

THE SPECIES OF *MACROPHTHALMUS*
(CRUSTACEA: BRACHYURA) IN THE
COLLECTIONS OF THE BRITISH MUSEUM
(NATURAL HISTORY)



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By R. S. K. BARNES

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SYNOPSIS

The British Museum holds twenty three species of the genus *Macrophthalmus* (Crustacea : Brachyura). Nine of these, *M. depressus*, *M. dilatatus*, *M. erato*, *M. grandidieri*, *M. laevimanus*, *M. parvimanus*, *M. pectinipes*, *M. tomentosus* & *M. transversus*, are redescribed and figured. Material from the Royal Society's 1967-1968 Expedition to Aldabra is also included. The convergence with certain sesarminine grapsids displayed by *M. hirtipes*, clinal changes in morphology in *M. dilatatus*, and the systematic value of a number of features of the genus are described and discussed, in addition to a review of the B.M. collection.

INTRODUCTION

THE following is a review of the British Museum collection of crabs of the genus *Macrophthalmus* Latreille (Ocypodidae : Macrophthalminae), it being the fifth contribution towards an eventual revision of this genus (see Barnes, 1966a ; 1966b ; 1967 ; 1968a). The review follows the same basic pattern as that of an earlier paper dealing with the species of this genus from Australia and adjacent regions (Barnes, 1967), and here only those species not covered by that publication will be fully described and figured, i.e. those marked by an asterisk in the list given below. Wherever possible, regression equations have been calculated to show the changes in the carapace length/breadth ratio and that of breadth of front/carapace breadth with changes in size (see Barnes, 1968b).

The collection contains material previously described and discussed by de Haan (1835), Adams & White (1848), Miers (1884 ; 1886), Lanchester (1900a ; 1900b), Laurie (1906 ; 1915), Calman (1927), Gordon (1931), Tweedie (1937) and McNeill (1968). Here, the two hundred and forty four specimens comprising the collected material are assigned to the following twenty three species :

<i>M. bosci</i> Audouin	52 specimens
? <i>M. brevis</i> (Herbst)	16 "
<i>M. convexus</i> Stimpson	11 "
<i>M. crassipes</i> H. M. Edwards	8 "
<i>M. crinitus</i> Rathbun	8 "
<i>M. definitus</i> Adams & White	6 "
* <i>M. depressus</i> Rüppell	27 "
* <i>M. dilatatus</i> (de Haan)	8 "
* <i>M. erato</i> de Man	9 "
<i>M. graeffei</i> A. M. Edwards	3 "
* <i>M. grandidieri</i> A. M. Edwards	10 "
<i>M. hirtipes</i> (Jacquinot)	8 "
<i>M. japonicus</i> (de Haan)	10 "
* <i>M. laevimanus</i> H. M. Edwards	1 "
<i>M. latifrons</i> Haswell	2 "
<i>M. latreillei</i> (Desmarest)	22 "
<i>M. pacificus</i> Dana	9 "
* <i>M. parvimanus</i> Guérin	1 ¹ "
* <i>M. pectinipes</i> Guérin	10 "

¹ Also included in this report are 13 specimens of *M. parvimanus* collected by the Royal Society's 1967-1968 Expedition to Aldabra.

<i>M. punctulatus</i> Miers	1	specimens
<i>M. telescopicus</i> (Owen)	13	„
* <i>M. tomentosus</i> Souleyet	4	„
* <i>M. transversus</i> (Latreille)	5	„

The collection therefore contains approximately two thirds of the probably valid species included in this genus. With respect to the validity, or otherwise, of a number of published species, the author has attempted to keep the majority of such discussion for a proposed full revision of *Macrophthalmus*. However, some comments have been made on a number of new synonymies which have become apparent during this study. One particularly difficult case to unravel at this juncture is centred around *M. brevis* (= *M. carinimanus* H. M. Edwards). A considerable number of minor variations and different geographical populations of this species have almost certainly been made the basis for a plethora of specific names, but an adequate treatment of this species must await the examination of more material from more localities. That part of the problem which impinges on *M. dilatatus* has, however, been dealt with in some detail. Other difficult cases are centred around *M. telescopicus* and *M. latreillei*.

In addition, the status of the following species has been deliberately excluded from discussion in this report—*M. consobrinus*, *M. graeffei*, *M. latipes*, *M. milloti* and *M. teschi*.

Any modern worker studying *Macrophthalmus* species from a large geographical area must very quickly become aware that the characters displayed by these organisms do not remain constant, but vary (a) with size of the animal, (b) amongst material from a single locality, and (c) from locality to locality. But as a result of the patchiness of much of the collecting which has produced the specimens examined, our knowledge of many species over much of their range is negligible. In a few cases clinal changes in morphology can be discerned (see *M. dilatatus*) and in more cases intermediate forms between two distinct structural types can be found. But often samples are inadequate for more than tentative judgements.

Complete synonymies are given only for those species not covered by Barnes (1967).

The dimensions given under "Material examined" headings below are of greatest carapace breadth.

A. Subgenus *MACROPHTHALMUS* Sensu stricto

1. *Macrophthalmus (Macrophthalmus) brevis* (Herbst, 1804)

Foreword

This is an extremely problematical species, with an intensely confused synonymy, but since very few specimens have been seen by the author, it would be premature to do more here than indicate the nature and magnitude of the problem.

Six species, *M. laevimanus* H. M. Edwards, *M. sandakani* Rathbun, *M. simdentatus* Shen, *M. malaccensis* Tweedie, *M. malayensis* Tweedie and *M. travancorensis* Pillai, have been described from the area between the Gulf of Manaar and Hainan Island.

Each is known only from one or two localities and between them they total only about twenty specimens. Further, none of these authors refers to any of the other authors' species.

Secondly, there are two very poorly known species, *M. sulcatus* H. M. Edwards and *M. brevis* (Herbst), known from approximately the same area. These eight species, judging from the published descriptions, all appear to grade into one another in a non-linear manner, and there are additional links to a ninth species, *M. dilatatus* (de Haan). Lastly, Lanchester's (1900a) record of *M. crassipes* H. M. Edwards and Tweedie's (1937) record of *M. c.f. crassipes* are not of that species, but together with Lanchester's *M. dilatatus carens* form a tenth unit related to the previous nine. All the material of '*M. brevis*' in the B.M. collection falls into this latter, tenth unit. The status of *M. sulcatus*, *M. sandakani* and *M. malaccensis* will be discussed under the section on *M. dilatatus*, and *M. laevimanus* and *M. malayensis* are considered in a separate section below.

MATERIAL EXAMINED. 8 ♂♂ (12.0–17.0 mm), 8 ♀♀ (11.8–19.7 mm). B.M. Reg. Nos—82.24, 1900.10.22.277–284 (Syntypes of *M. dilatatus carens*), 1900.10.22.285–292.

LOCATIONS. Singapore, Malacca.

COMMENTS. The material with the registration number of 82.24 is that collected by the "Alert" and identified by Miers as *M. dilatatus* (it is not recorded in the results of the "Alert" voyage—Miers, 1884—presumably as a result of an oversight); Lanchester (1900a) regarded it as being identical with his *M. dilatatus carens*. 1900.10.22.277–284 is the type material of the latter subspecies (Lanchester, 1900a), which was considered by Tweedie (1937) to be a series of juvenile *M. brevis*. That with the number of 1900.10.22.285–292 was recorded by Lanchester (1900a) as *M. crassipes*, and Tweedie was of the opinion that, together with his own *M. c.f. crassipes* material, it might form a new subspecies of *M. crassipes* (Tweedie, 1937).

All these specimens are juveniles, which increases the uncertainty of identification. 82.24 and 1900.10.22.277–284 are almost certainly of the same species, to which 1900.10.22.285–292 may belong, but there are a number of noticeable differences between the latter and the two former. What perhaps contributes most to their *incertae sedis* position is that, although juvenile, they are large and possess carapaces relatively longer than would be expected for their size. For example, the largest specimen (19.7 mm) has a carapace length one millimetre larger than that of a "*M. malaccensis*" of carapace breadth 21.8 mm.

2. *Macrophthalmus (Macrophthalmus) transversus* (Latreille, 1817)

Gonoplax transversus Latreille, 1817

Macrophthalmus transversus: Latreille, 1829; H. M. Edwards, 1837; H. M. Edwards, 1852; Cano, 1889; de Man, 1892; Tesch, 1915; Kemp, 1919

MATERIAL EXAMINED. 4 ♂♂ (17.0–23.0 mm), 1 ♀ (18.7 mm). B.M. Reg. Nos—1919.11.91–94, 1951.4.19.2.

LOCATIONS. Chandpur, Balasore (India).

DESCRIPTION. Front deflexed; markedly constricted between bases of ocular

peduncles ; smooth margined ; with almost straight anterior margin and faint median furrow.

Upper orbital border strongly curved, transversely directed ; margin studded with rounded granules increasing in size towards external orbital angle, granules nearest to that angle large and tubercular. Lower orbital border serrated by large, curved, pointed tubercles ; with from three to six very large, more or less flattened spines in centre (each approx. three times longer than normal tubercle and nine times the surface area).

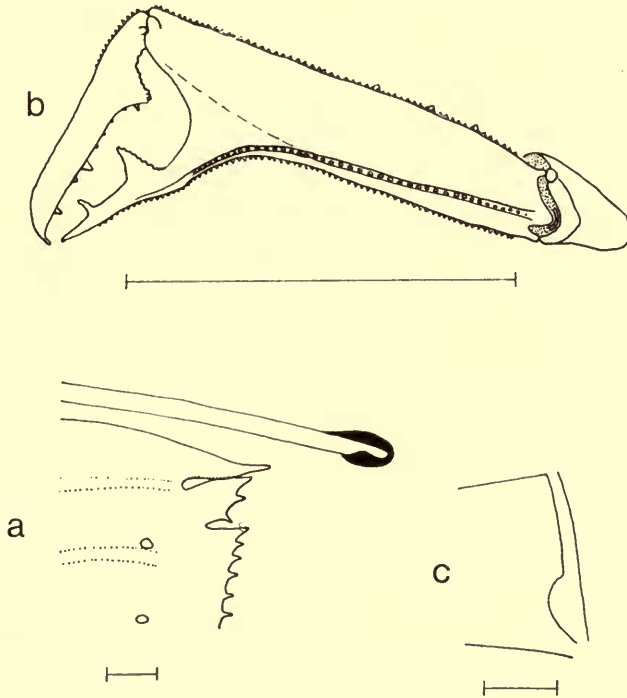


FIG. 1. *M. transversus*—a, anterolateral carapace teeth and ocular peduncle, b, left male chela (outer surface), c, external margin of ischium of external maxilliped. Scale lines a & c 1 mm., b, 1 cm.

Three well defined anterolateral teeth (see Fig. 1a). External orbital angle large, elongate, strongly pointed, directed straight outwards ; anterior margin with continuation of granulation of upper orbital border ; lower margin with rounded granules ; tip often formed by elongate tubercle ; separated from second lateral tooth by deep, narrow incision, wider and more U-shaped in juveniles. Second lateral tooth large, of the shape shown by Fig. 1a, directed outwards and forwards ; anterior margin with rounded granules ; convex or straight outer margin with three large tubercles (in adults), the largest anteriorly forming point of tooth, second in centre of margin, third at posterior angle directed posteriorly ; separated from third lateral tooth by deep, narrow incision. Third lateral tooth moderately large, triangular, pointed,

directed outwards and slightly forwards, with large tubercle at tip ; margins straight, outer margin smoothly continuous with lateral carapace margin.

Carapace completely covered with small, rounded granules ; with well defined, deep furrows ; with well defined, raised clumps of granules on branchial regions, each bearing one very large tubercle in its centre, accessory granules often lacking, "clump" then represented only by tubercle, additional similar tubercle often present between positions of first and second clumps (tubercle formed from second clump) ; with row of four to six smaller, pointed tubercles between branchial clumps or tubercles and lateral carapace margins ; with abruptly sloping sides ; without surface hair. Lateral margins posteriorly convergent, with row of about eight large tubercles on margin, evenly spaced from third lateral tooth to posterior angle of carapace, tubercle at that angle particularly large. With row of granules near to and subparallel with posterior margin. Greatest carapace breadth across external orbital angles. Female carapace without granules excepting on branchial and lateral regions.

Ocular peduncles very long and narrow, projecting beyond external orbital angle for between one tenth and one fifth of their length.

Male cheliped. (a) *Merus*. Upper margin with scattered granules and from one to three large spines centrally ; inner margin with row of tubercles along length, of which any number from two to six may be converted into very long spines (often differentially on the two meri, e.g. one with six, the other three) ; outer margin with scattered granules and one or two large spines distally. Inner surface without granules, with patch of hair centrally and proximally near inner margin ; outer surface with scattered granules near upper and outer margins ; lower surface with scattered granules near outer margin and thickish hair near inner margin.

(b) *Carpus*. Almost hairless. Outer surface with scattered granules, those near lower margin large and tuberculiform ; inner surface more or less smooth, except for a large spine near upper margin and similar spine in central region directed towards palm. Upper margin with scattered small granules ; lower margin with irregular tubercular granules.

(c) *Palm*. Very elongate. Outer surface closely covered with small, pointed granules ; with prominent longitudinal ridge bearing a row of small, pointed tubercles along crest ; anterior margin without notch. Inner surface closely covered with granules, with thick hair over whole surface, with exception of extreme proximal region and area near lower margin, with large spine, and accessory tubercles in large specimens, near to and directed towards carpus. Upper margin with row of from four to eight large spines, increasing in size towards carpus, with granules between spines ; lower margin with pointed granules as on outer surface (see Fig. 1b).

(d) *Index*. Markedly deflexed, elongate, very thin. Outer surface with small, sparse granules, with faint, feebly granular continuation of longitudinal ridge of palm, granules decreasing in size distally ; inner surface sparsely granular, with dense hair near cutting margin. Cutting margin with very large, tall, laterally flattened, pointed tooth in centre, tooth either spiniform with straight entire margins, or with a crenulated posterior margin (in some large specimens, the tooth may take the form of two divergent spines joined together at their base), a second smaller spiniform tooth, with entire margins, situated half way between larger tooth and tip of index, re-

mainder of margin usually without further conspicuous granules ; lower margin with pointed granules and few tubercles.

