BIOLOGICAL RESULTS OF THE SNELLIUS EXPEDITION XXIII. THE GENUS MACROPHTHALMUS (CRUSTACEA, BRACHYURA)

by

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This paper records the species of *Macrophthalmus* (Ocypodidae, Macrophthalmiae) collected by the Snellius Expedition during its exploration of the eastern region of the Malay Archipelago in the years 1929 and 1930. In addition, further material from this area in the collections of the Rijksmuseum van Natuurlijke Historie, Leiden, is included.

Full descriptions, figures and synonymies are given for those species recorded below which have not previously been covered by this author in his survey of *Macrophthalmus* (see Barnes, 1966a; 1966b; 1967; 1968a; 1970). To facilitate this, material of these species has also been examined from the collections of the National Museum, Singapore, the Muséum National d'Histoire Naturelle, Paris, and the British Museum (Natural History), London.

A full account of the localities mentioned below in connection with material from the Snellius Expedition has been given by Boschma (1936).

Sixteen species are included in this report; those redescribed are indicated by an asterisk in the list given below.

М.	abercrombiei Barnes	2	specimens
М.	bosci Audouin	36	"
* М.	brevis (Herbst)	3	**
М.	convexus Stimpson	48	,,
М.	crassipes H. M. Edwards	23	,,
*М.	crinitus Rathbun	39	,,
М.	definitus Adams & White	15	,,
* М.	dentatus Stimpson	I	,,
М.	erato De Man	4	,,
* М.	graeffei A. M. Edwards	2	,,
М.	latreillei (Desmarest)	2	,,
*М.	quadratus A. M. Edwards	6	"
М.	telescopicus (Owen)	7	,,
*М.	teschi Kemp	2	**
М.	tomentosus Souleyet	11	"
М.	sp. nov.	5	55

The species recorded from Darwin, Australia, and described by Barnes (1967) as *M. crinitus*, is not of that species. Here *M. crinitus* is redescribed, and the Australian material is described as a new species.

The author wishes to record his gratitude to the directors of the museums stated above for allowing the examination of material in their charge, and wishes in particular to thank Dr. L. B. Holthuis (Leiden), Dr. R. Serène (Singapore), Mme. D. Guinot (Paris), and Dr. A. L. Rice (London) for their help during this investigation.

Macrophthalmus Latreille, 1829 Subgenus Macrophthalmus Latreille, 1829 1. Macrophthalmus (Macrophthalmus) brevis (Herbst, 1804)

Cancer brevis Herbst, 1804.

Macrophthalmus brevis (Herbst): Tesch, 1915; Kemp, 1919; Tweedie, 1937; Barnes, 1970. nec Macrophthalmus brevis - Hilgendorf, 1869; De Man, 1880; Nobili, 1906.

Macrophthalmus carinimanus H. M. Edwards, 1837: Gray, 1847; H. M. Edwards, 1852; De Man, 1880; De Man, 1890; Ortmann, 1897; De Man, 1902.

nec Macrophthalmus carinimanus - Bianconi, 1851; Hilgendorf, 1878; Haswell, 1882; Lanchester, 1900b; McNeill, 1962.

Macrophthalmus simdentatus Shen, 1936.

Macrophthalmus travancorensis Pillai, 1951.

Macrophthalmus dilatatus carens Lanchester, 1900a.

Macrophthalmus sp. nov. Pillai, 1949.

Macrophthalmus crassipes H. M. Edwards: Lanchester, 1900a; Tweedie, 1937.

nec Macrophthalmus crassipes - H. M. Edwards, 1852; etc.

Snellius Expedition

Paleleh, Celebes; 22/viii/1929 - 2 8, 1 9.

Description (based on the above and material from the National Museum, Singapore). — Front deflexed, markedly constricted between bases of ocular peduncles; with smooth margins, straight or slightly bilobed anterior margin, smooth surface, faint median furrow.

Upper orbital border curved, somewhat backwardly sloping; margin beaded by small rounded granules. Lower orbital border serrated by large, widely spaced, tubercular granules, with one or two smaller pointed granules often alternating with the large.

Two large and one small anterolateral teeth. External orbital angle large, elongate, pointed, directed outwards and forwards (extent of forward orientation varying with age — in juveniles tooth aligned markedly forwards, i.e. up to approx. 45°, whilst with increase in size forward orientation decreases, so that in large adults tooth aligned only some 20° forward from the broad carapace axis; precise orientation subject to some variability in all

size groups however); anterior margin straight or slightly concave, with continuation of rounded granulation of upper orbital border; posterior margin convex or angled, with more pointed granules; separated from second lateral tooth by deep, narrow incision in adults, wider and more V-shaped in juveniles. Second lateral tooth large, more or less wedge shaped (see fig. Ia), pointed, directed outwards and forwards, projecting more or less equally with external orbital angle (in juveniles second lateral tooth tends to project slightly beyond external orbital angle, and vice versa in adults); anterior margin straight, with rounded granules; tip formed by tubercle; posterior margin convex, with large, curved, pointed tubercles; separated from third lateral tooth by distinct V-shaped incision. Third lateral tooth small, but distinct, triangular, pointed, often hidden beneath lateral carapace hair, directed outwards and slightly forwards; anterior margin straight, with rounded granules; posterior margin more or less straight, with tubercles as on that of second lateral tooth.

Carapace covered by small to medium sized rounded granules, largest and densest anterolaterally and near furrow separating cardiac and gastric regions, central gastric region almost smooth; with deep, well defined furrows; with distinct raised clumps of granules on branchial regions; without hair except a narrow band concealing lateral margins from level of third lateral tooth to base of third pereiopod; with abruptly sloping sides. Greatest carapace breadth across external orbital angles (in adults) or second lateral teeth (in juveniles), behind which lateral margins convergent. Lateral margins with large, bluntly pointed granules and row of hairs, concealed beneath lateral carapace hair. Posterior margin smooth.

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

Male cheliped. (a) Merus. Inner margin without granules over proximal four fifths, with pointed tubercles or rarely spines around distal angle, with thick hair over all but tuberculated angle; upper margin with fine hair proximally, with large, conical, pointed granules thickly scattered along margin, granules largest centrally; outer margin with small pointed granules on immediately proximal area, with large, scattered, pointed granules between latter and centre of margin, with conical, pointed, tubercular granules in irregular rows along next distal quarter, with single row of large conical tubercles distally, without hair. Inner surface with pointed granules near upper margin, especially distally, with narrow band of thick hair near centre of inner margin, diverging from that margin distally (band of hair occasionally more extensive), remainder smooth; lower surface with thick hair near inner margin, with pointed granules and scattered short hairs over remainder; outer surface with small granules distally, with sparse, scattered, short hairs over more or less smooth remainder.

(b) Carpus. Upper margin with dense rounded granules along whole length, with large, pointed, conical granules centrally, some of which being larger and tubercular, without spine; lower margin smooth proximally, with small, pointed, anteriorly directed granules distally. Outer surface with rounded granules near upper margin, otherwise smooth; inner surface with two large spines in centre, with large, conical, pointed granules above and below spines, with line of thick hairs up surface proximally to granular and spiniferous region.

(c) Palm. Elongate. Outer surface with dense, small, rounded granules over upper half, densest near upper margin, and along centre of anterior



Fig. 1. *M. brevis* (Herbst). a, adult anterolateral carapace teeth; a', juvenile anterolateral carapace teeth; b, outer face of male left chela. Scale lines: a, 5 mm; a', 3 mm; b, 10 mm.

margin, with longitudinal ridge, capped by row of granules, near to and subparallel with lower margin, area immediately above longitudinal ridge smooth, with small pointed granules over region between ridge and lower margin; inner surface with upper and distal region covered by mat of thick hair, underlying surface smooth, with proximal and lower region heavily granular, granules large and bluntly pointed, with large spine near articulation with carpus, with row of large thick hairs near to and parallel with upper margin. Upper margin with pointed granules, decreasing in size distally; lower margin with irregular pointed granules.

(d) Index. Deflexed. Outer surface with fine rounded granules near proximal section of cutting margin, with more strongly marked continuation of longitudinal ridge of palm, capped by row of small granules, with fine granules near lower margin; inner surface with continuation of mat of hair on palm over all but tip and region near lower margin, latter region with small granules. Lower margin with small pointed granules, largest and densest proximally; cutting margin with large, wedge shaped, crenulated tooth in centre and extending back towards base (see fig. 1b), with large rounded tubercles in row distal to tooth (pointed in juveniles).

(e) Dactylus. Curved. Outer surface smooth except for fine granules near upper margin and proximally; inner surface completely covered by mat of thick hair continuous with that on palm. Upper margin with small pointed granules proximally, smooth distally; cutting margin with small, quadrangular, crenulated tooth near base, with row of large, rounded or bluntly pointed tubercles distal to tooth as far as tip (sharply pointed in juveniles).

Pereiopod meri with small rounded granules, subterminal spine, and long fine hairs, densest proximally, on upper margins.

Male abdomen. Lateral margins of fourth and fifth segments slightly convex or straight, with large rounded convexity in morphologically anterior position on lateral margins of sixth segment. Anterior sternal segments and margins of sternal segments adjacent to abdomen granular.

External (3rd) maxilliped. Internal margin of ischium slightly convex or straight; external margin slightly sinuous, but predominantly straight through most of its length. Internal margin of merus convex; external margin with very poorly developed, somewhat flat, postero-external convexity; anterior margin moderately excavated.

