

The Indo-Pacific Pilumnidae II.

A revision of the genus *Rhizopa* Stimpson, 1858, and the status of the Rhizopinae Stimpson, 1858 (Crustacea, Decapoda, Brachyura)

Peter K.L. Ng

Department of Zoology, National University of Singapore, Kent Ridge, Singapore 0511, Republic of Singapore

ABSTRACT: The taxonomy of crabs of the small Indo-Pacific genus *Rhizopa* Stimpson, 1858, is very difficult mainly because the type species, *R. gracilipes* Stimpson, 1858, has never been described in detail or figured, and the single type specimen was almost certainly destroyed in the great Chicago Fire of 1871. To prevent any future doubt about the identity of the species, a neotype is designated. The genus *Rhizopa* is revised, and now contains only the type species, with one of the species previously assigned to the genus referred to a new genus, *Rhizopoides*, another to *Ceratoplax* Stimpson, 1858, and the third to the genus *Heteropilumnus* De Man, 1895. A neotype is designated for the type of the genus *Ceratoplax*, *C. ciliatus* Stimpson, 1858. The status and composition of the Rhizopinae is also discussed, as well as the taxonomy of some problematic species. The Rhizopinae is presently recognised to contain 20 genera: *Rhizopa*, *Rhizopoides*, *Ceratoplax*, *Heteropilumnus*, *Typhlocarcinus*, *Typhlocarcinops*, *Caecopilumnus*, *Mertonia*, *Xenophthalmodes*, *Zehntneria*, *Cryptocoeloma*, *Pseudocryptocoeloma*, *Pseudolithochira*, *Selwynia*, *Paraselwynia*, *Paranotonyx*, *Protonotonyx*, *Cryptolutea*, *Lophoplax*, and *Serratocoxa* gen. nov. The genera *Notoonyx*, *Scalopidia*, *Camatopsis*, *Chasmocarcinus*, *Chasmocarcinops*, *Hepthopelta*, *Megathesius*, *Speocarcinus*, *Acidops* and *Raoulia* gen. nov. are also excluded or removed from the subfamily. Specimens identified as "*Typhlocarcinodes piroculatus*" by Serène (1964) are presently referred to a new genus and species, *Raoulia limosa*. Three species previously placed in *Lophoplax* and *Ceratoplax* are transferred to a new genus, *Serratocoxa*, whilst specimens identified as *Typhlocarcinops transversa* by Takeda & Miyake (1968a) are referred to a new species, *Typhlocarcinops takedai*.

1. INTRODUCTION

Crabs of the family Pilumnidae Samouelle, 1819, *sensu* Guinot, 1978, commonly referred to as "Hairy Crabs" on account of their hirsutous carapaces and legs are extremely common in the Indo-Pacific, constituting one of the largest

families in the superfamily Xanthoidea MacLeay, 1838, *sensu* Guinot, 1978, with more than 250 species in some 30 genera. The identification of these crabs however, is usually extremely difficult due to the confused state of its taxonomy. Many genera and species have been so briefly characterised (and often poorly or not even figured) that their actual identities remain indeterminate. One such taxon is the genus *Rhizopa* Stimpson, 1858.

The genus *Rhizopa* was first established to accommodate a single new species Stimpson described from Hong Kong in 1858, *Rhizopa gracilipes*. Stimpson also erected a new family, the Rhizopidae for four of his new genera: *Rhizopa*, *Scalopidia*, *Typhlocarcinus* and *Ceratoplax*. Tesch (1918), Beurlen (1930), Balslev (1957), Serène (1968) and Guinot (1969c) followed Stimpson in recognising *Rhizopa* as monotypic. Serène (1971) subsequently described the second species, *R. sasekumari* from Peninsular Malaysia but had doubts about placing his species in this genus. Guinot (1971) also indicated that *Speocarcinus luteus* McNeill, 1929, from Australia might be a *Rhizopa*. Ng (1985) recognised, with some doubt, four species in the genus *Rhizopa* – *R. gracilipes*, *R. sasekumari* Serène, 1971, *R. luteus* (McNeill, 1929) and *R. yangae* Ng, 1985, and provided a provisional key to separate them.

Stimpson's description of *R. gracilipes* however, was extremely brief, and the absence of any figures makes it impossible to characterise the species with any degree of certainty. In his posthumously published paper of 1907, 'ghosted' by Mary Rathbun, which provided much more details and figures of the numerous species which Stimpson had described many years earlier, no mention was made of his Rhizopidae. In a footnote, Rathbun (*in* Stimpson, 1907) remarked that the "... family Rhizopidae, comprising two pages of Stimpson's "Prodrömus" and Nos. 144 to 148 inclusive, of the species, is missing from the manuscript of this report; also the illustrations of this family, as well as of other Ocyropodoidea. This gap existed in 1875 when the manuscript was examined by Prof. Sidney I. Smith, and it is probable that the missing parts were removed by Dr. Stimpson himself for further study and were destroyed in the Chicago Fire in 1871" (p. 95). Numbers 144 to 148, all new species, according to Stimpson (1858), were: 144. *Scalopidia spinosipes*, 145. *Rhizopa gracilipes*, 146. *Typhlocarcinus nudus*, 147. *Typhlocarcinus villosus*, and, 148. *Ceratoplax ciliatus*.

Evans (1967) records some of Stimpson's type material in the British Museum (Natural History) but her list does not include *Rhizopa* or any of the Rhizopidae. Other than these specimens, all of Stimpson's material must now be regarded as destroyed in the Chicago Fire which gutted the Chicago Academy of Sciences where the specimens were kept. There is no evidence to suggest that any other material is still extant. More details about the fire can be found in Rathbun *in* Stimpson (1907), Mayer (1918) and Evans (1967). Stimpson's brief description of *R. gracilipes*, the absence of figures and loss of the type has resulted in much confusion over the identity of the genus and species as well as the taxonomic validity of the Rhizopidae.

In an attempt to clarify the systematics of the genus *Rhizopa*, and in particular the identity of *R. gracilipes*, the author has examined most of the material which had previously been assigned by other authors to *R. gracilipes*. To prevent any future doubt and confusion over the identity of *R. gracilipes*, a neotype is designated, and figured in detail in this paper. The unusual structure of the male first pleopods, third maxillipeds and last pair of ambulatory legs of *R. gracilipes* suggest that the other species that are presently recognised as belonging to the genus *Rhizopa* should be removed, with *Rhizopa s. str.* containing only the type species, *R. gracilipes*. The other species have been referred to *Heteropilumnus*, *Ceratoplax* and a new genus, *Rhizopoides*.

With regards to the Rhizopidae, it was recognised as a subfamily of the family Goneplacidae Dana, 1851, by Alcock (1900), an approach followed by all later workers, and which was accepted by Balss (1957) in his classification of the Brachyura. Guinot (1969c) made reference to *Rhizopa* possessing many pilumnid characters and, in her revision of Brachyuran classification (1977, 1978, 1979), in which she reorganised the family Goneplacidae, affiliated the genus *Rhizopa* with the family Pilumnidae Samouelle, 1819, *sensu* Guinot, 1978. She (1978) also tentatively recognised the Rhizopinae *s. str.* as consisting of only a single genus, *Rhizopa*, and belonging to a special branch. The other genera were referred to her 'goneplacien' group of the Pilumnidae or out of the Pilumnidae altogether. Ng (1983) also preferred to exclude the Rhizopinae from consideration in his preliminary studies of the Pilumnidae. In his treatment of the genus *Rhizopa* however, Ng (1985) regarded *Rhizopa* as a true pilumnid taxon, but did not venture to deal with the Rhizopinae in detail. Serène (1984), in his monograph on the Indian Ocean Xanthoidea, did not even consider the Rhizopinae in his classification of the Pilumnidae. There is thus a need to better understand the detailed composition, relationship and validity of the Rhizopinae. The taxonomy of the Rhizopinae will be briefly reviewed and discussed in this paper.

Materials examined (or mentioned) are deposited in the Zoological Museum of the University of Copenhagen (ZMUC), United States National Museum of Natural History, Smithsonian Institution (USNM), British Museum (Natural History) (BMNH), Zoological Laboratory of the Kyushu University, Japan (ZLKU) and the Zoological Reference Collection, National University of Singapore (ZRC). All measurements provided are in millimetres, and are of the carapace breadth and length respectively. The abbreviations G1 and G2 are for the male first and second pleopods respectively.

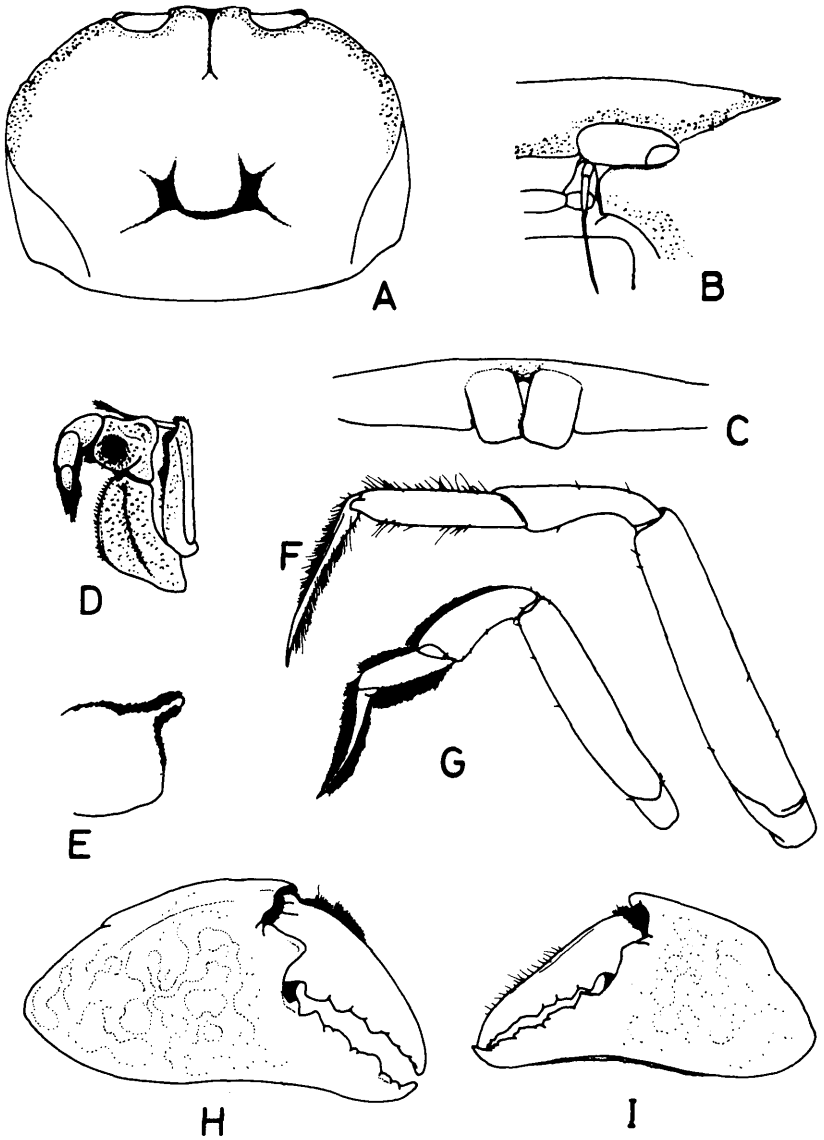


Figure 1. *Rhizopa gracilipes* Stimpson, 1858. A, B. Male, 8.8 by 6.1mm, USNM 39744; C-H Neotype Male, 9.7 by 7.0mm, ZMUC. A. Dorsal view; B. Left frontal view; C. Posterior margin of epistome; D. Left third maxilliped; E. Dorsal view of right carpus of cheliped; F. Left third ambulatory leg; G. Left last ambulatory leg; H. Right cheliped; I. Left cheliped.

2. TAXONOMY

Family Pilumnidae Samouelle, 1819, sensu Guinot, 1878

Subfamily Rhizopinae Stimpson, 1858

Genus Rhizopa Stimpson, 1858 s. str.

Rhizopa Stimpson, 1858: 95.

Type-species: *Rhizopa gracilipes* Stimpson, 1858, by monotypy.

Diagnosis: Carapace ovate, surfaces smooth, covered with very low pubescence, anterolateral margin almost entire. Cornea small. Merus of third maxilliped distinctly produced at anterolateral angle, ischium narrow in distal portion, resulting in gape in buccal cavity when third maxillipeds closed. Posterior margin of epistome with two rectangular tooth-like structures. Chelipeds smooth, margins cristate, occasionally with fringe of hairs, cutting edge of fingers with numerous low, blunt teeth; propodus of larger cheliped with large tooth-like structure that overlaps base of dactylus. Dactylus of last pair of ambulatory legs distinctly curving upwards. First male segment not reaching to bases of last pair of ambulatory legs, occupying only about half the space. Male genital openings coxosternal, opening via a narrow groove. G1 sinuous, tip short, blunt. G2 short, sinuous.

Remarks: Ng (1985) had provisionally recognised four species in this genus; the type *Rhizopa gracilipes*, *R. sasekumari*, *R. luteus* and *R. yangae*, but the present revision indicates that such a classification is unsatisfactory. With the present definition of the genus, *R. luteus* is transferred to the genus *Ceratoplax*, *R. yangae* to a new genus, *Rhizopoides*, and *R. sasekumari* to the genus *Heteropilumnus*. The genus *Rhizopa* thus again becomes monotypic.

Rhizopa gracilipes (Stimpson, 1858) (see Pl. 1, Fig. 1, 2)

Rhizopa gracilipes Stimpson, 1858: 95; Miers, 1886: 235; Rathbun, 1910: 34, Fig. 27; Tesch, 1918: 201; Serène, 1968: 91 (part); Guinot, 1969c: 698, Fig. 110a, b; Guinot, 1971: 1078; Naiyanetr, 1980: 41; Ng, 1985: 631

(not *Rhizopa gracilipes* Serène, 1964; Griffin & Campbell, 1969; Campbell & Stephenson, 1970; Griffin, 1972; Stephenson *et al.*, 1974)

Material examined. Neotype – 1♂, 9.7 by 7.0mm (ZMUC), Sound of Koh Chang, Gulf of Thailand, ca. 12°4'N, 102°24'E, 3 to 5 fms depth, leg. Th. Mortensen, between 24.xii.1899 and 6.i.1900.