(e) *Dactylus*. Markedly deflexed, elongate, very thin. Outer surface closely covered with small granules ; inner surface completely covered by mat of thick hair. Upper margin with small, pointed granules ; cutting margin with large, triangular, spiniform or crenulated tooth near base, with irregular number of small, cylindrical spines in distal half, with small, irregular granules and tubercles over remainder. Extreme tip of dactylus hooked.

Pereiopod meri with from one to six large spines on the distal part of posterior lower margin in large specimens.

Male abdomen with bulge in morphologically anterior half of lateral margins of sixth segment.

External maxilliped. Internal margin of ischium almost straight or slightly convex ; external margin with a marked and precise concavity proximally (see Fig. 1c), distal portion of margin smoothly but slightly convex. Internal margin of merus convex ; external margin smoothly convex, without differentiated convexities ; anterior margin shallowly concave.

First male pleopod almost straight, without well developed terminal process, without hair on internal margin except at tip.

Central convexity of epistome small and pointed.

DIMENSIONS. Over the size range examined, the carapace length/breadth ratio varies from 0.40 : 1 to 0.44 : 1, and the breadth of front/carapace breadth ratio from 0.12 : 1 to 0.13 : 1.

COMMENTS. *M. transversus*, the type species of the genus, is remarkable for the extremely thin chelae of both sexes (the female chela is as thin as that of the males and possesses similar spiniform teeth, but is otherwise not spiniferous) and for the extremely tubercular and spiniferous carapace, chelipeds and pereiopods, it being rivalled in the latter only by *M. pectinipes*.

As pointed out by Kemp (1919), the additional joint on the dactylus of the male cheliped, as described and figured by Tesch (1915), is the result of a partial fracture of the base of that finger in his specimen.

3. *Macrophthalmus (Macrophthalmus) parvimanus* Guérin, 1834

Macrophthalmus parvimanus Guérin, 1834 : H. M. Edwards, 1837 ; H. M. Edwards, 1852 ; Richters, 1880 ; Miers, 1884 ; Balss, 1934 ; Taylor, 1968

Macrophthalmus convexus kempii Gravely, 1927

Macrophthalmus convexus : Kemp, 1919 (part)

Macrophthalmus consobrinus : Crosnier, 1965

MATERIAL EXAMINED. 7 ♂♂ (8.1–24.9 mm), 7 ♀♀ (10.8–23.3 mm). B.M. Reg. No. 82.24, and Royal Society Expedition, Aldabra 1967–1968 (“Lagoon mud, Dune Jean Louis Creek, Aldabra, 18/xi/1967”).

LOCATIONS. Mahe (Kerala), Aldabra.

DESCRIPTION. Front deflexed ; markedly constricted between bases of ocular

peduncles ; smooth margined ; with straight or slightly bilobed anterior margin ; with shallow median furrow.

Upper orbital border curved, markedly backwardly sloping ; margin beaded by small, rounded granules. Lower orbital border serrated by large, evenly spaced, tubercular granules along entire length.

Two well defined and one very poorly defined anterolateral teeth (see Fig. 2a), beaded by small granules along all margins. External orbital angle large, pointed, directed outwards and forwards at its tip ; separated from much smaller second lateral tooth by wide, V-shaped or very narrow incision. Second lateral tooth small, pointed, triangular, directed straight outwards ; separated from third lateral tooth by very small incision. Third lateral tooth very small or absent.

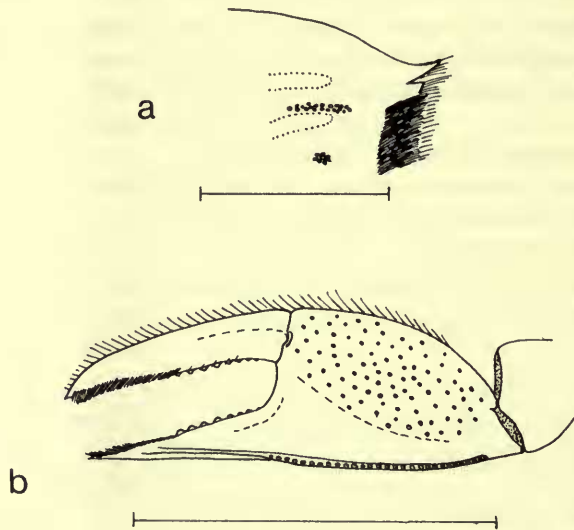


FIG. 2. *M. parvimanus*—a, anterolateral carapace teeth, b, left male chela (outer surface).
Scale lines—5 mm.

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

Ocular peduncles long and narrow, cornea extending as far as, or slightly beyond, tip of external orbital angle.

Male cheliped. Unique in that it is not sexually dimorphic in this species ; males with small, slender, weak chelae of the same pattern as found in the females of other *Macrophthalmus* species.

(a) *Merus*. Upper and inner margins with long, fine hair ; outer margin with row of very small granules. All surfaces without granules ; scattered hairs only on inner surface.

(b) *Carpus*. Without granules or tubercles. Upper margin with fringe of long hairs ; lower margin with few scattered hairs ; outer anterior margin with long hair mainly in lower portion. Both surfaces smooth.

(c) *Palm*. Outer surface finely granular, with longitudinal ridge very close to lower margin ; inner surface without granules, with square or rectangular patch of short thick hair centrally, with row of long, fine hairs near to and subparallel with upper margin. Upper margin with row of small granules and row of long, fine hairs ; lower margin with small granules on the longitudinal ridge (see Fig. 2b).

(d) *Index*. Undeformed. Outer surface smooth, except for marked, agranular continuation of longitudinal ridge near lower margin, and row of long hairs near distal cutting margin ; inner surface smooth, except for row of long hairs near distal cutting margin. Cutting margin without differentiated tooth except in large specimens, in which from eight to ten granules are associated to form a long, low tooth, from one to two fifths of the length of the margin away from its base, with row of rounded granules proximally ; lower margin smooth.

(e) *Dactylus*. Straight. Outer and inner surfaces smooth, apart from row of hairs near distal cutting margin. Cutting margin without differentiated tooth, except in large specimens in which five or six granules near the base are associated to form a distinct tooth, with few small granules proximally and centrally ; upper margin with fringe of long, fine hair.

Pereiopod meri, carpi and propodi with quite heavily granular surfaces and margins, upper margin of merus with row of hairs, and small subterminal spine.

Male abdomen. Lateral margins of sixth segment with bulge in morphologically anterior position. Sternal surfaces granular.

External maxilliped. Internal and external margins of ischium more or less straight through much of their length, distally convergent. Internal margin of merus convex ; external margin with marked posteroexternal convexity and faint anteroexternal convexity ; anterior margin with shallow concavity.

First male pleopod with very well developed terminal process, without hair on internal margin.

DIMENSIONS. Carapace length = 0.46 carapace breadth + 0.82 (Standard deviation 0.21), Breadth of front = 0.088 carapace breadth + 0.59 (Standard deviation 0.05).

COMMENTS. This species was shrouded in obscurity until the publication of Balss's (1934) paper, in which he showed that there was indeed a species of *Macrophthalmus* with juvenile-like adult male chelae. Previously most authors had accepted Tesch's (1915) contention that *M. parvimanus* was probably based on a female specimen of *Uca*.

M. parvimanus is, in fact, extremely closely related to the well known *M. convexus*, the only character separating the two species being the peculiar cheliped of the former species. The large (32.5 mm), abnormal male recorded by Kemp (1919) from the "upper end of the Gulf of Manaar" is clearly a specimen of *M. parvimanus*. Kemp noted that "The chela differs from that of the female [*M. convexus*] in only two points,—in the possession of rudimentary teeth on the fingers and in the hairy

covering of the inner surface" and that "In all other respects the specimen agrees precisely with normal examples of the species [*M. convexus*]" (Kemp, 1919 : 389 and see his Plate 24, fig. 2). The specimens recorded and described by Gravely (1927) as *M. convexus kempi*, from the Gulf of Manaar, also belong to this species. Of his specimens, Gravely (1927 : 150) states "As . . . the seven males (two small) in our collection all agree with this abnormal specimen [Kemp's] it is evident that they represent a distinct local race for which I propose the name *kempi*." Besides the Gulf of Manaar, however, this species is known from the Seychelles (the type locality) and nearby islands, and from Madagascar, since Crosnier's (1965) record of *M. consobrinus* was based on material of *M. parvimanus*. This was ascertained by the examination of part of Crosnier's material in the Muséum National d'Histoire Naturelle, Paris, through the courtesy of Dr. D. Guinot.

4. *Macrophthalmus (Macrophthalmus) dilatatus* (de Haan, 1835)

In this paper, *M. dilatatus* (*sensu* de Haan and subsequent authors) is regarded as the nominal subspecies of *M. dilatatus (sensu novo)* and *M. sulcatus*, *M. sandakani* and *M. malaccensis* are regarded as being synonymous and forming a second subspecies *M. dilatatus sulcatus* H. M. Edwards, 1852 (*comb. nov.*).

a. *M. dilatatus dilatatus* (de Haan, 1835)

Ocypode dilatata de Haan, 1835

Macrophthalmus dilatatus : H. M. Edwards, 1852 ; de Man, 1890 ; Ortmann, 1894a ; Ortmann, 1897 ; ? Doflein, 1904 ; Tesch, 1915 ; Sakai, 1934 ; Sakai, 1939 ; Sakai, 1965
nec Macrophthalmus dilatatus carens Lanchester, 1900a

MATERIAL EXAMINED. 2 ♂♂ (26.3 & 30.8 mm), 1 ♀ (31.5 mm). B.M. Reg. Nos—1935.3.19.37-38, 1961.6.5.92.

LOCATIONS. North China, Tokyo Bay or Sagami Bay (Japan).

DESCRIPTION. Front deflexed ; constricted between bases of ocular peduncles ; with smooth margins, slightly bilobed or straight anterior margin, shallow median furrow.

Upper orbital border markedly curved and almost transversely directed, with little backwards slope ; margin beaded by small, rounded granules. Lower orbital border serrated by large, widely spaced, tubercular granules, often with smaller granules alternating with the large.

Two well defined and one poorly defined anterolateral teeth (see Fig. 3a). External orbital angle narrow, elongate, pointed, directed outwards and forwards to a variable degree (varying from straight outwards to outwards and up to 20° forwards, measured from the transverse carapace axis) ; anterior margin with small granules continuous with those on upper orbital border ; posterior margin smooth ; separated from second lateral tooth by deep, but narrow incision. Second lateral tooth large, wedge-shaped, directed outwards and forwards ; anterior margin smooth or with small granules ; posterior margin straight or convex, with granules ; tip extends as

far as, or slightly beyond, that of external orbital angle ; separated from third lateral tooth by narrow incision. Third lateral tooth variable in size, directed outwards and forwards ; with granular margins.

Carapace of darkish colour, covered with medium sized granules to a variable extent, with central areas almost devoid of granules in some specimens ; with well defined, deep furrows ; with distinct raised clumps of tubercular granules on branchial regions ; with abruptly sloping sides. Greatest carapace breadth across external orbital angles and second lateral teeth, or across latter alone. Lateral margins posteriorly convergent, with rows of hair along length ; posterior margin granular.

Ocular peduncles long and narrow, cornea extending to tip of external orbital angle.

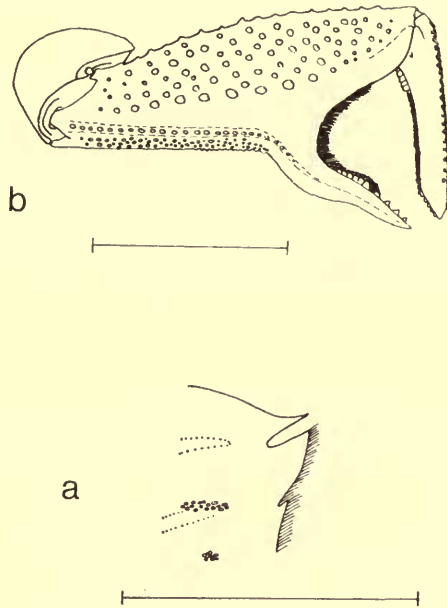


FIG. 3. *M. dilatatus dilatatus*—a, anterolateral carapace teeth, b, right male chela (outer surface). Scale lines—1 cm.

Male cheliped. (a) *Merus*. Upper margin with large tubercle centrally and patch of hair proximally ; inner margin densely haired, with one or two very large tubercles distally ; outer margin granular, with one or two large tubercles distally. Lower surface sparsely granular, with dense mat of hair near and continuous with that on inner margin, hair may extend over most of surface ; inner surface more or less smooth, with hair near inner margin ; outer surface with sparse hair near upper margin and sparse granules near outer margin.

(b) *Carpus*. Almost hairless. Outer surface smooth centrally, with scattered granules near upper and lower margins ; inner surface smooth, except for large tubercle dorsally and similar tubercle centrally near joint with palm. Lower margin with few, large granules distally ; upper margin with sparse row of granules distally.

(c) *Palm*. Elongate. Outer surface with very large, evenly spaced, rounded

tubercles in upper half, the lowest tubercles largest and forming a row (see Fig. 3b), area between row of tubercles and longitudinal ridge smooth, longitudinal ridge prominent and with large granules on crest decreasing in size towards index, area below ridge heavily granular, anterior margin with deep notch ; inner surface heavily haired over all but lower and proximal region, boundary to haired portion marked by row of granules and large spine near to and directed towards carpus, lower proximal region heavily granular, especially near lower margin. Upper margin with row of large tubercles, largest centrally ; lower margin granular.

(d) *Index*. Markedly deflexed in adults. Outer surface more or less smooth, except for low, agranular continuation of longitudinal ridge ; inner surface heavily haired near cutting margin, with small granules near lower margin. Cutting margin with long, low, crenulated tooth occupying proximal half to three fifths, with a few large granules distally in adults ; lower margin granular. In adults, index strongly curved near base, correlated with interdigital notch.

(e) *Dactylus*. Slightly curved, oriented almost vertically in adults. Outer surface smooth apart from row of granules near upper margin ; inner surface heavily haired (hair on inner surfaces of index and dactylus continuous with that on palm). Upper margin granular ; cutting margin with low tooth formed from four or five contiguous granules in a line at base, with rounded granules and dense hair along remainder. Base of cutting margins of index and dactylus widely separate.