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

Dimensions. — Too few specimens of this species have, as yet, been examined to permit any biometrical analyses to be undertaken. However, the

following expressions, derived from the material seen by this author, are given as a guide. Carapace length = 0.38 carapace breadth + 1.98. Breadth of front = 0.14 carapace breadth + 0.50.

Comments. — Much of the confusion surrounding M. brevis has resulted from the differences in orientation of the external orbital angle manifested by juveniles and adults, and from too great a reliance on the ratio of 4:Igiven by De Man (1890) and Tesch (1915) for the relationship between length and height of the palm of the male cheliped. Juveniles of all the brevis group of species (e.g. M. brevis, M. crassipes, M. dilatatus (De Haan)) possess forwardly directed external orbital angles, which are separated from the second lateral teeth by wide incisions. With increase in size in these species, the external orbital angle changes its orientation so that it becomes less forwardly directed and closer to the second lateral tooth. This change occurs at a comparatively small size in M. crassipes and M. dilatatus, but in M. brevis it does not take place until the animal is considerably larger (in the region of 20 mm carapace breadth, but this is subject to some variation). In M. laevimanus H. M. Edwards the juvenile condition is retained into the adult stage.

In juveniles of *M. brevis* the palm of the male cheliped is scarcely longer than high. With increase in size the length of the palm grows with positive allometry so that ratios of length to height of 2:1 and 3:1 are passed through before a final ratio of about 4:1 is attained.

Pillai (1951: 33) in his description of M. travancorensis distinguished that species from M. brevis by (a) the orientation of the external orbital angle, (b) the ratio of length to height in the palm of the male cheliped (3 : I as opposed to 4 : I), and by a few other characters in which he was mistaken as to the anatomy of M. brevis. This lack of knowledge with respect to the structure of adults of M. brevis is understandable in that the material described by De Man (as M. carinimanus) and redescribed by Tesch (from which the species was mainly known) contained no fully adult specimens.

Shen (1936) was apparently unaware of the similarity between his new species, M. simdentatus, and M. brevis, since he regarded it as being close to M. convexus and M. dilatatus, and made no reference to M. brevis. Both M. simdentatus and M. travancorensis are indistinguishable from M. brevis.

M. brevis can be distinguished from the related M. dilatatus by the absence in the former, and presence in the latter, of spines on the margins of the male cheliped merus and large rounded tubercles on the outer surface of the male cheliped palm. The two species are sympatric in part of the Malay Archipelago, M. dilatatus being represented by the malaccensis form of its southern subspecies M. dilatatus sulcatus (see Barnes, 1970). It is notable that this southern subspecies of M. dilatatus differs more from the sympatric M. brevis than does the allopatric northern subspecies M. d. dilatatus (see Mayr, 1965, etc.).

2. Macrophthalmus (Macrophthalmus) telescopicus (Owen, 1839) Snellius Expedition

Reef, Maratoea, Borneo; 14-18/viii/1929 — 2 &, I Q. Shore, Paleleh, Celebes; 22/viii/1929 — 1 &. Manoembai, Aru Islands; 11-14/x/1929 — 1 &. Koedingareng Lompo, Spermonde Archipelago; 3/ii/1930 — 1 Q.

Leiden Museum

In black silty sand, Kaipoeri, Koeroedoe Island, Geelvinck Bay, New Guinea (Stn 507); Natural Sciences Foundation Expedition; 10/ii/1956 – 19.

3. Macrophthalmus (Macrophthalmus) crassipes H. M. Edwards, 1852 Leiden Museum

Sandy beach near Boeti, E. of Merauke, south coast of Western New Guinea; 25/iii/ 1955; L. B. Holthuis, no. 728 – 12 8, 11 9.

4. Macrophthalmus (Macrophthalmus) convexus Stimpson, 1858 Snellius Expedition

Ternate; $25-27/ix/1929 - 1 \ Q$. Sapoeka besar, Postiljon Islands; $21-23/xii/1929 - 4 \ S, 3 \ Q$. Bima, Soembawa; $25/xii/1929 - 7 \ S, 2 \ Q$. Taliaboe, Soela Islands; $18/iii/1930 - 2 \ Q$. Haroekoe, Ambon; $3-7/v/1930 - 14 \ S, 9 \ Q$. Ambon; $11-17/ix/1930 - 1 \ S$. Flores; $18-19/viii/1930 - 1 \ S$. Kaledoepa, Toekang Besi Islands; $27/viii/1930 - 2 \ S, 2 \ Q$.

5. Macrophthalmus (Macrophthalmus) dentatus Stimpson, 1858

Macrophthalmus dentatus Stimpson, 1858: Stimpson, 1907; Rathbun, 1910a; Tesch, 1915.

Snellius Expedition

Dredged from 6-15 metres, Koepang, Timor; 4/xii/1929 - 1 9.

Description (based on material from the National Museum, Singapore). — Front narrow, markedly constricted between bases of ocular peduncles; with smooth margins and surface, straight anterior margin, distinct median furrow.

Upper orbital border curved, backwardly sloping; margin with small granules, rounded on inner quarter, pointed on remainder. Lower orbital border with small pointed granules, increasing in size towards external orbital angle. One very large and three or four smaller anterolateral teeth. External orbital angle very large, elongate, pointed, directed outwards and about 40° forwards, of the shape shown by fig. 2a; anterior margin without granules, posterior margin with small pointed granules; separated from second lateral tooth by distinct V-shaped incision. Remaining lateral teeth smaller, triangular, directed outwards and variably forwards, with small pointed granules on all margins, of somewhat variable relative sizes; separated from each other by V-shaped incisions; teeth occupying anterior four fifths of lateral margins.

Carapace surface smooth and shiny, without hair and without granules except on branchial regions, where five or six very short granular rows, of variable orientation, each composed of from two to six granules, are present



Fig. 2. *M. dentatus* Stimpson. a, anterolateral carapace teeth; b, outer face of male left chela; c, merus and ischium of left external maxilliped. Scale lines: a, b, 5 mm; c, 2 mm.

on each region, three of the rows situated near lateral margin, remaining two or three rows in longitudinal plane of insertion of last pereiopod (i.e. in positions of inner and outer longitudinal granular rows of *Mareotis*); circumgastric furrow conspicuous but not deep, other furrows visible but poorly marked. Greatest carapace breadth across external orbital angles, behind which lateral margins convergent. Posterior margin without granules.

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

Male cheliped. (a) Merus. Extremely elongate. Inner margin with series of pointed granules along length, largest distally, with long hairs over proximal two thirds; upper margin with small pointed granules and short sparse hair over proximal half, smooth over distal half; outer margin with large pointed granules along whole length, proximal granules scattered, distally aligned into one row. Inner and outer surfaces without granules or hairs; lower surface with pointed granules along inner half of distal margin and near proximal section of outer margin, remainder without granules or hair.

(b) Carpus. Elongate, without hair. Upper margin with row of large pointed granules along proximal third, with scattered, small, pointed granules over distal two thirds; lower margin with scattered, medium sized, forwardly directed granules. Outer surface without granules, smooth; inner surface with row of large pointed granules from proximal region of upper margin to distal and lower joint with palm, remainder smooth, without spines.

(c) Palm. Elongate, without hair except on anterior margin between bases of fingers. Outer surface without granules, excepting a number of very fine granules near upper and lower margins, without longitudinal ridge near lower margin; inner surface without granules, excepting a number of very fine granules near upper and lower margins, especially proximally, without spine near joint with carpus. Upper margin with scattered, very fine granules, with row of small, pointed, anteriorly directed granules, largest proximally; lower margin with fine, scattered, pointed granules.

(d) Index. Short, curved, slightly deflexed (see fig. 2b). Outer surface without granules, without longitudinal ridge; inner surface without granules, with row of long silky hairs near cutting margin. Lower margin with very fine granules proximally, smooth distally; cutting margin with large, triangular, smooth sided, spiniform tooth, slightly crenulated or smooth at tip, in centre, with one large and one small lobular protuberances between spiniform tooth and minutely serrated tip, with rounded protuberance between tooth and base (see fig. 2b), tip curved upwards.

(e) Dactylus. Strongly curved. Outer surface smooth, without granules;

inner surface smooth, without granules except near upper margin, with row of hairs near distal section of cutting margin. Upper margin finely granular, except over tip where smooth; cutting margin with small, flat tipped, quadrangular tooth near base, with series of abutting, flat or rounded topped granules extending to pointed and curved tip.

All segments of pereiopods elongate, especially meri. Merus with rows of small, pointed, outwardly directed granules along upper margin, latter with curved subterminal spine; without conspicuous hair, except over distal half of lower surfaces of meri of first and second pereiopods, where situated mat of short hair.

Male abdomen. Lateral margins of fourth segment slightly convex, of fifth segment straight, of sixth segment with large bulge in morphologically anterior half.

External maxilliped. Internal and external margins of ischium more or less straight, distally convergent. Merus broad and of little height; external margin projecting markedly beyond that of ischium; internal margin almost straight; external margin with very large posteroexternal convexity (see fig 2c) grading into slight anteroexternal convexity; anterior margin with shallow concavity.

First male pleopod curved, with moderately developed terminal process, with hair on internal margin near tip.

Central region of epistome broadly protuberant.

Dimensions. — Very little material of this species is known. In the specimens seen by this author the ratio of length to greatest breadth (carapace) ranged from 1:1.89 to 1:1.92 over a size range of 8.9 to 12.3 (mm, carapace breadth), and the breadth of the front to greatest carapace breadth ratio varied from 0.13: 1 to 0.12: 1.

