

## Crustacea: Decapoda, Brachyura

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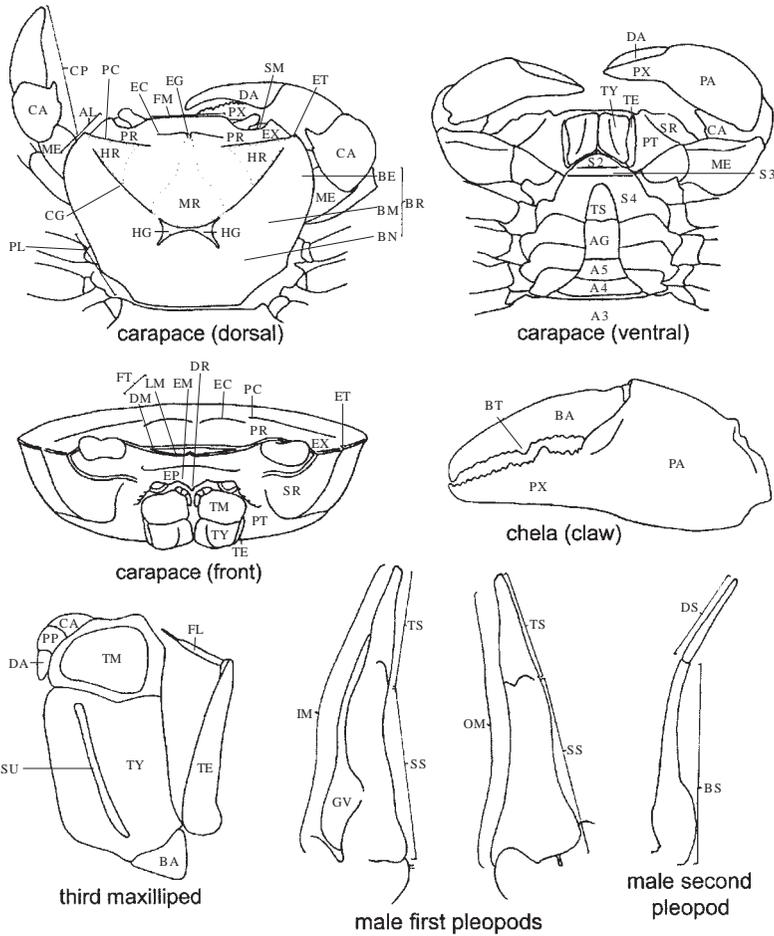
### INTRODUCTION

Of the estimated 6500 known species of brachyuran or true crabs, some 1000 are wholly freshwater. Southeast Asia has three families of freshwater crabs – Potamidae, Gecarcinucidae and Parathelphusidae (Ng 1998, 1990b; Cranbrook and Furtado 1988; Ng and Ambu 1998). These families are very diverse in Southeast Asia, particularly in Malaysia. In addition, members of several families, notably the Sesarmidae and Varunidae (both used to be in the Grapsidae), have many members that spend their adult lives in freshwater. Another family of crabs which has a few representatives in freshwater is the Hymenosomatidae, but most are not true freshwater crabs although they may be found some distance inland (Ng 1995c,d; Ng and Chuang 1996).

### GENERAL BIOLOGY

Freshwater crabs are significant organisms inhabiting Southeast Asian fresh waters, playing a key role in recycling nutrients through their scavenging of plant and animal material. However, they are relatively poorly known because of their secretive habits and difficult taxonomy.

They are present in almost all clean fresh water bodies, from lowlands to high mountains. Like all crabs, they breathe with gills, but they do not always need to be in water. As long as their gill chamber is moist or has a water bubble trapped inside, they are able to breathe and move about. As such, many species have become terrestrial or semi-terrestrial, burrowing in the rainforest floors, climbing trees or wandering deep in the rainforest. This is not at all surprising considering how moist Malaysian rainforests are. Even without rain, the forest floor is often damp; or with numerous swamps and small streams. Each morning, condensing dew also covers the forest with moisture. In addition, there are many plants that trap rainwater, forming temporary pools all over the forest, even many metres above the ground. Such small aquatic ecosystems, called phytotelms, provide crabs with moisture for their gills as well as food. Some crabs (e.g. *Geosesarma*) have been found in pitcher plants (*Nepenthes*) (Ng and Lim 1987) while on Pulau Tioman, *Pseudosesarma crassimanum* has been found scurrying around the nodes of *Pandanus* (Pandanus) and among the leaves of tapioca at night. Species of *Arachnothelphusa* are also known to climb shrubs and tall dipterocarp trees.



**Figure 1.** Technical terms. Carapace (dorsal) – BE: epibranchial region, BM: mesobranchial region, BN: metabranchial region, BR: branchial region, CA: carpus, CG: cervical groove, CP: cheliped, DA: dactylus, EC: epigastric cirstae, EG: epigastric groove, ET: epibranchial tooth, EX: external orbital tooth, HG: H-groove, HR: hepatic region, ME: merus, MR: mesogastric region, PC: postorbital cristae, PR postorbital region, PX: pollex, SM: supraorbital margin. Carapace (ventral) – A1-A6: abdominal segments 1 to 6, CA: carpus, DA: dactylus, PA: palm, PT: pterygostomial region, PX: pollex, TE: third maxilliped exopod, TY: third maxilliped ischium, ME: merus, S2-S4: sternites 2 to 4, SR: suborbital region. Carapace (front) – DM: dorsal margin of frontal median triangle, DR: downwardly-directed ridge of epistomal median lobe, EC: epigastric cristae, EM: epistomal median lobe, EP: epistome, ET: epibranchial tooth., EX: external orbital tooth, FM: frontal margin, LM: lateral margin of frontal median triangle, PC: postorbital cristae, PR: postorbital region, PT: pterygostomial region, SR: suborbital region, TE: third maxilliped exopod, TM: third maxilliped merus, TY: third maxilliped ischium. Chela (claw) – BT: distinctly-enlarged tooth, DA: dactylus, PA: palm, PX: pollex. Third maxilliped – BA: basis, CA: carpus, DA: dactylus, FL: exopod filament, PP: propodus, SU: sulcus, TE: exopod, TM: merus, TY: ischium. Male first and second pleopods – BS: basal segment, DS: distal segment, GV: groove for male second pleopods, SS: subterminal segment, TS: terminal segment.

Caves are yet another extreme habitat, but with their often damp environment, are ideal habitats for freshwater crabs. The huge caves of Gunung Mulu and Niah in Sarawak are home to some of the strangest and most primitive crabs in Asia (*Cerberusa*), but most such ecosystems are still poorly explored and more new species undoubtedly await discovery.

### Life cycle

True freshwater crabs (Potamidae, Gecarcinucidae, Parathelphusidae) do not need to return to the sea to release their eggs and larvae. They have relatively large eggs (a mm or more in diameter) and have direct development, i.e. with the eggs hatching into miniature versions of the adult. The females brood the juvenile crabs for short periods before releasing them. There are also a number of crabs (Sesarmidae, Varunidae) which live in freshwater but still need to return to the sea; they have small eggs which hatch out into free-swimming marine larvae (zoeae) and become part of the zooplankton fauna. After several weeks, these larvae metamorphose into miniature crabs that then slowly make their way inland. There is, however, one sesarmid genus, *Geosesarma*, whose members also have direct development, with their large eggs hatching out into miniature crabs or very advanced zoeae which do not need to feed, possessing instead, internal yolk reserves. They can thus be regarded as true freshwater crabs as they never need to return to the sea (Ng 1988).

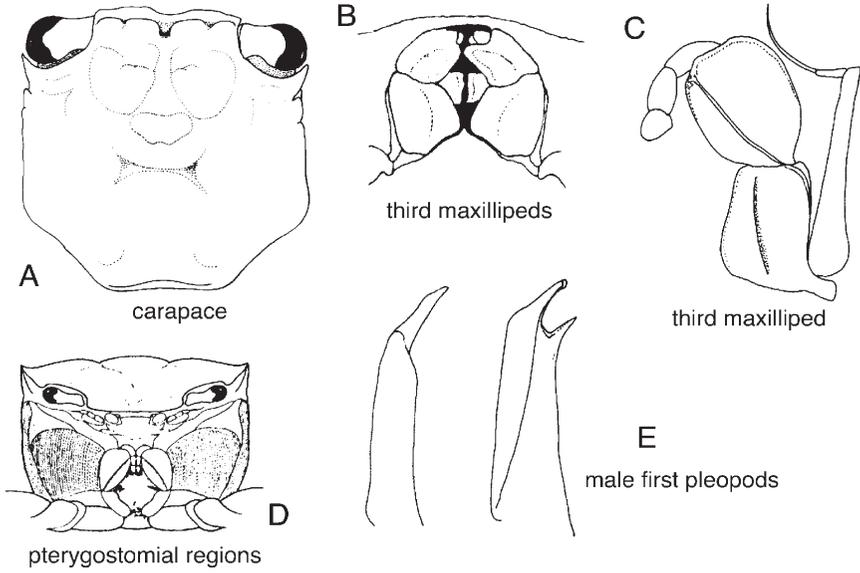
### REGIONAL TAXA

Currently, the families Potamidae, Gecarcinucidae and Parathelphusidae have between them 25 genera and 91 described species from Malaysia, Singapore and Brunei and, in the family Sesarmidae, there are 18 species of *Geosesarma* presently known. Two species of Hymenosomatidae, have been found thus far, viz. *Hymenicoides microrhynchus* Ng, 1995, and *Neorhynchoplax dentata* Ng, 1995.

