



## The position of the Hymenosomatidae MacLeay, 1838, within the Brachyura (Crustacea, Decapoda)

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### Abstract

The Hymenosomatidae is unique among the Brachyura on the basis of spermatozoal ultrastructure and morphological characters of the adults and larvae. The location of the hymenosomatid male gonopore, always a controversial question, is here shown to be sternal, not coxo-sternal. This disposition, analogous to the arrangement of Thoracotremata, contradicts all morphological characters that indicate a heterotreme affiliation, close to the Majoidea and Dorippoidea. Molecular data also support such an assignment. The multiple hymenosomatid plesiomorphies are reviewed. The exceptional male reproductive system, a new scheme for the Eubrachyura, is assumed, at least in part, to be the result of a strong carcinisation in an ancient, deeply rooted group, at present the most ecologically diverse in Brachyura. The presence of the Hymenosomatidae on the former Gondwanan landmasses and its worldwide pattern of distribution are consistent with the hypothesis of a Gondwanan origin of the family.

**Key words:** Brachyura, Eubrachyura, Thoracotremata, Heterotremata, Hymenosomatidae, Majoidea, Dorippoidea, male reproductive system, male gonopore, spermatozoa, coxo-sternal condition, carcinisation, larval development, megalopa, phylogeny

### Introduction

The placement of the Hymenosomatidae MacLeay, 1838, within the Brachyura Latreille, 1802, has been controversial at one time or another, the family being considered heterotreme, close to or within the Majoidea Samouelle, 1819 (e.g., Rathbun 1925; Richer de Forges 1976, 1977; Guinot & Richer de Forges 1997; Guinot & Bouchard 1998; Martin & Davis 2001; Ng *et al.* 2008) or thoracotreme, often close to the Pinnotheroidea De Haan, 1833 (e.g., H. Milne Edwards 1837; Alcock 1900; Garth 1958; McLay 1988). A new step has been achieved when Hymenosomatidae has been found to be unique among the Brachyura on the basis of the spermatozoal ultrastructure so that it was difficult to accommodate the family in the three brachyuran divisions, Podotremata Guinot, 1977, Heterotremata Guinot, 1977, and Thoracotremata Guinot, 1977 (Richer de Forges *et al.* 1997). This discovery conformed to a puzzling situation, the sternal emergence of the male ejaculatory duct and gonopore in Hymenosomatidae. This is a thoracotreme disposition in contradiction with all the morphological characters that indicate a heterotreme affiliation for the family (Guinot & Richer de Forges 1997). The presence in the Hymenosomatidae of seminal receptacles connected to sternal openings of sternite 5, the vulvae (Guinot 1979a: 186), the salient apomorphy of the Eubrachyura Saint Laurent, 1980, supports a eubrachyuran assignment. Nevertheless, the retention in the basal Hymenosomatidae (Odiomarinae Guinot, 2011) of dorsal uropods as in the basal Podotremata (Guinot & Bouchard 1998; Guinot 2011), so far unique among eubrachyurans, merits discussion. In addition, a wide range of other plesiomorphic features is present in hymenosomatids, notably a weak cephalic condensation, with the absence of orbits and proepistome in basal representatives and incomplete orbits even in the more derived taxa. The great number of unique and exceptional traits of Hymenosomatidae, in particular the absence of a megalopal stage in the larval development of all its members, as well as occurrence in marine, brackish and freshwater habitats (Lucas 1980), requires a reappraisal of character evolution in Hymenosomatidae. The basal position of Hymenosomatidae in the heterotreme Eubrachyura as recovered by a wide range of data, including molecular analysis, necessitates a reappraisal of the relationships of the family and has led to a re-evaluation of the phylogeny of Brachyura.

## Material and methods

Measurements, in millimetres, refer to carapace length  $\times$  carapace width. The following abbreviations are used: G1, first male pleopod, or first gonopod; mxp3, third maxilliped; P5, fifth pereopod.

A large number of hymenosomatids have been examined, in particular the material deposited in the Muséum national d'Histoire naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); and Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC). Only the main taxa that were examined and the species that have been dissected are cited below.

### Material examined.

*Amarinus lacustris* (Chilton, 1882), male  $4.6 \times 5.8$  mm, female  $4.7 \times 4.8$  mm, juv.  $2.0 \times 2.0$  mm, New Zealand, Auckland, Oratia stream (ZRC2010.0238)

*Cancrocaeca xenomorpha* Ng, 1991, male  $3.9 \times 4.6$  mm, paratype, Indonesia, Sulawesi, Maros, Lubang Batu Neraka cave (MNHN-B24450); ovig. female  $4.1 \times 5.2$  mm, Indonesia, Sulawesi Selatan, Gua Samanggi (ZRC 2007.0118)

*Elamena truncata* (Stimpson, 1858), male, Taiwan, Taipei (ZRC 1999.2062)

*Halicarcinus planatus* (Fabricius, 1775), male  $17.0 \times 21.0$  mm (dissected), ovig. female  $15.0 \times 20$  mm, Kerguelen Islands, Bouvier det. (MNHN-B25953); male  $15.0 \times 17.3$  mm (dissected), several males and females, South Pacific Ocean, Campbell Island (MNHN-B25960)