Comments. — M. dentatus is a most atypical species of Macrophthalmus, differing from all other species in that genus in a large number of features, involving the carapace, chelipeds and maxillipeds. The most marked of these peculiarities are: (a) the numerous anterolateral carapace teeth, occupying nearly the whole lateral margin, (b) the shape of the external orbital angle, (c) the numerous short granular rows on the branchial regions, (d) the extremely elongate male cheliped merus (seen also in a species being described by Dr. Serène), (e) the shape of the dactylus and index of the male chela (see fig. 2b), (f) the lobular protuberances on the cutting margin of the index, (g) the smooth spiniform tooth on the index (to some extent paralleled by M. transversus (Latreille)), and (h) the broad low external maxilliped merus (seen in incipient form in some species of the M. telescopicus group?).

Many of these modifications are of structures influenced by burrowing behaviour, i.e. respiratory and feeding systems, in the Brachyura (see Garstang, 1897; Verwey, 1930; etc.). It is here, perhaps, no coincidence that M. dentatus is also atypical in being sublittoral. Although, at the present state of knowledge, the function of these modifications in a sublittoral Macrophthalmus can not be suggested.

The isolated position of M. dentatus, with respect to its morphology, should perhaps be reflected by the establishment of a new subgenus. This author, however, is of the opinion that M. dentatus may have arisen from a 'proto-telescopicus' stock within the subgenus Macrophthalmus (i.e. from a M. graeffei-like species, prior to the elongation of the ocular peduncles), and that, at present, it is more meaningful to retain it in that grouping.

In species of the *M. telescopicus* group (*M. telescopicus, M. graeffei, M. latipes* Borradaile and the afore-mentioned new species) there is a tendency towards the development of a fourth lateral tooth (see Barnes, 1967), there are similarities with respect to the meri of the male cheliped and external maxilliped (see above) to *M. dentatus*, and it is possible to derive the form of *M. dentatus* from a 'proto-telescopicus' stock without serious difficulties. In addition to the length of the ocular peduncles, *M. dentatus* differs from *M. telescopicus*, etc., in the lack of a longitudinal ridge on the outer surface of the male cheliped propodus and in the presence of the short branchial granular rows.

6. Macrophthalmus (Macrophthalmus) graeffei A. M. Edwards, 1873

Macrophthalmus graeffei A. M. Edwards, 1873b: Ortmann, 1897; Laurie, 1915; Tesch, 1918; Barnes, 1970.

nec Macrophthalmus graeffei Ward, 1928. Macrophthalmus convexus - Tesch, 1915 (part); Stephensen, 1946. nec Macrophthalmus convexus Stimpson, 1858; etc.

Snellius Expedition

Dredged from 10-15 metres, Koepang, Timor; 2/xii/1929 — 1 &. Dredged from 6-15 metres, Koepang, Timor; 4/xii/1929 — 1 &.

Description (based on material from the Muséum National d'Histoire Naturelle, Paris, and the British Museum, London). — Front deflexed, markedly constricted between bases of ocular peduncles; with smooth margins, distinct median furrow, straight anterior margin with a concave excavation in mid line.

Upper orbital border backwardly sloping and nearly straight through much of its length; margin beaded by small pointed granules, increasing in size towards external orbital angle, those on outer half of margin directed towards that angle. Lower orbital border serrated by moderately large pointed granules, increasing in size towards external orbital angle.

Three well defined anterolateral teeth (see fig. 3a). External orbital angle large, elongate, narrow based, pointed, directed outwards and very slightly forwards; anterior margin with granules as on upper orbital border; posterior margin smooth; separated from second lateral tooth by wide U-shaped incision. Second lateral tooth large, elongate, with broader base than preceding tooth, pointed, directed outwards and very slightly forwards, projecting from half to three quarters as far as external orbital angle; margins with small pointed granules; separated from third lateral tooth by wide U-shaped incision. Third lateral tooth small, triangular, broad based, bluntly pointed, often hidden in carapace hair, directed outwards and very slightly forwards, projecting from half to one third as far as second lateral tooth; margins with small pointed granules.

Carapace smooth centrally, with small rounded granules on branchial and lateral regions, with three moderately well defined clumps of granules on branchial regions, with hair along extreme lateral borders from level of second or third lateral tooth posteriorly, with sparse hair in furrows; furrows distinct, especially circumgastric. Greatest carapace breadth across external orbital angles. Lateral margins with pointed granules and short hairs, subparallel posteriorly. Posterior margin smooth.

Ocular peduncles long and narrow; cornea extending beyond tips of external orbital angles for no more than half its length. Distal to cornea situated a small, narrow, short, blunt terminal protuberance (similar to that of *Macrophthalmus ceratophorus, Ocypode ceratophthalma, Uca stylifera, Tmethypocoelis ceratophora*, etc., except in incipient form).

Male cheliped. (a) Merus. Upper margin with rows of large, forwardly directed, pointed granules, largest centrally, with short hair over proximal half; inner margin heavily haired over a granular background; outer margin with small, forwardly directed, pointed granules, largest just distal of central. Inner surface without granules, with hair near upper and inner margins; outer surface smooth centrally, with scattered granules near outer margin and near extreme distal end of upper margin, with hair near upper margin proximally and centrally; lower surface with granules over outer half (i.e. that near outer margin), with thick hair over inner half (i.e. that near inner margin).

(b) Carpus. Without hair. Outer surface covered with pointed granules, largest near upper margin, except over proximal central region and in some specimens along central longitudinal axis; inner surface with small scattered granules, with line of small pointed granules along anterior margin, without

tubercles or spines. Upper margin with close covering of large, forwardly directed, pointed granules; lower margin with small, scattered, pointed granules.

(c) Palm. Outer surface with close covering of small rounded granules, except near base of index, with longitudinal ridge, capped by row of granules, near to and subparallel with lower margin, with small semi-circular excavation on anterior margin between bases of fingers; inner surface with three longitudinal bands of granules, one of medium sized, forwardly directed, pointed granules near upper margin, second of similar granules along central axis, third of small, pointed granules near lower margin, the two separating



Fig. 3. M. graeffei A. M. Edw. a, anterolateral carapace teeth; b, outer face of male right chela. Scale lines: a, 5 mm; b, 10 mm.

agranular bands smooth, with long sparse scattered hairs in upper granular band, with band of thick short hair along centre of anterior margin between bases of fingers, without tubercle near joint with carpus. Upper margin covered by medium sized, forwardly directed, pointed granules; lower margin with small, scattered, pointed granules.

(d) Index. Slightly deflexed. Outer surface without hair, with large pointed granules near cutting margin, with well developed continuation of longitudinal ridge of palm close to and subparallel with lower margin (see fig. 3b) bearing many small granules on its crest, granules largest distally, with smooth area between granules near cutting margin and longitudinal ridge, with small scattered granules below ridge; inner surface with band of thick short hair near cutting margin, continuous with that on palm, with more or less smooth remainder. Cutting margin with long, low, crenulated, wedge shaped tooth in central half, with few, large, triangular tubercles distally; lower margin with small, scattered, pointed granules except over tip. Extreme tip of index further deflexed.

(e) Dactylus. Curved. Outer surface with wide band of medium sized pointed granules near upper margin, granules largest distally, with narrow band of medium sized pointed granules near cutting margin, granules large distally where the two bands merge, intervening area centrally and proximally smooth; inner surface with band of short thick hair near cutting margin, with band of small granules near upper margin, largest distally, intervening area smooth. Upper margin with row of large, curved, pointed granules, those in centre largest and tubercular; cutting margin obscured by hair, with very small, scarcely differentiated, quadrangular tooth near base, distally with row of evenly spaced, rounded or pointed tubercles almost to tip.

Upper margins of pereiopod meri granular, with fringe of sparse hair, with subterminal spine.

Male abdomen. Fourth, fifth and sixth segments with convexities in morphologically anterior halves of lateral margins, that on sixth segment most pronounced. First sternal segment granular, second and third with granular abdominal margins.

External maxilliped. Internal margin of ischium convex; external margin smoothly but slightly concave. Internal margin of merus more or less straight; external margin with flattened posteroexternal convexity, with remainder of margin shallowly concave; anterior margin smoothly concave.

First male pleopod straight through terminal two thirds of its length, with well developed terminal process curved through about 90°, without hair on internal margin except at tip.

Dimensions. — The following expressions are intended only as a guide as comparatively few specimens have been examined. Carapace length = 0.53 carapace breadth + 0.34. Breadth of front = 0.12 carapace breadth + 0.32.

Comments. — As pointed out by Barnes (1970), Tesch (1915) was mistaken in synonymising this species with M. convexus; it shows clear affinities with M. telescopicus. The most obvious difference between the latter and M. graeffei lies in the comparatively shorter ocular peduncles of the species under consideration here.

The incipient terminal projection of the ocular peduncle ("style" — von Hagen, 1970) would appear not to be a preservation effect, as was earlier considered possible (Barnes, 1970), since it is present in a number of other specimens (e.g. Paris Museum collection) free from such effects.

Subgenus Mareotis Barnes, 1967

I. Macrophthalmus (Mareotis) tomentosus Souleyet, 1841

Leiden Museum

Soerabaja, E. Java; March 1923; P. Buitendijk — 4 3. Soerabaja, E. Java; Nov. 1926; P. Buitendijk — 2 3. Pasaroean, E. Java; Feb. 1927; P. Buitendijk — 1 3, 1 9. Tandjong Priok, W. Java; May 1927; P. Buitendijk — 1 9. Locality unknown — 1 3, 1 9.

