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**The Macrophthalminae of Australasia;
with a review of the evolution and morphological
diversity of the type genus *Macrophthalmus*
(Crustacea: Brachyura)**

R. S. K. BARNES

*N.A.T.O. Postgraduate Research Student, Zoology Department,
University of Queensland, Australia*

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The Macrophthalminae of Australasia; with a review of the evolution and morphological diversity of the type genus *Macrophthalmus* (Crustacea: Brachyura)

The Australasian species of the brachyuran subfamily Macrophthalminae Dana are little known both inside and outside Australasia. Eighteen Australasian species of five genera are here recorded, with keys given for their identification, from the collections in various Australasian institutions. Sixteen species are redescribed, and indications are given of the changes observed in the relative proportions (used taxonomically by many previous authors) with increase in size of the animals. The genus *Macrophthalmus* Latreille, is reviewed in the light of the greatly increased information available on many of the species since the last review by Tesch (1915). Six subgenera of *Macrophthalmus* are described and a key given for their identification; and the intrageneric evolution is discussed. A bibliography of taxonomic literature on the Macrophthalminae is included.

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INTRODUCTION

The Australasian species of the Indo-West Pacific subfamily Macrophthalminae have never been reviewed, as have the Japanese species (Sakai, 1939), the Indian species (Alcock, 1900; Kemp, 1919), the South African species (Barnard, 1950, 1955), the Malagasy species (Crosnier, 1965) and the Malay species (Tweedie, 1937).

The constituent genera of the subfamily have also received little attention. *Cleistostoma*, *Paracleistostoma* and *Tylodioplax* have received one review this century, that of Guinot & Crosnier (1963), while the only other genus to receive a review, *Macrophthalmus*, was last reviewed in 1915 by Tesch. This latter publication is now inadequate for several reasons. First, it is particularly inadequate as regards Australasian species since the Leiden Museum, upon whose collections the monograph was based, possessed at that time very little Australasian material, and species endemic to that region were characterised by merely repeating the all too brief original specific descriptions. Second, many new species have been described, and more material of many little known species has become available, since the publication of Tesch's review. Third, several authors (including Kemp, 1919, p. 391; Tweedie, 1941, p. 25) have pointed out inaccuracies in Tesch's characterizations of some species, and the present author has noted inaccuracies in those of other species. Fourth, Tesch made use of a number of relative proportions in defining and distinguishing between the reviewed species. On the use of these relative proportions Tweedie (1937, p. 163) has stated:—"The numerous species of this genus [*Macrophthalmus*] are notoriously difficult to identify with certainty, partly because the characters separating them are often vague and difficult to define and perhaps even more because in their postlarval development many species change their proportions in respect of both the carapace and chelipeds. These proportions have been largely used in defining and describing the species and such descriptions are not always made from fully adult specimens, or if they are, no account of developmental changes is given."

In this paper it is thus hoped to (a) place the little known Australasian fauna on record; (b) describe little known species *de novo* from material in various Australasian institutions, with changes observed with size in the relative proportions used by Tesch (1915), and others, documented; (c) review the morphological diversity seen in the genus *Macrophthalmus*, in the light of species described since 1915 and the increased knowledge available on other, then poorly known, species; (d) consolidate the, at present, scattered literature; and (e) to provide as complete as possible synonymies.

The terminology used follows that of Rathbun (1918, pp. 6-8, Figs 1, 2).

Measurements used are as follows:

Length of carapace is measured along the median line, from anterior to posterior margin.

Breadth of carapace is measured at the widest point.

Breadth of front is measured along the anterior margin.

Length of propodus of cheliped is measured from the articulation with the carpus to the tip of the immovable finger, along the lower margin.

Dimensions given under 'material examined' in the specific descriptions are those of carapace breadth.

(Measurements were made with vernier calipers or with a microscope eyepiece micrometer and are given correct to 0.1 mm, except in a few cases where they are given correct to the nearest 0.25 mm.)

THE SUBFAMILY MACROPHTHALMINAE DANA, 1852

Macrophthalminae Dana, 1852, p. 312; Miers, 1886, p. 237; Ortmann, 1894a, p. 741; Alcock, 1900, pp. 290-91; Tesch, 1918, p. 57; Sakai, 1939, p. 611.

The Macrophthalminae contains seven genera: *Macrophthalmus* Latreille, 1829; *Cleistostoma* de Haan, 1835; *Camptandrium* Stimpson, 1858; *Paracleistostoma* de Man, 1895; *Tylodiplax* de Man, 1895; *Leipocten* Kemp, 1915; and *Australoplax* Barnes, 1966b. (Barnes (1966b) having shown that of the three species placed in the genus *Euplax* H. Milne Edwards, 1852, two including the type species are to be referred to *Macrophthalmus* and the third to *Australoplax*; while the genus *Hemiplax* Heller, 1865 is in this paper fused with *Macrophthalmus*.) Of these seven genera, *Camptandrium* and *Tylodiplax* contain no Australasian species and are not dealt with in this paper.

The subfamily is almost exclusively Indo-West Pacific, occurring from South Africa (Barnard, 1950) in the west to Polynesia (Nobili, 1906c), and possibly Chile (H. Milne Edwards, 1852, but see Porter, 1913; Rathbun, 1918; Garth, 1957) in the east, and from Japan (Sakai, 1965) and Korea (Kim, 1958) in the north to Tasmania (Tweedie, 1941), New Zealand (Bennett, 1964) and Campbell Island (Filhol, 1885) in the south. The subfamily however also penetrates into the South Atlantic, for a short distance up the west coast of southern Africa (Barnard, 1954a).

All species are predominantly littoral, but a few have also been recorded sublittorally. They occur in burrows or under stones, in substrates ranging from soft mud to firm sand, in both estuarine and fully marine conditions.

KEY TO THE AUSTRALASIAN GENERA OF THE MACROPHTHALMINAE

- (1) (a) Pereiopods with transverse/oblique row of large tubercles across lower surfaces of meri. . . *Leipocten* Kemp
- (b) Pereiopods without any transverse or oblique rows of tubercles across lower surfaces of meri. . . 2
- (2) (a) Merus of external maxilliped larger than ischium; latter with large triangular anterointernal protruberance. . . 3
- (b) Merus of external maxilliped smaller than or subequal to ischium; latter without large triangular anterointernal protruberance. . . 4
- (3) (a) Carapace domed; front without well developed 'horns' at anterolateral angles. . . *Cleistostoma* de Haan
- (b) Carapace flattened; front with well developed anterolateral 'horns'. . . *Paracleistostoma* de Man
- (4) (a) Cutting margins of dactylus and immovable finger of male chelae obscured externally by dense hair; dactylus without differentiated tooth on cutting margin. . . *Australoplax* Barnes
- (b) Cutting margins of dactylus and immovable finger of male chelae not obscured externally by hair; dactylus with differentiated tooth on cutting margin. . . *Macrophthalmus* Latreille

Within the subfamily two distinct generic groups are present; one group consisting of *Macrophthalmus* and *Australoplax*, the other of *Cleistostoma*, *Paracleistostoma*, *Camptandrium*, *Tyloidiplax* and to a lesser extent *Leipocten*. The contrasting characters of these two groups of genera can best be shown in the form of the table below.

<i>Macrophthalmus</i> etc.	<i>Cleistostoma</i> etc.
1. Lateral carapace margins more or less straight, either parallel or posteriorly convergent. Anterolateral margins with 2-4 well demarkated teeth.	Lateral carapace margins parenthetical or divergent posteriorly. Anterolateral margins with blunt tooth-like protruberances or more commonly entire.
2. Ocular peduncles frequently long.	Ocular peduncles short.
3. Palm of male chela elongate. Immovable finger straight or deflexed downwards, cutting margin frequently with large tooth.	Palm of male chela short and globose or feeble. Immovable finger straight or deflexed upwards, cutting margin without differentiated tooth.
4. Abdomen of male composed of seven separate segments.	Abdomen of male with varying degrees of segmental fusion, usually segments two to five fused.
5. Merus of external maxilliped smaller than or subequal to ischium; subrectangular with breadth exceeding length. Ischium with length exceeding breadth. Two distal segments of palp large.	Merus of external maxilliped larger than ischium; sub-circular. Ischium with breadth exceeding length or subequal. Two distal segments of palp poorly developed.
6. First male pleopod straight or slightly curved.	First male pleopod recurved upon itself.

I. The Genus *Macrophthalmus* Latreille, 1829

Macrophthalmus Latreille, 1829, pp. 44-5; Ortmann, 1897, pp. 340-42; Alcock, 1900, pp. 375-83; Tesch, 1915, pp. 149-203; Kemp, 1919, pp. 383-94; Tweedie, 1937, pp. 163-69; Sakai, 1939, pp. 623-28; Barnard, 1950, p. 101; Crosnier, 1965, pp. 122-36.

Hemiplax Heller, 1865, p. 40; Tesch, 1918, p. 57; Sakai, 1939, p. 628.

Euplax H. Milne Edwards, 1852, p. 160; Tesch, 1918, p. 57 (part); Sakai, 1939, p. 630.

Generic description

Front. Narrow (ratio of breadth of front to breadth of carapace between 1: 3.0 and 1: 12.0), depressed; frequently with median furrow, constriction between bases of ocular peduncles, and bilobed anterior margin (never pointed).

Orbits. Long, narrow, furrows, occupying whole of anterior border of carapace between front and external orbital angles. Upper orbital border usually sinuous; disposed transversely or sloping backwards; usually studded with small rounded granules. Lower orbital border projecting, studded with large granules or tubercles.

Antennae. Moderately long, base short and situated in inner angle of orbit.

Epistome. Long and narrow. Central region with concavity, rounded convexity or straight.

Anterolateral carapace teeth. External orbital angle forms first lateral tooth. Tooth development variable, external orbital angle and second lateral tooth usually large, third lateral tooth usually small, fourth lateral tooth rarely present. Teeth directed outwards and forwards in varying degrees.

Carapace. Depressed; rectangular or trapezoid. Breadth always exceeding length, but ratio between two dimensions variable between 1:1.10 and 1:2.30. Lateral margins parallel or posteriorly convergent. Regions usually well demarkated, separated by furrows. Frequently granular or hairy.

Ocular peduncles. Generally long. Cornea reaching to, or beyond bases of external orbital angles.

Chelipeds. In males well developed, equal or subequal. Merus triangular in section; palm large and elongate, in adults length of propodus exceeding length of carapace; dactylus and immovable finger spoon-tipped, often deflexed downwards and inwards, differentiated tooth present on cutting margin of dactylus and frequently on immovable finger. In females poorly developed, without differentiated teeth on cutting margins of either immovable finger or dactylus.

Periopods. Second and third pairs large and subequal, first and fourth pairs small (fourth pair smallest). Meri long, triangular in section, and with distal subterminal spine on upper margins, often concealed in hair.

Male abdomen. Composed of seven, distinct, separate segments; the first two small, remainder excepting small telson, subequal. Narrow; lateral segmental margins converging more or less smoothly towards telson.

External (third) maxilliped. Subrectangular merus smaller than, or subequal to, ischium; with breadth exceeding length. Ischium large, with length exceeding breadth, without row of hairs across base. Well developed palp articulates at anteroexternal angle of merus. Maxillipeds leave small hiatus when folded.

First male pleopod. Straight or slightly curved.

Type species: *M. transversus* (Latreille, 1817).

Comments. Fifty-five species of the genus *Macrophthalmus* have been described, but of these probably only about 35 species are valid. These species exhibit a wide range of structural diversity, and *Macrophthalmus* is probably one of the most diverse of all brachyuran genera. All but three species (discussed later) however, fall into one or other of four large species-groups, each with its own characteristic and distinct facies. These species-groups are here described as subgenera and the relationships between the subgenera are later hypothesised.

The subgenera of Macrophthalmus

(a) *Macrophthalmus*.

Front narrow. Carapace relatively very broad (ratio of length to breadth in the order of 1 : 2.0), usually with small sparse granules or smooth; without longitudinal, transverse or oblique rows of granules on the branchial regions; with three verrucose granular clumps, however, longitudinally in line on each branchial region. Lateral teeth relatively narrow based and strongly pointed. Cornea extends to tip of, or beyond, external orbital angles. Central region of epistome with rounded protruberance. Longitudinal ridge present close to and parallel with lower margin, on outer surface of propodus of male chela; immovable finger and dactylus short compared with length of palm, latter often with large proximally directed tubercle on inner surface near carpal joint. Pereiopods relatively slender. Abdomen of male broad compared with length. External maxillipeds broad; merus markedly smaller than ischium; ischium large with little or no surface sculpturing.

The subgenus *Macrophthalmus* contains besides the type species, *M. transversus* (Latreille, 1817), the following: *M. brevis* (Herbst, 1804); *M. parvimanus* Guérin, 1834; *M. dilatatus* (de Haan, 1835); *M. telescopicus* (Owen, 1839); *M. crassipes* H. Milne Edwards, 1852; *M. sulcatus* H. Milne Edwards, 1852; *M. convexus* Stimpson, 1858; *M.*

dentatus Stimpson, 1858; *M. grandidieri* A. Milne Edwards, 1867; *M. graeffei* A. Milne Edwards, 1873b; *M. latipes* Borradaile, 1903; *M. consobrinus* Nobili, 1906c; *M. sandakani* Rathbun, 1914; *M. hilgendorfi* Tesch, 1915; *M. simdentatus* Shen, 1936; *M. malaccensis* Tweedie, 1937; *M. malayensis* Tweedie, 1937; *M. travancorensis* Pillai, 1951; *M. milloti* Crosnier, 1965.

(b) *Mareotis* subgen. n.

Front very narrow. Carapace moderately broad (ratio of length to breadth in the order of 1 : 1.4–1.5), usually with numerous large granules; with longitudinal and/or transverse rows of granules and/or hairs on the branchial regions; without verrucose clumps of granules. Lateral teeth broad based and rectangular. Cornea extends to base of external orbital angles. Central region of epistome with concave excavation. Longitudinal ridge on outer surface of male chela absent in most species, feeble if present; no proximally directed tubercle on inner surface of palm. Immovable finger and dactylus long compared with length of palm. Pereiopods large. Abdomen of male narrow compared with length. External maxilliped narrow; merus markedly smaller than ischium; ischium with marked surface sculpturing.

The subgenus *Mareotis* contains besides the type species, *M. japonicus* (de Haan, 1835), the following: *M. depressus* Rüppell, 1830; *M. tomentosus* Souleyet, 1841; *M. definitus* Adams & White, 1848; *M. pacificus* Dana, 1851; *M. setosus* H. Milne Edwards, 1852; *M. crinitus* Rathbun, 1913; *M. teschi* Kemp, 1919; *M. abercrombiei* Barnes, 1966a.

(c) *Mopsocarcinus* subgen. n.

Animals of small size. Front broad. Carapace subquadrate (ratio of length to breadth in the order of 1 : 1.2), smooth or with small granules; without conspicuous aggregations of granules into rows or clumps on branchial regions. Lateral teeth broad based, subrectangular, but pointed at anteroexternal angle. Ocular peduncles short and stout, cornea extending to base of external orbital angles. Central region of epistome straight. Palm of male chela somewhat inflated; longitudinal ridge on outer surface of propodus present; tubercle on inner surface absent; dactylus and immovable finger moderately short, immovable finger straight or deflexed only at tip. Pereiopods slender. Breadth of abdomen moderate. External maxilliped narrow; merus subequal to ischium; both merus and ischium heavily sculptured.

The subgenus *Mopsocarcinus* contains besides the type species, *M. boscii* Audouin/Savigny, 1825, the following: *M. quadratus* A. Milne Edwards, 1873a; *M. punctulatus* Miers, 1884; *M. erato* de Man, 1888b; *M. franchettii* Maccagno, 1936.

(d) *Venitus* subgen. n.

Animals of large size when adult. Front narrow. Carapace subquadrate (ratio of length to breadth in the order of 1 : 1.2–1.3), heavily granulated with large granules and/or tubercles; without well defined rows of granules (poorly defined rows of granules present in some specimens of some species, but never constantly in any species) and without verrucose clumps on branchial regions. Lateral teeth large, broad based, and elongate and sharply pointed in adults. Cornea extends to base of external orbital angles. Central region of epistome straight. Longitudinal ridge on outer surface of male chela absent; tubercle on inner surface absent; immovable finger of moderate length, undeflexed. Pereiopods large,

with large granules and/or spines on margins when adult. Abdomen of male large and elongate. External maxilliped of moderate breadth; merus markedly smaller than ischium, very broad (breadth slightly exceeding that of ischium); ischium with little surface sculpturing.

The subgenus *Venitus* contains besides the type species, *M. latreillei* (Desmarest, 1822), the following: *M. pectinipes* Guérin, 1839; *M. leptophthalmus* (H. Milne Edwards, 1852); *M. gastrodes* Kemp, 1915.

There remains three species that do not fall into any of the four subgenera so far proposed, these species all having been placed in the genus *Hemiplax* by various authors at one time or another. Two of the species are evidently closely related, but the third is distinct. *Hemiplax* is here incorporated into *Macrophthalmus* as a subgenus, while the third species, referred to above, which shows affinities neither with the subgenus *Hemiplax* nor with the other subgenera described, excepting in so far as the common generic characters, is placed in a separate subgenus.

(e) *Hemiplax* Heller, 1865.

Front broad. Carapace moderately broad (ratio of length to breadth in the order of 1 : 1.5), finely granulate; with transverse and oblique granular rows on each branchial region; without clumps of granules. Lateral teeth large, broad based, pointed. Cornea extends to base of external orbital angles; ocular peduncles being stout. Central region of epistome straight. Longitudinal carina present partially on lower margin and partially on outer surface of male chela in adults; no tubercle on inner surface of palm; carpus with spine on upper and inner margin; dactylus and immovable finger elongate, immovable finger deflexed and without a differentiated tooth. Pereiopods moderately well developed. Abdomen of male broad. External maxilliped narrow; merus subequal to ischium; merus and ischium sculptured.

The subgenus *Hemiplax* contains besides the type species *M. hirtipes* (Jacquinot, 1853), only *M. boteltobagoe* (Sakai, 1939).

(f) *Tasmanoplax* subgen. n.

Front of medium breadth. Carapace moderately broad (ratio of length to breadth in the order of 1 : 1.5), finely granulate; with two longitudinal granular rows in anterior/posterior position on each branchial region; without clumps of granules. Lateral teeth broad based and rectangular. Central region of epistome with large convexity. Cornea extends to base of external orbital angles. Longitudinal ridge present on outer surface of male chela; without tubercle on inner surface of palm; without spine on carpus; dactylus and immovable finger elongate, latter deflexed and without differentiated tooth. Pereiopod development moderate. Abdomen of male narrow. External maxilliped narrow; merus subequal to ischium; merus and ischium sculptured.

The subgenus *Tasmanoplax* contains only the type species *M. latifrons* Haswell, 1882b.

KEY TO THE SUBGENERA OF *MACROPHTHALMUS*

- | | |
|---|---------------------------|
| (1) (a) Epistome with central protruberance. | ...2 |
| (b) Epistome with straight or concave central region. | ...3 |
| (2) (a) Merus of external maxilliped subequal to ischium. | ... <i>Tasmanoplax</i> |
| (b) Merus of external maxilliped markedly smaller than ischium. | ... <i>Macrophthalmus</i> |

- (3) (a) Merus of external maxilliped subequal to ischium. . . . 4
- (b) Merus of external maxilliped markedly smaller than ischium. . . . 5
- (4) (a) Carapace subquadrate. . . . *Mopsocarcinus*
- (b) Breadth of carapace equal to approx 1.5 × length. . . . *Hemiplax*
- (5) (a) Epistome with marked concavity in central region. . . . *Mareotis*
- (b) Epistome with straight or slightly concave central region. . . . *Venitus*

*The Australasian species of the genus **Macrophthalmus***

(a) *Subgenus **Macrophthalmus***

KEY TO THE AUSTRALASIAN SPECIES OF THE SUBGENUS *MACROPHTHALMUS*

- (1) (a) Ocular peduncles not extending beyond tips of external orbital angles . . . 2
by more than half the length of the cornea, if at all.
- (b) Ocular peduncles extending beyond tips of external orbital angles by . . . *M. telescopicus*
more than length of cornea.
- (2) (a) Carapace surface coarsely granular; external orbital angle with tip close . . . *M. crassipes*
to, and on same level as, that of second lateral tooth; backwardly
directed tubercle present on inner surface of palm of male chela, near
carpal joint.
- (b) Carapace surface smooth; external orbital angle with tip separate from, . . . *M. convexus*
and projecting well beyond, that of second lateral tooth; no back-
wardly directed tubercle near carpal joint on inner surface of palm of
male chela.

1. *Macrophthalmus (Macrophthalmus) telescopicus* (Owen, 1839)

(Plate 1(a), Fig. 1)

Synonymy

Gelasimus telescopicus Owen, 1839, p. 78, Plate 24, Fig. 1.

Macrophthalmus telescopicus: H. Milne Edwards, 1852, p. 155; Dana, 1852, p. 314; Stimpson, 1858, p. 97; Ortmann, 1894a, p. 744; 1894b, p. 58; Rathbun, 1906, p. 834; Stimpson, 1907, p. 95; Tesch, 1915, p. 161, Plate 5; 1918, p. 58; Kemp, 1919, p. 387, Plate 24, Figs 10 & 11; Stephenson *et al.*, 1931, p. 56; Balss, 1934, p. 522; Tweedie, 1937, p. 164; Balss, 1938, p. 76; Sakai, 1939, p. 623, Plate 73, Fig. 1; Edmondson, 1946, p. 311, Fig. 185; Tinker, 1965, p. 122, Plate 49; Crosnier, 1965, p. 126.

Macrophthalmus compressipes Randal, 1839, p. 123; Gibbes, 1850, p. 180.

Macrophthalmus podophthalmus Souleyet, 1841, p. 241, Plate 3, Figs 6 & 7; H. Milne Edwards, 1852, p. 155; Haswell, 1882a, p. 88; Miers, 1886, p. 249; Lanchester, 1900, p. 760.

Macrophthalmus verreauxi H. Milne Edwards, 1848, p. 358; 1852, p. 155, Plate 4, Fig. 25; Hess, 1865, pp. 142 & 171; de Man, 1880b, p. 184; Haswell, 1882a, p. 89; Alcock, 1900, p. 377; Borradaile, 1903, p. 433; Nobili, 1906b, p. 317; Rathbun, 1910a, p. 322, Fig. 6; Laurie, 1915, p. 470.

Material examined. 23 ♂♂ (7.7–22.5 mm); 38 ♀♀ (7.75–28.5 mm).

Western Australia (Exmouth Gulf—Yampi Sound); Queensland (Cape York—Moreton Bay); New Caledonia (Oubatche); Lord Howe Island.

Description. Front deflexed; markedly constricted between bases of ocular peduncles; smooth margined, anterior margin being bilobed in males and straight in females; and with faint median furrow.

Upper orbital border curved and backwardly sloping; margin studded with medium sized granules. Lower orbital border 'serrated' by large granules along margin.

