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A REVIEW OF THE SENTINEL AND ALLIED CRABS (CRUSTACEA: BRACHYURA: MACROPHTHALMIDAE), WITH PARTICULAR REFERENCE TO THE GENUS *MACROPHTHALMUS*

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***ABSTRACT.* –** The systematic position and nature of the erstwhile ocypodid subfamily Macrophthalminae is reviewed; annotated keys to the macrophthalmid subfamilies and genera and to the extant species of the type genus *Macrophthalmus* are provided; and the subgenera and species groups of *Macrophthalmus* are described and discussed.

***KEY WORDS.* –** Ocypodoidea, Grapsoidea, Macrophthalminae, key, phylogeny.

INTRODUCTION

Much has happened with respect to the systematics of *Macrophthalmus* Desmarest, 1823, in the 30+ years since the author completed his revision of the genus and produced a key to its then-known species (Barnes, 1977). Several new species have been described and more is now known about the distribution, morphology, ecology and behaviour of others; several name changes have been made; and allozyme and molecular sequence data have challenged our understanding of relationships both within *Macrophthalmus* and within the larger group to which the sentinel crabs belong (data in Serène, 1977; Lewinsohn, 1977; Manning & Holthuis, 1981; Vannini & Valmori, 1981; Serène, 1981; Henmi, 1984; Tirmizi & Ghani, 1988; Zucker, 1988; Wada & Sakai, 1989; Kosuge, 1991; Takeda & Komai, 1991; Huang, Yu & Takeda, 1992; Karasawa & Matsuoka, 1992; Fransen, 1998; Apel & Türkay, 1999; Kitaura & Wada, 1999; Jennings, McLay & Brockenhoff, 2000; Henmi, 2000; Ng, Wang, Ho & Shih, 2001; Kobayashi & Kato, 2003; Kitaura, Nishida & Wada, 2002; Litulo, 2005; Litulo, Macia & Mantelatto, 2005; Nagai, Watanabe & Naruse, 2006; Schuwerack, Barnes, Underwood & Jones, 2006; Barnes & Davie, 2008; Naruse & Kosuge, 2008; etc., and references cited below). Two new allied genera have also been described (Davie, 1993, 2009) and other genera have been transferred into and out of close relationship with *Macrophthalmus* (see Ng, Guinot & Davie, 2008 and below). This paper seeks to provide a review of the current systematics of the group in the light of these developments, and to provide new keys to its genera and species.

THE FAMILY MACROPHTHALMIDAE

For many years, the genus *Macrophthalmus* and others believed at the time to be related to it were unquestionably regarded as representing a component subfamily of the Ocypodidae Rafinesque, 1815, and were thus thought to be relatively far removed systematically from members of the various genera then considered to form the Grapsidae MacLeay, 1838. Indeed, these two families were placed in different superfamilies (Ocypodoidea and Grapsoidea). This, for example, is the system adopted in the recent classifications of Martin & Davis (2001) and Sakai (2004). Molecular sequence data produced and analysed by Kitaura, Wada & Nishida (2002), however, strongly suggested that *Macrophthalmus* is more closely related to grapsids of the subfamily Varuninae H. Milne Edwards, 1853, and to some genera traditionally regarded as being members of the grapsid subfamily Sesarminae Dana, 1851 (i.e. *Metaplax* H. Milne Edwards, 1852, *Cyclograpsus* H. Milne Edwards, 1837, and *Helice* de Haan, 1833) than it is to any other crab within the Ocypodidae. This includes to the camptandriids that historically (following Tesch, 1918) had also been included within the Macrophthalminae Dana, 1851, until they were removed to form a separate subfamily within the Ocypodidae by Serène (1974) and later in several classifications (following Ng, 1988) to comprise a separate family within the Ocypodoidea. Kitaura et al.'s (2002) conclusions were confirmed by the sequence data of Schubart, Cannicci, Vannini & Fratini (2006) that indicated that *Macrophthalmus* is indeed more closely related to all grapsids, mictyrids and gecarcinids than it is to the typical ocypodid genera *Uca* Leach, 1814, and *Ocypode* Weber, 1795, or to *Heloecius* Dana, 1851. These sequence data

also showed that the erstwhile other ocypodid subfamilies *Camptandriinae* Stimpson, 1858, and *Dotillinae* Stimpson, 1858 (= *Scopimerinae* Alcock, 1900) also nestled within a group of grapsid and gecarcinid lines within the traditional Grapsoidea.

The families Ocypodidae and Grapsidae, let alone the superfamilies Ocypodoidea and Grapsoidea, may therefore have little real systematic or phylogenetic validity as currently constituted (see also Brösing, Richter & Scholtz, 2007). It must be said, however, that although these analyses of sequence data may seem completely to overthrow the systematic and phylogenetic status quo, those systematists actually concerned with the day-to-day business of macrophthalmine, varunine and sesarmine species had long realised how difficult it was in fact to decide wherein some of these species should be placed because of the considerable 'overlap in the familial definitions' (see, e.g., Davie, 1993).

Nevertheless, Ng et al. (2008) have recently strongly defended the traditional morphological basis of the higher systematic units within the thoracotrematan Brachyura and they defiantly retained the superfamilies Ocypodoidea and Grapsoidea, and included *Macrophthalmus* as a component genus of the Ocypodoidea whilst maintaining within the Grapsoidea the grapsid genera associated with *Macrophthalmus* by Kitaura et al. (2002) and Schubart et al. (2006). Their view that a concensus of both molecular and morphological approaches to the question is both possible and will ultimately emerge (Ng et al., 2008: 214), however, is perhaps over-optimistic in the light of controversies that have run for more than 10 years over the relationships on molecular *versus* morphological grounds of some arthropod groups (see, e.g., Giribet & Ribera, 2000; Cook, Yue & Akam, 2005). Pending further phylogenetic analysis of the entire 'Ocypodoidea' and 'Grapsoidea', the Macrophthalmidae seems best regarded as a separate family within the ocypodoid+grapsoid complex of the Thoracotremata Guinot, 1977 or within the Grapsoidea sensu Rathbun (1918) (see Kitaura et al., 2002), and likewise the Varunidae (see Schubart, Cuesta & Diesel, 2000; Schubart, Neigel & Felder, 2000; Schubart, Cuesta & Felder, 2002).

On this basis, the Macrophthalmidae comprises the four genera *Macrophthalmus*, *Australoplax* Barnes, 1966, *Enigmaplax* Davie, 1993, and *Lutogemma* Davie, 2009, together it has been argued (see Ng et al., 2008 for details) with two other genera that have long been regarded as belonging to other taxa entirely: *Ilyograpsus* Barnard, 1955 (hitherto usually placed in the Grapsidae: Grapsinae) and *Tritodynamia* Ortmann, 1894 (of the pinnotherid subfamily Asthenognathinae Stimpson, 1858). In the scheme put forward by Ng et al. (2008), each of the two latter genera is placed in its own subfamily within the Macrophthalmidae, the Ilyograpsinae Stevcic, 2005, and Tritodynamiinae Stevcic, 2005, respectively, whilst the more traditionally recognised macrophthalmid genera then constitute the Macrophthalminae Dana, 1851. Komai & Wada (2008), however, have recently argued strongly that *Ilyograpsus*, together with a related new genus, *Apograpsus* Komai & Wada, 2008, that they erect for a species originally described in *Ilyograpsus*, are even closer to the Macrophthalminae than proposed by Ng et al. (2008) and do not warrant separation from them in a distinct subfamily. Interestingly in the light of the suggested affinity between *Macrophthalmus* and the varunids on molecular grounds, the DNA sequence data of Cuesta, Schubart & Felder (2005) also suggest close relationships between some asthenognathines and the Varunidae; and Ng et al. (2008) transferred the genus *Asthenognathus* Stimpson, 1858 to that family. Further, Ng et al. (2008) considered that although seven species of *Tritodynamia* showed affinity with the Macrophthalmidae, two other species currently included in the genus are more likely to be related to the Varunidae.

The Macrophthalmidae is today restricted to the Indo-West Pacific, although fossil material of *Macrophthalmus* is known from former brackish-water deposits in Europe (Provence, France, and the Austrian Vienna Basin). Remy (1952) thought that *Macrophthalmus* originated in what is now the Mediterranean, although apart from a recent Lessepsian migrant into the eastern part of that sea, the family appears to have become extinct in the region of the Mediterranean basins in the late Miocene or early Pliocene. An Eocene-Oligocene origin considerably further east in the former Tethys Sea was argued by Barnes (1968). Nevertheless, it is curious that within the main subfamily, the Macrophthalminae, three of the four component genera are restricted to Australia, and so is one of the subgenera of *Macrophthalmus* whilst another is known only from New Zealand. Perhaps, as Davie (2009) suggests, the broad-fronted members of the subfamily comprise a separate lineage, that might then have evolved around Australia (although note below that the molecular sequence analysis of Kitaura, Nishida & Wada (2006) places the broad-fronted subgenus *Chaenostoma* as a highly derived form descended from narrow-fronted ancestors within *Macrophthalmus*).