Others – 12♂, 11♀ (2 with rhizocephalans, 1 ovigerous), 4 juvs. (ZMUC), 2♂, 3♀ (1 with rhizocephalan)(ZRC), 6♂ (largest 8.8 by 6.1mm), 7♀ (USNM 39744), 1♂, 1♀ (BMNH Nr. 1930.3.29.4-5), all same data as neotype ----- 1♂ (ZMUC), off Koh Kat, Gulf of Thailand, ca. 11°41'N, 102°37'E, 6 fms depth, leg.

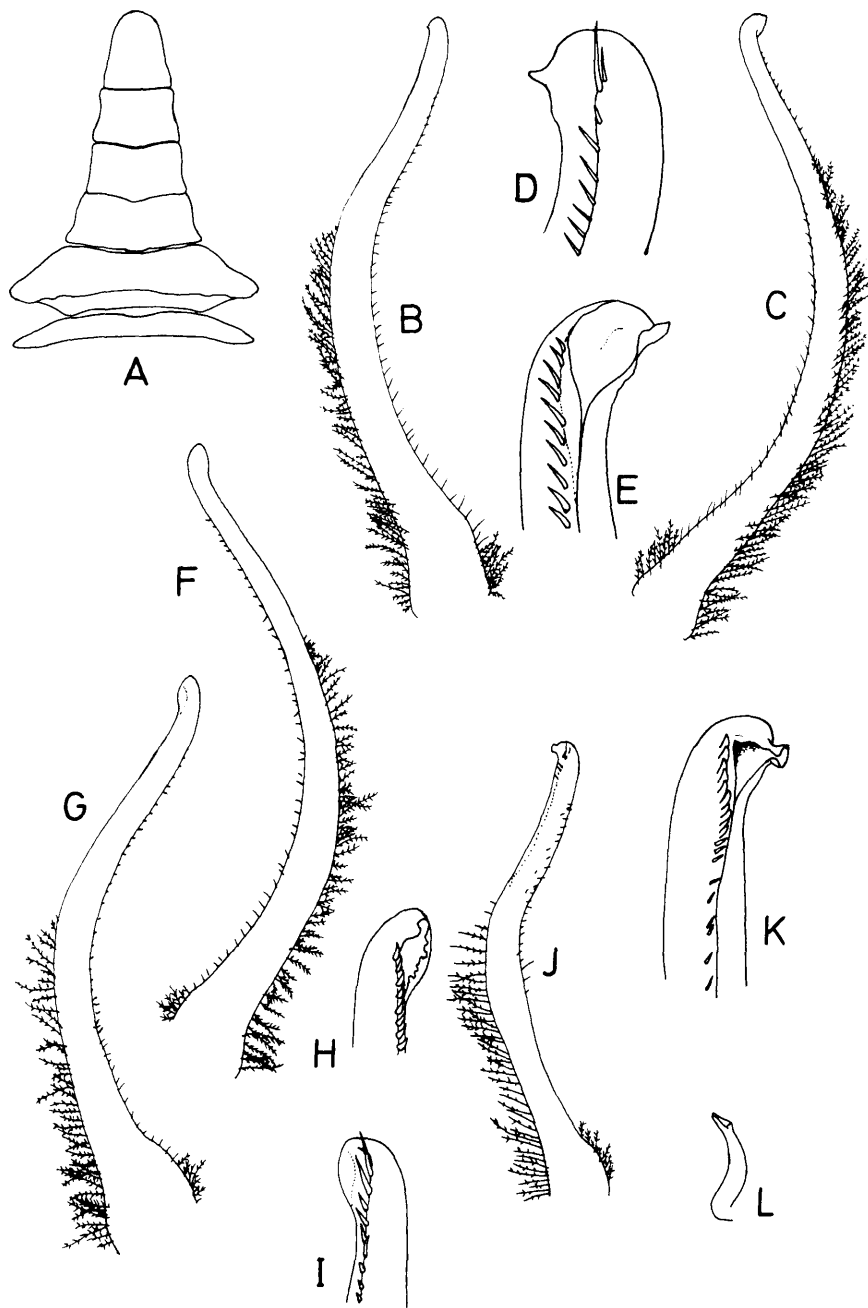


Figure 2. *Rhizopa gracilipes* Stimpson, 1858. A, F-I. Neotype male, 9.7 by 7.0mm, ZMUC; B-E. Male, 8.8 by 6.1mm, USNM 39744; J-L. Male, 8.8 by 6.3mm (after Guinot, 1969). A. Abdomen; B, C, F, G, J. Left G1; D, E, H, I, K. Tips of G1; L. Left G2.

Th. Mortensen, 26.i.1900 -----1♀ (ZMUC), off Koh Bidang, Gulf of Thailand, on mud and shell bottom, 9 fms depth, leg. Th. Mortensen. 18.i.1900 ----- 2 young ♂ (ZMUC), Sound of Koh Mak, Gulf of Thailand, ca. 11°51'N, 102°25'E, 5 to 6 fms depth, leg. Th. Mortensen, 17.ii.1900.

Description of male neotype. Carapace ovate, longitudinally convex, regions indistinctly demarcated, smooth, covered with very low pubescence. H-shaped central depressions distinct but shallow. Frontal margin sinuous, with small median notch which extends backwards to form a shallow Y-shaped groove. Anterolateral margin arcuate, convex, almost entire, vaguely divided into three lobes by depressions, the last most prominent; lined with short hairs. Posterolateral margin almost straight, parallel, adjacent areas with fine oblique striae and low pubescence. External orbital angle not clearly demarcated, merging with supraorbital and anterolateral margins, with supraorbital appearing confluent with anterolateral. Areas adjacent to front, supraorbital and anterolateral margins lined with fine, low, rounded granules, low pubescence and scattered short hairs. Posterior margin of carapace almost straight. Infraorbital margin smooth, entire. Suborbital, sub-branchial and pterygostomial regions covered with low, rounded granules, low pubescence and scattered short hairs. Antennules folding transversely, basal segment of antenna large, free, blocking orbital hiatus. Cornea small, without visible pigmentation. Posterior margin of epistome straight, with two median rectangular tooth-like structures, the grooves separating them very distinct. External surfaces of third maxillipeds covered with low, small rounded granules and scattered short hairs; merus of third maxillipeds quadrate with median depression, anterolateral angle distinctly produced; distal portion of ischium narrow, with distinct oblique median sulcus; exognath with distal triangular tooth-like structure, flagellum well developed, distally tipped with numerous long hairs.

Chelipeds asymmetrical. Right cheliped larger, surfaces convex, rugose; margins cristate; fingers shorter than palm; tips strongly hooked; dactylus with three teeth and one denticle; propodus with five teeth and large basal tooth-like structure that overlaps base of dactylus. Surface of palm of left cheliped slightly rugose, margins more distinctly cristate, ventral margin lined with small granules; tips of fingers hooked; dactylus with three teeth and four denticles, dorsal margin with hair; propodus with six teeth of varying sizes and broad, low basal tooth-like structure that overlaps base of dactylus slightly. Carpus squarish, with blunt but distinct spine on dorsal internal angle; areas on and adjacent to spine covered with low, small rounded granules and low pubescence. Merus and ischium not fused, freely articulating.

Ambulatory legs long, surfaces smooth, margins unarmed, third leg longest, surfaces with scattered short stiff hairs except on dactylus and propodus where hairs are longer and denser. Merus longest segment, dactylus of first three pairs almost straight except for hooked tip; dactylus of last pair distinctly upcurved throughout length.

Surfaces of sternum and abdomen covered with low rounded granules and scattered low pubescence. Abdomen with seven freely articulating segments; first short, broad, not reaching to base of last pair of ambulatory legs, occupying only about half the space; third as broad as but two to three times longer than first; fourth to fifth progressively more trapezoidal, sixth rectangular, seventh triangular, longer than sixth. Male genital opening coxosternal, opening via a narrow exposed canal leading from coxa of last pair of ambulatory legs. G1 long, slender, sinuous, tip blunted with open end. G2 short, sinuous.

Remarks. Miers (1886) was the first to record '*Rhizopa gracilipes*' after Stimpson (1858), and in a footnote to the Rhizopinae, he made the following comments; 'I very much doubt the generic distinctness of *Rhizopa gracilipes*, Stimpson (from Hong Kong), from this species [*Ceratoplax arcuata*]. In specimens, probably from the Chinese Seas, referred doubtfully to *Rhizopa gracilipes* in the British Museum, the ocular corneae are minute and inferior as in *Ceratoplax*, but the merus of the exterior maxillipeds is not produced at its antero-external angle; the basal antennal joint is more robust and quadrate. In the fully grown specimen, the frontal margin is entire, and the palms of the chelipeds are cristate and externally glabrous, as in Stimpson's description' (p. 235). Miers' specimens are however, not *R. gracilipes* as presently defined, since the merus of the third maxilliped is not produced at the anterolateral angle, as is the case for *R. gracilipes s. str.*

Rathbun (1910) subsequently recorded *R. gracilipes* in her study of the Danish material from the Gulf of Thailand (Siam), figuring the third maxilliped, larger cheliped and abdomen of a large male measuring 9.7 by 7.0mm.

Serène (1964), studying the material collected by Mortensen's Pacific Expedition (1914 to 1916), identified a male from Port Jackson, Australia, as belonging to *R. gracilipes* and provided a detailed description and figures of the specimen's G1, abdomen and third maxilliped. He compared his specimen with two females Rathbun (1910) had retained in the Copenhagen Museum as well as with her 1910 figures, and dismissed the differences between their anterolateral margins, third maxillipeds and chelipeds as variations. The present study however, shows that Serène's '*R. gracilipes*' is not conspecific with Stimpson's species but with '*Speocarcinus luteus*' McNeill, 1929, instead. Realising the confusion with the identity of the species however, Serène (1964) indicated that the 9.7 by 7.0mm male figured by Rathbun (1910) should be made the neotype of the species.

Rathbun however, had not provided a catalogue number for this or any of her Thai specimens. She only recorded that the specimen figured was collected from 'Koh Chang' in Thailand (Koh is Thai for island). The exact specimen Serène referred to is thus not known with certainty. Rathbun had indicated in the preface of her study of the Danish Expedition material that she had retained some of the specimens for the USNM when sufficient were available, but did not indicate which of these were actually retained in her records of the material examined. The whereabouts of the 9.7 by 7.0mm male was thus unknown.

Through the kind offices of Dr Torben Wolff of the ZMUC and Dr Raymond Manning of the USNM, the available *Rhizopa* specimens in their collections, containing both Rathbun's (1910) and Serène's (1964) material were sent to the author for examination. A pair which had been sent by the USNM to the BMNH on 25th November 1929 was also examined through the kindness of Dr Paul Clark. A male in the ZMUC was found to agree extremely well with Rathbun's figure, and, in accordance with Serène's suggestion, is here designated as the neotype of *R. gracilipes*.

It must be noted however that the area where Rathbun's material was collected is some 2300km southwest of the type locality Hong Kong. Stimpson's Hong Kong *R. gracilipes* is however, likely to be conspecific with Rathbun's since in characterising the genus *Rhizopa*, Stimpson (1858) writes, 'Hectognathopoda paullo hianta' (Third maxillipeds somewhat gaping)(p. 95), and this is exactly the condition observed in Rathbun's (1910) Thai specimens, in which the distal part of the ischium of the third maxilliped is rather narrow. The ischia of the third maxillipeds of Serène's (1964) '*R. gracilipes*' are much more quadrate and no distinct gape is observed when the third maxillipeds are closed. There is thus no likelihood that his '*R. gracilipes*', presently referred to *Ceratoplax luteus* (McNeill, 1929), is the true *R. gracilipes*. *Ceratoplax luteus* thus also cannot be a junior synonym of *R. gracilipes*.

The G1 of the neotype male is rather poorly preserved and very soft. The figure provided here of this structure (Fig. 2 F-I) may thus not be truly representative of the species. It is nevertheless, still very similar to that of other males from the same locality (Fig. 2 B-E) and that figured by Guinot (1969)(Fig. 2 J-I). The anterolateral margin of the neotype (Pl. 1A) is also more entire than that of smaller males (Fig. 1A), with the first anterolateral lobe almost undiscernible. The two rectangular median lobes of the posterior margin of the epistome are also straighter and closer to each other in smaller specimens. Otherwise, the neotype agrees excellently with the other specimens in all non-sexual aspects.

The unusual structure of the G1, with the tip distinctly blunted, makes its relationship with more typical pilumnids and other rhizopines unclear. Such a G1 structure however, is not unique in the Pilumnidae, and is also present in *Typhlocarcinus rubidus* Alcock, 1900, *Typhlocarcinops marginata* Rathbun, 1914 (both *vide* Serène, 1964), *Typhlocarcinops takedai* sp. nov. (as *T. transversa* Tesch, 1918, *vide* Takeda & Miyake, 1968a) and *Parapilumnus quadridentatus* De Man, 1895 (*vide* Gordon, 1931; Ng, 1983).

With regards to the hairiness of the chelipeds, this is a rather variable character. In many of the females, the dorsal and ventral margins of their mani and fingers are lined with long, silky hairs. This is absent in the larger males, but in some smaller males, some hairs are present. Only in the larger males are the chelipeds distinctly unequal. This difference is almost certainly associated with age and size, and cannot be used as a diagnostic character.

Griffin & Campbell (1969), in their studies of Australian material (including

Table 1. The genera and species belonging to *Rhizopinae*.