*Hymenicoides robertsi* Naruse & Ng, 2007, males  $4.0 \times 5.8$  mm –  $4.9 \times 5.7$  mm, 2 ovig. females  $3.8 \times 4.4$ ,  $4.2 \times 4.8$  mm, paratypes, Myanmar, Raknine State, market on Kaladan River (MNHN-B30393)

*Limnopilos sumatranus* Naruse & Ng, 2007, male  $4.6 \times 5.1$  mm, female  $5.4 \times 6.3$  mm, paratypes, Indonesia, Sumatra (MNHN-B30395)

*Neorhynchoplax mangalis* (Ng, 1988), ovig. female  $3.6 \times 3.3$  mm, Singapore (ZRC 1993.6752)

*Neorhynchoplax prima* Ng & Chuang, 1996, male, holotype, Indonesia, Pulau Bintan (ZRC 1994.4233)

*Odiomaris estuarius* Davie & Richer de Forges, 1996, male  $4.6 \times 4.3$  mm, holotype, New Caledonia, Dumbea estuary (MNHN-B25278); female  $5.4 \times 5.0$  mm, paratype, same data (MNHN-B25275)

*Odiomaris pilosus* (A. Milne-Edwards, 1873), male  $20.0 \times 22.6$  mm, New Caledonia (MNHN-B26146); several specimens (one male specimen dissected by M. Tavares in January 2011), New Caledonia, River Wé Waalu, G. Marquet & L. Taillebois coll. 22.10.2010 (MNHN-B32604)

*Sulaplax ensifer* Naruse, Ng & Guinot, 2007, ovig. female  $5.0 \times 6.5$  mm, paratype (ZRC 2007.0119); female  $4.0 \times 5.0$  m, Indonesia, Sulawesi Tenggara, Muna I. (MNHN-B30396)

*Trigonoplax unguiformis* (De Haan, 1839), female  $10.4 \times 14.5$  mm, 2 other females, ?Japan (NMNH13714); male  $6.1 \times 7.3$  mm, Western Australia, Passage Island (NMNH184973).

## Spermatozoa

The spermatozoa of Hymenosomatidae, studied in two species of *Odiomaris* Ng & Richer de Forges, 1996, *O. pilosus* (A. Milne-Edwards, 1873) and *O. estuarius* Davie & Richer de Forges, 1996, and in *Elamena vesca* Ng & Richer de Forges, 1996, significantly differ in at least nine major characteristics from those of all other brachyuran taxa that were investigated (Richer de Forges *et al.* 1997; Jamieson & Tudge 2000). The combination of spermatozoal characters, collectively and often individually, is so markedly distinctive from that of the families with which the Hymenosomatidae has traditionally been associated, the heterotreme Majoidea and thoracotremes such as Varunidae H. Milne Edwards, 1853, Ocypodidae Rafinesque, 1815, and Gecarcinidae MacLeay, 1838 (Jamieson *et al.* 1995), that Richer de Forges *et al.* (1997: 238, 239) recognized a “hymenosomatid-type of spermatozoon”. A “majid-hymenosomatid” relationship was not supported by spermatozoal ultrastructure, because the two families differed in the nine distinctive characters of the Hymenosomatidae (Jamieson & Tudge 2000). One of these hymenosomatid characters, the almost septate condition of the inner acrosome zone is, exceptionally, approached in the majoid *Cyrtomaia furici* Guinot & Richer de Forges, 1988 (Inachidae MacLeay, 1838) but could not be considered a convincing synapomorphy between the two families (Jamieson *et al.* 1998: 199, 204, 205). The highly developed projection of the acrosome from the nucleus in hymenosomatid spermatozoon recalls the totally emer-

gent acrosome of podotremes. A less pronounced emergence is seen in Anomura (Tudge 1995; Jamieson & Tudge 2000), dorippids (Jamieson & Tudge 1990, 2000) and majoids (Jamieson *et al.* 1998; Jamieson & Tudge 2000), and may represent the plesiomorphic condition in Brachyura. This structure is apomorphically increased in podotremes and may also have occurred independently in hymenosomatid spermatozoon, while thoracotremes and most heterotremes have completely withdrawn the acrosome (B.G.M. Jamieson, pers. comm. February 2011).

