



Odiomarinae nov. subfam., a new subfamily for two primitive genera of Hymenosomatidae MacLeay, 1838, with preliminary remarks on the family (Crustacea, Decapoda, Brachyura)

DANIÈLE GUINOT

Muséum national d'Histoire naturelle, Département Milieux et Peuplements aquatiques, 57 rue Cuvier, case postale 53, F-75231 Paris cedex 5, France. E-mail: guinot@mnhn.fr

Abstract

A new subfamily Odiomarinae **nov. subfam.** is erected to receive two primitive genera of the eubrachyuran family Hymenosomatidae MacLeay, 1838: *Odiomaris* Ng & Richer de Forges, 1996, and *Amarinus* Lucas, 1980, mostly from fresh and estuarine waters of the Indo-West Pacific region. The new subfamily is characterised by the presence of “intercalated platelets” on the male abdomen, either articulated and moveable or relatively less well demarcated. The hymenosomatid platelets are actually vestigial uropods that are similar to those, also showing as dorsal plates, of the podotreme Dynomenidae Ortmann, 1892, and Dromiidae De Haan, 1833. The hymenosomatid uropod differs from the podotreme ones by the deep socket that is excavated at its ventral side and thus corresponds to the typical eubrachyuran press-button system. The odiomarine socket is particularly interesting because it provides morphological and phylogenetic criteria for identifying podotreme uropods and eubrachyuran sockets as homologues. In addition to several other plesiomorphic characters, the retention of dorsal uropods in the Hymenosomatidae, a unique known case in the Eubrachyura Saint Laurent, 1980, and evidence of an ancient lineage, allows re-defining and preliminarily interpreting the exclusive combination of characters of the family and to reconsider its status within the Eubrachyura.

Key words: Crustacea, Decapoda, Brachyura, Eubrachyura Hymenosomatidae, Odiomarinae **nov. subfam.**, *Odiomaris*, *Amarinus*, Dorippidae, Inachoididae, uropod, pleotelson, socket, abdominal-locking mechanism, phylogeny

Introduction

The Hymenosomatidae MacLeay, 1838, which includes 118 species in 19 genera (updated from Ng *et al.* 2008: 108), recently removed from the Majoidea Samouelle, 1819, and elevated to a suprafamilial level, Hymenosomatoidea MacLeay, 1838 (Martin & Davis 2001: 74; Chen & Sun 2002: 34; Poore 2004: 390; Števcíć 2005: 101), has surprisingly not been credited with any subfamilies despite its many members and heterogeneous organisation. The large morphological variations of the rostrum, epistome, mouthparts, male and female abdomens, gonopods, and vulvae (Melrose 1975; Lucas 1980; Ng 1991; Ng & Chuang 1996; Guinot & Richer de Forges 1997; Davie 2002; Poore 2004; Naruse & Ng 2007a, 2007b; Naruse, Mendoza & Ng 2008; Naruse, Ng & Guinot 2008) nevertheless provide evidence for the presence of several distinct lineages in the Hymenosomatidae. The family presents actually a unique combination of characters within the Brachyura, some being plesiomorphic and others seemingly derived, the result of a strong carcinisation.

The distinctiveness of the Hymenosomatidae caught our attention for a long time (Guinot 1979: 110, 149, 215, 250), in particular the dorsal intercalated platelets on each side of the sixth somite of the male abdomen in genera such as *Odiomaris* Ng & Richer de Forges, 1996, and *Amarinus* Lucas, 1980 (Guinot & Richer de Forges 1997: 470, fig. 6A–E). The presence of several other plesiomorphic characters exhibited by these two genera justifies the establishment of a separate subfamily for them. The new subfamily, Odiomarinae **nov. subfam.**, is erected here to receive these primitive hymenosomatid representatives, as a prelude to a revision in progress of the eubrachyuran family Hymenosomatidae. It is likely that other taxa will be added to this subfamily in the future.

Material and methods

Measurements refer to carapace length \times carapace width, spines and teeth included. The following abbreviations are used in the text: G1, first male pleopod, or first gonopod; G2, second male pleopod, or second gonopod; mxp3, third maxilliped; P1–P5, first to fifth pereopods (P1 as chelipeds).

The material examined is deposited in the Muséum national d'Histoire naturelle, Paris (MNHN) and the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC).

Systematics

Eubrachyura Saint Laurent, 1980

Heterotremata Guinot, 1977

Hymenosomatidae MacLeay, 1838

Odiomarinae nov. subfam.

Genera included. *Amarinus* Lucas, 1980; *Odiomaris* Ng & Richer de Forges, 1996.

Diagnosis. Body dorsoventrally very flattened, cuticle thin. Carapace circular to oval, pear-shaped, with angles obtuse, rounded; posterolateral margin may be uneven, undulate, either unarmed or toothed. Dorsal surface flat, may be slightly concave; grooves varying from poorly to well defined, often not reaching lateral borders, with gastro-cardiac, thoracic grooves (terminology of Lucas 1980: fig. 1A). Hymenosomian rim continuous at base of rostrum. Rostrum unilobed, forming single, broad, spade-shaped lobe, directed downwards, base extending laterally over eyestalks, meeting postocular lobes. Eyestalks prominent. Antennules, antennae developed, usually visible dorsally. Epistome short. Pterygostomian lobe may be well marked. Mxp3 small but broad, operculiform; ischium approximately subequal to merus; palp slender. Thoracic sternum very wide; sternites 1–3 forming produced plate; sternites 4–8 medially fused; sutures 4/5–7/8 only lateral. Junction of sternite 4 with pterygostome pronounced, distinctly separating Milne Edwards openings from chelipeds. Chelipeds subequal, homomorph. Walking legs of moderate thickness, with sparse plumose setae; dactyli curved, without teeth or with one weak subdistal tooth on inner margin. Abdomens without fused somites (except for pleotelson) in both sexes; male abdomen triangular or with almost straight lateral margins parallel; presence of uropods showing as intercalated plates laterally at base of pleotelson, plates either prominent, moveable, or partially fused with pleotelson, or not well demarcated; pleotelson triangular or semicircular. Female abdomen with convex lateral margins, may form large, discoid plate, usually covering a brood cavity. G1 stout or more slender, spindle-shaped, curved base, remaining part nearly straight; distal portion with tip simple or with 2 or several lobes or processes; subterminal tufts of setae. Vulvae in unfused part of thoracic sternum, anteriorly displaced in intermediate position between inner ends of sutures 4/5, 5/6. Axial skeleton regularly compartmented, with parallel arrangement of phragmae in antero-posterior plane as well as above and below junction plate; sella turcica sole transversal binding.

Species included. *Odiomaris* Ng & Richer de Forges, 1996 (type species: *Elamena pilosa* A. Milne-Edwards, 1873, by original designation), with two species: *O. pilosus* (A. Milne-Edwards, 1873) and *O. estuarius* Davie & Richer de Forges, 1996.

Amarinus Lucas, 1980 (type species: *Elamena lacustris* Chilton, 1882, by original designation), with eleven species: *A. abatan* Naruse, Mendoza & Ng, 2008, *A. angelicus* (Holthuis, 1968), *A. crenulatus* Ng & Chuang, 1996, *A. lacustris* (Chilton, 1882), *A. laevis* (Targioni-Tozzetti, 1877), *A. latinasus* Lucas, 1980, *A. lutarius* Lucas & Davie, 1982, *A. paralacustris* (Lucas, 1970), *A. pristes* Rahayu & Ng, 2004, *A. pumilus* Ng & Chuang, 1996, *A. wolterecki* (Balss, 1934) (see below).

For the distinction of the two genera, see Ng & Richer de Forges (1996: 271, figs. 5–7).