Pereiopod meri with hair and small subterminal spine on upper margin, without conspicuous granules.

Male abdomen. Lateral margins of sixth segment with bulge in morphologically anterior half.

External maxilliped. Internal margin of ischium convex ; external margin more or less straight. Internal margin of merus convex ; external margin curving smoothly into anterior margin, without distinct posteroexternal convexity ; anterior margin smoothly concave.

First male pleopod curved, with well developed terminal process, without hair on internal margin except at tip.

DIMENSIONS. Too few specimens have been examined to permit any deductions from their dimensions, but using figures from the literature it can be seen that at a size (carapace breadth) of between 20 and 30 mm the carapace length/breadth ratio is in the range 0.47 : 1 to 0.49 : 1.

b. *M. dilatatus sulcatus* H. M. Edwards, 1852

Macrophthalmus sulcatus H. M. Edwards, 1852 : Alcock, 1900 ; Lenz, 1905 ; Tesch, 1915 ; Kemp, 1919 ; Chhappgar, 1957

nec Ortmann, 1894a

Macrophthalmus sandakani Rathbun, 1914 : Tesch, 1918

nec Rathbun, 1924

Macrophthalmus malaccensis Tweedie, 1937 : Crosnier, 1965

Macrophthalmus carinimanus : Lanchester, 1900b

MATERIAL EXAMINED. 3 ♂♂ (21.3–26.3 mm), 2 ♀♀ (19.5 & 23.6 mm). B.M. Reg. Nos—80.6 (part), 1900.12.1.23, 1937.11.15.167–168 (Syntypes of *M. malaccensis*).

LOCATIONS. Santubong, Selangor, "Malaysia".

DESCRIPTION. In this description, only those characters will be mentioned in which *M. dilatatus sulcatus* differs from *M. dilatatus dilatatus* (see above).

External orbital angle small to very small, narrow, triangular, pointed, directed straight outwards, with tip projecting backwards and occasionally across anterior margin of second lateral tooth (in specimens from western part of range, tooth then very small) or with tip projecting outwards and occasionally also slightly forwards (in specimens from eastern part of range, tooth then small), projecting less far laterally than second lateral tooth (see Fig. 4a).

Carapace of lightish colour, completely covered by dense, medium sized granules, without any smooth central regions. Relatively broad (see "Dimensions"), with greatest breadth across second lateral teeth.

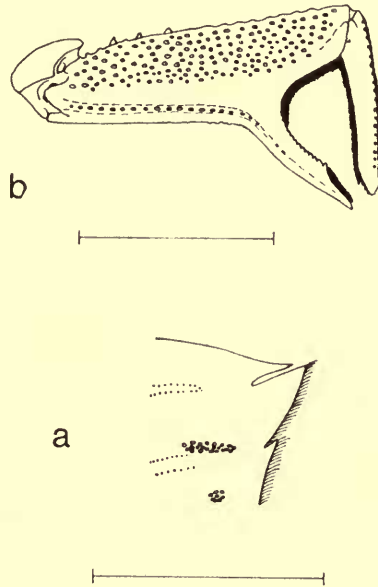


FIG. 4. *M. dilatatus sulcatus*—a, anterolateral carapace teeth, b, right male chela (outer surface). Scale lines—1 cm.

Male cheliped. (a) *Merus*. Upper margin with row of rounded granules along length, without large tubercle ; inner margin with four or five very large tubercles centrally and distally.

(c) *Palm*. Outer surface with many, large (but smaller than in the nominal subspecies) rounded granules in upper half, lowest granules not largest and not forming a distinct row (see Fig. 4b).

(e) *Dactylus*. Cutting margin with very small, low tooth, formed from four or five contiguous granules, near base, tooth inconspicuous and often hidden by hair.

DIMENSIONS. Too few specimens have been examined to permit any deductions

from their dimensions, but using figures from the literature it can be seen that at a size (carapace breadth) of between 17 and 26 mm, the carapace length/breadth ratio is in the order of between 0.41 : 1 and 0.45 : 1. Any further data cannot yet be given.

COMMENTS. It will be noticed that these two subspecies differ only in the degree of expression of a few characters. In *M. d. sulcatus*, (a) the external orbital angle is smaller, (b) the carapace is broader, lighter in colour, and more heavily granulated, (c) the tubercles or granules on the outer surface of the palm are smaller and more numerous, (d) the tooth on the dactylus is smaller, and (e) the tubercles on the inner margin of the merus are more numerous and those on the upper margin are not developed, when compared to *M. d. dilatatus*. In addition, the tooth on the index of the westernmost *M. d. sulcatus* is often larger.

Many of these differences of degree, however, appear to vary in a clinal manner, as far as the limitations of the material permit interpretation. In the Japanese material ("*dilatatus*"), the carapace is relatively narrowest, the external orbital angle is largest and directed most forwards, and the tuberculation of the palm is heaviest. In material from Singapore ("*malaccensis*"), the carapace is broader, the external orbital angle is smaller but is aligned in essentially the same direction as in the Japanese forms, although less forwards, and the granulation of the palm is still heavy with traces of alignment of the lowest granules. Thirdly, specimens from India and Mauritius ("*sulcatus*") show the smallest external orbital angles, with the tip directed backwards in some specimens, the broadest carapaces, and the least heavily developed granulation on the palm. Some features of the upper orbital border, the second lateral tooth, and the teeth on the fingers of the male cheliped also show trends consistent with such a clinal change.

Thus the series of "species", *M. dilatatus*—*M. malaccensis*—*M. sulcatus*, shows indications of a continuous change in a number of independent characters from the North East through to the South and West. Even the division into a northern and a southern subspecies may, therefore, be drawing a non-existent distinction, but "*sulcatus*" and "*malaccensis*" at our present state of knowledge appear to be more closely allied to each other than "*malaccensis*" is to "*dilatatus*". Only the collection of more material from the shores of the Bay of Bengal and of the South China Sea will tell whether or not this distinction is valid.

The similarities between "*dilatatus*", "*malaccensis*" and "*sulcatus*" which have led to their being synonymized here have already been described and discussed (see two previous "Descriptions"), there now remains the position of "*sandakani*" and Lanchester's (1900b) record of *M. carinimanus* to be considered. Rathbun's *M. sandakani* was based on a single female specimen from Sandakan, Borneo. Females of the different species within a given subgenus of *Macrophthalmus* are exceedingly difficult to distinguish, females and juveniles often sharing a common structural plan. Hence, separation of the species is usually based on the males. *M. sandakani*, however, does not depart from the structural characteristics exhibited by female specimens of "*malaccensis*", and it does not seem unreasonable, as no evidence to the contrary is apparent, to conclude that they are of the same species. Rathbun (1924) later described a juvenile male of her species from North West

Australia, but this was shown by Barnes (1967) to be almost certainly a young *M. crassipes*.

The material described by Lanchester (1900b) as *M. carinimanus* is in the British Museum, with the registration number of 1900.12.1.23. It is identical to the material described by Tweedie (1937), from a nearby locality, as *M. malaccensis* (Reg. No. 1937.11.15.167-168).

The relationship of *M. dilatatus* (*sensu novo*) to *M. brevis* will not be considered in this paper.

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

MATERIAL EXAMINED. 7 ♂♂ (5.6-35.0 mm), 6 ♀♀ (9.0-18.5 mm). B.M. Reg. Nos—83.22, 84.31 (part), 84.31 (part), 1892.4.18.17-20 (part), 1900.10.22.293, 1920.2.23.1, 1934.1.17.132, 1937.9.21.274-275 (part), 1937.9.21.274-275 (part), 1964.7.1.109, & Unregistered.

LOCATIONS. Zanzibar, Sudanese Red Sea, Singapore, Mindano (Philippines), Arafura Sea, Low Isles (Gt Barrier Reef), Torres Straits, Viti Levu (Fiji), Hawaii.

DIMENSIONS. The approximate equations derived from measurements of these specimens are given below.

Carapace length = 0.57 carapace breadth + 0.39, Breadth of front = 0.13 carapace breadth + 0.61.

The breadth of the carapace increases relative to the carapace length with increase in size of these specimens, as in other *Macrophthalmus* species, but contrary to the figures given previously for *M. telescopicus* (Barnes, 1968b). Only small samples have, as yet, been available; further material should resolve this discrepancy.

COMMENTS. The material with the registration number of 1937.9.21.274-275 (part) is that recorded by McNeill (1968), and that with 1900.10.22.293 is that recorded by Lanchester (1900a) as *M. podophthalmus*.

Similar variations in the length of the ocular peduncles and in the relative lengths of the anterolateral teeth to those noted by Barnes (1967) can be seen in the present material. The ocular peduncle projects beyond the external orbital angle for between one half (e.g. 1934.1.17.132 & Unregistered) and one eighth (e.g. 1892.4.18.17-20) of its length, and the external orbital angle : second lateral tooth : third lateral tooth ratio varies from 4 : 2 : 1, through 4 : 3 : 1 and 2 : 1 : 1, to 1 : 1 : 1. Variations in the shape of the tooth on the index of the male cheliped can also be noted.

6. *Macrophthalmus (Macrophthalmus) crassipes* H. M. Edwards, 1852

MATERIAL EXAMINED. 7 ♂♂ (10.7-25.0 mm), 1 ♀ (10.5 mm). B.M. Reg. Nos—1932.11.30.164, 1932.11.30.196-197.

LOCATIONS. Willy Creek & Broome (N.W. Australia).

DIMENSIONS. All the dimensions of these specimens fit the equations given by Barnes (1968b) for this species, to within one Standard Error.

7. *Macrophthalmus (Macrophthalmus) laevimanus* H. M. Edwards, 1852*Macrophthalmus laevimanus* H. M. Edwards, 1852*Macrophthalmus malayensis* Tweedie, 1937

MATERIAL EXAMINED. 1 ♂ (24.6 mm). B.M. Reg. No. 1937.11.15.166 (Holotype of *M. malayensis*).

LOCATION. Selangor.

DESCRIPTION. Front deflexed ; constricted between bases of ocular peduncles ; with smooth margins, slightly bilobed or straight anterior margin, and shallow media furrow.

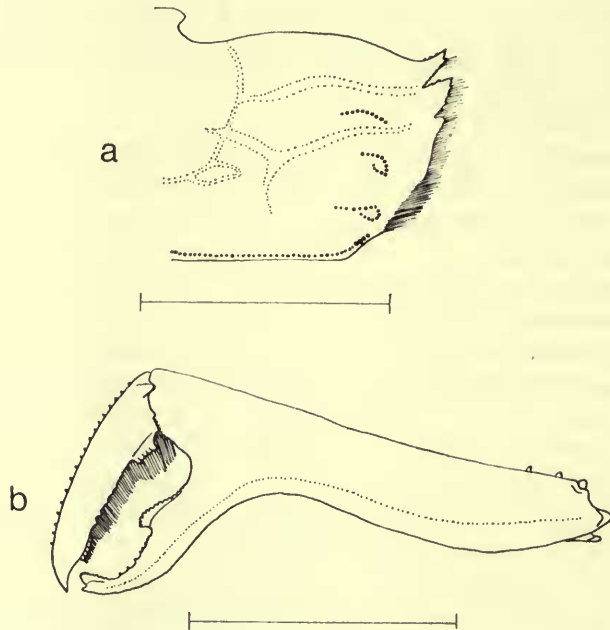


FIG. 5. *M. laevimanus*—a, anterolateral carapace teeth, b, right male chela (outer surface).
Scale lines—1 cm.

Upper orbital border markedly curved, almost transversely directed ; margin beaded by small, rounded granules. Lower orbital border serrated by large, widely spaced, tubercular granules, increasing in size towards external orbital angle, granules nearest external orbital angle, however, small and sparse.

Three well defined anterolateral teeth (see Fig. 5a). External orbital angle narrow, elongate, pointed, directed outwards and forwards at an angle of approx. 40° to transverse carapace axis ; anterior margin with small, rounded granules continuous with those on upper orbital border ; posterior margin with small, pointed granules, except near tip where smooth, granules directed forwards with respect to margin ; tip formed by large granule ; separated from second lateral tooth by wide V-shaped

incision, wider and more U-shaped in juveniles. Second lateral tooth large, wedge-shaped, pointed, directed outwards and forwards, but less forwards than external orbital angle ; anterior margin more or less straight, with pointed granules ; posterior margin convex, with pointed granules ; tip formed by large granule ; separated from third lateral tooth by distinct V-shaped incision. Third lateral tooth small, wedge-shaped, blunt, directed outwards ; with granular margins.

Carapace closely covered with medium-sized granules, largest anteriorly ; with well defined, deep furrows ; with very distinct, markedly raised clumps of tubercular granules, of the shape shown by Fig. 5a ; with abruptly sloping sides ; with row of granules close to and subparallel with posterior margin, of which terminal four or five granules distinctly larger than remainder. Greatest carapace breadth across second lateral teeth ; behind which lateral margins slightly convergent and with row of short, dense hair. Posterior margin smooth.

Ocular peduncles long and narrow ; cornea extending to middle of, or to two thirds the length of, external orbital angle.

Male cheliped. (a) *Merus*. Upper margin finely granular, with large tubercle centrally and smaller tubercle immediately proximal to latter, with patch of hair proximally, with few small tubercles proximal to central tubercle in large specimens ; inner margin with two to four large spines centrally or in distal half, with pointed tubercles over remainder, with long hair centrally and proximally ; outer margin with spine just distal of central, granular proximally, with row of pointed spines or large tubercles distal to spine, decreasing in size distally. Lower surface granular near outer margin, smooth centrally, with scattered hair near inner margin ; inner surface very feebly granular or smooth, with row of long hairs near to and subparallel with central region of inner margin ; outer surface finely granular near outer margin, with sparse scattered hair over more or less smooth remainder.

(b) *Carpus*. Elongate, almost hairless. Outer surface with scattered granules near upper and lower margins ; inner surface more or less smooth, except for two large spines dorsally and similar spine centrally near joint with palm. Lower margin with row of distally directed, pointed tubercles, largest distally, immediately proximal area smooth ; upper margin with one to three pointed tubercles proximal to dorsal spines, with row of distally directed, pointed tubercles distally and centrally.