Three well defined anterolateral teeth present. External orbital angle large, pointed, directed outwards and slightly forwards; anterior margin studded with granules, posterior margin smooth; separated from second lateral tooth by wide incision. Second lateral

tooth pointed, directed outwards and slightly forwards; both margins granular; base broader than preceding tooth; extending laterally for variable distance, sometimes extending as far as tip of external orbital angle (as in many females and a few males) or else extending to about half that distance (as in most males); separated from third lateral tooth by wide incision. Third lateral tooth pointed, directed outwards and slightly forwards; both margins granular; base broader than either of two preceding teeth; extending laterally for variable distance similarly to second lateral tooth. Posterior to third lateral tooth, small bulge present in carapace margin, in position of fourth lateral tooth of *M. latreillei* and *M. dentatus*.

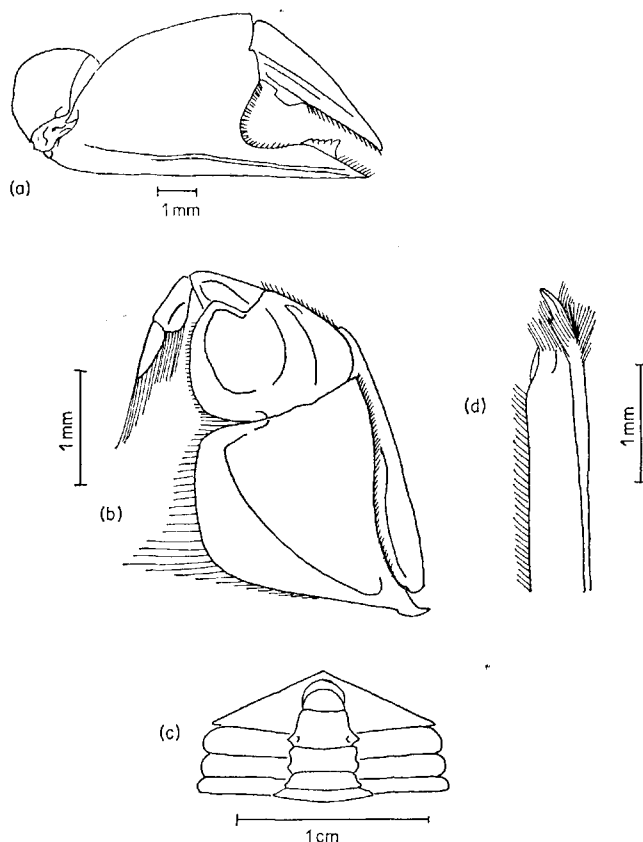


FIG. 1. *M. telescopicus*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

Carapace smooth, except on branchial regions where heavily granular and near postero-lateral margins where hairy; with indistinct furrows, excepting circumgastric; with poorly developed clumps of granules on branchial regions. Lateral margins with row of short hairs, margins parallel or slightly bulging posterior to bulge in position of fourth lateral tooth. Greatest carapace breadth between external orbital angles.

Ocular peduncles very long, extending beyond tips of external orbital angles by between two-elevenths and seven-twelfths of their length.

Male cheliped. (a) Merus. Upper margin with row of large tubercular granules; inner margin with fringe of long hairs; outer margin with medium sized granules. Lower surface heavily haired; inner and outer surfaces hairless and with scattered granules.

(b) Carpus. Outer surface covered with small granules; inner surface with scattered hairs and granules, latter forming a row near joint with propodus.

(c) Palm. Outer surface closely covered with small granules; granular ridge well developed, continuing onto immovable finger with reduction in granules; inner surface with dense mat of hairs distally and centrally (continuous with those of immovable finger and dactylus), granules proximally, centrally and near upper and lower margins. Upper and lower margins closely covered with granules.

(d) Immovable finger. Undeformed. Outer surface with granules near margins; inner surface heavily hairy. Cutting margin with long, crenulated, tooth in central region.

(e) Dactylus. Outer surface with close covering of small granules near upper margin; inner surface with mat of hairs near cutting margin and two parallel longitudinal rows of hairs near upper margin. Upper margin with series of tubercular granules; cutting margin with large quadrangular tooth near base and isolated conical tubercles over remainder.

Male abdomen. Lateral margins of fourth segment convergent towards fifth segment; of fifth segment concave; of sixth segment with sharply pointed protruberance in morphologically anterior position.

External maxilliped. Internal margin of ischium straight; external margin concave proximally and convex distally. Internal margin of merus convex; external margin smoothly curved; anterior margin deeply indented.

First male pleopod straight, with well-developed terminal process and without hairs on internal margin.

Dimensions and relative proportions

Carapace breadth (mm)	7.5	10.0	15.0	20.0	22.5
Carapace breadth Carapace length	1.58	1.66	1.66	1.66	1.66
Length of chela	♂ 0.46	0.53	0.70	—	—
Carapace breadth	♀ 0.37	0.37	0.38	0.39	0.39
Carapace breadth Breadth of front	5.07	5.41	5.66	5.75	5.79

Distribution. Red Sea (de Man, 1880b); India (Alcock, 1900); Singapore (Lanchester, 1900); Japan (Sakai, 1939); Australia (Haswell, 1882a; Miers, 1886); Pacific Islands (Owen, 1839; Gibbs, 1850; Tinker, 1965).

Comments. Tesch (1915) synonymised the *Gelasimus telescopicus* of Owen (1839), the *M. compressipes* of Randall (1839), the *M. podophthalmus* of Souleyet (1841), the *M. verreauxi* of H. Milne Edwards (1848) and the *M. telescopicus* (Owen) of the same author

(1852) into the one *M. telescopicus*. There exists no doubt that Owen's and Randall's species are synonymous, but doubt however exists over the status of Souleyet's and H. Milne Edwards' (1848) species. The distinction between these three 'species' is based on the form of the anterolateral teeth (degree of flatness and pointedness of the external orbital angle, etc.). Kemp (1919) accepted Tesch's synonymy only as a temporary measure and suggested that further research would be necessary to prove the three 'species' to be in fact synonymous. Crosnier (1965) examined specimens of *podophthalmus* and *verreauxi* which 'greatly resembled the types' and came to the conclusion that the differences between those two species and *telescopicus* were not sufficient to justify three separate species.

Although the author has seen specimens from a somewhat restricted area, the variations observed in these specimens permit certain conclusions, relating to the validity of Tesch's synonymy, to be made. A large degree of variation in the length of the ocular peduncles was noted, this variation showing no correlation with size or geographical area. A similar degree of variation was shown by the anterolateral teeth (with no correlation between teeth variations and size of the ocular peduncles); in some specimens the external orbital angles were directed partially forwards, in others straight outwards, and the size of the second lateral tooth varied from being half as long as the external orbital angles to being equisized with those teeth. In all other respects the various specimens, with the exception of those from Lord Howe Island, were identical. The Lord Howe Island specimens differed in the degree of expression of several characters from the other specimens seen. They showed (a) more anteriorly directed external orbital angles, (b) coarser and more extensive granulation on the branchial region, (c) more extensive hair on the inner surface of the male chela, (d) longer ocular peduncles, (e) slightly larger third lateral carapace teeth and (f) comparatively broader male abdominal segments, especially the sixth. These specimens may represent a geographical race of *M. telescopicus* on the isolated Lord Howe Island, insufficient specimens have however been examined to further determine their status.

The variation seen in the form of the external orbital angles in the other specimens has included specimens resembling Crosnier's figures of both *M. podophthalmus* and *M. verreauxi*, even within specimens from a single locality, and yet there appears to be no correlation between any of the variable characters that might indicate that *M. telescopicus* is in fact composed of a number of sibling species. Hence it would appear that *M. telescopicus* possesses a large degree of variation in a small number of characters, and if this species is shown to exhibit a similar variability in other parts of its range, then it would seem probable that Tesch's synonymy is substantially correct.

2. *Macrophthalmus (Macrophthalmus) crassipes* H. Milne Edwards, 1852

(Plate 1(b), Fig. 2)

Synonymy

Macrophthalmus crassipes H. Milne Edwards, 1852, p. 157; Hess, 1865, p. 142; Haswell, 1882a, p. 89; de Man, 1890, p. 76, Plate 4, Fig. 7; Ortmann, 1894a, p. 744; 1897, p. 345; Rathbun, 1910a, p. 323; Tesch, 1915, p. 174, Plate 7; Rathbun, 1924, p. 12; Tweedie, 1937, p. 164.

Macrophthalmus carinimanus: Haswell, 1882a, p. 88; McNeill, 1962, p. 41, Plate 2, Fig. 2; *nec* H. Milne Edwards, 1837, p. 65.

? *Macrophthalmus sandakani*: Rathbun, 1924, p. 12, Plate 1, Fig. 3; *nec* Rathbun, 1914, p. 82.

Material examined. 160 ♂♂ (6.7–37.0 mm); 118 ♀♀ (8.3–33.0 mm).

Queensland (Cape York–New South Wales border); New South Wales (Queensland

border—Sydney); Western Australia (Roebuck Bay); Northern Territory (Darwin); New Guinea (Port Moresby).

Description. Front deflexed; markedly constricted between bases of ocular peduncles; smooth margined; with bilobed anterior margin and median furrow.

Upper orbital border strongly curved and markedly sloping; margin 'beaded' by small granules. Lower orbital border 'serrated' by large tubercular granules.

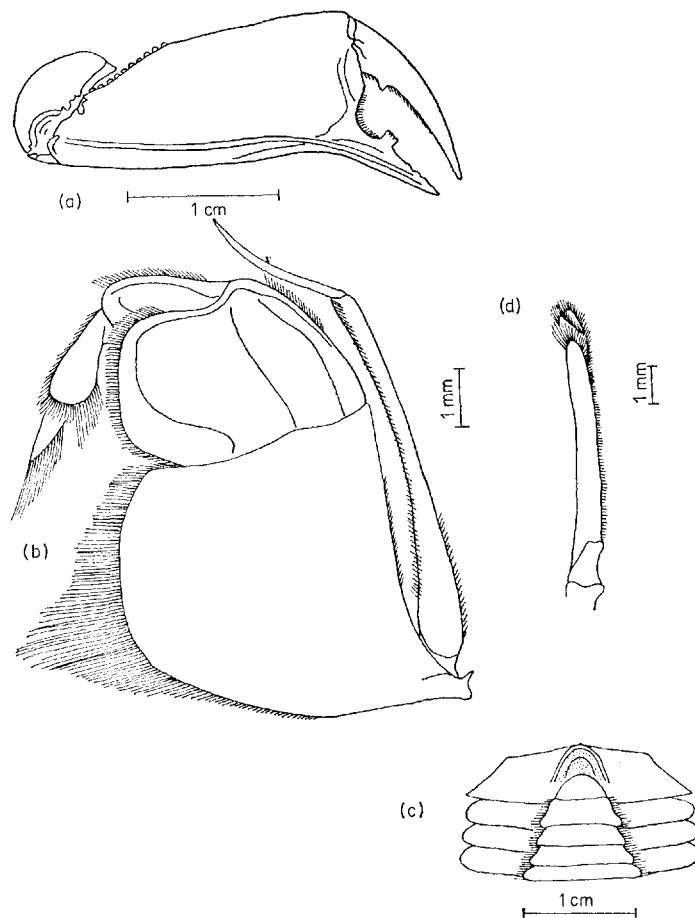


FIG. 2. *M. crassipes*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (right), sternal surface.

Two well defined and one poorly defined anterolateral teeth present. External orbital angle narrow, elongate, pointed, directed outwards and slightly forwards; anterior margin with granules continuous with those of upper orbital border, posterior margin smooth; separated from second lateral tooth by deep, but very narrow incision. Second lateral tooth large, wedge-shaped, directed outwards and slightly forwards; anterior margin smooth, posterior margin straight or concave, granular; tip extends to same level as that of external

orbital angle; separated from third lateral tooth by small, narrow incision. Third lateral tooth small or absent; if present both margins granular.

Carapace covered in small to medium sized granules; with well defined, deep furrows; with distinct clumps of granules on branchial regions; with abruptly sloping sides. Lateral margins markedly convergent posteriorly, with row of long hairs along length. Greatest carapace breadth between external orbital angles and second lateral teeth.

Ocular peduncles long and narrow; cornea not protruding beyond tip of external orbital angle.

Male cheliped. (a) Merus. Upper margin with few, isolated, tubercular granules in proximal half; inner margin hairy; outer margin with compact row of tubercles distally. Lower surface finely granulated and hairy on inner half; inner surface smooth proximally and with close covering of hair distally; outer surface more or less smooth.

(b) Carpus. Hairless. Outer surface smooth; inner surface with large spine and tubercular granules dorsally, and with a similar arrangement, but with more tubercular granules, ventrally and near joint with palm.

(c) Palm. Elongate. Outer surface finely granular near upper margin, smooth near lower margin except near strongly marked longitudinal ridge; inner surface heavily hairy (continuous with hair on immovable finger and dactylus), sparsely granular, but with individual granules larger than those on outer surface, with large spine or spines proximally, near and directed towards carpus. Upper margin with row of prominent granules along whole length; lower margin smooth.

(d) Immobile finger. Deflexed. Outer surface smooth to naked eye, except for continuation of longitudinal ridge, granular microscopically; inner surface densely hairy. Cutting margin with large, crenulated, quadrangular or hemispherical tooth, one third length of margin from base, and with series of large granules distally.

(e) Dactylus. Strongly curved. Outer surface smooth; inner surface heavily hairy. Cutting margin with small quadrangular tooth near base, distally with large granules; upper margin smooth.

Pereiopod meri with hair along upper margins concealing subterminal spines.

Male abdomen. Lateral margins of fourth segment convergent towards fifth segment; of sixth segment with bulge occupying morphologically anterior half.

External maxilliped. Internal margin of ischium convex; external margin straight. Internal margin of merus convex; external margin curving smoothly into anterior margin, without developed posteroexternal convexity; anterior margin shallow and concave.

First male pleopod slightly curved, with well developed terminal process and without hairs on internal margin.

Dimensions and relative proportions

Carapace breadth (mm)	7.0	10.0	15.0	20.0	25.0	30.0	35.0
Carapace breadth	1.75	1.90	2.00	2.05	2.11	2.15	2.22
Carapace length							
Length of chela	♂ 0.36	0.37	0.42	0.51	0.62	0.70	0.77
Carapace breadth	♀ 0.33	0.33	0.31	0.31	0.30	0.30	—
Carapace breadth	4.83	5.55	6.15	6.58	6.94	7.14	7.22
Breadth of front							

Distribution. Malaya (Tweedie, 1937); Gulf of Siam (Rathbun, 1910a); China (Ortmann, 1897); Caroline Islands (de Man, 1890); Australia (H. Milne Edwards, 1852).

Comments. This species is one of the commonest and most widespread Australian species.

Haswell (1882a) and McNeill (1962) both recorded the allied species *M. carinimanus* (= *M. brevis*, fide Tesch (1915)) from Australia, the former from Holborn Island and Sydney, the latter from Sydney alone. Both authors deposited their identified material in the Australian Museum, where the specimens were re-examined by the present author and found to be of *M. crassipes*.

Rathbun (1924) recorded *M. sandakani* as occurring near Cape Jaubert, Western Australia (the only Australasian record of this species). From her description of the specimen, and from her figuring of the chela (Fig. 3) and the dorsal surface of the entire animal (Plate I), it seems quite probable that the young male referred to belongs to *M. crassipes*, the author being unable to find any points of difference between the description and figures, and that species.

3. *Macrophthalmus (Macrophthalmus) convexus* Stimpson, 1858 (Plate 1(c), Fig. 3)

Synonymy

Macrophthalmus convexus Stimpson, 1858, p. 97; Miers, 1880, p. 307; Haswell, 1882a, p. 89; de Man, 1888a, p. 354, Plate 15, Fig. 4; Ortmann, 1894a, p. 745; 1897, p. 344; Alcock, 1900, p. 343; de Man, 1902, p. 493, Plate 19, Figs 6, 6(a); Stimpson, 1907, p. 97, Plate 13, Fig. 2; Rathbun, 1910a, p. 323, Plate 2, Fig. 3; Tesch, 1915, p. 175, Plate 7; 1918, p. 59; Kemp, 1919, p. 389, Plate 24, Fig. 2; Balss, 1922, p. 145; Boone, 1934, pp. 201–204, Plates 104–106; Tweedie, 1937, p. 163; Sakai, 1939, p. 625, Fig. 97; nec Stephenson, 1946, p. 191; Barnard, 1954b, p. 98 (fide Crosnier, 1965).

Macrophthalmus inermis A. Milne Edwards, 1867, p. 286; 1873a, p. 277, Plate 12, Fig. 5; Rathbun, 1906, p. 834.

Material examined. 52 ♂♂ (7.0–32.5 mm); 47 ♀♀ (9.0–31.0 mm).

Western Australia (Roebuck Bay); Queensland (Cooktown—Port Curtis); New Guinea (Daru Island); Solomon and Santa Cruz Islands; New Hebrides; Fiji; Gilbert Islands.

Description. Front deflexed; markedly constricted between bases of ocular peduncles; smooth margined; with bilobed anterior margin and median furrow.

Upper orbital border curved, backwardly sloping; margin 'beaded' with small granules. Lower orbital border 'serrated' by large tubercular granules.

Two well-defined and one poorly-defined anterolateral teeth present, 'beaded' with small granules along margins. External orbital angle large, pointed, directed outwards and forwards (tip in adults lying in same transverse plane as anterior margin of upper orbital border); separated from much smaller second lateral tooth by wide incision. Second lateral tooth small, pointed, directed straight outwards; separated from third lateral tooth by small incision. Third lateral tooth very small or absent.

Carapace smooth and shiny to naked eye (except for granular clumps on branchial regions), lateral areas microscopically granular; with faint, shallow furrows, excepting circumgastric; with well developed granular clumps on branchial regions. Lateral margins markedly convergent posteriorly, with rows of long silky hair along their lengths. Greatest carapace breadth between external orbital angles.

Ocular peduncles long and narrow; cornea only passing slightly, if at all, tip of external orbital angle.

Male cheliped. (a) Merus. Inner margin with series of granules and row of long, fine, hairs; upper and outer margins without granules or hairs. Inner surface with large granules; lower and outer surfaces finely granular.

(b) Carpus. Hairless. Outer surface smooth; inner surface with row of large tubercles near joint with palm.

(c) Palm. Hairless. Outer surface smooth above longitudinal ridge, heavily granular below ridge; inner surface finely granular, without spine near carpal

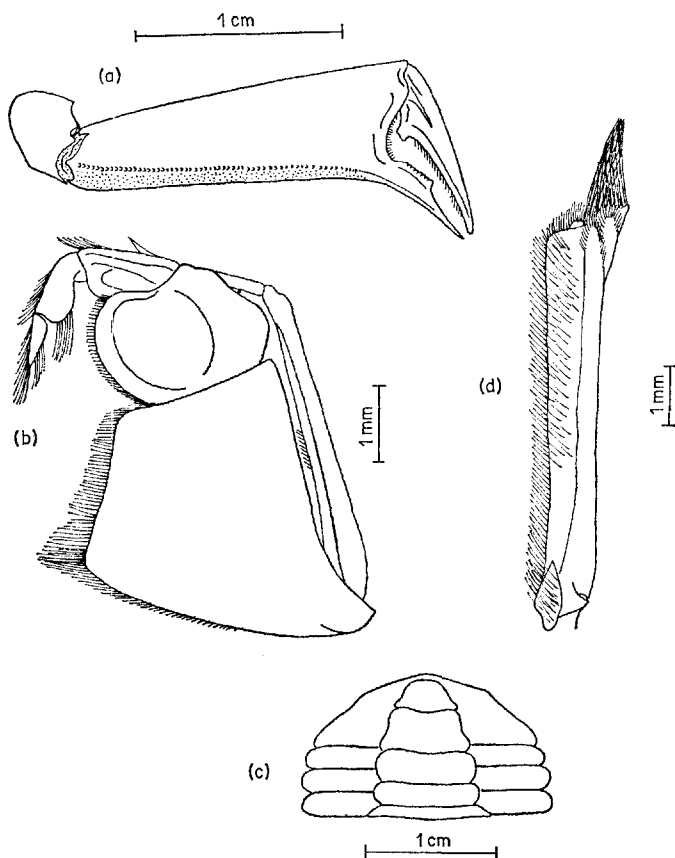


FIG. 3. *M. convexus*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

joint. Upper margin with row of small granules along entire length; lower margin irregularly granular.

(d) Immovable finger. Deflexed. Outer surface smooth except for continuation of longitudinal ridge; inner surface heavily hairy. Cutting margin with large, long, crenulated tooth in proximal half.

(e) Dactylus. Curved. Outer surface smooth; inner surface heavily hairy. Cutting margin with small quadrangular tooth near base, with granules distally.

Pereiopod meri with few fine hairs on upper margins.

Male abdomen. Lateral margins of last and penultimate segments with bulge in morphologically anterior positions; of other segments convex.

External maxilliped. Internal and external margins of ischium more or less straight, distally convergent. Internal margin of merus convex; external margin with almost semi-circular posteroexternal convexity and smaller anteroexternal convexity.

First male pleopod straight, with tuft of long terminal hairs, but without hair on internal margin.

Dimensions and relative proportions

Carapace breadth (mm)	7.0	10.0	15.0	20.0	25.0	30.0	33.0
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.75	1.82	1.88	1.94	1.97	2.04	2.18
$\frac{\text{Length of chela}}{\text{Carapace breadth}}$	♂ 0.43	0.45	0.49	0.58	0.70	0.75	—
	♀ —	0.33	0.33	0.33	0.33	0.34	—
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	5.83	6.25	7.14	7.55	8.06	8.22	8.25

Distribution. India (Alcock, 1900); Malaya (Tweedie, 1937); Indonesia (de Man, 1902); Japan (Sakai, 1939); Australasia (Miers, 1880; Boone, 1934); Pacific Islands (Rathbun, 1906).

Comments. The synonymy given agrees with that of Tesch (1915) in the placing of *M. inermis* as a synonym of *M. convexus*, but disagrees with Tesch and follows Laurie (1915) in separating *M. graeffei* from *M. convexus* as a distinct species.