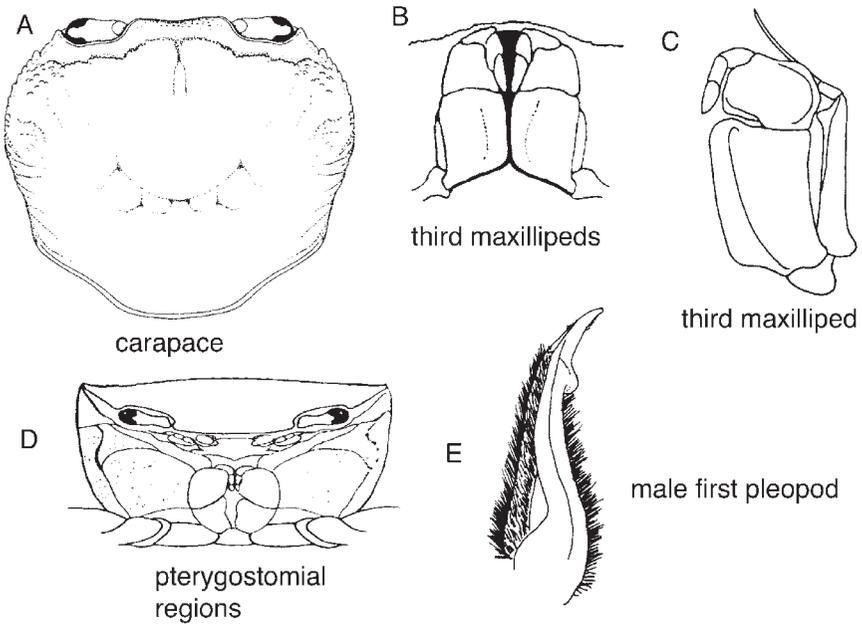
In the present work, we have included keys to all the genera of true freshwater crabs and freshwater grapsids known from Malaysia (Peninsular Malaysia, Sarawak and Sabah), Singapore and Brunei. In addition, we have included southernmost Thailand (south of the Isthmus of Kra) in the keys since most of the genera (and some of the species) occur there as well as in northernmost Peninsular Malaysia, the fauna in this area being more or less homogeneous.

### Key characters of freshwater crabs

The terminology for structure follows essentially that used by Ng (1988) (Fig. 1). Several genera and species are in the process of being described or the descriptions are in press. In such instances, no name has been applied. Keys to the various species in most of the genera treated here have been published in numerous papers (see generic descriptions).



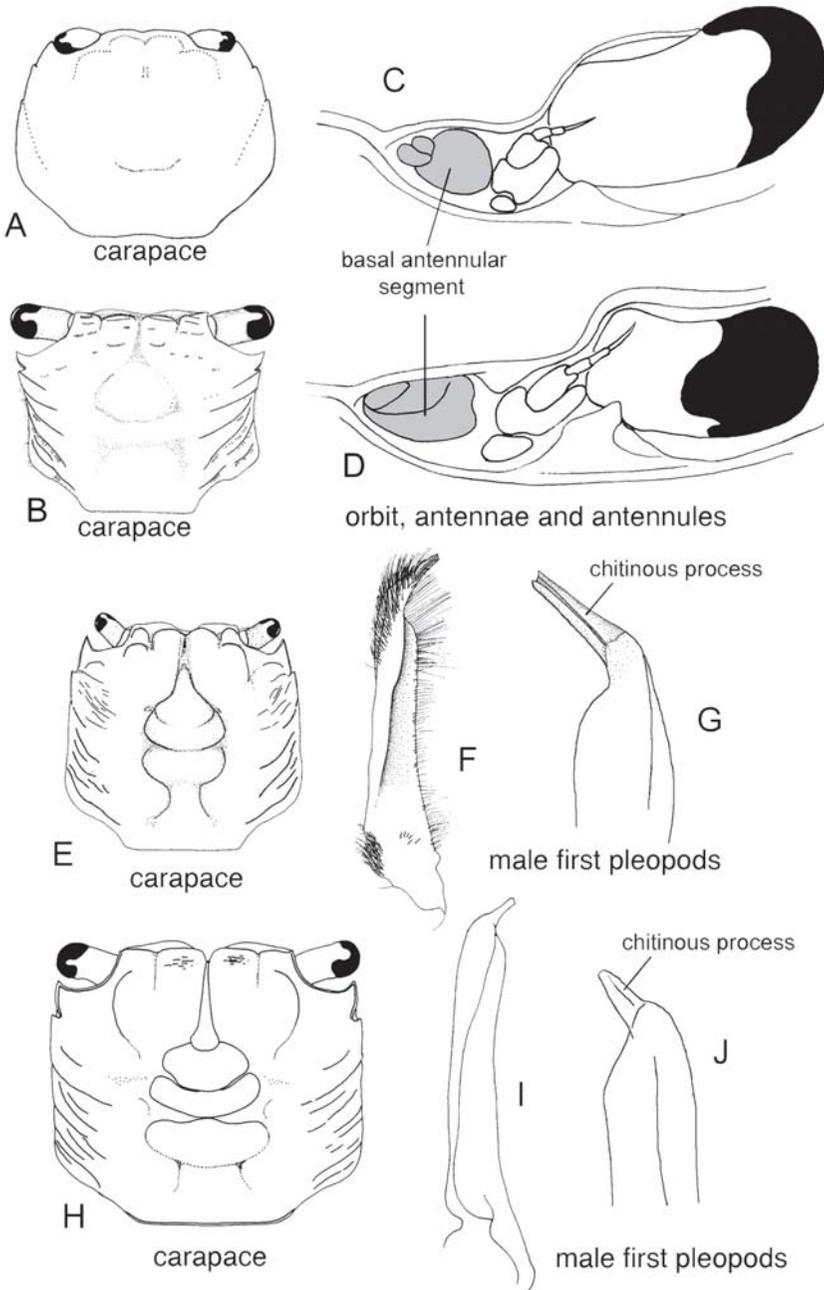
**Figure 2.** Family Sesarmidae. A – carapace; B – buccal cavity showing third maxillipeds; C – left third maxilliped; D – frontal view of carapace; E – left male first pleopods (denuded).



**Figure 3.** A – carapace; B – buccal cavity showing third maxillipeds; C – left third maxilliped; D – frontal view of carapace; E – left male first pleopods.