(c) *Palm*. Extremely elongate in adults. Outer surface with close covering of small granules over whole surface, with very poorly developed granular longitudinal ridge, especially so in adults, without deep, semi-circular anterior notch ; inner surface without hair, with close covering of small granules over whole surfaces, with large spine near joint with carpus. Upper margin coarsely granular, with row of pointed tubercles along length, largest at extreme proximal and distal ends, with the two most proximal tubercles very large and spiniform ; lower margin with granules as on outer and inner surfaces.

(d) *Index*. Markedly deflexed in adults. Outer surface with granules as on that of palm, with continuation of longitudinal ridge only feebly granular ; inner surface with granules as on that of palm, without hair excepting fringe around spooned tip. Lower margin with forwardly directed pointed granules, except at extreme tip ; cutting margin with large wedge-shaped, crenulated tooth occupying proximal half,

with smaller, tall, wedge-shaped, crenulated tooth at extreme tip (see Fig. 5b), with pointed tubercles between the two teeth. Tip of index deflexed upwards, through about 70° in adults.

(e) *Dactylus*. Slightly curved. Outer surface smooth near tip, finely granular over remainder, granules largest near upper and lower margins; inner surface with granules as on that of palm, with mat of hair over all but extreme distal and proximal regions, or over whole surface. Upper margin with rows of pointed granules, largest proximally; cutting margin with large, crenulated, subrectangular tooth near base, with row of large tubercles distal to tooth, the most distal four or five tubercles coalesced in large adults to form a distinct subterminal tooth, extreme tip without tubercles.

Pereiopod meri with very fine hair and subterminal spine on upper margins; upper and posterior lower margins with granules, remainder smooth.

Male abdomen. Lateral margins of sixth segment with bulge in morphologically anterior half. Margins of sternal segments granular near abdomen.

External maxilliped. Internal margin of ischium straight; external margin more or less straight. Internal margin of merus convex; external margin with moderately developed posteroexternal convexity, remainder curving smoothly into anterior margin; anterior margin with slight to moderate concavity.

First male pleopod curved, with well developed terminal process, without hair on internal margin.

COMMENTS. Mme Guinot has been so kind as to forward to the author photographs of the only known specimen of H. M. Edwards's *M. laevimanus*, collected by Leschenault at Pondichery and housed in the Muséum National d'Histoire Naturelle, Paris. These photographs show quite clearly that this specimen is indistinguishable from those described by Tweedie as *M. malayensis*, and hence the two species are here considered to be synonymous.

As stated earlier, comments on the status and affinities of this species will be delayed, pending a re-examination of *M. brevis*.

8. *Macrophthalmus (Macrophthalmus) convexus* Stimpson, 1858

MATERIAL EXAMINED. 8 ♂♂ (14.0–35.5 mm), 3 ♀♀ (8.6–24.1 mm). B.M. Reg. Nos—80.6 (part), 1908.10.27.14–15, 1910.3.29.19, 1929.8.1.11, 1930.12.2.109, 1935.3.19.33, 1950.12.1.22, & Unregistered.

LOCATIONS. Low Isles (Gt Barrier Reef), Torres Straits, Ki Islands (New Guinea), "Malaysia", Hong Kong, S. Formosa, Viti Levu (Fiji).

DIMENSIONS. The dimensions of these specimens fit the equations given by Barnes (1968b) for this species, to within one Standard Error.

COMMENTS. The material with the registration number of 1950.12.1.22 is that referred to by McNeill (1968).

9. *Macrophthalmus (Macrophthalmus) grandidieri* A. M. Edwards, 1867

Macrophthalmus grandidieri A. M. Edwards, 1867 ; A. M. Edwards, 1868 ; Lenz & Richters, 1881 ; Ortmann, 1894b ; Ortmann, 1897 ; Lenz, 1905 ; Tesch, 1915 ; Stebbing, 1917 ; Balss, 1934 ; Monod, 1938 ; Barnard, 1950 ; Fourmanoir, 1954 ; Crosnier, 1965

Macrophthalmus hilgendorfi Tesch, 1915 ; Barnard, 1950 ; Barnard, 1955

Macrophthalmus brevis : Hilgendorf, 1869 ; de Man, 1880 ; Nobili, 1906b

Macrophthalmus carinimanus : Bianconi, 1851 ; Hilgendorf, 1878

MATERIAL EXAMINED. 6 ♂♂ (21.0–29.7 mm), 8 ♀♀ (14.5–28.1 mm). B.M. Reg. Nos—1913, 2, 14, 11–12, 1928. 12. 1. 117–118, 1955. 3. 5. 109–112. (Also examined were four specimens collected by W. Macnae at Inhaca Island, S. Africa, by courtesy of Dr. J. C. Yaldwyn.)

LOCATIONS. Durban, Inhaca Island, Morrumbene Estuary (Mozambique).

DESCRIPTION. Front deflexed ; markedly constricted between bases of ocular peducles ; with smooth margins, slightly bilobed anterior margin, faint median furrow.

Upper orbital border strongly curved and somewhat backwardly sloping ; margin beaded with small granules. Lower orbital border serrated by large tubercular granules, with smaller granules often alternating with the large.

Three well defined anterolateral teeth present (see Fig. 6a). External orbital angle very small, pointed, directed outwards and often backwards so that its tip lies across the middle of the anterior margin of second lateral tooth (see Fig. 6b) ; anterior margin with small granules continuous with those on upper orbital border ; posterior margin smooth ; separated from second lateral tooth by narrow incision. Second lateral tooth very large, wedge shaped, bluntly pointed, directed outwards and forwards ; anterior margin with beading of small granules ; convex posterior margin with large tubercular granules ; tip extends well beyond that of external orbital angle ; separated from third lateral tooth by wide, V-shaped incision. Third lateral tooth relatively large in males, smaller in females, triangular, directed outwards and very slightly forwards, hidden in hair ; anterior margin with thick tuft of hair ; more or less straight posterior margin with few, inconspicuous granules.

Carapace surface covered with small granules ; with well developed, deep furrows ; with somewhat indistinct, but variably developed, raised clumps of granules on branchial regions ; with row of granules near to and subparallel with posterior margin ; with abruptly sloping sides covered with thick mat of hair. Lateral margins posteriorly convergent, hidden under carapace hair. Greatest carapace breadth across second lateral teeth.

Ocular peduncles long and narrow ; cornea not projecting beyond tip of second lateral tooth, but usually beyond that of external orbital angle.

Male cheliped. (a) *Merus*. Upper margin without granules, with patch of short thick hair proximally ; inner margin concealed under thick mat of long hair, without granules ; outer margin covered by large semi-circular granules. Lower surface with thick mat of long hair covering all but small proximal region near outer margin, latter granular ; inner surface smooth on upper portion, covered by mat of hair on lower portion, hair over lower portion of inner surface, inner margin and lower

surface continuous ; outer surface with granules near outer margin, with sparse scattered hair over remainder.

(b) *Carpus*. Almost hairless. Outer surface almost entirely smooth, but with few, very small, scattered granules near upper and lower margins ; inner surface smooth except for large spine centrally, occasionally with one or two smaller tubercles near joint with palm, without tubercle or spine dorsally. Lower margin with small scattered granules ; upper margin with few, small, widely spaced tubercles centrally.

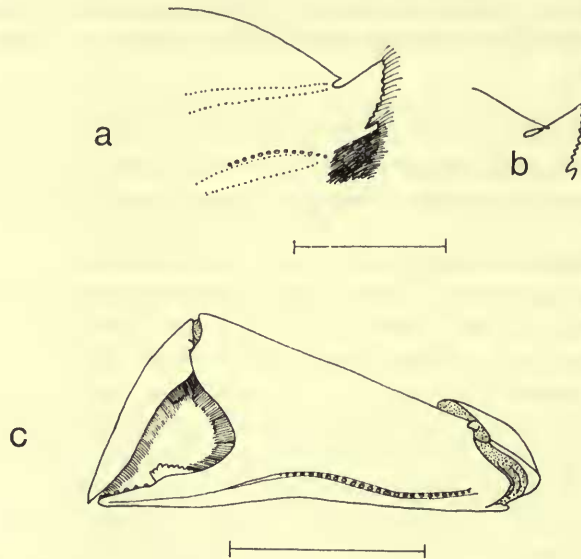


FIG. 6. *M. grandidieri*—a, anterolateral carapace teeth, b, external orbital angle variation, c, left male chela (outer surface). Scale lines—a & b 5 mm, c, 1 cm.

(c) *Palm*. Elongate. Outer surface covered by very fine granules, with prominent longitudinal ridge bearing row of rounded granules along crest (see Fig. 6c), anterior margin with deep notch, height increasing markedly distally ; inner surface heavily haired over upper and distal portion, with fine granules over lower and proximal portion, with large spine near to and directed towards carpus. Upper margin with row of large, pointed, tubercular granules, increasing in size proximally ; lower margin with small granules.

(d) *Index*. Deflexed in adults. Outer surface finely granular, with faint continuation of longitudinal ridge of palm, but without granules on crest ; inner surface heavily haired near cutting margin, finely granular over remainder. Cutting margin with large, crenulated, wedge-shaped or subrectangular tooth in centre, with variable number of pointed tubercles distally ; lower margin finely granular.

(e) *Dactylus*. Slightly curved. Outer surface with fine granules, densest near upper margin ; inner surface heavily haired (hair on inner surfaces of index and dactylus continuous with that on palm). Upper margin with row of pointed tubercular granules along length, on finely granular background ; cutting margin with

large, crenulated, subrectangular tooth near base, completely hidden under thick hair, with small, pointed, tubercular granules distally, margin completely obscured by thick hair.

Pereiopod meri with thick hair along upper margin concealing small subterminal spine.

Male abdomen with slight bulge in lateral margins of sixth segment, in morphologically anterior position.

External maxilliped. Internal margin of ischium convex or almost straight ; external margin convex distally, concave proximally. Internal margin of merus convex ; external margin with slight posteroexternal convexity ; anterior margin shallowly concave.

First male pleopod curved, with flat terminal process, with few hairs on internal margin near tip.

DIMENSIONS. Carapace length = 0.44 carapace breadth + 0.45 (Standard deviation 0.16), Breadth of front = 0.13 carapace breadth + 0.77 (Standard deviation 0.10).

COMMENTS. The synonymy given above follows the opinions of Balss (1934) and Crosnier (1965) with respect to the status of Hilgendorf's (1869 & 1878) and other authors' records of *M. brevis* and *M. carinimanus*, which Tesch (1915) described as a new species, *M. hilgendorfi*.

M. grandidieri is related to *M. dilatatus* and particularly to the southern and western subspecies *M. dilatatus sulcatus*. It differs from the latter principally in the lower degree of carapace granulation, with feebler branchial clumps, and in details of the male cheliped. In the latter, the merus lacks the large tubercles on the inner and outer margins, the carpus lacks the large tubercle on the dorsal portion of its inner surface, the palm lacks the row of granules on the inner surface, and the teeth on the fingers show a number of differences, when compared with *M. dilatatus sulcatus*. The two species are allopatric, *M. grandidieri* replacing *M. dilatatus* in Africa.

10. *Macrophthalmus (Macrophthalmus) graeffei* A. M. Edwards, 1873

Macrophthalmus graeffei A. M. Edwards, 1873a : Ortmann, 1897 ; Laurie, 1915 ; Tesch, 1918 nec Ward, 1928

Macrophthalmus convexus : Tesch, 1915 (part) ; Stephensen, 1945

MATERIAL EXAMINED. 3 ♀♀ (22.0–23.1 mm). B.M. Reg. No. 1934.1.17.133–135.

LOCATION. Sudanese Red Sea.

COMMENTS. As yet no male of this species has been examined by the author, and hence a description of *M. graeffei* and a discussion of its affinities will be postponed. It may be noted, however, that contrary to the opinion of Tesch (1915 ; 1918) it is evidently closely related to *M. telescopicus*, etc., and not to *M. convexus*.

The British Museum specimens are three of those collected on the Sudanese shores of the Red Sea and described by Laurie (1915). In these females, as noted by that author, the ocular peduncles terminate in a small rounded projection distal to the dilated region, wherein would presumably be located the cornea were it not detached

and freely moveable within the peduncle. It is difficult to ascertain from these specimens the shape of the peduncle in life, as the tissue within the cuticle is freely floating in a liquid matrix and the cuticle itself is soft and malleable. It is therefore possible that this terminal projection is an artifact, caused by differential softening of the cuticle, but if it is subsequently found to be genuine it may represent, in a very incipient form, the terminal projection of such species as *Ocypode ceratophthalma* and *Uca stylifera*.

B. Subgenus *MAREOTIS* Barnes, 1967

1. *Macrophthalmus (Mareotis) depressus* Rüppell, 1830

Macrophthalmus depressus Rüppell, 1830 : H. M. Edwards, 1837 ; H. M. Edwards, 1852 ; Heller, 1861 ; Paul'son, 1875 ; de Man, 1881 ; de Man, 1888a ; Henderson, 1893 ; ? de Man, 1895 ; Ortmann, 1897 ; Alcock, 1900 (part) ; Nobili, 1906a ; Nobili, 1906b ; Laurie, 1915 ; Tesch, 1915 ; Kemp, 1919 ; Calman, 1927 ; Gravely, 1927 ; Balss, 1934 ; Stephensen, 1945 ; Barnard, 1955 ; Chhappgar, 1957 ; Crosnier, 1965 ; Macnae, 1968 (part)
nec de Man, 1888b ; Lanchester, 1900b ; Grant & McCulloch, 1906 ; Etheridge & McCulloch, 1916
Macrophthalmus affinis Guérin, 1839a : Guérin 1839b ; H. M. Edwards, 1852
nec Haswell, 1882b

MATERIAL EXAMINED. 17 ♂♂ (7.0–30.8 mm), 10 ♀♀ (8.5–30.9 mm). B.M. Reg. Nos—85.14, 1892.7.15.233–234, 1913.10.30.6–7, 1926.1.26.130–133, 1934.1.17.136–137, 1955.3.5.104–108 (part), 1955.3.5.104–108 (part), 1963.10.24.8.

LOCATIONS. Mozambique, Sudan, Suez, Aden, Persian Gulf, Pamban.