(b) *Subgenus Mareotis*

KEY TO THE AUSTRALASIAN SPECIES OF THE SUBGENUS *MAREOTIS*

- (1) (a) Carapace with concave granular row on each protogastric region. ... *M. definitus*
 (b) Carapace without concave granular row on each protogastric region. ... 2
- (2) (a) Carapace without longitudinal rows of hair or granules on each branchial region. ... *M. abercrombiei*
 (b) Carapace with distinct longitudinal rows of granules and/or hairs, sub-parallel to each other and to the posterolateral carapace margins, on each branchial region. ... 3
- (3) (a) Greatest carapace breadth occurring across external orbital angles. ... *M. setosus*
 (b) Greatest carapace breadth occurring behind external orbital angles. ... 4
- (4) (a) No differentiated tooth on cutting margin of immovable finger of male chela. ... *M. pacificus*
 (b) Distinct tooth present on cutting margin of immovable finger of male chela. ... 5
- (5) (a) Inner surfaces of dactylus and immovable finger of chela heavily hairy. ... *M. crinitus*
 (b) Inner surfaces of dactylus and immovable finger without hair. ... *M. japonicus*

1. *Macrophthalmus (Mareotis) definitus* Adams & White, 1848

(Plate 1(d), Fig. 4)

*Synonymy**Macrophthalmus definitus* Adams & White, 1848, p. 51; Ortmann, 1897, p. 342; Rathbun, 1910b, p. 307, Plate 2, Fig. 1; Tesch, 1915, p. 198; 1918, p. 59; Barnes, 1966a, p. 46.*Macrophthalmus depressus*: Ortmann, 1894a, p. 745; *nec* Rüppell, 1830, p. 19.*Material examined*. 4 ♂♂ (18.0–21.25 mm); 3 ♀♀ (14.25–15.0 mm).

Solomon Islands (Ysabel Island).

Description. Front deflexed; constricted between bases of ocular peduncles; with deep median furrow; sparsely granular surface; straight anterior margin and with granules along proximal half of lateral margins.

Upper orbital border curved and transverse; margin studded with rounded granules. Lower orbital border studded with large tubercular granules decreasing in size towards external orbital angle.

Three distinct anterolateral teeth present, 'beaded' along outer margins with rounded granules. External orbital angle broad, rectangular, directed outwards and slightly forwards; anterior margin with granules continuous with those of upper orbital border; separated from second lateral tooth by wide U-shaped incision. Second lateral tooth large, broad, rectangular, projecting beyond former tooth; outer margins slightly divergent posteriorly; separated from third lateral tooth by wide V-shaped incision. Third lateral tooth broad, wedge shaped and bluntly pointed.

Carapace with heavily granular surface except over gastric, cardiac, intestinal and contiguous branchial regions which are smooth and shiny; with scattered hairs on branchial regions, densest marginally; with deep furrows; with two concave granular rows, one on each anteroprotogastric region; with transverse, concave, row of granules, extending from third lateral tooth across branchial region; with smaller, slightly concave, row of small granules above insertion of fourth pereopod; without clearly defined longitudinal granular rows, but with two short rows present in position of inner longitudinal row of other species in an anterior/posterior position. Greatest carapace breadth between third lateral teeth, behind which lateral margins subparallel and with row of hairs.

Ocular peduncles long and narrow; cornea extending to base of external orbital angle.

Male cheliped. (a) Merus. Inner margin with large rounded granules and long hairs; upper margin with long hairs; outer margin with irregular covering of granules. Inner surface heavily hairy; outer surface with similar hairy mat, but slightly less well developed; lower surface heavily granular.

(b) Carpus. Elongate. Upper margin irregularly granular; lower margin with row of large granules. Inner surface hairy, and with large tubercles near joint with palm; outer surface smooth to naked eye, microscopically with small granules in upper portion.

(c) Palm. Outer surface smooth to naked eye, microscopically with small granules, largest near upper margin, without longitudinal ridge; inner surface heavily hairy, with large granules near lower margin. Upper margin with row of granules; lower margin with scattered granules.

(d) Immobile finger. Deflexed. Outer surface smooth; inner surface densely hairy. Lower margin smooth; cutting margin with large crenulated tooth in centre, and large granules distal to tooth.

(e) Dactylus. Curved. Outer surface with microscopical granules; inner surface densely hairy. Upper margin with very small granules; cutting margin with small but distinct tooth near base, large granules distally.

Pereiopod meri large, tapered distally; with close covering of hair on both upper surfaces, rows of granules along all margins, row of long hairs and large distal spine on upper margin. Carpi and propodi hairy. Dactyli lanceolate.

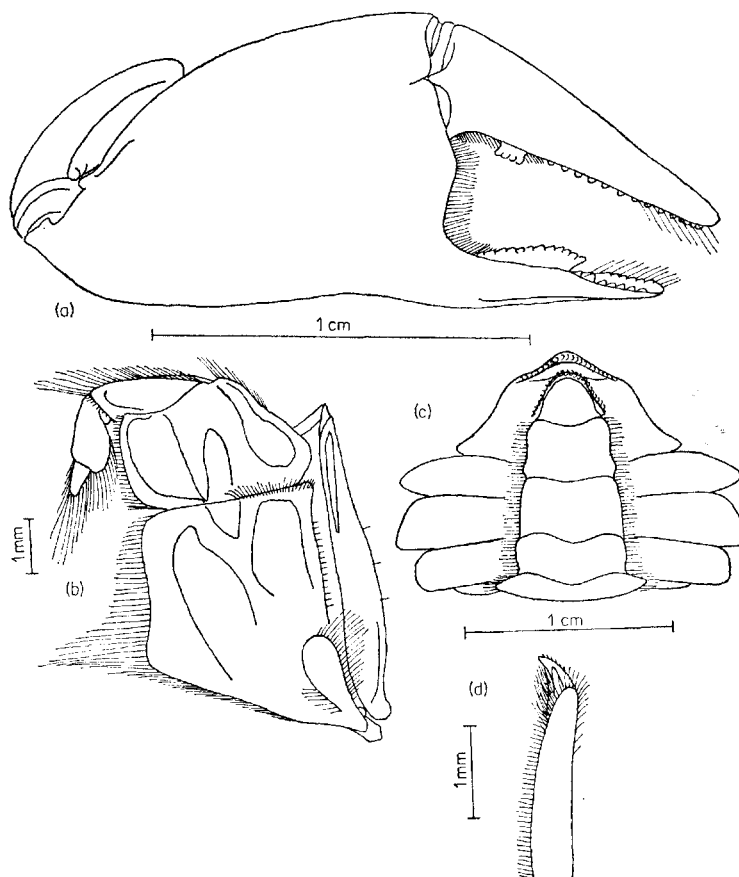


FIG. 4. *M. definitus*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

Male abdomen. Lateral margins of fourth segment convex, of sixth segment concave with slight convexity in morphologically anterior position. Third segment with marked, central, transverse ridge (also present in females).

External maxilliped. Internal margin of ischium concave; external margin straight. Merus with pronounced posteroexternal convexity.

First male pleopod slightly curved, with marked terminal and subterminal lobes, hair present on internal margin distally.

Dimensions of largest male examined (mm)

Carapace breadth = 21.25	Carapace length = 16.5
Length of propodus of chela = 15.0	Breadth of front = 2.9

Distribution. Philippines (Adams & White, 1848; Rathbun, 1910b).

Comments. The first record of this species from an area other than the Philippines.

2. *Macrophthalmus (Mareotis) abercrombiei* Barnes, 1966

Synonymy

Macrophthalmus abercrombiei Barnes, 1966a, pp. 43–47, Plate 8, Fig. 1.

Material examined. 3 ♂♂ (22.25–26.0 mm).

Queensland (South east Gulf of Carpentaria).

Comments. No further specimens have been discovered since the author described this species in 1966. One paratype has however been transferred from the Australian Museum to the Queensland Museum.

3. *Macrophthalmus (Mareotis) setosus* H. Milne Edwards, 1852

(Plate 2(a), Fig. 5)

Synonymy

Macrophthalmus setosus H. Milne Edwards, 1852, p. 159; Haswell, 1882a, p. 89; de Man, 1888a, p. 356, Plate 9, Figs 2, 2(a); Ortmann, 1897, p. 343; Tesch, 1915, p. 189; Etheridge & McCulloch, 1916, p. 12, Plates 5–6; Snelling, 1959, p. 70; McNeill, 1962, p. 42.

Macrophthalmus pacificus: Snelling, 1959, p. 70; *nec* Dana, 1851, p. 248.

Material examined. 133 ♂♂ (4.5–39.75 mm); 99 ♀♀ (7.75–38.0 mm).

Queensland (Port Curtis—New South Wales border); New South Wales (Queensland border—Sydney).

Description. Front deflexed; constricted between bases of ocular peduncles; with median furrow; smooth surface; almost straight anterior margin; and smooth margins.

Upper orbital border slightly curved and backwardly sloping; ‘beaded’ with small granules along margin. Lower orbital border serrated by tubercular granules.

Two distinct and one indistinct anterolateral teeth present. External orbital angle large, broad, rectangular; outer margin convex, both margins ‘beaded’ with small granules continuous with those on upper orbital border; separated from second lateral tooth by narrow fissure. Second lateral tooth similar in shape to preceding tooth but smaller than latter and projecting less outwardly; separated from third lateral tooth by narrow incision. Third lateral tooth small and completely hidden in thick hair.

Carapace surface with small granules, except over central regions, latter smooth; with variable amount of short hair, sometimes completely covering carapace; with shallow but distinct furrows; with transverse granular and hairy row extending from level of third lateral tooth across anterior branchial region; with short transverse row above insertion of fourth pereopod; with two longitudinal rows subparallel to each other and to postero-lateral carapace margins, on branchial region. Greatest carapace breadth occurring between external orbital angles, behind which lateral margins convergent. Lateral margins with row of short hairs.

Ocular peduncles long and narrow; cornea extending to base of external orbital angle.

Male cheliped. (a) Merus. Inner and upper margins heavily hairy; outer margin more or less smooth. Lower surface and upper regions of inner and outer surfaces heavily granulated, lower regions of inner and outer surfaces smooth.

(b) Carpus. Upper margin hairy; lower margin feebly granular. Inner surface with large granules and row of tubercles near joint with palm; outer surface with sparse smaller granules.

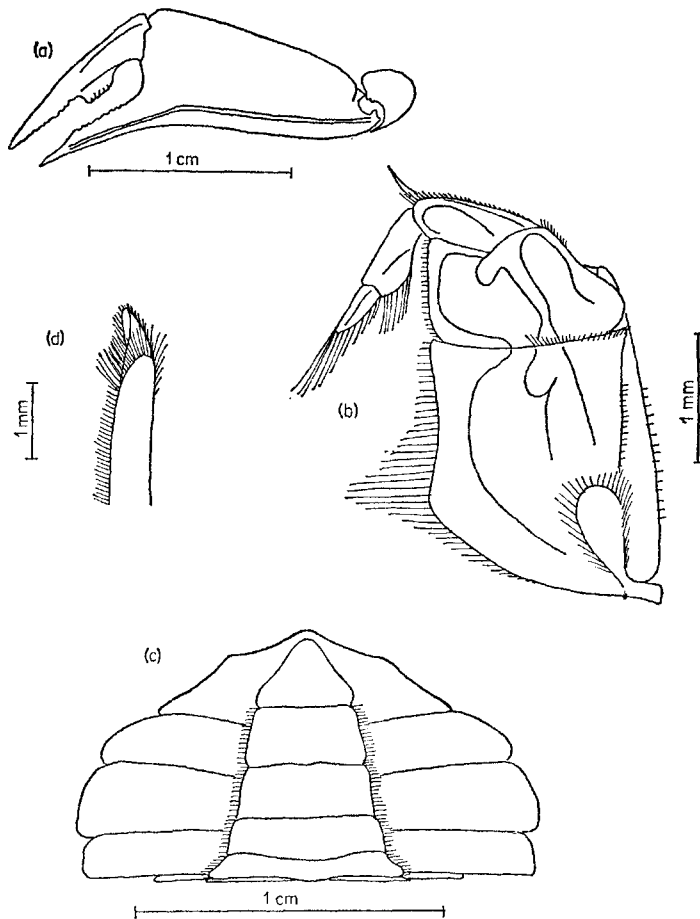


FIG. 5. *M. setosus*.

(a) Male chela (left), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

(c) Palm. Upper margin with irregular granules; lower margin with few granules. Inner surface finely granular and heavily hairy; outer surface with granules near upper margin, with inconspicuous and feebly developed longitudinal ridge running close to and subparallel with lower margin, and with smooth central area.

(d) Immovable finger. Deflexed. Outer surface smooth, with faint continuation of longitudinal ridge near lower margin; inner surface heavily hairy. Lower

margin smooth; cutting margin with longitudinal series of similar granules, slightly raised proximally, but without distinct tooth.

(e) Dactylus. Outer surface smooth; inner surface heavily hairy. Cutting margin with large, long, crenulated tooth occupying proximal quarter of the margin, with series of granules distally.

Pereiopod meri and carpi heavily hairy; lower margins and surfaces of meri granular, subterminal spine on upper margins small.

Male abdomen. Lateral margins of fourth, fifth and sixth segments more or less straight, of terminal segment concave.

External maxilliped. Internal margin of ischium markedly concave; external margin straight. Internal margin of merus almost straight; external margin with marked postero-external convexity. Merus-ischium suture transverse.

First male pleopod slightly curved, with marked terminal lobe and with hair on internal margin distally.

Dimensions and relative proportions

Carapace breadth (mm)	5.0	10.0	15.0	20.0	25.0	30.0	35.0
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.43	1.59	1.66	1.67	1.68	1.69	1.71
$\frac{\text{Length of chela}}{\text{Carapace breadth}}$	♂ 0.40	0.40	0.42	0.51	0.59	0.65	0.69
	♀ —	0.35	0.36	0.36	0.36	0.36	0.36
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	5.15	7.41	8.77	9.76	10.16	10.42	10.64

Distribution. Eastern Australia (H. Milne Edwards, 1852; Haswell, 1882a).

Comments. Juveniles of about 7.5 mm carapace breadth and under, differ markedly from adults in two features of carapace shape. In these juveniles the carapace breadth is not so markedly greater than the length as it is in adults (see 'relative proportions') and the position of greatest breadth occurs posterior to the external orbital angles, between the second and third lateral teeth. (Thus in these characters the juveniles are more typical of the subgenus *Mareotis* than the adults.) It is these juvenile *M. setosus* that Snelling (1959) recorded from the Brisbane River as *M. pacificus*. This was first suggested by Dr J. C. Yaldwyn of the Australian Museum (pers. comm.), and then confirmed by examination of Snelling's identified material in the Australian Museum and the University of Queensland Department of Zoology.

4. *Macrophthalmus (Mareotis) pacificus* Dana, 1851

(Plate 2(b), Fig. 6)

Synonymy

Macrophthalmus pacificus Dana, 1851, p. 248; 1852, p. 314, Plate 19, Fig. 4; Stimpson, 1858, p. 97; de Man, 1890, p. 79, Plate 4, Fig. 10; 1895, p. 579; Ortmann, 1897, p. 342; Tesch, 1915, p. 190, Plate 8; Kemp, 1919, p. 391; Rathbun, 1924, p. 13; Sakai, 1939, p. 628; Chhapgar, 1957, p. 514, Plate 15; Tweedie, 1950, p. 359; *nec* Rathbun, 1910b, p. 307, Plate 1, Fig. 3; Snelling, 1959, p. 70.

? *Macrophthalmus bicarinatus* Heller, 1868, p. 36, Plate 4, Fig. 2; de Man, 1902, p. 496.

Macrophthalmus quadratus: Boone, 1934, pp. 204–6, Plate 107–9; *nec* A. Milne Edwards, 1873a, p. 280.

Material examined. 46 ♂♂ (5.4–18.75 mm); 25 ♀♀ (6.75–22.0 mm).

Queensland (Cooktown—Port Curtis); New Guinea (Kaimare & Daru Island); Solomon Islands (Ysabel Island).

Description. Front deflexed; slightly constricted between bases of ocular peduncles; with smooth margins; straight anterior margin; deep median furrow.

Upper orbital border slightly curved and transverse; margin studded with very small granules, appearing smooth to naked eye. Lower orbital border studded with large tubercular granules, which increase in size towards epistome, granules immediately nearest epistome, however, small.

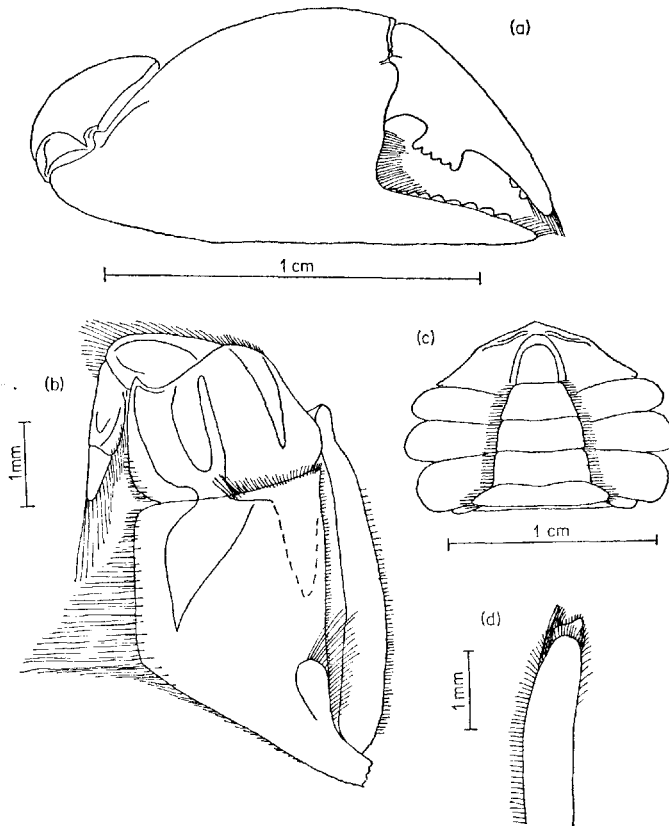


FIG. 6. *M. pacificus*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

Two large and one small anterolateral teeth present. External orbital angle broad, rectangular; with outer margins divergent posteriorly and with 'beading' of small granules; separated from second lateral tooth by deep but narrow incision. Second lateral tooth very broad, subrectangular, projecting beyond former tooth; outer margins divergent posteriorly and with 'beading' of small granules; separated from third lateral tooth by small but distinct incision. Third lateral tooth small, pointed and projecting as far as, or beyond, second lateral tooth.

Carapace surface smooth to naked eye, but microscopically with small granules; with inconspicuous furrows, excepting circumgastric; with granular ridge extending transversely across anterior branchial region from level of third lateral tooth; with small, transverse, concave, row of granules above insertion of fourth pereopod; with two longitudinal rows, subparallel to each other and to posterolateral carapace margins, on each branchial region, outer row broken into two sections by gap near anterior end, small anterior row set at angle to larger posterior row. Greatest carapace breadth across third lateral teeth, behind which lateral margins parallel and with row of hairs.

Ocular peduncles long and narrow; cornea extending to base of external orbital angle.

Male cheliped. (a) Merus. Inner margin with row of long hairs; upper margin with row of large tubercular granules; outer margin with small granules proximally and large tubercular granules distally. Inner surface smooth, with curved line of hairs along lower and distal borders, scattered hairs over remainder; outer surface hairless with scattered small granules; lower surface with dense mat of hair.

(b) Carpus. Upper margin with a few large granules distally; lower margin with small scattered granules. Inner surface hairless, with small scattered granules; outer surface with scattered small granules and hairs.

(c) Palm. Upper and lower margins without distinct rows of granules. Outer surface smooth to naked eye, microscopically with small scattered granules, without longitudinal ridge near lower margin; inner surface with scattered granules just visible to naked eye, with dense patch of hair centrally near distal margin (continuous with hair on immovable finger).

(d) Immobile finger. Undeformed. Outer surface with small scattered granules; inner surface with dense mat of hair near cutting margin. Lower margin with small scattered granules; cutting margin with series of large rounded granules, but without differentiated tooth.

(e) Dactylus. Curved, hairless except for fine hairs around spoon-tip. Outer and inner surfaces and upper margin with small scattered granules; cutting margin with large, crenulated tooth, with base narrower than cutting surface, in proximal half.

Pereopod meri, carpi and propodi granular, with only sparse hair on upper margins.

Male abdomen. Lateral margins of fourth and fifth segment straight, of sixth segment slightly sinuous.

External maxilliped. Internal and external margins of ischium more or less straight. Internal margin of merus straight; external margin with small posteroexternal convexity.

First male pleopod curved, with short terminal lobe, and hairs on internal margin distally.

Dimensions and relative proportions

Carapace breadth (mm)	5.0	10.0	15.0	20.0
Carapace breadth				
Carapace length	1.25	1.33	1.39	1.43
Length of chela	♂ 0.45	0.58	0.71	—
Carapace breadth	♀ —	0.42	0.43	0.44
Carapace breadth				
Breadth of front	5.55	6.45	7.04	7.14

Distribution. India (Chhapgar, 1957); Malaya (de Man, 1895); Borneo (Tweedie, 1950); Japan (Sakai, 1939); Australasia (Rathbun, 1924; Boone, 1934); Samoa (Dana, 1852).

Comments. The only previous record of this species from Australia is that of Rathbun (1924) who recorded a single male specimen from Broome, Western Australia.

The specimens from New Guinea and the Solomon Islands differed from those from Queensland in that they possessed more extensive pereopod hair and possessed a sparse covering of short hair over the carapace. Due, however, to the small number of specimens examined little significance can be placed on this.

5. *Macrophthalmus (Mareotis) crinitus* Rathbun, 1913

(Plate 2(c), Fig. 7)

Synonymy

Macrophthalmus crinitus Rathbun, 1913, p. 619, Plate 75, Fig. 3; Tesch, 1915, pp. 192–3; Kemp, 1919, p. 390, Plate 24, Fig. 7; Chhapgar, 1957, p. 515, Plate 15.

Macrophthalmus pacificus: Rathbun, 1910b, p. 307, Plate 1, Fig. 3; *nec* Dana, 1851, p. 248.

Macrophthalmus sp.: de Man, 1902, p. 495.

Material examined. 12 ♂♂ (3.1–13.5 mm); 1 ♀ (12.0 mm).

Northern Territory (Darwin).

Description. Front deflexed; slightly constricted between bases of ocular peduncles; with smooth margins; straight or faintly bilobed anterior margin; deep but narrow median furrow.

Upper orbital border curved and transverse; margin studded with small rounded granules. Lower orbital border studded along whole length with large tubercular granules, and with long hairs on outer quarter.

Two large and one small anterolateral teeth present. External orbital angle large, broad, subrectangular, with granules continuous with those on upper orbital border on anterior margin; outer margin convex, with rounded granules, margins of two teeth slightly divergent posteriorly; separated from second lateral tooth by wide V-shaped incision. Second lateral tooth large, very broad, directed outwards, projecting beyond former tooth; anterior margin straight, outer margin convex, studded with rounded granules; separated from third lateral tooth by very narrow incision. Third lateral tooth very small, pointed.

Carapace surface smooth centrally, with scattered granules on branchial and hepatic regions, and with variable short hair over whole surface, densest laterally; with distinct furrows but only circumgastric deep; with four rows of hairs on each branchial region, often obscured by carapace hair, indistinct transverse row extending across anterior branchial region from level of third lateral tooth; short, concave, transverse row above insertion of fourth pereopod; two longitudinal rows subparallel to each other and to posterolateral carapace margins; with prominent epigastric ridges. Greatest carapace breadth across second lateral teeth, behind which lateral margins subparallel and with row of hairs.

Ocular peduncles long and narrow; cornea extending to base of external orbital angles.