Ecology and geographical distribution. Both *Odiomaris* (Ng & Richer de Forges 1996, 2007; Guinot & Richer de Forges 1997; Marquet *et al.* 2003; Juncker & Poupin 2009) and *Amarinus* (Chilton 1915, as *Halicarcinus* pro parte; Walker 1969, as *Halicarcinus*; Melrose 1975, as *Halicarcinus* pro parte; Lucas 1972, as *Halicarcinus* pro

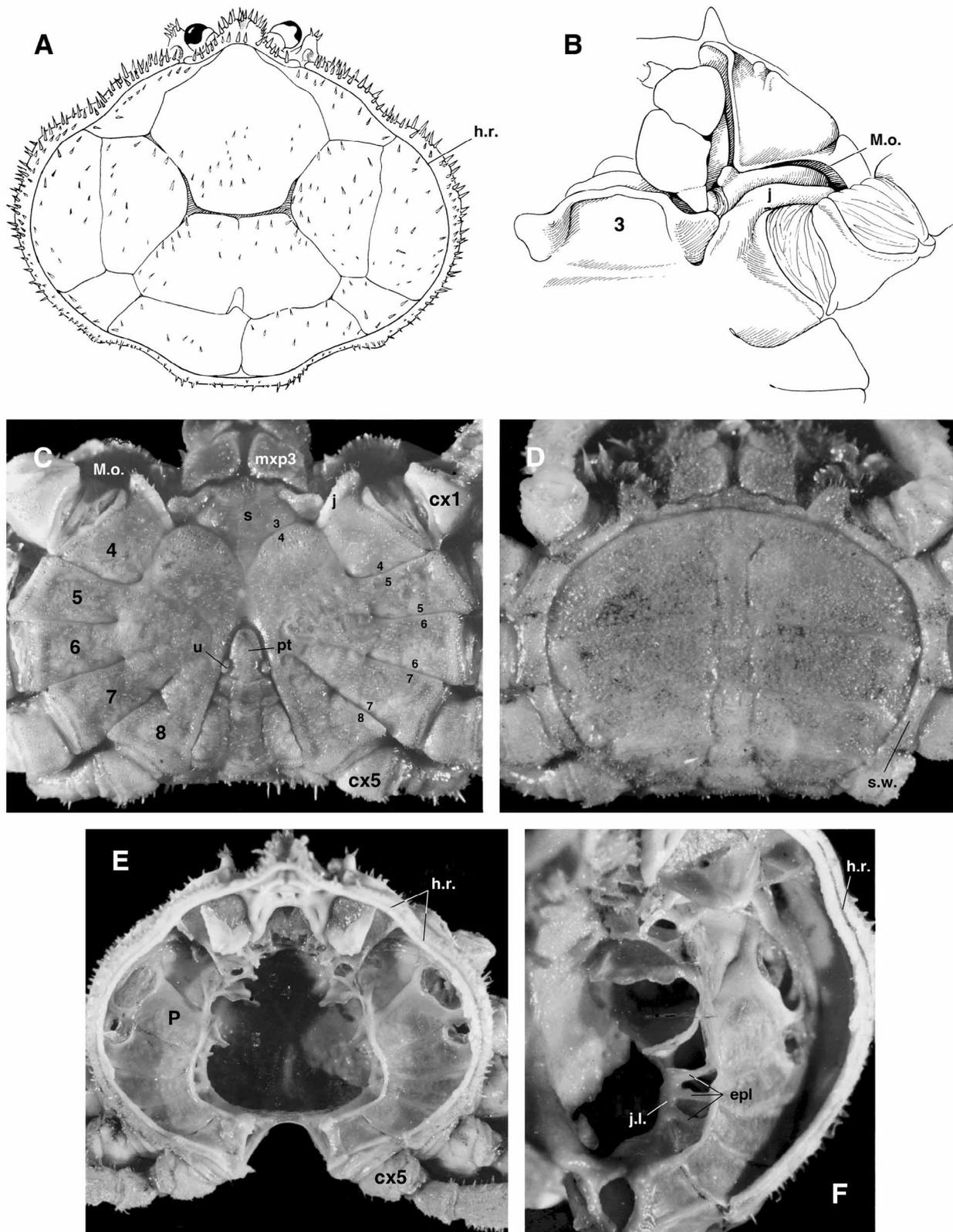


FIGURE 1. *Odiomaris pilosus* (A. Milne-Edwards, 1873), New Caledonia (MNHN). A–C, male 16.5 × 18.6 mm. A, carapace, dorsal view; B, pterygostome and mxp3 (setae and details not figured); C, ventral view; D, female: ventral view; E, male 17 × 20 mm: dorsal view after removal of carapace at level of hyemosomian rim; F, male: axial skeleton (prepared by Sylvie Secretan): lateral view. cx1, cx5, coxa of P1, P5; h.r., hyemosomian rim; j, sternum/pterygostome junction; j.l., junction line; epl, endopleurite; M.o., Milne Edwards opening; mxp3, third maxilliped; p, pleurite; pt, pleotelson (somite 6 fused to telson); s, sternal shield; s.w., sternal wall; u, uropod; 3–8, sternites 3–8; 3/4–7/8, thoracic sternal sutures 3/4–7/8.

parte; 1980; Lucas & Davie 1982; Wear & Fielder 1985; McLay 1988; Chuang & Ng 1994; Towers & McLay 1995; Ng & Chuang 1996; Davie 2002; Johnston & Robson 2005) inhabit inland freshwaters: rivers and streams with rapid currents, swamps, at an altitude of 1600 m in New Guinea for *A. angelicus* (Holthuis 1968: 112, as *Halicarcinus*), and may be sometimes confined to lakes in New Zealand (Lucas 1980; McLay 1988). They also inhabit low salinity waters in estuarine environments, having wide tolerance to salinities (e.g., *A. abatan*, see Naruse, Mendoza & Ng 2008). The presence of odiomarines in marine waters is questionable (see below). *Amarinus* is known from the Indo-West Pacific region: Philippines, Sulawesi, New Guinea, New Caledonia; mostly from Australia (mainland and islands); and New Zealand (McLay 1988). *Odiomaris* appears to be endemic to New Caledonia (Ng & Richer de Forges 1996, 2007), in rivers with rapid currents (G. Marquet, pers. com).