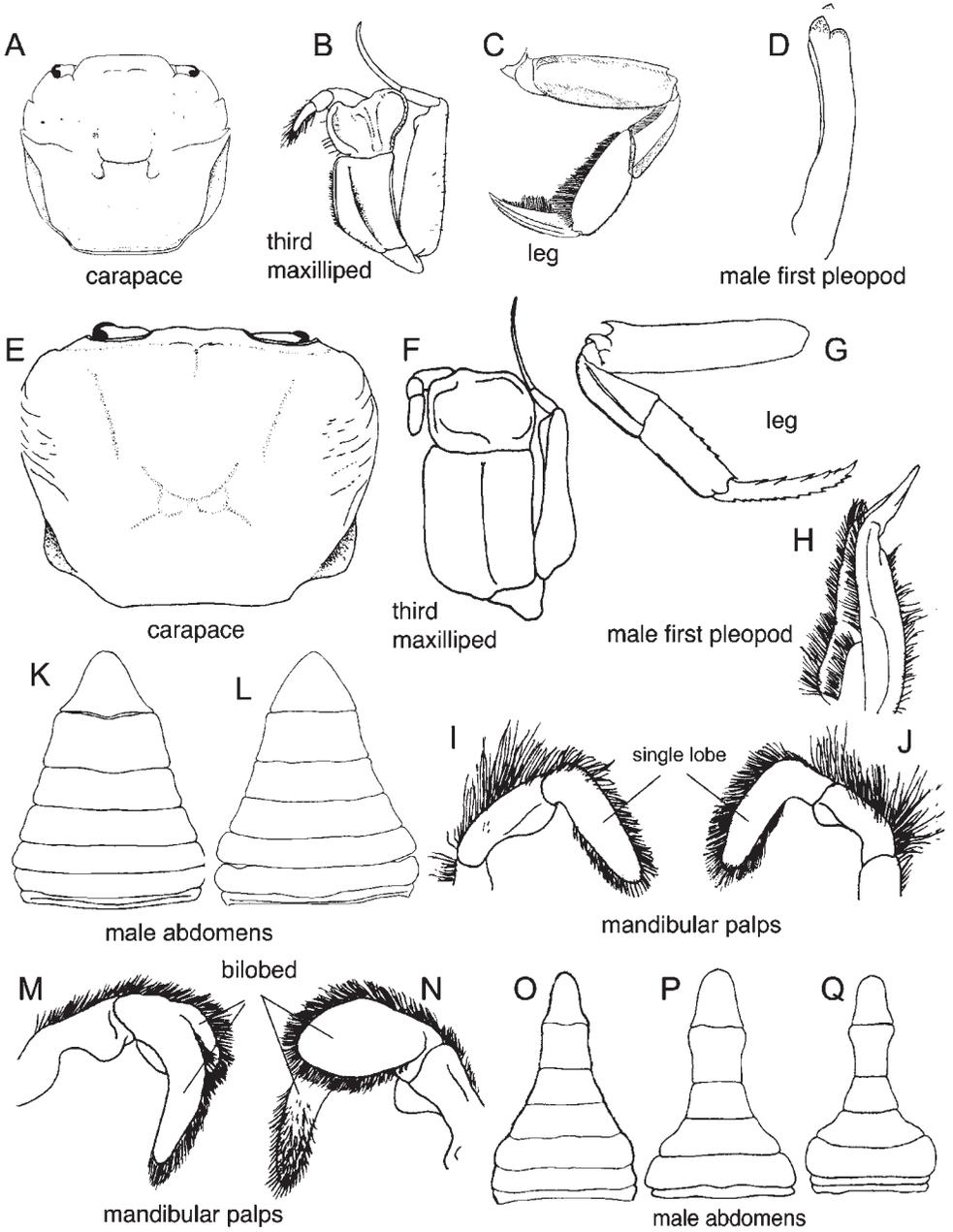
## KEY TO GENERA

1. Eyes very large relative to carapace, cornea often reaching to edges of carapace (Fig. 2A); third maxillipeds forming distinct rhomboidal gap between them when closed (Fig. 2B), ischium and merus with prominent oblique setose ridge (Fig. 2C); pterygostomial region with dense setae arranged in distinct regular pattern (Fig. 2D); male first pleopod with distinct pectinated lip or projection (Fig. 2E) ..... SESARMIDAE .. 2
- Eyes small relative to carapace, cornea never close to edges of carapace (Fig. 3A); third maxillipeds closing tightly, not forming rhomboidal gap between them (Fig. 3B), ischium and merus without distinct ridges (Fig. 3C); pterygostomial region with scattered setae or glabrous (Fig. 3D); male first pleopod without prominent pectinated lip or projection, or unpectinated throughout (Fig. 3E) ..... 5
2. Frontal margin distinctly shorter than posterior carapace margin (Fig. 4A); second and third pair of ambulatory legs long ..... *Sesarmoides*
- Frontal margin equal to or broader than posterior carapace margin (Fig. 4B); second and third pair of ambulatory legs not elongate ..... 3
3. Basal antennular segment swollen, rounded (Fig. 4C); adult females with large eggs (ca. 0.5–1.0 mm), direct or abbreviated larval development, completely freshwater ..... *Geosesarma*
- Basal antennular segment not swollen, broader than long (Fig. 4D); adult females with small eggs (distinctly less than 0.5 mm), larval development normal, marine ..... 4
4. Carapace with lateral margins gently diverging (Fig. 4E); male first pleopod with distal chitinous process slender, elongate (Fig. 4F,G) ..... *Sesarmops*
- Carapace with lateral margins parallel or almost so (Fig. 4H); male first pleopod with very short or very stout chitinous process slender (Fig. 4I,J) ..... *Pseudosesarma*
5. Carapace distinctly squarish, regions poorly developed, anterolateral margin with low teeth or lobes, rarely dentiform (Fig. 5A); exopod of third maxilliped very stout, anteroexternal angle of merus expanded, ear-like (Fig. 5B); legs with distal segments laterally flattened, densely lined with setae (Fig. 5C); male first pleopod very stiff, hard, tip bilobed with tip pectinated (Fig. 5D) ..... VARUNIDAE: *Varuna*
- Carapace usually quadrate to transversely ovate; regions usually distinct, anterolateral margin may be entire or with teeth, lobes or spines (Fig. 5E); exopod of third maxilliped slender, anteroexternal angle of merus not expanded (Fig. 5F); legs with distal segments subcylindrical to cylindrical in cross-section, not densely lined with setae (Fig. 5G); male first pleopod stiff but not hard, distal part normal, never pectinated (Fig. 5H) ..... 6
6. Mandibular palp with single terminal lobe (Fig. 5I,J); male abdomen distinctly triangular in shape (Fig. 5K,L) ..... POTAMIDAE .. 7
- Mandibular palp with terminal part bilobed (Fig. 5M,N); male abdomen T-shaped in shape to varying degrees (Fig. 5O–Q) ..... PARATHELPHUSIDAE, GECARCINUCIDAE ..12
7. Third maxilliped with well developed flagellum on exopod of third maxilliped which extends to at least half width of merus (Fig. 6A,B) ..... 8
- Third maxilliped without flagellum on exopod of third maxilliped, or if present, very short, distinctly less than half width of merus (Fig. 6C,D) ..... 10



**Figure 4.** Family Sesarmidae. A – *Sesarmoides*; C – *Geosesarma*; E–G – *Sesarmops*; H–J – *Pseudosesarma*. A, B, E, H – carapaces; C, D – frontal view of carapace showing orbit, antennae and antennules; F, G, I, J – male first pleopods.

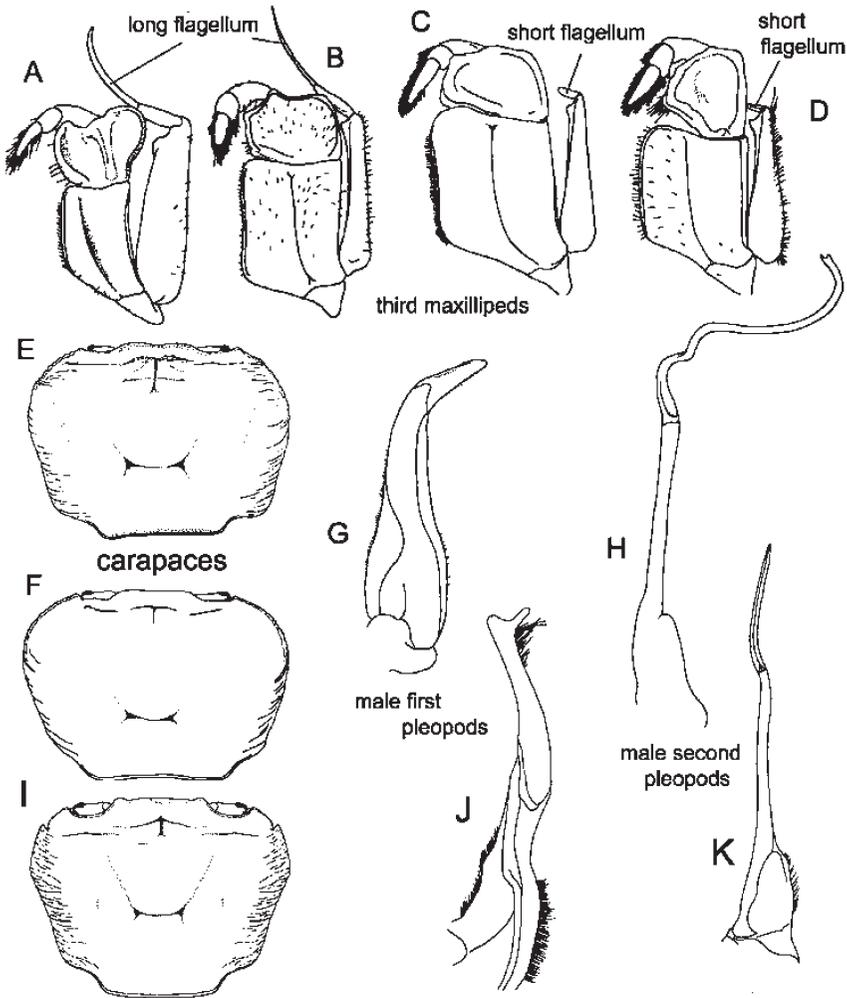
8. Dorsal surface of carapace relatively smooth, glabrous; epi- and postorbital cristae low, smooth (Fig. 6E,F); male second gonopod (Fig. 6H) at least twice length of male first gonopod (Fig. 6G) ..... *Ibanum* (Sarawak, Brunei)
- Dorsal surface of carapace with granules, striae, punctae and/or scattered setae; epi- and postorbital cristae distinct (Fig. 6I); male second gonopod shorter (Fig. 6K), subequal to or slightly longer than male first gonopod, never twice the length of male first pleopod (Fig. 6J) ..... 9
9. Male first gonopod very long, slender, distal part usually dilated to differing degrees (Fig. 7A–F) ..... *Isolapotamon* (Sarawak, Sabah, Brunei)
- Male first gonopod not elongate, usually gently or strongly curved inwards, sometimes hook-like, distal part gently tapering to tip (Fig. 7G–K) ..... *Johora* (southern Thailand, Peninsular Malaysia)
10. Carapace with reduced or without pigmentation; epigastric cristae weak or absent; eyes reduced, cornea degenerated to varying degrees (Fig. 8A, B); ambulatory legs slender, long; male second gonopod about twice length of male first gonopod (Fig. 8C, D) ..... *Cerberusa* (Sarawak)
- Carapace with normal pigmentation; epigastric cristae distinct; eyes normal (Fig. 8E,F); ambulatory legs not prominently elongate; male second gonopod shorter, subequal to or slightly longer than male first gonopod, never twice the length of male first pleopod (Fig. 8G,H) ..... 11
11. Male first gonopod with distinct subdistal swelling along inner margin between terminal and subterminal segments (Fig. 8I) ..... *Terrapotamon* (southern Thailand)
- Male first gonopod without distinct subdistal swelling along inner margin between terminal and subterminal segments, margin appears straight or gently curved (Fig. 8J) ..... *Stoliczia* (southern Thailand, Peninsular Malaysia)
12. Anterolateral margin with 4 teeth (including external orbital tooth) (Fig. 8K,L) ..... 13
- Anterolateral margin with 1–3 teeth (including external orbital tooth) (Fig. 8M–P) ..... 17
13. Male first pleopod very short, entire terminal segment swollen, resembling bird's head (Fig. 9A) ..... *Salangathelphusa* (southern Thailand, Peninsular Malaysia)
- Male first pleopod relatively more slender (at least distal half), elongate, terminal segment not swollen, although tip may sometimes be dilated (Fig. 9B–D) ..... 14
14. Male first pleopod with basal part prominently swollen, median part slender, elongate, tip dilated (Fig. 9E) ..... *Sayamia* (southern Thailand, Peninsular Malaysia)
- Male first pleopod with basal and median parts gently merging, tip always tapering or rounded, never dilated (Fig. 9F,G) ..... 15
15. Male first pleopod prominently curving inwards towards longitudinal median of abdominal cavity (Fig. 9H) ..... *Heterothelphusa* (Thailand, Peninsular Malaysia)
- Male first pleopod prominently curving outwards from longitudinal median of abdominal cavity (Fig. 9I) ..... 16



**Figure 5.** A–D – Family Varunidae, *Varuna*. I–L – Family Potamididae. A, E – carapaces; B, F – left third maxillipeds; C, G – walking legs; D – male first pleopod (denuded); H – male first pleopod; I, J, M, N – mandibular palps; K, L, O–Q – male abdomens.

