds; E, fourth ambulatory leg, propod and dactyl.

further differs from *Q. coronata* in having the supraorbital angle tuberculate, not spiniform, posterior propodal margin smooth, dactyl four-toothed, set with pinnate spinules, and a sinuous first male pleopod lacking the curved tip characteristic of *Q. coronata*.

Quadrella reticulata Alcock, 1898
Fig. 7D, E

Quadrella coronata reticulata Alcock, 1898: 227.

Quadrella reticulata—Sérène, 1973: 199, figs. 1, 7, 11–13, pl. 1a–d.

? *Quadrella coronata* var.—Nobili, 1906a: 143, 1906b: 294.

Material Examined.—Near Natuna Islands, South China Sea, 04°21'03"N, 115°58'50"E, 1938, 45 fms (82 m), leg. R. Young, 2 ♀♀ (NMS 1965.11.23 46–47).

Description.—Carapace globose. Anterolateral margins constricted behind postorbital spine, inflated. Epibranchial tooth well developed, acute. Posterolateral margins rounded. Submedian frontal lobes separated by rounded sulcus. Lateral lobes wider, less prominent than submedian pair, separated from latter by shallow, skewed indentation. Superior angles of orbits markedly tuberculate. Postorbital angle conical, acute. Inferior internal orbital tooth visible beyond supraorbital angle, extending as far forward as lateral lobe (Fig. 7D).

Anterior margin of buccal frame sinuous, minutely notched medially; anterior borders of efferent canals rounded, notched. Interantennular septum short, subquadrate. Exognath of external maxilliped nearly cylindrical, inner margin slightly scooped distally, bearing triangulate tooth. Inner margin of ischium of endognath produced, wide-angled, proximally tuberculate; merus subpentagonal.

Chelipeds granular. Anterior margin of ischium crenate, tuberculate, median tubercle spiniform. Merus, about 0.75 cl, anterior margin serrate with irregular triangular teeth, larger distally. Internal angle of carpus with 2 spines, distal spine larger. Manus, 1.3 cl, strongly tuberculate, tubercles larger on lower margin. Inner margin of ambulatory propodi spinose. First ambulatory leg 1.6 cl. On posterior margin of fourth ambulatory dactyl 13 triangular teeth, smaller proximally; cornute spines placed above 6 interior distalmost teeth. Short, irregular rows of spinules on interior and anterior surface (Fig. 7E).

Distribution.—Ceylon, Andaman Islands, Singapore, Japan.

Remarks.—*Quadrella reticulata* shares with both *Q. bispinosa* and *Q. boopsis* a serrulate merus of the cheliped. It differs from *Q. bispinosa* in the absence of a midanterolateral spine and in the number of teeth on the posterior margin of the dactyl; from *Q. boopsis* it can be distinguished on account of its relatively longer merus, more prominent anterior carpal spine, and in fresh material, the reticulate design on the carapace and chelipeds.

Alcock's description (1898) of *Q. coronata* var. *reticulata* is rather brief but mentions three distinctive features: the meshwork ornamentation on the carapace, the serrate anterior margin of the merus of the cheliped, and the granulate chelipeds. Serène (1973) elevated it to specific rank and enumerated the distinguishing characters between *Q. reticulata* and *Q. coronata*. According to Nobili (1906a, b) his specimens have on their carapace irregular reddish lines; his description, however, lacks sufficient evidence to verify identification with *Q. reticulata*.

Quadrella serenei, new species

Fig. 8A, B

Quadrella maculosa—Rathbun, 1911: 235 (part).

Quadrella cyrenae—Serène, 1975: 510, figs. 1–4, 13, pl. 1 (part), 1977: 51, 1984: 288, fig. 193, pl. 41d.

Not *Quadrella cyrenae* Ward, 1942: 45, pl. 3, figs. 5, 6 = *Q. maculosa* Alcock, 1898.

Material Examined.—Holotype, Fort Dauphin, Madagascar, October 1958, 50 m, coll. A. Crosnier, 1 ♂ (PM B8193), det. Serène *Q. cyrenae*.—South coast, Madagascar, 22°08'S, 43°08'E, 115–135 m, 5 June 1972, leg. FAO, 1 ♀ (PM B8195), det. Serène *Q. cyrenae*.—Seychelles, 63 m, 22 November 1968, 1 ♂, 1 ♀ (NMST 4365); 1 ♂ (NMST 4364); 27 November 1968, 1 ♀ (NMST 4363).—Cargados Carajos Islands, 1 September 1905, 45 fms (82 m), HMS Sealark, coll. J. S. Gardiner, 1 ♀ (USNM 41344).

Description.—Carapace globose, constricted behind postorbital teeth. Anterolateral borders inflated. Epibranchial tooth minute, rounded. Frontal lobes triangular, acute; V-shaped median sulcus, deeper than submedian indentation. Lateral teeth not jutting as far forward as submedian pair. Supraorbital angle tuberculate,