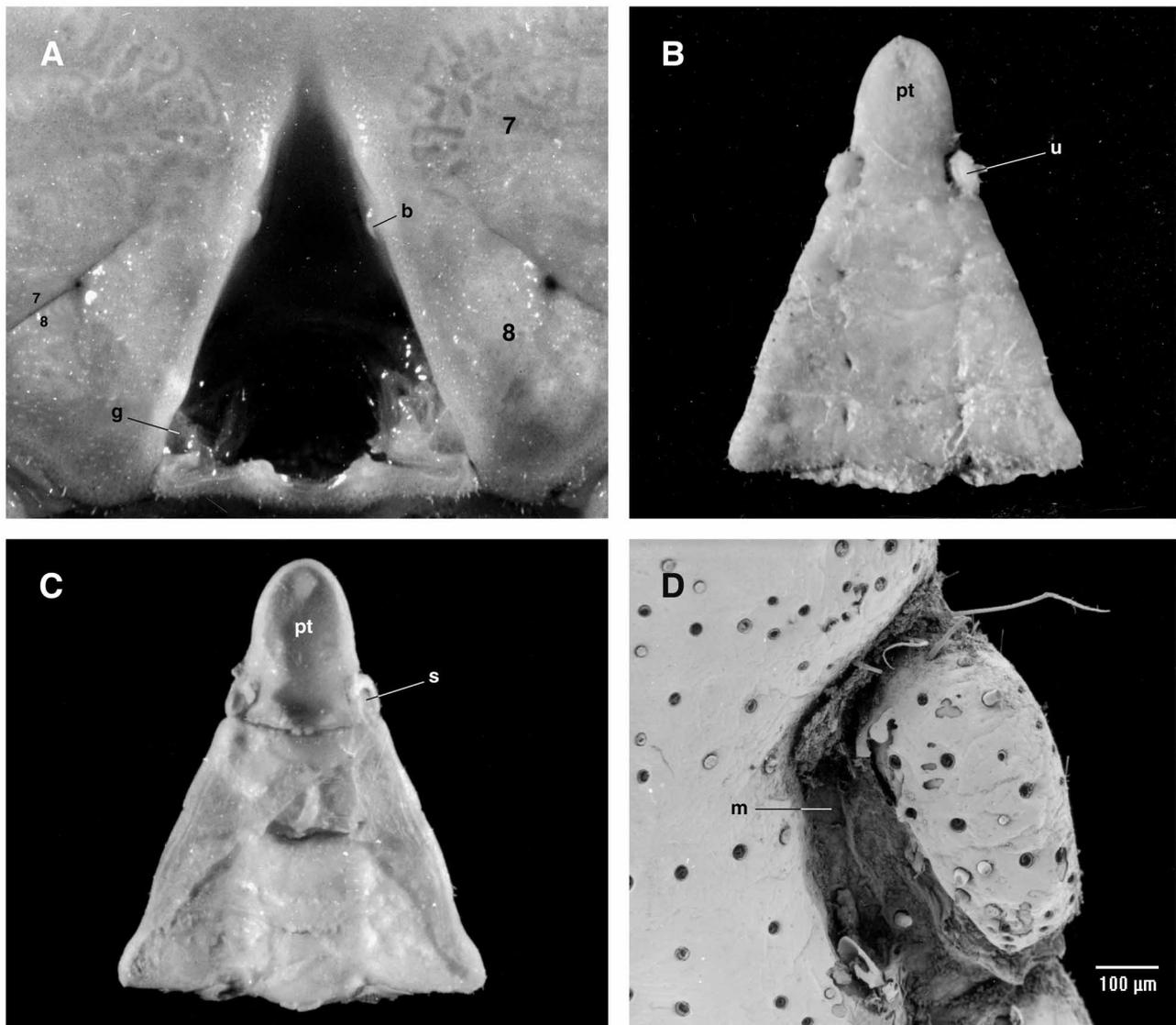


FIGURE 2. *Odiomaris pilosus* (A. Milne-Edwards, 1873), male 20.0 × 22.6 mm, New Caledonia (MNHN). A, thoracic sternum (abdomen removed) with press-button; B, C, male abdomen in dorsal and ventral views: moveable uropod with socket situated at pleotelson's base; D, vestigial uropod (electron micrograph) (all after Guinot & Richer de Forges 1997: figs. 6A–C, E). b, button of press-button system; g, gonopore; m, articulating membrane; pt, pleotelson (somite 6 fused to telson); s, socket; u, uropod; 7, 8, sternites 7, 8; 7/8, thoracic sternal suture 7/8. Scale bar: 100µm (D).

Remarks. The most significant trait of the Odiomarinae **nov. subfam.** is the presence of abdominal platelets on the male abdomen that are homologous to the dorsal vestigial uropods found in the Dromiidae De Haan, 1833, as already suggested by Holthuis (1968: 115) (see *Discussion*). The odiomarine uropods, located on each side of the pleotelson's base since the sixth abdominal somite is fused to the telson (pleotelson) as in all Hymenosomatidae, are moveable or, if they are not articulated, remain variously demarcated (Figs. 1C, 2B–D, 3A–C; A. Milne-

Edwards 1873: pl. 18, fig. 6b; Holthuis 1968: fig. 1d, as *Halicarcinus*; Lucas 1980: fig. 7A–D; Lucas & Davie 1982: fig. 9e; Ng & Chuang 1996: figs. 2D, 3E; Davie & Richer de Forges 1996: fig. 2C; Ng & Richer de Forges 1996: fig. 7B; Guinot & Richer de Forges 1997: figs. 4B–D, 6B–E; Guinot & Bouchard 1998: fig. 27; Rahayu & Ng 2004: fig. 2E; Naruse, Mendoza & Ng 2008: fig. 1e). The broad abdomen of the mature female is devoid of intercalated platelets (Fig. 1D).

The vestigial uropod at the pleotelson's base of the male abdomen is ventrally excavated in a deep socket, externally bordered by a thickened calcified margin and delimited by an articulating membrane (Fig. 2C). This socket is used as the complementary part of a "button" located on the thoracic sternite 5 (Fig. 2A), as usual in the Eubrachyura. Such platelets have so far not been reported in any Eubrachyura. Their persistence, or survival, in the Hymenosomatidae is evidence of the retention of an ancestral structure in a very ancient lineage. Odiomarinae **nov. subfam.** receives *Amarinus* and *Odiomaris*, which can be regarded among the more primitive hymenosomatids. The remaining genera are provisionally included in the Hymenosomatinae MacLeay, 1838, pending complete revision of the family in progress.

The plesiomorphic characters of Odiomarinae **nov. subfam.** include the male and female abdomens without fused somites (except for pleotelson), thus consisting of six elements (namely the maximum of somites existing in Hymenosomatidae); the thoracic sternum with anterior sternites forming a narrow, produced plate; the vulvae not much anteriorly displaced; the axial skeleton regularly compartmented, with parallel arrangement of phragmae in anteroposterior plane; and the G1 only curved in the proximal portion, then straight.

The taxonomy of the Hymenosomatidae, complicated by their small size, flat shape, and the often transparent carapace, has long been unstable. Despite recent investigations, some genera could be paraphyletic, and the placement of many species will need to be re-examined (e.g., see Ng & Chuang 1996). Provisionally, preferring a strict diagnosis of the Odiomarinae **nov. subfam.**, the subfamily cannot accommodate for the moment all the species that show faintly delimited uropods. *Amarinus*, as listed by Ng *et al.* (2008: 108), already contains various patterns for the carapace lateral margin (unarmed, regular, only undulate, or toothed), rostrum (continuous or not with the dorsal surface of the carapace), male abdomen (triangular or suboval), and G1 (stout or slender, tip simple or with lobes and processes).

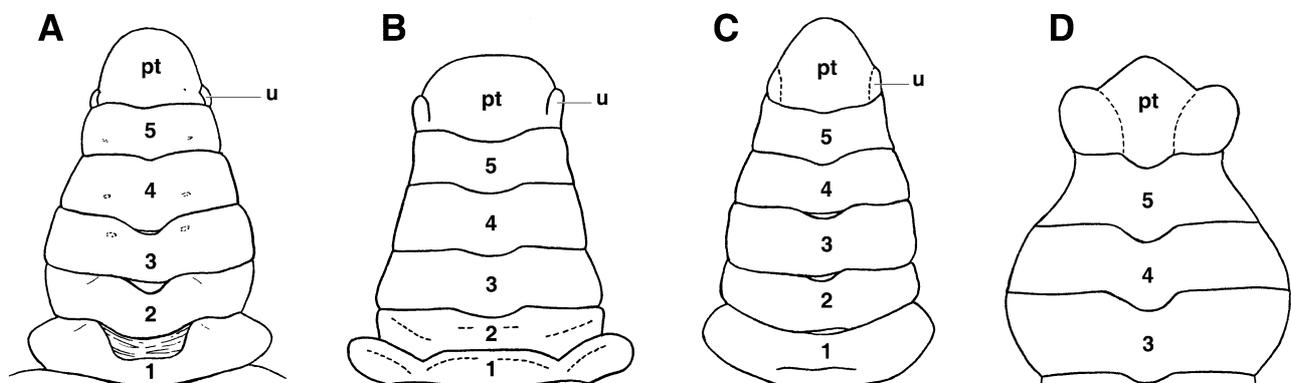


FIGURE 3. A–C. Male abdomen in the Odiomarinae **subfam. nov.**: five somites (1–5) + pleotelson, with intercalated platelets (uropods), entirely demarcated (A, B) or only demarcated by suture (dotted line) (C). A, *Amarinus angelicus* (Holthuis, 1968) (after Holthuis 1968: fig. 1d); B, *A. lutarius* Lucas & Davie, 1982 (after Lucas & Davie 1982: fig. 9e); C, *A. lacustris* (Chilton, 1882) (after Lucas 1980: fig. 7B); 3D. Male abdomen of *Hymenicoides carteri* Kemp, 1917 (after Kemp 1917: fig. 21): five somites (1–5) + trilobate pleotelson: inflated areas corresponding to uropods integrated to pleotelson. pt, pleotelson (somite 6 fused to telson); 1–5, abdominal somites 1–5; u, uropod.

Amarinus wolterecki has a male abdomen with six articles, a unilobed rostrum, and a spindle-shaped G1, but shows ten teeth on the lateral margins of the carapace, a rostrum that is continuous with the dorsal surface of carapace, and a G1 with well-defined, twisted folds and a simple tip (Holthuis 1968: 117; Ng & Chuang 1996: 12, fig. 3). *Amarinus pristis*, from western Papua, Indonesia (Rahayu & Ng 2004: 91, fig. 2; see also Naruse, Mendoza & Ng 2008: 431), with a carapace having a serrated lateral margin, a triangular rostrum, and with a truncate G1, is closer to *A. wolterecki* than to the other species of *Amarinus*. *Amarinus laevis*, the *Halicarcinus australis* (Haswell, 1882) of many authors, shows delimited uropods and a particular combination of characters: toothed lateral margins of the carapace, almost trifold rostrum, prominent antennal spines, truncate apex of the G1, chelae of large

males with a sac between bases of fingers, i.e., a pulvinus (Lucas 1980: 199, figs. 4C, 7A, 10D; Poore 2004: 393, figs. 119c, 121b, e, pl. 21f).

