The spermatheca in podotreme crabs (Crustacea, Decapoda, Brachyura, Podotremata) and its phylogenetic implications

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ABSTRACT

The thoracic sternum of the primitive crabs (Podotremata Guinot, 1977) is strongly modified in females at the level of the sutures 7/8, separating the last two sternites, which corresponds to a secondary specialization of the phragmae 7/8. Thus a paired spermatheca has developed, which is intersegmental, internalized and independent of the female gonopores on the coxae of the third pereopods. This is unique to the Podotremata, being completely distinct from the eubrachyuran seminal receptacle. The spermatheca is reviewed in all members of the Podotremata, in its external aspect and internal structure. Among the Dromiacea, a spermathecal tube becomes specialized in the Homolodromiidae, Dromiinae, and Hypoconchinae, while it is absent in the Dynomenidae and Sphaerodromiinae, suggesting that the Sphaerodromiinae are basal to the Hypoconchinae + Dromiinae and that the Dynomenidae are basal to the remaining dromiacean families. The phylogenetic implications are discussed, confirming the distinction of two basal clades, Dromiacea and Homolidea, the peculiar organization found in the Cyclodorippidae, Cymonomidae and Phyllotymolinidae, and the special condition of the Raninoidea. The paired spermatheca proves to be the strongest synapomorphy of the Podotremata, including two Cretaceous families. Hypotheses on female sperm storage and functioning of the spermatheca, on male sperm transfer and the role of gonopods in insemination, and on the modalities of fertilization are included. New data on the axial skeleton are provided. The study of the spermatheca, which has considerable systematic value in decapod phylogeny, leads to a discussion of the monophyly of the Brachyura, taking into account the paleontological data.

KEY WORDS
Spermatheca,
Podotremata,
Dromiacea,
Dromiidae,
Hypoconchinae,
Sphaeodromiinae,
Dynomenidae,
Homolodromiidae,
Homolidae,
Latreilliidae,
Poupiniidae,
Cyclodorippidae,
Cymonomidae,
Phyllotymolinidae,
Raninoidea,
phylogeny.

RÉSUMÉ

La spermathèque chez les crabes Podotremata (Crustacea, Decapoda) et ses implications phylogénétiques.

Le sternum thoracique des crabes primitifs (Podotremata Guinot, 1977) est fortement modifié chez la femelle au niveau des sutures 7/8, qui séparent les deux derniers sternites, ce qui correspond à une spécialisation secondaire des phragmes 7/8. Ainsi se développe une spermathèque paire, qui est intersegmentaire, internalisée et indépendante de l'orifice femelle sur la coxa du troisième péréiopode. Elle est une exclusivité des Podotremata, étant complètement distincte du réceptacle séminal eubrachyourien. La spermathèque est étudiée chez tous les représentants de Podotremata, dans son aspect externe et dans sa structure interne. Parmi les Dromiacea, un tube se spécialise chez les Homolodromiidae, Dromiinae et Hypoconchinae, tandis qu'il est absent chez les Dynomenidae et les Sphaerodromiinae, suggérant que les Sphaerodromiinae sont basaux par rapport aux Hypoconchinae + Dromiinae et que les Dynomenidae sont basaux par rapport aux autres familles de dromiacés. Les implications phylogénétiques sont discutées, confirmant la distinction de deux clades basaux, Dromiacea et Homolidea, l'organisation particulière des Cyclodorippidae, Cymonomidae et Phyllotymolinidae, ainsi que la condition tout à fait spéciale des Raninoidea. La spermathèque paire s'avère être la plus forte synapomorphie des Podotremata, y compris deux familles du Crétacé. Des hypothèses sur le stockage du sperme par la femelle, le fonctionnement de la spermathèque, le transfert du sperme, le rôle des gonopodes dans l'insémination et sur les modalités de fertilisation sont formulées. Des données nouvelles sur le squelette axial sont apportées. L'étude de la spermathèque, qui a une valeur considérable pour la phylogénie des décapodes, conduit à une discussion sur la monophylie des Brachyura, en tenant compte des données paléontologiques.

MOTS CLÉS
Spermathèque,
Podotremata,
Dromiacea,
Dromiidae,
Hypoconchinae,
Sphaeodromiinae,
Dynomenidae,
Homolodromiidae,
Homolidae,
Latreilliidae,
Poupiniidae,
Cyclodorippidae,
Cymonomidae,
Phyllotymolinidae,
Raninoidea,
phylogénie.