Male cheliped. (a) Merus. Inner margin with long hair and tubercular granules at distal angle; upper margin with long hair; outer margin with row of large pointed granules, largest distally. Inner surface with mat of hair distally and near inner margin; outer surface with granules proximally and near outer margin, hair near upper margin; lower surface with large rounded granules under mat of hair.

(b) Carpus. Upper and lower margins coarsely granular. Inner surface with small scattered granules and oblique row of large pointed tubercles; outer surface with small scattered granules.

(c) Palm. Upper and lower margins with scattered granules, largest on lower margin. Outer surface finely granular, granules largest and densest near upper margin, without longitudinal ridge near lower margin in adults, present in juveniles; inner surface heavily hairy distally and on upper half, with granules near lower margin.

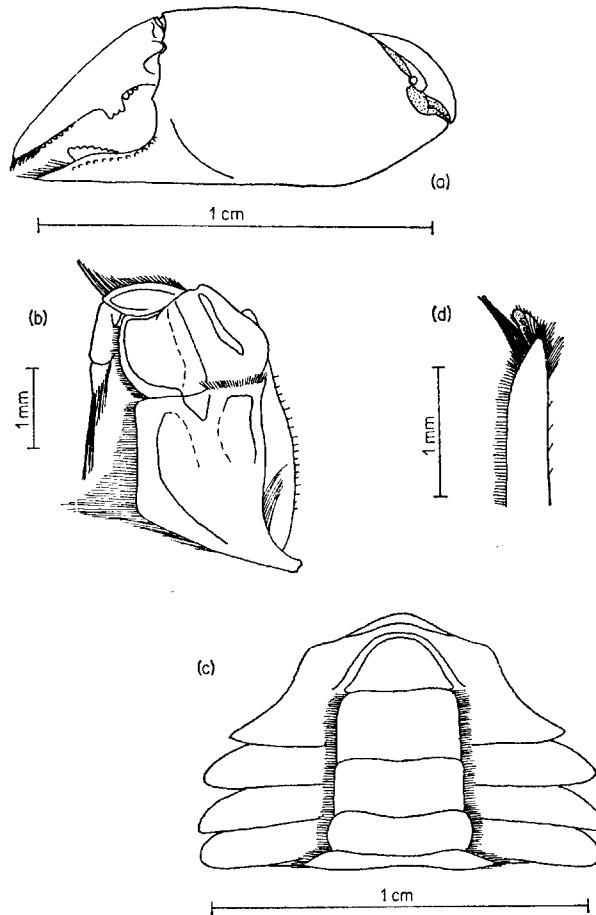


FIG. 7. *M. crinitus*.

(a) Male chela (left), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

(d) Immovable finger. Straight or slightly deflexed. Outer surface finely granular, without continuation of longitudinal ridge except in juveniles; inner surface with mat of hair. Lower margin finely granular; cutting margin with large, long, crenulated tooth in centre of margin (in adults).

(e) Dactylus. Curved. Outer surface finely granular; inner surface heavily hairy. Upper margin with scattered granules; cutting margin with large quadrangular tooth, one third length of margin from base, (in adults), in juveniles long, low, crenulated tooth present near base (tooth of adult possibly developed from distal section of juvenile tooth), remainder of margin with medium-sized granules.

Pereiopod meri, carpi and propodi with thick hair on upper margins and upper surfaces, hair concealing subterminal spines on meri.

Male abdomen. Lateral margins of fourth segment slightly convex; of fifth and sixth segments straight and parallel.

External maxilliped. Internal and external margins of ischium straight. Internal margin of merus convex; external margin with pronounced posteroexternal convexity.

First male pleopod slightly curved; with well developed terminal lobe, and hair on internal margin distally.

Dimensions and relative proportions

Carapace breadth	(mm)	3.0 (predicted)	5.0	7.5	10.0	13.0
Carapace breadth						
Carapace length		1.20	1.25	1.30	1.38	1.42
Length of chela	♂	0.37	0.45	0.51	0.60	0.77
Carapace breadth						
Carapace breadth		4.29	5.15	6.00	6.45	6.84
Breadth of front						

Distribution. India (Chhapgar, 1957); Mergui Archipelago (Kemp, 1919); Indonesia (Rathbun 1910b); Australia (present paper).

Comments. The Australian specimens differ from those described by Rathbun (1913) in details of the male chelae. The type male lacks a differentiated tooth on the immovable finger, and possesses a faint longitudinal ridge on the distal part of the outer surface of the palm, continued more distinctly onto the immovable finger. The juveniles examined by Rathbun possessed a much more distinct ridge on the palm than the type male. The juveniles from Darwin agree exactly with Rathbun's description, in that they lack the fore-mentioned tooth and possess the ridge. The largest Darwin specimen, however, although slightly smaller than Rathbun's type, has no ridge and possesses a tooth on the immovable finger. This largest specimen is similar to the type in the structure of the tooth on the dactylus, the juveniles however possess a much more elongate tooth (cf. adult *M. setosus*), although there are indications of a gradual reduction of the proximal section of the tooth with increase in size of the juveniles. The differences between Rathbun's specimens and the specimens from Darwin (both authors having only limited material at their disposal—Rathbun having only examined five specimens) would not appear to be basic differences in the nature of the chelae, but rather the attainment of adult characters at a slightly smaller size in the Australian specimens—Rathbun's type male then not being fully adult.

Tesch (1915), without having examined any material of *M. crinitus*, states that one of the characters of the species is a lack of longitudinal pubescent rows on the branchial region. Rathbun, however, in her original description (1913) makes no mention of the lack of

pubescent rows, but states instead that the species lacks distinct granular rows on the branchial region. In the Darwin specimens the longitudinal rows of hairs are clearly visible.

Rathbun indicated affinity between her species and *M. pacificus*. Tesch, however, and later Kemp (1919), denied close affinity of *M. crinitus* with *M. pacificus*, and placed its relationships with *M. boscii*. Although this species does bear a superficial resemblance to *M. boscii* (in shape of carapace and chelae), its basic structural features place it without doubt into the subgenus *Mareotis*, and in the opinion of the author within the subgenus its affinities are as Rathbun indicated (cf. *M. pacificus*).

6. *Macrophthalmus (Mareotis) japonicus* (de Haan, 1835)

(Plate 2(d), Fig. 8)

Synonymy

Ocypode japonica de Haan, 1835, p. 54, Plate 7, Fig. 1, Plate 15, Fig. 2.

Macrophthalmus japonicus: Gray, 1847, p. 38; Adams & White, 1848, p. 51; H. Milne Edwards, 1852, p. 158; Ortmann, 1894a, p. 746; 1897, p. 343; Tesch, 1915, p. 200, Plate 9; Parisi, 1918, p. 96; Balss, 1922, p. 145; Urita, 1926, p. 26; Yokoya, 1928, p. 779; Shen, 1932, p. 215, Plate 9, Figs 132 & 134; Sakai, 1934, p. 320; 1936, p. 215, Plate 60; 1939, p. 627, Plates 73 & 105, Fig. 98; 1965, p. 190, Plate 90.

Material examined. 4 ♂♂ (10·25–30·75 mm); 3 ♀♀ (21·5–29·25 mm).

Western Australia (Shark Bay).

Description. Front deflexed; constricted between bases of ocular peduncles; with smooth margins; granular surface; bilobed anterior margin; deep median furrow.

Upper orbital border curved, slightly backwardly sloping; margin studded with large tubercular granules along whole length. Lower orbital border studded with large tubercular granules similarly to upper border; inner four-fifths of border straight, outer fifth abruptly sloping.

Two large and one small anterolateral teeth present. External orbital angle large, broad, rectangular, pointed anteriorly, directed outwards and slightly forwards; outer margin with large tubercular granules; anterior margin with granules continuous with those of upper orbital border; separated from second lateral tooth by wide U-shaped incision. Second lateral tooth large, broad, rectangular, directed outwards, projecting beyond former tooth; both margins with tubercular granules, outer margin slightly convex; separated from third lateral tooth by small but distinct incision. Third lateral tooth small, conical, projecting outwards; outer margin with tubercular granules.

Carapace surface entirely covered by large granules, excepting over a small central area; with deep, wide, hair containing, furrows distinctly demarking regions; with transverse granular and hairy row extending across anterior branchial region from level of third lateral tooth; with similar transverse row above insertion of fourth pereopod; with two longitudinal granular and hairy rows on branchial region, subparallel to each other and to posterolateral carapace margins. Greatest carapace breadth across second lateral teeth, behind which lateral margins slightly convergent or parallel. Lateral margins with large granules and row of hairs.

Ocular peduncles long and narrow; cornea extending to base of external orbital angle.

Male cheliped. (a) Merus. Elongate. Inner margin hairy; upper margin with distal row of tubercular granules; outer margin finely granular. Outer surface with few scattered granules; inner and lower surfaces heavily hairy near inner margin, and with scattered granules over remainder.

(b) Carpus. Hairless. Upper margin with row of large tubercles; lower margin finely granular. Outer surface granular towards margins, more or less smooth centrally; inner surface with scattered large tubercular granules.

(c) Palm. Elongate. Upper margin with longitudinal row of large tubercles; lower margin finely granular. Outer surface finely granular, granules increasing in size towards carpus, without longitudinal ridge near lower margin, with slight depression near base of immovable finger; inner surface heavily granular, with narrow longitudinal band of hair near upper margin.

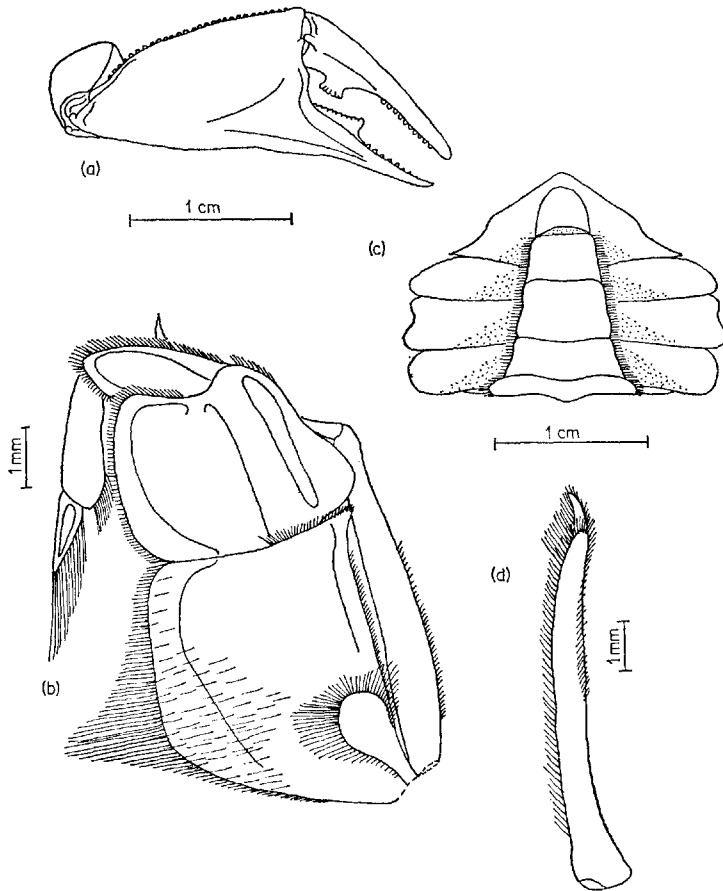


FIG. 8. *M. japonicus*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

(d) Immovable finger. Deflexed, hairless. Outer surface granular near upper and lower margins; inner surface heavily granular. Lower margin slightly granular proximally, smooth distally; cutting margin with large, wedge-shaped, crenulated tooth occupying proximal half of margin, distally with few large and many small tubercular granules.

(e) *Dactylus*. Curved, hairless. Outer surface with granules near upper and lower margins; inner surface heavily granular. Upper margin granular; cutting margin with large quadrangular crenulated tooth, wider at tip than at base, near base, and distally row of tubercular granules.

Pereiopod meri elongate; parallel upper and lower margins with rows of large granules; lower surfaces granular; upper margins with few hairs. Carpi granular and with longitudinal ridges. Propodi granular and with faint longitudinal ridges. Dactyli lanceolate.

Male abdomen. Lateral margins of fourth, fifth and sixth segments almost straight. Proximal and posterior margins of sternal segments granular.

External maxilliped. Internal and external margins of ischium almost straight, and sub-parallel. Internal margin of merus slightly convex; external margin with marked postero-external convexity. Raised areas of merus and ischium pitted.

First male pleopod slightly curved; with well developed terminal lobe, and hair on internal margin distally.

Dimensions (mm)

	Carapace breadth	Carapace length	Breadth of front	Length of chela
Largest male	30.75	20.75	3.0	23.5
Smallest male	10.25	7.5	1.5	4.0
Largest female	29.0	20.25	3.0	11.5
Smallest female	21.5	14.5	2.5	8.5

Distribution. Japan (Sakai, 1965); North China (Sakai, 1939); Singapore (Sakai, 1939); Australia (present paper).

Comments. These specimens from Western Australia differ from Japanese specimens in two characters. Firstly the inner surface of the palm of the male chela is without hair in Japanese forms (Tesch, 1915; Sakai, 1939), whereas in the Australian forms there is a narrow band of hair on the upper portion of that surface. Secondly the inner longitudinal granular row on the branchial region is, in Japanese forms, divided into two rows by a break in the centre (de Haan, 1835, Plate 15; Tesch, 1915; Sakai, 1939, Plate 105), whereas in the Australian forms the row is undivided. These differences may be sufficient to distinguish a distinct Australian geographical race of *M. japonicus*, but a greater number of specimens of the Australian form must first be obtained and examined.

The chela figured (Fig. 8(a)) is that of the largest male examined, and its characters appear to lie between 'c' and 'd' in Fig. 98 (Sakai, 1939, p. 627), and thus none of the specimens would appear to be fully adult, not yet having developed the fully adult male chelae (Sakai, 1939, Fig. 98(d)).

(c) Subgenus *Mopsocarcinus*

KEY TO THE AUSTRALASIAN SPECIES OF THE SUBGENUS *MOPSOCARCINUS*

- | | |
|--|---------------------------|
| (1) (a) Carapace surface granular. | ... <i>M. boscii</i> |
| (b) Carapace surface without granules. | ... <i>M. punctulatus</i> |

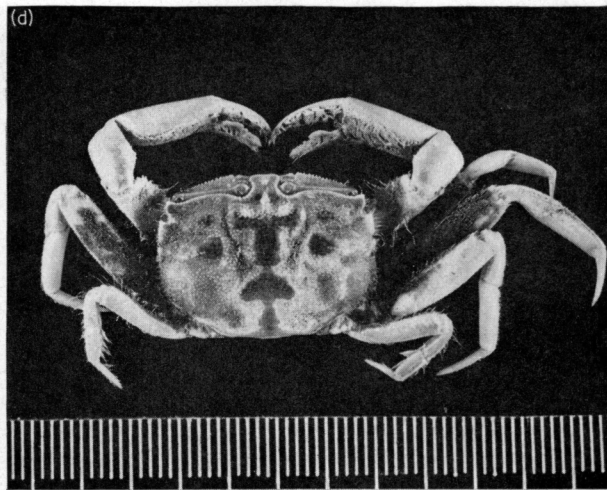
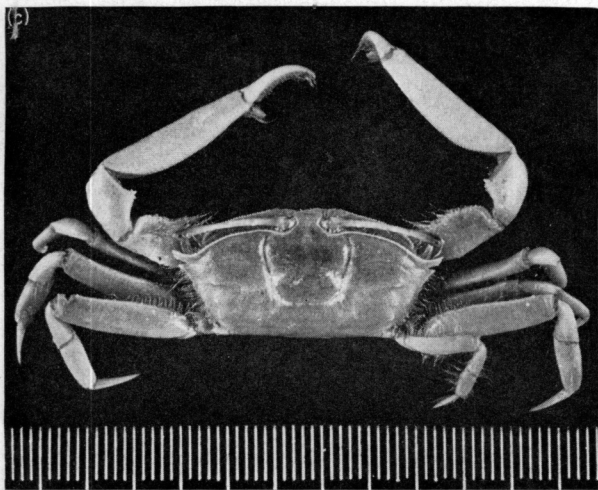
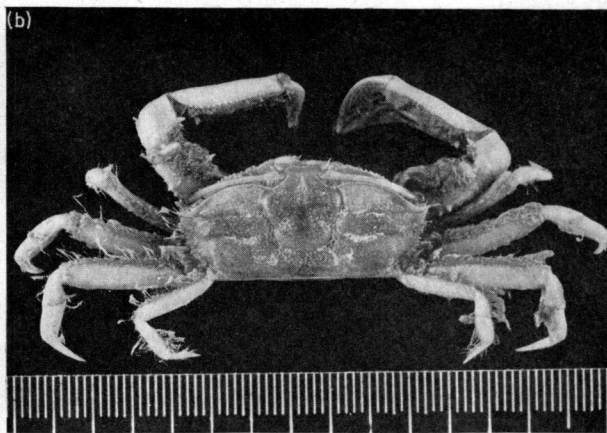
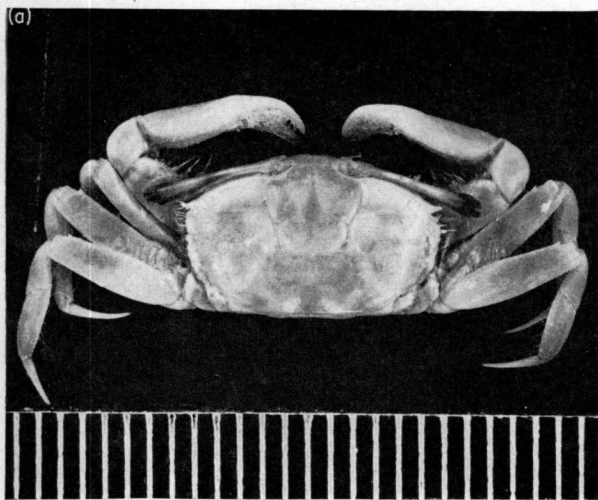


PLATE I. (a) *Macrophthalmus telescopicus* (A.M. No. P10408) ♂ dorsal surface.
 (b) *Macrophthalmus crassipes* (Z.D.U.Q.) ♂ dorsal surface.
 (c) *Macrophthalmus convexus* (Q.M. No. W1251) ♂ dorsal surface.
 (d) *Macrophthalmus definitus* (A.M. No. P7663) ♂ dorsal surface.

A.M., Australian Museum; W.A.M. Western Australian Museum; Q.M., Queensland Museum; Z.D.U.Q., Zoology Department, University of Queensland. Scale lines 1 mm apart.

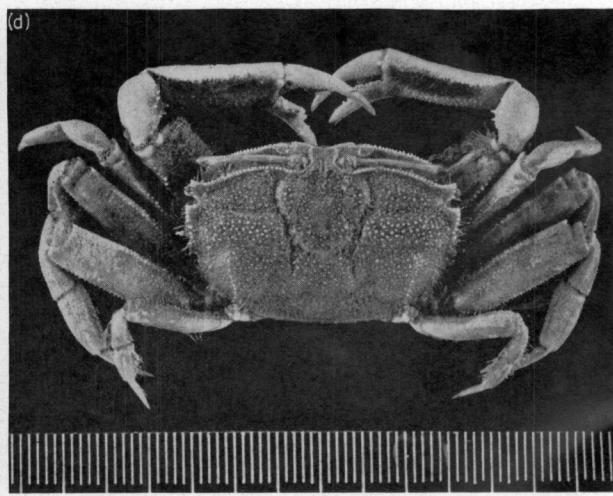
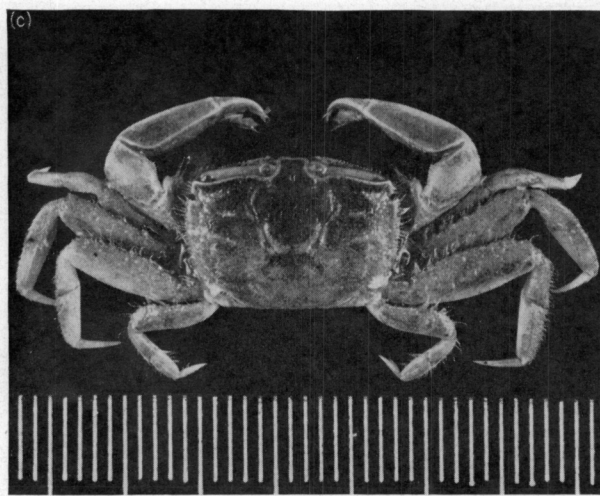
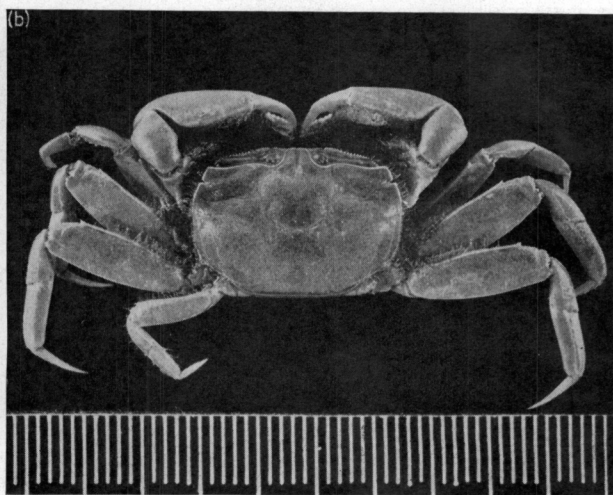
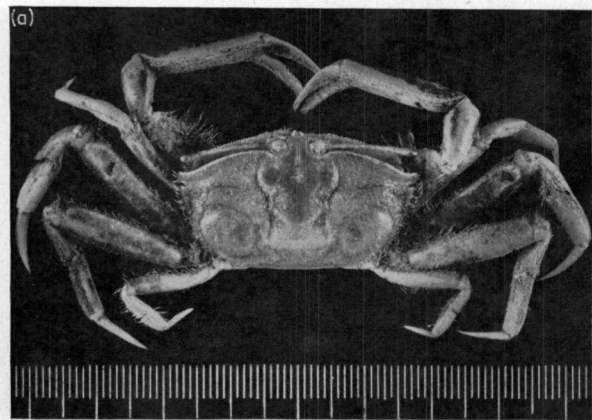


PLATE II. (a) *Macrophthalmus setosus* (Z.D.U.Q.) ♂ dorsal surface.
 (b) *Macrophthalmus pacificus* (A.M. No. P15124) ♂ dorsal surface.
 (c) *Macrophthalmus crinitus* (A.M. No. P15163) ♂ dorsal surface.
 (d) *Macrophthalmus japonicus* (W.A.M. No. 655-65) ♂ dorsal surface.