16. Male first pleopod with terminal and subterminal segments distinctly demarcated by suture (Fig. 9J) ..... *Geithusa*  
(Peninsular Malaysia)
- Male first pleopod with terminal and subterminal segments not demarcated (Fig. 9K) ..... *Siamthelphusa*
17. Anterolateral margin with 3 distinct teeth (including external orbital tooth) (Fig. 9L) ..... *Parathelphusa*  
(southern Thailand, Peninsular Malaysia, Sarawak, Sabah, Singapore, Brunei)
- Anterolateral margin with 1 or 2 teeth (including external orbital tooth) (Fig. 9M,N) ..... 18
18. Frontal median triangle well developed; dorsal and lateral cristae strong, completely fused (Fig. 9O) ..... 19
- Frontal median triangle incomplete; dorsal and lateral cristae absent and/or weak, sometimes strong, not completely fused (Fig. 9P) ..... 20
19. Larger adult male chela with gently curving fingers, rounded in cross-section (Fig. 10A); male first pleopod with sides of terminal segment gently tapering along most of length (Fig. 10B) ..... *Perithelphusa*  
(Sarawak)
- Larger adult male chela with pollex enlarged, laterally flattened, almost blade-like (Fig. 10C); male first pleopod with sides of terminal segment subparallel along most of length (Fig. 10D)...  
..... *Irmengardia*  
(Peninsular Malaysia)
20. Posterior margin of epistome with a broad median triangular tooth, lateral margins evenly concave (Fig. 10E); ischium of third maxilliped with shallow or undiscernible median sulcus, exopod short, without trace of flagellum (Fig. 10F) ..... GECARCINUCIDAE .. 21
- Posterior margin of epistome with a median triangular tooth, lateral margins sinuous (Fig. 10G); ischium of third maxilliped with distinct oblique median sulcus, exopod long with distinct flagellum (Fig. 10H) ..... 22
21. Carapace slightly broader than long, anterolateral margin entire, antero- and posterolateral margins not clearly demarcated, lateral carapace margins almost subparallel; ambulatory legs neither slender or elongate (Fig. 10I) ..... *Lepidothelphusa*  
(Sarawak)
- Carapace distinctly broader than long, anterolateral margin with one distinct tooth; antero- and posterolateral margins clearly demarcated, anterolateral margin convex, posterolateral margin converging towards posterior carapace margin (Fig. 10J); ambulatory legs slender, relatively elongate ..... *Phricotelphusa*  
(southern Thailand, Peninsular Malaysia)
22. Ambulatory legs very long, spider-like (Fig. 10K) ..... 23
- Ambulatory legs normal length, not elongate (Fig. 10L) ..... 24
23. Male first pleopod terminal segment short, less than a quarter length of entire structure (Fig. 10M); male second pleopod distal segment long, subequal in length or only slightly shorter than basal segment (Fig. 10N) ..... *Stygothelphusa*  
(Sarawak)

- Male first pleopod terminal segment short, less than a quarter length of entire structure (Fig. 10O); male second pleopod distal segment distinctly shorter than basal segment (Fig. 10P)...  
..... *Arachnothelphusa*  
(Sarawak, Sabah)
- 24. Carapace very swollen, egg-like, branchial regions prominently inflated (Fig. 11A), semiterrestrial to terrestrial in habits ..... *Terrathelphusa*  
(Sarawak, Brunei)
- Carapace with dorsal surface gently convex to almost flat, not swollen, branchial regions not distinctly inflated (Fig. 11B,C), fully aquatic species or found in muddy, swampy areas near water ..... 25



**Figure 6.** Family Potamididae. A–D – left third maxillipeds; E, F, I – carapaces; G, J – male first pleopods; H, K – male second pleopods.

25. Male abdomen relatively broadly T-shaped (Fig. 11D); male first pleopod with terminal segment stout, subtruncate (Fig. 11E) ..... *Sundathelphusa* (Sarawak, Sabah)
- Male abdomen narrowly T-shaped (Fig. 11F); male first pleopod with terminal segment slender (Fig. 11G) ..... 26 (Sarawak, Sabah, Brunei)
26. Male first pleopod terminal segment very short, conical, one quarter length of subterminal segment (Fig. 11H) ..... *Adeleana* (Sarawak)
- Male first pleopod terminal segment relatively longer, at least one third or more length of subterminal segment (Fig. 11I) ..... 27
27. Male first pleopod with stout, short terminal segment (Fig. 11J); male second pleopod with distal segment longer than half length of but shorter than basal segment (Fig. 11K) .. *Bakousa* (Sarawak)
- Male first pleopod slender to very slender; terminal segment cylindrical, rod-shaped or elongate, subequal to longer than half length of subterminal segment (Fig. 11L, N); male second pleopod with short distal terminal segment, less than 0.15 times length of basal segment (Fig. 11M) ..... 28 (Sarawak, Sabah, Brunei)
28. Carapace slightly ovate to distinctly quadrate, surfaces with cristae and striae distinct, often sharp; branchial regions gently convex to flat (Fig. 11B, C); male first pleopod with terminal segment cylindrical or rod-shaped, tapering to a tip (Fig. 11L) ..... *Thelphusula* (Sarawak, Sabah, Brunei)
- Carapace ovate, surfaces relatively smooth, with cristae and striae low; branchial regions distinctly convex; male first pleopod very slender, terminal segment elongate, thin, tip rounded (Fig. 11N) ..... *Coccosa* (Sarawak)

## FAMILY POTAMIDAE

This family has an Old World distribution and is not known east of Wallace's Line. They are the most speciose family in Indo-China. Most of the species live in relatively fast flowing waters and require clear, highly oxygenated waters. Many species also have semi-terrestrial habits, and can wander some distance from permanent water, especially during the wet season.

### Genus *Johora*

This is a wholly Malayan genus, with 14 species, viz. *J. aipooae* (Ng, 1986), *J. counsilmani* (Ng, 1985), *J. gapensis* (Bott, 1966), *J. grallator* Ng, 1988, *J. gua* Yeo, 2001, *J. hoiseni* Ng and Takeda, 1992, *J. johorensis* (Roux, 1936), *J. intermedia* Ng, 1986, *J. murphyi* Ng, 1986, *J. punicea* (Ng, 1985), *J. singaporensis* Ng, 1986, *J. tahanensis* (Bott, 1966), *J. thoi* Ng, 1990, *J. tiomanensis* (Ng and Tan, 1984), and is characterized by the presence of a long flagellum on the third maxilliped exopod. Of interest is that Pulau Tioman has five endemic species, including Peninsular Malaysia's only cavernicolous taxon (*J. gua*). One species is endemic to Singapore. Key and taxonomy of species are in Ng (1987a, 1988), Ng and Takeda (1992a), Yeo *et al.* (1999) and Yeo (2001).

### Genus *Stoliczia*

This is also a wholly Malayan genus with 15 species, viz. *S. bella* Ng and Ng, 1987, *S. changmanae* Ng, 1988, *S. chaseni* (Roux, 1934), *S. cognata* (Roux, 1936), *S. ekavibhathai* Ng and Naiyanetr, 1986, *S. goal* Ng, 1993, *S. karenae* Ng, 1993, *S. kedahensis* Ng, 1992, *S. leoi* (Ng and Yang, 1985), *S. pahangensis* (Roux, 1936), *S. panhai* Ng and Naiyanetr, 1986, *S. perlensis* (Bott, 1966), *S. rafflesi* (Roux, 1936), *S. stoliczkana* (Wood Mason, 1871) and *S. tweediei* (Roux, 1934). *S. panhai* and *S. ekavibhathai* are only known from southern Thailand. Members of this genus are easily recognized by the presence of a vestigial or absence of a flagellum on the exopod of the third maxilliped. Key and taxonomy of species are in Ng (1988, 1992a).

### Genus *Terrapotamon*

This genus is not yet known from northern Peninsular Malaysia per se but may well be found there. The two known southern Thai species, *T. abbotti* (Rathbun, 1898) and *T. palian* Ng and Naiyanetr, 1998, can be distinguished by their very stout male first pleopods and inflated carapace. These species are very colourful in life (red to yellow) with terrestrial habits and appear infrequently in the aquarium trade. Key and taxonomy of species are in Ng (1986a, 1988).