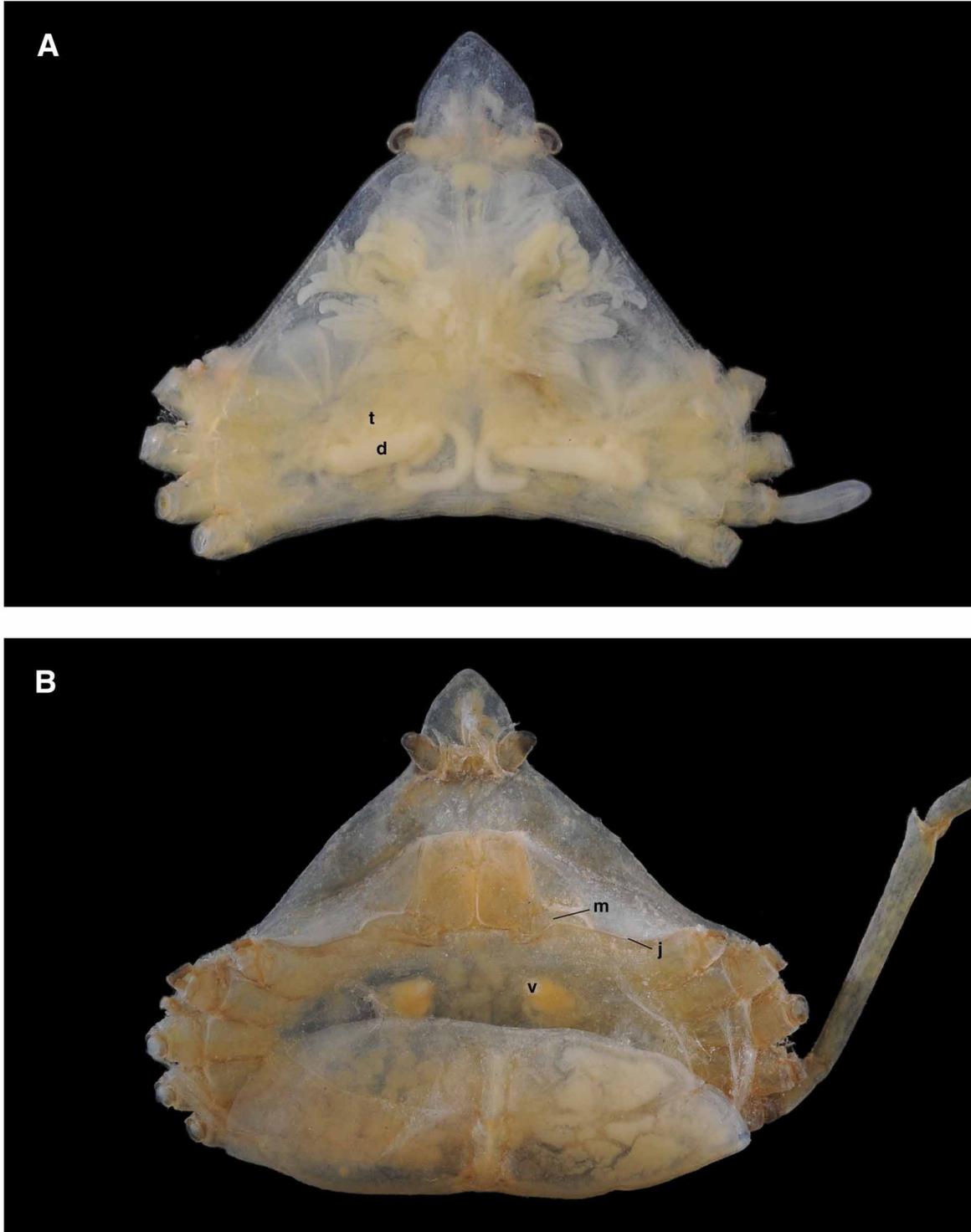
### Location of male gonopores

The male gonopore of Hymenosomatidae emerges in the form of a penis in the middle of sternite 8, at a clear distance from the P5 coxa and from sternal suture 7/8, thus in a posteriormost location in relation to sternite 8 (Fig. 1A; Guinot 1979a: fig. 53F; Guinot & Richer de Forges 1997: figs. 6A, 9). This sternal emergence of the hymenosomatid male gonopore has been a source of confusion, as clearly noted by Tesch (1918: 3): the only character justifying placement of Hymenosomatidae among the Catometopa (mostly corresponding to Thoracotremata) is the sternal opening, a trait that is “counterbalanced by a whole series of features showing a close relationship to the Oxyrhyncha and especially to the Maiidae” (see also Montgomery 1921: 95; Guinot 1979a: 215). In other words, is the Hymenosomatidae a heterotreme or a thoracotreme? The heterotreme-thoracotreme distinction results from two different trajectories of the vas deferens and its ejaculatory duct, either by way of the P5 coxa (Heterotremata) or directly through the sternum (Thoracotremata) (Guinot 1977; 1978: figs. 1, 2).

Based on absence of coxal male gonopores, H. Milne Edwards (1837: 35) assigned *Hymenosoma* Desmarest, 1825, to the Catometopa, but was later (1852: 103, 183) in favour of a separate tribe with some majid traits, establishing a link between *Ocyropodiens* and *Homoliens*. Ortmann (1893: 30; 1896: 416, 441, 442) noted a sternal location of the male gonopores, comparable to that of Leucosiidae Samouelle, 1819, and chose, however, a placement in the Majoidea Samouelle, 1819, perhaps in an “aberrant” group. Alcock (1900: 282, 291, 385) considered this was a “decided mistake” and included the Hymenosomatidae in the Catometopa. Despite its sternal male gonopores, the family was assigned to the Majoidea by Rathbun (1925: 561), hence the common name of “false spider crabs”. The Hymenosomatidae was considered thoracotreme, often close to Pinnotheridae De Haan, 1833 (Haswell 1882; Miers 1886; Alcock 1900; Garth 1958; Guinot 1978; McLay 1988; Chen & Sun 2002), and some workers have even synonymised it with this family (e.g., Hodgson 1902; Hutton 1904; Baker 1906). Richer de Forges (1976, 1977) considered the sternal emergence of the male openings to be deceptive. A coxo-sternal condition was supposed (without dissection) by Guinot & Richer de Forges (1997) and Guinot & Bouchard (1998), who suggested a close relationship of the Hymenosomatidae with the Inachoididae Dana, 1851, a majoid family rehabilitated by Drach & Guinot (1982, 1983; see also Guinot 1984).