Rhizopa gracilipes Stimpson, 1858

Ceratoplax ciliata Stimpson, 1858

Ceratoplax inermis (Haswell, 1881)

Ceratoplax glaberrima (Haswell, 1881)(=*C. punctata* Baker, 1907)

Ceratoplax hispida Alcock, 1900

Ceratoplax fulgida Rathbun, 1914

Ceratoplax truncatifrons Rathbun, 1914

Ceratoplax luteus (McNeill, 1929)

Ceratoplax laevimarginatus (Yokoya, 1933)

Typhlocarcinus villosus Stimpson, 1858

Typhlocarcinus nudus Stimpson, 1858

Typhlocarcinus rubidus Alcock, 1900

Typhlocarcinus craterifer Rathbun, 1914

Typhlocarcinus dentatus Stephensen, 1945

Typhlocarcinus thorsoni Serène, 1964

Caecopilumnus hirsutus Borradaile, 1903

Caecopilumnus piroculatus (Rathbun, 1911)

Caecopilumnus crassipes (Tesch, 1918)

Typhlocarcinops canaliculata Rathbun, 1909

Typhlocarcinops arcuata (Miers, 1884)

Typhlocarcinops decrescens Rathbun, 1914

Typhlocarcinops marginata Rathbun, 1914

Typhlocarcinops ocularia Rathbun, 1914

Typhlocarcinops angustipes Tesch, 1918

Typhlocarcinops transversa Tesch, 1918

Typhlocarcinops gallardoi Serène, 1964

Typhlocarcinops stephenseni Serène, 1964

Typhlocarcinops tonsurata Griffin & Campbell, 1969

Typhlocarcinops genkaiiae Takeda & Miyake, 1972

Typhlocarcinops takedai sp. nov.

Mertonia lanka Laurie, 1906

Mertonia integra (Haswell, 1881)

Xenophthalmodes moebii Richters, 1880

Xenophthalmodes dolichophallus Tesch, 1918

Xenophthalmodes morsei Rathbun, 1932

Xenophthalmodes brachyphallus Barnard, 1955

Zehntneria villosa (Zehntner, 1894)

Zehntneria amakusae (Takeda & Miyake, 1969)

Zehntneria miyakei Takeda, 1972

Zehntneria novaeinsulicola Takeda & Kurata, 1977

Table 1 continued.

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- Rhizopoides yangae* (Ng, 1985)
- Lophoplax bicristata* Tesch, 1918
Lophoplax sculpta (Stimpson, 1858)
Lophoplax takakurai Sakai, 1935
- Serratocoxa teschi* (Serène, 1971)
Serratocoxa granulosa (MacGilchrist, 1905)
Serratocoxa sagamiensis (Sakai, 1935)
- Heteropilumnus stormi* De Man, 1895
Heteropilumnus ciliatus (Stimpson, 1858)
 (= *Heteropanope cristadentatus* Shen, 1936)
Heteropilumnus longipes (Stimpson, 1858)
Heteropilumnus fimbriatus (H. Milne Edwards, 1834)
 (= *Pilumnus pilosus* Fulton & Grant, 1906)
Heteropilumnus setosus (A. Milne Edwards, 1873)
Heteropilumnus trichophoroides (De Man, 1895)
 (= *Pilumnus borradailei* Rathbun, 1909)
Heteropilumnus trichophorus (De Man, 1895)
Heteropilumnus angustifrons (Alcock, 1900)
Heteropilumnus hirsutior (Lanchester, 1900)
Heteropilumnus cristatus (Rathbun, 1909)
Heteropilumnus lanuginosus (Klunzinger, 1913)
Heteropilumnus splendidus (De Man, 1929)
Heteropilumnus amoyensis (Gordon, 1931)
Heteropilumnus granulimanus Ward, 1933
Heteropilumnus mikawaensis Sakai, 1969
Heteropilumnus sasekumari (Serène, 1971)
Heteropilumnus sp. nov. Ng & Tan, in press
- Cryptocoeloma haswelli* Rathbun, 1923
- Pseudocryptocoeloma parvus* Ward, 1936
Pseudocryptocoeloma symmetrinudus Edmondson, 1951
- Pseudolithochira integra* (Miers, 1884)
Pseudolithochira decharmoyi (Bouvier, 1915)
- Selwynia laevis* Borradaile, 1903
- Paraselwynia ursina* Tesch, 1918
- Paranotonyx curtipes* Nobili, 1906
- Pronotonyx laevis* (Miers, 1884)
- Cryptolutea lindemanensis* Ward, 1936
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specimens from Port Jackson), accepted Serène's (1964) identification of *R. gracilipes* as correct, and believed that '*Rhizopa gracilipes*' was actually conspecific with *Speocarcinus luteus* McNeill, 1929. They had compared the type material of *Speocarcinus luteus* with Serène's detailed descriptions and figures and found them identical. They figured the chelipeds and third maxillipeds of their specimens, noting that the chelipeds of the two sexes were different, and that McNeill's (1929) figure of the third maxilliped of *Speocarcinus luteus* was inaccurate, the anterolateral angle of the merus of the third maxilliped not as strongly produced as the figures seem to indicate. Consequently, they synonymised the two species, with *Rhizopa gracilipes* having priority. Campbell & Stephenson (1970) and Griffin (1972) subsequently referred more specimens from southeastern Australia and Moreton Bay (Australia) respectively to *R. gracilipes*, as did Stephenson *et al* (1974) for his lists of benthic invertebrates from southern Moreton Bay.

Guinot (1969c, 1971), after studying material from Trat Bay in the Gulf of Thailand (*ca.* 12°07'N, 102°34'E), which is very near where Rathbun's (1910) material was collected, expressed doubts as to Serène's (1964) conclusions, citing striking differences in the structure of the G1 and male cheliped between her specimen and Serène's '*Rhizopa gracilipes*' from Australia. She regarded *Speocarcinus luteus* as a distinct taxon, and indicated that it might be better to regard it as a distinct species of *Rhizopa*. Guinot (1969c), like Rathbun (1910), obviously regarded the Thai specimens to be representative of the true *R. gracilipes*. Ng (1985), after briefly reviewing the genus *Rhizopa*, concurred with Guinot's suppositions, and relegated all Australian records of '*R. gracilipes*' by Griffin & Campbell (1969), Campbell & Stephenson (1970) and Griffin (1972) to *Rhizopa luteus*.

The affinities of *Rhizopa* with the other pilumnid genera is unclear. Miers (1886) first commented on the tremendous similarity between *Rhizopa* and *Ceratoplax*, indicating that they might be synonymous. Externally, these two genera have only been effectively separated by the degree of pigmentation in their eyes, a character first cited by Stimpson (1858) and subsequently used by Alcock (1900) and Tesch (1918). Such a difference however, is a quantitative rather than a qualitative one, and is unlikely to be useful when a full spectrum of species are compared, and it is certainly not a reliable phylogenetic character. The easiest and most reliable way of separating *Rhizopa* from *Ceratoplax* is to use the width of the distal portion of the ischia of their third maxillipeds. The distal portion of the ischium of the third maxilliped in *Rhizopa* is rather narrow whereas that of *Ceratoplax* is distinctly quadrate.

Rhizopoides gen. nov.

Type-species: *Rhizopa yangae* Ng, 1985: 627

Diagnosis. Carapace ovate, surfaces smooth, with very low pubescence, anterolateral margins cut into distinct teeth. Anterolateral angle of merus of third

maxillipeds distinctly produced, ischium quadrate. Surfaces of larger cheliped smooth, glabrous, fingers gaping at base when closed, cutting edge of dactylus almost entire except for prominent median tooth. Dactylus of last ambulatory leg gently downcurved. G1 sinuous, tip elongate, tapering. G2 short, sinuous.

Etymology. The genus is named in allusion to its close resemblance to *Rhizopa*.

Rhizopoides yangae (Ng, 1985)

Rhizopa yangae Ng, 1985: 627, Figs. 1A-H, 2E-F

Material examined. Holotype - 1♂, 7.3 by 5.0mm (ZRC Nr. 1984.3.31.1), shallow water, muddy substrate, coral reef, Sentosa Island, Singapore, 1°14'34"N, 103°49'42"E, leg. P. K. L. Ng, vi.1982.

Remarks. Described from a single male collected from Singapore, *Rhizopa yangae* is now made the type of a new genus, *Rhizopoides*. *Rhizopoides yangae* has a combination of characters that makes its affiliation with known genera in the Rhizopinae very difficult. The distinctly cut anterolateral margin with well developed teeth is only found in some species of *Heteropilumnus* but the absence of long hairs on the carapace and legs, and a smooth and glabrous major cheliped makes it very difficult to place the species in this genus. Very few rhizopines have the anterolateral margin as distinctly cut and well developed as in *Rhizopoides yangae* (eg. *Typhlocarcinus dentatus* Stephensen, 1945, and *Heteropilumnus mikawaensis* Sakai, 1969). Its placement in the genus *Rhizopa s. str.* also cannot be justified considering its well developed anterolateral teeth, quadrate third maxilliped ischium, downcurved last ambulatory dactylus, the cutting edge of the dactylus and propodus of the cheliped with one large, blunt median tooth and two subdistal low denticles respectively, the fingers gaping when closed, and the sinuous and tapered tip of the G1. A new genus has therefore been established to accommodate this unusual species.

The structure of the ischia of the third maxillipeds of *Rhizopoides* is however, very close to that of *Ceratoplax*, but the two can easily be separated by the structure of their anterolateral margins. In *Ceratoplax*, the anterolateral margin is entire or faintly cut into lobes, whereas in *Rhizopoides*, three distinct teeth (including the external orbital angle) are discernible.

The original male was collected from under a rock on very muddy substratum in the intertidal region, which agrees fairly well with the known luteophilous habits of most rhizopines.

Genus Ceratoplax Stimpson, 1858

Ceratoplax luteus (McNeill, 1929) comb. nov.

Speocarcinus luteus McNeill, 1929: 152, Fig. 1-4, Pl. 36

Rhizopa gracilipes Serène, 1964, Fig. 2, Pl. 17A; Griffin & Campbell, 1969: 142, Fig. 2A-C, 6A; Campbell & Stephenson, 1970: 286; Griffin, 1972: 84; Stephenson, Williams & Cook, 1974: 115

[*Speocarcinus*] *luteus* Guinot, 1971: 1079

Rhizopa luteus Ng, 1985: 631

Material examined: 1♂, 3.5 by 10.0mm (ZMUC), Port Jackson, Watson's Bay, Australia, 6 to 9m depth, sand and skraber bottom, leg. Th. Mortensen, 8.x.1914

Remarks. *Ceratoplax luteus* was originally described from the genus *Speocarcinus* Stimpson, 1859, from two males and two females dredged from a muddy bottom in Salamander Bay, Port Stephens, New South Wales, Australia, in six fathoms of water. The type male, 21.0 by 15.0mm was figured in detail, but as Griffin & Campbell (1969) noted on reexamining the type, the figure of its third maxillipeds is inaccurate, with the anterolateral angle of the merus not as strongly produced as the figure seems to indicate. They also remarked that the degree of tuberculation on the outer surface of the cheliped is highly variable with sex and age, from smooth to strongly granular.

Serène (1964) briefly questioned the composition of the genus *Speocarcinus*, noting that McNeill's *Speocarcinus luteus* '... semble appartenir a un genre different de celle de Tesch et toutes deux a un autre que *Speocarcinus*' (... seems to belong to a genus different from that of Tesch [for *Speocarcinus celebensis*] and the other two species in *Speocarcinus*)(p. 194). Guinot (1969c) remarked that *Speocarcinus* is a fundamentally American taxon, and the Indo-Pacific species currently assigned to this genus should be referred elsewhere. *Speocarcinus s. str.* was revised by Guinot (1969c) and Felder & Rabalais (1986), and is now regarded as containing only five American species. The detailed descriptions and figures of *Speocarcinus* provided by Guinot (1969c) and Felder & Rabalais (1986), notably of their male abdomen (segments three to five fused), G1s (stout, slightly sinuous, with many scattered sharp spines on distal portion) and G2s (with a relatively long basal segment) clearly show that the genus *Speocarcinus* is not affiliated to the rhizopines or pilumnids as presently defined.

Ng (1985), concurring with Guinot's (1971) views on the affinities of '*Speocarcinus luteus*' with *Rhizopa*, tentatively transferred the species to the genus. But considering the present observations of the differently structured third maxilliped ischium and G1 of *Rhizopa gracilipes*, it was felt that it would be better to refer McNeill's species to another genus, as Ng (1985) had suggested. The strongly produced anterolateral angle of the third maxilliped excludes it as being a member of the genus *Typhlocarcinus* or *Typhlocarcinops* Rathbun, 1909, which have blunt and rounded anterolateral angles, despite their close external resemblance. It however fits perfectly into the genus *Ceratoplax* as presently defined with regards to the meral structure of its third maxillipeds and convex anterolateral margin. All specimens identified by Serène (1964), Griffin & Campbell (1969), Campbell & Stephenson (1970), Griffin (1972) and Stephenson *et al* (1974) as *Rhizopa gracilipes* from various parts of Australia must now be referred to *Ceratoplax luteus* instead.

The larvae of *Ceratoplax luteus* have been obtained by Professor Jack G.

Greenwood (det. as '*Rhizopa gracilipes*', in litt., 13 April 1984), and he has kindly informed the author that the zoeae have typically pilumnid characters (*vide* Rice, 1980; Ng, 1983)(Greenwood, personal communication). Other than the zoeae of two *Heteropilumnus* species, this is only the second rhizopine genus whose larvae is known, and supports the inclusion of the species, genus and subfamily in the Pilumnidae.

Genus Heteropilumnus De Man, 1895

Heteropilumnus sasekumari (Serène, 1971) comb. nov.

Rhizopa ? *sasekumari* Serène, 1971: 915, Pl. 5A; Guinot, 1971: 1079

Rhizopa sasekumari Ng, 1985: 631, Fig. 2A-D; Davie, 1985: 261, 262

Material examined. Holotype - 1♀, 16.2 by 10.6mm (ZRC Nr. 1969.12.4.7), Port Swettenham, Peninsular Malaysia, littoral mud, leg. A. Sasekumar, 28.x.1968.

Others - 1♀ (ZRC Nr. 1965.11.23.51), Labuan, Sabah, East Malaysia (Borneo), in mangrove, leg. 1938

Remarks. The placement of this species in the genus *Rhizopa* has always been in doubt, and even Serène (1971) was uncertain as to whether it was really a *Rhizopa*, although he did not comment in any detail. Guinot (1971) also listed this species under the genus *Rhizopa* with some reservation. Ng (1985) redescribed the species on the basis of the type material and reluctantly followed Serène's nomenclature. He suggested why '*Rhizopa sasekumari*' may not be a true *Rhizopa* especially with regards to its hirsutous carapace and chelipeds, and the fingers of the cheliped possessing numerous distinct cutting teeth. The G1 of the species is unknown. The available characters however, strongly suggest that '*R. sasekumari*' is more closely affiliated with the genus *Heteropilumnus*, which is itself in urgent need of revision.