1. *Macrophthalmus (Mopsocarcinus) boscii* Audouin/Savigny, 1825

(Plate 3(a), Fig. 9)

Synonymy

Macrophthalmus boscii Audouin, 1825, Plate 2, Fig. 1; Krauss, 1843, p. 40, Plate, 2, Fig. 5; Lenz & Richters, 1881, p. 425; Kemp, 1919, p. 383, Plate 24; Balss, 1935a, p. 141; Barnard, 1950, p. 103, Fig. 20; Fourmanoir, 1954, p. 3, Fig. 3; Crosnier, 1965, p. 134, Figs 244–8; Barnes, 1966b, p. 371.

Euplax boscii: H. Milne Edwards, 1852, p. 160; A. Milne Edwards, 1873a, p. 281; de Man, 1880a, p. 71; Miers, 1884, p. 540; 1886, p. 252; de Man, 1888a, p. 357; Ortmann, 1894b, p. 58; Lenz, 1905, p. 367; Nobili, 1906b, p. 319; Stebbing, 1910, p. 329; Tesch, 1918, p. 60; Sakai, 1939, p. 630, Fig. 100.

Cleistostoma boscii: Dana, 1852, p. 313, Plate 19, Fig. 3.

Chaenostoma orientale Stimpson, 1858, p. 97; 1907, p. 98.

Chaenostoma crassimanus Stimpson, 1858, p. 97; 1907, p. 98.

Material examined. 24 ♂♂ (6.25–13.0 mm); 15 ♀♀ (6.25–10.0 mm).

Queensland (Cooktown—Port Curtis); New Guinea (Daru Island); Solomon Islands (Guadalcanal); Santa Cruz Islands (Vanikoro); New Caledonia (Noumea & Oubatche).

Description. Front deflexed; slightly constricted between bases of ocular peduncles; with smooth margins; granular surface; slightly bilobed anterior margin; deep median furrow.

Upper orbital border curved, moderately backwardly sloping; margin studded with small granules, granules slightly increasing in size towards external orbital angle. Lower orbital border studded with wide-based, triangular granules throughout length, granules slightly increasing in size towards external orbital angle.

Two large and one small anterolateral teeth present. External orbital angle large, subrectangular, pointed anteriorly, directed outwards and forwards (so that tip of tooth is in same transverse plane as forward margin of upper orbital border); anterior margin concave, with continuation of granulation of upper orbital border; outer margin convex and with small granules, margins converging posteriorly; separated from second lateral tooth by distinct V-shaped incision. Second lateral tooth large, broad, bluntly pointed anteriorly, directed outwards and slightly forwards; outer margin slightly convex and with small granules; separated from third lateral tooth by small incision. Third lateral tooth small, pointed, hidden in carapace hair.

Carapace surface entirely covered with small, evenly scattered granules; with few scattered hairs, densest on branchial regions; with deep, distinct furrows, giving carapace 'lumpy' appearance; without distinct granular rows on branchial regions, (in some specimens, however, two indistinct, small, longitudinal rows of granules and hairs present on each branchial region, and very faint short row present above insertion of fourth pereopod). Greatest carapace breadth occurs across external orbital angles or second lateral teeth, behind which lateral margins subparallel, and with row of hairs.

Ocular peduncles slightly longer than breadth of front, stout; cornea extending to base of external orbital angle.

Male cheliped. (a) Merus. Inner, outer and upper margins with longitudinal rows of large tubercular granules, those of inner and outer margins largest distally, those of upper margin largest proximally; inner margin and carpal border with long hairs. Outer surface with few scattered granules; inner surface with very few small scattered granules and densely hairy towards inner margin; lower surface without granules, densely hairy towards inner margin.

(b) Carpus. Upper margin with row of small pointed granules; lower margin smooth. Outer surface smooth; inner surface with granules near joint with palm and with clump of hairs centrally.

(c) Palm. Inflated. Upper and lower margins with few scattered granules continuous with those on outer surface. Outer surface smooth to naked eye, microscopically with small granules, with longitudinal, feebly granular, ridge one-third height of palm from lower margin and subparallel to that margin; inner surface densely hairy, with scattered granules beneath the hair.

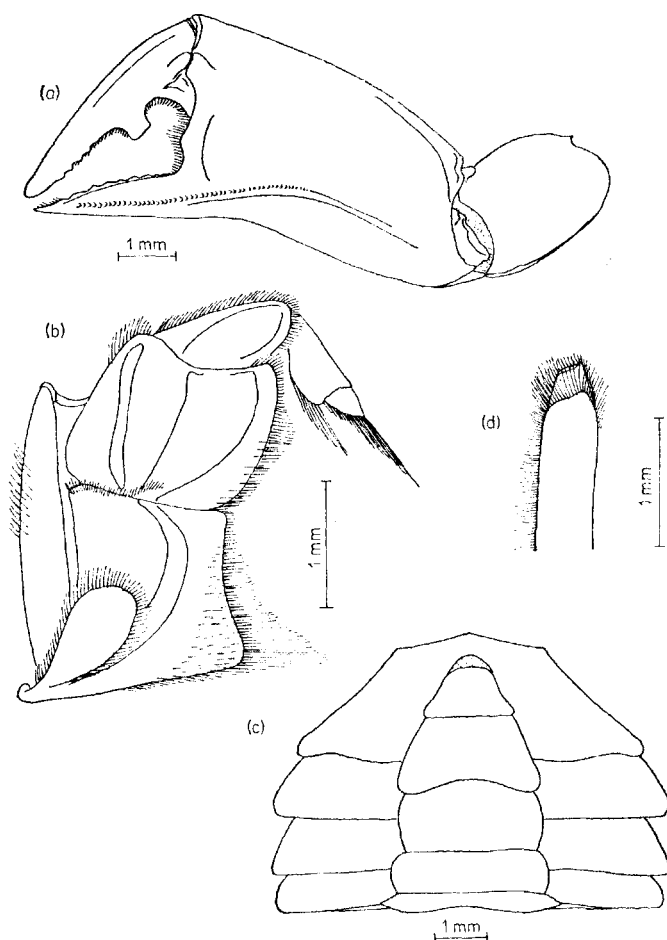


FIG. 9. *M. boscii*.

(a) Male chela (left), outer surface. (b) External maxilliped (right), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

(d) Immovable finger. Slightly deflexed. Outer surface smooth, except for continuation of longitudinal ridge on palm, latter strongly granular; inner surface hairy near cutting margin. Lower margin smooth; cutting margin without differentiated tooth but with granules along whole length (excepting spooned-tip).

(e) Dactylus. Curved. Outer surface smooth; inner surface densely hairy. Upper margin finely granular; cutting margin with large rectangular tooth in proximal third, distally with triangular granules.

Upper margins of pereopod meri with long hair.

Male abdomen. Lateral margins of fourth segment convex; of fifth segment slightly convex or straight; of sixth segment with convexity in morphologically anterior position; of seventh segment concave.

External maxilliped. Internal and external margins of ischium concave. Internal margin of merus convex; external margin straight.

First male pleopod slightly curved; with short terminal lobe, and hair on internal margin distally.

Dimensions and relative proportions

Carapace breadth (mm)	6.0	8.0	10.0
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.28	1.27	1.26
$\frac{\text{Length of chela}}{\text{Carapace breadth}}$	♂ 0.40	0.62	0.71
	♀ 0.33	0.35	0.37
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	4.61	4.57	4.35

Distribution. South Africa (Barnard, 1950); Madagascar (Crosnier, 1965); Red Sea (Nobili, 1906b); Indonesia (Tesch, 1918); Japan (Sakai, 1939); Australasia (A. Milne Edwards, 1873a; Miers, 1884; Balss, 1935a).

Comments. The relationships of this species to the genus *Euplax* has been dealt with by Barnes (1966b).

The relative decrease in breadth of the carapace and increase in breadth of the front, with increase in size, in the specimens examined is curious, representing a reversal of the usual trend seen in *Macrophthalmus*. Stress cannot, however, be placed on this feature, at the present time, in view of the small number of specimens examined.

2. *Macrophthalmus (Mopsocarcinus) punctulatus* Miers, 1884

(Plate 3(b), Fig. 10)

Synonymy

Macrophthalmus punctulatus Miers, 1884, p. 237, Plate 25, Fig. a; Tesch, 1915, p. 187; Snelling, 1959, p. 70.

Material examined. 38 ♂♂ (3.4–10.75 mm); 19 ♀♀ (4.1–8.75 mm).

Queensland (Moreton Bay); New South Wales (Trial Bay—Sydney).

Description. Front deflexed; not constricted between bases of ocular peduncles; with smooth margins; slightly bilobed anterior margin; median furrow; without granules on surface.

Upper orbital border curved and slightly backwardly sloping; margin smooth, without granules. Lower orbital border studded with large tubercular granules along whole length.

Two large and one small anterolateral teeth present. External orbital angle large, broad, pointed anteriorly, directed outwards and forwards (tip in adults on same transverse plane as base of front); anterior margin smooth, straight or slightly concave; outer margin straight, minutely serrated by small granules, two margins convergent posteriorly; separated from second lateral tooth by deep V-shaped incision. Second lateral tooth large,

broad, bluntly pointed anteriorly, directed outwards and slightly upwards; outer margin straight, or slightly convex, minutely serrated by small granules; separated from third lateral tooth by small incision. Third lateral tooth small but distinct, conical, directed outwards and upwards.

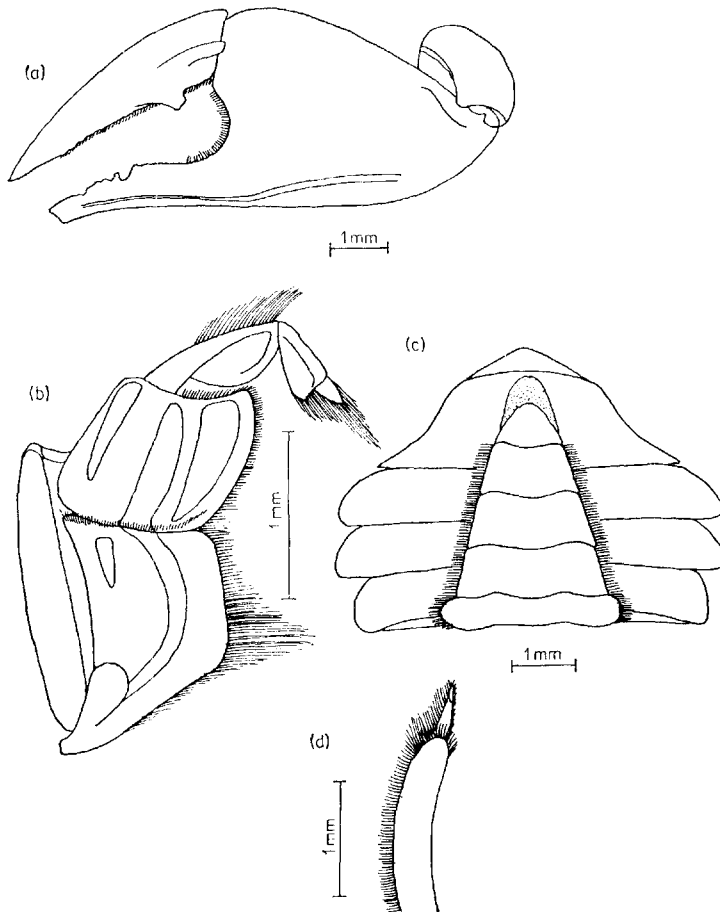


FIG. 10. *M. punctulatus*.

(a) Male chela (left), outer surface. (b) External maxilliped (right), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

Carapace surface completely without granules, shiny; with few scattered hairs, mainly on branchial regions; with indistinct furrows, excepting deep circumgastric; without rows of hairs on branchial regions. Greatest carapace breadth occurs across third lateral teeth or further posteriorly. Lateral margins with row of hairs.

Ocular peduncles subequal to, or less than, breadth of front, stout; cornea extending beyond base of external orbital angle but falls short of tip of latter.

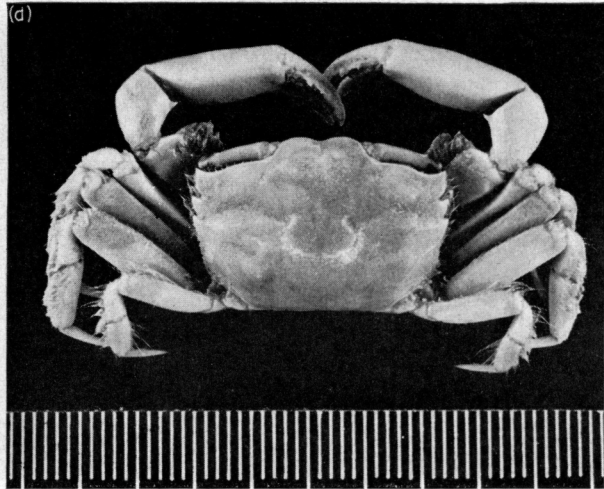
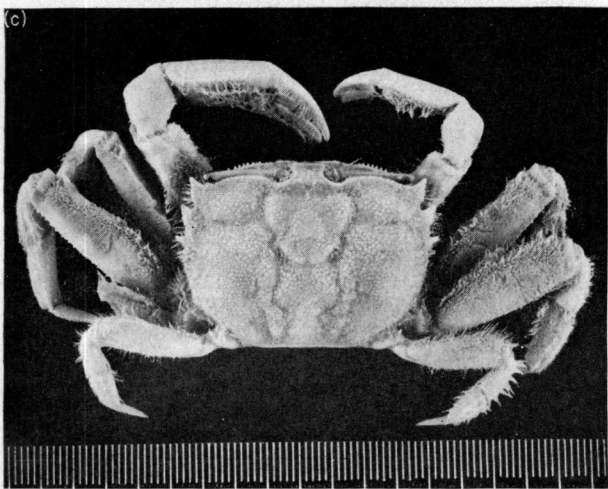
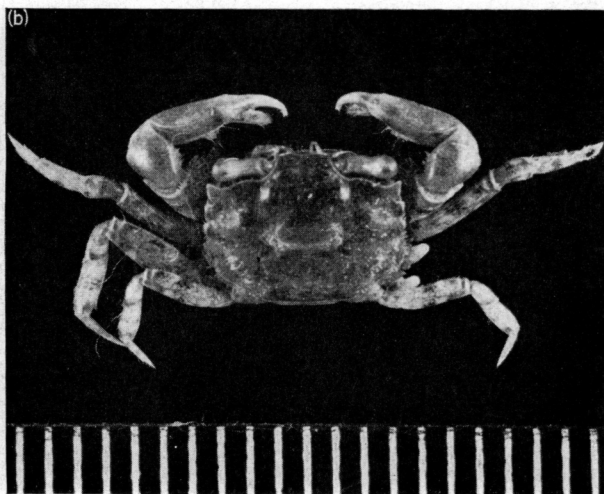
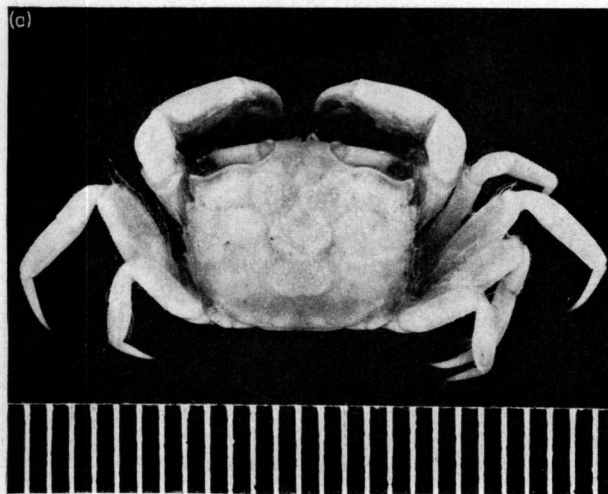


PLATE III. (a) *Macrophthalmus boscii* (A.M. No. P10409) ♂ dorsal surface.
 (b) *Macrophthalmus punctulatus* (A.M. No. P15154) ♂ dorsal surface.
 (c) *Macrophthalmus latreillei* (W.A.M. No. 648-65) ♂ dorsal surface.*
 (d) *Macrophthalmus hirtipes* (A.M. No. P9958) ♂ dorsal surface.

*Right chela atypical—partially regenerated.

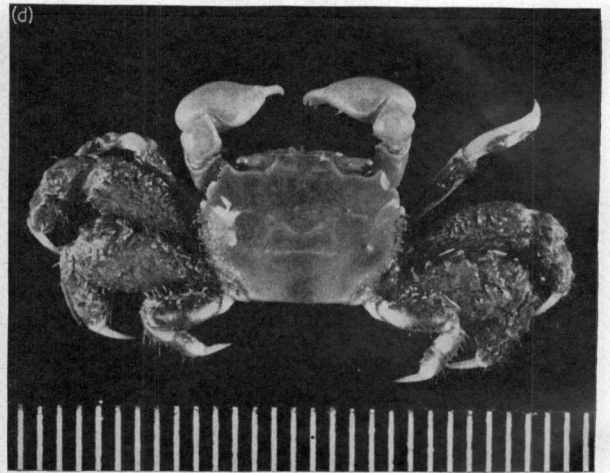
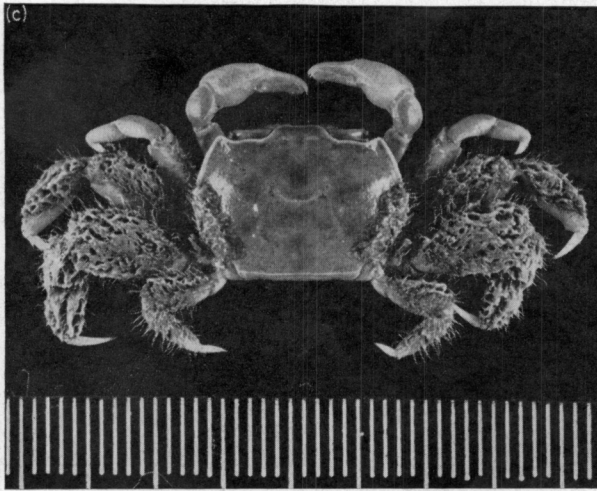
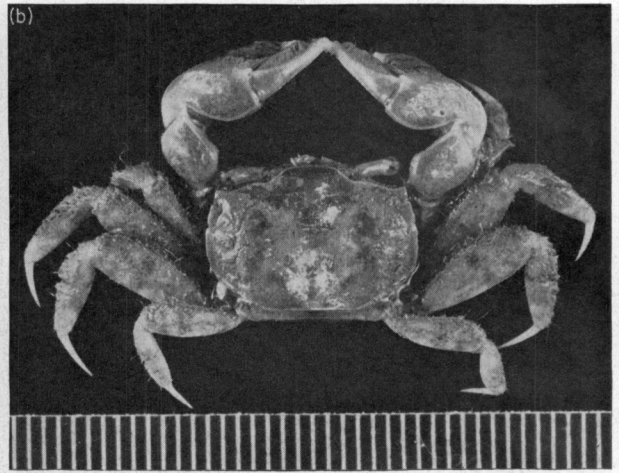
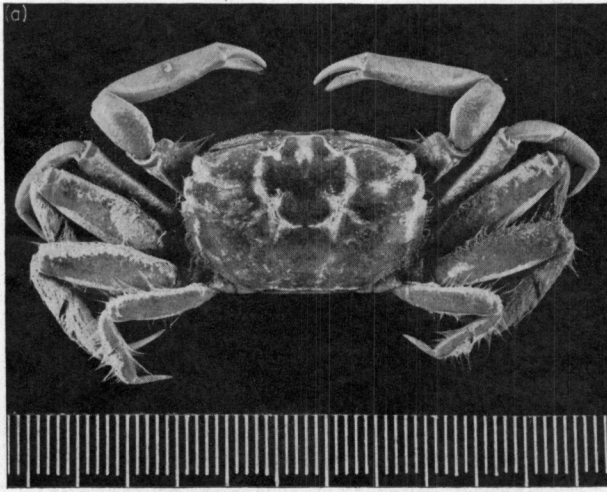


PLATE IV. (a) *Macrophthalmus latifrons* (A.M. No. P7266) ♂ dorsal surface.
 (b) *Australoplax tridentata* (Z.D.U.Q.) ♂ dorsal surface.
 (c) *Cleistostoma wardi* (A.M. No. P15161) ♂ dorsal surface.
 (d) *Paracleistostoma mneilli* (A.M. No. P12907) ♂ dorsal surface.

Male cheliped. (a) Merus. Completely without granules; inner surface densely hairy.

(b) Carpus. Without granules, and with very few hairs.

(c) Palm. Inflated, large, with length slightly exceeding breadth. Upper and lower margins smooth. Outer surface without granules, except on slightly raised longitudinal ridge, close to and subparallel with lower margin; inner surface without granules, with distally dense mat of hair (continuous with those of immovable finger and dactylus).

(d) Immovable finger. Undeformed. Outer surface smooth except for continuation of longitudinal ridge on palm; inner surface heavily hairy. Lower margin smooth; cutting margin with large, semi-circular, hair fringed concavity at base, long low crenulated tooth in proximal half, small granules in distal half, extreme tip granuleless and deflexed.

(e) Dactylus. Curved. Outer surface smooth; inner surface heavily hairy. Upper margin smooth; cutting margin with large rectangular tooth near base, with few granules distally.

Upper margins of pereopod meri fringed with hair, distal segments very hairy.

Male abdomen. Lateral margins of fourth, fifth and sixth segments straight.

External maxilliped. Internal margin of ischium straight or slightly convex; external margin concave. Internal margin of merus convex; external margin straight.

First male pleopod slightly curved; with well developed terminal lobe, and hair on extreme distal portion of internal margin.

Dimensions and relative proportions

Carapace breadth (mm)	3.5	5.0	7.0	9.0	10.5
Carapace breadth	1.27	1.31	1.32	1.33	1.34
Carapace length					
Length of chela	♂ 0.46	0.60	0.74	0.84	0.90
Carapace breadth	♀ —	0.43	0.43	0.43	—
Carapace breadth	3.60	3.80	3.85	3.91	3.92
Breadth of front					

Distribution. Eastern Australia (Miers, 1884; Snelling, 1959).

Comments. *M. punctulatus* possesses a large number of features usually associated with juveniles, and in particular with juveniles of *M. boscii*, e.g. the lack of carapace granulation and the relatively poor development of the granulation and the longitudinal ridge of the male cheliped. The possibility that this species has been founded on juvenile specimens of another species is however negated by the size and development of the male chelae, which are larger in *M. punctulatus* than in identical carapace-sized specimens of *M. boscii*, the only known Australian species closely related to *M. punctulatus*. However the juvenile character of this species suggests the possibility of its having evolved in Australia from *M. boscii*, or a species not too different from *M. boscii*, by neoteny.

(d) *Subgenus Venitus*

Contains only one Australasian species, *M. latreillei*.

1. *Macrophthalmus (Venitus) latreillei* (Desmarest, 1822)

(Plate 3(c), Fig. 11)

Synonymy

Gonoplax latreillei Desmarest, 1822, p. 99, Plate 9, Figs 1 & 4.