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INTRODUCTION

The females of some groups of decapod crustaceans do not possess a specialized reproductive region or any apparent external modification for sperm deposit. Sperm is simply deposited on the exterior of the female, on its thoracic sternal surface or even on the coxae, as in pagurids (Manjón-Cabeza & García Raso 2000). More largely, a receptacle for sperm storage is unknown in the Anomura H. Milne-Edwards, 1832 (McLaughlin & Lemaitre 1997). In these examples there is no external evidence of sexual dimorphism at the ventral surface of the body, except for the location of the male and female gonopores, the protrusions of the vas deferens on the male P5 coxae (Subramoniam 1977; Tudge 2003; Tudge & Lemaitre 2004), and eventual modification of the abdomen and abdominal appendages. In contrast, the female sternum in the remaining decapods may be modified by having a variable number of thoracic sternites with simple evaginations or invaginations of the exoskeleton or more complex formations that shield enclosed structures, the thelycum and spermatheca. The female genital area may serve for temporary external attachment or prolonged internalized storage of spermatophores, for the deposit of male accessory substances, for genital contact with the male during copulation and to transfer sperm to internal receptacles (Bauer 1986, 1991, 1994). In several groups (stenopodid shrimps, palinurid lobsters) the male anterior pleopods are not modified for sperm transfer, and insemination and fertilization are assumed to take place as the eggs pass over the spermatophores on their way for their attachment to the pleopods. In the Paguroidea Latreille, 1802 the male of *Clibanarius vittatus* (Bosc, 1802) (Diogenidae Ortmann, 1892) only emits material containing spermatophores onto sterna of the females, and ventral surfaces of the male/female pair are simply apposed during copulation (Hess & Bauer 2002; Scelzo *et al.* 2004). Conversely, in other groups (caridean and penaeoidean shrimps, cambarid crayfishes, nephropid lobsters, as well as brachyuran crabs), placement of the sperm on the exterior of the female or within spermathecae or inside vulvae is achieved by means of anterior male pleopods (gonopods), which are variously modified.

In the Brachyura there is a complete insemination unit formed by three organs in the male: the penis which emerges from coxa or from thoracical sternum, and is introduced into the base of G1 or inserted laterally; and the two first pairs of pleopods, the gonopods, which are modified into copulatory organs for the sperm transfer to the female. In the Brachyura the copulation involves the use of these three organs, which act together as a single reproductive apparatus.

For some time (Guinot 1977, 1978, 1979a, b; Guinot & Bouchard 1998; Guinot & Tavares 2001, 2003) we have considered that a comprehensive view of the morphology and systematics of the Brachyura Latreille, 1802 could hardly be achieved without a detailed study of ventral surface of the body. Characters of the thoracic sternum are hardly or not taken into account in the diagnoses presented in valuable recent papers (Chen & Sun 2002) and are rarely figured or used in keys. A new view of the Brachyura will possibly emerge with a more accurate picture of the thoracic sternum, which bears the spermathecae or the vulvae. A robust synapomorphy of the Brachyura is the pairing of the seminal receptacles, either independent from the oviducts and associated with the thoracic sternal sutures 7/8 (spermathecae *sensu* Tavares & Secretan 1993) or associated with the oviducts that open on the sixth somite. Seminal receptacles are absent in most Decapoda Reptantia or, if present, they are unpaired and medially located.

The use of the sternal plate and the genital structures, which are situated ventrally (penis, gonopods, male and female gonopores, internalized spermatheca), provides useful information on phylogenetic relationships and has allowed the separation of the Brachyura Latreille, 1802, into two main groups. On one hand, the Podotremata Guinot, 1977, with male and female gonopores on the pereopods (fifth and third coxae, respectively), a strictly "appendicular" organization, always accompanied by a paired, integumental, spermatheca that lack connections with the oviducts.