Davie (1985) reported this species, as *Rhizopa sasekumari*, from mangroves in Australia, noting that it is '... a cryptic species and rather difficult to collect only represented from the east coast by two or three specimens, and therefore, it is quite possible it will be found more generally in northern Australia, as collections are expanded' (p. 261). He also recorded the species (in his Table 2, p. 262) as being found in Singapore, but the present author has no records or know of any literature citing the species from Singapore. It is likely that he had mistaken the type locality of 'Port Swettenham, Malaisie' (Serène, 1971: 915) as being in Singapore.

The status of the subfamily Rhizopinae Stimpson, 1858

The family Rhizopinae was established by Stimpson, 1858, to accommodate four of his new genera, *Rhizopa*, *Scalopidia*, *Typhlocarcinus* and *Ceratoplax*, with their main similarities being a partly mobile antenna, small and immobile eyes, an undivided palate, and the sexual openings being coxal but opening in the sternum via a narrow canal. In Miers' (1886) system of classification, Stimpson's

family was relegated as part of the subfamily Carcinoplacinae, family Ocypodidae. Miers recognised three sections in his Carcinoplacinae: Rhizopinae, Euryplacinae Stimpson, 1870, and Carcinoplacinae H. Milne Edwards, 1852, in spite of the sectional nomenclature he chose to adopt. Miers defined the section 'Rhizopinae' as a group '... whose antero-lateral margins are arcuated, and in the characters drawn from the front, orbits and outer maxillipeds, but the antero-lateral margins are usually entire, rarely dentated, and the post abdomen of the male does not cover the whole width of the sternum at the base (except perhaps sometimes in *Typhlocarcinus*)' (p. 234). The genera he included in this section were *Rhizopa*, *Scalopidia*, Stimpson, 1858, *Typhlocarcinus* Stimpson, 1858, *Ceratoplax* Stimpson, 1858, *Notonyx* A. Milne Edwards, 1873, *Xenophthalmodes* Richters, 1880, and *Cryptocoeloma* Miers, 1884, the last with some doubt. He also noted that the '... species are all of small size and are exclusively Oriental or Indo-Pacific forms' (p. 223). Ortmann (1894, 1896) raised both the Carcinoplacinae and the section Gonoplacinae, subfamily Ocypodinae, of Miers to full family status, hence elevating Miers' 'section Rhizopinae' to subfamily Rhizopinae. Alcock (1900) modified Ortmann's system, combining his Carcinoplacidae and Gonoplacidae into one family, the Gonoplacidae, with each having subfamily status, equal in rank with his other subfamilies, Pseudorhombilinae Alcock, 1900, Prionoplacinae and Hexapodinae. Stebbing (1902) commented that the proper spelling of the type genus of the family is *Goneplax* Leach, 1815, and not '*Gonoplax*' as used by previous authors. The family should thus be spelt as Goneplacidae instead. Tesch (1918) followed Alcock (1900) in recognising the Rhizopinae merely as a subfamily of the family Goneplacidae. Summarising their conclusions, the Rhizopinae is characterised by a nearly smooth carapace which is broader than long, with the front narrow; anterolateral margins convex, usually entire or almost so; shallow orbits; poorly developed eyes (especially the cornea) which are or almost immobile; tendency for the antennules to fold obliquely in their fossae or not at all; and a short antennal flagellum. Alcock (1900) records the male openings as sternal, but the real opening as observed by Stimpson (1858) for *Rhizopa s. str.* is coxal, and the apparent opening in the sternum is due to a very narrow canal formed by the sternal plates connecting the coxal to the sternal opening. Alcock (1900) also noted that the male abdomen (ie. the first segment) '...does not nearly cover the space between the last pair of ambulatory legs' (p. 287). Tesch (1918) takes a broader and more flexible understanding of this last character, dismissing the use of this character by Rathbun (1910) to establish a new subfamily, the Typhlocarcinopsinae. Rathbun had characterised her subfamily by its broad first male abdominal segment which covers almost the entire space between the last pair of ambulatory legs. Tesch (1918) notes, '... that in many of the Rhizopinae the first segment of the male abdomen presents a clear tendency to enlarge and become broader than the third segment' (p. 199), and '...except for this slight difference, is absolutely and intimately related to *Typhlocarcinus* Stimpson, as regards all principal features'

(p. 200). Consequently, he includes the genus *Typhlocarcinops* Rathbun, 1909, in the subfamily Rhizopinae as defined by Alcock (1900), an action which the present author agrees with.

Tesch (1918) recognised 15 genera in his Rhizopinae: *Rhizopa*, *Ceratoplax*, *Typhlocarcinus*, *Typhlocarcinodes* Alcock, 1900, *Typhlocarcinops*, *Notonyx* A. Milne Edwards, 1873, *Chasmocarcinus* Rathbun, 1898, *Selwynia* Borradaile, 1903, *Paranotonyx* Nobili, 1906, *Paraselwynia* Tesch, 1918, *Camatopsis* Alcock & Anderson, 1899, *Hephthopelta* Alcock, 1899, *Megaethesius* Rathbun, 1909, *Mertonia* Laurie, 1906, and *Xenophthalmodes* Richters, 1880. Sakai (1939, 1965), in his treatment of the Japanese rhizopines, accepted Tesch's system of classification, and subsequently (1976) added a fossil genus, *Arges* De Haan, 1833, allied to *Xenophthalmodes*, to the subfamily. Balss (1957) in his compilation and classification of the Brachyura, added three more genera, *Acidops* Stimpson, 1871, *Pronotonyx* Ward, 1936, and the fossil genus *Microplax* Glaessner, 1928. This scheme of classification was reluctantly accepted by Serène (1964) in his treatment of the material from Dr Th. Mortensen's 1914 to 1916 Pacific Expedition. Serène (1964) however, suggested that the genera *Chasmocarcinus*, *Hephthopelta*, *Chasmocarcinops*, *Camatopsis*, *Megaethesius* might possibly be separated from the Rhizopinae and into a new subfamily, the Chasmocarcininae (p. 196). He (1965) subsequently recognised this as a separate subfamily with the above genera and adding two others, *Scalopidia* and *Mertonia*. He (1965) also recognised the Typhlocarcinopsinae, with the genera '*Thyphlocarcinops*' (spelling erroneous) and '*Thyphlocarcinodes*' (spelling erroneous). Later (1968) however, in his interpretation of the Rhizopinae, he recognised nine genera in the subfamily: *Rhizopa*, *Ceratoplax*, *Notonyx*, *Pronotonyx*, *Paranotonyx*, *Selwynia*, *Paraselwynia*, *Typhlocarcinus* and *Xenophthalmodes*, using Rathbun's (1910) Typhlocarcinopsinae to contain the remaining genera of Tesch's Rhizopinae with the addition of *Chasmocarcinops* Alcock, 1900, but made no mention of his Chasmocarcininae.

Takeda & Shimazaki (1974) recognised six subfamilies in the Goneplacidae: Carcinoplacinae H. Milne Edwards, 1852; Chasmocarcinopsinae Serène, 1964; Goneplacinae Dana, 1851, Hexapodinae Miers, 1886; Prionoplacinae Alcock, 1900; and Rhizopinae. Their 'Chasmocarcinopsinae' was almost certainly a misspelling, and actually referring to the Chasmocarcininae instead. Their Rhizopinae contained all of Serène's (1964) genera except with the addition of *Acidops* and *Typhlocarcinops*. They also resurrected the family Chasmocarcininae while dissolving the Typhlocarcinopsinae Rathbun, 1910. The genus *Zehntneria* Takeda, 1972, was also placed in the Carcinoplacinae, whilst *Typhlocarcinodes*, *Chasmocarcinus*, *Hephthopelta*, *Megaethesius*, *Scalopidia*, *Camatopsis* and *Mertonia* were included in the Chasmocarcininae.

Guinot (1969a, b, c, 1971), in her preliminary revisions of the goneplacid taxa, recognised the genera *Ceratoplax*, *Typhlocarcinus*, *Typhlocarcinops*, *Heteropilumnus* De Man, 1895, *Mertonia*, *Lophoplax* Tesch, 1918, *Galene* De Haan,

1833, *Halimede* De Haan, 1835, *Parapanope* De Man, 1895, *Rhizopa* and part of the *Litocheira* Kinahan, 1856, as having pilumnid affinities but did not go so far as to recognise them as a distinct group or actually transfer them to the Pilumnidae. Guinot (1969c) commented as for the other genera in Tesch's (1918) Rhizopinae, some may not be 'pilumnien'. She (1969c, 1971) also noted that the genus *Lophoplax* Tesch, 1918, which had been placed in the Prionoplacinae, might belong to her 'lignée pilumnienne' instead. Earlier (1969a), she indicated that the genera *Ser* Rathbun, 1929, *Cryptolutea* Ward, 1936, and *Homoiplax* Rathbun, 1914, might also belong to this group, but she did not examine this further. Later (1978), in her more comprehensive revision of brachyuran classification, she chose not to recognise the composition of the Rhizopinae of earlier workers (she had split and reorganised the Goneplacidae on the grounds of its heterogeneity) and tentatively placed the Rhizopinae *s. str.* and a single genus, *Rhizopa*, in the family Pilumnidae '... mais appartenant à dans un rameau spécial' (but belonging in a special branch)(p. 275). This was only done as a stop-gap measure, as Guinot (1978) correctly noted, the group being still unstable, but she did not want the group to be confused with the other 'Pilumnidae Catométopes' (p. 275).

Ng (1983), in his study of pilumnid systematics and xanthoid evolution, supported Guinot's (1978) actions, and remarked that the genus *Typhlocarcinodes* is unlikely to be a member of the family Pilumnidae since the male abdomen and gonopods as figured by Serène (1964) for *Typhlocarcinodes piroculatus* (Rathbun, 1911) were unlike those of known pilumnids. Serène's specimens of *T. piroculatus* are presently referred to a new genus and species (see p. 93) and not regarded as conspecific with Rathbun's species. *Typhlocarcinodes s. str.* however, remains excluded from the Pilumnidae (see p. 92). Felder & Rabalais (1986) recommended that *Chasmocarcinus* be retained in the Chasmocarcininae with the other genera.

The present designation of a neotype for *Rhizopa gracilipes* permits a clearer definition of this problematic subfamily. The validity of the Rhizopinae remains questionable but it does have practical, if not phylogenetic value. As Guinot (1978) had noted, it represents a group of pilumnids with 'goneplacien' (ie. catometopous) tendencies but not necessarily being phylogenetic in composition. In fact, some genera like *Heteropilumnus* have both 'pilumnien' as well as 'goneplacien' characters.

In her understanding of the Pilumnidae, Guinot (1978) recognises two main groups; 1., which is basically the Pilumninae of Balss' (1957), with the addition of several genera; and 2., which is the 'goneplacien' group, consisting of the genera *Heteropilumnus*, *Ceratoplax*, *Typhlocarcinus*, *Typhlocarcinops*, *Lophoplax*, *Mertonia*, and some of the species that have been assigned to *Litocheira* Kinahan, 1856. This 'goneplacien' group of Guinot's is actually part of the 'pilumnien' line, but at the 'goneplacien' grade (Guinot, *in litt.*, 2 February 1987).

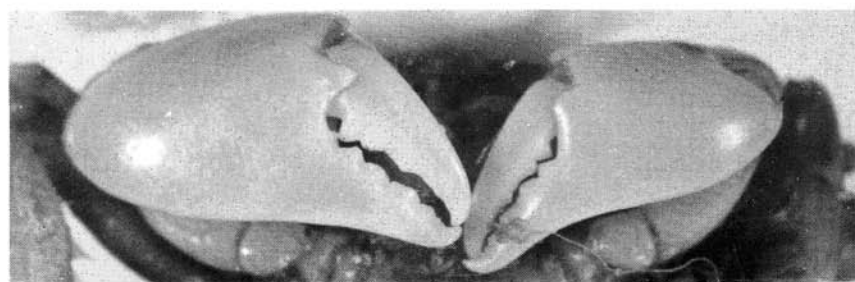
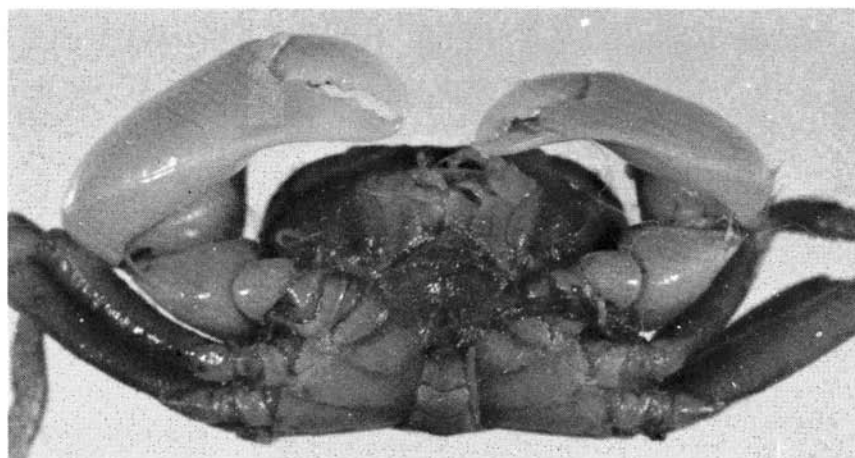
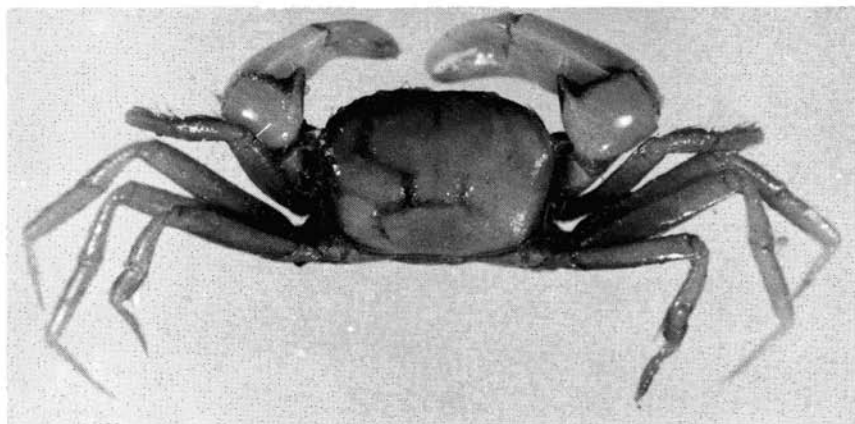


Plate 1. *Rhizopa gracilipes* Stimpson, 1858. Neotype male, 9.7 by 7.0mm, ZMUC.