Some genera and species in which the uropods are not still recognizable could prove to also belong to the basal Hymenosomatidae possibly close to the Odiomarinae **nov. subfam.** One such case is *Hymenicoides* Kemp, 1917. The trilobate pleotelson of the type species *H. carteri* Kemp, 1917 (Kemp, 1917: fig. 21; Guinot & Richer de Forges 1997: fig. 4E; Naruse & Ng 2007a: 18) and of *H. robertsi* Naruse & Ng, 2007, may be interpreted as having the uropods integrated into the pleotelson (Fig. 3D; Guinot & Bouchard 1998: 685), with the inflated areas at the pleotelson's base corresponding to the deep sockets functioning with the sternal buttons, as clearly shown by Naruse & Ng (2007a: fig. 1a, b). *Hymenicoides* shows several plesiomorphic features similar to those of *Amarinus* and *Odiomaris*, in particular the five-articulated abdomen plus the pleotelson in both sexes, and a weakly grooved carapace (Naruse & Ng 2007a: figs. 2a, b, 4a, b 5c, d). Both *H. carteri* and *H. robertsi* have, however, narrow, pediform mxp3, thus separated by a wide gap (Kemp 1917: fig. 16; Guinot & Richer de Forges 1997: fig. 3A; Naruse & Ng 2007a: fig. 4b), which is indicative of a primitive condition (a limb-like appendage is assumed to be the ancestral character state as shown by the most primitive homolodromioids and homoloids; see Guinot 1995; Guinot & Richer de Forges 1995), differing from the stout, operculiform mxp3 of *Amarinus* and *Odiomaris* (Fig. 1B, C; Holthuis 1968: figs. 2a, b, 3a, as *Halicarcinus*; Lucas & Davie 1982: figs. 8b, 9c; Ng & Richer de Forges 1996: fig. 6C, D, G; Davie & Richer de Forges 1996: fig. 1B; Guinot & Richer de Forges 1997: figs. 1D, 2D; Rahayu & Ng 2004: fig. 2B). In contrast to *Odiomaris* (with triangular abdomens) and *Amarinus* (abdomen with roughly parallel margins, weakly narrowing distally), in *Hymenicoides* the male abdomen is wider, with irregular margins, the female abdomen less oval, the rostrum absent or weak, and the stout G1 strongly bent in its distal half (Kemp 1917: fig. 21; Naruse & Ng 2007a: figs. 2a, b, 4a, 5a–d). The location of the vulvae about at the level of the inner ends of sutures 5/6 (Naruse & Ng 2007a: 22), instead of being more anteriorly projected as in many Hymenosomatidae, is also a plesiomorphic character of *Hymenicoides* (see below). *Limnopilos* Chuang & Ng, 1991 (Chuang & Ng 1991: 364, fig. 1), a genus closely allied with *Hymenicoides*, should be examined concurrently with *Hymenicoides*. *Hymenicoides* and *Limnopilos* share several plesiomorphic characters, such as the pediform mxp3, the six-articulated abdomen in both sexes, the inflated areas at the pleotelson's base of the male abdomen (Naruse & Ng 2007a: 26). The pediform shape of the mxp3 of *Hymenicoides* and *Limnopilos* indicates a basal position in comparison to *Odiomaris* and *Amarinus*, the evolutionary rate being not the same for all the morphological characters.

There are also plesiomorphic characters in *Cancrocaeca* Ng, 1991, in which the male and female abdomens have, as in the odiomarine, five freely articulating somites plus the pleotelson, the G1 is straight in its two distal thirds and has several distal processes and subterminal tufts of setae (Ng 1991: figs. 6, 7; Ng & Chuang 1996: fig. 5f; Guinot & Richer de Forges 1997: fig. 9A; Naruse & Ng 2007a: 19; Naruse, Ng & Guinot 2008: fig. 1d, e). The uropods, however, are not visible externally. Ng (1991: 61) had pointed out that the closest genus to *Cancrocaeca* was *Amarinus*, although *Cancrocaeca xenomorpha* is a highly modified taxon because of its troglolitic habits (pale coloration, blindness, long walking legs).

A provisional hypothesis is that *Hymenicoides* and *Limnopilos* form, with *Cancrocaeca*, a sublineage very close to the Odiomarinae **nov. subfam.**, the precise relationships remaining to be clarified. It should be noted that the vulva has an operculum in the known species of the three genera (Ng 1991: fig. 4E; T. Naruse pers. comm.). In these three genera, the carapace is rounded and weakly grooved, the rostrum absent or very weak, the mxp3 narrow, and the male abdomen wide and subcircular. Inclusion of *Hymenicoides*, *Limnopilos* and *Cancrocaeca* in the Odiomarinae **nov. subfam.** should be only made in relation to the level of generality of the characters chosen to differentiate the other hymenosomatids in the future classification.

A few taxa assigned to different genera in the literature, such as some species of *Elamenopsis* A. Milne-Edwards, 1873 (see Naruse & Ng 2007b) and *Elamena* H. Milne Edwards, 1837, are in need of a reappraisal. The status of *E. truncata* (Stimpson, 1858) is puzzling because, in addition to cryptic uropods, it has a G1 and mxp3 that are not substantially different from those of the Odiomarinae **nov. subfam.** (see Ng & Chuang 1991: fig. 30C, I, J).

Elamenopsis guinotae Poore, 2010, shows some of the typically odiomarine characters, in particular the prominent uropods, six-articulated male abdomen, and spindle-shaped G1 (Poore 2010: fig. 2c, d, b, table 1). Its marine habitat (in eastern Bass Strait at 14–15 m depth, Victoria, Australia), however, contrasts to the fresh or brackish environment of the abovementioned odiomarine. In any case, all its features are typical of *Elamenopsis* species as noted by Ng & Chuang (1996) and Naruse & Ng (2007b), some of them being very close to the odiomarine.

The status of *Hymenosoma hodgkini* Lucas, 1980, from marine and brackish waters of Australia, and with demarcated uropods, deserves some preliminary remarks. The abdomen is “sculptured making segmentation difficult to distinguish”, thus the number of somites is uncertain, 4 and 5 may be fused according to Lucas (1980). It will be necessary to establish if the following characters allow its assignment to the odiomarine: G1 with a dense zone of denticles on abdominal side; pterygostomal lobe developed, clearly visible; third female abdominal somite with posterolateral bulges (Lucas 1980: 169, 170, figs. 2E, 6H, 7I, 10B, C; Davie 2002: 246; Poore 2004: 395, figs. 120e, 121c, f). No specimens were unfortunately available for study.

Halicarcinus whitei (Miers, 1876), endemic from New Zealand, was described by Melrose (1975: 74, fig. 33D) as having on the male abdomen a remnant of the suture separating the sixth somite from the telson, a character not confirmed by McLay (1988: 380). This stage, preceding the complete fusion of the last two abdominal elements and leading to the formation of the pleotelson, could well be the most plesiomorphic case of the male abdomen occurring in the Hymenosomatidae.

Halicarcinus bedfordi Montgomery, 1931, has a triangular abdomen as in *Odiomaris pilosus* and *O. estuarius*, but without visible uropods; its pointed, projecting rostrum and several others distinguishing characters (Montgomery 1931: 425, pl. 27, fig. 3; Lucas 1980: 181, figs. 3A, 5E, 6N, 7G, 9E, F; Davie 2002: 245; Poore 2004: 394, fig. 120b; Rahayu & Ng 2004: 88) do not permit a clear assignment.

The Hymenosomatinae emend., which provisionally receives all the hymenosomatids other than the odiomarine genera, includes taxa with diverse shapes of carapace (varying from rounded to trapezoidal or triangular; rostrum varying from weak to much projected), male abdomen (composed of a variable number of fused somites) (Guinot & Richer de Forges 1997: figs. 4, 5A–I), various types of female abdomens (Guinot & Richer de Forges 1997: fig. 7), and a G1 usually with a strong curvature. As such, the Hymenosomatinae emend. appears to be paraphyletic. The reclassification of the group is currently under study.