By definition, a coxo-sternal condition is actually still coxal since the ejaculatory duct first perforates the P5 coxa and prolongs as the penis, which is covered by the posterior sternite(s) and becomes visible again on the sternum after emerging from a “secondary” aperture. The coxo-sternal condition occurs in several heterotreme groups, either as a simple trend or as an exclusive condition, e.g., in Dorippoidea MacLeay, 1838, Goneplacidae MacLeay, 1838, Litocheiridae Števc̆ić, 2005, and Palicoidea Bouvier, 1898. The coxo-sternal condition is thus different from the thoracotreme condition, in which the ejaculatory duct directly perforates the thoracic sternum without a detour by the P5 coxa. Evidence is here presented (Fig. 1A; see *Results*) for the exclusively thoracic emergence of the male duct in hymenosomatids, but not a coxo-sternal condition.

The taxonomy of Hymenosomatidae has therefore undergone several major changes, the family being most often considered heterotreme, as a part of Majoidea (Ng *et al.* 2008: 108), or in its proximity (Melrose 1975; Poore 2004). A suprafamilial rank, Hymenosomatoidea MacLeay, 1838, had even been proposed (Guinot 1978; Martin & Davis 2001; Chen & Sun 2002; Števc̆ić 2005). Lucas (1980: 152), in his comprehensive review, posed the question of the position of Hymenosomatidae but did not resolve the issue. The higher-level taxonomic position of Hymenosomatidae was not discussed in the most recent papers (e.g., Ng & Chuang 1996; Van den Brink 2006; Naruse & Ng 2007a, 2007b; Naruse, Ng & Guinot 2008; Naruse, Mendoza & Ng 2008; Van den Brink & McLay 2009; McLay & Van den Brink 2009; Naruse & Komai 2009; Teske *et al.* 2009).



**FIGURE 1.** *Trigonoplax unguiformis* (De Haan, 1839). A, male 6.1 x 7.3 mm, Western Australia, 19 m, coral, sponge and some sea grass, A.B. Williams det. 1981 (USNM 184973) (all fragile legs missing): male reproductive system visible through decalcified, transparent carapace, showing the testis and vas deferens, with ejaculatory duct connecting directly to the sternum, distant from P5 coxa; B, female 10.4 x 14.5 mm, ?Japan (USNM 13714): wide sternum/pterygostome junction, large brood cavity, with anteriorly displaced vulvae. d, vas deferens; j, sternum/pterygostome junction; m, Milne Edwards's openings separated from chelipeds and filled by flabelliform Mxp3 coxae; t, testis; v, vulva.

## Other morphological data

The hymenosomatid carapace is poorly calcified, with a thin cuticle, generally with a furrow (“hymenosomian groove”) entirely encircling its dorsal surface, and most often with several deep grooves that define several plate-like surfaces, an unusual pattern among brachyurans. Several distinctive characters may be enumerated (Lucas 1980; Ng & Chuang 1996; Guinot & Richer de Forges 1997): peculiar disposition of the eyes (absence of orbits and proepistome in the plesiomorphic state; orbits remaining incomplete in the derived hymenosomatid taxa) and cephalic appendages (antennules vertically folded and dorsally exposed; no antennal fossa and antennae extended forwards); thoracic sternum with sternites 4–8 considerably enlarged (Fig. 1B); sutures 4/5–7/8 laterally restricted; sterno-abdominal cavity of males generally reduced in length; male and female abdomens never having more than five somites, always with the formation of a pleotelson (somite 6 fused to the telson) and, often, fusion of additional somites to the pleotelson so that the abdomen may consist of only three elements; press-button for abdominal locking situated on the undivided part of the thoracic sternum; abdominal sockets located at the base of the pleotelson, thus belonging as usual to the last abdominal somite (somite 6); presence in some genera (*Odiomaris* and *Amarinus*) of defined intercalary platelets, completely articulated, moveable, homologous to the uropods of the Dromiidae De Haan, 1833, but with the sockets situated ventrally, the platelets being slightly discernible (Holthuis 1968: 115; Lucas 1980: fig. 7; Guinot & Richer de Forges 1997: figs. 4A–E, 6B–E; Guinot & Bouchard 1998: 658, fig. 27; Guinot 2011: figs. 1C, 2, 3A–C); mature females with brood cavity and pseudovulvae (Ng & Chuang 1996: 60, fig. 26D); sternum/pterygostome junction variously developed, substantially developed e.g., in *Trigonoplax* H. Milne Edwards, 1853; unusual Milne Edwards’s openings (Fig. 1B; Guinot 1979a: fig. 30A; Guinot & Richer de Forges 1997: figs. 1D, 3; Guinot 2011: fig. 1B, C); vulvae variously displaced anteriorly (Barnard 1950: 67; Richer de Forges 1976; Guinot 1979a: 186); axial skeleton regularly compartmented, with a parallel arrangement of the phragmae in the anteroposterior plane (Secretan 1998: 1763, figs. 19, 20; Guinot 2011: fig. 1E, F); retaining of apposition optics (Meyer-Rochow & Reid 1994).

The assertions by Saint Laurent (1980) that Guinot (1978, 1979a, 1979b) considered the existence of intermediate forms between Podotremata and Eubrachyura, as well as regarding the coxo-sternal condition as intermediate towards the thoracotreme organisation, are unfortunate misinterpretations. This has caused some confusion (e.g., Rice (1981a: 288; 1983: 321, 325). No true intermediates between the coxo-sternal and thoracotreme conditions have been found.

