

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 mcneilli* (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
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.27	1.31	1.32	1.33	1.34
Length of chela Carapace breadth	♂ 0.46	0.60	0.74	0.84	0.90
	♀ —	0.43	0.43	0.43	—
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	3.60	3.80	3.85	3.91	3.92

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 granulatus 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.

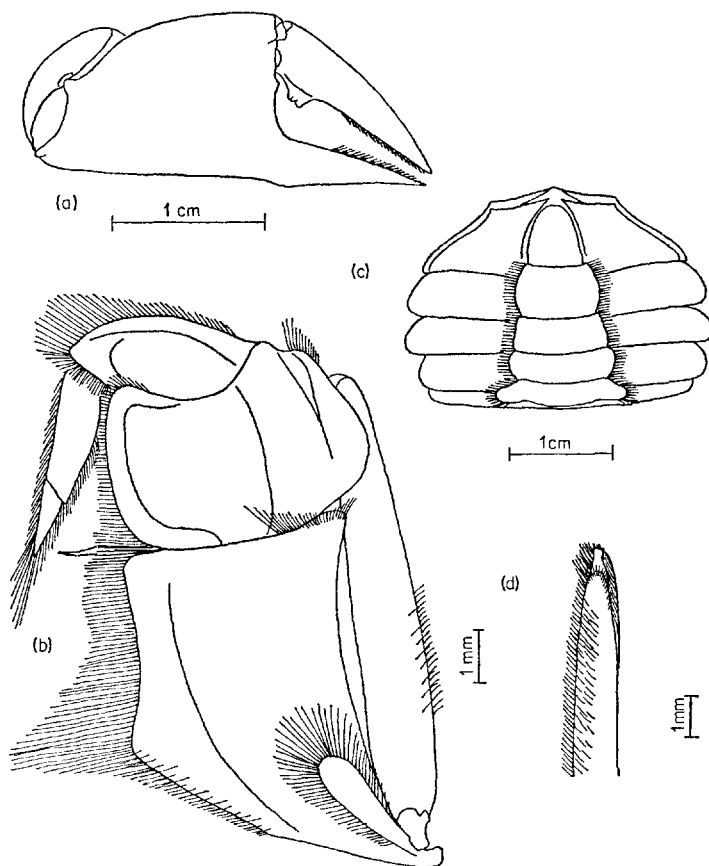


FIG. 11. *M. latreillei*.

(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
$\left. \begin{array}{l} \text{Length of chela} \\ \text{Carapace breadth} \end{array} \right\}$	♂ 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.)

(e) *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.

Metaplax 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 protruberance, 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.

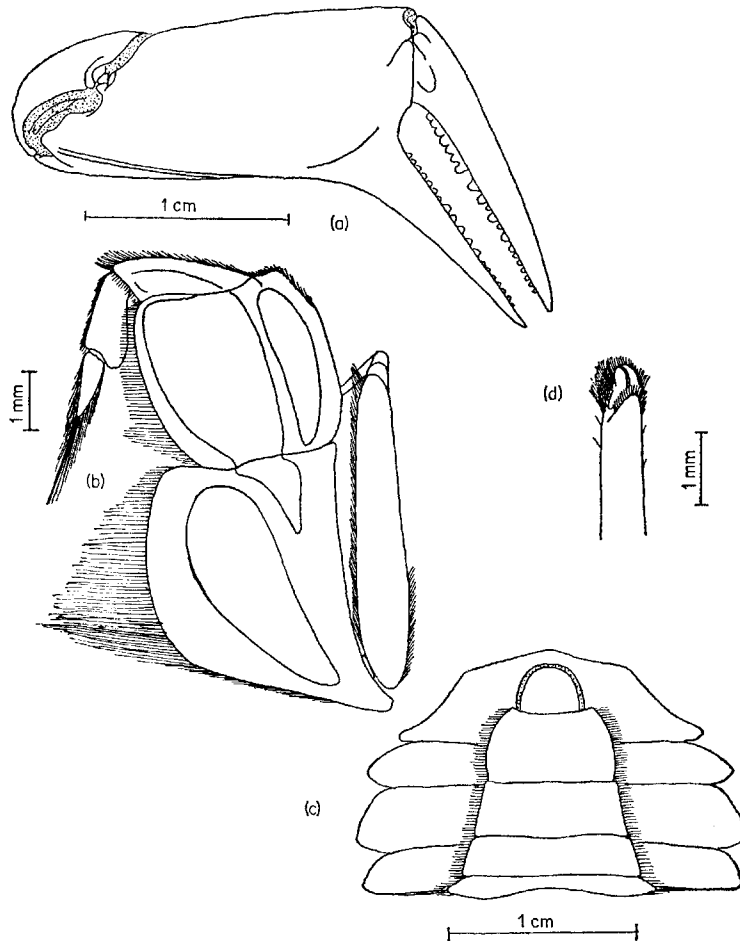


FIG. 12. *M. hirtipes*.