Macrophthalmus latreillei: H. Milne Edwards, 1837, p. 66; A. Milne Edwards, 1865, p. 193; 1873a, p. 278, Plate 13, Fig. 3; Ortmann, 1894a, p. 747; Laurie, 1906, p. 427, Plate 2, Fig. 12; Rathbun, 1910b, p. 306; Tesch, 1915, p. 181; 1918, p. 59; Kemp, 1919, p. 385; Rathbun, 1924, p. 13; Tweedie, 1937, p. 163; Sakai, 1939, p. 626; Suvatti, 1950, p. 154; Barnard, 1955, p. 22; Chhapgar, 1957, p. 513, Plate 14; Crosnier, 1965, p. 131, Figs 239–242; Barnes, 1966a, p. 46.

Macrophthalmus desmaresti Lucas, 1839, p. 567, Plate 20.

Macrophthalmus serratus Adams & White, 1848, p. 51; H. Milne Edwards, 1852, p. 159; Stimpson, 1858, p. 97; Miers, 1886, p. 250, Plate 20, Fig. 1; Stimpson, 1907, p. 96, Plate 13, Fig. 3; Rathbun, 1910a, p. 323; Etheridge & McCulloch, 1916, p. 11, Plate 4.

Macrophthalmus polleni Hoffmann, 1874, p. 19, Plate 4, Figs 27–30; de Man, 1879, p. 66; Lenz & Richters, 1881, p. 4, Figs 24–27.

Macrophthalmus laniger Ortmann, 1894a, p. 746, Plate 23, Fig. 15.

Macrophthalmus granulosus de Man, 1904, pp. 266–274, Plate 10, Fig. 5; Ward, 1941, p. 3.

Macrophthalmus affinis: Haswell, 1882a, p. 88; *nec* Guérin, 1839a, p. 172.

Macrophthalmus depressus: Grant & McCulloch, 1906, p. 21; Etheridge & McCulloch, 1916, p. 13, Plate 6; *nec* Rüppell, 1830, p. 19.

Material examined. 34 ♂♂ (6.2–59.5 mm); 17 ♀♀ (13.5–40.0 mm).

Western Australia (Freemantle & Broome); Queensland (Townsville—Bundaberg); New Guinea (Kaimare & Daru Island).

Description. Front deflexed; markedly constricted between bases of ocular peduncles; with small granules along margins; granular surface; bilobed anterior margin; median furrow.

Upper orbital border slightly curved, transverse; margin studded with small granules. Lower orbital border serrated by tubercular granules.

Three well-defined, large, and one small, anterolateral teeth present, anterior three teeth with granular margins. External orbital angle large, sharply pointed, directed outwards and forwards (tip in some transverse plane as forward margin of upper orbital border); outer margin convex; separated from second lateral tooth by wide incision. Second lateral tooth of equal size, or slightly larger than former tooth, sharply pointed, directed outwards and slightly forwards, projecting beyond external orbital angle; separated from third lateral tooth by wide incision. Third lateral tooth large, sharply pointed, directed outwards, projecting beyond two preceding teeth; separated from fourth lateral tooth by shallow incision. Fourth lateral tooth small, very small or absent.

Carapace surface heavily granular, with large rounded granules; with variable amount of hair (some specimens completely covered with hair, others with hair only in carapace furrows and scattered on branchial regions); with deep, conspicuous carapace furrows, especially circumgastric; without granular clumps but in some specimens rows of granules on branchial regions (some specimens completely without granular rows, others of identical size with two longitudinal rows, subparallel to each other and to posterolateral carapace margins, on branchial region). Greatest carapace breadth occurs across third lateral teeth, behind which lateral margins subparallel or slightly convergent. Lateral margins with small granules and row of hairs.

Ocular peduncles long and narrow; cornea extending to base of external orbital angles.

Male cheliped. (a) Merus. Inner and upper margins with long hair, upper margin with row of granules; outer margin granular. Inner and outer surfaces heavily hairy; lower surface heavily granular.

(b) Carpus. Upper and lower margins and inner surface heavily granular, inner surface hairy; outer surface granular in upper portion, hairy over lower portion.

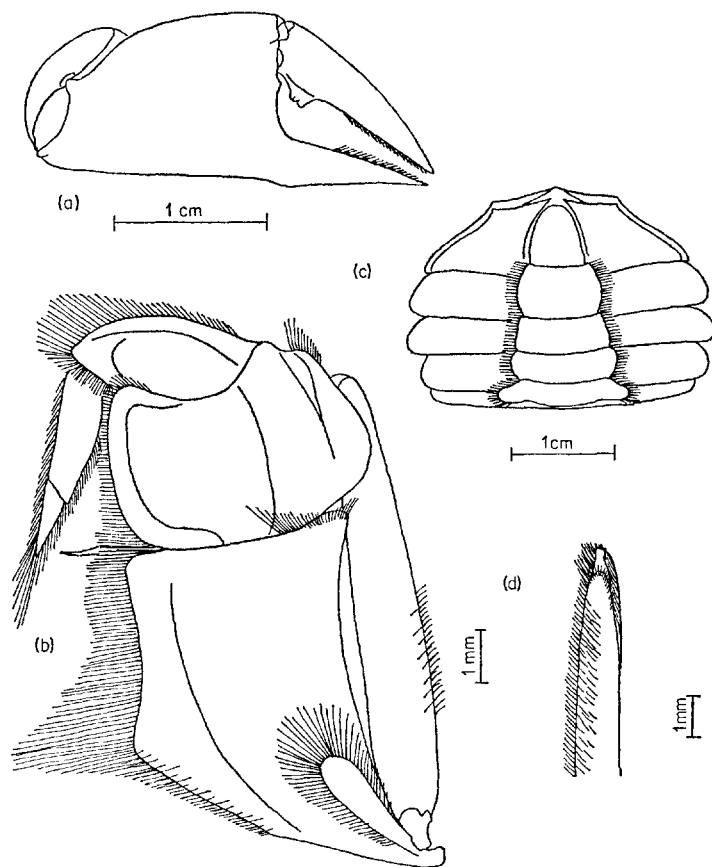


FIG. 11. *M. latreillei*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

(c) Palm. Upper margin with row of large granules; lower margin with scattered granules. Outer surface smooth to touch, without longitudinal ridge near lower margin; inner surface heavily hairy in upper and distal portions, heavily granular in lower and proximal portions.

(d) Immovable finger. Undeformed, except in very large specimens, in which slightly or moderately deflexed. Outer surface smooth; inner surface heavily hairy. Lower margin smooth; cutting margin without differentiated tooth, except in very large specimens, with row of equisized granules externally and with shorter row of granules,

internally and distally, in very large specimens small low crenulated tooth in centre of cutting margin.

(e) Dactylus. Curved. Outer surface smooth; inner surface heavily hairy. Upper margin with row of medium-sized granules along whole length; cutting margin with large, quadrangular, crenulated tooth near base, distally with small number of widely spaced cylindrical granules.

Pereiopod meri heavily granular and with variable hair; upper margins with large granules and large terminal curved spines, often with dense hair; lower and posterior margins with large granules, or in large specimens with very large, cylindrical, equally-spaced tubercles; lower surfaces granular; upper surfaces heavily hairy. Carpi hairy, with in large specimens longitudinal rows of large tubercles. Rows continued, in large specimens, along propodi. Dactyli lanceolate.

Male abdomen. Lateral margins of fourth and sixth segments convex; of fifth segment straight.

External maxilliped. Internal and external margins of ischium concave. Merus wide; internal margin convex; external margin with posteroexternal convexity merging into anteroexternal convexity.

First male pleopod straight; with moderately developed terminal lobe, and with hair on internal margin only at extreme distal end; sternal surface haired.

Dimensions and relative proportions

Carapace breadth (mm)	10.0	15.0	20.0	25.0	30.0	35.0	40.0	59.5 (1 specimen)
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.25	1.27	1.31	1.35	1.36	1.38	1.40	1.51
$\frac{\text{Length of chela}}{\text{Carapace breadth}}$	♂ 0.37	0.39	0.43	0.48	0.54	0.63	0.71	0.81
	♀ —	—	—	0.41	0.41	0.40	0.40	—
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	6.89	7.50	7.84	8.06	8.15	8.20	8.20	9.15

Distribution. South Africa (Barnard, 1955); Madagascar (Crosnier, 1965); India (Kemp, 1919); Malaya (Tweedie, 1937); Gulf of Siam (Rathbun, 1910a); Philippines (Laurie, 1906); Japan (Sakai, 1939); Australia (Rathbun, 1924); New Caledonia (A. Milne Edwards, 1873a).

Comments. This large species has been the subject of much taxonomic confusion as can be seen by reference to the synonymy. This has, to a large degree, been caused by the variability displayed by the species with respect to age (or more correctly size) and geographical distribution, particularly in the form of the chelae, the carapace surface and the anterolateral teeth.

Tesch (1915) was of the opinion that this species was remarkable for the small size of its chelae in the male. Two authors (A. Milne Edwards, 1873a and Miers, 1886), however, had both previously figured specimens in which the relative size of the chela could not be termed remarkably small, and Laurie (1906) had figured a series of male chelae, showing differences in size and shape relative to the overall size of the animal, the differences shown being of similar character to those seen in other species. The confusion can only have been caused by the large size attained by *M. latreillei*, hence a relatively small

specimen (relative to other specimens of the same species) with 'juvenile chelae' is still relatively large compared with other species of the genus, and thus without a knowledge of the total size range of the species the chelae would appear to be small.

Juveniles of this species possess blunt, subrectangular anterolateral teeth (see Crosnier, 1965, Fig. 242), these teeth increasing in size and pointedness with increase in total size (see Crosnier, 1965, Fig. 241). The degree of carapace hairiness also varies with total size and geographical location (see following); and *M. latreillei* is similar to other species of the genus in showing a variation in many relative proportions with increase in size (see 'Relative proportions').

Even though working on specimens of this species from a small area of its total range, geographical variations have become apparent. Specimens from New Guinea possessed hairless carapace surfaces, well developed tubercles on the lower margins of the pereopod meri, and relatively long dactyli and immovable fingers, the latter deflexed at the tip, on the male chelae. Specimens from St. Lawrence, Queensland, possessed extensive carapace hair, but lacked tubercles on the lower margins of the pereopod meri. The largest specimen seen, from Bundaberg, Queensland, lacked a hairy covering to the carapace, possessed well-developed pereopod tuberculation, and possessed rows of granules on the branchial region—lacked by the two previous groups of specimens. Specimens probably from Fiji, lacked the pereopod tuberculation and possessed relatively short dactyli and immovable fingers on the male chelae. Specimens from Townsville, Queensland possessed very extensive carapace hair.

Thus various authors (Adams & White, 1848; Hoffmann, 1874; Ortman, 1894a) described as new species different stages in the attainment of the 'fully adult characters' and local variations of the one species. The species of Desmarest (1822), Lucas (1839) and de Man (1904) were described from subfossil material, (the species occurring plentifully as a subfossil).

Considering the large size of this species and its probably wide range in Australia, it is not a little surprising that only one record, that of Rathbun (1924), of the occurrence of this species, or a species directly synonymous with it, in Australia, exists. Haswell (1882a), however, recorded a species which he doubtfully assigned to *M. affinis* (a synonym of *M. depressus*) from Holborn Island, Queensland. Later Grant & McCulloch (1906) recorded a species, which they stated agreed with that identified by Haswell as *M. affinis*, from Port Curtis, Queensland, and thus assigned it to *M. depressus*. In 1916, Etheridge & McCulloch, recorded a species, which 'did not differ' from those recorded by Haswell and Grant & McCulloch, as a subfossil, and figured an example of a 'typical recent Australian specimen' of that species (which they termed *M. depressus*, following Grant & McCulloch). This figure (Plate 6) is a typical example, not of *M. depressus*, but of *M. latreillei*. Thus it would seem as if the species referred to by all the previous authors is in fact *M. latreillei*. The specimens identified by Haswell were located in the Australian Museum (with the registration number of P1537) and proved to be misidentified specimens of *M. latreillei*, but the precise specimens referred to by Grant & McCulloch and Etheridge & McCulloch could not be located with absolute certainty, although two specimens from Port Curtis, labelled *M. depressus* and identified by Grant & McCulloch (reg. no. G5979), and a specimen from near Freemantle, labelled *M. depressus* and identified by Etheridge & McCulloch (reg. no. P3678) were found to be *M. latreillei*. (Apart from the previous references, *M. depressus* has not been recorded from Australia.)

(c) *Subgenus Hemiplax*

Contains only one Australasian species, *M. hirtipes*.

1. *Macrophthalmus (Hemiplax) hirtipes* (Jacquinot, 1853)
(Plate 3(d), Fig. 12)

Synonymy

Cleistotoma (?) *hirtipes* Jacquinot, 1853, p. 69, Plate 6.

Metaplex hirtipes Heller, 1862, p. 521.

Hemiplax hirtipes: Heller, 1865, p. 40, Plate 4, Fig. 3; Miers, 1876, p. 34; Filhol, 1885, p. 365; Miers, 1886, p. 251; Chilton, 1909, p. 608; Tesch, 1918, p. 57; Kemp, 1919, p. 384; Chilton & Bennett, 1929, p. 759; Richardson, 1949, p. 36; Ralph & Yaldwyn, 1956, p. 74, Fig. 41; Bennett, 1964, p. 85.

Macrophthalmus hirtipes: Thompson, 1902, p. 462; 1913, p. 237.

Material examined. 22 ♂♂ (10.5–30.2 mm); 15 ♀♀ (9.25–29.25 mm).

New Zealand (Westport, Christchurch, Dunedin).

Description. Front deflexed; unconstricted between bases of ocular peduncles; with smooth margins; finely granular surface; bilobed anterior margin; deep, narrow, median furrow.

Upper orbital border curved, transverse; margin studded in large specimens with small granules. Lower orbital border studded with tubercular granules, slightly increasing in size towards external orbital angles.

Three well developed, pointed, anterolateral teeth present. External orbital angle large, broad, directed outwards and forwards; convex outer margin studded with medium sized granules; separated from second lateral tooth by wide U-shaped incision. Second lateral tooth large, conical, directed forwards and outwards, projecting slightly beyond external orbital angle; with slightly concave anterior margin and slightly convex outer margin, latter studded with medium sized granules; separated from third lateral tooth by wide U-shaped incision. Third lateral tooth only slightly smaller than preceding tooth; directed forwards and outwards, projecting slightly beyond former two teeth; anterior and outer margins straight, latter studded with large granules.

Carapace surface covered with fine granules, densest on hepatic regions; with distinct furrows; with transverse row of granules extending across anterior branchial region from level of third lateral tooth; with oblique row of granules extending from third lateral tooth to position above point of insertion of fourth pereopod, diverging posteriorly from posterolateral carapace margins; with short concave row extending transversely across posterior branchial region from termination of former row to directly above point of insertion of fourth pereopod. Greatest carapace breadth occurs between third lateral teeth, behind which lateral margins subparallel. Anterolateral margins with fringe of hair; posterolateral margins studded with rounded granules.

Ocular peduncles short and stout, length of peduncle being less than breadth of front at narrowest point; cornea extending to base of external orbital angle.

Male cheliped. (a) Merus. Inner margin with rounded granules beneath row of long coarse hairs; outer margin with scattered granules distally; upper margin with row of small pointed granules, and fringe of long hair proximally. Inner, outer and lower surfaces with small, very sparse granules; hair only near inner and carpal margins on inner surface distally.

(b) Carpus. Upper margin with large, triangular, pointed protuberance, just proximal to the midpoint; lower margin smooth. Outer surface without

granules, except for granular ridge running obliquely from meral joint to midpoint of upper margin; inner surface smooth.

(c) Palm. Elongate, hairless, and without granules visible to naked eye. Upper margin with row of small granules proximally, and with very small granules distally; lower margin with very small granules, continuous with those on inner and outer surfaces. Outer surface with very small granules, and with granular longitudinal carina near lower margin; inner surface with very small granules.

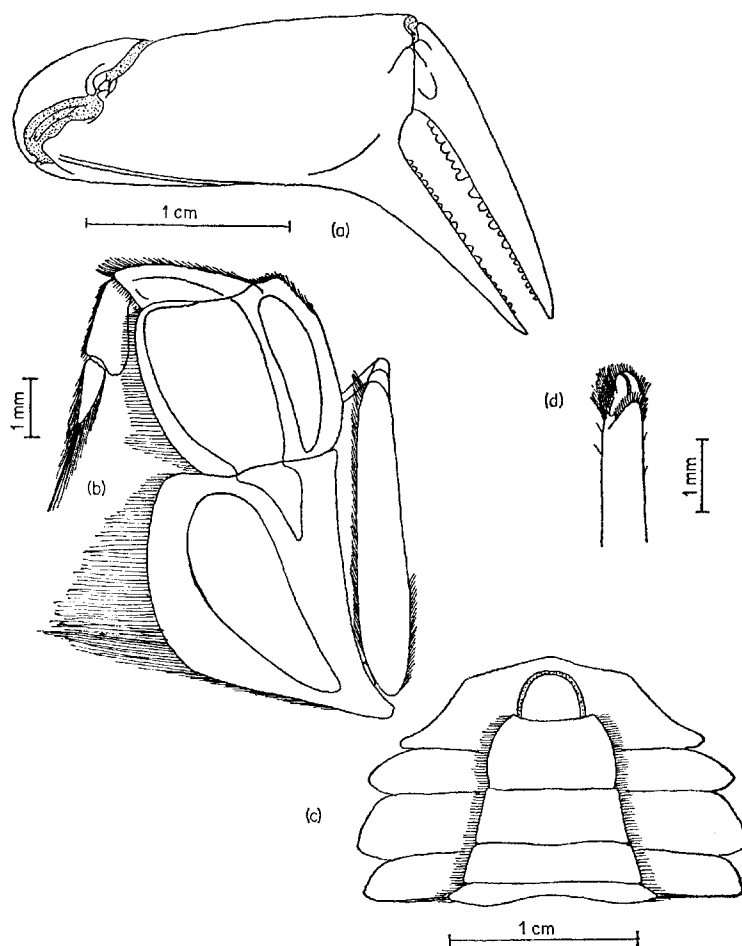


FIG. 12. *M. hirtipes*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

(d) Immovable finger. Markedly deflexed. Outer surface with microscopical granules, and continuation of carina near lower margin; inner surface with dense mat of hair near cutting margin, and microscopical granules near lower margin. Lower margin microscopically granular; cutting margin with row of large, pointed, conical granules along whole length, excluding extreme tip, without differentiated tooth.

(e) Dactylus. Curved. Outer surface with microscopical granules; inner surface with dense mat of hair. Upper margin with very small scattered granules; cutting margin with long, low, crenulated tooth near base, distally with granules as on cutting margin of immovable finger.

Pereiopod meri, except that of fourth pereiopod, almost completely without hair; upper margins with longitudinal rows of rounded granules and distinct spine distally; lower surfaces with small scattered granules.

Male abdomen. Lateral margins of fourth and fifth segments evenly convergent posteriorly; of sixth segment convex. Breadth of sixth segment markedly exceeding breadth of base of seventh segment.

External maxilliped. Merus and ischium of approximately equal breadth. Internal margin of ischium convex; external margin straight throughout most of its length. Merus subrectangular; internal and external margins convex; anterior margin with very shallow depression.

First male pleopod straight; with moderately developed terminal lobe; without heavy development of hair on internal or external margins of shaft.

Dimensions and relative proportions

Carapace breadth (mm)	10.0	15.0	20.0	25.0	30.0
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.41	1.42	1.43	1.44	1.46
$\frac{\text{Length of chela}}{\text{Carapace breadth}}$	♂ — ♀ 0.42	0.56	0.65	0.74	0.82
		0.43	0.44	0.44	—
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	3.38	3.43	3.45	3.46	3.47

Distribution. New Zealand (Bennett, 1964); Campbell Island (Filhol, 1885); Samoa (Jacquinot, 1853).

Comments. Several authors, including Chilton & Bennett (1929) and Bennett (1964), have previously tentatively synonymized the *Cleistotoma* (sic) (?) *hirtipes* of Jacquinot (1853) with the *Metaplex*, and later *Hemiplax*, *hirtipes* of Heller. Bennett, however, states that the two species have been synonymized mainly because of the coincidence of their specific names, and he regarded their grouping together into a single species as being highly provisional. Jacquinot, himself, was not sure of the generic affinities of his species, placing it provisionally in *Cleistostoma*, but recognizing its affinities with *Macrophthalmus*. Jacquinot's illustrations of *C.* (?) *hirtipes* (Plate 6, Figs 3, 3(c)) are identical with specimens of *M. hirtipes* from New Zealand examined by the author, (except in the form of the merus of the external maxilliped, which as figured by Jacquinot, has its length markedly exceeding its breadth, due to the position of the internal margin, which however seems likely to have been incorrectly drawn or caused by that part of the appendage being broken), and hence in this paper the two species are considered to be synonymous. No further Samoan material has been discovered.

Thompson (1902) considered '*Hemiplax hirtipes*' to consist of two species, *Hemiplax hirtipes* sensu strictu, and *Macrophthalmus hirtipes*, which, and only which, Thompson considered to be synonymous with Jacquinot's species, Heller's species being completely

distinct. Thompson later changed his mind and stated in correspondence with Chilton (quoted in Chilton & Bennett, 1929) that it was possible that '*Hemiplax hirtipes*' was the juvenile of the '*Macrophthalmus hirtipes*'. The differences between the two species (as they were originally considered by Thompson) were based on the size of the male chelae, the *H. hirtipes* of Heller possessing very small chelae, and the *M. hirtipes* of Jacquinot possessing large chelae. Since Heller (and Miers) saw only small specimens, Thompson's later opinion is consistent with the growth changes seen in the male chelae of other *Macrophthalmus* species.

(f) Subgenus ***Tasmanoplax***

Contains only one species, *M. latifrons*.

1. *Macrophthalmus (Tasmanoplax) latifrons* Haswell, 1882

(Plate 4(a), Fig. 13)

Synonymy

Macrophthalmus latifrons Haswell, 1882b, p. 549: 1882a, p. 90; Tesch, 1915, p. 189.

Microphthalmus (sic) latifrons: Fulton & Grant, 1906, p. 19.

Hemiplax latifrons: Etheridge & McCulloch, 1916, p. 13, Plates 4 & 6; Hale, 1927, p. 186, Fig. 187; Tweedie, 1941, p. 25, Fig. 10.

Material examined. 34 ♂♂ (8.25–29.3 mm); 21 ♀♀ (8.0–24.0 mm).

Victoria (Port Phillip); Tasmania (Orford—Margate).

Description. Front deflexed; slightly constricted between bases of ocular peduncles; with smooth margins; microscopically granular surface; arcuate anterior margin; median furrow.

Upper orbital border curved, transverse; margin studded with very small granules, appearing smooth to naked eye. Lower orbital border studded with large tubercular granules throughout whole length.

Two large and one small anterolateral teeth present, 'beaded' on the outer margins with small granules. External orbital angle large, pointed anteriorly, subrectangular, directed outwards and forwards; anterior margin concave, with granules continuous with those of upper orbital border; outer margin convex; separated from second lateral tooth by wide V-shaped incision. Second lateral tooth broad, blunt, rectangular, projecting beyond former tooth, with posteriorly divergent outer margins; separated from third lateral tooth by distinct V-shaped incision. Third lateral tooth small, pointed, directed outwards, projecting beyond two preceding teeth.