The Rhizopinae thus, according to Guinot (*in litt.*, 22 March 1986, 2 February 1987) is part of the same clade as the Pilumninae (as presently defined), but at a different grade in pilumnid evolution. For the moment, this subfamily is recognised as a taxon for practical reasons. Whether the taxon is an artificial one, or truly represents a monophyletic grouping can only be determined through detailed future studies of the various genera. In addition to the characters enumerated by previous authors, three very important characters must be added to the definition of the subfamily - a slender, simple and sinuous G1, a short and sinuous G2, and a male abdomen which is triangular with all the seven segments distinct and articulating. The present understanding of the Rhizopinae is thus, much broader than that accepted by Guinot (1978) and encompasses her second group of Pilumnidae (the 'goneplacien' group) as well as some genera she had not treated. The subfamily Rhizopinae is now recognised to contain the following genera: *Rhizopa*, *Rhizopoides*, *Ceratoplax*, *Typhlocarcinus*, *Typhlocarcinops*, *Caecopilumnus* Borradaile, 1903, *Pronotoonyx*, *Paranotoonyx*, *Selwynia*, *Paraselwynia*, *Mertonia*, *Xenophthalmodes*, *Lophoplax*, *Heteropilumnus*, *Cryptocoeloma* Miers, 1884, *Pseudocryptocoeloma* Ward, 1936, *Pseudolitochira* Ward, 1942, *Cryptolutea* Ward, 1936, *Zehntneria* Takeda, 1972, and *Serratocoxa* gen.nov. The genus *Cryptolutea* is also included in the Rhizopinae for the first time. The taxonomy of these genera, as well as others which have been placed in or affiliated with the Rhizopinae but presently transferred out or excluded, viz. *Speocarcinus*, *Ser*, *Homoioplax*, *Notonyx*, *Scalopidia*, *Camatopsis*, *Chasmocarcinus*, *Chasmocarcinops*, *Hephthopelta*, *Megathesius*, and *Acidops* will also be discussed. The taxonomy of some of the more problematic species will also be dealt with. The pilumnine genus *Viaderiana* Ward, 1942, will also be reviewed in view of its close relationship with some of the rhizopine genera.

Genus Rhizopa Stimpson, 1858 (see p. 73)

Genus Rhizopoides gen. nov. (see p. 80)

Genus Ceratoplax Stimpson, 1858

Serène (1968) recognised eight species in the genus, and Guinot (1969) remarked that '... des espèces attribuées à ce genre soient des Goneplacidae de la lignée pilumnienne. Le genre doit être révisé car il est certainement hétérogène' (... the species attributed to this goneplacid genus are of the 'pilumnien' line. The genus is heterogeneous and needs to be revised)(p. 698). *Ceratoplax villosa* (Zehntner, 1894) was later referred to a new genus, *Zehntneria* by Takeda (1972). Miers (1886) had noted that the genus *Ceratoplax* is extremely close to *Rhizopa*, and could only be effectively be separated by the degree of degeneration of the eyes. As discussed earlier, this character is unlikely to be reliable, and the shape of ischium of the third maxilliped is more useful instead. In fact, Stimpson, in characterising the genus *Ceratoplax*, writes, 'Hectognathopoda.....non hianta;

meri angulo externo prominente' (Third maxillipeds not gaping, external angle of merus prominent) (p. 96). The G1s of *Rhizopa* are also blunt-tipped whereas in those of known *Ceratoplax*, the tip is elongated and tapered. McNeill's (1929) '*Speocarcinus luteus*' (= Serène's (1964) '*Rhizopa gracilipes*') is presently referred to *Ceratoplax* on the basis of these characters.

Less can be said of the other species which Serène (1968) had referred to *Ceratoplax*, and the inclusion of several of these must be regarded as tentative until their types can be reexamined. The species described as *Speocarcinus laevimarginatus* by Yokoya (1933) from Japan cannot be retained in that genus as presently defined. The form of the mouthparts and male abdomen clearly places it in the genus *Ceratoplax* instead, although Serène (1964) had indicated that it might be a *Typhlocarcinus*. Two of the species, *C. inermis* and *C. glaberrima* were originally placed in the genus *Pilumnus* Leach, 1815, but Rathbun (1923) correctly referred them to *Ceratoplax*. Rathbun (1923), after comparing types, also synonymised *Ceratoplax punctata* Baker, 1907, with *C. glaberrima*. '*Ceratoplax laevis* Miers, 1884' was transferred to a new genus, *Pronotoonyx* by Ward (1936). Miers' (1884) *Ceratoplax arcuata* is presently transferred to the genus *Typhlocarcinops*. Zehntner (1894) had also described a new species, *Ceratoplax leptochelis* but Tesch (1918) commented that it is more likely to be a *Panopeus* or *Melia*, with Balss (1938) tentatively referring it to the genus *Lybia* H. Milne Edwards, 1834 (Family Xanthidae MacLeay, 1838 *sensu* Guinot, 1978). Recent revisions (Serène, 1984) accept it as a *Lybia*. The type of the genus *Ceratoplax*, *C. ciliatus* is poorly known, and like the type of *Rhizopa*, *R. gracilipes*, was almost certainly lost in the 1871 Chicago Fire. To prevent future misidentification and confusion about its identity, the specimen figured by Tesch (1918) is designated the neotype. It is a male 14.5 by 11.0mm, collected from the West Coast of Salawatti near New Guinea at a depth of 18m and is in the Amsterdam Museum.

Two species are currently transferred out of *Ceratoplax* into a new genus, *Serratocoxa* gen. nov.: *C. granulosa* MacGilchrist, 1905, and *C. sagamiensis* Sakai, 1935, because of the unusual serrated plate-like structure on their ambulatory coxa, which is absent in all other *Ceratoplax* species.

The structure of the last ambulatory leg seems to vary in the genus, with species like *C. ciliata*, *C. arcuata*, *C. hispida*, and *C. luteus* being downcurved, whilst *C. truncatifrons* and *C. laevimarginatus* have upcurved ones. It would appear that this character could be used to split *Ceratoplax* into two groups, but in view of the scarcity of specimens of most of the various species, and the dearth of information about interspecific variation, the present author prefers to adopt a more conservative approach and keep the genus intact.

Genus Typhlocarcinus Stimpson, 1858

Typhlocarcinus was established by Stimpson (1858) for two species, but his diagnosis was too brief to characterise the genus clearly. Tesch (1918) regarded *Typhlocarcinus* as different from the closely related *Ceratoplax* by the anterola-

teral angle of the merus of the third maxilliped being rounded and not produced, and the pigment of the eyes almost absent. He noted one exception, *T. craterifer* Rathbun, 1914, in which the anterolateral angle of the merus of the third maxilliped is produced and the eyes black. *Typhlocarcinus craterifer* is only known from females from the Philippines (Rathbun, 1914) and South Africa (Serène, 1964), and its status is very uncertain. Rathbun (1914) provided no figures, and Serène's (1964) figure of the third maxilliped has the anterolateral angle of the merus rounded, not produced, and if Tesch's (1918) interpretation is to be followed, may not represent *T. craterifer*, especially considering the great distance separating the two localities. Serène (1964) however, argues for the conspecificity of the Filipino and South African specimens since his specimens agree very well with Rathbun's (1914) description in almost all other respects, and correctly notes that Tesch's interpretation is subjective. A reexamination of the type would be most desirable to clarify these two views. The genus has since being expanded to include six species (see review by Serène, 1964). Some taxa have been transferred out (eg. *Typhlocarcinus integifrons* Miers, 1881, to *Typhlocarcinodes* Alcock, 1900), but the definition of the genus has remained essentially unchanged since Tesch (1918). Like the genus *Ceratoplax*, two of the species have the dactylus of the last ambulatory leg upcurved, *T. nudus* Stimpson, 1858 (*vide* Tesch, 1918) and *T. dentatus* Stephensen, 1945 (*vide* Stephensen, 1945; Serène, 1964). Again, whether this character merits the establishment of a separate genus for the species with the dactylus upcurved is debatable. The type of the genus, *T. villosus*, has the dactylus downcurved.

Genus Typhlocarcinops Rathbun, 1909

This genus was established by Rathbun (1909), and made the type of a new subfamily, Typhlocarcinopsinae Rathbun, 1910. She further elaborated on the subfamily and genus in 1910. Although the subfamily has been used by several authors, the present author agrees with Tesch (1918) that it should be synonymised with the Rhizopinae. The genus was originally characterised by the first male abdominal segment being very broad, reaching to the bases of the last pair of ambulatory legs. Otherwise, in general appearance they are identical to *Typhlocarcinus*. Tesch (1918) amended Rathbun's diagnosis, noting that the tendency for the expansion of the first male abdominal segment can also be found in *Typhlocarcinodes*, and hence unreliable as a generic character. To differentiate *Typhlocarcinops* and *Typhlocarcinodes*, he used the character of the posterior margin of the epistome. In *Typhlocarcinops*, this structure is prominent and distinct, whereas in *Typhlocarcinodes*, it is sunken into the buccal region, being indistinct. The antennules in this genus, thus almost meet the upper margins of the third maxillipeds. With the genus *Typhlocarcinodes* now revised and *Typhlocarcinodes s. str.* now removed from the Rhizopinae, these characters now apply for *Caecopilumnus*, to which almost all of Tesch's *Typhlocarcinodes* species have now being transferred. *Typhlocarcinops* was originally established with

Typhlocarcinops canaliculata Rathbun, 1909, as type.

The species described by Rathbun (1911) as *Typhlocarcinops piroculatus* is confusing. In her description, she listed three females (one adult and 2 juveniles) as her type material, describing the adult female in detail. Yet, in the legend to her plates, the two photographs (Pl. 20, figs. 1, 2) of the species were labelled as the type male. The photograph showing the ventral view of the species also seems to confirm the legend, showing a narrow, triangular abdomen, characteristic of males. Considering the size of the specimen (7.2 by 5.6mm), which is usually the adult size for these crabs, in all likelihood, the 'female' type description was a typographical error. She had also described the abdomen as having all the segments free, the first being very broad, as is characteristic of her genus *Typhlocarcinops*. Her placement of this species in the genus *Typhlocarcinops* is further indication that the adult specimen of the species she had in front of her was a male. In the absence of a male, the determination of the genus would have been extremely difficult, if not impossible. Tesch (1918) later transferred *T. piroculatus* to the genus *Typhlocarcinodes*, using the character of the strength of the posterior epistomal margin. The specimens described by Barnard (1955) and Serène (1964) as belonging to this species have been referred to *Raoulia limosa* gen. et sp. nov. instead.

The identity of *T. transversa* Tesch, 1918, is also of some interest. The merus of the third maxilliped figured by Tesch (1918) differs slightly from that by Serène (1964) in that the anterolateral angle appears to be more produced. Serène's figure however, is rather diagrammatic and direct comparisons would need to be made to confirm their conspecificity. Takeda & Miyake (1968a) also recorded this species from the East China Sea, figuring the G1. They noted however, that their specimens were different from Tesch's in having the carapace '... rather well sculptured medially, the lateral border of the carapace is provided with three blunt teeth which are formed by three U- shaped interruptions, and finally the outer surface of the palm is smooth beneath the pubescence, its upper border being rounded except near the proximal end' (p. 571). The type description of *T. transversa* however, indicates that the regions of the carapace are almost absent except for the longitudinal groove near the front, the three blunt teeth of the anterolateral margin are separated by wide gaps, and the outer surface of the palm granulose, with the upper borders sharply keeled. The East China Sea specimens are also very different (described but not compared by Takeda & Miyake) in the shape of the dactylus of the last ambulatory leg, being '... prominently upturned' (Takeda & Miyake, 1968a: 570). That of *T. transversa* s. str. is straight or slightly downcurved (*fide* Tesch, 1918; Serène, 1964). The specimens from the East China Sea almost certainly represent an undescribed species, for which the name *Typhlocarcinops takedai* sp. nov. is proposed:

***Typhlocarcinops takedai* sp. nov.**

Typhlocarcinops transversa Takeda & Miyake, 1968a: 569, Pl. 6A, Fig. 8a, b; Takeda, 1973: 54

(not *Typhlocarcinops transversa* Tesch, 1918)

Diagnosis. Carapace quadrate, surface well sculptured medially, covered with short pubescence, with long hairs on lateral borders. Front medially grooved, each lobe slightly arched. Third maxillipeds almost completely covering buccal cavern, merus quadrate, anterolateral angle produced. Anterolateral margin with three blunt teeth, bordered by small, thick granules, separated by relatively narrow U-shaped sinuses. Upper border of palm of cheliped rounded except for bluntly crested proximal end, surfaces almost smooth. Ambulatory legs unarmed, dactylus of last pair distinctly upcurved. First male abdominal segment very broad, reaching to base of last pair of legs. G1 sinuous, slender, tip blunted.

Etymology. The species is named in honour of Dr Masatsune Takeda.

Material (fide Takeda & Miyake, 1968a). Holotype - 1♂, 7.8 by 5.2mm, ZLKU No. 12535, 29°0.1'N, 124°48.1'E, 82m depth, leg. H. Yamashita, 29.vi.1962
Paratypes - 2♂(1 with *Sacculina*), 1♀, ZLKU No. 12536, 28°47'N, 124°50'E, 102m depth, leg. H. Yamashita, 30.vi.1962

Typhlocarcinops takedai bears a striking resemblance to *Rhizopa gracilipes* s. str., especially with regards to the blunted G1 and upcurved dactylus of the last ambulatory leg. The first male abdominal segment of *R. gracilipes* is however, not as broad as that typical for *Typhlocarcinops* species, and the ischium of the third maxillipeds of this genus is also not distally narrowed.

The species described as *Ceratoplax arcuata* by Miers (1884) cannot be maintained in Stimpson's (1858) genus as presently defined. Miers' figure of the male abdomen clearly shows the first male segment as being very broad, reaching to the bases of the last pair of ambulatory legs, typical for *Typhlocarcinops*. Its epistome moreover, is distinct, excluding its inclusion in the genus *Typhlocarcinodes* or *Caecopilumnus*. Consequently, Miers' species is transferred to *Typhlocarcinops*. It was described from Port Darwin, Australia.