ANNOTATED KEY TO MACROPHTHALMID SUBFAMILIES AND GENERA

1. Carapace without anterolateral teeth, transversely oval or hexagonal with its greatest breadth (which is some twice its length) near posterior carapace margin, and with lateral margins markedly converging anteriorly so that distance between external orbital angles < 60% of greatest carapace breadth; dactyl of external (third) maxilliped large, flattened, articulating at the base of the propodus, so that palp appears biramous .... *Tritodynamia* (Tritodynamiinae)
   [A group of smallish (< 20 mm carapace breadth) crabs restricted to East Asian waters from the South China Sea to the Sea of Japan that typically occur in mud flats as commensals in the burrows of sedentary polychaetes, enteropneusts, etc. Naruse & Ng (2009) are describing a new species of *Tritodynamia* from Singapore. Yang & Tang (2005) give a key to all the species traditionally included and the group is currently being revised by P. J. F. Davie and N. K. Ng.]
   – Carapace with anterolateral teeth, rectangular, with its greatest breadth located anteriorly to posterior carapace margin, and with its lateral margins not markedly converging anteriorly, if at all, so that distance between external orbital angles > 70% of greatest carapace breadth; dactyl of external maxilliped small,

cylindrical, articulating with distal tip of propodus, so that palp is uniramous ..... 2 (Macrophthalminae)

2. Carapace longer than broad ..... *Apograpsus*
[Monotypic for *A. paantu* (Naruse & Kishino, 2006), a minute species of brackish-water crab (< 7 mm in largest carapace dimension) currently known only from the Ryukyu Islands.]
– Carapace broader than long 3

3. Carapace with 4 anterolateral teeth, the first 3 large with external orbital angle and 3rd lateral tooth larger and/or more pointed than 2nd lateral; lateral angle of lower orbital border with S-shaped corner; male cheliped small and with chelae not swollen relative to the pereiopods, with tips of fingers spooned ... *Ilyograpsus*
[A group of very small (< 12 mm carapace breadth) crabs that occur intertidally in marine or more usually estuarine conditions, often in association with mangroves, on mud, under stones or amongst leaf litter in pools, from Mozambique, around the northern shores of the Indian Ocean and the western shores of the Pacific to Japan, to New Caledonia and to Queensland, Australia. The genus, currently containing five species viz. *I. paludicola* (Rathbun, 1909), *I. rhizophorae* Barnard, 1955, *I. nodulosus* Sakai, 1983, *I. vannini* Sawada, Hosogi & Sakai, 2005, and *I. daviei* Komai & Wada, 2008, is treated in detail by Sawada, Hosogi & Sakai (2005) and Komai & Wada (2008).]
– Carapace usually with no more than 3 anterolateral teeth of which only one or both of first 2 large, the 3rd never larger than 2nd, if four (or more) teeth present then male chelipeds large and longer than pereiopods; lateral angle of lower orbital border without S-shaped corner; male cheliped usually large and with greatly developed chelae, but if chelipeds small and chelae not enlarged then carapace without 4 anterolateral teeth 4

4. Cutting margins of the fingers of the male chelae completely obscured in external view by mat of hair; ischium of external maxilliped with line of hairs running transversely across surface in proximal half ..... *Australoplax*
[A monotypic genus restricted to the east coast of Australia; *A. tridentata* (A. Milne Edwards, 1873) being a small (carapace breadth up to 15 mm) inhabitant of intertidal muds, especially those associated with mangroves.]
– Cutting margins of fingers of chelae visible in external view, without obscuring mat of hair; ischium of external maxilliped without transverse line of hairs across surface 5

5. Tips of fingers of chelae not spooned, either pointed or flattened; front either broad (breadth between bases of ocular peduncles > 40% distance between tips of external orbital angles) or, if narrower, then palp of external maxilliped bearing elongate setae extending to sternum 6
– Tips of fingers of chelae spooned; front narrow, its breadth between bases of ocular peduncles < 40% distance between tips of external orbital angles; palp of external maxilliped without elongate setae ..... *Macrophthalmus*
[A widespread and abundant genus occurring throughout the Indian and west and central Pacific Oceans, from South Africa, Red Sea and Arabian Gulf in the west to Sea of Japan in the north, to Hawaii and Tuamotu Archipelago in the east, and to Tasmania and New Zealand in the south, with one species now extending into the eastern Mediterranean as a Lessepsian migrant (Ksiunin & Galil, 2003; Ates, Katagan & Kocatas, 2006). Several subgenera and some 46 species are currently recognized, ranging in size from < 10 to > 80 mm carapace breadth, and in habitat from high in the intertidal zone to >80 m depth in the subtidal, and from rocky shores to very soft muds. There the majority deposit feed on microphytobenthos and/or detrital organics, although some scrape algae from hard substrata (Wada & Wowor, 1989; Kosuge & Davie, 2001) or browse macrophytes (Woods & Schiel, 1997); the consumption of living or dead animal material has also been recorded (Kitaura & Wada, 2005). Species of *Macrophthalmus* most characteristically dominate sheltered, finely particulate, marine, lagoonal and estuarine sediments, both coralline and clastic. Many subtidal species probably await discovery. A key to the males of all living species and subspecies is given below; several others are known only from fossil material, dating back at least to the Miocene. Komai, Goshima & Murai (1995) provide a key to the females of the 17 species that occur on the Andaman Sea coast of Thailand, although not all *Macrophthalmus* females can easily be identified to species.]

6. Front broad, its breadth between bases of ocular peduncles > 40% distance between tips of external orbital angles; palp of external maxilliped without very long setae on inner margins reaching to sternum; legs laterally flattened ..... *Enigmaplax*
[A monotypic genus restricted to the east coast of Australia; *E. littoralis* Davie, 1993, being a very small (carapace breadth < 10 mm) inhabitant of intertidal and shallow subtidal seagrass meadows, algal mats and benthic rocks.]
– Front narrow, its breadth between bases of ocular peduncles < 30% distance between tips of external orbital angles; palp of external maxilliped with very long setae reaching to sternum; legs sub-cylindrical ..... *Lutogemma*
[A monotypic genus restricted to the north coast of Australia; *L. sandybrucei* Davie, 2009, being a very small (carapace breadth < 10 mm) inhabitant of shallow subtidal seagrass meadows and soft sediments in estuaries and the sheltered coastal sea, where it presumably suspension feeds using its peculiar elongate maxillipedal setae.]

ANNOTATED KEY TO LIVING *MACROPHTHALMUS* SPECIES (MALES)

1. With stridulatory apparatus; i.e. with short horny ridge on inner margin, or on inner surface near inner margin, of cheliped merus, & lower orbital border with small number of large triangular protuberances along its outer section occupying at least one fifth of that margin 2
– Without such stridulatory apparatus, although lower orbital border may be regularly serrated by granules 7

2. Carapace and propodus of fourth pereiopod with large spines or spiniform tubercles ..... *M. dentipes*
[Very large (up to 80+ mm carapace breadth) inhabitant of soft mudflats around the Arabian Gulf and Arabian Sea. This species was previously widely known under the name *M. pectinipes* Guérin, 1839 (Holthuis 1995).]
– Carapace and propodus of penultimate pereiopod without large spines or spiniform tubercles 3

3. Inner surface of palm of chela with large spine near articulation with carpus ..... *M. erato*
[Small (< 15 mm carapace breadth) inhabitant of stony mudflats or those with mangrove pneumatophores along the northern shores of the eastern Indian Ocean, eastern Malesia and the South China Sea.]
– Inner surface of palm of chela without spines 4

4. Anterolateral teeth of carapace narrowly separated from each other, their external margins forming a smooth curve .....
..... *M. tomentosus*

[Large (up to 35+ mm carapace breadth) Malesian mudflat species occurring from Andaman Sea and Taiwan, through the Philippines to New Caledonia.]

– Anterolateral teeth, or at least external orbital angles and second lateral teeth, separated from each other by wide V- or U-shaped gap, so anterolateral carapace margins appearing jaggedly toothed 5

5. Inner surface of palm of chela with mat of hair; outer surface of palm and index with row of granules near to and subparallel with lower margin ..... *M. quadratus*
[Small (< 12 mm carapace breadth) inhabitant of burrows or crevices beneath driftwood, stones or around mangrove pneumatophores in scattered localities from Thailand to Ryukyu Islands, and through Malaysia and Indonesia to New Caledonia.]

– Inner surface of palm of chela without mat of hair; outer surface of palm and index without row of granules near lower margin 6

6. Greatest carapace breadth across external orbital angles and/or second lateral teeth; index of chela not deflexed .... *M. boteltobagoe*
[Very small (< 10 mm carapace breadth) inhabitant of holes excavated by e.g. sipunculans in limestone rocks and on gravelly mudflats from Taiwan and the Ryukyu Islands, Hong Kong to New Guinea.]

– Greatest carapace breadth across third lateral teeth; index of chela noticeably deflexed ..... *M. holthuisi*
[Very small (< 10 mm carapace breadth) inhabitant of mud-filled depressions in or around mangrove habitats from the Ryukyu Islands, through Indonesia, to New Guinea.]

7. Ocular peduncles with a thin terminal filament (style) projecting distally beyond the cornea 8

– Ocular peduncles without a style 9

8. Cornea projecting beyond tip of external orbital angles for only half its length at most; style short ..... *M. graeffei*
[Medium-sized (up to ca. 25 mm carapace breadth) species known mainly from scattered sublittoral localities from Samoa, New Caledonia and New Guinea to the Red Sea and Arabian Gulf, and now also established in the eastern Mediterranean from Israel to the Aegean Sea.]

– Ocular peduncles extremely elongate so that whole cornea located well beyond carapace lateral margins; style long (subequal to rest of peduncle in length) and segmented .... *M. ceratophorus*
[Large (up to 45+ mm carapace breadth) species known only from limited sublittoral material from southern Japan to Taiwan and in Seychelles.]

9. Ocular peduncles extremely elongate, at least half of length of cornea located beyond lateral carapace margins 10

– Cornea not extending beyond lateral margin of carapace for half length of cornea, if at all 17

10. Carapace at least twice as broad as long; cheliped merus with long spines on all its margins ..... *M. transversus*
[Medium-sized (carapace breadth up to ca. 25 mm) species known from soft intertidal sediments around the Bay of Bengal, Andaman Sea and Strait of Malacca.]

– Carapace less than twice as broad as long; cheliped merus with or without granules or tubercles but never with long spines 11

11. Ocular peduncle projecting beyond lateral carapace margin for less than 25% of its length, so that cornea located beyond lateral carapace margin for no more than its total length .... *M. ryukyuanus*
[A very small species (up to 10mm carapace breadth) known only from two specimens dredged from a depth of some 20 m off one of the Ryukyu Islands, Japan.]