**Larvae.** The hymenosomatid zoeae, no more than three stages in marine species, present particular, even unique characters (reduced antennules and antennae, only a vestigial coxal endite on the second maxilla armed with a single seta, loss of the outer three processes on the telson, loss of the pleopods), and there is no megalopal stage (Muraoka 1977; Terada 1977; Richer de Forges 1977; Rice 1980, 1981a, 1981b, 1983; Fukuda 1981; Rabalais & Gore 1985; Krishnan & Kannupandi 1988; Tirmizi & Kazmi 1991; Dornelas *et al.* 2003). The freshwater species have a direct development (Lucas 1971; Wear & Fielder 1985): for example, *Amarinus lacustris* is known to carry ca. 35 eggs (Lucas 1980: 202, table 4); the cave-dwelling *Sulaplax ensifer* Naruse, Ng & Guinot, 2008, possesses the largest eggs (mean 1.19 mm, n = 10) and the smallest clutch size (17 eggs) known for any hymenosomatid crab; a female *Neorhynchoplax bovis* (Barnard, 1946) contained 13 juveniles under the abdomen (Barnard 1950: 72) (Naruse, Ng & Guinot 2008: 31).

Gurney (1938: 78), based on the larval characters of Hymenosomatidae, stated “if it were possible to construct a system for the Brachyura upon the zoea alone, then the three families Leucosiidae, Pinnotheridae, and Hymenosomatidae would have to be placed together”. A relationship between Hymenosomatidae and Pinnotheridae was supported by larval evidence (Gurney 1942; Wear 1967, 1968; Lucas 1971; see also Wear & Fielder 1985), but Rice (1980: 348) discounted this possibility. The larval morphology of hymenosomatids shows that they “could not have evolved from any of the extant thoracotrematous groups” (Rice 1983: 326). The family is distinguished from all other brachyuran families by the absence of a true megalopa in marine and brackish species as well as in freshwater representatives (Broekhuysen 1955; Melrose 1975; Richer de Forges 1977; Lucas 1971, 1972, 1975, 1980; Rice 1980, 1981a, 1983; Rabalais & Gore 1985; Wear & Fielder 1985; Horn & Harms 1988). According to Felder *et al.* (1985: 183) the first juvenile crab is equivalent to a postlarval stage (or decapodid) in the form of a benthic megalopa.

## Molecular data

A molecular analysis based on small subunit nuclear ribosomal RNA by Ahyong *et al.* (2007: 583, figs. 2, 4) supported the heterotreme status of the Hymenosomatidae, although with indecisive results “regarding a hymenosomatid-majid alliance, either in terms of topological robustness or resolution, although majoids and hymenosomatids are always in proximity to or near the 'base' of the eubrachyurans”. The odiomarine *Amarinus lacustris* (Chilton, 1882), basal in the family (Guinot 2011), was recovered as the sister taxon of the dorippid *Dorippoides facchino* (Herbst, 1785), indicating a dorippid + hymenosomatid clade within the Heterotremata. Significantly, the majoid–hymenosomatid assemblage was always associated with the dorippids, the majoids having a low position among the eubrachyurans. Ahyong *et al.* (2007: 583) concluded “the sister to the remaining eubrachyurans lies among the majoids–hymenosomatids–dorippids”. From another molecular analysis using three mitochondrial markers Teske *et al.* (2009: 31) preliminarily concluded that the Hymenosomatidae was “not part of the Majoidea”.

## Reproductive biology

The biology of reproduction of the small-sized hymenosomatids, with peculiar strategies, is noteworthy. Breeding may occur throughout the year (Hill & Forbes 1979; Johnston & Robson 2005; Van den Brink & McLay 2009; McLay & Van den Brink 2009). Copulation may occur before the puberty moult of females and involves prepubertal males, exceptional traits in the Brachyura. Females of *Halicarcinus planatus* (Fabricius, 1775) are able to re-mature their ovaries while they are ovigerous, probably a phenomenon unique among the Brachyura (Diez & Lovrich 2010); their postlarval development suggests an anomalous growth process (Vinuesa & Ferrari 2008).

## Results

The question of whether or not there is a true sternal emergence of the male gonopore in hymenosomatids has been successfully elucidated here by dissections. Dissections of *Halicarcinus planatus* and of freshly collected *Odiomaris pilosus* demonstrated a direct emergence of the ejaculatory duct through the thoracic sternum without passing through the P5 coxa. Moreover, examination of *Trigonoplax unguiformis* (De Haan, 1839), which has a remarkably transparent carapace, unambiguously showed that the ejaculatory duct does not connect the P5 coxa and, instead, directly joins a median region on the thoracic sternum. This configuration, first highlighted to me with an example of *Neorhynchoplax mangalis* (Ng, 1988) by T. Naruse (pers. comm. September 2010), is clearly visible in the photographed specimen of *T. unguiformis* (Fig. 1A). A coxo-sternal condition therefore does not occur in the Hymenosomatidae, and the sternal emergence is actually comparable to that of the Thoracotremata.