The anterolateral angle of the merus of the third maxilliped in *Typhlocarcinops* is of two types; distinctly produced (eg. *T. arcuata*, *T. transversa*, *T. takedai*) or rounded (eg. *T. canaliculata*, *T. stephensi*, *T. decrescens*, *T. marginata*, *T. gallardoi*). Whether this justifies the establishment of a separate taxon for the first group (the type of *Typhlocarcinops* being *T. canaliculata*) is beyond the scope of this paper. The use of this character to separate *Ceratoplax* and *Typhlocarcinus* has been questioned by several authors, but for want of anything better, all workers have followed it.

Genera Typhlocarcinodes Alcock, 1900, *Caecopilumnus* Borradaile, 1903, and *Raoulia* gen. nov.

The genus *Typhlocarcinodes* currently contains four species, the type, *T. integrifrons* (Miers, 1881), *T. hirsutus* (Borradaile, 1903), *T. piroculata* (Rathbun, 1911) and *T. crassipes* Tesch, 1918 (fide Serène, 1968). *Typhlocarcinodes* was established by Alcock (1900) without naming a type but he mentioned Miers'

species from Africa in his comparisons with a broken specimen he had. Tesch (1918) named the type as *T. integifrons*, but Takeda (1973) and Takeda & Shimazaki (1974) commented that since '..... Alcock established the present genus *Typhlocarcinodes* on the damaged unnamed specimen, and compared Miers' species, it is questionable, as Tesch, Monod, and Serène (1964) designated, that *Typhlocarcinodes integifrons* Miers is the type species of the present genus.' (Takeda, 1973: 52). Takeda (1973) believed that '..... it is rather natural to think that the Atlantic species (*Typhlocarcinodes integifrons*) represents another undefined genus' (p. 52), and only *T. crassipes*, *T. hirsutus* and *T. pirocylatus* belongs to the genus *Typhlocarcinodes*. Holthuis & Manning (1981) however, citing Article 69(a)(ii) of the International Code of Zoological Nomenclature, vindicated the nomenclatural legality of Tesch's action. Tesch noted that the type differed from the other three Indo-Pacific species in two important aspects, viz., the antennular flagellum of Miers' species is multiarticulate, hairier and longer than the peduncle, and the first male abdominal segment does not cover the sternum, whereas in the other three species, the flagellum is shorter than the peduncle, almost glabrous and has only five to six segments, and the first male abdominal segment reaches to the bases of the last pair of ambulatory legs. Monod (1956), Serène (1964) and Takeda (1973) further questioned the congenicity of the four species and gave indications that two or more genera might be involved. Holthuis & Manning (1981) noted that if this view was accepted, the name *Caecopilumnus* Borradaile, 1903, which was synonymised with *Typhlocarcinodes* by Tesch (1918), would have to be applied for the three Indo-Pacific species. Borradaile (1903), in establishing this taxon, had already commented on the close affinities of his genus with *Typhlocarcinodes*. The present author accepts the differentiation of *Caecopilumnus* from *Typhlocarcinodes*, with *Typhlocarcinodes* containing only the type species, *T. integifrons*. The other three Indo-Pacific species are now referred to *Caecopilumnus*.

Typhlocarcinodes integifrons, as presently defined however, cannot be retained in the Rhizopinae since its third to fifth male abdominal segments are fused, the G1 stout and cylindrical, with both the flagellum and the basal segment of the G2 elongated (*vide* Barnard, 1955; Forest & Guinot, 1966), and clearly non-pilumnid in structure. *Typhlocarcinodes integifrons* was originally described on the basis of a pair of specimens dredged from a depth of 18 to 28 metres, on a partly shelly and muddy substrate from Goree Bay, near Goree Island in Senegambia (Miers, 1881). He had placed the species in the genus *Typhlocarcinus* Stimpson, 1858, with some doubt, noting that the '... different genera of this family [Rhizopidae, present Rhizopinae] described by Stimpson are apparently separated by characters of small importance' (p. 260). Bals (1922) also seems to have accepted this classification although he inexplicably listed his record as '*Typhlocarcinodes (Typhlocarcinus) integifrons*', treating Stimpson's genus, *Typhlocarcinus*, as a subgenus of *Typhlocarcinodes*. In his

1957 compilation however, Balss recognised *Typhlocarcinus* as an independent genus. The gonopods of *Caecopilumnus* species remain undescribed, and the genus is retained in the Rhizopinae until shown otherwise.

With regards to *Caecopilumnus piroculatus*, Serène (1964) identified a male from Jolo, Indonesia to this species under the genus *Typhlocarcinodes*. He figured the third maxilliped, male abdomen and G1, and remarked that his male had the abdominal segments three to five fused, like Barnard's (1955) specimen, in contrast to Tesch's (1918) figure of the species which showed all the segments free. He suggested that it was due to the fact that Tesch's specimen was a juvenile. This however, is extremely unlikely since the fusion of these segments occurs at a very early stage in the crab's development (first few crab stages after the megalopa)(see Martin *et al.* 1984). Moreover, Ng (1983) and Ng & Rodriguez (1986) had demonstrated the value of the structure of the male abdomen (whether segments three to five are fused or articulate) in brachyuran taxonomy. Consequently, Serène's specimen must be referred to another taxon. Considering the fusion of the male abdominal segments, and the unusual G1 (which is non-pilumnid in all respects), and the very long G2, it is the author's opinion that it should be recognised as a new genus and species. The following diagnosis is provided:

Raoulia gen. nov.

Type-species: *Typhlocarcinodes piroculatus* Serène, 1964
(not *Typhlocarcinops piroculatus* Rathbun, 1911)

Diagnosis. Anterolateral margins arcuate, regions of carapace poorly defined, surfaces shining, smooth. Margins of carapace and legs with short hairs. Anterolateral angle of merus of third maxilliped rounded, not distinctly produced, exognath narrow. First segment of male abdomen narrow, very broad, reaching to base of last pair of ambulatory legs; third to fifth segments fused, with only edges of sutures still visible; sixth segment rectangular, lateral sides concave; seventh segment triangular, broader than long, tip rounded. G1 stout, relatively straight, distal half much more slender than proximal, tip tapered, with several subdistal spines. G2 long, with flagellum almost as long as basal position.

Etymology. The genus is named in honour of the late Dr Raoul Serène.

Raoulia limosa sp. nov.

Typhlocarcinodes piroculatus Barnard, 1955: 35, Fig. 16; Serène, 1964: 237, Pl. 21A, Fig. 15
(not *Typhlocarcinus piroculatus* Rathbun, 1911; ? Balss, 1938)

Diagnosis. As for genus

Etymology. The specific name is derived from the Latin for muddy, 'limosus', in allusion to the luteophilous habits of the crab.

Material (*vide* Serène, 1964). Holotype - 1♂, 8.25 by 6.25mm, ZMUC Nr. M58,

off Marongas, Jolo, Indonesia, ca 45m depth, leg. Th. Mortensen, Pacific Expedition 1913-1916, 20.iii.1914.

The identity of Barnard's (1955) specimen cannot be confirmed, but included under the synonymy of *Raoulia limosa* for the moment. Barnard's specimens differ from Serène's in having the third to fifth male abdominal segments completely fused (sutures not visible at all), the seventh segment relatively longer, and the G1 appearing straighter. None of these differences are however significant, especially since Barnard's male specimen (11.5mm in breadth) is larger than Serène's. The genus *Raoulia* is monotypic. Balss (1938) also recorded *Typhlocarcinodes piroculatus* from the Gilbert Islands, but since his specimen was a female, its actual generic identity cannot be determined.

Genus Xenophthalmodes Richters, 1880

The genus is currently believed to contain four species (Serène, 1968), although the status of some of these are rather doubtful. The type species, *X. moebii* Richters, 1880, was described from Black River, Mauritius, and recently refigured by Türkay (1981). The genus is easily distinguished in having its carapace more elongated, being more semicircular, with the front narrow but prominent, the antennules folding transversely and appearing cramped, and the anterolateral angle of the merus of the third maxilliped rounded. The last character easily differentiates *Xenophthalmodes* from the closely related genus *Mertonia*. The male abdomen of *Xenophthalmodes* is typically rhizopine but the G1s of *X. moebii* and *X. dolichophallus* Tesch, 1918, (*vide* Barnard, 1950; Guinot, 1977, 1979) are very unusual in that they extend beyond the last abdominal segment. The structure of the G1s however, although not distinctly sinuous, are slender and simple and can be relatively easily derived from typical pilumnid ones. The structure of their G1s are similar to some unusual pilumnids like *Halimede*, *Galene* and *Bathypilumnus* Ng & Tan, 1984 (*vide* Ng, 1983; Ng & Tan, 1984). Consequently, the genus is retained in the Rhizopinae. In *X. brachyphallus* Barnard, 1955, however, the G1 is distinctly sinuous, like typical pilumnids, and does not extend beyond the last abdominal segment (*vide* Barnard, 1955).

Genus Mertonia Laurie, 1906

Established by Laurie (1906) for his new species, *Mertonia lanka* for a pair of specimens from the Gulf of Manaar, the genus *Mertonia* closely resembles *Xenophthalmodes* but can be separated by the anterolateral angle of the merus of the third maxilliped being produced (not rounded), the ratio of the fronto-orbital breadth to the carapace breadth, ratio of frontal to carapace breadth, more ventral position of the orbits, small but distinct eyes, antennules folding in a different direction, and the more plumose antennal flagellum. Guinot (1969c) had remarked that '... L'espèce-type du genre *Mertonia* Laurie, *M. lanka* Laurie, appartient à la lignée pilumnienne' (... the type species of the genus *Mertonia*

Laurie, *M. lanka* Laurie, belongs in the 'pilumnien' line)(p.699). The two species in the genus *Mertonia* appear to be valid rhizopines. Laurie (1906) did not figure the male abdomen of his species but Yokoya (1936) did, and together with Stephensen's (1945) and Serène's (1964) excellent figures of the G1, there is little doubt as to it being a different genus from *Xenophthlamodes*, and its pilumnid affinities.

Genus Heteropilumnus De Man, 1895

The genus was originally established for two species, *Heteropilumnus stormi* De Man, 1895, (type species) and *H. fimbriatus* (H. Milne Edwards, 1834). Balss (1933) transferred three species from the genus *Pilumnus* Leach, 1815, *P. trichophorus* De Man, 1895, *P. trichophoroides* De Man, 1895, and *P. lanuginosus* Klunzinger, 1913, and seven species from *Litocheira* Kinahan, 1856, *L. angustifrons* Alcock, 1900, *L. ciliata* Stimpson, 1858, *L. cristata* Rathbun, 1909, *L. decharmoyi* Bouvier, 1915, *L. setosa* (A. Milne Edwards, 1873), *L. splendida* De Man, 1929, and *L. subintegra* (Lanchester, 1900), to the genus *Heteropilumnus*. As noted later, Ward (1942) had referred *L. decharmoyi* to his new genus *Pseudolitochira*. Balss (1933) also tentatively retained *L. affinis* Tesch, 1918, *L. amoyensis* Gordon, 1931, *L. beaumonti* Alcock, 1900, *L. glabra* Baker, 1906, *L. integra* Miers, 1884, *L. quadrispinosa* Zehntner, 1894, and *L. inermis* Borradaile, 1902, in *Litocheira* (type species *L. bispinosa* Kinahan, 1856). According to Balss (1933), *Heteropilumnus* and *Litocheira s. str.* can be separated by the form of their endostomial ridges; strong in *Litocheira* but absent or weak in *Heteropilumnus*. The G1s of the two genera also appear to differ significantly, those of *Heteropilumnus* being sinuous and slender, typically pilumnid (*vide* Gordon, 1931; Miyake, 1939; Ng & Tan, in press), whereas in *Litocheira s. str.*, it is short, stout, and short (*vide* Miers, 1886; Barnard, 1950). In this respect, *L. amoyensis* (type locality Amoy, southern China) cannot be retained in the genus *Litocheira* since its G1 is slender and sinuous (Gordon, 1931). The species is presently transferred to the genus *Heteropilumnus*. The form of the endostomial ridges in *H. amoyensis* is not known. The species described and figured as *L. amoyensis* by Stephensen (1945) is certainly a *Heteropilumnus*, but may actually represent another species; being much less pubescent, the G1 more slender, the tip more tapered and elongated, the apical region having two long spines, as well as a series of smaller ones, and the right and left G1s not crossing over near the tip.

Sakai (1939, 1976) subsequently added two more species to the genus, *H. longipes* (Stimpson, 1858) and *H. quadrispinosa* (Zehntner, 1894). With regards to the transfer of *H. quadrispinosa* from *Litocheira*, Sakai (1939) commented that the species had '... No ridge that define the efferent branchial channel, while in the *Litocheira* they may be present' (p. 54). Serène (1968) listed 14 species in the genus *Heteropilumnus*, essentially following Balss' (1933) classification, retaining *H. amoyensis* and *H. quadrispinosa* in the genus *Litocheira*. In the latest treatment, *H. quadrispinosa* was transferred to the genus *Viaderiana* Ward, 1942

(*vide* Takeda, 1971; Serène, 1971). Sakai (1969) subsequently described a new species, *H. mikawaensis* from Japan, while Ng & Tan (in press) resurrected *H. hirsutior* (Lanchester, 1900), a taxon originally described as a variety of *H. subinteger* and since synonymised with this species by most authors. Ng & Tan (in press) also pointed out that *H. subinteger* is an invalid name since it was cited as a replacement name for *L. integra* Miers, 1884, with the same type specimen, and violates the rules of nomenclature. They consequently established a new name, (*H. sp. nov.*) for Lanchester's species. The genus *Heteropilumnus* thus currently contains 17 species, including *H. sasekumari*.