– Ocular peduncle projecting beyond lateral carapace margin for at least 25% of its length, so that cornea located beyond lateral carapace margin for more than its own length 12

12. Terminal segments of last pereiopod flattened and paddle-shaped; with furrow demarcating the front from remaining carapace ..... *M. latipes*
[Known only from sublittoral material from Seychelles and Maldives; insofar as is known, very small (< 10 mm carapace breadth).]

– Terminal segments of last pereiopod not especially flattened nor paddle shaped; no furrow separating the front from remaining carapace 13

13. With 4 distinct anterolateral carapace teeth; length of cheliped merus > carapace length ..... *M. philippinensis*
[Small (< 12 mm carapace breadth) inhabitant of sublittoral sediments; known only from limited material from the Philippines, Vietnam and Taiwan.]

– With no more than 3 anterolateral carapace teeth; length of cheliped merus < carapace length 14

14. Ocular peduncles extend beyond tip of external orbital angle for < 36% of their length and for less than a distance equal to twice length of cornea ..... *M. milloti*
[Medium-sized (up to 20+ mm carapace breadth) inhabitant of intertidal soft sediments from east Africa to Hawaii and northern Australia.]

– Ocular peduncles extend beyond tip of external orbital angle for > 38% of their length and for more than a distance equal to twice the length of the cornea 15

15. With poorly differentiated teeth on cutting margins of chelae; lower margin of index concave; may attain a carapace breadth of >35mm ..... *M. telescopicus*
[Large inhabitant of mostly subtidal soft sediments from scattered localities throughout the western and central Pacific Ocean.]

– With distinct teeth on cutting edges of chelae; lower margin of index straight or convex; carapace breadth < 25 mm 16

16. Lower margin of index of chela straight; second and third anterolateral teeth of carapace spiniform and sharp; branchial regions with soft pubescence ..... *M. serenei*
[Medium-sized (up to some 25 mm carapace breadth) inhabitant of mostly intertidal soft sediments from scattered localities from the Red Sea and East Africa to southern Japan, the Tuamotus and Lord Howe Island.]

– Lower margin of index of chela with distinct convexity; second and third anterolateral teeth of carapace indistinct and lamellar; branchial regions naked (sublittoral) ..... *M. microfylacas*
[Small (< 15mm carapace breadth) inhabitant of coralline sediments from shallow sublittoral localities in Japan.]

17. Carapace with 4 or 5 anterolateral teeth, external orbital angle largest and marking position of greatest carapace breadth; carapace smooth and shiny ..... *M. dentatus*
[Small (< 15 mm carapace breadth) inhabitant of sublittoral sites scattered through the South China Sea from Hainan Island to Timor.]

– Carapace with 2–4 anterolateral teeth, if 4 present then carapace surface heavily granular and external orbital angles not marking position of greatest carapace breadth 18

18. Central region of epistome with a protuberance 19
– Central region of epistome straight or with a concavity 31

19. Inner surface of palm of chelae with at least 1 spine near articulation with carpus 20
– Inner surface of palm of chelae without spines 27

20. Merus of cheliped with granules or tubercles on its margins, but without spines except, in some, around distal angle of inner margin 21
– Merus of cheliped with spines on some or all of its margins, not counting any around distal angle of inner margin 22

21. External orbital angle very small and projecting less than second anterolateral tooth ..... *M. grandidieri*
[Large (up to 35 mm carapace breadth) inhabitant of muddy sandflats and seagrasses along eastern coast of Africa from South Africa to Gulf of Oman.]
– External orbital angle elongate and more or less projecting equally with second anterolateral tooth ..... *M. brevis*
[Medium-sized (up to 30 mm carapace breadth) inhabitant of firm muddy sandflats from Bay of Bengal to Ryukyu Islands and Malesia.]

22. Cutting margin of index of chelae with 2 teeth, one near tip; external orbital angle and second anterolateral tooth separated by wide incision 23
– Index of chelae with 1 tooth on its cutting margin, without one near tip; external orbital angle and second anterolateral tooth separated by a narrow incision 24

23. Lines of tubercular granules on branchial regions hook-shaped; dactylus of chelae with mat of hair over whole or almost whole of inner surface ..... *M. laevimanus*
[Medium-sized (carapace breadth > 25 mm) inhabitant of muddy sandflats around the Bay of Bengal and Strait of Malacca.]
– Granules on branchial regions in clumps or lines but not in hook-shaped rows; inner surface of dactylus of chelae without mat of hair ..... *M. laevis*
[Large (carapace breadth >30 mm) inhabitant of muddy sandflats in the Arabian Gulf and Arabian Sea.]

24. Second anterolateral tooth projecting markedly beyond external orbital angle 25
– External orbital angle projecting as far as second anterolateral tooth 26

25. External orbital angle projecting < half as far as second anterolateral tooth; tip of cornea projecting distinctly beyond tip of second anterolateral tooth; index of chela with distinct quadrangular tooth on cutting margin ... *M. sulcatus sulcatus*
[Medium-sized (up to 30mm carapace breadth) inhabitant of muddy sandflats in Arabian Gulf and Arabian Sea.]
– External orbital angle projecting > half as far as second anterolateral tooth; tip of cornea not projecting beyond tip of second anterolateral tooth; index of chela with indistinct, very low to slightly dome-shaped tooth on cutting margin .... *M. sulcatus malaccensis*
[Medium-sized (up to 30 mm carapace breadth) inhabitant of muddy sandflats in the Bay of Bengal and western Malesia, where it replaces *M. sulcatus sulcatus*.]

26. Outer surface of palm of chela with large hemispherical tubercles over upper half ..... *M. abbreviatus*
[Large (up to 35+ mm carapace breadth) inhabitant of muddy sandflats from South China Sea to southern coasts of Korea and Japan. Before 1981, *M. abbreviatus* was widely known under the name *M. dilatatus* (de Haan, 1835).]
– Outer surface of palm of chela finely granular, without hemispherical tubercles over upper half ..... *M. crassipes*
[Large (carapace breadth >35 mm) inhabitant of muddy sandflats from northern and eastern Australia to the Carolines and Hainan Island.]

27. External orbital angle larger than and projecting beyond second anterolateral tooth; carapace breadth twice carapace length; branchial regions with clumps of granules 28
– External orbital angle smaller than and not projecting as far as second anterolateral tooth; carapace breadth 1.5 × carapace length; branchial regions without clumps of granules (although rows of granules may be present) 30

28. Chelae large & elongate (equivalent to those of other species) with clearly differentiated teeth on cutting margins of fingers ..... *M. convexus*
[Large (carapace breadth up to 35 mm) inhabitant of high-level sand- or mudflats from the Andaman Sea and Ryukyu Islands, through Malesia to Hawaii, the Tuamotu Archipelago and Queensland.]
– Chelae small and feeble (as in female *Macrophthalmus*) with poorly differentiated or no teeth 29

29. Index of male chela with poorly differentiated, long low tooth along proximal half of cutting margin; tip of male first pleopod prolonged ..... *M. parvimanus*
[Medium-sized (carapace breadth up to 30 mm) inhabitant of mudflats at scattered localities from East Africa through the Indian Ocean and Malesia as far east as the Solomon Islands.]
– Index of male chela with small, quadrangular tooth in centre of cutting margin; tip of male first pleopod truncated .... *M. consobrinus*
[Medium-sized (carapace breadth up to 30 mm) inhabitant of river-mouth mudflats in the Gambier Islands in the Central Pacific Ocean.]

30. Index of chela without a tooth on cutting margin; outer surface of palm and index of chela with longitudinal ridge near to and subparallel with lower margin ..... *M. latifrons*
[Medium to large (up to 30+ mm carapace breadth) mudflat species restricted to south-eastern Australia.]
– Index of chela with a large, wedge-shaped tooth on cutting margin; outer surface of chela without longitudinal ridge near lower margin ..... *M. teschi*
[Medium-sized (up to 25 mm carapace breadth) inhabitant of mudflats through western Malesia.]

31. Merus and ischium of external maxilliped subequal (length of ischium < 1.4×length of merus); front broad (its breadth across base of ocular peduncles > 20% of distance between tips of external orbital angles) 32
– Merus of external maxilliped distinctly smaller than ischium (length of ischium > 1.5 × length of merus); front narrow (its breadth across bases of ocular peduncles < 18% of distance between tips of external orbital angles) 34

32. Cheliped carpus with large pointed protuberance on upper margin; medium to large-sized (up to 30+ mm carapace breadth); restricted to New Zealand ..... *M. hirtipes*

[Associated with low-tidal level sandy mudflats and with the seagrass *Zostera* sp. in estuaries and lagoons; often relatively nomadic and not occupying permanent burrows.]

– Cheliped carpus without protuberance on upper margin; small (< 15 mm carapace breadth); not occurring in New Zealand 33

33. Carapace surface granular ..... *M. boscii*
[Widespread species usually occurring under stones, in rock crevices or in sandy tide-pools at high tidal levels in rocky areas from eastern shores of Africa to Japan, Australia and Fiji.]

– Carapace surface without granules ..... *M. punctulatus*
[Inhabitant of high-shore mud and stony areas, restricted to south-western and eastern Australia.]

34. Inner surface of palm of chelae without mat of hair 35

– Inner surface of palm of chelae with mat of hair concealing at least part of surface 38

35. Dactylus of chela with very large tooth near centre of cutting margin; inner surface of palm of chelae with longitudinal row of hairs near to and subparallel with upper margin .... *M. barnesi*
[Known only from limited material from depths of 10+ m from Taiwan, Philippines, New Guinea and Seychelles; existing material probably of no more than young adults, < 25 mm carapace breadth.]

– Dactylus of chela with tooth near base of cutting margin; inner surface of palm of chelae without row of hairs as above .. 36

36. Branchial regions of carapace without distinct longitudinal rows of granules; carapace margins smoothly converging anteriorly ..... ***M. abercrombiei***
[Only five specimens of this species currently known, from the shores of the Torres Strait and Gulf of Carpentaria; existing material obtained from the shallow sublittoral and (though adult) is < 20 mm carapace breadth.]