## Discussion

A study of the sexual openings in the Brachyura (Guinot, Tavares & Castro in progress) examines carcinisation in all Brachyura, a process involving the broadening of the thoracic sternum and subsequent anatomical readjustments, in particular a displacement of the male gonopore, its “migration” from the P5 coxa (appendicular location) to sternite 8 (thoracic location). The term “migration” as used here only refers to a radical change in the location without a continuum between the two character states. In evolving a wider thoracic sternum, the Hymenosomatidae has modified the trajectory of the vas deferens. The male gonopore originates on sternite 8 because the distal duct perforates the sternal surface and passes through it, so the penis is completely inserted in the sternum (Fig. 1A), thus developing as in the thoracotreme disposition. The hymenosomatid male gonopore is analogous to the thoracotreme gonopore, but only a histological study could show if the male reproductive system has a strictly similar organisation in Hymenosomatidae and in thoracotremes such as Grapsoidea MacLeay, 1838, or Ocypodoidea Rafinesque, 1815. A sternal male gonopore has evolved homoplasically in the Hymenosomatidae and in the Thoracotremata. Hymenosomatidae is undoubtedly eubrachyuran (the presence of vulvae rejects a podotreme affiliation) and heterotreme (see above). Thus, the arrangement of the male system in hymenosomatids contradicts the

assumption, as in the dichotomy proposed by Guinot (1977), that only two different anatomical arrangements are present in male Eubrachyura, both the heterotreme and thoracotreme conditions. This also challenges the assumption that the only way for a heterotreme crab to evolve during the process of carcinisation (involving the broadening of the thoracic sternum) is to adopt the coxo-sternal condition, actually a coxal condition (Guinot, Tavares & Castro in progress).

Indeed, the hymenosomatid condition could cast doubt on the heterotreme-thoracotreme distinction. The fact that Hymenosomatidae is not a typical heterotreme results from an extreme state of carcinisation in the group (the broadest thoracic sternum known in Brachyura) suggestive of a long-term evolutionary history. It is here envisaged that the broad hymenosomatid thoracic sternal plate is a trait of an old, extremely carcinised clade instead of pertaining to a recent, derived family. So the extant representatives exhibit sternal characters that seem to characterise an advanced crab whereas in fact they belong to a primitive group, with these characters evolving *de novo* and independently from other heterotreme lineages. Even though the thoracic sternum in Brachyura may sometimes obscure phylogenetic information and its interpretation needs a careful evaluation, it remains nevertheless a reliable character to infer polarity in phylogenetic reconstruction. Although the fossil record does not yet provide any evidence, no fossil hymenosomatids being so far known due to their small size, flat body, and poorly calcified carapace (De Grave *et al.* 2009: 35), the hymenosomatid lineage is here believed to have evolved very early in eubrachyuran history, which appears as deeply rooted in phylogenetic trees. This is in agreement with the idea of Chilton (1915: 318) that, judging from its distribution, *Amarinus lacustris* “must be of considerable antiquity” and with the hypothesis that Hymenosomatidae arose prior to the breakup of Gondwana. This is in contrast to Walker (1969) and Lucas (1970) who suggested a recent origin, and to Teske *et al.* (2009) who rejected a “Gondwanan origin hypothesis” for the genus *Hymenosoma*. The presence of the Hymenosomatidae on the former Gondwanan landmasses and its pattern of distribution, including Antarctica, Africa, Madagascar, South America and the Australian continent, as well as the Arabian Peninsula and the Indian subcontinent (Kemp 1917; Lucas 1980; Lucas & Davie 1982; McLay 1988; Tirmizi & Kazmi 1991; Chuang & Ng 1994), are consistent with a Gondwanan origin of the family, as proposed here.

At the same time Hymenosomatidae possesses many highly modified features. This conforms with and casts light on the multiple singular traits of the group, in particular the numerous archaic features of the spermatozoa (some podotreme similarities), morphology (vestigial uropods), and molecular characteristics (basal position in the Eubrachyura). The “reduction” observed in the zoeae may be considered “derived” (Nelson & Platnick 1981; see also Marques & Pohle 1998) but, as in the case of the thoracic sternum, it provides additional support for the hypothesis that the Hymenosomatidae is an ancient lineage. The elimination of a true megalopa stage, a form of accelerated development that is considered as an advantage in a reduced pelagic life (Lucas 1970, 1971, 1975; Rabalais & Gore 1985; Gore 1985), may be linked to the ancestry of the lineage. The distinctive larval traits of the hymenosomatid zoeae that were assumed to be doubtfully “advanced” (e.g., Rice 1980, 1983) may well be the consequence of this early branching and long evolutionary history. A separate evolutionary history from a very early period and an independent acquisition of a thoracotreme condition, as hypothesised by Rice (1983: 327), are consistent with all data. Extant hymenosomatids may be, apart from podotreme crabs, among the most conservative living derivatives of an ancient brachyura fauna.

Why has a coxo-sternal condition not prevailed in the Hymenosomatidae whereas it occurs in many heterotreme families that have acquired a wide thoracic sternum such as the Dorippidae MacLeay, 1838, Ethusidae Guinot, 1977, Euryplacidae Stimpson, 1871, Palicidae Bouvier, 1898, and others? In all these brachyurans displaying a coxo-sternal condition, the male gonopore is situated on the P5 coxa close to suture 7/8 and, when the distance between the two P5 and the medially situated gonopods increases, the penis becomes longer, is located in a groove and, ultimately, covered because of the dorsal junction of the sternites 7 and 8, so that it becomes apparent on the sternum (Guinot 1969: figs. 1–8, 15, 16; 1979b: 45, figs. 2B3, 3). It is hypothesised here that such a transformation cannot be applied to a gonopore on a P5 coxa situated distant from the suture 7/8, which probably was a posterior location in the hymenosomatid ancestor as in the modern representatives.