Carapace surface covered with very small, closely set, granules; with deep, distinct, furrows; with short, poorly defined, transverse granular row extending across anterior branchial region from level of third lateral tooth; with two short granular rows, in anterior/posterior position in same longitudinal plane, in position of outer longitudinal branchial row of other species (e.g. *M. japonicus*); with short granular row above insertion of fourth pereopod. Greatest carapace breadth occurs between third lateral teeth, behind which lateral margins parallel. Lateral margins with small granules and row of fine hairs.

Ocular peduncles long and narrow; cornea extending to base of external orbital angle.

Male cheliped. (a) Merus. Inner margin with row of granules distally and with hair along whole length; upper margin with few long hairs centrally and with row of granules centrally and distally; outer margin hairless, with row of widely spaced, rounded granules

along whole length. Outer surface and lower surface hairless, with few scattered small granules; inner surface without granules, with convex row of hairs along inner and distal margins.

(b) Carpus. Elongate, hairless. Upper and lower margins with scattered granules. Outer surface with very small, scattered, granules; inner surface with few granules near joint with palm.

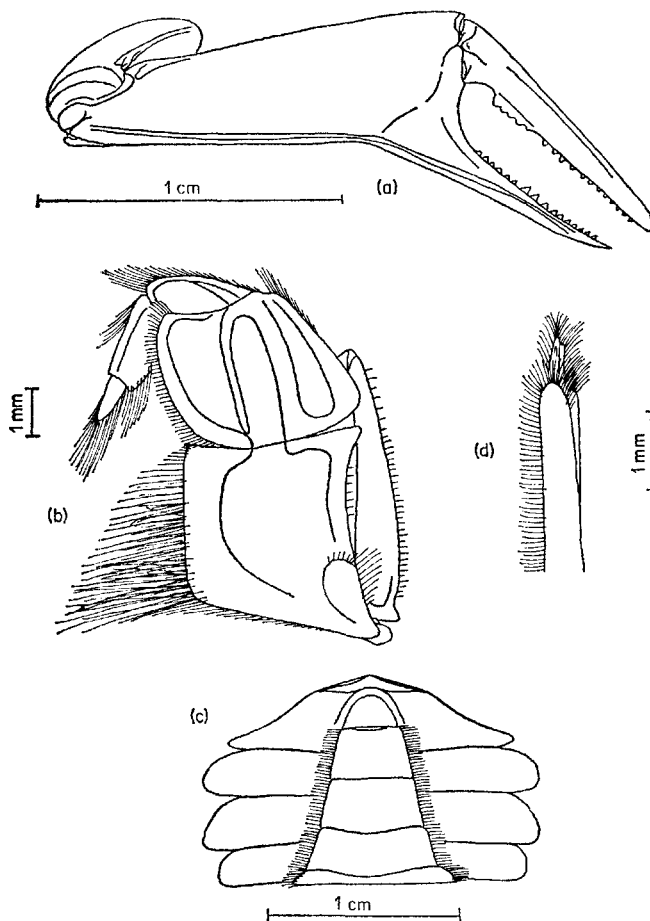


FIG. 13. *M. latifrons*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

(c) Palm. Elongate, hairless. Upper and lower margins with concentrations of the scattered granules on inner and outer surfaces. Inner and outer surfaces covered with very small, scattered granules, densest on inner surface; outer surface with slightly raised ridge close to and subparallel with lower margin.

(d) Immovable finger. Markedly deflexed. Inner and outer surfaces and lower margin with small scattered granules; outer surface with continuation of longi-

tudinal ridge on palm. Cutting margin without distinct tooth, with longitudinal series of pointed granules.

(e) Dactylus. Straight. Inner and outer surfaces and upper margin with small scattered granules. Cutting margin with long, low, crenulated tooth near base, distally with pointed granules.

Pereiopod meri with granular upper margins and lower surfaces; upper margins hairy. Carpi and propodi of second and third pereiopods heavily felted.

Male abdomen. Lateral margins of fourth, fifth and sixth segments straight, and smoothly convergent to seventh segment. Sternum with small scattered granules.

External maxilliped. Internal margin of ischium straight; external margin concave. Internal margin of merus convex; external margin straight through much of its length; anterior margin with shallow depression.

First male pleopod straight or very slightly curved; with well developed terminal lobe; without hair on internal margin.

Dimensions and relative proportions

Carapace breadth (mm)	10.0	15.0	20.0	25.0
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.54	1.56	1.57	1.57
$\frac{\text{Length of chela}}{\text{Carapace breadth}}$	♂ 0.41	0.58	0.76	0.87
	♀ 0.38	0.39	0.40	0.41
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	5.00	5.36	5.56	5.73

Distribution. South-east Australia (Fulton & Grant, 1906—Victoria; Hale, 1927—South Australia; Tweedie, 1941—Tasmania).

Comments. This species is the only ocypodid recorded by Hale (1927) from South Australia, and only species of the subfamily Macrophthalminae recorded from either Victoria or Tasmania.

II. The genus *Australoplax* Barnes, 1966

Australoplax Barnes, 1966b, pp. 371–372.

Type species: *A. tridentata* (A. Milne Edwards, 1873b).

Comments. This genus contains only one described species, *A. tridentata*, which is probably endemic to Australia.

1. *Australoplax tridentata* (A. Milne Edwards, 1873b)

(Plate 4(b), Fig. 14)

Synonymy

Cleistostoma tridentatum A. Milne Edwards, 1873b, p. 82.

Australoplax tridentata: Barnes, 1966b, pp. 372–374, Plate 24, Figs 1 & 2.

Chaenostoma tridentatum: de Man, 1896, pp. 93–95, Plate 3, Fig. 5 (not Fig. 4 as in text).

Euplax tridentata: McCulloch, 1913, p. 321; Tesch, 1918, p. 59; Rathbun, 1926, p. 177; Stephenson *et al.*, 1931, p. 42; Snelling, 1959, p. 70.

Metaplax hirsutimana Grant & McCulloch, 1906, p. 21, Plate 1, Fig. 3.

Material examined. 107 ♂♂ (2.7–15.3 mm); 66 ♀♀ (3.9–14.0 mm).

Queensland (Cooktown—New South Wales border); New South Wales (Queensland border—Sydney).

Description. Front broad, deflexed, unconstricted between bases of ocular peduncles; with smooth margins, lateral margins posteriorly divergent; smooth surface; obtusely pointed anterior margin; wide median furrow.

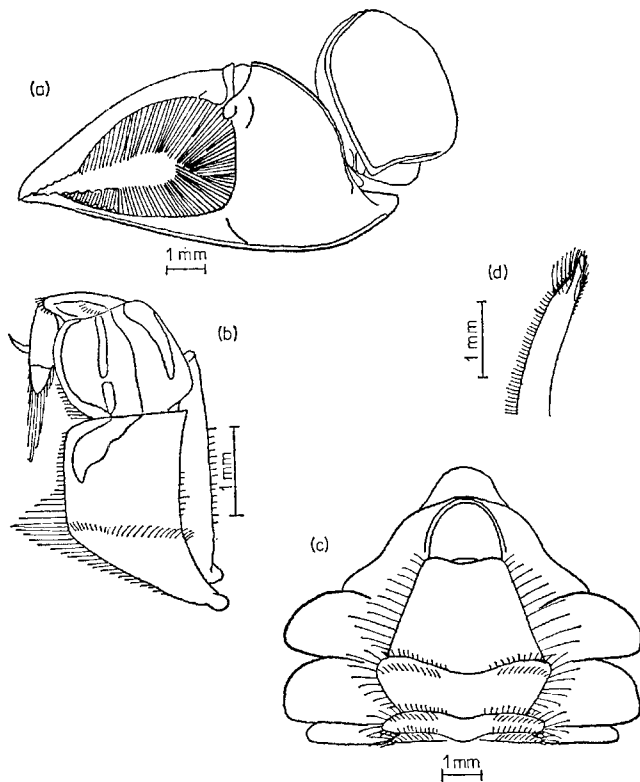


FIG. 14. *A. tridentata*.

(a) Male chela (left), outer surface. (b) External maxilliped, (left) outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (left), sternal surface.

Upper orbital border curved, backwardly sloping; margin without granules. Lower orbital border in males without granules, with small but marked concavity in central region; in females regularly studded with large tubercular granules.

Two large and one small anterolateral teeth present. External orbital angle large, rectangular, pointed anteriorly, directed outwards and forwards; with straight anterior margin; outer margin slightly convex, studded with a few very small granules; separated from second lateral tooth by small, but distinct, V-shaped incision. Second lateral tooth broad, rectangular, bluntly pointed anteriorly, directed outwards, projecting beyond former tooth; with straight, posteriorly divergent outer margins; separated from third lateral tooth by small incision. Third lateral tooth very small, pointed.

Carapace subquadrate. Surface smooth, without granules; with sparse, scattered, short hairs on branchial regions; with indistinct furrows, excepting circumgastric; with slightly raised epigastric, gastric, cardiac and intestinal regions. Greatest carapace breadth across bases of second pereopods. Lateral margins with row of short fine hairs.

Ocular peduncles short and stout; cornea extending almost to tip of external orbital angle.

Male cheliped. (a) Merus. Upper and outer margins with longitudinal series of small granules; inner margin with series of large tubercular granules along whole length, distal angle convex and with six large tubercles along crest. Surfaces without granules; inner surface, only, with scattered hairs.

(b) Carpus. Without hair or granules, except a few small granules on inner surface.

(c) Palm. Semi-globose. Upper and lower margins with longitudinal carinae, that of lower margin continuing along immovable finger. Outer and inner surfaces without granules; inner surface with mat of hair distally.

(d) Immobile finger. Inflexed. Inner and outer surfaces without granules, both with dense mats of hair near cutting margin. Cutting margin with longitudinal series of granules, completely obscured by hair, without differentiated tooth.

(e) Dactylus. Curved. Inner and outer surfaces without granules, both with dense mats of hair near cutting margin. Upper margin with longitudinal series of small granules; cutting margin with longitudinal series of granules, completely obscured by hair, without differentiated tooth.

Upper margins of pereopod meri, carpi, and propodi with mat of short brownish hairs and sparse longer black hairs.

Male abdomen broad. Lateral margins with long, sparse, black hair; of third segment convex; of fourth and fifth segments posteriorly divergent; of sixth segment posteriorly convergent. Sixth segment very large, seventh segment small.

External maxilliped. Merus subquadrate; internal margin convex; external margin straight; anterior margin with very shallow depression. Ischium with transverse/oblique row of hairs across base; internal and external margins straight.

First male pleopod curved; with well developed terminal lobe; with hair on internal margin distally.

Dimensions and relative proportions

Carapace breadth (mm)	5.0	7.5	10.0	12.5	15.0
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.33	1.39	1.39	1.40	1.42
$\frac{\text{Length of chela}}{\text{Carapace breadth}}$	♂ 0.56	0.66	0.75	0.81	0.88
	♀ 0.48	0.49	0.49	0.50	—
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	3.57	3.75	3.87	4.03	4.11

Distribution. Eastern Australia (Rathbun, 1926; Barnes, 1966b); Samoa (?), (A. Milne Edwards, 1873b).

Comments. The history of this species has been discussed by Barnes (1966b).

III. The genus *Cleistostoma* de Haan, 1835

Cleistostoma de Haan, 1835, p. 55; Tesch, 1918, pp. 61–62; Sakai, 1939, p. 631; Guinot & Crosnier, 1963, p. 607.

Type species: C. dilatatum (de Haan, 1835).

Comments. The genera *Cleistostoma* and *Paracleistostoma* are very closely related, being separated on only two characters—the degree of doming of the carapace, and the presence or absence of anterolateral projections on the front (Tesch, 1918; Sakai, 1939; Barnard, 1950). Guinot & Crosnier (1963) have shown that a complete series exists between animals with a domed carapace and without anterolateral ‘horns’ on the front (i.e. *Cleistostoma*) and animals with a flattened carapace and with well-developed ‘horns’ (i.e. *Paracleistostoma*). Guinot & Crosnier did not, however, synonymise the two genera, and this paper uncritically follows the status quo in treating the two groups as distinct genera.

Nine species have been described in the genus *Cleistostoma* of which two have since been transferred to other genera. Two species have been described from Australia, of which one is, in this paper, transferred to the genus *Paracleistostoma*. There then remains one species of this genus in Australasia.

1. *Cleistostoma wardi* Rathbun, 1926

(Plate 4(c), Fig. 15)

Synonymy

Cleistostoma wardi Rathbun, 1926, p. 178, Plate 14; Snelling, 1959, p. 70; Guinot & Crosnier, 1963, p. 607.

Material examined. 44 ♂♂ (10.25–18.6 mm); 21 ♀♀ (8.5–17.0 mm).

Queensland (Cairns—Moreton Bay).

Description. Front broad, deflexed, unconstricted between bases of ocular peduncles; with smooth margins, lateral margins posteriorly divergent; smooth surface; arcuate anterior margin; wide median furrow; without well developed anterolateral ‘horns’.

Upper orbital border slightly curved, transverse; margin without granules; external orbital angle directed forwards and outwards. Lower orbital border with large, widely spaced, tubercles on proximal two-thirds, and very small, closely set, granules and hairs on distal third. Ocular peduncle separated from lower orbital border by inwardly projecting shelf.

Epistome trilobate; central region with long, sharply pointed, projection.

Carapace domed; without anterolateral teeth; without granules on surface; with dense mats of hair on posterolateral branchial regions, mat consisting of large number of short, fine, soft hairs and sparse long, stiff, hairs; with indistinct furrows, excepting circumgastric; well marked epigastric ridges; depressed hepatic regions; with finely milled ridge close to and parallel with posterior carapace margin. Greatest carapace breadth occurs just anterior of the branchial hair (i.e. two-fifths of the carapace length from external orbital angle). Lateral margins arcuate, finely milled by small, closely set, granules.

Ocular peduncles short and stout (shorter than breadth of front).

Male cheliped. (a) Merus. Margins with longitudinal rows of medium sized granules and sparse hairs. Surfaces without granules, hairless excepting longitudinal row of hairs on inner surface close to and parallel with inner margin.

(b) Carpus. Globose. Longitudinal series of small granules along upper margin; lower margin smooth. Outer surface without granules; inner surface with row of small granules and hairs close to and parallel with upper margin.

(c) Palm. Large and globose. Upper margin with longitudinal row of small granules; lower margin without granules. Inner and outer surfaces without granules, and without hairs except for small row of hairs on inner surface close to and subparallel with upper margin.

(d) Immovable finger. Undeformed; broad, but of small height. Lower margin and inner and outer surfaces without granules or hairs. Cutting margin with small concavity at base, without differentiated tooth, with three longitudinal rows of small granules.

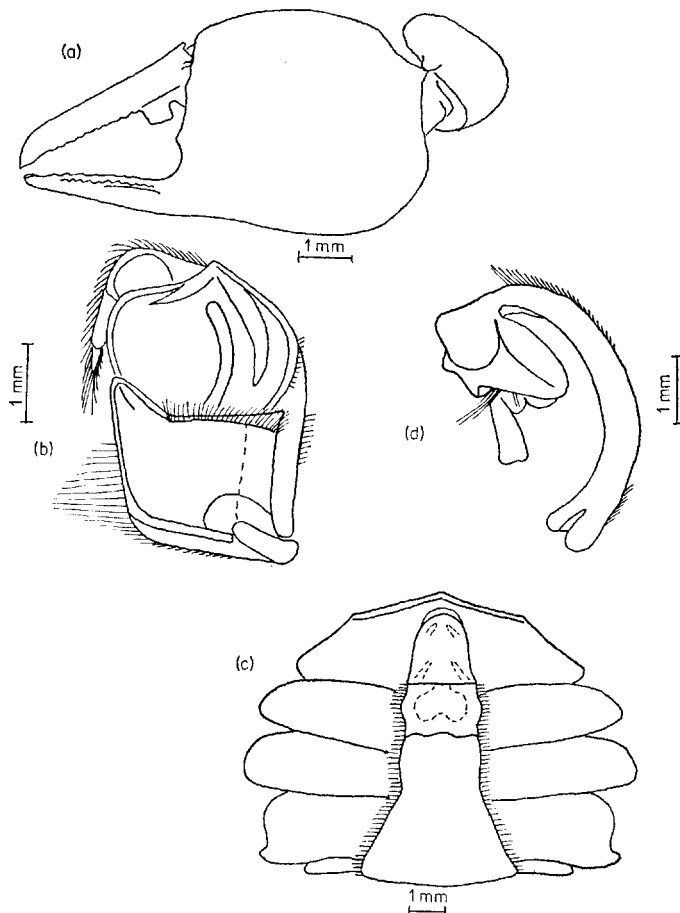


FIG. 15. *C. wardi*.

(a) Male chela (left), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (right), sternal surface.

(e) Dactylus. Broad, straight. Inner and outer surfaces without granules or hairs. Upper margin with longitudinal row of small granules; cutting margin with large, cylindrical, crenulated tooth near base, longitudinal series of granules distally.

Second, third and fourth pereopods with dense hairy covering (hair of same two types as present on branchial region) on upper margins and upper surfaces of meri, carpi and

propodi. First pereiopod with hair only in longitudinal row along upper margin of merus.

Male abdomen with second to fifth segments (inclusive) fused, a partial suture remaining between second and third segments. Lateral margins of sixth segment convex.

Merus of external maxilliped, markedly larger than ischium, subcircular; with shallow depression on anterior margin. Ischium with pronounced triangular protruberance at anterointernal angle; with row of hairs along suture with merus; with straight internal and external margins.

First male pleopod recurved. Distal portion swollen; with terminal tuft of hair and long terminal lobe.

Dimensions and relative proportions

Carapace breadth (mm)	10.0	12.5	15.0	17.5
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.38	1.43	1.43	1.43
$\frac{\text{Length of chela}}{\text{Carapace breadth}}$	♂ 0.33	0.38	0.47	0.58
	♀ 0.31	0.31	0.31	---
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	4.55	4.70	4.78	4.80

Distribution. Moreton Bay, Queensland (Rathbun, 1926; Snelling, 1959).

Comments. The range of this species, previously known only from Moreton Bay, Queensland, has now been extended up the Queensland coast to Cairns (approximately 1200 miles), but is still unknown outside of that state.

IV. The genus *Paracleistostoma* de Man, 1895

Paracleistostoma de Man, 1895, pp. 581–590: 1896, p. 90; Tesch, 1918, p. 63; Tweedie, 1937, pp. 157–159; Guinot & Crosnier, 1963, pp. 608–609.

Type species: *P. depressum* de Man, 1895.

Comments. Nine species have been described in this genus, a tenth is here added by the transference of a species from *Cleistostoma*, this species then being the only Australasian species of this genus (see also comments on the genus *Cleistostoma*).

1. *Paracleistostoma mcneilli* (Ward, 1933) **comb. n.**

(Plate 4(d), Fig. 16).

Synonymy

Cleistostoma mcneilli Ward, 1933, p. 390, Plate 21, Fig. 1; Snelling, 1959, p. 70; Guinot & Crosnier, 1963, p. 607.

Material examined. 34 ♂♂ (3.5–10.5 mm); 18 ♀♀ (4.6–10.3 mm).

Queensland (Port Curtis—Moreton Bay).

Description. Front broad, deflexed, unconstricted between bases of ocular peduncles; with smooth margins; smooth surface; wide median furrow; slightly pointed anterior margin, with well-developed anterolateral ‘horns’.

Upper orbital border curved, transverse; margin with ‘beading’ of small granules. Lower orbital border with small granules along entire length. Ocular peduncle separated from lower orbital border by inwardly projecting shelf.

Epistome trilobate; central lobe sharply pointed.

Carapace depressed; without granules on surface (except on well defined granular ridges); without surface hair; with indistinct furrows, excepting circumgastric; with prominent epigastric ridges; raised central cardiac, intestinal and branchial regions; with three lobular, tooth-like, anterolateral projections. External orbital angle large, pointed, directed forwards and outwards; with concave anterior margin, convex outer margin.

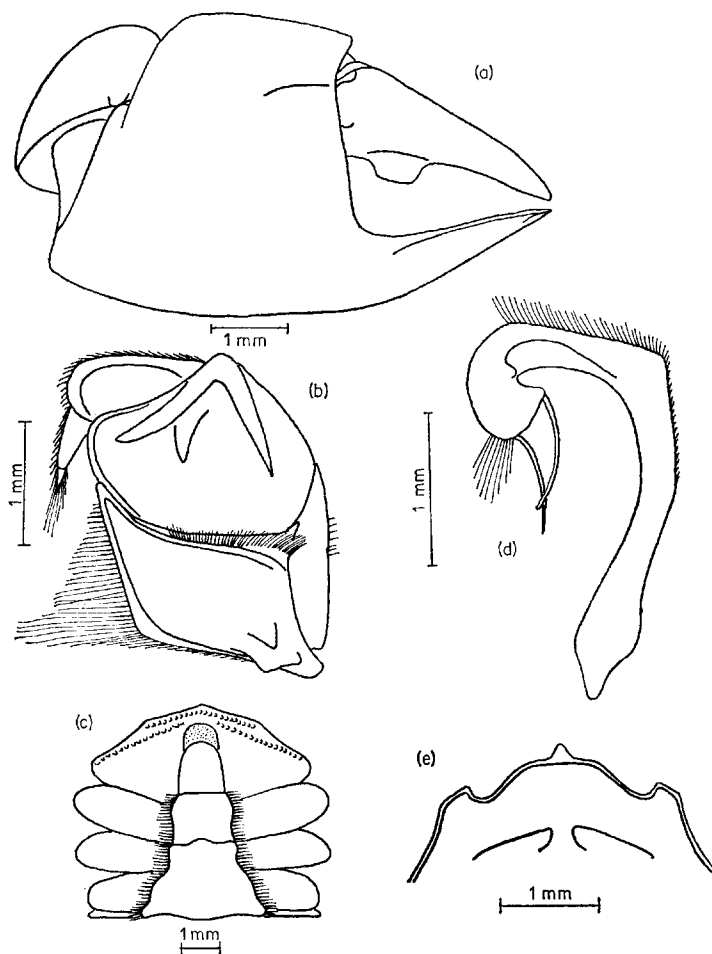


FIG. 16. *P. mcneilli*.

(a) Male chela (right), outer surface. (b) External maxilliped (left), outer surface. (c) Male abdomen and sternum. (d) 1st male pleopod (right), sternal surface. (e) Front.

Second lateral tooth small, broad-based, directed outwards, upwards and slightly forwards, projecting beyond former tooth. Third lateral tooth similar in size and shape to second lateral tooth, but projecting beyond latter. Cardiac region with well defined transverse ridge; faint diagonal ridge extends from end of cardiac ridge to third lateral tooth; granular ridge, running subparallel to posterolateral carapace margin, extends from

base of third lateral tooth to position above point of insertion of fourth pereopod, where it joins a transverse granular ridge, running close to and parallel with posterior carapace margin. Greatest carapace breadth occurs across third lateral teeth. Lateral margins arcuate, 'beaded' with small granules.