Larvae are known only for *H. ciliatus* (*vide* Takeda & Miyake, 1968b) and *H. hirsutior* (unpublished data), significant differences being observed in their rostrum, being very short (as in most pilumnids) in *H. hirsutior*, but very long in *H. ciliatus*. The genus is certainly heterogeneous in composition, and many of the species still await detailed redescriptions. Takeda (1977b) had noted that the difficulty in effectively separating *Heteropilumnus* from *Pilumnus* is '... mainly due to the variability of hairiness and partly to the diagrammatic figures so far published' (p. 86). The definition of the genus remains vague, being characterised by its quadrilateral carapace, usually entire or indistinctly cut anterolateral margin, and the presence of a fringe of long hairs lining the frontal and anterolateral margins. The form of the endostomial ridges, a character used by Balss (1933) and Sakai (1939, 1976) is still not known for many species. Moreover, it also seems to vary, being present in *H. hirsutior*, poorly developed in *H. sp. nov.*, and absent in *H. ciliatus* and *H. longipes*.

Genus Cryptocoeloma Miers, 1884

Cryptocoeloma was established by Miers (1884) for specimens he identified as *C. fimbriatum* (H. Milne Edwards, 1834). He also believed that Haswell's (1882) '*Pilumnus fimbriatus*' was conspecific with his species. De Man (1895) however, showed that Haswell's and Miers' species was not conspecific with Milne Edwards', and Rathbun (1923) applied a new name for Miers' species, *C. haswelli*. The author has examined a syntypic female contained in the BMNH and a male from the ZRC, and there is little doubt that although the species has many typical pilumnid characters like a very hirsutous carapace and legs, as well as a simple and slender G1, its carapace shape is distinctly 'goneplacien', and is hence included in the Rhizopinae. The genus can easily be recognised by having its anterior margins (frontal, anterolateral and supraorbital) completely entire, forming one unbroken line, the supraorbital margin being undiscernible. The anterior margins are also fringed with long, silky hairs, the other regions of the carapace being almost glabrous. The G1 is typically pilumnid but is not distinctly sinuous. Its taxonomy will be discussed in greater detail by Ng & Holthuis (in press) and Ng (in press).

Genus Pseudolitochira Ward, 1942

Ward (1942) established a new genus, *Pseudolitochira* for Miers' (1884) species, '*Litochira integra*', diagnosing it as having a '... Carapace broader than long, almost flat, regions not defined. Anterolateral margins entire or with rudimentary teeth. Front less than half the width of the carapace, abruptly declivous. Antennae standing in the orbital hiatus. Chelipeds equal in size' (p. 100). This species is very poorly known, and it is not possible to place it with any certainty. Although his description of the genus only mentioned the type species *P. integra*, in his list of crustacea from Mauritius, Ward (1942) also recorded '*L. decharmoyi* Bouvier, 1915' as belonging to his new genus *Pseudolitochira* (p. 52).

Bouvier's species had earlier been referred to the genus *Heteropilumnus* by Balss (1933), and followed by Serène (1968). Neither of these authors were apparently aware of Ward's action. Serène (1968) recognised only one species in *Pseudolitochira*, '*P. integer*'. As already pointed out by Ng & Tan (in press), since the generic name *Pseudolitochira* is feminine, the correct specific name used should be *integra* instead. Sakai (1955, 1976), apparently unaware of Ward's (1942) paper, maintained the species in the genus *Heteropilumnus*. The characteristics of the genus are clearly of the 'goneplacien' pilumnid type, and is consequently referred to the Rhizopinae for the time being.

Genus Pseudocryptocoeloma Ward, 1936

The genus *Pseudocryptocoeloma* was erected by Ward (1936) for *P. parvus* Ward, 1936, a small and unusual species from Queensland, Australia. He noted that that the taxa had a carapace which was three quarters as long as it is broad, the posterior regions of the carapace are flat, smooth and shining, and the anterolateral angle of the merus of the third maxilliped subauriculate. He cited three characters as differentiating *Pseudocryptocoeloma* from *Cryptocoeloma*, viz., the eyes being visible from dorsal view, anterolateral margins of the carapace lined with hairs of unequal length, and the exposed dorsal posterior parts of the carapace being smooth and polished. Ward also separated *Pseudocryptocoeloma* from *Heteropilumnus* by the structure of its cheliped, having an entire anterolateral margin, and a wider posterior margin of the carapace. Neither of the first two mentioned characters however, are very reliable and likely to be variable (see Griffin & Campbell, 1969; Ng & Tan, in press). The only useful character separating *Pseudocryptocoeloma* from *Heteropilumnus* seems to be the much more squarish carapace of *Pseudocryptocoeloma*, which in *Heteropilumnus*, is more rectangular. The segmentation of the male abdomen was not mentioned. Edmondson (1951) later described a second species, *P. symmetrinudus* from Samoa. The status of the genus as a rhizopine pilumnid must be held in question until the male abdomen and gonopods of either species of this genus are known.

Genus Paranotonyx Nobili, 1906a

Paranotonyx was established by Nobili (1906a, b) for a single species, *P. curtipes*

Nobili, 1906a, based on a 6.5 by 4.0mm female from the Red Sea. The genus is characterised by the dactylus of the palp of the third maxilliped having long hairs, the anterolateral angle of the merus produced, anterolateral margin entire, and posterolateral margins concave and converging. *Paranotonyx* is close to *Notonyx* and *Ceratoplax* but '... les maxillipèdes qui ont le merus dilaté très large, et aussi long quel'ischium. Le 'palpe' des maxillipèdes est font, son dernier article est pourvu de longs poils les forme de ses maxillipèdes distingue ce genre de *Ceratoplax* et de *Notonyx*' (... meri of the maxillipeds are very broadly dilated, and also longer than the ischia. The palps of the maxillipeds has long hairs on its last segment [dactylus] the form of the maxillipeds distinguishes the genera *Ceratoplax* and *Notonyx*)(Nobili, 1906b: 298). Nobili (1906b) also noted that '... les doigts sont un peu crochus et courts; sur les pattes de la troisième et de la quatrième paire ils mesurent à peine la moitié de la longueur des propodites. Dans les *Notonyx* et *Ceratoplax* les pattes sont beaucoup plus longues' (... the fingers being slightly hooked and short, the dactylus of the third and fourth pair of ambulatory legs being scarcely half the length of the propodus. In *Notonyx* and *Ceratoplax*, the dactylus is much longer)(p. 299). It has never been reported since, and males are unknown. Its classification in the Rhizopinae is provisional.

Genus Pronotonyx Ward, 1936

Pronotonyx laevis (Miers, 1884) was described from the Arafura Sea. Miers (1884) had originally placed his species in the genus *Ceratoplax* with some doubt, but Ward (1936) on examining several specimens from Queensland, Australia, felt a new, monotypic genus, *Pronotonyx* was necessary. *Pronotonyx* was diagnosed as having a broad, smooth and shining carapace, a very wide front (a third of the carapace width), an auriculate anterolateral angle on the merus of the third maxilliped, and the basal segment of the male abdomen almost reaching the base of the last pair of ambulatory legs. Its inclusion in the Rhizopinae is provisional.

Genus Selwynia Borradaile, 1903

Selwynia was established for the species *S. laevis* Borradaile, 1903, based on a single male from Hulule, Male Atoll in the Maldive and Laccadive Archipelagoes. The male abdomen and gonopods were not figured. Based on Borradaile's rather brief description and figures, *Selwynia* is very unusual amongst known rhizopines (indeed among known pilumnids) for an almost complete absence of hair, strongly built chelipeds and shortness of the ambulatory dactylus. Until the type can be reexamined however, it is very tentatively placed in the Rhizopinae.

Genus Paraselwynia Tesch, 1918

Tesch (1918) erected a new genus and species, *Paraselwynia ursina* for a single female collected from Tual in the Kei Islands, ostensibly allied to *Selwynia*, but differing significantly in having the anterolateral angle of the merus of the third

maxillipeds much more produced, the ambulatory legs being narrower, with the dactylus long and narrow, and being very hirsutous on the carapace and legs. Lack of a male however, makes its status as a rhizopine provisional.

Genus Cryptolutea Ward, 1936

Ward (1936) described a new genus and species, *Cryptolutea lindemanensis* from Queensland, Australia, which resembles *Rhizopa* and *Rhizopoides* externally and has all the male segments free, with the basal segment narrower than the distal ones. It is thus likely to be a true rhizopine, and is included in the subfamily for the first time. Guinot (1969a) had however, indicated that *Cryptolutea* might belong to her 'lignée pilumnienne'. The species appears to be related to *Cryptocoeloma haswelli* Rathbun, 1923, but differs in having the anterolateral margin more arcuate and unarmed, the eyes visible dorsally on denudation of the carapace, the hairs on the anterior margins being coarse and short, and the cheliped being more heavily built. *Cryptolutea lindemanensis* also bears a striking resemblance to *Ceratoplax luteus* (McNeill, 1929), but Ward (1936) separated the two taxa by his species having the merus of the third maxillipeds being more rectangular and the fingers of the larger cheliped shorter and thicker, with the palm shorter. The latter two characters are known to be variable in the related genus *Heteropilumnus* (fide Ng & Tan, in press) and thus cannot be relied upon. As for the form of the anterolateral angle of the merus of the third maxilliped being rectangular in *Cryptolutea* but produced in *Ceratoplax luteus*, Griffin & Campbell (1969) had remarked that McNeill's (1929) figures of the species were inaccurate; the anterolateral angle of the merus in *Ceratoplax luteus* being much less produced than his figures seem to indicate. *Cryptolutea lindemanensis* may thus eventually prove to be synonymous with *Ceratoplax luteus*, but until a direct comparison of the types of the two species is possible, Ward's genus and species are retained.

Genus Zehntneria Takeda, 1972

The genus was established by Takeda (1972) for three species, *Ceratoplax villosa* Zehntner, 1894, *Litocheira amakusae* Takeda & Miyake, 1969, and *Z. miyakei* Takeda, 1972, with the type being Zehntner's species. The fourth species, *Z. novaeinsulicola* was subsequently described by Takeda & Kurata (1977). The genus is characterised by its close resemblance to *Ceratoplax* but being more tomentose, the fingers of the chelipeds not strongly bent, and the male genital openings coxal. In *Ceratoplax* s. str., these openings are either sternal or coxosternal (sensu Guinot, 1977, 1978, 1979). In appearance, *Zehntneria* resembles *Pseudolitochira* Ward, 1942, but the anterolateral margin of *Pseudolitochira* is almost entire and the chelipeds equal in size. The generic significance of these differences however, is debatable since these structures are known to be variable even within species, and the structure of the G1 and position of the male genital openings in *Pseudolitochira* are not yet known.

Genus Lophoplax Tesch, 1918, and *Serratocoxa* gen. nov.

Tesch (1918) erected this genus on the basis of its members having the ‘... carapace thickly pubescent, granulate beneath the fur and with the various regions distinct, lateral margins all along with a series of blunt, depressed teeth, front strongly deflexed, bilobed. Chelipeds heavy, meropodite and carpodite pubescent, like the carapace. First segment of abdomen entirely occupying the space between the bases of the posterior legs, second segment much narrower, third segment again produced laterally, but not reaching to the coxopodites of the last legs; last segment of sternum exposed at anterior corners’ (p. 196). He designated his new species, *L. bicristata* as the type species, and suggested that Stimpson’s (1858) *Pilumnoplax sculpta* should also be included in the genus *Lophoplax*. Two other species, *L. takakurai* Sakai, 1935, from Yosihama (Japan) and *L. teschi* Serène, 1971, from the South China Sea were subsequently described. Both species were described only on the basis of females.

Takeda (1977a) recorded the second specimen of *L. sculpta* known from collections in the Ryukyu Islands, as well as the first male of *L. takakurai* from Shibushi Bay (Japan). Although he did not figure the G1s or male abdomen of either species, he noted that they had ‘... the *Pilumnus*-type male first pleopods’ (p. 122), a clear indication of the *Lophoplax*’s pilumnid affinities. Tesch (1918) had earlier figured his *L. bicristata* as having all the male abdominal segments distinct.

Tesch (1918), Beurlen (1930), Sakai (1939, 1976) and Balss (1957) had placed *Lophoplax* in the subfamily Prionoplacinae Alcock, 1900, family Goneplacidae. Guinot (1971, 1978) however, indicated that *Lophoplax* should be placed in the ‘goneplacien’ group of the Pilumnidae s. str., which Takeda’s (1977) rediscovery of *L. sculpta* seems to vindicate. Consequently, the genus is placed in the Rhizopinae.

Whilst Tesch’s genus is certainly valid, the composition of the genus is uncertain. Serène & Lohavanijaya (1973), in giving a detailed description and figures of *L. teschi*, noted the presence on ‘... the posterior border of the ambulatory legs of a denticulated wing-like plate covering the ischium’ (p. 76). Their Pl. 19C shows this character very clearly. This structure is also present in *Ceratoplax sagamiensis* Sakai, 1935, and *C. granulosa* MacGilchrist, 1905, but absent in the other *Lophoplax* species. Sakai (1935) commented that for the ambulatory legs of *C. sagamiensis*, the ‘... coxa of each pair is dorsally provided with a process, which terminates in 4 or 5 pectinated processes’ (p. 85). MacGilchrist (1905) described the process on *C. granulosa* as ‘tortoise-foot-like’. Serène & Lohavanijaya (1973) noted that these three species, *L. teschi*, *C. sagamiensis* and *C. granulosa* were certainly congeneric and may warrant a separate genus for themselves but took no formal steps to give it a name. The present author agrees with Serène & Lohavanijaya (1973) that these three species should be regrouped in a separate genus. Considering the distinctiveness of the unusual ambulatory coxa, a new taxon is easily justified. A diagnosis of the new genus, *Serratocoxa*, is provided below.

Genus *Serratocoxa* gen. nov.

Type-species: *Lophoplax teschi* Serène, 1971: 916

Diagnosis. Carapace distinctly quadrate, the anterolateral margin arcuate, almost entire, indistinctly lobed or appearing serrated. Anterolateral angle of merus of third maxilliped produced. Coxa of ambulatory legs with denticulated plate which partially covers ischium. Dactylus of last ambulatory leg downcurved. First male abdominal segment broader than third, reaching to base of last pair of ambulatory legs. G1 sinuous, slender. G2 short, sinuous.

Etymology. The name is derived from the Latin 'serratus' for serrated, and the coxa of the leg.