Although peculiar, the external morphology of the Hymenosomatidae, which demonstrates a heterotreme and not thoracotreme affiliation, shows evident relationships with crabs such as the Inachoididae Dana, 1851, Inachidae MacLeay, 1838 (Guinot & Richer de Forges 1997), and as well as the Dorippidae. The possible relationships between Hymenosomatidae and Dorippidae, never mentioned by taxonomists, are documented on the basis of morphological features by Guinot, Tavares & Castro (in progress). This view is supported by genetic results of Ah Yong

*et al.* (2007: 583) that placed the Hymenosomatidae in a basal position among the Eubrachyura close to Dorippoidea, both dorippids and majoids occupying a “low” position in Eubrachyura. A phylogeny inferred from nuclear protein-coding genes by Chu *et al.* (2009: figs. 1, 3) similarly suggested a basal position of the Dorippidae, clustering with Majoidea. The relationships between majoids and dorippoids are, however, difficult to discern mostly because of the lack of a modern, comprehensive study of the Majoidea.

The view that the Hymenosomatidae is basal in Eubrachyura and closely related to Dorippoidea is actually supported by consistent datasets. Both dorippid and hymenosomatid clades are deeply rooted and are represented in the living fauna by highly modified taxa: the Dorippoidea (including Ethusidae), which displays various states of a coxo-sternal condition (Guinot, Tavares & Castro in progress), and the Hymenosomatidae, which exhibits a novation that could be termed “sternitrema”. Both clades show a high diversity, which is linked to their ancestral origin and early diversification.

In a cladistic analysis of combined morphological and spermatozoal characters, *Neodorippe* formed the plesiomorphic sister-group of all other investigated eubrachyurans (Jamieson *et al.* 1995: fig. 1B; see also Jamieson 1994: 390, 391; Jamieson & Tudge 1990; hymenosomatid spermatozoa were yet to be investigated). In analysis of only spermatozoal characters in the same study (Jamieson *et al.* 1995: fig. 1A), however, majoids formed the plesiomorphic sister-group of all other eubrachyurans. With regard to the Hymenosomatidae, the spermatozoa of *Odiomaris* have the components typical of eubrachyuran (heterotreme and thoracotreme) spermatozoa, but differ significantly from all other investigated eubrachyurans in at least nine characteristics. The more noteworthy of which are: presence of an epiopercular dome; the acrosome smaller in volume than the nucleus, longer than wide, and strongly emergent, being surrounded only basally by nuclear material; the thin, putative inner acrosome zone that is anteriorly almost septate owing to several longitudinal corrugations; and the unique helical and posterolateral disposition of the nuclear arms. From a purely spermatological perspective, *Odiomaris*, *Elamena*, and, provisionally, all hymenosomatids were thus excluded from the Thoracotremata nor they were readily placeable in the Heterotremata (Richer de Forges *et al.* 1997). The projection (emergence) of the acrosome from the nucleus is complete in podotremes, and partial in dorippids and majoids as well as in anomurans. Emergence of the acrosome may, therefore, be plesiomorphic for brachyurans while the complete (podotremes) or strong (hymenosomatids) emergence may represent an independently apomorphic development from this state. The hypothesis by Jamieson & Tudge (2000: 72), based on spermatozoal ultrastructure, that Hymenosomatidae may “have acquired the thoracotreme condition of the genital pores independently of the Thoracotremata”, confirmed in the present paper, today reveals to be a reliable prediction.

A molecular analysis based on the sequence data from 16S rDNA gene of five species supported the recognition of a monophyletic Dorippidae consisting of two main lineages (Fan *et al.* 2004). Another more complete phylogenetic tree inferred from three mitochondrial genes (16S rRNA, 12S rRNA, and cytochrome *c* oxidase subunit I) by Sin *et al.* (2009) showed several distinct lineages concurring with groupings based on the overall carapace morphology and structure of the G1s. The dorippid G1s are so variable within the family (Holthuis & Manning 1990: 6) that even by themselves they denote the existence of multiple subfamilies. A reappraisal of the Dorippidae based on morphological traits, combined with genetic data, allows at least four subfamilies to be recognised (Guinot & Lai in progress). Similarly, despite heterogeneous organisation and large morphological variations (rostrum, cephalic appendages, mouthparts, male and female abdomens, gonopods, vulvae), the Hymenosomatidae had surprisingly not been subdivided into subfamilies before the establishment of the Odiomarinae for the most basal hymenosomatids (Guinot 2011). The heterogeneous family Hymenosomatidae is presently being revised (Naruse, Guinot & Ng in progress).