Discussion

The loss of the biramous uropods, thus of a tail fan (Wilson 1996), is the strongest synapomorphy of the Eubrachyura. It is accepted by all carcinologists that the dorsal plates characteristic of the basal Podotremata Guinot, 1977, i.e., the Dynomenidae Ortmann, 1892, and the great majority of Dromiidae, represent “vestigial uropods”. The intercalated platelets that are present in the primitive taxa of the Hymenosomatidae, the unique known case in the Eubrachyura, are homologous to the podotreme uropods. The sternal condition of the vulvae in all the Hymenosomatidae, including *Odiomaris* and *Amarinus*, obviously indicates that the family belongs in the Eubrachyura. The uropods may be moveable in both the Dromiidae and Odiomarinae **nov. subfam.** (see below). There is, however, an important difference between the odiomarine uropod and the dromiid ones. The dromiid uropod acts with a coxal structure situated on an appendage, and thus *aside* (Guinot & Bouchard 1998). In contrast, the odiomarine uropod is ventrally excavated into a deep socket, situated *below* the dorsal platelet and thus corresponds to the typical eubrachyuran press-button system for abdominal locking.

The odiomarine socket is particularly interesting because it provides morphological criteria for identifying uropods and sockets as homologues (Hennig 1966; Wiley 1981; Wägele 1996). The similarity of position (topographic and position in relation to other parts) is obvious. In dorsal view, the moveable hymenosomatid platelet closely reminds a dromiid or dynomenid uropod, except that its internal surface is excavated into a socket. In researching the criterion of special similarity between uropods and sockets, one needs to investigate similarities of structure as well as ontogenetic resemblance through histology.

The criterion of phylogenetic position may reinforce homologues in reviewing the uropod pattern in all Brachyura (Guinot & Bouchard 1998: table 3). Appendages of the sixth abdominal somite showing as rudimentary ventral, sometimes slightly bifid lobes in the Homolodromiidae Alcock, 1900 (Guinot 1995: figs. 5, 25) might probably be considered a transitional stage between the biramous decapod uropods and their reduced, impaired brachyuran homologues. In the Dromiidae, which are more carcinised, the appendages of the sixth abdominal somite, the traditionally so-called “vestigial uropods”, are present in many genera as freely articulated, moveable dorsal plates. They are often used to hold the abdomen, with the abdominal or uropodal border being often ventrally or laterally modified (Guinot & Bouchard 1998: fig. 2B; Guinot & Tavares 2003: table 1). Ventral lobes that are present in some primitive Dromiidae do not play a role in the abdominal-locking mechanism. Only a few

dromiids are devoid of dorsal plates or ventral lobes (Poore 2004). The large dorsal plates of the Dynomenidae are never modified to act as a press-button mechanism, even when a sternal structure is present (apomorphy) in the more derived representatives, i.e., the Dynomeninae Ortmann, 1892 (Guinot 2008). Neither abdomen nor uropods are modified in the Dynomenidae, and the abdomen is only loosely applied on the sternum, only restricting its sideways movements (McLay 1999). The podotreme uropod lacks a ventral socket (that could be used when applied on a surface) and only acts as a full-lock system, while the ventrally excavated odiomarine platelet bears a socket and operates as a typical press-button (Fig. 2). The intercalated platelets of the Hymenosomatidae correspond to the abdominal sockets of other eubrachyuran crabs and, as such, constitute the abdominal complementary parts for the locking of the abdomen, being used for this purpose.

In the larger brachyuran evolutionary scheme, when uropods as dorsal plates or ventral lobes are lost, sockets are uniformly developed in the same location on abdominal somite 6. The trends towards loss of abdominal appendages are components of the carcinisation process in the Decapoda Latreille, 1802, and the novelty represented by the socket may be regarded as the character state presence of uropod. Brachyura that possess lobe-shaped ventral uropods (Homolodromiidae, Hypoconchinae Guinot & Tavares, 2003, a few Dromiinae De Haan, 1833) or plate-shaped dorsal uropods (Sphaerodromiinae Guinot & Tavares, 2003, most Dromiinae, Dynomenidae) are recognized to be more basal than those having sockets at the same location, i.e., the Homoloidea De Haan, 1839 (Guinot & Richer de Forges 1995), Lyredinae Guinot, 1993 (Guinot 1993), and the Eubrachyura. Thus, the criterion of position is strengthened by a strict and constant location of ventral lobes, dorsal plates, intercalated platelets, and sockets on abdominal somite 6 in all the Brachyura.

Some eubrachyuran taxa show sockets that appear atypically positioned, i.e., on the last abdominal element (pleotelson), similarly to those of the Hymenosomatidae. There are cases in the Majoidea such as the Inachoididae Dana, 1851 (Guinot & Richer de Forges 1997: figs. 11C, 12C, D, 13B, 14B; Guinot & Bouchard 1998: fig. 20A–F) and the Inachidae MacLeay, 1838 (Guinot & Richer de Forges 1997: fig. 15A, B), in which they are located at the pleotelson's base in being a part of the same abdominal sixth somite. This can be easily explained because all these taxa show a similar fusion of abdominal somite 6 with the telson. The criterion of continuance through intermediate forms may be provided by the presence of moveable dorsal uropods in the Dromiidae, moveable intercalated platelets in the Odiomarinae **nov. subfam.**, and fully incorporated uropods in other heterotreme taxa.

The homology between uropod and socket is supported by the following arguments:

(1) All the Podotremata that have vestigial uropods (dorsal plates or ventral lobes) are devoid of abdominal sockets (Homolodromiidae, Dromiidae, and Dynomenidae).

(2) All the Homoloidea, which have no trace of appendage-like or dorsal or lobiform uropods, possess sockets ("homolid press-button", with the button on sternite 4), as well in the primitive family Poupiniidae Guinot, 1991, as in the Homolidae De Haan, 1839, and Latreilliidae Stimpson, 1858.

(3) All brachyuran crabs that lack uropods possess sockets. Examples of brachyuran crabs devoid of both uropods and sockets are very few (Guinot & Bouchard 1998: 677). The Raninoidea De Haan, 1839, can be considered as having lost the locking mechanism structures that are only retained in its most primitive representatives, the Lyreidinae Guinot, 1993. The Cyclodorippoidea Ortmann, 1892, is practically the only brachyuran group in which there is no known trace of uropods or sockets, the abdominal-locking mechanism being quite different (Guinot & Bouchard 1998).

Accordingly, it may be assumed that the appendages of the sixth abdominal somite are practically present in all the Decapoda, but with different patterns: as a biramous appendage, foliaceous ramus, rasp, ventral lobe, dorsal plate, intercalated platelet, or socket. According to Dixon *et al.* (2003: 954) the Brachyura have "telsons and uropods that are 'de-specialized', meaning that they are reduced (or absent) and apparently serve no major function". It seems, on the contrary, that the Brachyura cannot be defined by the absence of uropods, and the term "vestigial uropod" is an oversimplification. The eubrachyuran socket actually corresponds to a "vestigial uropod", as well as the dromiid uropod. The brachyuran uropod actually presents a wealth of character states: the dromiid dorsal uropod (without a socket) and the odiomarine ones with a functional socket, as well as the eubrachyuran socket that is the complementary part of the typical press-button.

The transformation of the uropod-socket, which seemingly has required a substantial modification, is exemplified by the configuration of the Odiomarinae **nov. subfam.**, where the uropod varies from completely articulated (Figs. 1C, 2B, D, 3A) to variously incorporated to the sixth somite (Fig. 3B, C). There is a trend for the fusion of the intercalated platelets (uropods) with the pleotelson in the Hymenosomatidae, the external sutures becoming

faintly marked, and finally the platelets become entirely incorporated in the sixth somite at the pleotelson's base, remaining still recognizable by an inflated area or, in some genera, without a visible external indication. The transformation series of the moveable intercalated platelets into fused plates, followed by their complete integration to the abdomen in a pleotelson, illustrates the stages towards the apomorphic condition found in male Hymenosomatinae. When the delimited platelets have disappeared, the sockets remain excavated on the ventral surface of the sixth somite, as a variously deep depression, delimited by a calcified margin. This conforms to the condition found in all Eubrachyura. In the odiomarine postpubertal females, as in most eubrachyuran mature females, the widened abdomen does not bear sockets anymore and it is not held against the thorax. The socket presents variable forms in the Eubrachyura, from rounded to elongated (Guinot & Bouchard 1997: fig. 26B, D; Bouchard 2000: 217). The morphology of the socket remains actually poorly known.