– Branchial regions of carapace with distinct longitudinal rows of granules; carapace margins not smoothly converging anteriorly 37

37. External orbital angle rectangular, not projecting as far as second lateral tooth and not directed anteriorly ..... *M. japonicus*
[Large (up to 40 mm carapace breadth) inhabitant of mudflats from Japan and Korea to Singapore. Tai & Song (1984) divided this species into two subspecies but stated that 'In many areas, there are intermediate forms. Absolute separation of these forms is often impossible.': for these reasons, this proposed subdivision is not followed here.]

– External orbital angle pointed, directed partly anteriorly and projecting as far as second lateral tooth (sibling species of the above, differentiated more behaviourally than morphologically) ..... ***M. banzai***
[Medium-sized (up to 30 mm carapace breadth) inhabitant of mudflats from Japan and Korea to Taiwan and south coast of China.]

38. Carapace with concave granular row on each protogastric region ..... ***M. definitus***
[Large (exceeding 30 mm carapace breadth) inhabitant of mudflats from the Andaman Sea and around the western rim of the Pacific Ocean from the Ryukyu Islands to the Solomon Isles and Queensland.]

– Carapace without concave granular rows on protogastric regions 39

39. Greatest carapace breadth across external orbital angles, where breadth > 1.7 times carapace length; outer surface of palm and index of chela with longitudinal ridge near lower margins; index deflexed ..... ***M. setosus***
[Large (up to 40mm carapace breadth) mud-burrowing species restricted to east coast of Australia.]

– Carapace broadest posterior to external orbital angles, where breadth < 1.7 times carapace length; if longitudinal ridge present on outer surface of palm and index of chela then index not deflexed 40

40. Whole inner surface of palm of chela obscured by mat of hair 41

– At least part of inner surface of palm of chela free from thick hair 42

41. Central region of epistome straight; index with large wedge-shaped tooth on its cutting margin ..... ***M. teschi***
[Medium-sized (up to 25 mm carapace breadth) inhabitant of mudflats through the Bay of Bengal and western Malesia.]

– Central region of epistome with distinct concavity; index with low poorly-differentiated tooth on cutting margin .... ***M. depressus***
[Large (up to 35+ mm carapace breadth) inhabitant of mudflats through the western Indian Ocean.]

42. Inner surface of palm of chela with longitudinal band of hair along upper half; index of chela deflexed ..... ***M. pistrosinus***
[Medium to large-sized (carapace breadth >30+ mm) inhabitant of sandy mudflats in Shark Bay, Western Australia.]

– Hair on inner surface of palm of chela not as above; index of chela scarcely or not at all deflexed 43

43. Outer surface of index of chela with longitudinal granule-capped ridge running along centre, subparallel with lower margin .... *M. crinitus*
[Medium-sized (up to 25 mm carapace breadth) inhabitant of mudflats scattered from the Gulf of Aden, through Malesia to southern Japan.]

– Outer surface of index of chela without longitudinal ridge 44

44. Cutting margin of index of chela with a differentiated tooth; carapace breadth < 40 mm 45

– Cutting margin of index of chela without a differentiated tooth, except in individuals of > 45 mm carapace breadth 47

45. Carapace with thick hair laterally and longitudinal rows of hairs on branchial regions ..... *M. darwinensis*
[Little-known inhabitant of mangrove-associated mudflats in northern Australia and New Caledonia, all existing material < 15 mm carapace breadth.]

– Carapace without thick lateral hair and without longitudinal rows of hairs branchially 46

46. Cutting margin of index of chela with distinct, tall, prominent tooth ..... *M. leptophthalmus*
[Known for certain only from northern shores of the Bay of Bengal; limited existing material all < 25mm carapace breadth.]

– Cutting margin of index of chela with indistinct, long, low, crenulated tooth ..... ***M. dagohoyi***
[Small (< 20 mm carapace breadth) inhabitant of shallow subtidal organic muds in Bohol, Philippines.]

47. Carapace smooth to naked eye; inner surface of dactylus of chela without mat of hair ..... ***M. pacificus***
[Medium-sized (up to 25 mm carapace breadth) inhabitant of (often mangrove-associated) mudflats around the western Pacific rim from Korea to northern Australia and Samoa, and on both sides of the Malay-Thai peninsula (and possibly India).]
– Carapace surface heavily granular; inner surface of dactylus of chela heavily haired ..... ***M. latreillei***
[Very large (up to 60+ mm carapace breadth) inhabitant of low shore and subtidal muds from Mozambique to Japan and Australasia.]

SUBGROUPS WITHIN THE GENUS *MACROPHTHALMUS*

It is evident that morphologically the species keyed out above fall into a number of distinct clusters or subgroups spanning a wide range in body form, several of which have been given subgeneric rank; indeed intrageneric diversity within *Macrophthalmus* must be one of the greatest in the Brachyura.

Macrophthalmus (*Chaenostoma)* Stimpson, 1858
(Fig. 1A)

Small, carapace breadth < 15 mm; ocular peduncles short and stout, not projecting beyond lateral carapace margins, subequal in length to breadth of front or shorter; front broad, not constricted between bases of ocular peduncles, where its breadth is 20–30% the distance between external orbital angles; ischium of external maxilliped some 1.25 times length of merus; carapace with breadth < 1.3 times length, with lateral margins parallel, with broad-based subrectangular anterolateral teeth, without conspicuous aggregations of granules into rows or clumps on branchial regions; central region of posterior border of epistome straight; males without stridulatory apparatus; fingers of male chela short with index straight or slightly downflexed, and with a differentiated tooth only on dactylus. Intertidal, but unusually for *Macrophthalmus*, mainly associated with rocky or stony habitats.

Two species are included in *Chaenostoma* (= *Mopsocarcinus* Barnes, 1967): *M. boscii* Audouin, 1825 (type species) and *M. punctulatus* Miers, 1884. This subgenus was suggested by Barnes (1967) to approximate the form of the ancestral *Macrophthalmus*, but the molecular sequence analysis of Kitaura, Nishida & Wada (2006) places it as a highly derived form.

Macrophthalmus (*Euplax*) H. Milne Edwards, 1852
(Fig. 1B)

Small to medium-sized (< 25 mm carapace breadth); corneas reduced, ocular peduncles elongate but not projecting beyond lateral carapace margins, much longer than breadth of front; front narrow but not constricted between bases of ocular peduncles, where its breadth is ca. 15% the distance between external orbital angles; ischium of external maxilliped > 1.7 times length of merus; carapace with breadth ca. 1.3 times length, with lateral margins converging anteriorly, so that greatest carapace breadth occurs posterior to anterolateral teeth, with small, blunt anterolateral teeth, without specific system of rows or clumps of granules or hairs on branchial regions; central region of posterior border of epistome concave; fingers of male cheliped short with index straight or slightly upcurved and with differentiated teeth on both dactylus and index. Shallow subtidal.

Euplax contains two species: *M. leptophthalmus* (H. Milne Edwards, 1852) (type species) and *M. dagohoyi* Mendoza & Ng, 2007. The name *M. gastrodes* Kemp, 1915, was considered by Barnes (1977) to be a synonym of *M. leptophthalmus*, a view shared by Mendoza & Ng (2007), but Ng et al. (2008) list it, presumably erroneously, as a valid species within the subgenus *Venitus* (below). The separation of this subgenus from *Venitus* is discussed by Mendoza & Ng (2007).

Macrophthalmus (*Hemiplax*) Heller, 1865
(Fig. 1C)

Medium-sized, up to 30+ mm carapace breadth; ocular peduncles short and stout, not projecting beyond lateral carapace margins, subequal in length to breadth of front or shorter; front very broad, not constricted between bases of ocular peduncles, where its breadth is ca. 35% the distance between external orbital angles; ischium of external maxilliped some 1.3 times length of merus; carapace with breadth ca. 1.5 times length, with lateral margins diverging anteriorly, with large, broad-based, pointed anterolateral teeth, branchial regions with rows of granules including oblique row extending from 3rd anterolateral tooth to position above insertion of 4th pereiopod and transverse row extending from tip of 3rd anterolateral tooth; central region of posterior border of epistome straight; males without stridulatory apparatus; fingers of male chela elongate with index downflexed and a differentiated tooth only on dactylus; breadth of base of male telson < breadth of 6th abdominal segment. Intertidal.

Hemiplax is a monotypic subgenus for *M. hirtipes* (Jacquinot, in Hombron & Jacquinot, 1846), restricted to New Zealand, the only macrophthalmid in that region. Its zoeal larval stage is similar to that of *Heloecius cordiformis* (H. Milne Edwards, 1837) (currently in the monotypic family Heloeciidae) but is unlike those of the other *Macrophthalmus* species so far investigated (Wear, 1968; Fielder & Greenwood, 1985), albeit that the larval stages of relatively few species are known.

Macrophthalmus (*Macrophthalmus*) Desmarest, 1823
(Figs. 2A, 2B, 2C; 3A, 3B)

Large, up to 40 mm carapace breadth; ocular peduncles elongate to extremely elongate, projecting or not projecting beyond lateral carapace margins, much longer than breadth of front; front narrow, constricted between bases of ocular

peduncles, where its breadth is 7–17% the distance between external orbital angles; ischium of external maxilliped > 1.7 times length of merus; carapace with breadth > 1.5 and usually > 2 times length, with large, well-developed, outwardly directed, pointed anterolateral teeth of which external orbital angle often narrowly-based, with lateral margins diverging anteriorly, branchial regions without longitudinal or transverse granular rows of granules but with three distinct clumps of granules longitudinally aligned; central region of posterior border of epistome with a central protuberance; fingers of male chelae short to elongate with index straight or downflexed, differentiated teeth on both dactylus and index, inner surface of palm often with large spine near joint with carpus. Intertidal to subtidal, the intertidal species usually in firmer, sandier substrata than those inhabited by *Mareotis*.