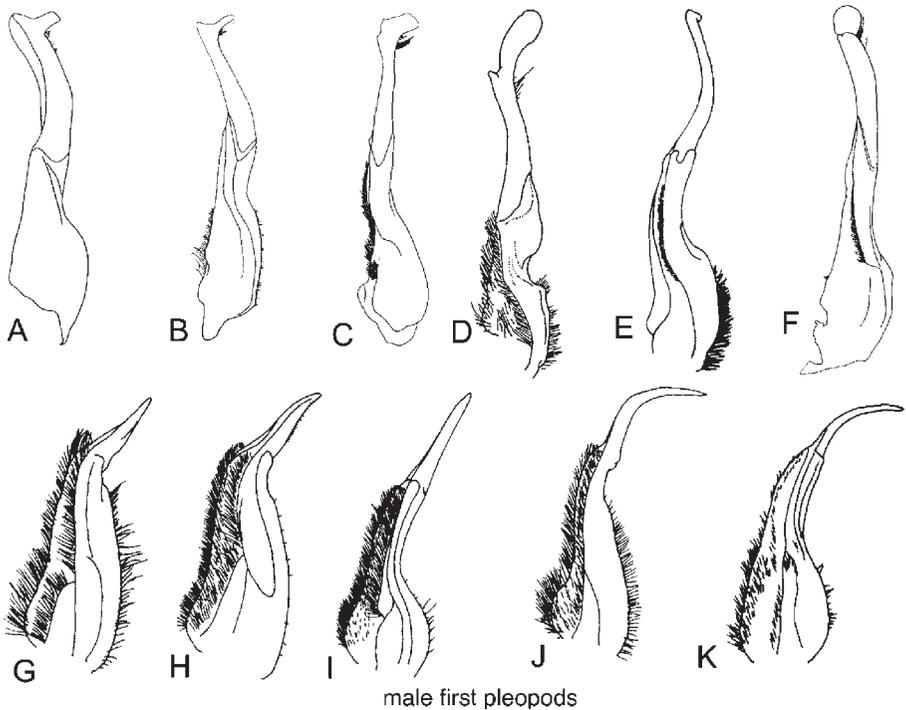


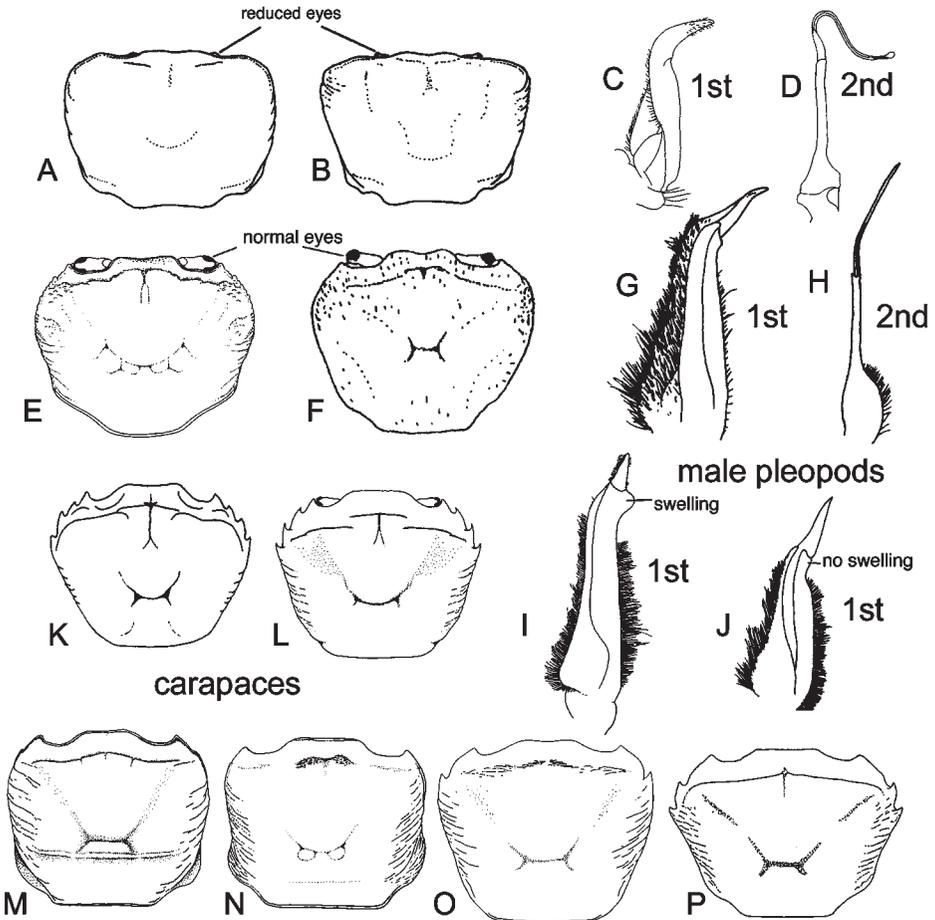
Figure 7. Family Potamidae. A–F – *Isolapotamon*; G–K – *Johora*. Male first pleopods.

### Genus *Cerberusa*

A genus with two cavernicolous species, the type of which is the only known completely blind Sundaic freshwater crab. Both species are known only from the limestone caves of northern Sarawak. Key and taxonomy of species are in Holthuis (1979).

### Genus *Ibanum*

This is probably an ancient genus from northern Borneo with a long male second pleopod and allied to *Cerberusa* but not possessing any cave-living features. Two species are known from Sarawak, *I. aethes* Ng, 1995, and *I. pilimanus* Ng and Jongkar 2004, and other species have been found also in Brunei (unpublished data). Key and taxonomy of species are in Ng (1995b) and Ng and Jongkar (2004).



**Figure 8.** A–D – *Cerberusa*; I – *Terrapotamon*; J – *Stoliczia*. A, B, E, F, K–P – carapaces; C, G, I, J – male first pleopods; D, H – male second pleopods.

### **Genus *Isolapotamon***

Members of this wholly Bornean and Philippine (Mindanao) genus have a very long and slender male first pleopod in which the distalmost part is dilated into various shapes. Eleven species are known from Sarawak, Sabah and Brunei, viz. *I. anomalum* (Chace, 1938), *I. bauense* Ng, 1987, *I. borneensis* Ng and Tan, 1998, *I. collinsi* Holthuis, 1979, *I. consobrinum* (De Man, 1899), *I. doriae* (Nobili, 1900), *I. griswoldi* (Chace, 1938), *I. grusophallus* Ng and Yang, 1986, *I. ingeri* Ng and Tan, 1998, *I. kinabaluense* (Rathbun, 1904) and *I. nimboni* Ng, 1987. One Sarawak species, *I. stuebingi* Ng, 1995, is a junior synonym of *I. nimboni* (unpublished data). Key and taxonomy of species are in Holthuis (1979), Ng (1987b, 1995b), Ng and Tan (1998).

### **FAMILY GECARCINUCIDAE**

The validity of this family is not certain and may be synonymous with Parathelphusidae. Only two genera are known from the area of study, one in northern Peninsular Malaysia, another in Sarawak.

### **Genus *Phricotelphusa***

Members of this genus mainly occur in Myanmar and southern Thailand, and are characterized by their relatively small size and montane habits. They are mainly aquatic. Only two species are known from northwestern Peninsular Malaysia, *P. hockpingi* Ng, 1986, and *P. gracilipes* Ng and Ng, 1987. Key and taxonomy of species are in Ng (1988, 1994).

### **Genus *Lepidothelphusa***

A monotypic and unusual genus and is the only known Bornean gecarcinucid and parathelphusid which has no flagellum on the exopod of the third maxilliped. *L. cognetti* (Nobili, 1903) is known only from Sarawak. This species appears to be closely associated with shale formations and has been found in caves. Key and taxonomy of species are in Bott (1970).