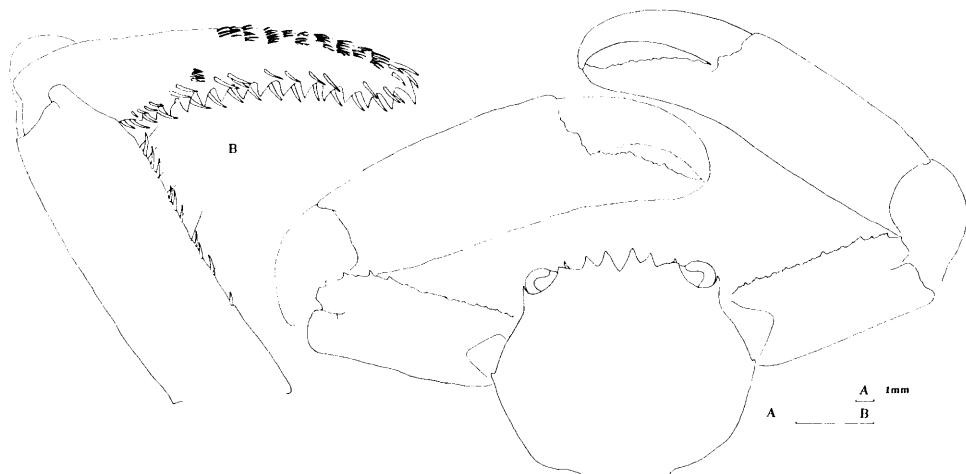


Fig. 8. *Quadrella serenei*, new species. A, holotype, Madagascar, carapace and chelipeds. B, female, Cargados Carajos Islands, fourth ambulatory leg, propodus and dactyl.

distalmost tubercle largest. Postorbital tooth long, acute. Infraorbital tooth conical, almost as prominent as lateral teeth (Fig. 8A).

Interantennular septum stout, rounded. Anterior edge of buccal frame sinuous, imperceptibly notched medially; notched lips at termination of exhalant canals. Exognath of exterior maxillipeds hourglass-shaped; tooth at anterior margin rounded. Margin of ischium of endognath with minute tubercles on posterior half; merus with distal exterior angle extended, distal internal angle obliquely cut, inner margin rounded.

Frontal edge of ischium of cheliped with several rounded tubercles; merus, about four-fifths cl, with row of raised tubercles anteriorly, successively larger and more acuminate distally. Carpus rounded. Chela swollen, microscopically granulate.

First ambulatory leg less than twice cl; propodus, longer than dactyl, with 16 cornute spines on posterior margin. On posterior margin of first ambulatory dactyl 13 triangular teeth, imperceptibly diminishing in size proximally; on internal margin, slightly above triangular teeth, row of 14 cornute spines; on anterior border of dactyl irregular rows of short setae. Apical dactylar tooth acuminate, curved, cornute. Propodus of fourth ambulatory leg stout, only slightly longer than dactyl, posterior margin armed with 10 spines. On posterior margin of fourth ambulatory dactyl 14 triangular teeth, on internal border 15 spines (Fig. 8B).

Distribution.—Madagascar, Seychelles, Cargados Carajos Island.

Remarks.—Rathbun (1911) listed under *Quadrella maculosa* a specimen of *Q. serenei* (see *Q. maculosa*). Serène (1975) described, illustrated, and photographed material collected in Madagascar as *Q. cyrenae*. Even though Serène formerly expressed his reservation (1975: 511): "Ces imprécisions, sinon incertitudes, voire contradictoires, m'avaient conduit (Serène, 1973) à faire de *cyrenae* un synonyme de *maculosa*," he adopted Ward's identification. On examining the Madagascan specimens, kindly lent by Dr. Crosnier of the Muséum National d'Histoire Naturelle, they were found to differ from *Q. maculosa* (=*Q. cyrenae* Ward) and *Q. lewinsohni* with which it shares a tuberculate merus of the cheliped (see above).

KEY TO *HEXAGONALIA* AND *QUADRELLA*

1. Interorbital margin bilobed. Thoracic sternum oval. First sternites forming flattened arch. Last abdominal segment elongate. Double row of teeth on posterior margin of ambulatory dactyls. First male pleopod with pinnate appendages..... *Hexagonalia brucei*
- Interorbital margin cut into 4 triangular lobes. Thoracic sternum rounded. First 3 sternites forming arcuate triangle. Last abdominal segment twice as wide as long. Single row of triangular teeth on posterior margin of dactyls. First male pleopod distally setose or spinulose..... *Quadrella* (2)
2. Posterior margin of ambulatory propodi smooth, devoid of spines..... 3
- Posterior margin of ambulatory propodi spinose..... 4
3. Midway between postorbital and epibranchial teeth no spine. Anterior margin of ischium of cheliped minutely tuberculate. On posterior margin of ambulatory dactyl 4 triangular teeth..... *Quadrella nitida*
- With intermediate anterolateral spine. Anterior margin of cheliped ischium tuberculate, median tubercle prominent. On posterior margin of last ambulatory dactyl 7 teeth..... *Quadrella bispinosa*
4. Anterior margin of cheliped merus bearing 7–10 long, curved, regularly spaced spines. On posterior margin of ambulatory dactyls 8 teeth, strongly diminishing in size proximally. Tip of first male pleopod incurved..... *Quadrella coronata*
- Anterior margin of cheliped merus serrate or tuberculate. On posterior margin of ambulatory dactyls 13 or more teeth. First male pleopod sinuous..... 5
5. Merus two-thirds carapace length..... *Quadrella boopsis*
- Merus longer than two-thirds carapace length..... 6
6. Anterior margin of cheliped merus serrate..... *Quadrella reticulata*
- Anterior margin of cheliped merus tuberculate..... 7
7. Anterior margin of cheliped carpus prominently spinose. Epibranchial spines prominent..... *Quadrella maculosa*
- Anterior inner margin of cheliped carpus rounded. Epibranchial tooth rounded, tuberculate..... 8
8. Submedian frontal lobes separated by wide U-shaped sulcus. Eyes protuberant, cornea extending beyond postorbital angle. Minute tuberculation on anterior margin of cheliped merus..... *Quadrella lewinsohni*
- Submedian frontal lobes separated by V-shaped sulcus. Eyes not protuberant. Cheliped merus with raised tubercles anteriorly, successively larger and more acuminate distally..... *Quadrella serenei*

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