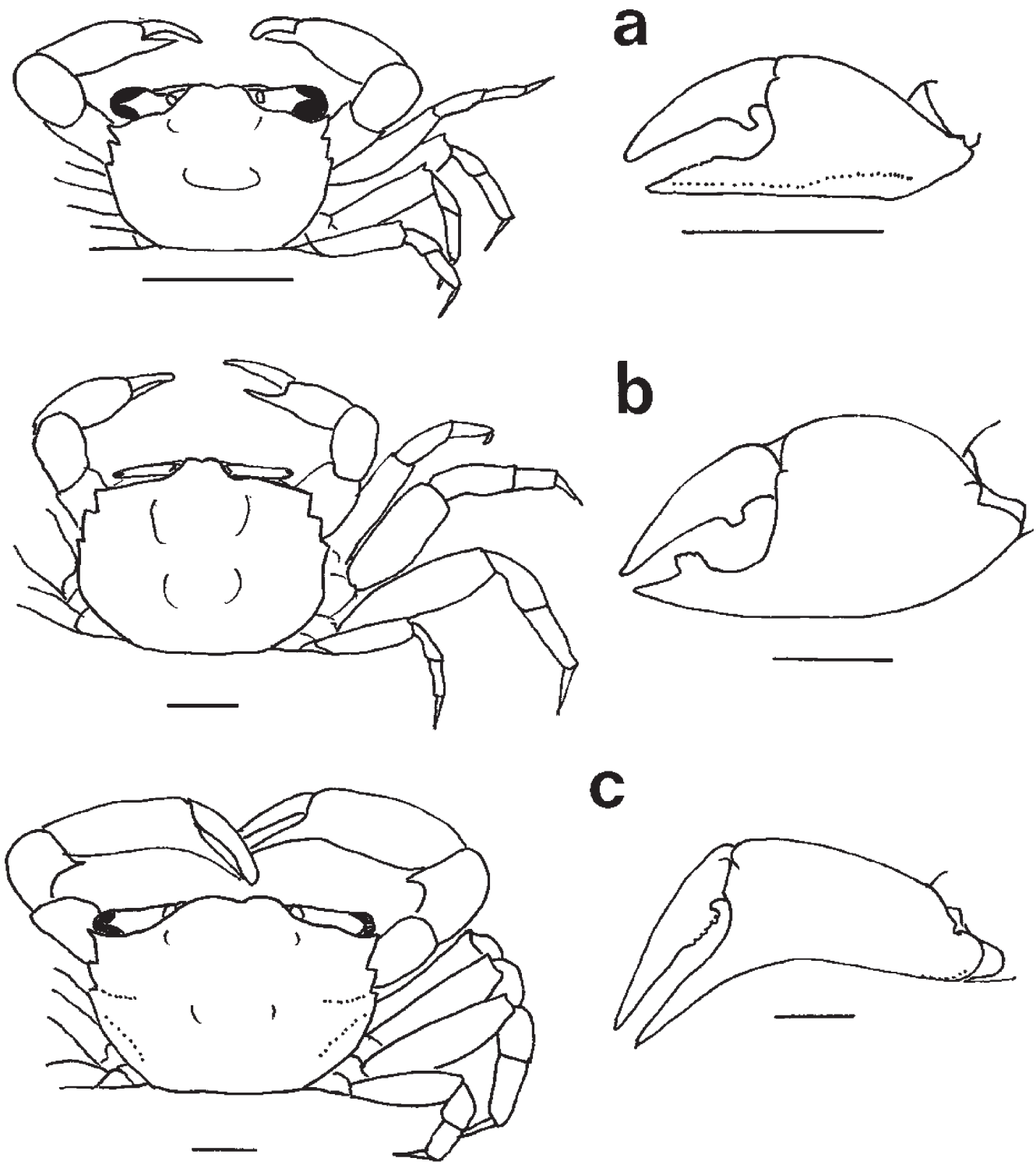

Fig. 1. Form of the carapace and adult male chela of subgroups of the genus *Macrophthalmus* I: (a) subgenus *Chaenostoma*, (b) subgenus *Euplax* and (c) subgenus *Hemiplax*. Scale bars = 5mm.

The type subgenus contains 21 species, divisible into two speciose groups and three small ones, two of them monotypic:

The *Macrophthalmus telescopicus* group

This comprises: *M. ceratophorus* Sakai, 1969, *M. graeffei* A. Milne Edwards, 1873, *M. latipes* Borradaile, 1903, *M. microfylacus* Nagai, Watanabe & Naruse, 2006, *M. milloti* Crosnier, 1965, *M. philippinensis* Serène, 1971, *M. ryukyuanus* Naruse & Kosuge, 2008, *M. serenei* Takeda & Komai, 1991 ('*M verreauxi* H. Milne Edwards, 1848' in Barnes, 1976; 1977) and *M. telescopicus* (Owen, 1839). In these species (Fig. 2A), the ocular peduncles are extremely elongate so that part of, and usually all, the cornea is positioned beyond the lateral carapace margins and in several of the species the peduncle projects beyond the carapace for half its total length; the tip of peduncle also sometimes bears a terminal style projecting beyond the cornea. Other distinguishing

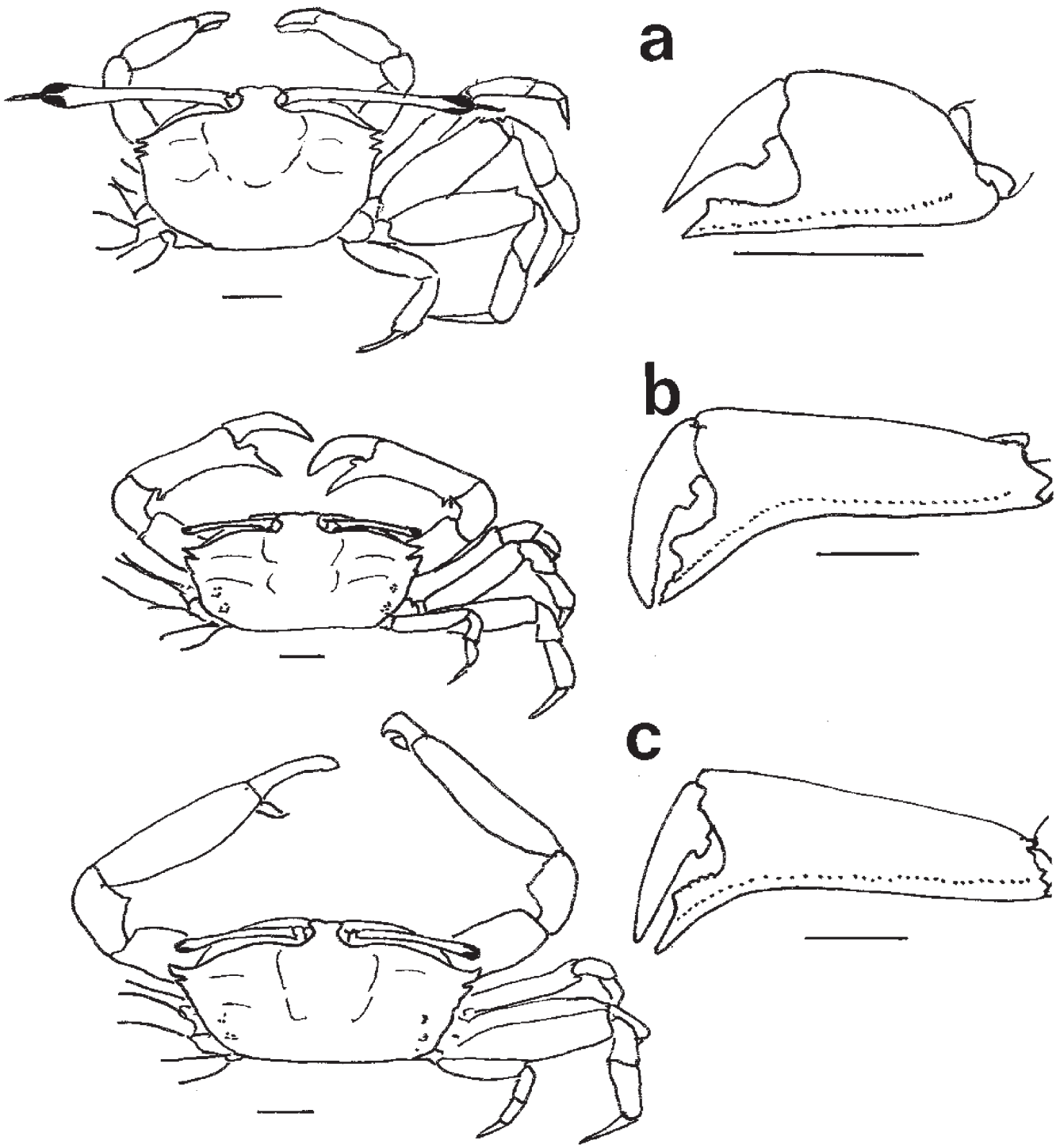

Fig. 2. Form of the carapace and adult male chela of subgroups of the genus *Macrophthalmus* II, the subgenus *Macrophthalmus* part 1: (a) *M. telescopicus* group, (b) *M. brevis* group, and (c) *M. convexus* group. Scale bars = 5mm.

features include: front relatively broad (breadth 13-17% that of carapace); carapace moderately broad (breadth = 1.5–1.7 × length), with three variably-developed but usually spiniform anterolateral teeth; male chela without spine near carpal joint, with short fingers and undeflexed index. A mainly sublittoral group (in depths of up to 80m), though *M. milloti* and *M. serenei* are common intertidally.