### **FAMILY PARATHELPHUSIDAE**

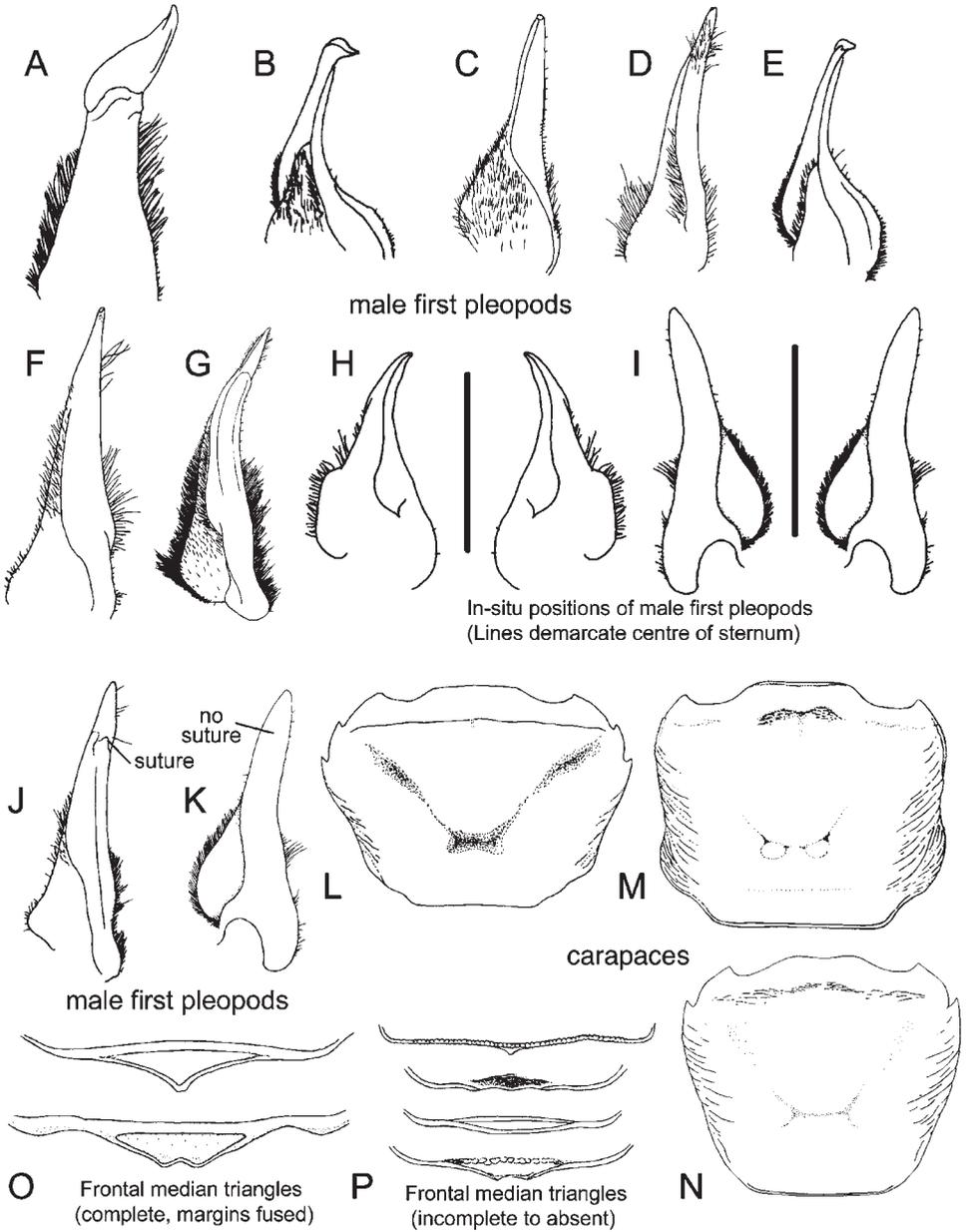
This is a large family of freshwater crabs which occurs from lowlands to mountains, stagnant pools to open waters and also terrestrial habitats. Sundathelphusidae is a junior synonym of this family.

### **Genus *Adeleana***

This genus occurs in Borneo and Sumatra with three species. Sarawak has one cavernicolous species, *A. chapmani* Holthuis, 1979. Taxonomy of species is in Holthuis (1979).

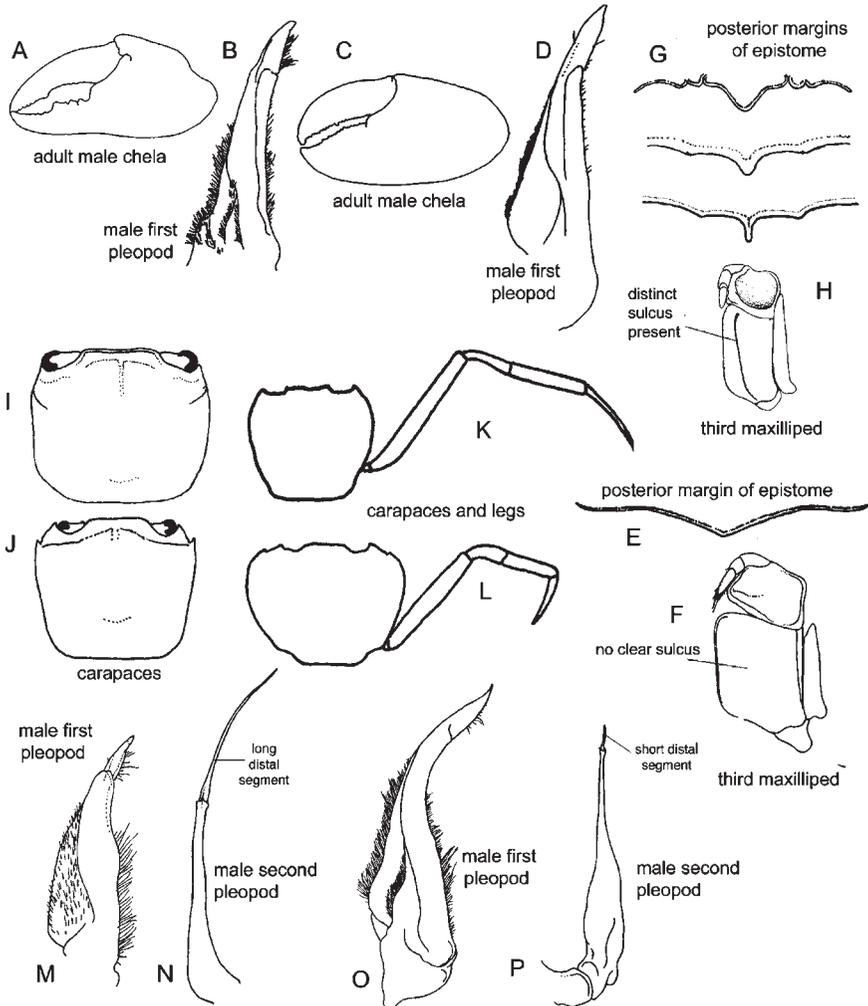
### **Genus *Thelphusula***

All members of this genus are Bornean, seven of which occur in Sarawak, Sabah and Brunei, viz. *T. baramensis* (De Man, 1902), *T. dicerophilus* Ng and Stuebing, 1990,



**Figure 9.** Family Parathelphusidae. A – *Salangathelphusa*; H – *Heterothelphusa*; J – *Geithusa*; I, K – *Siamthelphusa*; L – *Parathelphusa*. A–G, J, K – male first pleopods; H, I – in-situ positions of pair of male first pleopods in thoracic sternal cavity; L–N, carapaces; O, P – frontal median triangles of carapace from frontal view.

*T. granosa* Holthuis, 1979, *T. luidana* (Chace, 1938), *T. sabana* Tan and Ng, 1998, *T. styx* Ng, 1989, and *T. tawauensis* Tan and Ng, 1998. Most are deep forest species with semi-terrestrial habits. One species, *T. dicerophilus* is associated with rhinoceros mud pools in Sabah (presumably using the semi-permanent water source and feeding on the insects within); and another, *T. styx*, occurs in caves of Gunung Mulu. Key and taxonomy of species are in Ng (1991b) and Tan and Ng (1998).



**Figure 10.** A–D, G, H, O, P – Family Parathelphusidae; A, B – *Perithelphusa*; C, D – *Irmengardia*; M, N – *Stygothelphusa*; O, P – *Arachnothelphusa*. E, F, I, J – Family Gecarcinucidae; I – *Lepidothelphusa*; J – *Phricotelphusa*. A, C – left adult male chelae; B, D, M, O – male first pleopods; E, G – posterior margins of epistomes; F, H – left third maxillipeds; I, J – carapaces; K, L – schematic figure of carapace showing relative lengths of third walking legs; N, P – male second pleopods.

### **Genus *Coccusa***

This small genus contains only three known species, one from eastern, another from western Kalimantan; with *C. cristicervix* Ng and Jongkar 2004, only recently described from southern Sarawak. Key and taxonomy in Tan and Ng (1998) and Ng and Jongkar (2004).

### **Genus *Bakousa***

A wholly Bornean genus characterized mainly by its distinctive male first and second pleopod structures. It superficially resembles some *Thelphusula* and *Adeleana* species. Only one species is known: *B. sarawakensis* Ng, 1995, from fast-flowing streams in Bako National Park in Sarawak. Key and taxonomy of species are in Ng (1995a).

### **Genus *Arachnothelphusa***

The spider-like legs and ovate carapaces of these forest-dwelling terrestrial and tree-climbing species are very distinct. Three species are known from Sabah, *A. kadamaiana* (Borradaile, 1900), *A. rhadamanthysi* Ng and Goh, 1987, and *A. terrapes* Ng, 1991; and the genus is also in Sarawak (unpublished data). These are very agile crabs and are frequently found climbing trees in wet forests. Key and taxonomy of species are in Ng (1991b).

### **Genus *Stygothelphusa***

The squarish carapace and extremely long ambulatory legs easily distinguishes the obligate cave-dwelling species in this genus. Two species are known from Sarawak, viz. *S. bidiensis* (Lanchester, 1900) and *S. nobilii* (Colosi, 1920). The latter species had been placed in *Arachnothelphusa* but recent information (unpublished data) indicates it is a valid *Stygothelphusa* species. These crabs are always associated with limestone formations, living in caves. Their long legs and pale colouration are characters typically associated with cavernicoles. Key and taxonomy of species are in Ng (1989b).

### **Genus *Terrathelphusa***

All members of this genus are terrestrial species with prominently swollen carapaces. Three species are known from Sarawak and Brunei, viz. *T. kuchingensis* (Nobili, 1901), *T. ovis* Ng, 1997, and *T. telur* Ng, 1997; the last apparently a Bruneian endemic. Key and taxonomy of species are in Ng (1989c, 1997b) and Ng and Jongkar (2004).