Ocular peduncles short and stout (shorter than breadth of front).

Male cheliped. (a) Merus. Upper and inner margins evenly studded with large granules throughout length; outer margin with large tubercles, in greatest concentrations proximally and distally. Surfaces without granules or hairs.

(b) Carpus. Smooth, without granules, with hairs only on upper margin.

(c) Palm. Large and globose, without granules or hairs.

(d) Immovable finger. Inflexed upwards. Surfaces and lower margin without granules; cutting margin with few, small, isolated granules, without differentiated tooth.

(e) Dactylus. Curved. Surfaces and upper margin without granules; cutting margin with large quadrangular tooth near base, distally with a few, very small, granules or smooth.

Meri of all four pereopods, and carpi and propodi of all except first pereopod, covered on all surfaces with mat of thick brownish hair. Carpus and propodus of first pereopod hairless.

Male abdomen with second to fifth segments (inclusive) fused, fused mass with highly sinuous lateral margins. Lateral margins of sixth segment with bulge in morphologically posterior position. Seventh segment elongate.

Merus of external maxilliped, markedly larger than ischium, subcircular; with shallow depression on anterior margin. Ischium with pronounced triangular protruberance at anterointernal angle; with row of hairs near suture with merus; with straight internal margin; concave external margin.

First male pleopod recurved. Distal portion swollen; with two long terminal filaments; with clump of hair distally.

Dimensions and relative proportions

Carapace breadth (mm)	5.0	7.5	10.0
Carapace breadth			
Carapace length	1.25	1.32	1.34
Length of chela	♂ —	0.37	0.59
Carapace breadth	♀ 0.25	0.28	0.29
Carapace breadth			
Breadth of front	3.70	3.80	3.81

Distribution. Southern Queensland (Ward, 1933; Snelling, 1959).

Comments. Guinot & Crosnier (1963) suggested the transference of this species (and also *Paracleistostoma japonicum* Sakai, 1934) from their respective genera to the genus *Camptandrium* on account of the three anterolateral teeth present in both species. All the species of *Camptandrium* possess anterolateral teeth, but one or more species in each of the genera *Cleistostoma*, *Paracleistostoma* and *Tylodiplax* also possess anterolateral protruberances in varying degrees of definition, and hence the mere presence of anterolateral teeth would

not seem sufficient to transfer a species to *Camptandrium*. The external maxilliped, and particularly the merus of that appendage, appears to have a characteristic form in the genera *Camptandrium* and *Tylodioplax* (see Rathbun, 1909, p. 109; Kemp, 1915, Fig. 14; Guinot & Crosnier, 1963, Fig. 6, etc.) and a different, but equally characteristic, form in the genera *Cleistostoma* and *Paracleistostoma* (see Tesch, 1918, Plate 3, Fig. 2(c); Rathbun, 1926, p. 178; Tweedie, 1937, Figs 5(b), 6(b), etc.). The external maxilliped of the species under discussion shows clear relationships with that of the latter two genera (cf. Figs 15(b), 16(b) and fewer with *Camptandrium* (and *Tylodioplax*). The chelae and pereopods also show affinities with *Cleistostoma* and *Paracleistostoma*, rather than with the former genera. Thus the author must disagree with Guinot & Crosnier and suggest affinities of this species with *Cleistostoma* and *Paracleistostoma*. Within these two genera, the characters of the carapace and front of this species place it in the genus *Paracleistostoma* (see comments on the genus *Cleistostoma*).

V. The genus *Leipocten* Kemp, 1915

Leipocten Kemp, 1915, pp. 244–247, Plate 12, Figs 16–20; Balss, 1935b, p. 47; Tweedie, 1937, p. 162.

Type species: L. sordidulum Kemp, 1915.

Comments. Kemp (1915), in describing the genus, placed it in the Xanthidae, regarding it either as constituting a new subfamily, or as an aberrant member of the Eriphiinae Alcock, 1898. Balss (1935b) suggested the removal of the genus from the Xanthidae and its inclusion within the Macrophthalminae (Ocypodidae). Tweedie (1937) further suggested that, within the latter subfamily, the affinities of *Leipocten* were 'with that section of the subfamily which includes the genera *Paracleistostoma* and *Camptandrium* rather than with the genus *Macrophthalmus*' (p. 162), basing his statement on the structure of the first male pleopod. The author is in complete agreement with Balss and Tweedie regarding the affinities of this genus; Tweedie's opinion being reinforced by the structure of the external maxilliped, the male abdomen, the chelae and the carapace.

The genus contains only one described species, *L. sordidulum*.

1. *Leipocten sordidulum* Kemp, 1915

Synonymy

Leipocten sordidulum Kemp, 1915, pp. 244–247, Plate 12, Figs 16–20; Balss, 1935b, p. 47; Tweedie, 1937, p. 162, Fig. 7; Sakai, 1939, p. 635, Fig. 105; Snelling, 1959, p. 70.

Material examined. 6 ♂♂ (4.2–6.5 mm); 3 ♀♀ (4.75–7.2 mm).

Queensland (Brisbane River).

Distribution. Madras, India (Kemp, 1915); Singapore and Malay Peninsula (Tweedie, 1937); Formosa (Sakai, 1939); Brisbane River, Australia (Snelling, 1959).

Comments. This species has been so adequately described by Kemp (1915), Tweedie (1937) and Sakai (1939), particularly Kemp, that any further description or figuring here is unnecessary. Sufficient to note that the Australian specimens examined show the same variations as noted by Kemp in his Indian specimens.

DISCUSSION

Macrophthalminae fauna of Australasia

Eighteen species of five genera have here been recorded from Australasia. The following species should be removed from the fauna list, as having been recorded on misidentifications: *M. depressus* (= *M. affinis*), *M. brevis* (= *M. carinimanus*), and probably *M. sandakani*. Ortmann's record (1894a) of *M. sulcatus* is also, as Kemp (1919, p. 388) has pointed out, 'almost certainly erroneous', and Ward's record (1928) of *M. graeffei* from the Capricorn Islands, Queensland, still remains unconfirmed, and is probably erroneous. Of two species, *M. tomentosus* and *M. quadratus*, almost certainly validly recorded from Australasia (New Caledonia), by A. Milne Edwards (1873a), the author has seen no specimens.

*Evolution of the genus **Macrophthalmus***

The following discussion is an attempt to derive phylogenetic relationships within the genus *Macrophthalmus* in the light of the foregoing review of the systematics and morphology, and to determine some of the more important selective pressures that have resulted in the diversity seen.

From a study of seemingly unspecialised structures and structures present throughout the genus it can be hypothesised that the ancestral *Macrophthalmus* was probably of the following structure: 'Subquadrate carapace, with a broad unconstricted front, short ocular peduncles, smooth or moderately granular surface. Semiglobose male chelae, with moderately long fingers, the immovable finger being straight and without a differentiated tooth, the dactylus being curved and with a small quadrangular tooth near the base of the cutting margin, and a longitudinal ridge on the outer surface of the palm and immovable finger close to and subparallel with the lower margin. Slender pereopods with a small subterminal spine on the upper margins of the meri. External maxillipeds with subequal merus and ischium. Epistome with a straight central region. Male abdomen with seven distinct segments, the first two small, the five distal segments with straight lateral margins evenly convergent from the third to the seventh segment. Slightly curved or straight first male pleopod'. This ancestral *Macrophthalmus* probably occupied under-stone or small-burrow microhabitats in muddy sand, littoral or estuarine environments.

The species of the subgenus *Mopsocarcinus* are most similar to this hypothetical ancestral form, and in particular *M. boscii* shows little divergence from the latter. Amongst *Mopsocarcinus* only *M. quadratus* and *M. erato* show marked specializations, in that a cheliped merus/lower orbital border stridulating apparatus is present in the males (see Guinot-Dumortier & Dumortier 1960).

The species of the subgenus *Mareotis* have diverged from the ancestral form and have evolved a characteristic facies. *M. crinitus* retains more primitive characters, i.e. is structurally nearer to the hypothesized ancestral form, than any other species in this group. This species has retained the longitudinal ridge on the palm in its juvenile stages, possesses somewhat indistinct hairy rows on the carapace and relatively poorly-developed surface granulation and has retained an undeflexed immovable finger. *M. pacificus* is closely allied to the latter species, but lacks the ridge on the palm even in the juveniles, the immovable finger remaining undeflexed. It possesses a specialized feature in that the surface carapace granulation is secondarily (?) lost. *M. abercrombiei* and *M. definitus* have diverged from a crinitus-like form, but show a specialisation in the suppression of the longitudinal

granular rows of the branchial region. They show, however, the deflexed immovable finger, the heavy surface granulation (but with certain central smooth areas), and the lack of the ridge on the palm, as in the typical species of this group. *M. japonicus*, *M. depressus*, *M. teschi* and *M. tomentosus* have also probably diverged from a crinitus-like form, and share many characters with the two former species, but have retained and strongly developed the longitudinal granular rows of the branchial region. *M. tomentosus* has developed a specialized stridulating mechanism, independently of *M. quadratus* and *M. erato*, but which closely resembles that structure in those species (de Man, 1888b). *M. setosus* probably represents an early divergence from forms near the base of the *Mareotis* line. It differs from other species in that group in the retention of a longitudinal ridge (albeit feebly developed) on the palm in the adult, in a relatively broader carapace, and in the location of the position of the greatest carapace breadth between the external orbital angles. In the juveniles, however, the greatest carapace breadth occurs further posteriorly, as in all other species in the subgenus.

A second line showing divergence from the ancestral form and the evolution of a characteristic facies is that of the subgenus *Macrophthalmus*. Extant species which resemble the hypothetical transitional forms between the ancestral form and species such as *M. brevis* have not been discovered, and subfossil or fossil material of them does not at present exist. Three closely related species, *M. telescopicus*, *M. latipes* and *M. milloti*, and also *M. dentatus* can be regarded as specialised forms that have diverged from these transitional species however. Both groups of species have evolved an intermediate carapace shape (length : breadth \simeq 1 : 1.6–1.7), but show marked specialisations that place them off the direct evolutionary line (and have perhaps allowed them to survive in the face of competition from the more highly evolved species). The three closely related species have evolved very elongate ocular peduncles, which project well beyond the tips of the external orbital angles (in some specimens of *M. telescopicus* examined, by as much as seven-twelfths of their total length), while the other species, *M. dentatus*, has evolved a fourth anterolateral tooth (Stimpson, 1907). The remaining species in the subgenus have evolved a very similar morphological facies, with the partial exception of two species showing non characteristic specializations. *M. transversus* has independently evolved ocular peduncles of the same type as seen in *M. telescopicus*, etc. and also shows specializations of the male chelae, which are unusually weak and slender (Tesch, 1915). This latter character has evolved to a further degree in *M. parvimanus*, a species restricted to the Seychelles and nearby islands, in which the male chelae resemble the female chelae of other species of the genus (Balss, 1934). The ocular peduncles of this species do not project beyond the external orbital angles, however. All but three of the 'typical' *Macrophthalmus* (s.s.) species possess a characteristic proximally directed tubercle on the inner surface of the palm of the male chela, near the carpal joint, often associated with the development of tubercles on the carpus itself. Three species, *M. convexus*, *M. graeffei* and *M. consobrinus*, showing close affinity in many seemingly non adaptive characters, have diverged from the remaining species and lack the forementioned tubercle. These latter remaining species can be divided into two groups on characters of the external orbital angle. In one group, including *M. sulcatus* and *M. grandidieri* which have a centre of geographical distribution in East Africa and the western Indian Ocean, the external orbital angle is small and its tip falls well short of that of the second lateral tooth, in some cases the tip being directed backwards and partially across the latter tooth. While in the second group, including *M. brevis*, *M.*

dilatatus and *M. crassipes*, which have a centre of geographical distribution in Indonesia, the external orbital angle is large and its tip projects equally out from the carapace to that of the second lateral tooth.

The third line showing divergence from the ancestral form and the evolution of a characteristic facies is that of the subgenus *Venitus*. These species have retained a number of ancestral characters, and have attained the largest size of any species in the genus. Although distinct from all other species, some characters of the external maxilliped and carapace possibly indicate an ancestry of this group close to that of *Mareotis*. Two species have evolved specialisations previously seen in other species; *M. pectinipes* has independently evolved a stridulating mechanism of the same type as seen in *M. quadratus*, *M. erato* and *M. tomentosus*, and *M. latreillei* has evolved a fourth anterolateral tooth, parallelling *M. dentatus* in this character.

The two remaining subgenera represent isolated lines showing a curious mixture of ancestral characters and specialisations parallelling a number of other evolutionary lines. Both groups only occur at the present time in geographically isolated areas, the subgenus *Tasmanoplax* in the extreme south east of Australia, and *Hemiplax* in New Zealand and Formosa; only in Formosa are there other species of the subfamily also present. Thus it would appear that either the groups have evolved their peculiar facies in isolation, or that the extant species represent the remains of once widely distributed evolutionary lines, which have survived only in isolated areas lacking in more highly evolved forms, perhaps *Tasmanoplax* is a case of the former and *Hemiplax* the latter.

Tasmanoplax has retained the broad front, the longitudinal ridge on the palm, and external maxilliped, etc., of the hypothetical ancestral form, has parallellled the species of *Mareotis* in the presence of granular rows on the branchial region (the rows being of a different construction in *Tasmanoplax* than in *Mareotis*, however) and in the shape of the anterolateral teeth, has parallellled *Macrophthalmus* (s.s.) in the character of the epistome, and has parallellled *Hemiplax* in characters of the chelae.

Hemiplax has, similarly to *Tasmanoplax*, retained a number of basic ancestral characters, has parallellled other groups in other characters (the precise characters differing, however, in the two subgenera) and has evolved a number of specialised characters without parallel in other groups. *Hemiplax* has retained the ancestral broad unconstricted front, the short stout ocular peduncles, the straight central region of the epistome (cf. *Tasmanoplax*) and the form of the external maxillipeds; has parallellled *Mareotis* in the presence of transverse granular rows on the branchial region, but has evolved a unique oblique granular row on that region; has parallellled *Tasmanoplax* in some aspects of the structure of the male chela, but has evolved a large triangular protruberance on the carpus of the male cheliped, to some extent parallelling the tubercles present in some species of the subgenus *Macrophthalmus*; and has evolved a somewhat distinctive abdomen.

It is here hypothesised that one of the main selective pressures influencing the adaptive radiation within the genus *Macrophthalmus* has been that of predation. This pressure has resulted in two series of structural modifications, (a) those of the ocular peduncles, and (b) those concerned with increasing the speed and efficiency of the burrowing mechanisms.

The species of *Mopsocarcinus* probably rely, and the hypothetical ancestral form probably relied, on their small size and reclusive habits to escape from predation. The more specialized species however have increased their size and have evolved specializations specifically to avoid predators. It has been seen that in the majority of *Macroph-*

thalmus species, i.e. the species of the subgenera *Mareotis*, *Macrophthalmus*, *Venitus* and to a lesser extent *Tasmanoplax*, a trend for the reduction in breadth of the front, correlated with an increase in length of the ocular peduncles, has evolved. An increase in the length of the ocular peduncles, which in life are held vertically above the animal, confers several advantages: (1) the animal can still receive information about conditions above the surface of the substratum whilst its body is completely hidden (i.e. buried) below the surface, thus decreasing the chance of a potential predator being aware of the presence of the crab; (2) the higher the corneas of the crab are from the surface of the substratum, i.e. the longer the ocular peduncles are (the cornea being situated terminally), the greater the area of substratum potentially visible, and thus a potential predator's movements can be detected when the predator is a greater distance away from the crab; and (3) with overlapping fields of vision some degree of depth perception may be possible (Waterman, 1961). If a selective pressure does exist for increased length of the ocular peduncles, the length of the latter can theoretically be increased in one of two ways from the state of the peduncles in the ancestral form (and *Mopsocarcinus*). The peduncle can be lengthened so that its tip projects beyond the external orbital angle, or the breadth of the front can be reduced, effectively increasing the proximal rather than the distal section of the peduncle (or by a combination of the two, discussed later). If the peduncle is lengthened so as to project beyond the outer margin of the orbit, the eye can no longer be retracted into the safety of the orbital canal in times of danger, but is continually exposed; whereas if the peduncle is elongated by a reduction in the breadth of the front, the eye can still be retracted into the orbital housing, and is not continually exposed to predators. Thus *a priori* it would seem that a selective advantage would exist in the latter case, rather than in the former, since in only four species does the cornea project beyond the external orbital angle for any length, all other species with elongate peduncles have evolved them correlated with a reduction in breadth of the front only, *M. telescopicus*, *M. milloti*, *M. latipes* and *M. transversus* as has already been noted have evolved narrow constricted fronts and greatly elongated ocular peduncles projecting well beyond the external orbital angles. It is almost certain that the reduction in breadth of the front preceded the great elongation of the peduncles in the evolutionary history of the four species and that the latter is a secondary specialization. This specialization would seem to have occurred in spite of the considerable selective pressure acting against the development of completely unprotected eyes. In all four species the selective pressure 'overriding' the latter pressure may have been due to the otherwise heavy predation on the species that would have ensued, perhaps due to different factors in the different species. The nature of these factors is difficult to determine, several factors suggest themselves but none are particularly satisfactory. *M. telescopicus*, *M. milloti* and *M. latipes* are all comparatively small species, although larger than those of *Mopsocarcinus*, which as already hypothesised may rely in part on their very small size to escape from predation, they are however smaller than most other species of this genus. Perhaps these species, by virtue of their size, would be very vulnerable to predation from, for example, littorally feeding small birds. The great elongation of the peduncles might then have evolved in response to the need for the crabs to burrow as deeply as possible from the surface into the substratum, yet still receive optic information from above the surface. *M. transversus* as has already been noted is remarkable for the feeble nature of the chelae of the males, if the chelae are used as weapons of defence, then those of this species would surely be inadequate, and the elongate peduncles might have

evolved to compensate for the added vulnerability of this species. *M. parvimanus*, however, possesses even smaller chelae than the previous species, and would thus seem to be at an even greater disadvantage, but has not evolved the greatly elongate ocular peduncles.

It has also been hypothesised that mechanisms increasing the speed and efficiency of burrowing have been evolved. Species of *Macrophthalmus* (s.l.) burrow by means of sideways digging motions, i.e. the carapace of the crab entering the substratum lateral margin first. The crab that can burrow beneath the surface of the substratum fastest at the approach of a predator is likely to be at a selective advantage over a crab that can only do so more slowly. Two mechanisms increasing the speed of burrowing have been evolved by this genus: (1) increasing the size and strength of the pereopods and (2) streamlining the carapace along the axis of entry into the burrow, i.e. with increase in size, increasing the breadth of the carapace relative to the length (thus decreasing the relative length of the lateral margins). The latter mechanism alone has been evolved by the species of the subgenus *Macrophthalmus*, and the streamlining of the carapace reaches its peak in this group (with a ratio of length to breadth in adults in the order of 1 : 2), the pereopods remaining slender. The lateral borders of the carapace are also strongly sloping towards the lateral margins, in this group, facilitating entry into the substratum. Both mechanisms have evolved in the subgenera *Mareotis*, *Hemiplax* and *Tasmanoplax*. The streamlining of the carapace is much less marked than in the previous group (ratio of length to breadth in adults in the order of 1 : 1.4–1.5), but the pereopods have correspondingly evolved into powerful digging structures. The species of *Venitus* have retained the subquadrate carapace shape of the hypothetical ancestral form, and have also attained very large size. It would thus seem that the large unstreamlined carapaces of these species would restrict rapid burrowing in anything other than very soft mud, and it is precisely that habitat from which most Australian specimens of *M. latreillei* have been recorded (e.g. W. Macnae m.s. collection notes). The pereopods, however, have evolved into large, seemingly efficient, digging structures, with series of spines and tubercles along the margins of several of the segments of the limbs, possibly further increasing their efficiency. It is also possible that the large size of these species when adult is in itself a deterrent to some potential predators, and that the need for rapid burrowing is less marked than in smaller species.

Thus it can be hypothesized that the selective advantage in the two main trends seen in the morphology of *Macrophthalmus* (s.l.) species is in the avoidance of predation from at least some of the potential predators. The selective advantages conferred by other characters, e.g. shape of anterolateral teeth, shape of male abdomen, pattern of surface carapace granulation, etc., however, cannot be explained in terms of single external factors, but have probably evolved in response to a whole complex of differing pressures.

Geographical distribution

The 20 species of Macrophthalminae occurring in Australasia (the 18 species reviewed in this paper together with *M. tomentosus* and *M. quadratus*) can be divided into three zoogeographical groupings: widespread species, i.e. those species with a known distribution encompassing almost the whole range of the subfamily; Indo-West Pacific species, i.e. those species distributed over the eastern part of the range of the subfamily and absent from Africa and the western Indian Ocean; and the Endemic species. Differences can be detected in the Australasian distribution of the endemic species on the one hand and the non-endemic species on the other.

The widespread species, i.e. *M. boscii*, *M. latreillei* and *M. telescopicus*, and the Indo-West Pacific species, i.e. *M. convexus*, *M. crassipes*, *M. crinitus*, *M. definitus*, *M. japonicus*, *M. pacificus*, *M. tomentosus* and *L. sordidulum* are restricted to the tropical areas of Australasia and the zones of interlap between the tropical and temperate zones. Only two species, *M. latreillei* and *M. crassipes*, extend into the truly temperate zones, the former extending to Freemantle on the western coast of Australia (approximately 32°S.), and the latter to Sydney on the eastern coast (approximately 34°S.). Although some of these species show very restricted Australasian distributions (although this may be more apparent, due to the lack of collecting in the relevant areas, than real), the other species, known from more than one area, show widespread distributions throughout the tropical regions of both eastern and western Australia.

The endemic species, however, show no such restriction to the tropical regions, and show more restricted distributions than the non-endemic species, all endemic species being confined to eastern Australasia, (two of the 'endemic' species, *M. hirtipes* and *A. tridentata*, have also been recorded once from Samoa; the record of the latter species is however doubtful (see de Man, 1896) and that of the former has not been confirmed, the only record being in 1853 (Jacquinot, 1853)). Two species, *M. abercrombiei* and *M. quadratus*, known from very restricted localities, do appear to be confined to the tropical regions, the former to the south eastern portion of the Gulf of Carpentaria and the latter to New Caledonia. *M. punctulatus*, *M. setosus*, *M. hirtipes*, *M. latifrons* and *P. mcneilli*, however, occur only to the south of the tropic of Capricorn. Two other endemic species show a distribution along the eastern coast of Australia in both temperate and tropical regions. *A. tridentata* and *C. wardii* occurring as far north as Cooktown (approximately 15° 30' S.). *M. latifrons* and *M. hirtipes* occur at the southern limit of the range of the subfamily.

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