The Hymenosomatidae, which includes 119 species in 19 genera (updated from Ng *et al.* 2008: 108), is distributed worldwide, being particularly widespread throughout the southern hemisphere, also circumpolar in the subantarctic region, and is found in a wide variety of environments: from the open ocean (244 m depth for *Halicarcinus lucasi* Richer de Forges, 1993, see Richer de Forges 1993; about 500 m depth for *H. tongi* Melrose, 1975, see Melrose 1975), estuarine and brackish waters (Lucas & Davie 1982), inland fresh waters (e.g., Lucas 1980; Lucas & Davie 1982; McLay 1988; Ng & Chuang 1996), swamps at an altitude of 1600 m (Holthuis 1968: 112), pools of arid zones (Kemp 1917; Ali *et al.* 1995, 2000), caves (Ng 1991; Naruse, Ng & Guinot 2008); it may be also symbiotic with echinoderms (Lucas 1980: 224; Poore 2004: 390). Hymenosomatids are probably the most ecologically diverse group of crabs, indicative of successful morphological adaptations, with the freshwater taxa present everywhere (including Philippines, India, Sulawesi, New Guinea, New Caledonia, Australia and New Zealand).

All data sets from independent traits are congruent, and the unique combination of characters exhibited by the modern hymenosomatids, some plesiomorphic and others seemingly derived, is assumed to be at least partly the result of a strong carcinisation in an ancient group. This group branched off early from typical brachyuran (and, with a reasonable degree of certainty, eubrachyuran; see below) stem. It is conceivable that the highly modified spermatozoa of hymenosomatids would have lost traces of their origin though the emergent acrosome (albeit secondarily increased) may be a plesiomorphic relic of this origin. The absence of the megalopal stage in larval development is a loss acquired during the evolution of the group. It is here suggested that hymenosomatids, majoids and dorippids have a common ancestor, and that hymenosomatids and majoids subsequently diverged (hence the morphological and molecular similarities between hymenosomatids and the basal majoids such as inachoidids and inachids) while dorippids retained these ancestral relations. The root could also be near a podotreme-like ancestor of all three before the separation of the two major brachyuran groups, podotremes (coxal female and male openings, plus a paired spermatheca; perhaps with uropods) and eubrachyurans (sternal female openings, the vulvae, and either coxal or sternal male openings): this hypothesis, however, contradicts the traditional view of eubrachyuran monophyly. The monophyly of the hymenosomatid group is not questioned here, although the available evidence suggests that it consists of several distinct sublineages. Taxonomically, hymenosomatids may be grouped, at least provisionally, in the superfamily Hymenosomatoidea in close proximity to the Majoidea and Dorippoidea.

This would leave unchanged the diagnosis of the Heterotremata by Guinot (1977: 1050; italics are original): “Section that contains those families of Brachyura whose representatives are *all* sternitreme for the female orifice and *some* representatives *at least* are peditreme for the male orifice” (*Section qui contient les familles de Brachyours dont tous les représentants sont sternitèmes pour l’orifice femelle et dont certains représentants, au moins, sont péditrèmes pour l’orifice mâle*), opposed to that of the Thoracotrema: “Section that contains those families of Brachyura whose *all* representatives are sternitreme for the female orifice and also for the male orifice” (*Section qui contient les familles de Brachyours dont tous les représentants sont sternitrèmes pour l’orifice femelle et aussi pour l’orifice mâle*). Moreover, the assertion that the hymenosomatid precursor had a coxal male gonopore conforms to the definition of a monophyletic clade that must consist of an ancestor organism and all its descendants (Hennig 1966). It can be stated that a coxal perforation is present in all other heterotreme families. This disposition has been demonstrated by a number of dissections especially in the various taxa displaying a coxo-sternal condition (Guinot, Tavares & Castro work in progress).

The identification in Thoracotremata of crabs with, eventually, a “false” sternal emergence of the penis, still remains a problem, in particular the highly specialised Pinnotheroidea and Cryptochiroidea Paulson, 1875. These two groups were provisionally removed from the Thoracotremata by Guinot & Richer de Forges (1997: 496, table 1). Their catometope, thoracotreme affiliation has not been recently questioned (for Pinnotheroidea, see von Sternberg & Cumberlidge 2001). Their spermatozoa remain unknown.

The hypothesis of a coxo-sternal condition in the Pinnotheroidea can now be rejected after several dissections (M. Tavares, pers. comm. February 2011), and possible affinities with the Hymenosomatidae are far from evident, at least for some morphological characters in adults. Pinnotheroid zoeae share, however, with the hymenosomatid zoeae (and also leucosiid zoeae) some features that may be regarded as independently evolved (Lucas 1971; Rice 1980, 1983; Wear 1967; Wear & Fielder 1985). According to Rice (1983: 327) the Pinnotheridae have the most advanced thoracotreme zoeae and could not have been ancestral to any other group. A molecular analysis by Palacios-Theil *et al.* (2009) supports the Pinnotheroidea as Thoracotremata (see also Wetzer *et al.* 2009). Similarly, molecular data recover the Cryptochiroidea as thoracotremes within the Grapsoidea MacLeay, 1838, probably closely allied to the Grapsidae (Wetzer *et al.* 2009). A reappraisal of these two groups is, however, needed.

The subsection Heterotremata consists of two groups: (1) with a perforation of the P5 coxa (including the coxo-sternal condition) in the true heterotremes: all known Heterotremata (hymenosomatids excluded), represented by about 70 families; (2) with a perforation of the sternum, distant from the suture 7/8: the “sternitreme” Heterotremata, at least for now represented by the sole family Hymenosomatidae.

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