### **Genus *Irmengardia***

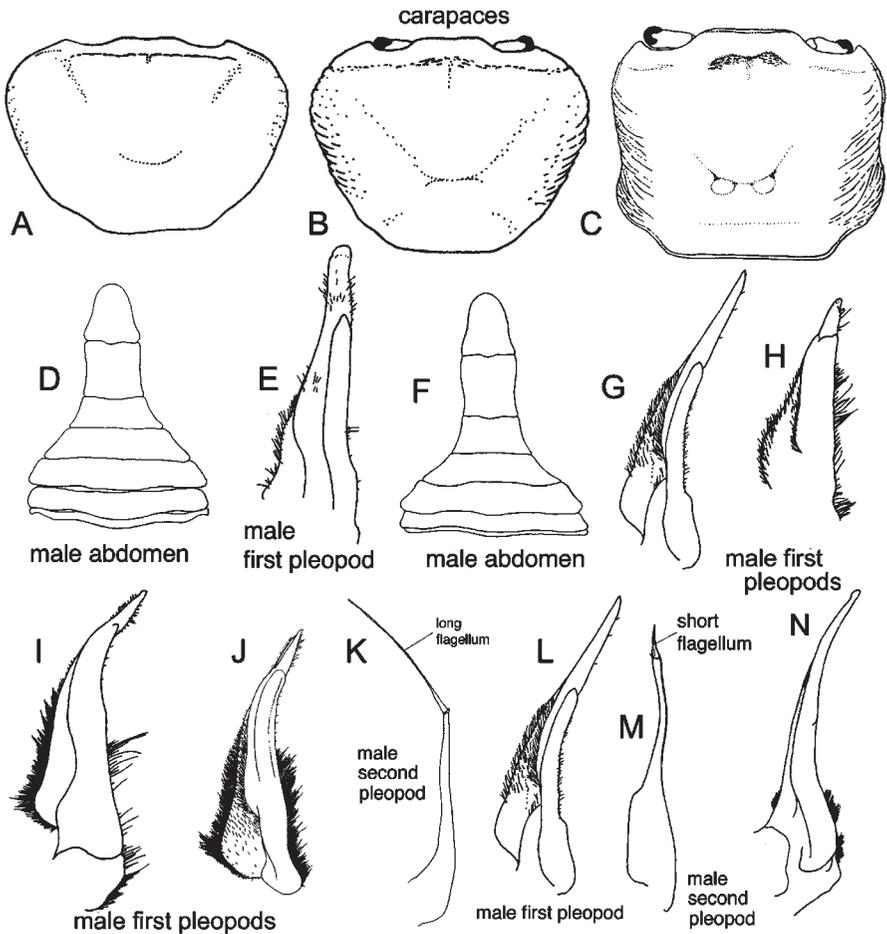
There are only three species in this genus, known only from Peninsular Malaysia, Singapore and Riau Islands (Indonesia). The species from Malaysia and Singapore are *I. didacta* Ng and Tan, 1991, *I. johnsoni* Ng and Yang, 1985, and *I. pilosimana* (Roux, 1936). All are completely aquatic and live in relatively slow-flowing waters with dense leaf litter and submerged vegetation. Key and taxonomy of species are in Ng (1988) and Ng and Tan (1991).

### Genus *Perithelphusa*

A Bornean genus, the members possessing a simple male first pleopod and usually a distinct epibranchial tooth. Two species are known from Sarawak, *P. borneensis* (Von Martens, 1868) and *P. lehi* Ng, 1986; both occurring in slow-flowing shallow waters or almost stagnant pools with dense submerged leaf litter and vegetation. Key and taxonomy of species are in Bott (1970) and Ng (1986b)

### Genus *Sundathelphusa*

This genus is more speciose in Sulawesi, the Moluccas and the Lesser Sunda Islands. The two known Bornean species are characterized by their rugose carapaces and



**Figure 11.** Family Parathelphusidae. A – *Terrathelphusa*; B, C, M – *Thelphusula*; N – *Coccusa*; D, E – *Sundathelphusa*; H – *Adeleana*; J, K – *Bakousa*. A–C, carapaces; D, F – male abdomens; E, G, H–J, L, N – male first pleopods; K, M – male second pleopods.

broad T-shaped abdomens. Two species are known from Sarawak and Sabah, *S. aspera* Ng and Stuebing, 1989, and *S. tenebrosa* Holthuis, 1979. Key and taxonomy of species are in Holthuis (1979) and Ng and Stuebing (1989).

### Genus *Parathelphusa*

This is a very speciose genus with over 30 species, occurring from southern Thailand to Sulawesi. Ten species are known from the Malaysian region, viz. *P. maculata* De Man, 1879, *P. maindroni* Rathbun, 1902, *P. malaysiana* Ng and Takeda, 1992, *P. nagasaki* Ng, 1988, *P. ovum* Ng, 1995, *P. oxygona* Nobili, 1901, *P. pulcherrima* (De Man, 1902), *P. reticulata* Ng, 1990, *P. sarawakensis* Ng, 1986, and *P. valida* Ng and Goh, 1987. Most are lowland species, occurring in relatively slow-flowing waters, although some are semi-terrestrial. *P. sarawakensis*, however, lives in fast flowing, gravel-strewn streams. Of ecological interest are two species which are found in the highly acidic waters of freshwater and peat swamps (*P. maindroni* in Peninsular Malaysia; *P. reticulata* in Singapore) (Ng, 1990c, 1993). Taxonomy of species is in Bott (1970), Ng (1988, 1990a, c, 1995b), Ng and Goh (1987) and Ng and Takeda (1992). Because the genus *Parathelphusa* is so common and ecologically significant in the area of study, we provide a much-needed key to the species from Malaysia, Singapore and Brunei.

### Key to species of *Parathelphusa*

1. Ambulatory meri without distinct, sharp dorsal subterminal spine on any of the legs, sometimes blunt, stump-like structure may be present (Fig. 12A) ..... *P. sarawakensis* (Sarawak)
- Ambulatory meri with distinct, sharp dorsal subterminal spine on at least some of the legs (Fig. 12B) ..... 2
2. Postorbital crista meeting anterolateral margin between first and second epibranchial teeth or at base of second tooth (Fig. 12C,D) ..... 3 (Sarawak, Sabah, Peninsular Malaysia)
- Postorbital crista meeting anterolateral margin at base of first epibranchial tooth (Fig. 12E) ... 6
3. Outer margin of first epibranchial tooth smooth (Fig. 12G) or gently serrated (Fig. 12H); postorbital crista meeting anterolateral margin at base of second epibranchial tooth (Fig. 12G,H); male first pleopod very stout, distal part not dilated subterminally before tip, opening "flared" (Fig. 12I) ..... *P. pulcherrima* (Sarawak, Brunei, Sabah)
- Outer margin of first epibranchial tooth always entire (Fig. 12F); postorbital crista meeting anterolateral margin between first and second epibranchial teeth (Fig. 12F); male first pleopod stout or slender, distal part dilated just before very slender tip, or not dilated subterminally before tip, opening slightly "flared" (Fig. 12J) ..... 4 (Pulau Tioman, Sabah)
4. Carapace very flat, gastric regions not inflated, not distinctly convex (Fig. 12P); male first pleopod slender, distal part dilated subterminally before slender tip, resembling "sparrow's head" (Fig. 12K) ..... *P. nagasaki* (Pulau Tioman)

- Carapace convex to distinctly convex, gastric regions appear inflated (Fig. 12Q); male first pleopod stout, slightly sinuous, tip subtruncate (Fig. 12L,M) ..... 5 (Sabah)
- 5. Carapace convex, gastric regions inflated (Fig. 12R); male first pleopod almost straight, tip directed upwards (Fig. 12N) ..... *P. valida* (Sabah)
- Carapace strongly convex, gastric regions strongly inflated (Fig. 12S); male first pleopod curving outwards, C-shaped (Fig. 12O) ..... *P. ovum* (Sabah)
- 6. Proximal part of outer margin of male first pleopod with distinct cleft (Fig. 13A) ..... *P. maculata* (Peninsular Malaysia, Singapore)
- Proximal part of outer margin of male first pleopod entire without distinct cleft (Fig. 13B) ..... 7
- 7. Tip of male first pleopod terminal segment rounded, folds forming blunted end, outer margin of subterminal segment straight or sinuous (Fig. 13C) ..... *P. oxygona* (Sarawak)
- Tip of male first pleopod terminal segment tapering, folds forming a sharp point, outer margin of subterminal segment straight (Fig. 13D) ..... 8 (Singapore, Peninsular Malaysia)
- 8. Epibranchial teeth in adults small, outer margin of teeth strongly convex, anterolateral margin appears strongly rounded (Fig. 13E); outer margin of male first pleopod very straight, distal part of terminal segment very slender, sharp, opening very small (Fig. 13F) ..... *P. reticulata* (Singapore)
- Epibranchial teeth in adults triangular, normal, outer margin of teeth straight or gently convex, anterolateral margin not strongly rounded (Fig. 13G); outer margin of male first pleopod almost straight, distal part of terminal segment slender, sharp, opening small (Fig. 13H) .... *P. maindroni* (Peninsular Malaysia)

### Genus *Siamthelphusa*

Members of this genus are lowland dwellers often in clean, shallow streams with water plants and gravel substrate. Only one species is known from northern Malaysia, *S. improvisa* (Lanchester, 1901). The genus is very speciose in Thailand. Key and taxonomy of species are in Ng (1988), Ng and Ng (1987) and Ng and Naiyanetr (1997).

### Genus *Salangathelphusa*

A monotypic genus with one southern Thai and northern Malaysian species, *S. brevicarinata* (Hilgendorf, 1882). It occurs in at the bases of waterfalls and other fast-flowing streams. The male first pleopod is very stout and short. Key and taxonomy of species are in Bott (1968b, 1970) and Ng (1988).