The Hymenosomatidae thus shows several characteristic patterns: moveable platelets, which is the plesiomorphic condition (Odiomarinae **nov. subfam. pro parte**); simple and no longer articulated platelets, with variously distinct sutures (Odiomarinae **nov. subfam. pro parte**); structures dorsally recognisable at pleotelson' base (*Hymenicoides*, *Limnopilos*); and prominences variously marked; external indications lost (other hymenosomatids). All of these structures play the same role in covering the acute buttons of the press-button mechanism and firmly locking the abdomen.

Status of the family Hymenosomatidae

The taxonomy of the Hymenosomatidae, a group generally consisting of small, peculiar, cryptic crabs, often called "false spider crabs" or "crown crabs" (alluding to the flat body), has undergone several major changes. A suprafamilial level among the Heterotremata, Hymenosomatoidea is sometimes used (Martin & Davis 2001; Poore 2004; Števcíć 2005). The family has been considered either a heterotreme, as a family of the Majoidea or in the proximity of the Majidae Samouelle, 1819 (Richer de Forges 1976, 1977; Guinot & Richer de Forges 1997; Ng *et al.* 2008: 108; De Grave *et al.* 2009: 35; Schweitzer *et al.* 2010: 93), or a thoracotreme, often close to the Pinnotheridae De Haan, 1833 (H. Milne Edwards 1837; Haswell 1882; Miers 1886; Alcock 1900; Garth 1958; Guinot 1978; McLay 1988), even with the genera included in this family (Hodgson 1902; Hutton 1904; Baker 1906). Its position is most often not mentioned at all (Ng & Chuang 1996; Van den Brink 2006; Naruse & Ng 2007a; Naruse, Mendoza & Ng 2008; Naruse, Ng & Guinot 2008; Van den Brink & McLay 2009; McLay & Van den Brink 2009; Naruse & Komai 2009; Teske *et al.* 2009). The dilemma, briefly discussed by Guinot (1979: 215), results from the apparently sternal location of the male gonopores (Lucas 1980: 151; Davie 2002: 341; Poore 2004: 390) and, at the same time, from the evident relationships with crabs as the Inachidae and Inachoididae, thus suggesting a heterotreme, and not thoracotreme, affiliation. The disposition of the male gonopore actually seems to be coxo-sternal, waiting a satisfactory internal dissection that would correctly show the trajectory of the vas deferens, either via the P5 coxa (as in the Heterotremata) or through the sternum (as in the Thoracotremata Guinot, 1977).

The molecular analysis by Ahyong *et al.* (2007: 583, figs. 2, 4) established the heterotreme status of the Hymenosomatidae, with indecisive results "regarding a hymenosomatid-majid alliance", the majoids and hymenosomatids always occupying a low position in the Eubrachyura. *Amarinus lacustris* was recovered as the sister taxon of the dorippid *Dorippoides facchino* (Herbst, 1785), indicating a dorippid + hymenosomatid clade within the Heterotremata. On the basis of another molecular analysis, Teske *et al.* (2009: 31) preliminarily concluded that the Hymenosomatidae was "not part of the Majoidea".

All members of the Hymenosomatidae are remarkable by the absence of a true megalopa in the marine and brackish species (which have three free larval stages) as well as in the freshwater representatives (with direct development) (see Rice 1980; Wear & Fielder 1985). This characteristic, plus a unique combination of zoeal characters, places it apart from all other Brachyura (Richer de Forges 1977; Melrose 1975; Lucas 1971, 1972, 1975, 1980; Rice 1980, 1981; Wear & Fielder 1985). The zoea of most hymenosomatids bears a single lateral seta on the antenna, supposed to be a vestigial exopod (Dornelas *et al.* 2003: 2593, table 1).

The spermatozoal ultrastructure of the Hymenosomatidae, studied in two species of *Odiomaris* (Richer de Forges *et al.* 1997) and in *Elamena vesca* Ng & Richer de Forges, 1996 (B.G.M. Jamieson, unpublished data), is also unique among the Brachyura. The sperm differs significantly in at least by ten major characters from all the other taxa that were investigated, particularly those families with which they have been associated, the Majidae

sensu lato and the Pinnotheridae. So unusual is the hymenosomatid sperm that, from a purely spermatological point of view, “it is difficult to accommodate the hymenosomatids in any of the three brachyuran divisions, Podotremata, Heterotremata, and Thoracotremata” (Richer de Forges *et al.* 1997: 233, 241). This opens the way to another, new interpretation.

The lack of any known fossil record (Lucas 1970: 275; 1980: 225; De Grave *et al.* 2009: 35; Schweitzer *et al.* 2010: 93) due to the small, fragile condition of hymenosomatids, is not evidence of a relatively recent origin. Contrary to Walker (1969) and Lucas (1970), who suggested a recent origin, Chilton (1915) hypothesised that *Amarinus lacustris* was an ancient species that arose prior to the breakup of Gondwana, thus possibly Cretaceous, a hypothesis that could illuminate the ancestry of the odiomarine.

The persistence of vestigial uropods as dorsal plates in the Odiomarinae **subfam. nov.** (Figs. 2, 3), the only known case in the Eubrachyura is, in addition to the other plesiomorphic characters, evidence of an ancient lineage. An early origin of the subfamily Odiomarinae **subfam. nov.** is assumed here. The hymenosomatid clade is itself deeply rooted in the brachyuran evolutionary process, and should be basal in the Eubrachyura. Studies in progress on the family Hymenosomatidae and, more extensively, on the brachyuran plesion, are revealing new, unexpected insights on the phylogenetic relationships of the family, with its probable inclusion in a peculiar grouping that takes into consideration the perplexing morphological, larval, and spermatozoal information (Guinot, Tavares & Castro work in progress; Guinot, Naruse & Ng work in progress). The closest families reveal to be the Dorippidae MacLeay, 1838, the Inachoididae, and the Inachidae. The available though unpublished datasets support the molecular tree of Ah Yong *et al.* (2007) that suggests a majoid–hymenosomatid–dorippoid clade.

Acknowledgements

I am grateful to J.-F. Dejouannet (IRD, MNHN, Département Systématique et Évolution, Paris) for the preparation of the illustration. Thanks to P.K.L. Ng (Tropical Marine Science Institute, National University of Singapore), who made available the rich hymenosomatid collection in his Institution, and for critical comments, T. Naruse (University of the Ryukyus, Okinawa) for valuable discussions, and to P. Castro (California State Polytechnic University, Pomona, U.S.A.) for precious comments on the manuscript.

References

- Ahyong, S.T., Lai, J.C.Y., Sharkey, D., Colgan, D.J. & Ng, P.K.L. (2007) Phylogenetics of the brachyuran crabs (Crustacea: Decapoda): the status of Podotremata based on small subunit nuclear ribosomal RNA. *Molecular Phylogenetics and Evolution*, 45(2), 576–586.
- Alcock, A. (1900) The Brachyura Catometopa, or Grapsoida. Materials for a carcinological fauna of India. No. 6. *Journal of the Asiatic Society of Bengal*, 69(2, 3), 279–456.
- Baker, W.H. (1906) Notes on South Australian Decapod Crustacea. Part 1. *Transactions of the Royal Society of South Australia*, 28, 146–161.
- Bouchard, J.-M. (2000) *Morphologie fonctionnelle des systèmes de rétention de l'abdomen chez les Brachyours (Crustacea Decapoda). Microstructures; implications phylogénétiques et systématiques*. Unpublished PhD thesis, Muséum national d'Histoire naturelle, Paris, 694 pp.
- Chen, H. & Sun, H. (2002) Brachyura. Marine primitive crabs. In: *Fauna Sinica, Invertebrata*, vol. 30. *Arthropoda, Crustacea*. Editorial Committee of Fauna Sinica, Academia Sinica, Science Press, Beijing, China, xiii + 597 pp. [In Chinese with English abstract]
- Chilton, C. (1915) A freshwater crab and its distribution in Australia and New Zealand. *Transactions of the New Zealand Institute*, 47, 316–320.
- Chuang, C.T.N. & Ng, P.K.L. (1991) Preliminary descriptions of one new genus and three new species of hymenosomatid crabs from Southeast Asia (Crustacea: Decapoda: Brachyura). *Raffles Bulletin of Zoology*, 39(2), 363–368.
- Chuang, C.T.N. & Ng, P.K.L. (1994) The ecology and biology of Southeast Asian false spider crabs (Crustacea: Decapoda: Brachyura: Hymenosomatidae). *Hydrobiologia*, 285, 85–92.
- Davie, P.J.F. (2002) Crustacea: Malacostraca: Eucarida (Part 2): Decapoda-Anomura, Brachyura. In: Wells, A. & Houston, W.W.K. (Eds.) *Zoological Catalogue of Australia*, vol. 19.3B. CSIRO Publishing Australia, Melbourne, xiv + 641 pp.
- Davie, P.J.F. & Richer de Forges, B. (1996) Two new species of false spider crabs (Crustacea: Brachyura: Hymenosomatidae) from New Caledonia. *Memoirs of the Queensland Museum*, 39(2), 257–262.
- De Grave, S., Pontcheff, N.D., Ahyong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M.,