(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
$\left. \begin{array}{l} \frac{\text{Length of chela}}{\text{Carapace breadth}} \end{array} \right\}$	♂ —	0·56	0·65	0·74	0·82
	♀ 0·42	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 *Metaplax*, 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 *Cleistotoma*, 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 Jacquinet 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.

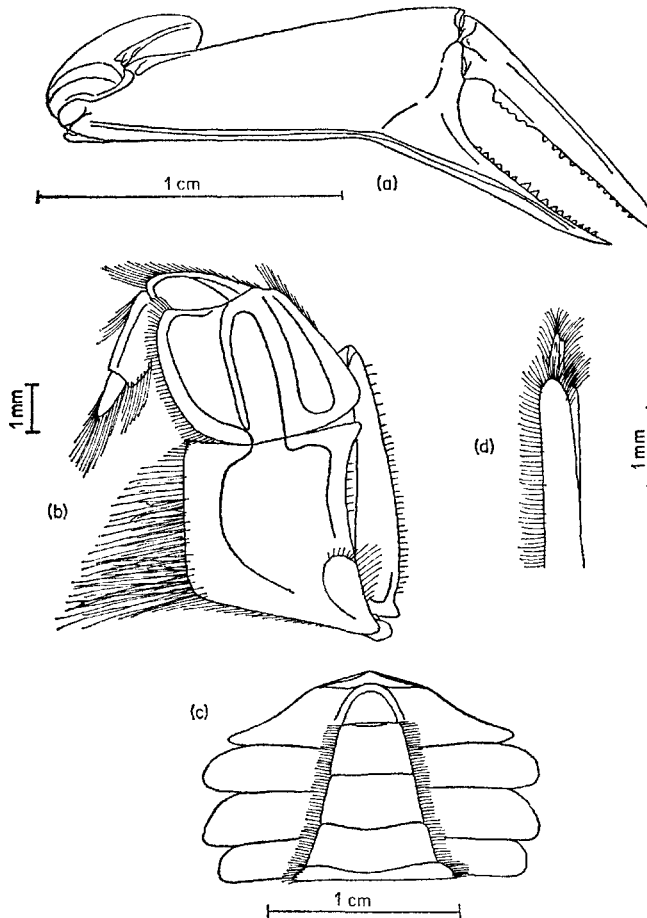


FIG. 13. *M. latifrons*.

(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
Length of chela } $\frac{\text{Carapace breadth}}{\text{Carapace breadth}}$	♂ 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 hirsutumana 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.

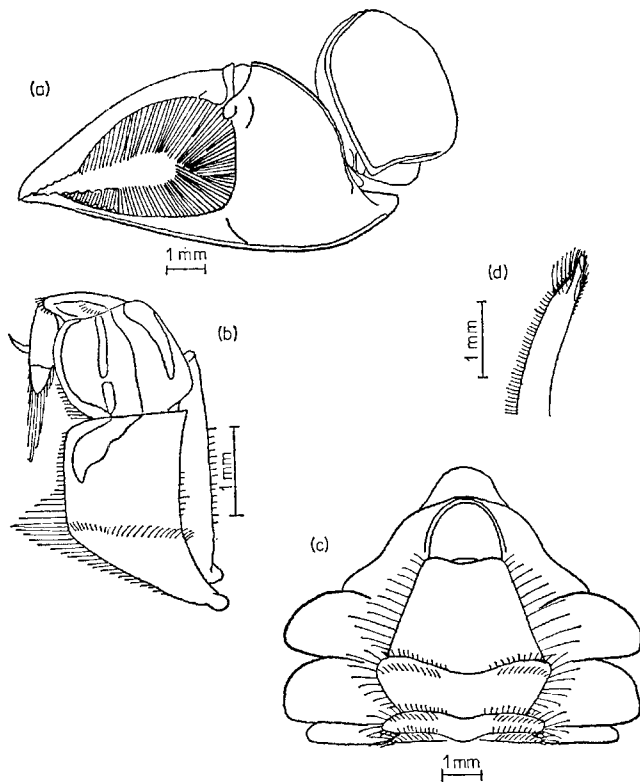


FIG. 14. *A. tridentata*.

(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
$\left. \begin{array}{l} \text{Length of chela} \\ \text{Carapace breadth} \end{array} \right\}$	♂ 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.