The *Macrophthalmus brevis* group

This comprises: *M. abbreviatus* Manning & Holthuis, 1981, *M. brevis* (Herbst, 1804), *M. crassipes* H. Milne Edwards, 1852, *M. grandidieri* A. Milne Edwards, 1867, *M. laevimanus* H. Milne Edwards, 1852, *M. laevis* A. Milne Edwards, 1867 and *M. sulcatus* H. Milne Edwards, 1852 which is divisible into a western *M. sulcatus sulcatus* and an eastern *M. sulcatus malaccensis* Tweedie, 1937 (see Barnes 1970 for details under the name *M. dilatatus sulcatus*). In this group (Fig. 2B), the corneas are not positioned beyond lateral carapace margins and no style is present; carapace very broad (breadth > 2 × length), with a small pointed external orbital angle and larger, broad-based, flat, second lateral tooth; front narrow (breadth < 14% that of carapace); male chela with spine/s near carpal joint, with elongate and usually downflexed fingers. Intertidal in muddy sandflats. The names *M. gallardoi* Serène, 1971, *M. hilgendorfi* Tesch, 1915 and *M. sandakani* Rathbun, 1914 listed by Ng et al. (2008) as extant species are still, as earlier (Barnes, 1977), regarded by this author as being synonyms of species within this group.

The *Macrophthalmus convexus* group

This intertidal group comprises only *M. consobrinus* Nobili, 1906, *M. convexus* Stimpson, 1858 and *M. parvimanus* Guérin, 1834 (Fig. 2C). Although broadly similar to the *M. brevis* group above, it was shown to be separate by allozyme and molecular sequence data (Horii, Kitaura, Wada & Nishida, 2001; Kitaura et al., 2006), and morphologically it differs from them in possessing a large, flat, forwardly curved external orbital angle and in lacking the spine on the palm of the male chela. Like the *M. brevis* group, however, the corneas do not project, the carapace is broad (breadth > 2 × length) and the front narrow (breadth < 10% that of carapace). The status of the various isolated geographical populations of *M. parvimanus* is currently somewhat uncertain. It is possible that several populations of *M. convexus* have given rise to *M. parvimanus*-like forms in different areas. Poupin (e.g. 1997) has been followed here and the Gambier Islands form, *M. consobrinus*, included as a distinct species, pending revision of the group. The *M. convexus* group is closely allied with the *M. telescopicus* group on both allozyme and molecular sequence data, and the two appear only distantly related to the *M. brevis* group (Horii et al., 2001; Kitaura et al., 2006).

Macrophthalmus transversus

The intertidal type species of the genus, *M. transversus* (Latreille, 1817) (Fig. 3A), does not fit easily into any of the three subgroups above, although it does possess the typical broad carapace (breadth > 2 × length) and narrow front (breadth ca. 12% that of carapace) of the subgenus. It has extremely long ocular peduncles with projecting corneas like the *M. telescopicus* group and anterolateral teeth equivalent to those of the *M. brevis* group, but is singular in its elongate, deflexed and highly laterally flattened, blade-like chelae which bear spiniform teeth on their cutting margins; the chelae, however, do bear the typical spine of the *M. brevis* group on the palm near the carpal joint. The carapace, chelipeds and pereiopods also bear tubercles and spines to a degree greater than any other species in the genus except the very large *M. (Venitus) dentipes* (Barnes, 1970).

Macrophthalmus dentatus

The equally singular *M. dentatus* Stimpson, 1858 (Fig. 3B), only known from sublittoral material, similarly possesses the characteristic broad carapace (greatest breadth 2 × length), narrow front (breadth 10% that of carapace) and elongate but not projecting ocular peduncles of the subgenus *Macrophthalmus*, but although it otherwise shares some features with the *M. telescopicus* group (extremely elongate cheliped meri, short undeflexed fingers on the chelae) it is aberrant within the genus in possessing 4-5 anterolateral teeth occupying most of the lateral carapace margins, of which the external orbital angle is very large and flaring forwards and outwards, and in details of its carapace granulation, external maxilliped structure, and some other features (see Barnes, 1971).

Macrophthalmus (*Mareotis*) Barnes, 1967

(Figs. 3C, 4A)

Large, up to 40 mm carapace breadth; ocular peduncles elongate but not projecting beyond lateral carapace margins, much longer than breadth of front; front narrow, usually constricted between bases of ocular peduncles, where its breadth is 8–15% distance between external orbital angles; ischium of external maxilliped > 1.5 times length of merus (usually 1.7–2.5 times); carapace with breadth 1.3–1.7 times length (and in one species > 1.8 times length), with large, broad-based, subrectangular anterolateral teeth, with lateral margins subparallel or arched (so that greatest carapace breadth not across external orbital angles or even second anterolateral teeth), with longitudinal and/or transverse rows of granules and/or hairs on branchial regions but without clumps of granules; central region of posterior border of epistome straight, with marked concavity or (in some populations of one species) with a central protuberance; males of one species with stridulatory apparatus as described below in *Paramareotis*; fingers of male chelae usually elongate with index downflexed and with differentiated teeth on both

index and dactylus or on dactylus only. Intertidal, usually in relatively soft muds.

Twelve species are included which have been divided between two subgroups on morphological grounds (the groups A and B of Komai et al., 1995):

The *M. crinitus* group

In *M. crinitus* Rathbun, 1913, *M. darwinensis* Barnes, 1971, and *M. pacificus* Dana, 1851 (Fig. 3C) the front is relatively broad and unconstricted, the central region of epistome is straight, the characteristic longitudinal ridges of the branchial

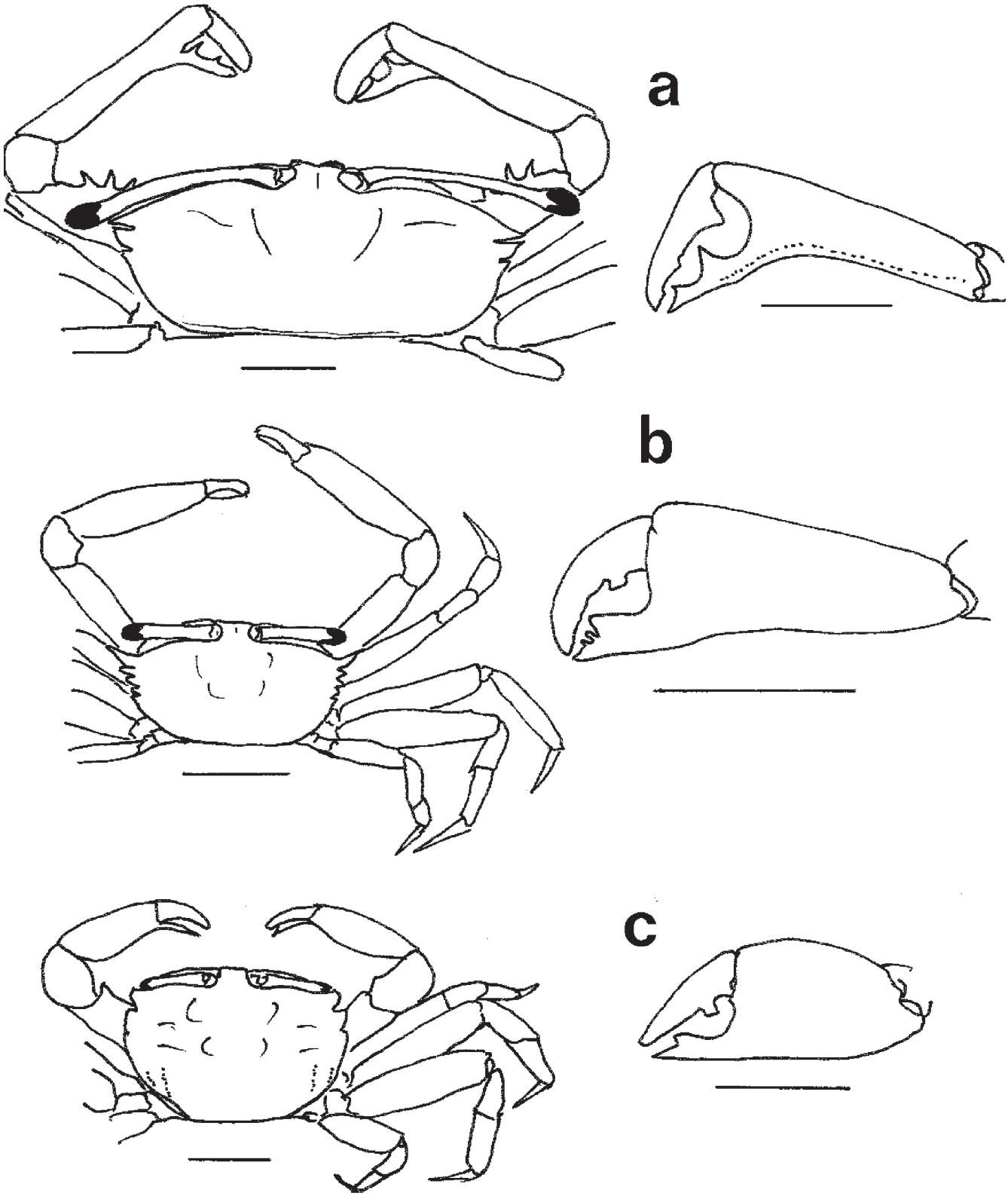

Fig. 3. Form of the carapace and adult male chela of subgroups of the genus *Macrophthalmus* III: (a, b) the subgenus *Macrophthalmus* part 2, *M. transversus* (a) and *Macrophthalmus dentatus* (b); (c) the *M. crinitus* group of the subgenus *Mareotis*. Scale bars = 5mm.

regions are poorly marked, and the fingers of the male chela are short, with an undeflexed index. The specimen described by Pretzmann (1974) as *M. pacificus tjiljapensis* in fact belongs to *M. definitus* in the other subgroup of *Mareotis*.