- Fransen, C.H.J.M., Goulding, L.Y.D., Lemaitre, R., Low, M.E.Y., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., Tshudy, D. & Wetzer, R. (2009) A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology*, Supplement 21, 1–109.
- Dixon, C.J., Ah Yong, S.T. & Schram, F.R. (2003) A new hypothesis of decapod phylogeny. *Crustaceana*, 76(8), 935–975.
- Dornelas, M., Paula, J. & Macia, A. (2003) The larval development of *Hymenosoma orbiculare* Desmarest, 1825 (Crustacea: Decapoda: Brachyura). *Journal of Natural History*, 37(21), 2579–2597.
- Garth, J.S. (1958) Brachyura of the Pacific coast of America, Oxyrhyncha. *Allan Hancock Pacific Expeditions*, 21(1), xxii + 499; (2), 501–854.
- Guinot, D. (1978) Principes d'une classification évolutive des Crustacés Décapodes. Brachyours. *Bulletin Biologique de la France et de la Belgique*, 112(3), 211–292.
- Guinot, D. (1979) Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. *Mémoires du Muséum national d'Histoire naturelle*, sér. A, Zoologie, 112, 1–354.
- Guinot, D. (1993) Données nouvelles sur les Raninoidea de Haan, 1841 (Crustacea Decapoda Brachyura Podotremata). *Comptes rendus de l'Académie des Sciences*, sér. 3, 316(11), 1324–1331.
- Guinot, D. (1995) Crustacea Decapoda Brachyura: Révision des Homolodromiidae Alcock, 1900. In Crosnier, A. (Ed.), Résultats des Campagnes MUSORSTOM, vol. 13. *Mémoires du Muséum national d'Histoire naturelle*, 16, 155–282.
- Guinot, D. (2008) A re-evaluation of the Dynomenidae (Decapoda, Brachyura, Podotremata), with the recognition of four sub-families. *Zootaxa*, 1850, 1–26.
- Guinot, D. & Bouchard, J.-M. (1998) Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema*, 20(4), 613–694.
- Guinot, D. & Richer de Forges, B. (1995) Crustacea Decapoda Brachyura : Révision de la famille des Homolidae de Haan, 1841. In: Crosnier, A. (Ed.), Résultats des Campagnes MUSORSTOM, vol. 13. *Mémoires du Muséum national d'Histoire naturelle*, 13, 283–517.
- Guinot, D. & Richer de Forges, B. (1997) Affinités entre les Hymenosomatidae MacLeay, 1838 et les Inachoididae Dana, 1851 (Crustacea Decapoda Brachyura). *Zoosystema*, 19(2–3), 453–502.
- Guinot, D. & Tavares, M. (2003) A new subfamilial arrangement for the Dromiidae de Haan, 1833, with diagnoses and description of new genera and species. *Zoosystema*, 25(1), 43–129.
- Haswell W.A. (1882) *Catalogue of the Australian stalk- and sessile-eyed Crustacea*. Sydney, The Australian Museum, xxiv + 324 pp.
- Hennig, W. (1966) *Phylogenetics Systematics*. University of Illinois Press, Urbana, 263 pp.
- Hodgson, T.V. (1902) Crustacea. In: Lankester, E.R., *Report on the Collections of Natural History made in the Antarctic Regions during the Voyage of the "Southern Cross"*. XI. British Museum, London, pp. 228–261.
- Holthuis, L.B. (1968) On Hymenosomatidae (Crustacea Decapoda Brachyura) from fresh water, with the description of a new species. *Beaufortia*, 15(195), 109–121.
- Hutton, F.W. (1904) *Index Faunae Novae Zelandiae*. Dulau, London, 372 pp.
- Johnston, K. & Robson, B.J. (2005) Habitat use by the hymenosomatid crab *Amarinus lacustris* (Chilton) in two south-eastern Australian rivers. *Marine Freshwater Research*, 56(1), 37–744.
- Juncker, M. & Poupin, J. (2009) Crustacés de Nouvelle-Calédonie (Décapodes & Stomatopodes). Illustration des espèces communes et liste documentée des espèces terrestres et des récifs. *Rapport Scientifique du CRISP (Coral Reef Initiative for the South Pacific)*, 1–20.
- Kemp, S. (1917) Notes on Crustacea Decapoda in the Indian Museum. X. Hymenosomatidae. *Records of the Indian Museum*, 13(5), 243–279.
- Lucas, J.S. (1970) Breeding experiments to distinguish two sibling species of *Halicarcinus* (Crustacea: Brachyura). *Journal of Zoology* (London), 160, 267–278.
- Lucas, J.S. (1971) The larval stages of some Australian species of *Halicarcinus* (Crustacea, Brachyura, Hymenosomatidae). I. Morphology. *Bulletin of Marine Science*, 21(2), 471–490.
- Lucas, J.S. (1972) The larval stages of some Australian species of *Halicarcinus* (Crustacea, Brachyura, Hymenosomatidae). II. Physiology. *Bulletin of Marine Science*, 22(4), 824–840.
- Lucas, J.S. (1975) The larval stages of some Australian species of *Halicarcinus* (Crustacea, Brachyura, Hymenosomatidae). III. Dispersal. *Bulletin of Marine Science*, 25(1), 94–100.
- Lucas, J.S. (1980) Spider crabs of the family Hymenosomatidae (Crustacea: Brachyura) with particular reference to Australian species: Systematics and Biology. *Records of the Australian Museum*, 33(4), 148–247.
- Lucas, J.S. & Davie, P.J.F. (1982) Hymenosomatid crabs of Queensland estuaries and tidal mud flats, including descriptions of four new species of *Elamenopsis* A. Milne-Edwards and a new species of *Amarinus* Lucas. *Memoirs of the Queensland Museum*, 20(3), 401–419.
- Marquet, G., Keith P. & Vigneux, E. (2003) Atlas des poissons et des crustacés d'eau douce de Nouvelle-Calédonie. *Patri-moines naturels*, 58, 1–282.
- Martin, J.W. & Davis, G.E. (2001) *An updated classification of the Recent Crustacea*. Natural History Museum of Los Angeles County, Science series 39, 124 pp.
- McLay, C.L. (1988) Brachyura and crab-like Anomura of New Zealand. *Leigh Laboratory Bulletin*, 22, i-v, 1–463.
- McLay, C.L. (1999) Crustacea Decapoda: Revision of the Family Dynomenidae. In: Crosnier, A. (Ed.), Résultats des Cam-