2. Macrophthalmus (Mareotis) definitus Adams & White, 1848

Snellius Expedition

Beach, Bima, Soembawa; 25/xii/1929 - 2 \Im . Taliaboe, Soela Islands; 10/iii/1930 - 6 \Im , 7 \Im .

3. Macrophthalmus (Mareotis) quadratus A. M. Edwards, 1873

Macrophthalmus quadratus A. M. Edwards, 1873a: Tesch, 1915; Barnes, 1967. nec Macrophthalmus quadratus Boone, 1934; McNeill, 1968.

Snellius Expedition

Beach, Manoembai, Aru Islands; 11-14/x/1929 – 2 8, 4 9.

Description (based on the above and part of A. M. Edwards's original material from New Caledonia from the Muséum National d'Histoire Naturelle, Paris). — Front deflexed, slightly constricted between bases of ocular peduncles; with proximal halves of lateral margins granular, deep 18

median furrow, sparsely granular surface; anterior margin bilobed in males, less so in females.

Upper orbital border strongly curved, moderately sloping backwards; margin studded with small, pointed, slightly curved granules, increasing in size towards and inclined towards external orbital angle. Lower orbital border of males with about seven bluntly pointed granules on inner quarter of border, granules increasing in size towards external orbital angle; with three large triangular protuberances, with their apices immediately above their internal basal angles and with their heights smoothly diminishing towards external orbital angle, directed ventrally and occupying remainder of border, protuberance in centre of border (the most internal) largest. Lower orbital border of females regularly studded with large tubercular granules; granules largest towards epistome, but those immediately nearest to latter small.

Two large and one small anterolateral teeth (see fig. 4a). External orbital angle large, broad, almost triangular, strongly pointed anteriorly, directed outwards and forwards; anterior margin with pointed, slightly curved granules continuous with those on upper orbital border over basal half, distal half smooth; outer margin straight, with small pointed granules along posterior section, smooth near tip; posterior margin straight, making a small angle with outer margin, with small rounded granules or smooth; separated from second lateral tooth by wide U-shaped incision. Second lateral tooth large, broad, triangular, directed outwards, projecting slightly less far outwards than former tooth, tip strongly pointed, often formed by large tubercle; anterior margin smooth; convex outer margin with large, pointed, conical granules along length; posterior half of tooth variably hidden by carapace hair; separated from third lateral tooth by small U- or V-shaped incision. Third lateral tooth very small, triangular, with rounded tip, directed outwards, hidden by carapace hair; with conical pointed granules along outer margin.

Carapace surface covered with small rounded granules, excepting over smooth central gastric, cardiac and intestinal regions; with variable amount of short scattered hair on branchial regions and in carapace furrows, hair denser along lateral borders, with distinct furrows demarcating regions, with convex epigastric ridges, each with a row of granules on crest, on each side of median furrow at base of front, with short row of granules above insertion of fourth pereiopod, with moderately distinct transverse alignment of granules extending across anterior branchial region from level of third lateral tooth, variably developed, without longitudinal rows of granules on branchial regions, but with granules in such a position and of such a size as to be possibly regarded as incipient rows. Greatest carapace breadth across tips of external orbital angles, behind which lateral margins straight and slightly convergent. Lateral margins with rounded granules beneath row of hairs, all hidden by posterolateral hair.

Ocular peduncles somewhat short and stout; cornea extending to centre of external orbital angle.

Male cheliped. (a) Merus. Inner margin with short horny ridge, of length about one fifth that of merus, situated close to but just distal of, centre of margin, ridge mounted on short flange, no longer than length of ridge, arising from inner surface at angle of approx. 90°, distal to ridge margin with series of large, curved pointed tubercles continuing around distal margin of inner surface, proximal to ridge series of smaller, conical, pointed tubercles along margin; outer margin with series of large, curved,



Fig. 4. M. quadratus A. M. Edw. a, anterolateral carapace teeth; b, outer face of male left chela. Scale lines: a, 2 mm; b, 5 mm.

pointed tubercles, largest distally; upper margin with similar tubercles, largest centrally, and with moderately dense hair mainly proximally. Inner surface without granules, with thick hair near ridge on inner margin; outer surface with small scattered granules and short thick hair; lower surface without granules, with short scattered hairs.

(b) Carpus. Upper margin with three or four short pointed tubercles on central region, remainder coarsely granular; lower margin moderately granular. Outer surface coarsely granular over upper and lower thirds, less granular centrally and proximally; inner surface with few, pointed, short tubercles in central region, smooth elsewhere.

(c) Palm. Short and high (see fig. 4b). Upper margin with irregular series of small, pointed and rounded granules along length; lower margin with granules as on outer surface. Outer surface very closely covered with small rounded granules, without longitudinal ridge near lower margin, but with line of granules in a similar position only just discernable against the granular background; inner surface covered by thick short hair except over extreme lower proximal area, without granules, tubercles or spines beneath hair.

(d) Index. Straight. Outer surface with granules as on palm, without longitudinal ridge, but with line of granules along centre of surface showing greater distinctness than that on palm, with which it is continuous; inner surface with thick hair proximally, continuous with that on palm, smooth elsewhere. Lower margin more or less smooth; cutting margin with long, low, crenulated tooth along central three quarters to three fifths of margin, of the shape shown by fig. 4b, without further granules.

(e) Dactylus. Curved. Outer surface with granules as on that of palm; inner surface with short thick hair near cutting margin over proximal half, hair continuous with that on palm, without granules. Upper margin with granules as on outer surface; cutting margin with large, almost square, slightly crenulated tooth, one third the length of margin from base, with conical granules distally near tip.

Pereiopod meri with short thick hair along upper margins; upper margin of propodus of third pereiopod with thick hair; without conspicuous hair on other margins and surfaces.

External maxilliped. Internal margin of ischium concave; external margin straight through much of its length. Internal margin of merus convex; external margin smoothly convex, without differentiated convexities; anterior margin markedly excised.

Male abdomen. Lateral margins of fourth and fifth segments straight, of sixth segment with small protuberance in centre of margin.

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

Epistome with straight central region.

Dimensions. — Over the size range examined (7.0-10.1 mm carapace breadth), the carapace length to breadth ratio varied from 1:1.34 to 1:1.48, and the breadth of front to carapace breadth ratio from 0.20:1 to 0.21:1.

Comments. — M. quadratus is in many respects an intermediate between the subgenera *Mopsocarcinus* (into which it was provisionally placed by Barnes, 1967, on the basis of the then available descriptions) and *Mareotis*, and as with other such intermediates the higher taxon to which it is assigned is mainly one of individual preference. In view of the affinities shown by this species to M. erato and M. crinitus, both primitive members of *Mareotis* (see Barnes, 1970, and below), it is here placed in the latter subgenus.

M. quadratus and M. erato differ in the larger and more prominent external orbital angle of the former, in details of the stridulatory apparatuses, in the even more indistinct branchial rows of M. quadratus, in the lack of a spine on the inner surface of the male cheliped palm in that species (useful as a diagnostic character), and in a few details of the granulation and tooth structure of the male cheliped. The similarities between these two species, however, far outweigh these differences, the similarities extending to several seemingly trivial details of cheliped granulation pattern. M. crinitus is perhaps more closely allied to M. erato than to M. quadratus, and can be distinguished from the latter two by its lack of a stridulatory apparatus.

M. quadratus would appear to be a more primitive species of *Mareotis* than even *M. erato* and *M. crinitus*. All three species show primitive characters in the straight central region of the epistome, the undeflexed index, the line of granules along the region adjacent to the lower margin of the propodus, etc. But *M. quadratus* further shows extremely ill defined branchial granular alignments, of what can be described as an incipient character, and further approximates to the *Mopsocarcinus* state in the prominent external orbital angles, across which lies the position of greatest carapace breadth. Although *M. quadratus* is, as stated, more primitive than *M. crinitus* in most of its structure, it is more advanced in details of its cheliped anatomy. In *M. quadratus*, the longitudinal ridge on the outer surface of the male cheliped palm and index (present in *Mopsocarcinus*) is reduced to a row of granules (as it is in *M. erato*), whilst in *M. crinitus* the ridge is retained on the index. This may argue a diphyletic origin for *Mareotis*.

4. Macrophthalmus (Mareotis) erato De Man, 1888

Leiden Museum

Soerabaja, E. Java; Dec. 1927; P. Buitendijk - 1 8, 3 9.

5. Macrophthalmus (Mareotis) crinitus Rathbun, 1913

Macrophthalmus crinitus Rathbun, 1913: Tesch, 1915; Kemp, 1919; Chhapgar, 1957; Barnes, 1970.

nec Macrophthalmus crinitus - Barnes, 1967; Barnes, 1968b. Macrophthalmus pacificus - Rathbun, 1910b. nec Macrophthalmus pacificus Dana, 1851; etc. Macrophthalmus sp. De Man, 1902.

Snellius Expedition

Ternate; 29/ix/1929 — 14 3, 12 9. Beach, Ambon; 6/v/1930 — 1 3, 2 9. Ambon; 11-17/ix/1930 — 4 3, 4 9.

Leiden Museum

Sea Fishery Station, Hollandia-Haven; N.E. Western New Guinea; 28/xii/1954; L. B. Holthuis — I 3, I 2.

Description (based on the above and material in the British Museum, London). — Front deflexed, slightly constricted between bases of ocular peduncles; with proximal halves of lateral margins moderately granular, straight or slightly bilobed anterior margin, deep but narrow median furrow.

Upper orbital border strongly curved and transverse; margin studded with small pointed granules, increasing in size and becoming more sharply pointed towards external orbital angle. Lower orbital border studded along whole length with large, slightly curved, tubercular granules.