The *M. japonicus* group

The *M. japonicus* group comprises *M. abercrombiei* Barnes, 1966, *M. banzai* Wada & Sakai, 1989, *M. definitus* Adams & White, 1848, *M. depressus* Rüppell, 1830, *M. japonicus* (de Haan, 1838) (the type species of *Mareotis*), *M. setosus* H. Milne Edwards, 1852, *M. pistrosinus* Barnes & Davie, 2008, *M. teschi* Kemp, 1919, and *M. tomentosus* Souleyet, 1841 (which possesses the stridulatory apparatus) (Fig. 4A). In these, the front is narrow and markedly constricted, the central region of epistome bears a concavity (except in *M. teschi* – see below), the characteristic transverse and longitudinal branchial ridges of *Mareotis* are usually well-marked, and the fingers of the male chela are elongate with the index being strongly downflexed especially in large individuals. The morphology of *M. teschi* appears somewhat less straightforward than seemed earlier (Barnes, 1971) in that a north-south cline is now evident: Thai populations (Komai et al., 1995) display a relatively parallel-sided carapace and straight central region of the epistome; in Indonesia (Barnes, 1971) the second lateral tooth projects beyond the external orbital angle and the central region of the epistome is protuberant; whereas material examiner by the author from Selangor in peninsular Malaysia is equivalent to that from Thailand in its epistome but to that from Indonesia in the form of its anterolateral carapace teeth.

Molecular sequence data (Kitaura et al., 2006) confirm the existence of two groupings within *Mareotis* but not the two identified on morphological grounds by Komai et al. (1995). Sequence analysis groups *M. darwinensis* and *M. definitus* on the one hand, but, on the other, groups *M. banzai*, *M. japonicus*, *M. tomentosus*, *M. pacificus* and *M. pistrosinus*, and allies them with the subgenus *Venitus* and the *M. convexus* and *M. telescopicus* groups of *Macrophthalmus* sensu stricto instead (see Fig. 6). The allozyme data of Horii et al. (2001), however, which did not include *M. darwinensis*, grouped *M. definitus* with *M. japonicus* and *M. banzai* in a *Mareotis* cluster distinct from although allied to *M. convexus* and the *M. telescopicus* group.

Macrophthalmus (*Paramareotis*) Komai, Goshima & Murai, 1995
(Fig. 4B)

Small, carapace breadth < 15 mm; ocular peduncles short and stout, not projecting beyond lateral carapace margins, subequal in length to breadth of front or shorter; front broad, not constricted between bases of ocular peduncles, where its breadth is 20–30% distance between external orbital angles; ischium of external maxilliped ca. 1.25 times length of merus; carapace with breadth 1.3–1.6 times length, with lateral margins subparallel, with broad-based subrectangular or pointed anterolateral teeth, without conspicuous aggregations of granules into rows or clumps on branchial regions (indistinct rows present in some); central region of posterior border of epistome usually straight (with convexity in one species); males with stridulatory apparatus in all species (i.e. with short horny ridge on ventoroflexor margin, or on inner surface near ventoroflexor margin, of cheliped merus, and lower orbital border with 1–2 large triangular protuberances occupying at least one fifth of that margin); fingers of male chela short with index straight or slightly downflexed and with differentiated teeth on both fingers. Intertidal, with one species often occurring in holes in limestone rocks and the others often associated with mangrove pneumatophores.

Four species are included: *M. boteltobagoe* (Sakai, 1969), *M. erato* de Man, 1888, *M. holthuisi* Serène, 1973, and *M. quadratus* A. Milne Edwards, 1873 (the type), Kosuge & Davie (2001) having demonstrated that *M. boteltobagoe* and *M. holthuisi* are distinct species *contra* the opinion of Barnes (1976). Molecular sequence data (Kitaura et al., 2006) suggest that *M. erato* + *M. quadratus* are only distantly related to *M. holthuisi* + *M. boteltobagoe*, but instead are related to the *M. brevis* group of the subgenus *Macrophthalmus*.

Macrophthalmus (*Tasmanoplax*) Barnes, 1967
(Fig. 5A)

Medium-sized, up to 30+ mm carapace breadth; ocular peduncles elongate but not projecting beyond lateral carapace margins, longer than breadth of front; front moderately narrow, not constricted between bases of ocular peduncles, where its breadth is ca. 20% distance between external orbital angles; ischium of external maxilliped ca.1.2 times length of merus; carapace with breadth 1.5–1.6 times length, with lateral margins subparallel, with large, broad-based, subrectangular anterolateral teeth, branchial regions with transverse and longitudinal rows of granules; central region of posterior border of epistome with large convexity; males without stridulatory apparatus; fingers of male chelae elongate with index downflexed and with clearly differentiated tooth on dactylus only. Intertidal in soft sediments.

This is a monotypic subgenus for *M. latifrons* Haswell, 1882, restricted to south-eastern Australia, the only macrophthalmid in that region. It appears to differ behaviourly from other *Macrophthalmus* in that allocleaning (foraging on the carapace or walking legs of other conspecific individuals) is not displayed (Kitaura & Wada, 2004).

Macrophthalmus (*Venitus*) Barnes, 1967
(Fig. 5B)

Often very large (up to 80+ mm carapace breadth, and leg span of up to 30 cm); ocular peduncles elongate but not projecting beyond lateral carapace margins, much longer than breadth of front; front narrow, constricted between bases of ocular peduncles, where its breadth is 5–15% the distance between external orbital angles; ischium of external

maxilliped > 1.7 times length of merus; carapace with breadth from, in small species/individuals, 1.3 to, in large species/individuals, 1.7 times length, with lateral margins subparallel or diverging posteriorly, with large and often projecting, broad-based, subtriangular, pointed anterolateral teeth (especially in large adults), heavily granular surface but without specific system of rows or clumps of granules; central region of posterior border of epistome straight; males of one species (*M. dentipes*) with stridulatory apparatus as described above in *Paramareotis*; fingers of male chelae usually moderately elongate with index straight and with a differentiated tooth only on dactylus; pereipods often with large tubercles or spines. Low intertidal and subtidal, in very soft muds; intertidally, the mouth of the burrow is often located in a large, water-filled, saucer-shaped depression.

Venitus contains three species: *M. barnesi* Serène, 1971, *M. dentipes* Lucas, 1836, and *M. latreillei* (Desmarest, 1817)

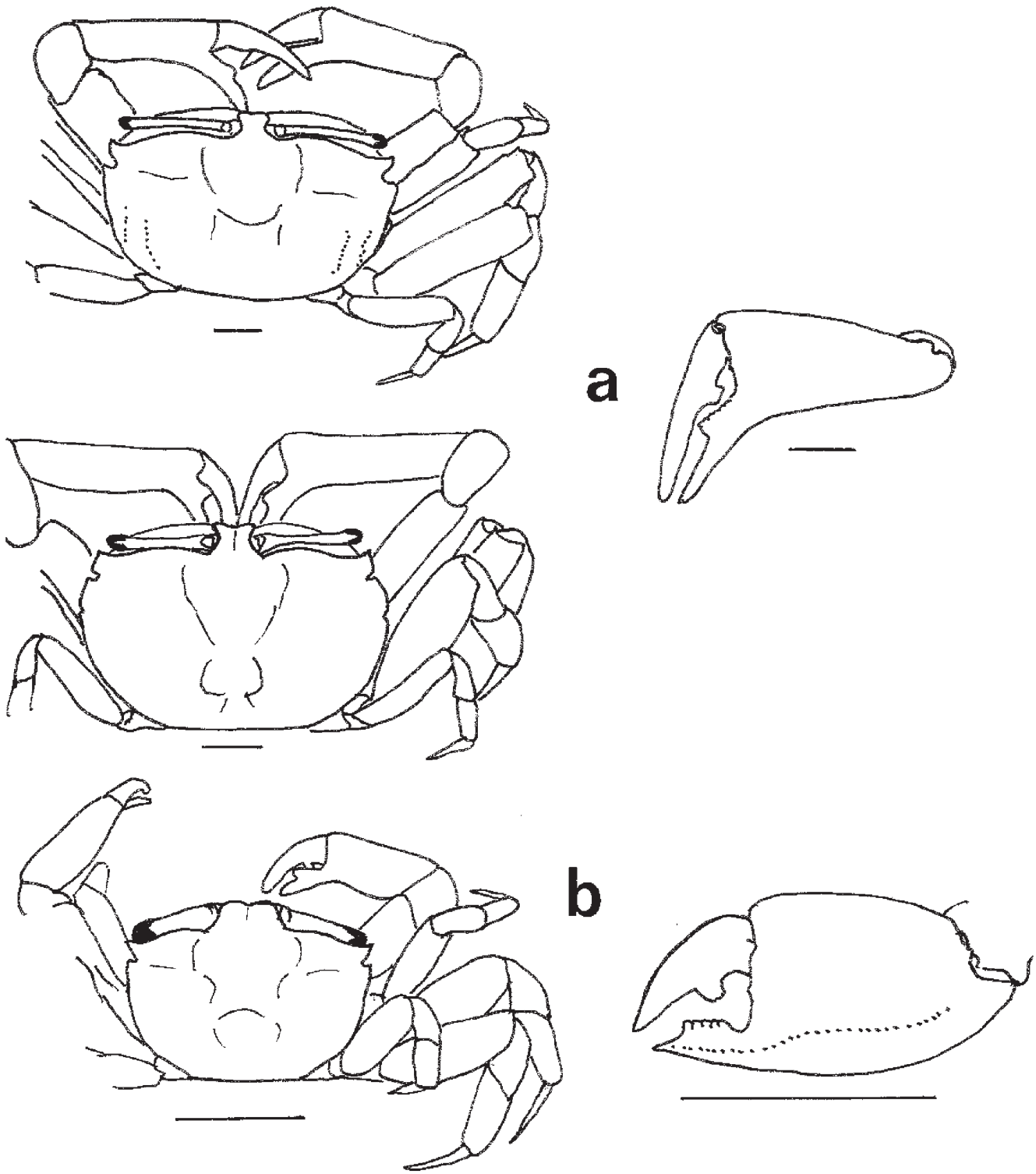

Fig. 4. Form of the carapace and adult male chela of subgroups of the genus *Macrophthalmus* IV: (a) the *M. japonicus* group of the subgenus *Mareotis* (both the relatively parallel-sided and relatively rounded carapace types), and (b) subgenus *Paramareotis*. Scale bars = 5mm.