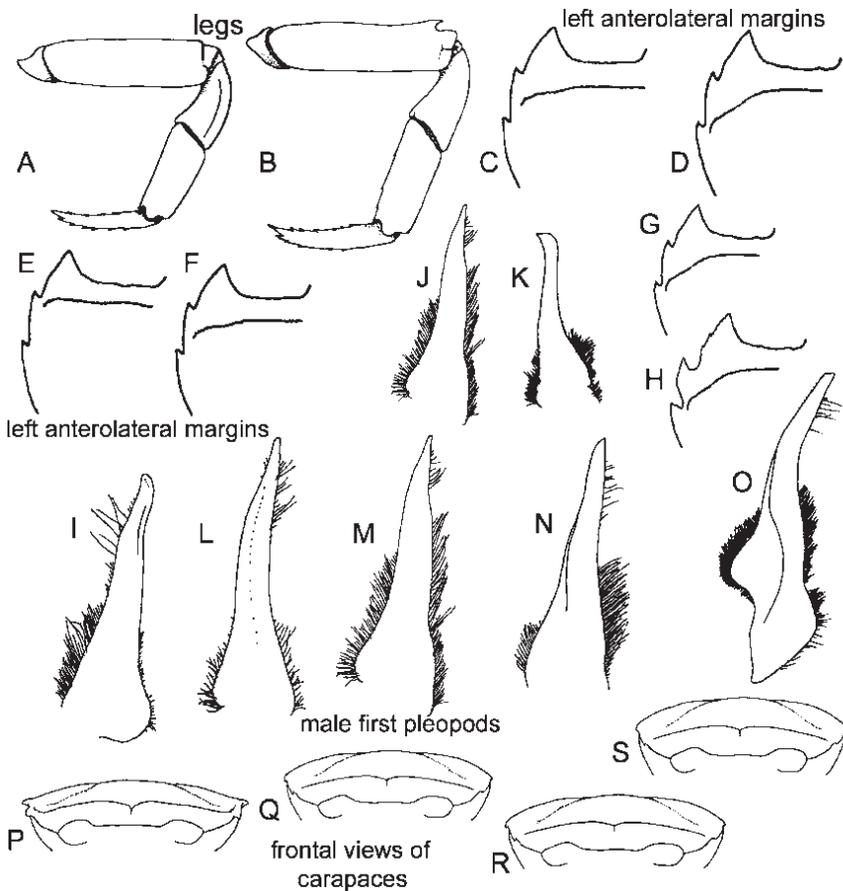
### Genus *Heterothelphusa*

A genus known only from Peninsular Malaysia and Thailand thus far. The male first pleopod of the type species is unusually bent inwards. The species in the genus occur in fast flowing waters as well as swamps. Two species are known from

northwestern Peninsular Malaysia, viz. *H. fatum* Ng, 1997, and *H. insolita* Ng and Lim, 1986 (unpublished data). One species (*H. fatum*) appears regularly in the aquarium trade, their placid habits making them good communal tank subjects. Key and taxonomy of species are in Ng (1988, 1997a), Ng and Lim (1986) and Ng and Naiyanetr (1993).

### Genus *Sayamia*

This genus was split off from *Somanniathelphusa* (now restricted to Thailand) and only one species is known for certain from northern Peninsular Malaysia, *S. sexpunctata* (Lanchester, 1906). This species is common in rice fields and still waters. In rice fields, they are regarded as pests as they feed on the young plants and weaken the bunds. Key and taxonomy of species are in Bott (1968b, 1970), Ng (1988) and Ng and Ng (1987).



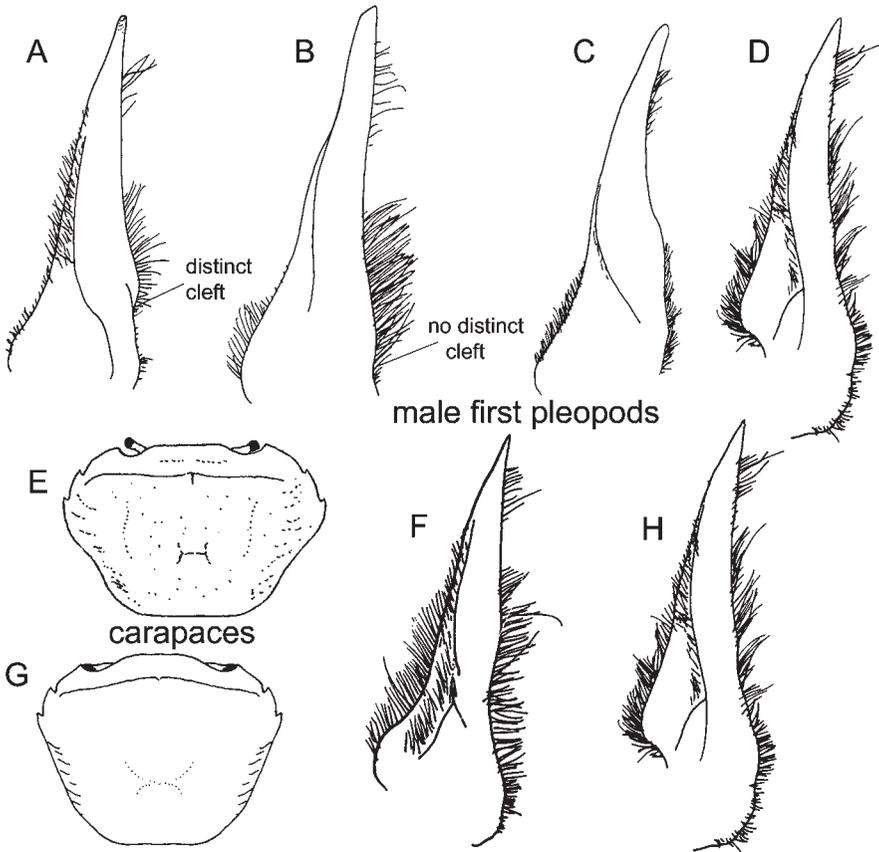
**Figure 12.** Family Parathelphusidae, *Parathelphusa*. A, B – walking legs; C, H – left sides of carapaces showing anterolateral margins; I–O – male first pleopods; P–S – frontal view of carapaces showing different degrees of inflation.

### Genus *Geithusa*

Members of this genus have three epibranchial teeth on each side of the carapace, the male abdomen is T-shaped but without any constrictions between segments four to six, and the male first pleopod is separated into the terminal and subterminal segments. Only two species are known, both from northeastern Peninsular Malaysia, *G. lentiginosa* Ng, 1992, and *G. pulchra* Ng, 1989. Key and taxonomy of species are in Ng (1989a, 1992b).

### FAMILY VARUNIDAE

The Varunidae and Sesarmidae used to be subfamilies in the better known family Grapsidae, but there is increasing evidence that all are distinct families. For the varunids, the most often seen is *Varuna yui* Hwang and Takeda 1986 (Fig. 5A–D), a species which spends much of its adult life in the open sea but sub-adults can be found many kilometres inland in low-lying areas.



**Figure 13.** Family Parathelphusidae, *Parathelphusa*. A – *P. maculata*; C – *P. oxygona*; E, F – *P. reticulata*; G, H – *P. maindroni*. A–D, F, H – male first pleopods; E, G – carapaces.

## FAMILY SESARMIDAE

Most sesarmids are mangrove denizens but several genera have made their way into freshwaters. All of them, however, with the exception of members of one genus (*Geosesarma*), need to return to the sea to release their planktonic larvae. One of the more peculiar and common are three species of *Pseudosesarma*, *P. bocourti* (A. Milne-Edwards, 1869)(Fig. 4 H–J), *P. crassimanum* (De Man, 1887) and *P. edwardsi* (De Man, 1888), which may occur deep inland. *Pseudosesarma bocourti* is interesting because it likes muddy areas and even peat swamps, its flattened chelae being distinctive (Ng 1995a). In nearby Southeast Asian countries, members of two other genera have members that enter freshwaters, *Sesarmops* (Fig. 4E–G) and *Sesarmoides* (Fig. 4A), and as they may also be present in the area of study, they have been included in the generic key.

### Genus *Geosesarma*

This completely terrestrial/freshwater genus does not need to return to the sea to reproduce, its large eggs hatching out directly into very advanced zoeae with internal yolk or as miniature versions of the adult. Some Indonesian species even carry their young on their backs (Ng and Tan 1995). A few species are nepenthophilous (i.e. associated with pitcher plant cups) (Ng and Lim 1987), using the water in these cups for respiration as well as feeding on the insect material within. The highest diversity of species is known from Peninsular Malaysia, but this is merely because this area is the best explored. Eighteen species are known at present from the Malaysian region, viz. *G. albomita* Yeo and Ng, 1999, *G. aurantium* Ng, 1995, *G. bau* Ng and Jongkar 2004, *G. cataracta* Ng, 1986, *G. foxi* (Kemp, 1918), *G. gracillimum* (De Man, 1902), *G. insulare* Ng, 1986, *G. johnsoni* (Serène, 1968), *G. katibas* Ng, 1995, *G. malayanum* Ng and Lim, 1986, *G. nemesi* Ng, 1986, *G. penangense* (Tweedie, 1940), *G. peracca* (Nobili, 1903), *G. sabanus* Ng, 1992, *G. sarawakense* (Serène, 1968), *G. serenei* Ng, 1986, *G. scandens* Ng, 1986 and *G. tiomanicum* Ng, 1986. Key and taxonomy of species are in Ng (1988, 1992c, 1995b,d) and Ng and Jongkar (2004).

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