Two large and one small anterolateral teeth (see fig. 5a). External orbital angle large, broad, subrectangular, directed forwards and outwards, pointed; anterior margin with pointed granules continuous with those on upper orbital border; straight or convex outer margin with pointed granules; separated from second lateral tooth by wide V-shaped incision. Second lateral tooth large, very broad, directed outwards, projecting beyond former tooth; anterior margin more or less straight, with rounded or pointed granules; convex outer margin irregularly studded with rounded or pointed granules, with row of long thick hairs; whole tooth variably obscured by carapace hair; separated from third lateral tooth by narrow incision. Third lateral tooth small, pointed, directed forwards and outwards; margins with rounded or pointed granules; obscured by carapace hair.

Carapace surface smooth centrally, with scattered granules on branchial

and hepatic regions, with variable short hair over whole surface, densest laterally, with distinct furrows, but only circumgastric deep, with prominent epigastric ridges, with four rows of hairs on each branchial region, often obscured by carapace hair, transverse row extending across anterior branchial region from level of third lateral tooth, short concave row above insertion of fourth pereiopod, two longitudinal rows subparallel to each other and to lateral carapace margin, without granular rows. Greatest carapace breadth across second or third lateral teeth, behind which lateral margins subparallel. Lateral margins with row of long thick hairs, obscured by carapace hair.

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

Male cheliped. (a) Merus. Inner margin completely obscured by thick hair, without granules; upper margin with row of pointed granules and sparse long hair; outer margin with scattered granules proximally, with row of pointed tubercular granules distally, all obscured by thick hair. Inner surface with thick mat of hair distally and near inner margin, otherwise smooth; outer surface with granules proximally and near outer margin, with hair near outer and upper margins; lower surface with mat of hair, underlying surface smooth, without granules.

(b) Carpus. Upper margin with large pointed granules centrally, with scattered rounded granules elsewhere; lower margin finely granular. Outer surface with rounded granules, largest and more pointed near upper margin; inner surface finely granular, with a few pointed tubercular granules near lower margin, with patch of thick hair centrally.

(c) Palm. Short (see fig. 5b). Upper margin with row of small pointed granules; lower margin with scattered small pointed granules. Outer surface with close covering of fine rounded granules, largest and densest near upper margin, without longitudinal ridge in adults, but with line of granules in a similar position only just discernable against the granular background, granular row more marked in juveniles; inner surface with dense hair distally and on upper half, with granules near lower margin.

(d) Index. Straight. Outer surface finely granular, with longitudinal ridge, most marked distally, along centre, bearing row of granules on crest, ridge more marked in juveniles; inner surface with mat of hair near cutting margin, continuous with that on palm, with granules near lower margin. Lower margin finely granular; cutting margin with series of abutting pointed granules along whole length, without differentiated tooth.

(e) Dactylus. Curved. Outer surface finely granular; inner surface with mat of hair. Upper margin with scattered granules; cutting margin with

large, quadrangular, crenulated tooth, one third length of margin from base, with area immediately distal to tooth smooth, with pointed granules in series near tip.

Pereiopod meri with thick hair on upper margins, and posterior lateral surfaces, without hair on lower and anterior lateral surfaces, with subterminal spine on upper margin. Posterior lateral surfaces of carpi and propodi of second and third pereiopods with mat of short hair.

Male abdomen. Lateral margins of fourth segment slightly convex, of fifth segment straight, of sixth segment with central, or morphologically anterior, rounded convexity.

External maxilliped. Internal margin of ischium concave; external margin more or less straight. Internal margin of merus convex; external margin with moderately developed postero-external convexity; anterior margin shallowly concave.



Fig. 5. *M. crinitus* Rathbun. a, anterolateral carapace teeth; b, outer face of male left chela. Scale lines: a, 5 mm; b, 10 mm.

First male pleopod slightly curved, with moderately developed terminal process, with hair on internal margin distally.

Dimensions. — The following expressions have been derived from 45 specimens with a size range of 9.0-20.5 mm (carapace breadth). Carapace length = 0.67 carapace breadth + 1.16. Breadth of front = 0.13 carapace breadth + 0.46.

Comments. — The description and figures given by Barnes (1967) of M. crinitus from Darwin, Northern Australia, are not of that species, but of an allied form described as new below, the two species differing mainly in the structure of the male cheliped.

M. crinitus is a primitive member of *Mareotis*, related to *M. pacificus*, *M. erato*, *M. quadratus* and the new species, as indicated earlier. The comments of Barnes (1967) with respect to the affinities of this species still stand, except for those referring to the longitudinal ridge and teeth of the male chela.

Macrophthalmus (Mareotis) darwinensis sp. nov.

Macrophthalmus crinitus - Barnes, 1967; Barnes, 1968b. nec Macrophthalmus crinitus Rathbun, 1913; etc.

Syntypes: In burrows near low tide, mangrove mudflats, 400 yards from Fannie Bay Hotel, Darwin, Northern Territory, Australia; 14/iii/1966; M. Hamon; Australian Museum Reg. No. P15163 -- 12 3, 1 9.

Description. — A full description of this species has already been given by Barnes (1967: 221-223, fig. 7a-d) under the name M. crinitus. This will not be repeated here, but a short diagnosis will be given differentiating this species from M. crinitus.

"As *M. crinitus* except — margins of front smooth; upper orbital border moderately curved, with rounded granules; anterolateral teeth with rounded granules; male cheliped merus — inner margin with long hair and tubercular granules at distal angle, upper margin with long hair, outer margin with row of large pointed granules, largest distally, without mat of hair, lower surface with large rounded granules beneath mat of hair; male cheliped palm — outer surface without longitudinal ridge or row of granules in adult, with longitudinal ridge in juveniles; male cheliped index — outer surface without longitudinal ridge or row of granules in adult, with longitudinal ridge in juveniles, cutting margin with large, long, crenulated tooth in centre in adults; lateral margins of sixth segment of male abdomen straight; internal margin of ischium of external maxilliped straight; first male pleopod with well developed terminal process." Dimensions. — The following expressions are approximate only, being based on only 13 specimens. Carapace length = 0.65 carapace breadth + 0.78. Breadth of front = 0.12 carapace breadth + 0.34 (Barnes, 1970).

Comments. — M. darwinensis differs from M. crinitus mainly in the structure of the male cheliped. In this it shows an advance over the condition found in M. crinitus. The longitudinal ridge on the palm is confined to the juvenile phase, no trace remaining in the adult, and a differentiated tooth is developed on the cutting margin of the index. The index, however, remains undeflexed and the palm is short. Further primitive features (shared with M. crinitus) are the lack of granular rows on the branchial regions and the unexcavated central region of the epistome.

6. Macrophthalmus (Mareotis) teschi Kemp, 1919

Macrophthalmus teschi Kemp, 1919. nec Macrophthalmus teschi - Gordon, 1931. Macrophthalmus depressus - De Man, 1888; De Man, 1895; Alcock, 1900 (part). nec Macrophthalmus depressus - Rüppell, 1830; etc.

Leiden Museum

Soerabaja, E. Java; Nov. 1926; P. Buitendijk — 1 8, 1 9.

Description (based on the above and material from the National Museum, Singapore). — Front deflexed, constricted between bases of ocular peduncles; with arcuate anterior margin, granular proximal halves of lateral margins, smooth surface, distinct median furrow.

Upper orbital border slightly curved, transversely directed; margin beaded by small rounded granules, those on outer half more pointed and inclined towards external orbital angle. Lower orbital border with small concavity about one third the length of margin from epistomal end, concavity with a few short hairs arising from near its base; inner four fifths straight (with exception of the concavity), with regular series of large, rounded tipped tubercles, outer fifth abruptly sloping, without tubercles.

Two clearly defined and one poorly defined anterolateral teeth (see fig. 6a). External orbital angle small, subrectangular, directed outwards and slightly forwards; slightly concave anterior margin with small rounded granules continuous with those on upper orbital border; slightly convex outer margin with small rounded granules and row of short hairs; posterior margin smooth; separated from second lateral tooth by wide U-shaped incision. Second lateral tooth large, broad, triangular, directed outwards, forwards and upwards, projecting beyond external orbital angle, bluntly pointed

anteriorly; slightly convex anterior margin with small, rounded, outwardly directed granules near tip, basal portion smooth; outer margin slightly convex, with small, rounded or bluntly pointed granules and short hairs along whole length; separated from third lateral tooth by very small V-shaped incision. Third lateral tooth very small, wedge shaped, directed outwards, projecting beyond second lateral tooth, with rounded tip; margins with granules and hairs, as on outer margin of second lateral tooth.

Carapace surface covered by fairly sparsely distributed, medium sized granules, particularly sparse over gastric region, with short fine hair in furrows, with sparse hair variably over carapace surface, particularly concentrated laterally and posteriorly, with few, large, stiff hairs near and on branchial granular rows and on hepatic regions; with four granular and hairy rows on each branchial region, of which hairs are most noticeable (granular nature of rows best detected on a dry carapace) - transverse row extending across anterior branchial region from incision separating second and third lateral teeth, row most clearly demarcated near that incision, short transverse row above insertion of fourth pereiopod, two longitudinal rows subparallel to each other and to lateral carapace margin, of which outer row the better defined, inner row somewhat sinuous anteriorly, --- granules comprising rows of similar size to those on general carapace surface; with deep circumgastric furrow, remaining furrows shallow and often inconspicuous. Greatest carapace breadth across third lateral teeth, behind which lateral margins more or less parallel, with rounded granules and short hairs. Internal border of posterior margin beaded with very small rounded granules.