DESCRIPTION. Front deflexed ; constricted between bases of ocular peduncles ; with granular surface, deep median furrow, faintly bilobed anterior margin ; with proximal half of lateral margins granular, remainder smooth.

Upper orbital border curved, slightly backwardly sloping ; margin studded with rounded granules. Lower orbital border with inner four fifths straight and serrated by large, rounded, tubercular granules ; outer fifth abruptly sloping, without granules.

Two large and one small anterolateral teeth (see Fig. 7a). External orbital angle large, broad, rectangular, pointed anteriorly, directed outwards and slightly forwards ; anterior margin with granules continuous with those on upper orbital border ; outer margin with similarly rounded granules ; separated from second lateral tooth by wide, deep, U-shaped incision. Second lateral tooth large, broad, rectangular, directed outwards, projecting beyond former tooth ; anterior and convex outer margins with rounded granules, partly hidden under hair in many individuals ; separated from third lateral tooth by small, U-shaped incision. Third lateral tooth small, triangular, projecting outwards ; outer margin with rounded granules ; hidden under carapace hair in many specimens.

Carapace surface entirely covered by medium sized granules, central gastric region only sparsely covered ; with variable amount of hair (centred mainly in furrows and laterally, but some specimens almost hairless, and others covered excepting central gastric, cardiac and intestinal areas) ; with deep wide furrows, especially circum-gastric, often partly concealed by hair ; with four granular and hairy rows on each

branchial region—transverse row, often inconspicuous, extending across region from level of third lateral tooth, smaller transverse row above insertion of fourth pereopod, two longitudinal rows, inner sinuous, subparallel to each other and to posterolateral carapace margin. Greatest carapace breadth across second lateral teeth, behind which lateral margins parallel or somewhat convergent. Lateral margins with rounded granules and long hairs.

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

Male cheliped. (a) *Merus*. All three margins with fine granules completely obscured by thick hair. Inner and lower surfaces completely hidden under thick mats of hair ; outer surface with dense hair near upper margin and scattered hair over remainder. No conspicuous granules on any surfaces.

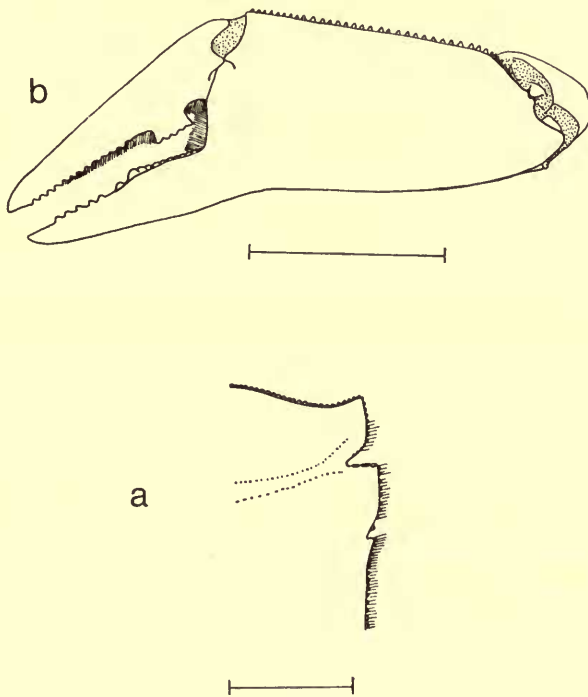


FIG. 7. *M. depressus*—a, anterolateral carapace teeth, b, left male chela (outer surface).
Scale lines—a 5 mm, b 1 cm.

(b) *Carpus*. Elongate. Both margins and inner surface completely obscured by thick mat of hair, beneath which no conspicuous granules. Outer surface finely granular over upper half, smooth over lower.

(c) *Palm*. Moderately heavy. Upper margin with longitudinal row of pointed granules ; lower margin finely granular. Outer surface finely granular, without longitudinal ridge near lower margin (see Fig. 7b) ; inner surface with fine granules completely obscured by thick hair covering whole surface.

(d) *Index*. Deflexed. Outer surface finely granular ; inner surface completely hidden by thick hair, beneath which finely granular. Lower margin with fine granules, densest proximally ; cutting margin with very long, low, crenulated tooth extending from base for a distance equal to more than half the margin's length, distally with rounded or pointed granules.

(e) *Dactylus*. Slightly curved. Upper margin and outer surface finely granular ; inner surface completely obscured by thick mat of hair (hair mats on inner surfaces of palm, index and dactylus continuous) ; cutting margin with large, quadrangular, crenulated tooth near base, with pointed granules distally.

Pereiopod meri with all margins and surfaces hidden by thick hair ; hair also over most carpi and propodi to a variable extent.

Male abdomen. Lateral margins of fourth, fifth and sixth segments almost straight ; surfaces of segments sparsely granular. Anterior sternal segments granular and hairy.

External maxilliped. Internal and external margins of ischium almost straight. Internal margin of merus convex ; external margin with large posteroexternal convexity and much smaller anteroexternal convexity ; anterior margin with moderately developed concavity.

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

DIMENSIONS. Carapace length = 0.66 carapace breadth + 0.11 (Standard deviation 0.39), Breadth of front = 0.11 carapace breadth + 0.45 (Standard deviation 0.12).

COMMENTS. This well known species has been remarkably free from controversy, perhaps because the only feature in which it exhibits any marked degree of variation is the degree of carapace hairiness. Kemp (1919) separated a form under the name of *M. teschi* from this species, and the synonymy given above uncritically follows the *status quo* in regarding this species as valid.

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

MATERIAL EXAMINED. 7 ♂♂ (15.0–31.0 mm), 3 ♀♀ (11.0–26.1 mm). B.M. Reg. Nos—74.2, 1900.10.22.294, 1926.5.20.5, 1939.3.19.41–42, 1961.3.20.2 (Paratype).

LOCATIONS. Singapore, China (Chekiang, Shantung, Yanghokou), Japan.

DIMENSIONS. In the equations given below, data from the Australian specimens described by Barnes (1967) have been included.

Carapace length = 0.66 carapace breadth + 0.38 (Standard deviation 0.52), Breadth of front = 0.068 carapace breadth + 1.13 (Standard deviation 0.18).

COMMENTS. All these specimens lack hair on the inner surface of the palm of the male cheliped as is typical of this species, whereas the Australian specimens described by Barnes (1967) possess a narrow band of hair in that region. The second described difference between the two forms of *M. japonicus*, that of a continuous, uninterrupted inner longitudinal branchial row in the Australian specimens, is, however, also shown by the North Chinese material (1939.3.19.41–42). It is probable that this structure

is subject to considerable variation over much, if not all, of the range of this species, as found in other members of this subgenus (e.g. *M. tomentosus*). It would be interesting to examine adults of this species from Singapore (so far only juveniles are known) in order to ascertain the hairiness of the inner surface of the palm. In northern forms hair is lacking, whilst it is present in southern specimens.

3. *Macrophthalmus (Mareotis) tomentosus* Souleyet, 1841

Macrophthalmus tomentosus Souleyet, 1841 : H. M. Edwards, 1852 ; A. M. Edwards, 1873b ; de Man, 1888b ; Alcock, 1900 ; Tesch, 1915 ; Kemp, 1919 ; Balss, 1922 ; Tweedie, 1937 ; Sakai, 1939 ; Barnes, 1967

MATERIAL EXAMINED. 2 ♂♂ (24.4 & 32.7 mm), 2 ♀♀ (25.2 & 26.0 mm). B.M. Reg. Nos—86.52, 1935.3.19.45.

LOCATIONS. Mergui, Amoy.

DESCRIPTION. Front deflexed ; constricted between bases of ocular peduncles ; with deep median furrow, sparsely granular surface, straight or slightly convex anterior margin ; with proximal half of lateral margins granular, remainder smooth.

Upper orbital border curved, slightly forwardly sloping ; margin studded with large rounded granules increasing in size towards external orbital angle. Lower orbital border with inner four fifths of margin straight and bearing large tubercular granules increasing in size towards external orbital angle, with outer fifth abruptly sloping and bearing three or four long, low, flattened granules beneath fringe of long hairs.

Two large and one small anterolateral teeth (see Fig. 8a). External orbital angle large, broad, rectangular, pointed anteriorly, directed outwards and forwards ; anterior margin with granules continuous with those on upper orbital border ; outer margin almost straight, with rounded or moderately pointed granules, margins of the two teeth markedly posteriorly divergent ; separated from second lateral tooth by deep, narrow, U-shaped incision. Second lateral tooth very large, very broad, rectangular, pointed anteriorly, directed outwards and forwards ; anterior margin with few or no granules ; outer margin more or less straight, with moderately pointed granules, outer margins of the two teeth markedly posteriorly divergent, so that posterior portion of the tooth projects well beyond anterior portion, which itself projects well beyond external orbital angle (thereby giving a noticeably narrowed carapace anteriorly) ; separated from third lateral tooth by deep, very narrow, U-shaped incision. Third lateral tooth fairly small, broad, triangular, pointed, directed outwards and forwards ; outer margin with granules as on second lateral tooth ; projecting well beyond latter.

Carapace surface, excepting smooth central gastric region, entirely covered with medium sized granules ; furrows indistinct, excepting well marked circumgastric and circumcardiac ; with very poorly defined transverse granular row extending across branchial region from level of third lateral tooth, with well defined transverse row above insertion of fourth pereopod, with two longitudinal granular rows on each branchial region subparallel to each other and to posterolateral carapace margins,

inner row sinuous and often broken in one or two places anteriorly ; posterolateral branchial region with short sparse hair. Greatest carapace breadth across third lateral teeth, behind which lateral margins parallel or even slightly convex (in which case, greatest carapace breadth occurs further posteriorly). Lateral margins with rounded or moderately pointed granules and short hair. Posterior margin granular.

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

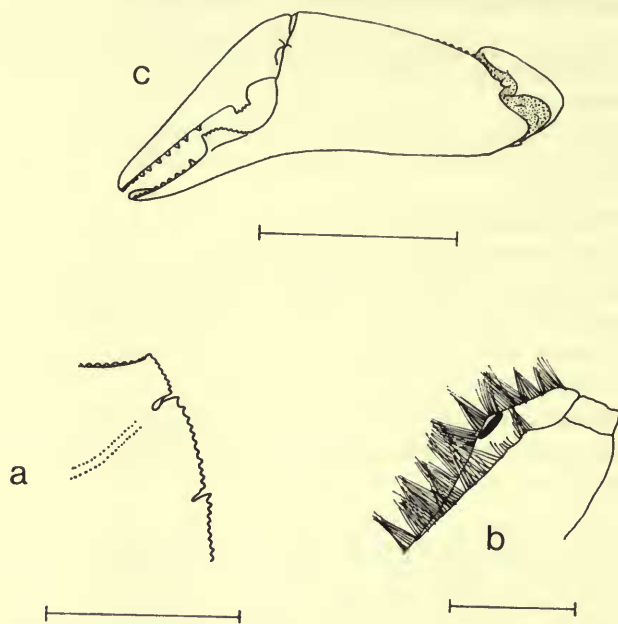


FIG. 8. *M. tomentosus*—a, anterolateral carapace teeth, b, distal region of inner surface of merus of male cheliped, c, left male chela (outer surface). Scale lines—a & c 1 cm, b 5 mm.

Male cheliped. (a) *Merus*. Elongate. Inner margin with row of long hairs ; upper margin with row of pointed granules, largest centrally and distally, and long hairs ; outer margin with scattered pointed granules. Inner surface with row of long hairs near inner margin and diverging from that margin distally, with sparse short hairs over most of surface, with a horny ridge (see Fig. 8b), one eighth the length of the inner margin in length, situated very close to that margin at a distance of about two thirds to three quarters the length of the merus away from the ischium ("musical crest" or "stridulatory ridge") ; outer surface with sparse granules and very short hairs on upper half and near outer margin ; lower surface with scattered granules over half contiguous with outer margin and three large pointed granules near inner margin and ischium.

(b) *Carpus*. Hairless. Upper and lower margins with scattered pointed granules. Outer surface with small pointed granules, except over smooth central area ; inner surface granular and with row of large spines near joint with palm.

(c) *Palm*. Elongate. Upper margin with rows of pointed granules, largest proximally; lower margin finely granular. Outer surface finely granular, granules largest near upper margin and proximally, without longitudinal ridge near lower margin; inner surface more heavily granular, with longitudinal row of hairs near upper margin and with sparse mat of short hair over upper distal region.

(d) *Index*. Markedly deflexed in adults. Outer surface finely granular; inner surface with line of long fine hairs near cutting margin, finely granular proximally, more or less smooth distally. Lower margin finely granular proximally, more or less smooth distally; cutting margin with large, wedged shaped, crenulated tooth in proximal half (see Fig. 8c), with spiniform tubercles in distal half.

(e) *Dactylus*. Slightly curved. Outer surface finely granular; inner surface more heavily granular, with mat of very short hair on proximal half near cutting margin and line of long hairs down centre of surface. Upper margin with fine scattered granules, largest proximally; cutting margin with fairly small, quadrangular, crenulated tooth near base, with row of spiniform tubercles distal to tooth.

Pereiopod meri with thick hair on upper margins and on upper portions of lateral surfaces; anterior lower margins with medium sized, moderately pointed granules; posterior lower margins with large pointed granules. Propodi and carpi of second and third pereiopods with mats of hair; carpi of those appendages with granular ridges.

Male abdomen. Lateral margins of fourth and fifth segments straight, of sixth segment parenthetically convex. Sternal segments granular near abdomen.

External maxilliped. External margin of ischium straight, apart from a distal protuberance at anterior/external margin junction near joint with merus; internal margin slightly concave. Internal margin of merus straight; external margin with marked posteroexternal convexity and very small anteroexternal convexity; anterior margin deeply excised.

First male pleopod slightly curved; with well developed terminal lobe; without hair on internal margin except at tip.

DIMENSIONS. Only four specimens have been examined, but these do not depart from the general pattern seen in *Mareotis* and the changes in shape with increase in size will probably be found to be not too dissimilar to the expressions –

Carapace length = $0.66 \text{ carapace breadth} + 1.0$, and Breadth of front = $0.10 \text{ carapace breadth} + 0.25$.