Thus, two female apertures are present in the Podotremata: the oviductal opening (female genital opening or female gonopore) on the coxa of the third pereopod, with a role in egg laying; and a separate sternal aperture (spermathecal aperture) leading to internalized spermatheca. On the other hand, the assemblage Heterotremata Guinot, 1977-Thoracotremata Guinot, 1977 (the Eubrachyura Saint Laurent, 1980), with the male gonopore either on the coxa of the fifth pereopod or on the corresponding sternite, and a unique female orifice (vulva) on the sixth somite, connected with the oviduct. The region for the storage of sperm has been variously termed the sperm sac (Churchill 1919), copulatory pouch (Broekhyusen 1936) and seminal receptacle (Pyle & Cronin 1950; Ryan 1967), but it is named spermatheca by most authors (Hartnoll 1968). The eubrachyuran seminal receptacle is only an enlargement (Hartnoll 1968: fig. 1; 1969: 161, 175, 177; Guinot 1978: figs 1, 2; 1979a: 171, fig. 38) or a part of the female gonad, and the eubrachyuran vulva serves for a multiple role: copulation and release of eggs, as well as for sperm storage.

It has long been known that the thoracic sternum of the podotreme females is traversed along more or less of its full extent by two oblique, almost longitudinal main sutures, the "sternal grooves" or "sternal furrows" of the early authors. Gordon (1949, 1950, 1963, 1966) remarkably showed the importance of the anterior extensions of the sutures between the two last thoracic somites, i.e. the sternal sutures 7/8. It has been demonstrated that in the Brachyura, such as in the Nephropidae Dana, 1852, the sternal thoracic sutures 7/8 correspond to phragmae derived from two adjacent segments (segments 7 and 8) and composed of two infoldings (Drach 1971; Secretan 1980, 1991, 1998; Secretan-Rey 2002). The peculiar structure that is the podotreme spermatheca corresponds to a special invagination of the endosternite 7/8 along the line of the suture (Gordon 1950, 1963, 1966; Hartnoll 1975, 1979).

In following Gordon's lead, the term "spermatheca" was strictly defined by Tavares & Secretan (1993) for the Brachyura, as being only the internalized structure derived from sternal modifications of two adjacent segments in females, basically a split between the two plates of the intersegmental phragma, one derived from sternite 8 and the other one from sternite 7. According to these two authors, the intersegmental or intertagmal, internal, and *paired* spermatheca, as a secondary specialization of the phragma 7/8, is unique to the Podotremata. This anatomical definition permits to clarify the features of the podotreme spermatheca, that is a definite storage organ, and to distinguish it from the eubrachyuran seminal receptacle.

Thus, in the Podotremata, the posterior part of the female thoracic sternum is especially modified for a sexual function. In the podotreme group the sternal phragmae 7/8 are variously modified to form the paired spermatheca, which is a more or less differentiated complex structure, with a similar topographic position and the same function. Although there is an homogeneous ground plan, the examination of both external and internal anatomy of the spermathecae, including skeletal ones, reveals an unexpected wealth of patterns at the level of families, subfamilies, genera and species (Guinot & Tavares 2001: 522, 523, fig. 10). In the podotreme spermathecae, the immediate and externally visible differences concern location of their apertures on the sternal plate, and their shape and size. For example, in the Homolodromiidae Alcock, 1900, Dynomenidae Ortmann, 1892 and in the Sphaerodromiinae Guinot & Tavares, 2003, the apertures of the spermathecae are situated behind or about the level of the female gonopores on the P3 coxae. In the Dromiinae De Haan, 1833, adult females are known to have their thoracic sternites 7 and 8 growing forward and encroaching on the preceding sternites (6, 5 and even 4), thus occupying much of the ventral surface of the cephalothorax (Fig. 1A). As a result, the dromiine sternum appears externally as completely distorted and sexually dimorphic. The moving of sutures 7/8 and of their apertures in the anterior part of thoracic sternum is found in the Dromiinae and, in a lesser extent, in the Hypoconchinae Guinot & Tavares, 2003. This is thus a character used to distinguish these two subfamilies from the Sphaerodromiinae (Guinot & Tavares 2003). A feature shared by all the three dromiacean families (Homolodromiidae, Dromiidae Dynomenidae) is the generally small spermathecal aperture, a condition linked with the shape of the gonopods, mainly as regards the long and needle-like second gonopod. The extension of the female sutures 7/8 and their apertures in the anterior part of the thoracic sternum is not exclusive to Dromiinae and Hypoconchinae. It is found, at variable extent, in Cyclodorippoidea Ortmann, 1892, which shows a wide sternal thoracic sternum and sutures 7/8 that are sometimes greatly advanced, notably in certain Cyclodorippidae Ortmann, 1892, although not corresponding to the same pattern (Fig. 28).