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

Male cheliped. (a) Merus. Inner margin with medium sized, pointed granules along whole length, with short dense hair mainly distally, with sparse long hairs scattered along length; upper margin with small rounded granules beneath line of long stiff hairs and short dense hair obscuring margin, especially distally; outer margin without hair, with coarse, dense, pointed, medium sized granules along length. Inner surface with short dense hairs and sparse long hairs distally and near distal regions of inner and upper margins, remaining area smooth, without granules; lower surface with hair near distal portion of inner margin, with dense, small to medium sized, pointed granules, largest near outer margin, over all but region near proximal section of inner margin, where smooth, without any mats of hair; outer surface with short hair over upper half, densest near upper margin, with small pointed granules near outer margin, smooth centrally.

(b) Carpus. Upper margin with small spine centrally, with small densely

scattered, rounded granules over whole length, with long hairs and variable short hair proximal to spine; lower margin with short dense hair over more or less smooth background. Outer surface with fine granules, largest and densest near upper margin, region near lower margin almost smooth; inner surface with large pointed granules along anterior margin, largest dorsally, heavily haired.

(c) Palm. Outer surface completely covered by dense fine granules, with



Fig. 6. *M. teschi* Kemp. a, anterolateral carapace teeth and outer region of lower orbital border; b, outer face of male left chela. Scale lines: a, 5 mm; b, 10 mm.

larger pointed granules near proximal region of lower margin, without longitudinal ridge or row of granules near lower margin; inner surface completely covered by mat of thick hair, with medium sized granules beneath the hair near proximal region of lower margin height of granular band progressively diminishing distally, remainder of surface smooth beneath hair, without spine near articulation with carpus. Upper margin with densely scattered fine granules as on outer surface; lower margin with densely scattered, large, pointed granules proximally, granules diminishing in size distally.

(d) Index. Deflexed. Outer surface covered by dense fine granules proximally, granules reduced distally so that tip smooth, without longitudinal ridge or row of granules near lower margin; inner surface with continuation of mat of hair on palm proximally and near cutting margin, region near lower margin without granules or hair. Lower margin with fine granules proximally, smooth distally; cutting margin with large, wedge shaped, crenulated tooth (see fig. 6b) on basal half, distally with irregular, tall or conical, pointed tubercles to tip.

(e) Dactylus. Curved. Outer surface covered by dense fine granules, as over those of palm and index; inner surface completely obscured by mat of thick hair continuous with that on palm. Upper margin with dense fine granules as on outer surface; cutting margin with large, elongate, rectangular, crenulated tooth occupying proximal third to quarter of margin, distally with large, tall, pointed tubercles to tip.

Pereiopod meri with short thick hair along upper margins, not concealing subterminal spines, with very short sparse hair over posterior lateral surfaces, not otherwise haired. Carpi of second and third pereiopods with thick mat of hair concealing posterior lateral surfaces and upper (i.e. outer) portion of anterior lateral surface. Propodi of second and third pereiopods with thick mat of hair concealing anterior and posterior lateral surfaces.

Male abdomen with all but terminal segment fringed with long hairs. Lateral margins of fourth and sixth segments smoothly and slightly convex; of fifth segment more or less straight. Sternal segments with granules over their abdominal halves.

External maxilliped. Internal margin of ischium concave; external margin more or less straight through much of its length. Merus elongate; internal margin straight; external margin with moderately developed posteroexternal convexity grading more or less smoothly into very small anteroexternal convexity; anterior margin with small concavity.

First pleopod somewhat curved, with well developed terminal process curved through about 80°; external margin heavily haired, hair extending over regions of sternal and abdominal surfaces adjacent to external margin; without hair on internal margin except at tip.

Central region of epistome with rounded protuberance.

Dimensions. — Over the size range of 11.5-17.0 mm (carapace breadth) examined, the carapace length to breadth ratio varied from 1:1.44 to 1:1.55, and the breadth of front to carapace breadth ratio from 0.12:1 to 0.14:1.

Comments. — M. teschi is remarkable for the shape of the central region of its epistome. In all the primitive members of Mareotis this region is straight, and in all the advanced members (except M. teschi) it shows a marked concave excavation. M. teschi appears to parallel the species of the subgenus Macrophthalmus, all of which possess a protuberant central region of the epistome. The functions of the differing shapes of this structure are, however, unknown.

7. Macrophthalmus (Mareotis) abercrombiei Barnes, 1966

Leiden Museum

South coast of Frederik Hendrik Island, S.W. Western New Guinea; 10/ii/1955; D. C. Zwollo — 1 &, 1 Q.

Comments. — This is only the second record of this species, originally described from the Gulf of Carpentaria, Northern Australia, the number of specimens of it known now being five.

This material includes the first recorded female M. abercrombiei. The female shows faint longitudinal granular rows on its branchial regions, absent in the male specimens known; the New Guinea material is otherwise similar to that described earlier (Barnes, 1966a).

Subgenus Mopsocarcinus Barnes, 1967 Macrophthalmus (Mopsocarcinus) boscii Audouin, 1825

Snellius Expedition

Mamoedjoe; 5/viii/1929 - 1 &. Beach, Paleleh, Celebes; 22/viii/1929 - 3 &, 2 &. Kera, Timor; 15-16/xi/1929 - 2 &, 2 &. Koepang, Timor; 25/xi/1929 - 1 &. Beach, Ternate; 1-2/iv/1930 - 1 &. Beach, Ternate; 29/ix/1930 - 1 &. Beach, Ternate; 29/ix/1930 - 1 &. Beach, Ternate; 29/ix/1930 - 1 &. Beach, Ambon; 6/v/1930 - 1 &. Ambon; 11-17/ix/1930 - 9 &, 3 &. Ambon; 14/x/1930 - 2 &. Morotai; 1/x/1930 - 2 &. Ende, Flores; $6\cdot8/xi/1930 - 3 \&$.

Subgenus Venitus Barnes, 1967 1. Macrophthalmus (Venitus) latreillei (Desmarest, 1817)

Snellius Expedition

Ake Selaka, Kaoe Bay, Halmaheira; 28/v/1930 - 2 8.

2. Macrophthalmus (Venitus) sp. nov.

Macrophthalmus aff. latreillei: Barnes, 1970.

Leiden Museum

In pasty sand at 5-9 fathoms, in lagoon 1³/₄ miles N.E. of Mios, Woendi Island, Padaido Group, New Guinea (Stn. 484); Natural Sciences Foundation Expedition — 1 8, 4 9.

Description (based on material in the British Museum, London). — Front deflexed, markedly constricted between bases of ocular peduncles; with smooth margins, granular and hairy surface, straight anterior margin, deep hair-filled median furrow.

Upper orbital border strongly curved, slightly backwardly sloping; margin studded with irregular, moderately large, sharply or bluntly pointed granules, with long hairs along whole length. Lower orbital border with rounded or bluntly pointed tubercles, densest and largest near epistome, with long hairs along whole length.

Three well defined anterolateral teeth. External orbital angle moderately large, subrectangular, broad, bluntly pointed, projecting only slightly outwards and very slightly forwards (see fig. 7a); concave anterior margin with rounded granules continuous with those on upper orbital border; outer margin straight or convex, with series of rounded or bluntly pointed granules; separated from second lateral tooth by shallow, wide, U-shaped incision; tooth often hidden by carapace hair. Second lateral tooth moderately large, broad, triangular, with rounded tip, projecting upwards and slightly outwards; whole tooth situated further laterally than external orbital angle; curved margins with rounded or bluntly pointed granules; separated from third lateral tooth by very shallow, wide, U- or V-shaped incision; tooth often hidden by carapace hair. Third lateral tooth smaller than the preceding, broad, triangular or an obtuse protuberance in form, with rounded tip, projecting slightly outwards and somewhat upwards; whole tooth situated further laterally than second lateral tooth; curved margins with small, rounded or bluntly pointed granules; tooth often hidden by carapace hair. No fourth lateral tooth, but nearest granule on lateral margin larger than its fellows and tubercular.

Carapace markedly narrowed anteriorly, heavily granular on elevated

regions excepting over smooth central cardiac, central gastric and intestinal regions, granules largest and densest along borders of circumgastric and circumcardiac furrows, depressed areas of carapace smooth; with thick pelt of long fine hairs over anterior third to half of carapace variably developed, with thick short hair over lateral carapace borders and anterior branchial region; circumgastric and circumcardiac furrows very deep and distinct, remaining furrows poorly developed; without differentiated rows or clumps of granules on branchial region. Greatest carapace breadth across third lateral teeth (or further posteriorly), behind which lateral margins slightly bulging. Lateral margins with close row of large rounded granules and row of short hairs. Posterior margin smooth, but with row of small granules, largest near insertion of fourth pereiopod, very close to and subparallel with that margin in large specimens.

Ocular peduncles long and narrow; cornea projecting to tip of external orbital angle, or slightly beyond latter, but not beyond lateral limit of carapace.

Male cheliped. (a) Merus. Inner margin with few, large bluntly pointed granules, largest centrally, with scattered hairs centrally and thick row of long hairs distally; upper margin with row of long hairs, with scattered, very small granules, with few larger granules in distal half, with moderately large subterminal spine distally; outer margin with scattered, medium sized, bluntly pointed granules, of which distal 6-8 granules largest, tubercular and aligned. Inner surface without granules, except immediately adjacent to upper and inner margins, without hair, except row near central region of inner margin; outer surface with irregular scattering of very small granules, with larger granules close to central and proximal regions of outer margin, with irregular scattering of very short hairs; lower surface with thickly scattered rounded granules, densest near outer margin, without hair, except along extreme distal margin.