(type species). The names *M. serratus* Adams & White, 1849 and *M. vietnamensis* Serène, 1971 listed by Ng et al. (2008) as extant species are still, as earlier (Barnes, 1977), regarded by this author as being synonyms of species within this group.

Relationships between the subgroups

Clearly there is considerable lack of agreement between clades identified by analyses of allozyme data and of nucleotide sequences from mitochondrial 16S rRNA (Horii et al., 2001; Kitaura et al., 2006) (Fig. 6) and those based on morphological similarity/difference, and Kitaura et al. (2006) identify a correlation between type of sediment inhabited and morphology indicating that considerable functional convergence in body form may have occurred between members of different clades. To date, however, considerably less than half the *Macrophthalmus* species, and no representatives at all from four of the subgroups identified above, have been subject to molecular analysis. Although, therefore, a case could clearly be made for elevating some or all of the subgroups within *Macrophthalmus* to generic level, it might be wise to await a complete set of molecular data and more information derived therefrom and from further morphological analyses on the monophyly or otherwise of putative genera and on potential phyletic relationships between them before so doing. Equivalent molecular sequence data on the relationships between *Macrophthalmus* and the other genera in the family would also be valuable.

ACKNOWLEDGEMENTS

I am most grateful to Peter Dworschak of the Naturhistorisches Museum, Vienna, Austria, for sending me information on the *Macrophthalmus pacificus tjiljapensis* material in his care; and, for their invaluable comments and advice, to Peter Davie of the Queensland Museum, Australia, Peter Ng of the National University of Singapore and Keiji Wada of the Nara Women's University, Japan.

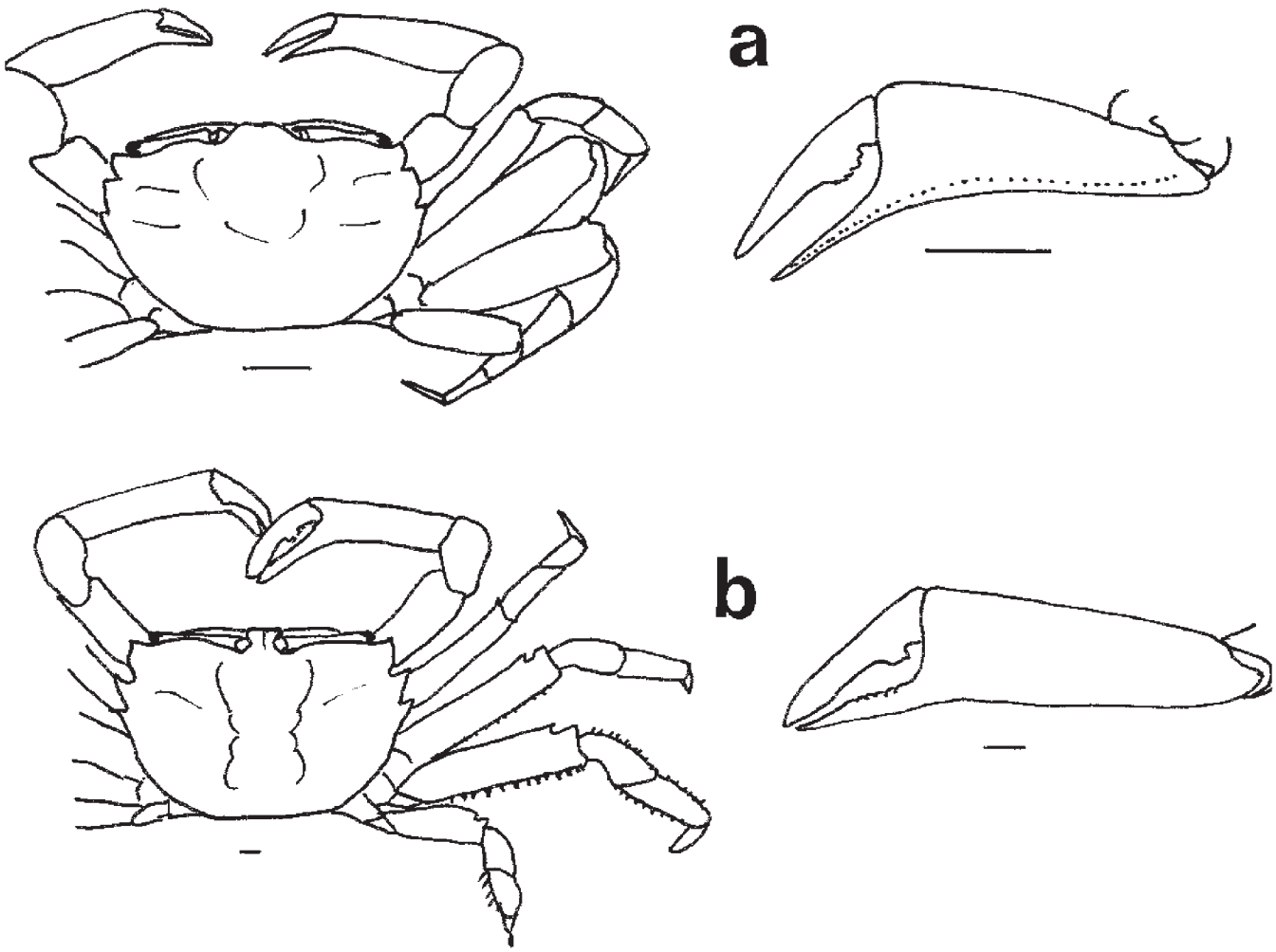

Fig. 5. Form of the carapace and adult male chela of subgroups of the genus *Macrophthalmus* V: (a) subgenus *Tasmanoplax* and (b) subgenus *Venitus*. Scale bars = 5mm.

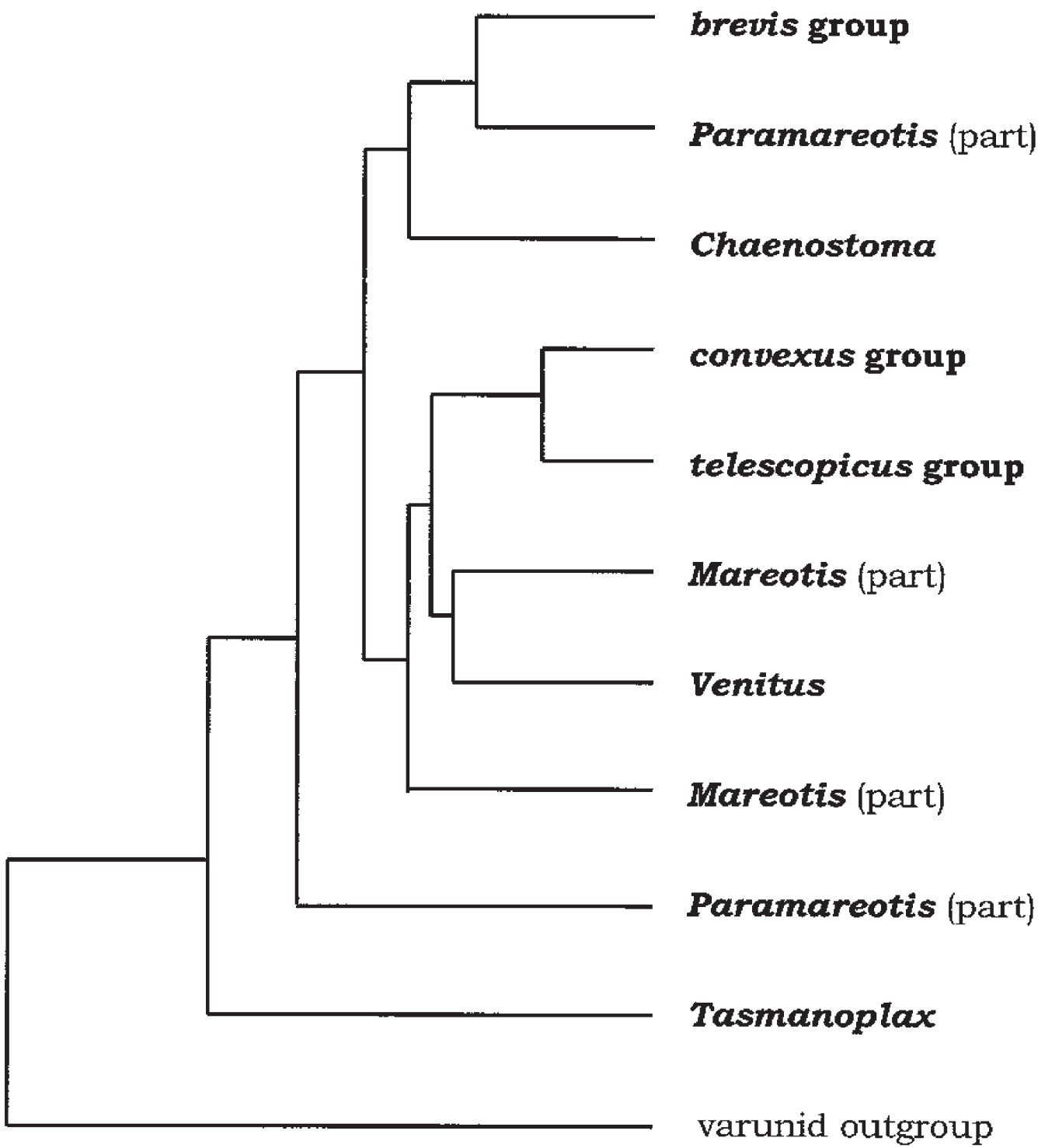

Fig. 6. The relationships between and within some subgroups of *Macrophthalmus* suggested by the nucleotide sequence analyses of Kitaura et al. (2006).

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