COMMENTS. This is one of the four *Macrophthalmus* species, representing three different subgenera, possessing a horny ridge on the merus of the male cheliped and a specialised series of tubercles on the lower orbital border, which have been suggested to function as a stridulatory apparatus. Although it is difficult to postulate any other function for this apparatus, none of the species concerned have, as yet, been observed or heard stridulating, and no auditory receptors have, as yet, been located (the sound produced, however, may not have an intraspecific function, but may be “directed” towards other organisms).

Morphologically, the most interesting aspect of these structures is their extreme similarity in the four species, which have presumably evolved them independently

(see *M. pectinipes* and *M. erato*), although *M. erato* and *M. tomentosus* may possibly have inherited them from a common ancestor.

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

MATERIAL EXAMINED. 5 ♂♂ (10.0–30.5 mm), 1 ♀ (10.2 mm). B.M. Reg. Nos—43.6 (Holotype), 1930.12.2.215, 1935.3.19.34–36.

LOCATIONS. Philippines, Hong Kong, Canton.

DIMENSIONS. In the equations given below, data from the Australasian specimens described by Barnes (1967) have been included.

Carapace length = 0.68 carapace breadth + 1.33 (Standard deviation 0.98),
Breadth of front = 0.12 carapace breadth + 0.39 (Standard deviation 0.13).

COMMENTS. The male specimen with the registration number of 1930.12.2.215 is that recorded from Hong Kong by Gordon (1931) as *M. teschi* (although with reservations concerning its specific identity). Its assignment to *M. definitus* has also been suggested by Shen (Unpublished B.M. catalogue notes).

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

MATERIAL EXAMINED. 4 ♂♂ (15.1–23.3 mm), 5 ♀♀ (16.0–24.5 mm). B.M. Reg. Nos—72.7, 1900.12.1.24, 1908.10.27.12–13, 1930.12.2.211–214, 1935.3.19.43–44.

LOCATIONS. Buntal (Malaysia), Hong Kong, Philippines, Formosa.

DIMENSIONS. The dimensions of these specimens do not depart from the equations already given for this species (Barnes, 1968b) by more than one and a half Standard Errors.

COMMENTS. The specimen with the registration number 1900.12.1.24 is that recorded from Buntal, Malaysia, by Lanchester (1900b) as *M. depressus*. As with the previous species, the identity of this specimen as recorded above was also noted by Shen (Unpublished B.M. catalogue notes).

6. *Macrophthalmus (Mareotis) erato* de Man, 1888

Macrophthalmus erato de Man, 1888b : de Man, 1895 ; Koelbel, 1897 ; Alcock, 1900 ; Rathbun, 1910 ; Tesch, 1915 ; Kemp, 1919 ; Tweedie, 1937 ; Chopra & Das, 1937

MATERIAL EXAMINED. 5 ♂♂ (8.2–13.3 mm), 4 ♀♀ (8.5–13.0 mm). B.M. Reg. Nos—86.52, 1937.11.15.162–165, 1939.3.19.39–40.

LOCATIONS. Mergui, Johore, Canton.

DESCRIPTION. Front deflexed ; slightly constricted between bases of ocular peduncles ; with proximal halves of lateral margins granular ; anterior margin bilobed in males, straight or slightly bilobed in females ; with deep median furrow ; sparsely granular surface.

Upper orbital border strongly curved, slightly backwardly sloping ; margin

studded with small, pointed, slightly curved granules, increasing in size towards and inclined towards external orbital angle. Lower orbital border in males, with 3-5 rounded tubercles on inner quarter of border, tubercles increasing in size towards external orbital angle; with one large triangular protuberance, its apex almost immediately above its internal basal angle and with its height smoothly diminishing towards external orbital angle, occupying central half of border; with one or two small triangular protuberances on external quarter (see Fig. 9a). In females, lower orbital border studded with large tubercular granules along whole length, granules largest centrally.

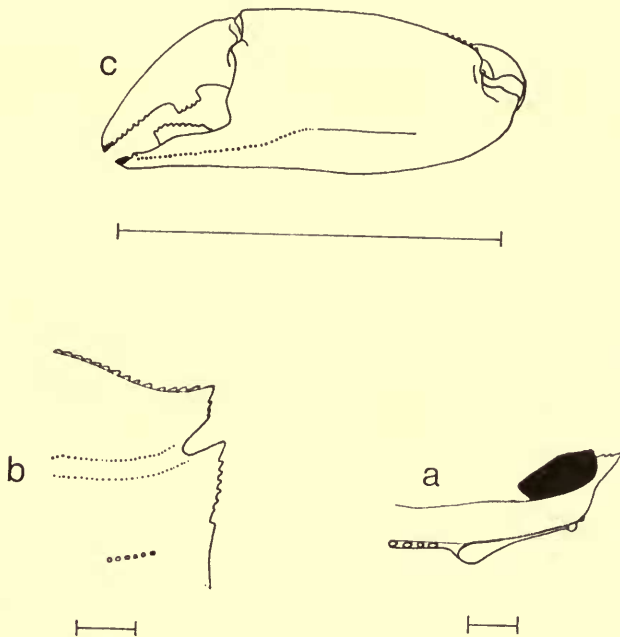


FIG. 9. *M. erato*—a, lower orbital border of male, b, anterolateral carapace teeth, c, left male chela (outer surface). Scale lines—a & b 1 mm, c 1 cm.

Two large and one very small anterolateral teeth (see Fig. 9b). External orbital angle large, broad, subrectangular, directed outwards and forwards, strongly pointed anteriorly; anterior margin with pointed, slightly curved granules continuous with those on upper orbital border; outer margin with a few large pointed granules centrally; separated from second lateral tooth by wide U-shaped incision. Second lateral tooth large, broad, triangular, directed outwards and forwards, projecting beyond external orbital angle, tip strongly pointed; anterior margin smooth or almost smooth; straight or slightly convex outer margin with large, pointed, conical granules along length; posterior half of tooth hidden by carapace hair; separated from third lateral tooth by shallow, almost non-existent, V-shaped incision. Third lateral tooth very small, triangular, with rounded tip, hidden by carapace hair.

Carapace surface covered with small rounded granules, excepting over smooth

central gastric and cardiac regions and over abruptly sloping posterolateral borders, latter covered by thick hair ; with variable amount of scattered hair over remainder out of carapace surface, mainly laterally and in carapace furrows ; with deep distinct furrows demarcating regions ; with convex epigastric ridges, each with row of granules, on each side of median furrow at base of front, in large specimens ; with four indistinct hairy (and sometimes somewhat granular) rows on each branchial region,—very indistinct transverse row extending across anterior branchial region from level of third lateral tooth, short transverse row above insertion of fourth pereopod, and two longitudinal rows subparallel to each other and to posterolateral carapace margins. Greatest carapace breadth across tips of second lateral teeth. Posterolateral margins convex, with row of long hairs concealed by posterolateral carapace hair.

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

Male cheliped. (a) *Merus*. Inner margin with series of large pointed tubercles along length, continuing around distal margin of inner surface, tubercles largest distally ; outer margin with series of similar tubercles ; upper margin with series of large, squat, pointed tubercles along distal four fifths of its length, tubercles largest centrally, and with hair on centre of margin, densest proximally. Inner surface without granules, with patch of hair distally, with line of hairs close to and subparallel with inner margin, with short horny ridge of length about one fifth of that of merus situated close to and just distal to centre of inner margin, ridge mounted on flange extending further distally and making an acute angle with plane of inner surface ; outer and lower surfaces covered by thick short hair, lower surface without granules beneath hair, outer surface with few scattered granules near upper margin.

(b) *Carpus*. Upper and lower margins and outer surface coarsely granular, upper margin with two or three large tubercular spines on central region ; inner surface with row of about six large pointed tubercles on crest running up centre.

(c) *Palm*. Upper margin with series of large, squat, conical granules along length, largest centrally ; lower margin with densely scattered point granules. Outer surface closely covered with small pointed granules, without longitudinal ridge near lower margin, but with line of granules in a similar position in some specimens, the line being only just discernible against the scattered granular background ; inner surface covered by thick hair except over extreme lower proximal area, without noticeable granulation beneath hair except near lower margin where heavily granular, with large spiniform protuberance directed at right angles to surface half way between upper and lower margins and about one third the length of the palm from articulation with carpus.

(d) *Index*. Straight, but slightly deflexed at tip. Outer surface with granules as on palm, without longitudinal ridge, but with line of granules along centre of surface showing greater distinctiveness than that on palm with which it is continuous ; inner surface with thick hair, continuous with that on palm, near cutting margin, smooth near lower margin. Lower margin with granules as on lower margin of palm over proximal half, distal half smooth ; cutting margin with large, long, crenulated, subrectangular tooth, of length just less than half that of margin, in a position just

proximal of central (see Fig. 9c), with few conical granules in centre of remaining distal margin.

(e) *Dactylus*. Curved. Outer surface with granules as on outer surface of palm ; inner surface heavily haired, hair continuous with that of palm. Upper margin with densely scattered, small, pointed granules, continuous with those on outer surface ; cutting margin with large quadrangular tooth, one third the length of margin from base, with series of conical granules distal to tooth.

Pereiopod meri with thick hair on upper margins ; upper lateral surfaces of meri, carpi and propodi of third pereiopods heavily haired, similar surfaces of second pereiopods often heavily haired.

External maxilliped. Internal margin of ischium concave ; external margin straight through much of its length. Internal margin of merus convex ; external margin smoothly convex or with posteroexternal convexity ; anterior margin shallowly excavated.

Male abdomen. Lateral margins of sixth segment smoothly convex, of fourth and fifth segments slightly convex or straight.

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

Epistome with straight central region.

DIMENSIONS. Too few specimens have been examined to gain an accurate impression of the changes in various relative carapace proportions with increase in size of the animals. But, as a guide, the regression equations derived from these specimens are given below.

Carapace length = 0.64 carapace breadth + 0.71 (Standard deviation 0.21),
Breadth of front = 0.12 carapace breadth + 0.70 (Standard deviation 0.10).

COMMENTS. In his descriptions of subgenera of *Macrophthalmus*, Barnes (1967) placed this species in the subgenus *Mopsocarcinus*, on the basis of the published descriptions and figures. However, although the central region of the epistome is not at all excavated, the other morphological features of this species indicate a position within the subgenus *Mareotis*. Of particular significance in this respect are the narrow front, hairy branchial rows, the overall shape of the male chela, the lack of a longitudinal ridge on the outer surface of the male palm, the sculpturing of the external maxilliped and the relative sizes of its component segments, and the approximate value of the growth coefficient.

M. erato shows many affinities with *M. crinitus*, and would appear to be a primitive member of its subgenus, as indicated by the straight epistome, the poorly developed branchial rows, the undeflexed index, and the longitudinal row of granules on the outer surface of the palm (which crowns a ridge in species of *Mopsocarcinus*). Comparison between the description of *M. crinitus* given by Barnes (1967) and the foregoing description of *M. erato* shows the extreme similarity of these two species, the most obvious feature separating them being the stridulatory apparatus of the present species. The spine on the inner surface of the palm in *M. erato* is a further distinguishing character, such spines being unknown in other *Mareotis* species and being otherwise known only in species of the nominate subgenus of *Macrophthalmus*.

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

MATERIAL EXAMINED. 5 ♂♂ (13.6–18.1 mm), 3 ♀♀ (14.8–20.5 mm). B.M. Reg. Nos—1892.4.18.14–16, 1892.4.18.17–20 (part), 1892.4.18.21.

LOCATIONS. Ambon, Ternate, Mindano.

DIMENSIONS. The thirteen specimens of this species known from Australia show changes in their dimensions with size according to the following expressions (Barnes, unpublished).

Carapace length = 0.65 carapace breadth + 0.78 (Standard error 0.17), Breadth of front = 0.12 carapace breadth + 0.34 (Standard error 0.04). These Indonesian specimens differ considerably in their proportions. Their carapace lengths are on average about half a millimetre greater, and their fronts one third of a millimetre broader, than would be expected on the basis of the Australian material. As, however, so few specimens have been examined, little can as yet be concluded from this.

COMMENTS. Other differences between these specimens and the Australian material described previously (Barnes, 1967) can be seen in the structure of the male chela. The juvenile Australian forms possess a longitudinal ridge on the outer surface of the palm and lack a tooth on the index, whilst the only adult examined (13.5 mm) lacked the ridge and possessed a differentiated tooth. The Indonesian forms, although adult and without exception larger than the largest Australian specimen, all show a faint trace of a longitudinal ridge and only the smallest individual possesses a tooth on the index, and then only fully developed on one of the chelae.

C. Subgenus *VENITUS* Barnes, 19671. *Macrophthalmus (Venitus) latreillei* (Desmarest, 1817)

MATERIAL EXAMINED. 5 ♂♂ (9.9–44.0 mm), 4 ♀♀ (24.7–45.2 mm), 1 subfossil of unknown sex (c. 38 mm). B.M. Reg. Nos—60.15, 84.31, 1930.12.2.210, 1931.5.15.32, 1934.1.16.162, 1937.11.15.161, 1954.6.24.1.

LOCATIONS. Gulf of Manaar, Bengal?, Queensland, N.W. Australia, Singapore, Hong Kong, Kobe (Japan).

MATERIAL OF *M. aff. latreillei*. 7 ♂♂ (5.9–21.8 mm), 5 ♀♀ (15.3–19.8 mm). B.M. Reg. No. 1960.6.9.4–10. Philippines.

DIMENSIONS. The dimensions of the above material fall within the range of the expressions given by Barnes (1968b) for this species.