(b) Carpus. Upper margin with row of large pointed granules, with long hairs, densest proximally; lower margin with medium sized pointed granules and long hair. Outer surface smooth centrally, with small granules near upper and lower margins, with very short scattered hairs over upper half and proximally, with long hairs near lower margin; inner surface with row of large, long, pointed granules and long hairs up centre, with one or two small conical tubercles above upper end of granular row, remainder smooth.

(c) Palm. Short and high. Upper margin with series of large, conical, pointed granules along proximal half, with smaller rounded granules over distal half; lower margin with fine granules. Outer surface completely covered by fine granules, with larger granules in a narrow band contiguous

with upper margin, without longitudinal ridge or row of granules near lower margin; inner surface with covering of small pointed granules on lower proximal region, with narrow band of small granules contiguous with upper margin, with areas of fine granules interspersed with smooth areas over remainder, without any mats of hair, with a longitudinal row of long hairs close to and parallel with upper margin passing along the surface, without



any spine near joint with carpus, with a few conical granules on anterior margin in clump between bases of fingers.

(d) Index. Straight. Outer surface covered by scattered fine granules, without longitudinal ridge; inner surface with very sparse fine granules, with row of long hairs close to and parallel with cutting margin from base to tip and extending for short distance onto palm. Lower margin smooth; cutting margin with series of granules linearly aggregated to form a long, low, crenulated 'tooth' extending from tip almost to base (see fig. 7b).

(e) Dactylus. Outer surface with sparse very fine granules; inner surface with similar granulation, with continuation of the row of hairs near upper margin of palm along whole length at distance of about one third depth of finger from upper margin. Upper margin with fine granules and short hairs; cutting margin with very large, rectangular, crenulated tooth just proximal of central, with rounded or flat granules distal to tooth.

Pereiopod meri with large, pointed, tubercular granules, row of hairs and subterminal spine on upper margins; with large, pointed, tubercular granules along posterior lower margins. Carpi of second and third pereiopods with row of pointed tubercular granules beneath thick hair on outer (i.e. upper) margin, with rows of pointed tubercular granules along anterior lateral surface, beneath thick hair. Propodi of second and third pereiopods with row of pointed tubercular granules, beneath thick hair, on outer margin, with thick hair on proximal region of anterior lateral surface. Dactyli broad and lanceolate.

External maxilliped. Internal margin of ischium more or less straight; external margin concave proximally, convex distally. Internal margin of merus slightly convex; external margin with slight posteroexternal convexity grading smoothly into convex anterior region; anterior margin moderately excavated.

Male abdomen without transverse ridge across third segment, with lateral margins of fourth and fifth segments more or less straight, with slight convexity just anterior (morphologically) of centre in lateral margins of sixth segment. Sternal segments granular.

First male pleopod more or less straight; with moderately developed terminal process, without hair on internal margin except at extreme tip, with external margin very heavily haired, hair extending over both surfaces.

Comments.

A description of this species is at present in press (Serène, in press). Dr. Serène has kindly provided the author with his manuscript description of the species, from which it is apparent that the Leiden Museum material

and that described earlier (Barnes, 1970) from the Philippines differ in no important details from Dr. Serène's specimens.

A KEY TO THE LIVING SPECIES OF MACROPHTHALMUS

The following key refers only to those 31 living species of this genus seen and redescribed by this author (i.e. Barnes, 1966a; 1967; 1970; present paper; and unpublished redescription of M. latipes) and to four unquestionably valid species (M. boteltobagoe, M. ceratophorus, M. leptophthalmus and a second new species being described by Dr. Serène as yet unexamined. Although, therefore, it is incomplete, in that seven still problematical species are excluded (many of which, however, probably being non valid), it is hoped that it will be of some use, at least until Macrophthalmus has been fully revised.

The key has not been constructed to follow a phylogenetic or systematic sequence, and therefore relative positions within it do not necessarily indicate affinity; instead, obvious, but arbitrary, characters have been used in an attempt to ensure the swift and unambiguous identification of the contained species. This notwithstanding, final identification should always be ascertained by reference to the appropriate specific descriptions.

N.B. Only adult males should be used when attempting to identify species of this genus.

1.	Short horny ridge present on inner margin, or on inner surface near inner margin, of merus of male cheliped; lower orbital border of males with small number of large
1 a .	triangular protuberances occupying at least one fifth of the margin 2. No horny ridge on merus of male cheliped; with lower orbital border of males
	gular protuberances
2.	Carapace and propodus of penultimate pereiopod with large spines or spiniform tubercles
2a.	Carapace and propodus of penultimate pereiopod without large spines or spiniform tubercles
3	Inner surface of palm of male chela with large spine near articulation with carpus
3a.	Inner surface of palm of male chela without spines
4 .	Carapace distinctly narrowed anteriorly; index of male chela markedly deflexed tomentosus Soulevet
4a.	Carapace not narrowed anteriorly (greatest carapace breadth across external orbital angles); index of male chela straight . 5.
5.	Inner surface of palm of male chela with mat of hair; outer surface of palm and index of male chela with row of granules near lower margin. quadratus A. M. Edw.
5a.	Inner surface of palm of male chela without mat of hair; outer surface of palm and index of male chela without row of granules near lower margin .
	boteltobagoe (Sakai)
6.	Ocular peduncles with cornea projecting beyond tip of external orbital angle for at least one third of its length

6a.	Ocular peduncle with cornea not projecting beyond tip of external orbital angle or second lateral tooth (whichever projects the farther) for more than one quarter
7.	of its length, if at all
	on all its margins
7a.	granules and/or tubercles on its margins, but never spines
8.	Terminal segments of last pereiopod flattened and paddle shaped . latipes Borradaile
8 a .	Terminal segments of last pereiopod not especially flattened and not paddle shaped 9.
9.	Ocular peduncles with only part of cornea projecting beyond tip of external orbital angle
9a.	Ocular peduncle with whole of cornea projecting beyond tip of external orbital angle
10.	Ocular peduncle with slender terminal filament distal to cornea. cerato phorus Sakai
10a.	Ocular peduncle without any filament distal to cornea
11.	Four distinct anterolateral carapace teeth; length of merus of male cheliped> carapace length
11a.	Three distinct anterolateral carapace teeth; length of merus of male cheliped <
	carapace length
12.	Carapace with four or five anterolateral teeth, external orbital angle largest and
	marking position of greatest carapace breadth; general carapace surface smooth
	and shiny
1 2a .	Carapace with two to four anterolateral teeth, if four present then carapace
	surface heavily granular and external orbital angle not marking position of
	greatest carapace breadth
13.	Central region of epistome with a protuberance
13a.	Central region of epistome straight or excavated
14.	Inner surface of palm of male chela with spine or spines near articulation
	with carpus
14a.	Inner surrace of paim of male cheia without spines
15.	merus of male cheliped with granules and/or tubercles on its margins, but without
150	Marys of male challened with poince on some or all of its marging discounting any
15a.	around distal angle of inner margin
16	External orbital angle very small and projecting far less outwards than second
10.	lateral tooth arandidieri A. M. Edw.
16a.	External orbital angle large and more or less equiprojecting with second lateral
x ou.	tooth
17.	Index of male chela with two differentiated teeth (one near the tip) on its cutting
	margin; external orbital angle and second lateral tooth separated by wide incision laevimanus H. M. Edw.
172	Index of male chela with one differentiated tooth (without one near tip) on its
. <i>,</i>	cutting margin; external orbital angle and second lateral tooth separated by
18	Second lateral tooth projecting markedly beyond external orbital angle
10.	dilatatus sulcatus H. M. Edw.
18 a .	External orbital angle and second lateral tooth more or less equiprojecting . 19.
19.	Utter surface of paim of male cheia with large nemispherical fubercies over
	upper nair
iya.	hemispherical tubercles crassible H M Fdw
20	External orbital angle larger than and projecting beyond second lateral tooth:

	carapace approx. twice as broad as long; branchial regions with clumps of granules
20a.	External orbital angle smaller than, and not projecting as far as second lateral tooth; carapace approx. one and a half times as broad as long; branchial regions
21	Male chela large and elongate, with clearly differentiated teeth on cutting margins
21a.	Male chela small and feeble (equivalent to those of <i>Macrophthalmus</i> females), with poorly differentiated teeth on cutting margins of the fingers <i>parvimanus</i> Guérin
22.	Index of male chela without a differentiated tooth on cutting margin; outer surface of palm and index of male chela with longitudinal ridge near lower margin .
22a.	Index of male chela with a differentiated tooth on cutting margin; outer surface of palm and index of male chela without longitudinal ridge near lower margin.
23. 222	Merus of external maxilliped subequal; front broad
23a. 24.	Carpus of male cheliped with large pointed protuberance on upper margin.
24a.	Carpus of male cheliped without a protuberance on upper margin . 25.
25.	Carapace surface granular bosci Audouin
25a.	Carapace surface without granules punctulatus Miers
26.	Inner surface of palm of male chela without any mats of hair
26a.	Inner surface of palm of male chela with mat of hair concealing at least part of surface
27.	Dactylus of male chela with very large tooth near centre of cutting margin; inner surface of palm of male chela with longitudinal row of hairs near to, and parallel with upper margin
27a.	Dactylus of male chela with coth near base of cutting margin; inner surface of solar of male chela without row of hairs
28.	Distinct longitudinal rows of granules on branchial regions of carapace; carapace not markedly, narrowed anteriorly
28a.	No longitudinal rows of granules on branchial regions of carapace; carapace markedly parcound anteriorly
29.	Carapace with concave granular row on each protogastric region
202	Carapace without concave granular rows on protograstric region 30.
30.	Greatest carapace breadth across external orbital angles; outer surface of palm and index of male chela with longitudinal ridge near lower margin; index deflexed
30a.	Carapace with greatest breadth situated posterior to external orbital angles; if longitudinal ridge present on outer surface of palm and index of male chela, then
31.	index undeflexed
	depressus Ruppell
31a.	At least part of inner surface of pair of male chela inter irom thick hair . 32.
32.	half; index of male chela deflexed
32a.	chela scarcely, or not at all deflexed

1) *M. japonicus* appears twice in the above key, — the Japanese and Chinese form in couplet 28, and the Australian form in couplet 32.