In the Homolidea De Haan, 1839 sutures 7/8, although very oblique, remain short and restricted to posterior part of the sternum, and the spermathecal apertures are large (more so than in Dromiacea), leading to a sexually dimorphic sternum. Both gonopods are stout, and the second is thick, cylindrical, and with a terminal orifice.

In the Raninoidea, the basic structure is as in the other Podotremata, with paired spermathecae lying within endosternite 7/8. But, due to the strong dorsal flexion of the posterior portion of the sternum and its narrow shape, spermathecal apertures are situated anteriorly on sternite 7 and very close to the median line so that the paired spermatheca appears as a single median one. The subfamilial subdivision of the family is supported by the disposition of the paired spermatheca (Guinot 1993b). The first male gonopods are modified, being more or less folded in a tubular structure and apposed to act together in entering the closely placed spermathecal apertures (Gordon 1963, 1966; Hartnoll 1979; Guinot 1979a).

To our present knowledge, the similarity in the position (topographic homology and similar position in relation to other parts) of the podotreme spermatheca is evident. Nevertheless, ignoring the importance of the spermatheca, most of the authors questioned the monophyly of the Podotremata. The Podotremata was unrecognized in the classification of Martin & Davis (2001) in which the Raninoidea De Haan, 1833 and the Cyclodorippoidea Ortmann, 1892, i.e. the Archaeobrachyura, were placed within the Eubrachyura, a scheme that makes the eubrachyuran diagnosis complicated. It is obvious that the relationships of the so-called "primitive" crabs remain unclear (Feldmann 2003). We nevertheless consider the presence of the paired spermatheca connected with the sternal sutures 7/8 a criterium valid enough to justify the podotreme grouping. Assuming that our interpretation of monophyletic Brachyura is correct (robust synapomorphies are the pairing of the receptacles *sensu lato*, i.e. podotreme spermatheca or eubrachyuran seminal receptacle, and the male reproductive apparatus consisting of three organs which act together: penis, G1, G2), the debate concerning the monophyly of the Podotremata is a crucial issue. The classification of Martin & Davis (2001) would be confirmed if such a monophyly is not demonstrated and if the archaeobrachyura, as a whole or partly, proves to be more related to the Heterotremata-Thoracotremata assemblage than to the Podotremata (Dromiacea and Homoloidea).

The Podotremata exhibits several markedly different patterns of coxal morphology of the last pereopod, which is related to sperm transfer (Guinot & Tavares 2003). In the Dromiacea characterized by short female sternal sutures 7/8 (Homolodromiidae, Dynomenidae and Sphaerodromiinae) the male P5 coxa is totally modified, elongated as a continuous hard extension (coxal plate), and simply enclosing the penis. In the two other dromiid subfamilies (Dromiinae and Hypoconchinae), with long female sternal sutures 7/8 and apertures of spermathecae located more anteriorly than the female genital openings on the third pereopods, a long, sclerotized and mobile penial tube is present. This penial tube is unique to members of the subfamilies Dromiinae and Hypoconchinae. In the Homolidea, the coxa of the male fifth pereopod is not especially modified, and the penis looks like a simple papilla (Guinot 1979a). In the Archaeobrachyura Guinot, 1977, the male coxa is diversely modified, extending into a long, hard process in some raninids (coxal plate; see Serène & Umali 1972) or bearing a long penial tube in the cyclodorippine *Tymolus daviei* Tavares, 1997 (p. 262, fig. 1).

Thus, mating that requires a particular arrangement of the male copulatory system, involving both gonopods and the penes, probably depends on the condition of the spermathecae.

All Podotremata are characterized by the marked change in the alignment of the arthrodial cavities of posterior pereopods, with the last thoracomere(s) tilted upwards, often almost perpendicular to preceding ones. All podotreme families have the last two pairs of pereopods (P4 and P5) or the last pair alone (P5) modified and capable of carrying a camouflaging object, that is known in most representatives (Homolodromiidae, Dromiidae, Homolidae, Latreilliidae, Cyclodorippidae) (Guinot *et al.* 1995). In the Dynomenidae and the Raninoidea, in which carrying behaviour is absent, there is also a dorsal location of the arthrodial cavity of the P5.