COMMENTS. The variations in structure noted in Australasian material of this species were with respect to (a) the hairiness of the carapace, (b) the tuberculation of the pereopods, (c) the length of the fingers of the male chelae, (d) the pattern of branchial region granulation, and (e) the various changes correlated with increase in size (Barnes, 1967). Comparable variation can be seen in the specimens under consideration here. This is best expressed in tabular form –

Material	Pereiopod tuberculation	Branchial granulation	Carapace hair	Length of fingers
84.31	Absent	Feeble rows	In furrows only	Long
1930.12.2.210	Absent	No rows	In furrows only	Very long
1937.11.15.161	Absent	No rows	Moderately hairy	Short
1931.5.15.32	Marked	Feeble rows	Very hairy	Average
60.15	Absent	Feeble or no rows	Moderately hairy	Moderately long
1934.1.16.162	Absent	Feeble row on 1 side only	Slight	Average

The twelve specimens from the Philippines (1960.6.9.4-10) differ markedly in a number of respects from typical members of *M. latreillei*, these differences being mainly associated with the male cheliped. The palm of the chela is somewhat globose, and the fingers are long (up to half the chelar length), straight, and taper smoothly to a point, the index being inclined upwards in large specimens. The male cheliped is without the thick hair on the inner and outer surfaces of the merus, and on the inner surfaces of the palm, index and dactylus characteristic of *M. latreillei*. The only hair present on the inner surfaces of the chela is a longitudinal row near to and parallel with the upper margins of the palm and dactylus, and a similar row near to and parallel with the cutting margin of the index. The dactylus bears a large, somewhat centrally placed tooth on its cutting margin. In females, the chelae are elongate and of little height. Other differences between the Philippine material and *M. latreillei* are to be found in the anteriorly narrowed carapace, the distribution of carapace hair, the granulation of the posterior carapace margin, and the surface of the third abdominal segment.

Dr. R. Serene has described a number of new species of *Macrophthalmus* in a paper shortly to be published (pers. comm.), and he has kindly provided manuscript descriptions of these species. The 1960.6.9.4-10 specimens clearly belong to one of the new species described by Dr. Serene, and hence they will not be considered further in the present paper.

The material from the Gulf of Manaar (1934.1.16.162) is part of that described and figured by Laurie (1906), and that from Japan (84.31) is part of that discussed by Miers (1886).

2. *Macrophthalmus (Venitus) pectinipes* Guérin, 1839

Macrophthalmus pectinipes Guérin, 1839a : Guérin, 1839b ; H. M. Edwards, 1852 ; Henderson, 1893 ; Ortmann, 1897 ; Alcock, 1900 ; Tesch, 1915 ; Kemp, 1919 ; Chhapgar, 1957
Macrophthalmus simplicipes Guérin, 1839a : Guérin, 1839b ; H. M. Edwards, 1852
Macrophthalmus guerini H. M. Edwards, 1852

MATERIAL EXAMINED. 9 ♂♂ (24.6-73.0 mm), 1 ♀ (40.0 mm). B.M. Reg. Nos—1899.6.17.83-87, 1892.9.16.2-6.

LOCATIONS. Fao (Iraq), Sind (W. Pakistan).

DESCRIPTION. Front deflexed ; markedly constricted between bases of ocular

peduncles ; with smooth margins and surface, markedly bilobed anterior margin, very deep median furrow.

Upper orbital border curved, slightly backwardly sloping ; margin with tall, slender, pointed tubercles, directed somewhat towards external orbital angle, increasing in length slightly towards that tooth. Lower orbital border with about four to six rounded tubercles on inner two ninths of margin ; five or six very large, long, flat protuberances along remainder, inner three or four of which being low triangles in form with rounded apex directly over or very close to inner basal angle of triangle, outer two (i.e. those closest to external orbital angle) more hemispherical ; outer third or quarter of margin with row of hairs (see Fig. 10a) ; in males. In females, inner two thirds of margin with rounded tubercles, outer third with pointed tubercles directed towards front.

Two large and one small anterolateral teeth (see Fig. 10b). External orbital angle large, broad, subrectangular, strongly pointed anteriorly, directed outwards and forwards ; anterior margin with two to four tall, slender, pointed tubercles as on upper orbital border ; tip formed by large, but similar tubercular spine ; outer margin with few, small granules and fringe of long hairs ; posterior margin generally smooth ; separated from second lateral tooth by deep, wide, U-shaped incision. Second lateral tooth large, broad, almost triangular with apex directed outwards, slightly forwards and upwards ; apex formed by large, pointed, tubercular spine ; anterior margin with few rounded granules or smooth ; outer margin more or less straight with evenly spaced, rounded or slightly pointed granules and fringe of long hairs ; separated from third lateral tooth by distinct V-shaped incision (incision and posterior of outer margin obscured by carapace hair). Third lateral tooth small, triangular, pointed, directed outwards and slightly forwards ; outer margin with few rounded granules ; tooth obscured by carapace hair.

Carapace surface with large, tall, scattered tubercles, rounded on central regions and pointed on branchial regions. In adult males, tubercles generally extending over whole carapace, excepting central cardiac and intestinal regions, with a density of approx. 15-20/sq.cm. ; in females and juveniles, tuberculation much less marked, tubercles occurring mainly on branchial regions with only few more centrally. Carapace with deep conspicuous furrows ; with granules on branchial regions ; with thick hair over abruptly sloping sides, hair longest and densest in region of third lateral tooth, and scattered hair in furrows ; without any aggregations of tubercles or granules into clumps and without conspicuous rows of granules, although in some specimens some of the branchial tubercles exhibit some form of longitudinal alignment. Greatest carapace breadth across tips of second lateral teeth, behind which lateral margins subparallel or slightly convergent. Lateral margins with pointed tubercles and row of hairs ; posterior margin smooth or with granules in large specimens.

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

Male cheliped. (a) *Merus*. Extremely elongate. Inner margin developed into a projecting flange, at right angles to inner surface and continuous in a straight line with plane of lower surface, extending over distal five sixths of margin ; flange of

greatest height at extreme proximal end, tapering smoothly distally; on crest of flange a horny ridge, one tenth as long as inner margin; proximal to ridge, margin with few rounded granules and row of long hairs; distal to ridge, double row of large, pointed, tubercular spines, increasing in size distally. Upper margin with row of pointed granules and row of hairs in proximal half, with scattered granules or smooth

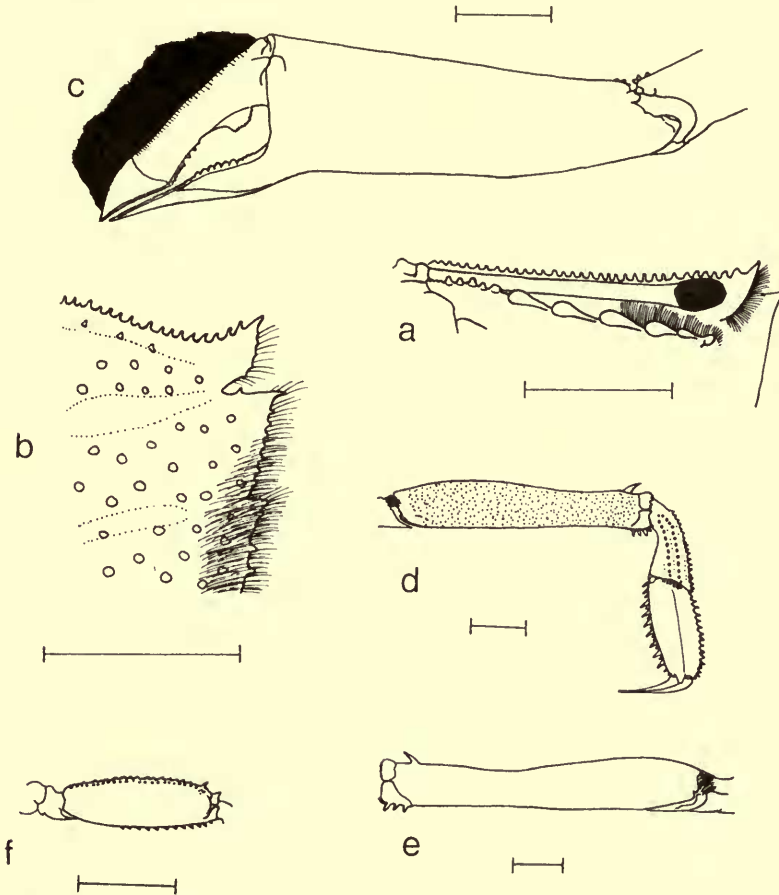


FIG. 10. *M. pectinipes*—a, lower orbital border of male, b, anterolateral carapace teeth, c, left male chela (outer surface), d, third male pereiopod (posterolateral surface), e, merus of third pereiopod of large male (posterolateral surface, with granular detail omitted), f, merus of third pereiopod of juvenile male (posterolateral surface). Scale lines—1 cm.

in distal half; outer margin with dense pointed granules and from seven to ten large, pointed, tubercular granules in row near joint with carpus. Inner surface with scattered rounded granules over distal two thirds or smooth; lower surface with pointed granules over outer half, with variable, short, thin hair over underside of flange; outer surface smooth along central line, with pointed granules and thin short hair near outer margin, with very few small granules and thin short hair near upper margin. Females without flange.

(b) *Carpus*. Upper margin with row of large pointed tubercles ; lower margin smooth. Outer surface smooth, except for a few, small, pointed granules near proximal lower margin and row of similar granules near to and parallel with upper margin ; inner surface with spine near joint with palm, with short fine hair over most of surface, many individuals with scattered pointed granules over upper half.

(c) *Palm*. Elongate. Upper margin with row of broad based, pointed granules, largest proximally ; lower margin finely granular. Outer surface finely granular, without longitudinal ridge near lower margin ; inner surface finely granular, with patch of long hair near distal portion of upper margin, with scattered hair near base of dactylus and above base of index.

(d) *Index*. With extremely elongate tip, deflexed in adults ; with abrupt angulation about half way along the finger in both sexes, so that distal half of index makes an angle of approx. 140° with proximal half, distal half being directed inwards. Outer surface finely granular proximally, smooth distally ; inner surface finely granular, with row of hairs along internal border of markedly spooned cutting margin. Lower margin finely granular ; cutting margin with series of broad pointed granules, joined together at their bases, along anterior half (i.e. as far as angle), forming long low "tooth", distally without granules but with minute serrations in the horny sheath usually found only at the tip of the finger in other *Macrophthalmus* species, but here extending for approx. half the length of cutting margin.

(e) *Dactylus*. With extremely elongate tip ; curved ; with abrupt angulation almost two thirds of length of dactylus from base in both sexes, as on index. Outer surface finely granular, except at tip where smooth, with long hair near upper margin ; inner surface finely granular near base, smooth distally, with scattered hairs over surface and long hair near upper margin. Upper margin with thick mat of very long hair, often extending for a distance greater than height of dactylus above that finger (see Fig. 10c) ; cutting margin with large, long, rectangular tooth, crenulated at tip, near base, distal to tooth with row of granules as far as angle, from angle to tip with minute serrations in horny sheath as on index.

Pereiopod meri of second and third walking legs large, very elongate (especially the third), all surfaces and margins with close covering of large, rounded or pointed granules, without noticeable hair, with a number of large curved spines on distal margins near joints with carpi, largest ventrally. Carpi of first three pereiopods with longitudinal rows of spines along upper (outer) surface (1st carpus with one row, 2nd with one well developed and two moderately developed rows, 3rd with two well developed and one more feeble row – very large specimens with three or four well developed rows) ; carpi of third pereiopod with a few large spines distally on lower (inner) surface near posterior surface of articulation with propodus. Propodi of second and third pereiopods with row of large curved spines along upper margin ; propodi of third pereiopods with row of very large curved spines along lower margin and with mat of short hair over upper half of anterior lateral surface ; mat also extending over much of upper (i.e. outer, as above) half of anterior lateral surface of carpi. Dactyli broad (see Fig. 10d & e). Fourth pereiopod small, with hair fringed margins, excepting lower margins of merus and carpus.

Male abdomen. Lateral margins of fourth, fifth and sixth segments more or less

straight, those of fourth and fifth segments slightly anteriorly convergent, those of sixth parallel. Sixth segment with slight depression in lateral regions near joint with seventh segment, often associated with slight concavity in lateral margins where affected by the depression. Sides of seventh segment slightly concave, segment otherwise a broad based triangle.

External maxilliped. External margin of ischium straight or slightly sinuous ; internal margin slightly concave. Internal margin of merus straight ; external margin with large, flattened posteroexternal convexity, without anteroexternal convexity ; anterior margin shallowly concave.

First male pleopod curved, with very long terminal lobe directed externally at an angle of approx. 75° to the longitudinal axis of pleopod shaft at tip, without hair on internal margin except at tip, external margin and abdominal surface heavily haired.

Central region of epistome straight.

DIMENSIONS. *M. pectinipes* is the largest species of *Macrophthalmus* by a considerable margin, and is probably the largest ocypodid. The largest of the specimens here examined (73.0 mm) had a total span of approx. 30 cm.

As with *M. erato*, the equations given below can only be a guide, as so few specimens have been examined.

Carapace length = 0.56 carapace breadth + 0.55 (Standard deviation 0.34),
Breadth of front = 0.076 carapace breadth + 0.65 (Standard deviation 0.21).

COMMENTS. Juvenile males differ in several respects from the adults. The most marked feature in which they differ is the comparative "normality" of the pereopod meri (see Fig. 10f & c.f. Fig. 10d & e) as opposed to the highly aberrant adult structure. In addition, they show many (*circa* 18) small rounded granules along the inner section of the lower orbital border (i.e. between the epistome and the triangular plates) ; the greatest carapace breadth across the elongate and pointed external orbital angles ; a lack of marked tuberculation on the carapace surface (the smallest male here examined possessed only a number of small tubercles arranged in a longitudinal row on the branchial region in an equivalent position to the inner row of *Mareotis*) ; and the pereopod meri lack the heavily granular surfaces, but possess a row of spines along the upper margin and a similar row along the posterior lower margin of the 2nd and 3rd meri.

As pointed out by Tesch (1915), the variation in the extent of tuberculation of the carapace and the differences observed between the juveniles and adults, and between the two sexes, in this species have resulted in the description of two such morphs as *M. simplicipes* and *M. guerini*.

D. Subgenus *MOPSOCARCINUS* Barnes, 1967

1. *Macrophthalmus (Mopsocarcinus) bosci* Audouin, 1825

MATERIAL EXAMINED. 28 ♂♂ (2.5–14.5 mm), 24 ♀♀ (4.5–12.7 mm). B.M. Reg. Nos—81.31, 81.37, 82.24, 84.31, 1937.9.21.270–273 (part), 1937.9.21.270–273 (part), 1937.9.21.270–273 (part), 1937.9.21.270–273 (part), 1951.9.13, 1955.6.22.3–5.