References

- ALCOCK, A., 1900. Materials for the carcinological fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. Journ. Asiat. Soc. Bengal, 69 (2): 279-486.
- * BARNES, R. S. K., 1966a. A new species of the genus Macrophthalmus Latreille, 1829 (Decapoda: Brachyura: Ocypodidae) from the Gulf of Carpentaria, Queensland. Proc. Roy. Soc. Queensland, 78 (4): 43-47.
 - ----, 1966b. The status of the genus Euplax H. Milne Edwards, 1852; and a new genus, Australoplax, of the subfamily Macrophthalminae Dana, 1851 (Brachyura: Ocypodidae). Aust. Zool., 13: 370-376.
 - -----, 1967. The Macrophthalminae of Australasia; with a review of the evolution and morphological diversity of the type genus Macrophthalmus (Crustacea: Brachyura). Trans. zool. Soc. London, 31: 195-262.
 - -----, 1968a. On the affinities of three fossil ocypodid crabs and their relevance to the time and place of origin of the genus Macrophthalmus (Crustacea: Brachyura). Journ. Zool., London, 154: 333-339.
 - -----, 1968b. Aspects of the Australasian zoogeography of the Macrophthalminae (Brachyura: Ocypodidae). Proc. Linn. Soc. London, 179: 67-75.
 - -----, 1970. The species of Macrophthalmus (Crustacea: Brachyura) in the collections of the British Museum (Natural History). Bull. Br. Mus. nat. Hist. (Zool.), 20 (7): 203-251.
 - BIANCONI, G. G., 1851. Specimina zoologica Mosambicana quibus vel novae vel minus notae animalium species illustrantur, 5: 47-88. (Bononiae).
 - BOONE, L., 1934. Scientific results of the world cruise of the yacht "Alva", 1931, William K. Vanderbilt commanding. Crustacea: Stomatopoda and Brachyura. Bull. Vanderbilt mar. Mus., 5: 1-210.
 - BOSCHMA, H., 1936. Biological Data. The Snellius Expedition, 6: 1-29.
 - CHHAPGAR, B. F., 1957. On the marine crabs (Decapoda: Brachyura) of Bombay State. 2. Journ. Bombay nat. Hist. Soc., 54: 503-549.
 - DANA, J. D., 1851. Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e Classe Reipublicae Faederatae duce, lexit et descripsit. Proc. Acad. nat. Sci. Philad., 5: 247-254, 267-272.
 - GARSTANG, W., 1897. Contributions to marine bionomics. 2. The function of anterolateral denticulations of the carapace in sand-burrowing crabs. Journ. mar. biol. Ass., U.K., 4: 396-401.
 - GORDON, I., 1931. Brachyura from the coasts of China. Journ. Linn. Soc. London, (Zool.), 37 (254): 525-558.

GRAY, J. E., 1847. List of the specimens of Crustacea in the collection of the British Museum. (London).

HAGEN, H.-O. VON, 1970. Zur Deutung langstieliger und gehörnter Augen bei Ocypodiden (Decapoda, Brachyura). Forma et Functio, 2: 13-57.

HASWELL, W. A., 1882. Catalogue of the Australian stalk and sessile eyed Crustacea. (Sydney).

HERBST, J. F. W., 1804. Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten, 3 (4). (Berlin).

HILGENDORF, F., 1869. Crustaceen. In: C. C. VON DER DECKEN, Reisen in Ost-Africa, 3: 69-116, 147. (Berlin).

—, 1878. Die von Herrn Dr. W. Peters gesammelten Crustaceen. Mber. Deutsch. Akad. Wiss. Berl., 1878: 782-851.

KEMP, S., 1919. Notes on Crustacea Decapoda in the Indian Museum. No. 13. The Indian species of Macrophthalmus. Rec. Indian Mus., 16: 383-394.

LANCHESTER, W. F., 1900a. On a collection of Crustacea made at Singapore and Malacca. 1. Crustacea Brachyura. Proc. zool. Soc. London, 1900: 719-770.

-----, 1900b. On some malacostracous crustaceans from Malaysia in the collection of the Sarawak Museum. Ann. Mag. nat. Hist., (7) 6: 249-265.

LAURIE, R. D., 1915. Reports on the marine biology of the Sudanese Red Sea. No. 21. On the Brachyura. Journ. Linn. Soc. London, (Zool.) 31: 407-475.

McNEILL, F., 1962. Crabs of the Sydney foreshores. Aust. Mus. Mag., 14 (2): 37-43.

----, 1968. Crustacea, Decapoda & Stomatopoda. Sci. Rep. Gt Barrier Reef Exped., 7: 1-98.

- MAN, J. G. DE, 1880. On some new species of Gelasimus and Macrophthalmus. Notes Leyden Mus., 2: 67-72.
- —, 1888. Report on the podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum. Part 2. Journ. Linn. Soc. London, (Zool.) 22 (137): 65-129.
- -----, 1890. Carcinological studies in the Leyden Museum. No. 4. Notes Leyden Mus., 12: 49-126.
- —, 1895. Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Zool. Jb. (Syst.), 8: 485-609.
- ----, 1902. Die von Herrn Prof. Kükenthal im Indischen Archipel gesammelten Decapoden und Stomatopoden. Abh. Senckenb. naturforsch. Ges., 25: 467-929.

MAYR, E., 1965. Animal species and evolution. (Harvard).

- MILNE EDWARDS, A., 1873a. Faune carcinologique de la Nouvelle Calédonie. 2. Nouv. Archs Mus. Hist. nat. Paris, 9: 155-332.
- —, 1873b. Description de quelques Crustacés nouveaux du Muséum Godeffroy. Journ. Mus. Godeffroy, 1 (4): 77-88 (253-264).

MILNE EDWARDS, H., 1837. Histoire naturelle des Crustacés, 2: 1-531. (Paris).

----, 1852. Observations sur les affinités zoologiques et la classification naturelle des Crustacés. Ann. Sci. nat. Zool., (3) 18: 109-166.

NOBILI, G., 1906. Faune carcinologique de la Mer Rouge, Décapodes et Stomatopodes. Ann. Sci. nat. Zool., (9) 4: 1-347.

ORTMANN, A., 1897. Carcinologische Studien. Zool. Jb. (Syst.), 10: 258-372.

PILLAI, N. K., 1949. On two new species of crabs from Travancore. Proc. Indian Sci. Congr., 35 (3): 195.

-----, 1951. Decapoda (Brachyura) from Travancore. Bull. Res. Inst. Univ. Travancore, 2c: 1-46.

RATHBUN, M. J., 1910a. The Danish Expedition to Siam, 1890-1907. 5. The Brachyura. K. Danske Vidensk. Selsk. Skr., (7) 4: 303-367. ----, 1910b. Decapod crustaceans collected in the Dutch East Indies and elsewhere by Mr. Th. Barbour in 1906-1907. Bull. Mus. comp. Zool. Harvard, 52: 305-317.

----, 1913. Descriptions of new species of crabs of the family Ocypodidae. Proc. U.S. natn. Mus., 44: 615-620.

RÜPPELL, E., 1830. Beschreibung und Abbildung von 24 Arten kurzschwanziger Krabben als Beitrag zur Naturgeschichte des Rothen Meeres. (Frankfurt).

SERÈNE, R., in press. Bull. Mus. Nat. Hist. nat. Paris.

SHEN, C. J., 1936. On a collection of brachyuran Decapoda from Hainan Island, with descriptions of three new species. Chin. Journ. Zool., 2: 63-80.

- STEPHENSEN, K., 1946. The Brachyura of the Iranian Gulf, with an appendix on the male pleopoda of the Brachyura. Dan. scient. Invest. Iran, 4: 57-237.
- STIMPSON, W., 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit. Pars V. Crustacea Ocypodidae. Proc. Acad. nat. Sci. Philad., 10: 31-40, 93-110.

-----, 1907. Report on the Crustacea, Brachyura and Anomura collected by the North Pacific Exploring Expedition, 1853-1856. Smithson. misc. Coll., 49: 1-240.

TESCH, J. J., 1915. The catometopus genus Macrophthalmus as represented in the collection of the Leiden Museum. Zool. Meded. Leiden, 1: 149-204.

-----, 1918. The Decapoda Brachyura of the Siboga Expedition. 1. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. Siboga Exped., 39c: 1-148.

- TWEEDIE, M. W. F., 1937. On the crabs of the family Ocypodidae in the collection of the Raffles Museum. Bull. Raffles Mus., 13: 140-170.
- VERWEY, J., 1930. Einiges über die Biologie ost-indischer Mangrovekrabben. Treubia, 12: 169-261.
- WARD, M., 1928. The Crustacea of the Capricorn and Bunker Groups, Queensland. Aust. Zool., 5: 241-246.