Serène & Lohavaniyaya (1973) also recorded a male of *S. teschi* from the type locality of (which they labelled as the paratype), but although the male abdomen and G1 was not figured, they were described. The gonopods of *S. teschi* are '... pilumnien, the pleopod 1 (G1) distally curved and the pleopod 1 [G2?] short ...' (p. 76). The second 'pleopod 1' was certainly a typographical error, the authors actually referring to the G2 instead. The genus *Serratocoxa* is thus certainly rhizopine, and presently contains three species, *S. teschi*, *S. granulosa*, and *S. sagamiensis*. *Lophoplax* on the other hand, has now been restricted to include *L. bicristata*, *L. takakurai*, and *L. sculpta*.

Genus *Speocarcinus* Stimpson, 1859

The revision of this genus by Guinot (1969c) and Felder & Rabalais (1986) clarifies its taxonomy considerably. The genus was established by Stimpson (1859) for his new species, *S. carolinensis* from South Carolina. The revised and restricted genus *Speocarcinus* is now a wholly American Atlantic taxon, with five species: *S. carolinensis*, *S. granulimanus* Rathbun, 1893, *S. spinicarpus* Guinot, 1969c, *S. lobatus* Guinot, 1969c, and *S. monotuberculatus* Felder & Rabalais, 1986. All have their third to fifth male abdominal segments fused, their G1s relatively stout, straight and lined with spines, and G2 relatively elongated. *Speocarcinus californiensis* Lockington, 1877, was referred to a new genus, *Malacoplax* Guinot, 1969a, whilst *S. ostreaticola* Rathbun, 1910, was synonymised with *Prionoplax ciliata* Smith, 1870, with doubt (Guinot, 1969a, c). The three species of Indo-Pacific *Speocarcinus* listed by Serène (1968) : *S. luteus* McNeill, 1929, *S. laevimarginatus* Yokoya, 1933, and *S. celebensis* Tesch, 1918, are clearly not belonging to *Speocarcinus*, as suggested by Serène (1964) and Guinot (1969c, 1971). They have all been transferred to other genera.

Speocarcinus luteus and *S. laevimarginatus* are now placed in the genus *Ceratoplax*. As for *S. celebensis*, Serène (1964) indicated that the species might be closer to *Viaderiana* Ward, 1942. Little is known of *S. celebensis*, having only been recorded from Celebes (Sulawesi) (Tesch, 1918, type locality) and the Java Sea (Serène, 1964). Tesch (1918) described the male abdomen as having seven distinct segments, and Serène's specimen was a female. The G1 and G2s are unknown. Since the shape of the carapace is very close to *Viaderiana*, and the

anterolateral margin only bears two blunt teeth (excluding the external orbital angle), Tesch's species is tentatively referred to the genus *Viaderiana*.

Genera Homoioplax Rathbun, 1914, and Ser Rathbun, 1931

Both these poorly known taxa were suspected of being possible 'pilumnien' crabs by Guinot (1969a), but are excluded from the Rhizopinae in this study until their G1s are known. *Homoioplax* was established by Rathbun (1914) for a new species, *H. haswelli*, specimens of which Miers (1884) had called '*Pseudorhombila vestita* var. *sexdentata* Haswell, 1882'. Rathbun (1914) correctly interpreted the true identity of Miers' species, but it was left to Tesch (1918) to describe the genus and species in detail. The male abdomen consists of seven segments but the shape, as well as the form of the carapace is more akin to those of the genus *Carcinoplax* H. Milne Edwards, 1852, and the G1s, when known, will probably support its placement in that group, not the Rhizopinae. *Ser* was established for *Ser fukiensis* Rathbun, 1931, from Fukien, China, and was placed by Rathbun (1931) in the subfamily Carcinoplacinae on account of its third male abdominal segment covering the entire space between the last pair of ambulatory legs. The carapace of *Ser* however, closely resembles *Ceratoplax*, and according to Rathbun's (1931) photographs of the species, the anterolateral margin of the merus of the third maxilliped is also produced. It must be excluded from *Ceratoplax* and the Rhizopinae for the moment because Rathbun (1931) indicated that the '... appendages of the second [male abdominal] segment are bent obliquely upward just beyond the middle and the extremities are curved downward in a ring' (p. 84). Obviously referring to the G2, the length of this structure clearly suggests that *Ser* is not a pilumnid, which have very short and sigmoid G2s. The length of the G2 is unusual even for the Carcinoplacinae, and is shorter than those known for the genus *Carcinoplax* (fide Guinot, 1969b; Guinot & Richer de Forges, 1981a, b; Chen, 1984). On the other hand, if Rathbun had accidentally confused the G1 with the G2 (very unlikely), then the description provided by her would indicate that *Ser* is a pilumnid, the shape being diagnostic for many members of the group. Rathbun's paper was dated as 'December 1929', but the back cover indicated that the actual date of publication was 'July 31st 1931'.

Genus Notonyx A. Milne Edwards, 1873

This genus was established by A. Milne Edwards (1873) for his species, *N. nitidus*. Alcock (1900) subsequently described a second species, *N. vitreus* from India. Although this genus has always been included in the subfamily Rhizopinae, Stephensen's (1945) and Serène & Umali's (1972) figures of the G1 and G2 of *N. nitidus* suggest against its inclusion in the Rhizopinae as presently defined. Although all the male abdominal segments are articulate, the G1 and G2 are clearly non-pilumnid. The male abdomen is also distinctly triangular in shape and much broader than those of other rhizopines.

Genus Acidops Stimpson, 1871

This is a poorly known genus described on the basis of one species, *Acidops fimbriatus* Stimpson, 1871 from western America. On the basis of information supplied to him by Dr John Garth (*in litt.*), Monod (1956) synonymised *Epimelus* A. Milne Edwards, 1878, (its type, and only species is *E. cessaci* A. Milne Edwards, 1878, described from West Africa) with *Acidops*, with the latter having priority. The genus *Acidops*, according to Monod, therefore contained only two species. Tesch (1918) examined a cotype male of *Epimelus cessaci* in the RMNH, comparing it with *Typhlocarcinodes*. Although Tesch implied that the two genera were closely related, he did not include *Epimelus* in his list of rhizopine genera. Balss (1957), probably following up on Tesch's suggestions, formally included *Epimelus* in the Rhizopinae. Monod (1956) had noted (but without figures) that the G2 of *Acidops* is longer than the G1, and agreed in the transfer of *Acidops* from the pilumnids to the Goneplacidae. Guinot & Ribeiro (1962) figured the G1 and G2 of *A. cessaci*, neither of which are pilumnid or rhizopine in character. The genus *Acidops* is thus removed from the Rhizopinae as presently defined.

Remaining genera

The genera *Scalopidia* (= *Hypophthalmus* Richters, 1881, *vide* Miers, 1886), *Camatopsis*, *Chasmocarcinus*, *Chasmocarcinops*, *Hepthopelta*, *Megathesius* and *Acidops* are clearly neither rhizopines or pilumnids in the present sense, their third to fifth abdominal segments being completely fused, their G1s straight, stout, lined with spines, and G2s elongated (Tesch, 1918; Stephensen, 1945; Monod, 1956; Serène, 1964; Felder & Rabalais, 1986). The exact place in the Brachyura of these genera remains uncertain.

Genus Viaderiana Ward, 1942

Ward (1942), in establishing this genus, characterised it being covered with long, soft (flexible) hairs, two well developed frontal lobes, longer antennae, and very long ambulatory legs. Only one species was apparently recognised by him, the type, *Viaderiana typica* Ward, 1942, described from a single female collected from Mahebourg, Mauritius. He did however, compare his species with '*Litocheira quadrispinosa* Zehntner, 1894', a species which Balss (1933), Monod (1938) and Miyake (1939) had retained in the genus *Litocheira*. but was transferred by Sakai (1939, 1976) to *Heteropilumnus*. From Ward's (1942) comparisons however, it would appear that he regarded Zehntner's species as also being in the genus *Viaderiana*, although he never stated this explicitly. Serène (1968) however, retained *Litocheira quadrispinosa*, *L. affinis*, *L. amoyensis* Gordon, 1931, *L. beaumonti* Alcock, 1900, and *L. aranea* Tesch, 1918, in the genus *Litocheira* Kinahan, 1856, recognising only the type species in *Viaderiana*. Takeda (1971) provided a detailed redescription of the genus and *V. typica*, adding the following notes to Ward's diagnosis; '... carapace quadrate and covered with hairs of various length. Dorsum smooth with ill-defined areolae.

Frontal region declivous with two well-developed lobes. Each lobe with rather produced lateral lobule. Anterolateral border of carapace with two spines or spiniform teeth excluding external orbital angle, and sometimes with a rudimental tooth behind them ...' (p. 196). Four other species were also included by Takeda (1971) in the genus *Viaderiana*: *V. affinis* (Teach, 1918), *V. aranea* (Tesch, 1918), *V. beaumonti* (Alcock, 1900), and *V. quadrispinosa* (Zehntner, 1894), although as he himself admitted, this was done '... chiefly as a matter of convenience ...' (p. 197). Almost simultaneously, Serène (1971), in recording a male of *V. typica* from Vietnam, recognised also added four species to the genus *Viaderiana*, other than *V. typica* and *V. quadrispinosa* (the latter species probably included on the basis of Ward's (1942) original implications): *V. affinis*, *V. longipes* (A. Milne Edwards, 1873), *V. elegans* (De Man, 1887), and *V. taeniola* (Rathbun, 1906). The latter three species were originally classified in the genus *Pilumnus*. Serène's (1971) inclusion of these species in the genus *Viaderiana* is based almost entirely on the form of their anterolateral margins, with only two prominent teeth (excluding the external orbital angle) on each side, the last being absent, vestigial or very small. Serène (1971) also appended an important comparison of *Viaderiana* with *Pilumnus*, with which he believed shared many similarities. *Viaderiana*, according to Serène (1971) differed from *Pilumnus* in three main areas; viz., 1. the appearance of the carapace, being more delicate, more or less quadrangular and flatter, the borders of the anterolateral margin very short, armed with two weak teeth-like spines; 2. the fingers of the chelipeds long, cutting teeth with well developed teeth, the carpus with a spine on the inner angle, the ambulatory legs long and thin; and 3. the presence of a transverse fringe of very fine, silk-like hairs lining the length of the frontal margin. Only in the last character is there an overlap with *Heteropilumnus*.

Serène (1971) had also noted that *Pilumnus cursor* A. Milne Edwards, 1873, *P. spinicarpus* Grant & McCulloch, 1906, *P. striatus* De Man, 1888, *P. neglectus* Balss, 1933, *P. turgidulus* Rathbun, 1911, and *P. rotumanus* Borradaile, 1900, also resembled *Viaderiana*, but their carapaces were more convex and their anterolateral margins have three well developed teeth. *Pilumnus striatus* and *P. rotumanus* however, also have their last anterolateral tooth distinctly reduced compared to the first two, and in all general appearances, closely resemble species presently placed in the genus *Viaderiana*. *Pilumnus striatus* is known only from the type material of four females and two males from Amboina (Moluccas)(*fide* De Man, 1888), while *P. rotumanus* is only known from three females, one each from Rotuma, South Pacific (Borradaile, 1900), Xisha Islands (Paracel Islands), South China Sea (Dai & Lan, 1981), and the Cocos Keeling Islands, eastern Indian Ocean (Ng, 1983). Ng & Tan (1984) also described a new species, *P. demani*, on the basis of a male from Nhathrang Bay, Vietnam. Like *P. striatus*, the last anterolateral tooth of *P. demani* is reduced (but still present as a distinct spine unlike *P. striatus*). These three species are now included in the genus *Viaderiana*. The species described by Tesch (1918) as *Speocarcinus*

celebensis should also tentatively be referred to *Viaderiana* since it has only two blunt anterolateral teeth and a quadrate carapace.

The male abdomen of *Viaderiana* is typically triangular shaped, being broader than the more typical pilumnids and rhizopines. The G1 is only known for *P. demani* (fide Ng & Tan, 1984), and differs from those of typical rhizopines and pilumnids in being much stouter, the tip being strongly hooked. The genus is certainly closer to the Pilumninae *s. str.* than to the Rhizopinae as presently recognised, but in the more quadrate carapace, and the tendency to have some of their anterolateral spines reduced, the genus *Viaderiana* approaches the Rhizopinae. The form of the endostomial ridges in the genus appears to vary, being almost absent in *V. quadrispinosa* (fide Sakai, 1939, 1976), but well developed in *V. demani* (fide Ng & Tan, 1984).

As for the other species allied to *P. cursor* by Serène (1971), less can be said. The author is still in the midst of revising this complex of species (which includes *Pilumnus longicornis* Hilgendorf, 1878). Until these species can be properly characterised and the degree of intraspecific variation determined, their relationship to the genus *Viaderiana* and Rhizopinae remains uncertain.

3. CONCLUSION

The genera and species that are presently recognised as belonging to the Rhizopinae are listed in Table 1. The first species listed in each genus is its type.

In summary, the Rhizopinae *s. str.* contains 20 genera with 74 recognised species. Many of the taxa are still poorly known, and their place in the subfamily is highly provisional. The Rhizopinae still cannot be properly defined, and important characters like the position of the male genital openings are still unknown for many taxa. At the moment, it varies from coxal (eg. *Cryptocoe-loma*) to coxosternal (eg. *Rhizopa*). Geographically, the subfamily is confined to the Red Sea, Indian Ocean and West Pacific. East Pacific and Atlantic genera (eg. *Typhlocarcinodes* and *Acidops*) previously assigned to the Rhizopinae have been shown to possess characters not typical for the subfamily and the Pilumnidae, and have consequently been transferred out. Ecologically, almost all seem to be luteophilous taxa, occurring from shallow to deep waters, but less often in the intertidal zone. The small size, reduced cornea, short antennae and upcurved last ambulatory dactylus of many species are clearly adaptations to this habitat, and probably explain why they are externally so different from the more typical Pilumnidae. In the more conservative and very important characters of the G1, G2 and larval structures however, they are without doubt, pilumnids.

The problems associated with pilumnid systematics are not easily resolved, and the present revision of the Rhizopinae must be regarded as no more than a very preliminary attempt. The composition of the Pilumnidae remains an unsettled question, and even the latest proposal by Serène (1984) is by no means

satisfactory. In fact, the results of the author's ongoing studies of the family (unpublished data) conflicts with Serène's scheme in many respects. Clearly, much more work needs to be done before a clearer understanding of the Pilumnidae can be achieved.

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