1964.7.10.7-8, 1966.1.24.4-7, 1966.1.24.8-13, 1966.1.24.14, 1966.1.25.15, 1966.1.24.16-20, 1966.1.24.21-25 (part), 1966.1.24.21-25 (part), Unregistered.

LOCATIONS. Inhaca, Mozambique, Dar es Salaam, Mombasa, Red Sea, Monte Bello Is (Australia), Low Isles & Three Isles (Gt Barrier Reef), Queensland, Fiji.

DIMENSIONS. The equations given by Barnes (1968b), slightly modified by the incorporation of data from the above specimens are -

Carapace length = 0.77 carapace breadth + 0.21 (Standard deviation 0.21),
 Breadth of front = 0.21 carapace breadth + 0.16 (Standard deviation 0.10).

COMMENTS. The material under the registration number 1937.9.21.270-273 is that collected by the Great Barrier Reef Expedition and recorded by McNeill (1968) under the name of *M. quadratus*. *M. quadratus* is a very inadequately known species, having never been seen since A. M. Edwards (1873b) published his original description of material from New Caledonia. It can, however, be immediately distinguished from *M. bosci* by its possession of a stridulatory apparatus on the lower orbital border and cheliped merus of the male. None of the Barrier Reef specimens possess this apparatus.

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

MATERIAL EXAMINED. 1 ♂ (7.3 mm). B.M. Reg. No. 81.31 (Holotype).

LOCATION. Port Jackson (Sydney).

E. Subgenus *HEMIPLAX* Heller, 1865

Macrophthalmus (Hemiplax) hirtipes (Jacquinot, 1853)

MATERIAL EXAMINED. 4 ♂♂ (7.3-28.0 mm), 4 ♀♀ (6.2-27.9 mm). B.M. Reg. Nos—84.31, 86.56, 1899.7.18.7-8.

LOCATIONS. Dunedin, Queen Charlotte Sound (New Zealand).

DIMENSIONS. The above specimens fit the equations given by Barnes (1968b) within two Standard Errors (length : breadth) and one Standard Error (front : breadth).

COMMENTS. A point of great interest with respect to the subgenus *Hemiplax* is the great similarity displayed by this group to certain sesarmine grapsids, particularly to those of the genera *Metaplax* and *Helice*. This resemblance must have been apparent to Heller (1862), since he described specimens of this species as a new form of *Metaplax*! The similarity is displayed by (a) the shape of the front, (b) the carapace shape, and particularly the shape of the anterolateral teeth, (c) the short, stout ocular peduncles, (d) the shape of the central region of the epistome, (e) the presence of an oblique row of granules on the branchial region of the carapace, extending from the posterior region of the third lateral tooth to a position above the insertion of the fourth pereopod, the rows on the two branchial regions converging posteriorly (this oblique row in *Hemiplax* is not found in other *Macrophthalmus* species), (f) the presence of a transverse granular row extending across the branchial

region from the tip of the third lateral tooth, and a concave granular row immediately above the fourth pereopod insertion, and (g) the breadth of the sixth abdominal segment markedly exceeding the breadth of the base of the seventh segment (again not occurring in other *Macrophthalmus* species).

By virtue of its gross external morphology, *Hemiplax* is, therefore, likely to be confused with these Sesarminae. The structure of the male chela and of the external maxilliped, however, show typical *Macrophthalmus* patterns and depart radically from those of the Sesarminae; its true affinities are also shown by a number of other features in which these grapsids and the Macrophthalminae differ.

It can be seen that, in general, *Hemiplax* has approached the grapsid pattern of gross external morphology, rather than vice versa, which raises the question of why these ocypodids should have evolved such a similar facies to the sesarminae. Answers to such a question can only be sought by a close examination of the ecology and behaviour of the relevant species, the convergent modifications being mainly associated with burrowing and respiration (Garstang, 1897; Verwey, 1930). Undoubtedly, however, the geographical isolation of the *Hemiplax* species from their congeners has been a factor of major importance in their evolution. *M. hirtipes* is, for example, the only ocypodid crab in the New Zealand fauna, and it may be significant that the sole New Zealand ocypodid should so greatly resemble the more plentiful, and presumably more successful, grapsids.

Only two other known species are referable to the subgenus *Hemiplax*: *M. major* (Glaessner), a large (c. 52 mm), subquadrate carapaced species known only from the Lower Pleistocene of New Zealand, and *M. boteltobago* (Sakai), known only from one specimen from Formosa. A third species, as yet undescribed and known only from a Pliocene cephalothorax from New Zealand, may be referable to this subgenus (Glaessner, 1960). Therefore only one *Hemiplax* species is known from a region other than New Zealand, and from a region in which other members of the Ocypodidae are also present. Serene (pers. comm.), however, is of the opinion that *M. boteltobago* should be assigned to *Mopsocarcinus* and not *Hemiplax*, and if he is correct *Hemiplax* species are known only from New Zealand, a region lacking in other ocypodids.

F. Subgenus *TASMANOPLAX* Barnes, 1967

Macrophthalmus (Tasmanoplax) latifrons Haswell, 1882

MATERIAL EXAMINED. 1 ♂ (24.0 mm), 1 ♀ (21.5 mm). B.M. Reg. No. 1955.3.4. 1-2.

LOCATION. Westernport (S.E. Australia).

DIMENSIONS. The measurements of the above specimens agree, to within one Standard Error, with the expressions given for this species by Barnes (1968b).

DISCUSSION

Descriptions of sixty six different species of crabs referable to *Macrophthalmus* may be found in the literature, of which ten were based on fossil or subfossil remains.

Of one species, *M. laevis* A. M. Edwards, almost nothing is known. Twenty five of the remaining sixty five have been reliably shown to be synonyms, leaving twenty seven probably valid species (including three known only from fossil material) and thirteen doubtful species, of which only between three and six are likely to be valid. This gives a total of between thirty and thirty three valid *Macrophthalmus* species and of between twenty seven and thirty living species (and to the author's knowledge a further five new species are at the moment "in press").

As the author has now examined twenty four of these species, this is a suitable moment to briefly consider what characters are of use to the systematist working on this genus.

Two characters, much used in other brachyuran groups, are of little or no importance in *Macrophthalmus*. These are the morphology of the first male pleopod and colouration, which in this genus is uniform and drab effecting concealment against the uniform, drab background of the frequented mud and sand flats. Excepting the two basic divisions into which the Macrophthalminae can be partitioned (see Barnes, 1967 : 201), which are well characterized by differences in gross pleopod morphology (and for which 'Linearpleopoda' and 'Curvipleopoda', for *Macrophthalmus*, etc., and *Cleistostoma*, etc., respectively, would be apt names at the tribal level), differences between the pleopods at the subgeneric and specific levels are trivial and dwarfed by differences shown by other skeletal elements.

At the subgeneric level, several gross differences in major structural components are apparent. These are : (a) the relative breadth of the front, and to some extent correlated with this the length and cross-sectional diameter of the ocular peduncles, e.g. the growth coefficient of the front as compared with the carapace breadth is c. 0.29 in *Hemiplax*, c. 0.22-0.23 in *Mopsocarcinus*, c. 0.09-0.16 in *Macrophthalmus* (*sensu stricto*), and within the latter range in the three other subgenera ; (b) the length/breadth ratio of the carapace, e.g. the growth coefficient of the length as compared with the breadth is c. 0.43-0.46 in *Macrophthalmus* (with the exception of *M. telescopicus*), c. 0.64-0.68 in *Mareotis* (with the exception of *M. setosus*), and c. 0.70-0.78 in *Mopsocarcinus* ; (c) the presence or absence of granular rows or clumps on the carapace ; (d) the gross form of the anterolateral carapace teeth ; (e) the shape of the central region of the epistome ; (f) the sculpturing and relative sizes of the merus and ischium of the external maxilliped ; (g) the presence or absence of a longitudinal ridge on the outer surface of the male chela, and a number of other features of gross chelar form ; (h) the size and tuberculation of the pereopods ; and (i) the shape of the sixth abdominal segment in the male.

The majority of these subgeneric points of difference are those of gross carapace morphology and can be seen in both sexes. They are probably related to the different environments frequented by the different subgenera. For example, *Mareotis* species most commonly occur in predominantly muddy substrates and are frequently estuarine, whilst *Macrophthalmus* (*sensu stricto*) species most commonly occur in substrates containing a fair percentage of 'sand' and are less frequently estuarine (for that reason, if for no other), and *Mopsocarcinus*, of which all species are relatively small, often occurs under stones, etc. Many of the areas of difference enumerated above can be correlated with the demands made on the systems of feeding, burrowing,

respiration, etc, by the various substrates, with due regard for the size of the animal concerned.

Specific differences within the subgenera are of a very different nature. Some species are characterized by the markedly atypical character of one or more structures, e.g. the greatly elongated ocular peduncles of *M. transversus* and *M. telescopicus*, but most species can only be separated with confidence on features shown solely by the male sex. These differences are mainly ones of ornamentation patterns on the cheliped, but again some species can be characterised by the possession of markedly atypical features, e.g. the thin chelae of *M. transversus*, the non-dimorphic chelae of *M. parvimanus*, and the stridulatory apparatus of *M. tomentosus*, *M. erato*, *M. pectinipes* and *M. quadratus*. But before discussing the nature of the specific differences exhibited by the majority of species, brief mention will be made of those features of the morphology of *Macrophthalmus*, which, although they are within certain limits modified in different directions by different species, are subject to considerable variation within a number of individual species and are therefore dubious characters upon which to base specific distinctions, especially if only limited material is available.

Characters subject to variation in *Macrophthalmus* are of three types,—those showing sexual dimorphism, those varying with size of the animal, and those exhibiting differences amongst animals of the same size and sex in a single population (often in practice from a single locality) or in geographically separated populations. The first and second types show many similarities, since juvenile males show many resemblances to adult females, but small and large adult males also often differ considerably. Further, some characters which vary on an age or a sex basis also vary geographically and within localities. Characters subject to such variation are: degree and extent of carapace granulation and hairiness, shape and orientation of anterolateral carapace teeth (especially with size), shape of anterior margin of front, relative carapace and chela proportions (the former with size, the latter with size and sex), hairiness of the male cheliped, degree of surface granulation of the male cheliped, size and shape of the teeth on the cutting margins of the male chela, extent of granulation and/or tuberculation of the pereopods, etc. Some characters are particularly variable in particular species, e.g. length of ocular peduncle and relative sizes of the anterolateral teeth in *M. telescopicus*, shape of the anterolateral teeth in *M. latreillei*, and carapace surface and pereopod granulation and tuberculation in *Venitus*.

What then remains for use as specifically diagnostic characters? Many of the variable characters briefly outlined above vary within fairly well defined limits and usually such characters can be utilized (with caution) if only adult males are made the basis of the classification. In *Macrophthalmus* (*sensu stricto*) and *Mareotis*, which contain between them some seventy percent of the probably valid living species of this genus, closely related species (i.e. those sharing a very similar morphological facies) without exception show constant differences of type or range in various features of their male chelipeds. These differences include the presence or absence of a large tubercle on the inner surface of the palm (in *Macrophthalmus*); the presence, number, or absence of spines on the inner surface of the carpus; the granulation

and tuberculation on the various surfaces and margins of the merus and index ; the size, number and distribution of granules on the outer surface of the palm ; the degree of deflexion of the index ; the presence or absence of differentiated teeth on either finger ; and (with caution) the distribution of hair on the cheliped ; in addition to the relative lengths and heights of the constituent segments. Other distinguishing features can be noted from the preceding systematic account. The other subgenera show similar differing characteristics, but as they contain few species each, the problem is not nearly so acute.

The features by which the various species differ and which are subject to least variation are then those manifested by the male chelipeds, whilst the females and juveniles of some species can only be identified with difficulty and uncertainty. It is tempting to draw parallels between this genus and other ocypodids, such as *Uca*, in which much of the taxonomy is based on the detailed structure of the male chelae. The latter appendages are used in behavioural exchanges intraspecifically and may function as specific isolating mechanisms. Few *Macrophthalmus* species have had their intraspecifically oriented behaviour investigated and therefore too many parallels cannot legitimately be drawn. But as no other functional significance for the different variations on a granular theme is apparent, either this or "side effects" of predominantly behavioural or physiological genes remain the most probable explanations of these specific distinguishing characters.

TAXONOMIC CONCLUSIONS

1. *M. sulcatus*, *M. sandakani* and *M. malaccensis* are synonymous and together form a southern and western subspecies of *M. dilatatus*, *M. dilatatus sulcatus*. Lanchester's (1900b) record of *M. carinimanus* is also of this subspecies. *M. dilatatus* (*sensu de Haan*), "*M. malaccensis*" and "*M. sulcatus*" form a series, progressing from north east to south west, along which clinal changes in a number of characters can be discerned.

2. *M. erato* is a primitive member of the subgenus *Mareotis*, and not *Mopsocarcinus* as earlier suggested (Barnes, 1967). It is evidently closely related to *M. crinitus*.

3. The following changes in synonymy are necessary, as the records were based on misidentifications :

Species recorded	Author	Identity of record
<i>M. convexus</i> ("abberant male")	Kemp, 1919	<i>M. parvimanus</i>
<i>M. consobrinus</i>	Crosnier, 1965	<i>M. parvimanus</i>
<i>M. depressus</i>	Lanchester, 1900b	<i>M. pacificus</i>
<i>M. teschi</i>	Gordon, 1931	<i>M. definitus</i>
<i>M. quadratus</i>	McNeill, 1968	<i>M. bosci</i>

4. *M. convexus kempfi* Gravely is synonymous with *M. parvimanus*, a species very closely related to *M. convexus*.

5. *M. malayensis* Tweedie is synonymous with *M. laevimanus* H. M. Edwards.

6. The status of *M. brevis* (= *M. carinimanus*) cannot be fully unravelled at the present time. Lanchester's (1900a) record of *M. crassipes* is not of that species, but may provisionally be grouped with *M. brevis*, although the material is best regarded as *incertae sedis*, together with *M. dilatatus carens* Lanchester, 1900, pending a revision of *M. brevis*.

7. *M. hirtipes* has converged with sesarmine grapsids of the genera *Metaplax* and *Helice* in the structure of a number of carapace features mainly associated with burrowing and reoxygenation of the water in the branchial cavities.

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