- pagnes MUSORSTOM, Volume 20. *Mémoires du Muséum national d'Histoire naturelle*, 180, 427–569.
- McLay, C.L. & Van den Brink, A.M. (2009) Relative growth and size at sexual maturity in *Halicarcinus cookii* (Brachyura: Hymenosomatidae): why are some crabs precocious moulters? *Journal of the Marine Biological Association of the United Kingdom*, 89(4), 743–752.
- Melrose, M.J. (1975) The marine fauna of New Zealand: Family Hymenosomatidae (Crustacea, Decapoda, Brachyura). *Memoirs of the New Zealand Oceanographic Institute*, 34, 1–123.
- Miers, E.J. (1886) Report on the Brachyura collected by H.M.S. Challenger during the years 1873–76. In: *Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873-76 Under the Command of Captain George S. Nacres, R.N., F.R.S. and the Late Captain Frank Touse Thompson, R.N.*, Zoology, vol. 17 (49). HMSO, London, Edinburgh and Dublin, L + 362 pp., pls. 1–29.
- Milne-Edwards, A. (1873) Recherches sur la faune carcinologique de la Nouvelle-Calédonie. *Nouvelles Archives du Muséum d'Histoire Naturelle*, (Paris), 9, 155–332.
- Milne Edwards, H. (1837) *Histoire Naturelle des Crustacés Comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux*. Libraries Encyclopédique de Roret, Paris. vol. 2, 531 pp.
- Montgomery, S.K. (1921) Some Hymenosomatidae from the Swan River. *Journal and Proceedings of the Royal Society of Western Australia*, 6(2), 93–96.
- Montgomery, S.K. (1931) Report on the Crustacea Brachyura of the Percy Sladen Trust Expedition to the Abrolhos Islands under the leadership of Professor W.J. Dakin, in 1913; along with other crabs from Western Australia. *Journal of the Linnean Society, Zoology*, 37, 405–465.
- Naruse, T. & Komai, T. (2009) A new species of the false spider crab genus *Halicarcinus* (Decapoda: Brachyura: Hymenosomatidae) from Okinawa Island, Japan. *Bulletin of the National Museum of Nature and Science, Series A (Zoology)*, Supplement 3, 175–181.
- Naruse, T., Mendoza, J.C.E. & Ng, P.K.L. (2008) Descriptions of five new species of false spider crabs (Decapoda: Brachyura: Hymenosomatidae) from the Philippines. *Marine Biology Research*, 4, 429–441.
- Naruse, T. & Ng, P.K.L. (2007a) On the taxonomy of the genus *Hymenicoides* Kemp, 1917 (Crustacea: Decapoda: Brachyura: Hymenosomatidae), with resurrection of *Limnopilos* Chuang & Ng, 1991, and descriptions of two new species. *Zootaxa*, 1621, 17–31.
- Naruse, T. & Ng, P.K.L. (2007b) On a new species of *Elamenopsis* from Singapore, with notes on *Crustaenia palawanensis* (Serène, 1971) (Crustacea: Decapoda: Brachyura: Hymenosomatidae). *Raffles Bulletin of Zoology*, 55(1), 121–155.
- Naruse, T., Ng, P.K.L. & Guinot, D. (2008) Two new genera and two new species of troglobitic false spider crabs (Crustacea: Decapoda: Brachyura: Hymenosomatidae) from Indonesia, with notes on *Cancrocaeca* Ng, 1991. *Zootaxa*, 1739, 21–40.
- Ng, P.K.L. (1991) *Cancrocaeca xenomorpha*, new genus and species, a blind troglobitic freshwater hymenosomatid (Crustacea: Decapoda: Brachyura) from Sulawesi, Indonesia. *Raffles Bulletin of Zoology*, 39(1), 59–73.
- Ng, P.K.L. & Chuang, C.T.N. (1996) The Hymenosomatidae (Crustacea: Decapoda: Brachyura) of Southeast Asia, with notes on other species. *Raffles Bulletin of Zoology*, Supplement 3, 1–82.
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. (2008) Systema Brachyurorum: Part 1. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*, Supplement 17, 1–286. [Updates at <http://rmbn.nus.edu.sg/research/cotw/supplement17.php>]
- Ng, P.K.L. & Richer de Forges, B. (1996) The Hymenosomatidae (Crustacea: Decapoda: Brachyura) of New Caledonia, with descriptions of two new genera and two new species. *Memoirs of the Queensland Museum*, 39(2), 263–276.
- Ng, P.K.L. & Richer de Forges, B. (2007) The Brachyura of New Caledonia. In: Payri, C.E. & Richer de Forges, B. (Eds.), *Compendium of marine species of New Caledonia*. Documents scientifiques et techniques, II7, seconde édition. IRD, Nouméa, pp. 315–331.
- Poore, G.C.B. (2004) Marine decapod Crustacea of southern Australia. A guide to identification. CSIRO Publishing, Collingwood, Melbourne, 517 pp.
- Poore, G.C.B. (2010) *Elamenopsis guinotae*, a new spider crab from Bass Strait, Australia (Brachyura, Hymenosomatidae). In: Castro, P., Davie, P.J.F., Ng, P.K.L. & Richer de Forges, B. (Eds.), *Studies on Brachyura: a Homage to Danièle Guinot*. *Crustaceana Monographs*, 11, 261–267.
- Rahayu, D.L. & Ng, P.K.L. (2004) The Hymenosomatidae (Crustacea, Decapoda, Brachyura) of Timika (Irian Jaya, Indonesia). *Zoosystema*, 26(1), 87–94.
- Rice, A.L. (1980) Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London*, 35, 271–424.
- Rice, A.L. (1981) Crab zoeae and brachyuran classification: a re-appraisal. *Bulletin of the British Museum of Natural History*, 40(5), 287–296.
- Richer de Forges, B. (1976) *Etude du crabe des îles Kerguelen Halicarcinus planatus (Fabricius) (Decapoda, Brachyura, Hymenosomatidae)*. Unpublished doctoral thesis, Université Pierre et Marie Curie. Océanographie Biologique. Paris.
- Richer de Forges, B. (1977) *Etude du crabe des îles Kerguelen Halicarcinus planatus (Fabricius)*. *Bulletin du Comité national Français de la Recherche antarctique (CNFRA)*, 42, 71–133.
- Richer de Forges, B., Jamieson, B.G.M., Guinot, D. & Tudge, C.C. (1997) Ultrastructure of the spermatozoa of Hymenosomatidae (Crustacea: Brachyura) and the relationships of the family. *Marine Biology*, 130, 233–242.
- Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H. & Schweigert, G. (2010) Systematic list of fossil decapod crus-

- tacean species. *Crustaceana Monographs*, 10, 1–230.
- Štević, Z. (2005) The reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura). *Natura Croatica*, 14, Supplement 1, 1–159.
- Teske, P.R., McLay C.L., Sandoval-Castillo, J., Papadopoulos, I., Newman, B.K., Griffiths, C.L., McQuaid, C.D., Barker, N.P., Borgonie, G. & Beheregaray, L.B. (2009) Tri-locus sequence data reject a “Gondwanan origin hypothesis” for the African/South Pacific crab genus *Hymenosoma*. *Molecular Phylogenetics and Evolution*, 53, 23–33.
- Towers, D.J. & McLay, C.L. (1995) Rare hymenosomatid, *Amarinus lacustris* (Chilton 1882) found in Mangere river, Northland (Brachyura: Hymenosomatidae). *New Zealand Natural Science*, 22, 91–93.
- Van den Brink, A.M. (2006) *The reproductive ecology and biology of the pill-box crab: Halicarcinus cookii Filhol, 1885 (Brachyura: Hymenosomatidae)*. MSc thesis. Canterbury University, Christchurch, NZ.
- Van den Brink, A.M. & McLay, C.L. (2009) Use of the sterile male technique to investigate sperm competition in a pill box crab, *Halicarcinus cookii* Filhol, 1885 (Brachyura: Hymenosomatidae). *Journal of Crustacean Biology*, 29(1), 62–69.
- Wägele, J.-W. (1996) First principles of phylogenetic systematics, a basis for numerical methods used for morphological and molecular characters. *Vie et Milieu*, 46(2), 125–138.
- Walker, K. (1969) The ecology and distribution of *Halicarcinus lacustris* (Brachyura: Hymenosomatidae) in Australian inland waters. *Australian Journal of Marine and Freshwater Research*, 20, 163–173.
- Wear, R.G. & Fielder, D.R. (1985) The marine fauna of New Zealand: Larvae of the Brachyura (Crustacea Decapoda). *Memoirs of the New Zealand Oceanographic Institute*, 92, 1–90.
- Wiley, E.O. (1981) *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, New York, xv + 439 pp.
- Wilson, G.D.F. (1996) Of uropods and isopod crustacean trees: a comparison of "groundpattern" and cladistic methods. *Vie et Milieu*, 46(2), 139–153.