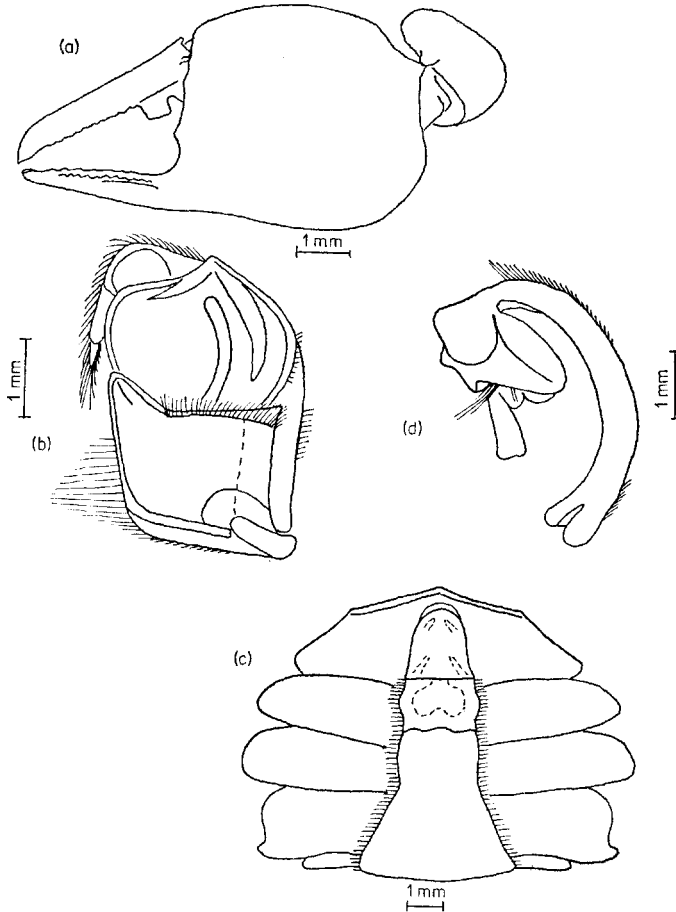


FIG. 15. *C. wardi*.

(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 pereopod 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
Length of chela 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.

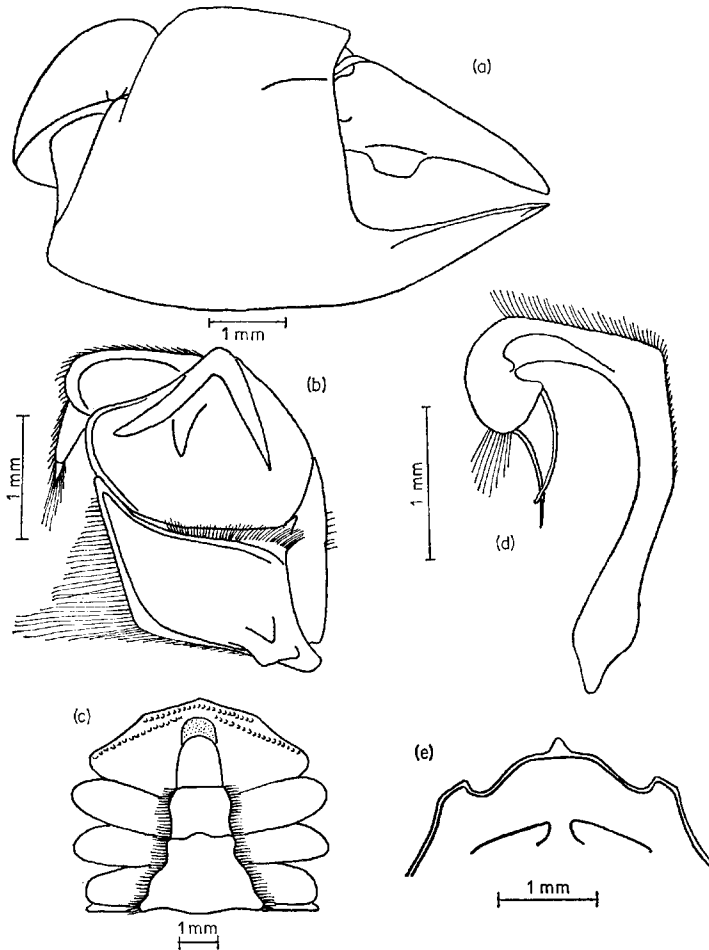


FIG. 16. *P. mcneilli*.

(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
$\frac{\text{Carapace breadth}}{\text{Carapace length}}$	1.25	1.32	1.34
$\left. \begin{array}{l} \text{Length of chela} \\ \text{Carapace breadth} \end{array} \right\}$	♂	—	0.37
	♀	0.25	0.28
$\frac{\text{Carapace breadth}}{\text{Breadth of front}}$	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, 1888*b*). *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 Fremantle 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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