This investigation reviews the morphology of the spermatheca in the 10 or 11 extant families and two fossil families of Podotremeta. It necessitates to describe, at least partly, the thoracic sternum and the axial skeleton.

We follow the classification already used by Guinot & Tavares (2003: 45). Section Podotremata, with three subsections: Dromiacea De Haan, 1833, with two superfamilies: Homolodromioidea Alcock, 1900 (one family: Homolodromiidae Alcock, 1900) and Dromioidea De Haan, 1833 (two families: Dromiidae De Haan, 1833, with three subfamilies Dromiinae De Haan, 1833, Hypoconchinae Guinot & Tavares, 2003, Sphaeodromiinae Guinot & Tavares, 2003; and Dynomenidae Ortmann, 1892); subsection Homolidea De Haan, 1839, with one superfamily: Homoloidea (three families: Homolidae De Haan, 1839, Latreilliidae Stimpson, 1858, and Poupiniidae Guinot, 1991); subsection Archaeobrachyura Guinot, 1977, with two superfamilies: Cyclodorippoidea (three families grouped for the moment *for convenience*: Cyclodorippidae Ortmann, 1892, Phyllotymolinidae Tavares, 1998, Cymonomidae Bouvier, 1897) and Raninoidea De Haan, 1839 (two families: Raninidae De Haan, 1839 and, perhaps, Symethidae Goeke, 1981).

MATERIAL AND METHOD

The species that were studied come from the collection deposited in the Muséum national d'Histoire naturelle, Paris (MNHN), generally preserved in 75° alcohol, and as far the material allowed. The examination of the spermatheca necessitated that the specimens are dissected and prepared for the study of the skeleton, by an immersion in a hot potassium hydroxyde (KOH) bath, to remove the soft tissues (Secretan-Rey 2002). To facilitate location of the pleurites it was preferable to cut the pereopods and only keep their arthrodial cavities, except for the P3 coxae bearing the female gonopores. The infoldings along the posteriomedian margin of sternite 8 were cut away in order to expose the endosternite 7/8, and dissections were necessary to show the internal details of the spermathecal structures. The best way to locate the spermatheca was by the arthrodial cavities of P4 and P5, i.e. in a caudal view of the crab.

For the axial skeleton we follow the terminology of Gordon (1950, 1963, 1966), Hartnoll (1979), Secretan (1998) and Secretan-Rey (2002). To write the name of the carcinologist De Haan versus de Haan (Fransen *et al.* 1997), we follow the spelling recommended by C. H. J. M. Fransen, Nationaal natuurhistorisch Museum, Leiden (pers. comm. 28.V.2004).

To preserve the custacean family name Dromiidae De Haan, 1833 (type genus *Dromia* Weber, 1795) and to remove homonymy with the insect family name Dromiidae Bonelli, 1810 (type genus *Dromius* Bonelli, 1810), an application has been proposed, so that the correct spelling of the coleopteran family will be Dromiusidae Bonelli, 1810 (Deuve *et al.* 2004).

Measurements refer to carapace length × carapace width (cw), in including the spines. The following abbreviations are used in the text: G1, first male pleopod or first gonopod; G2, second male pleopod or second gonopod; mxp1-mxp3, first to third maxillipeds; P1-P5, first to fifth pereopods; Pl, pleopods.

LIST OF THE SPECIES THAT WERE DISSECTED

Representatives of all the podotreme genera were examined, and the following species were completely (or partly) dissected:

- Homolodromiidae: *Homolodromia kai* Guinot, 1993; *H. bouvieri* Doflein, 1904; *Dicranodromia doederleini* Ortmann, 1892.
- Dynomenidae Ortmann, 1892: *Dynomene pilumnoides* Alcock, 1900; *Metadynomene tanensis* (Yokoya, 1933).
- Dromiidae De Haan, 1833:

1) Dromiinae De Haan, 1833: *Cryptodromia tuberculata* Stimpson, 1858; *Dromia marmorea* Forest, 1974; *D. personata* (Linnaeus, 1758); [*Dromia*] *dormia* (Linnaeus, 1763); [*Dromia*] *wilsoni* (Fulton & Grant, 1902); *Dromidiopsis indica* (Gray, 1831) n. comb.; *Epigodromia areolata* (Ihle, 1913); *Frodromia ?atypica* (Sakai, 1936); *Lauridromia intermedia* (Laurie, 1906); *L. dehaani* (Rathbun, 1923); *Lewindromia unidentata* (Rüppell, 1830); *Moreiradromia sarraburei* (Rathbun, 1910); *Stebbingdromia plumosa* (Lewinsohn, 1984); *Sternodromia spinirostris* (Miers, 1881); *S. monodi* (Forest & Guinot, 1966); *Takedromia cristatipes* (Sakai, 1969).
2) Hypoconchinae Guinot & Tavares, 2003: *Hypoconcha panamensis* Smith, 1869.
3) Sphaerodromiinae Guinot & Tavares, 2003: *Sphaerodromia lamellata* Crosnier, 1994; *S. kendalli* (Alcock & Anderson, 1894).

- Homolidae De Haan, 1839: *Homola ranunculus* Guinot & Richer de Forges, 1995; *Paromola bathyalis* Guinot & Richer de Forges, 1995; *Moloha majora* (Kubo, 1936); *Moloha* aff. *majora* (Kubo, 1936); *Homolomannia sibogae* Ihle, 1912.
- Latreilliidae Stimpson, 1858: *Latreillia valida* De Haan, 1839.
- Poupiniidae Guinot, 1991: *Poupinia hirsuta* Guinot, 1991.
- Cyclodorippidae Ortmann, 1892:

1) Cyclodorippinae Ortmann, 1892: *Tymolus daviei* Tavares, 1997.
2) Xeinostomatinae Tavares, 1992: *Krangalangia spinosa* (Zarenkow, 1970).

- Raninidae De Haan, 1839:

1) Lyreidinae Guinot, 1993: *Lyreidus tridentatus* De Haan, 1841.
2) Ranininae De Haan, 1839: *Ranina ranina* (Linnaeus, 1758).
3) Raninoidinae Lörenthey & Beurlen, 1929: *Raninoides bouvieri* Capart, 1951; *Raninoides* sp.; *Notopoides latus* Henderson, 1888.

- Dakoticancridae Rathbun, 1917: *Dakoticancer australis* Rathbun, 1917 (fossil, not dissected).
- Etyidae Guinot & Tavares, 2003: *Etyus martini* Mantell, 1844 (fossil, not dissected).

GENERAL STRUCTURE OF THE SPERMATHECA

The spermatheca, issued from the phragma formed by the two sternites 7 and 8 and being a part of the invagination of the axial skeleton at the level of the suture 7/8 (Fig. 1B), results from the separation of the two sheets of the phragma. A cavity is formed to receive and store the spermatic material. This cavity only opens externally and does not communicate with the interior. Used as a storage organ, it must protect its content against the external environment. The apposition of the two sheets and of the concerned external sclerites, sometimes with the overlapping of the infoldings, permits isolation of the sperm.

Because it is formed by phragma 7/8, the spermatheca is easily located by arthrodial cavities of P4 and P5 that it separates. In most Podotremata the sternum bends more or less abruptly at the level of the posterior somites, and thus the phragma 7/8 is oblique, roughly perpendicular to sternal plate. The spermatheca may be completely (its aperture excepted) calcified externally (Dromioidea), or consists of a poorly calcified area with several membranous parts (Homoloidea). In external view of the sternum, the opening is visible (at distal or subdistal part of the suture 7/8), either by a small orifice (Dromioidea *pro parte*), or by a slit (Dromioidea *pro parte*, Homoloidea, Cyclodorippoidea) or by a sunken pit (Raninoidea).

HISTORICAL ACCOUNT

The term "vulvae" was used at first to name the two median openings of eubrachyurans, which are situated on the sternum (sternite 6) and connected to the oviducts (Desmarest 1825: 63; H. Milne-Edwards 1834: 257, 262). But, in describing *Dromia* and the allied taxa which he included in the Anomura, H. Milne-Edwards (1837: 193) did not find these sternal female openings. The spermatheca was not seen by these authors. Thus, the gonopore on the P3 coxa was considered to be the only opening for reproduction, and the same name "vulva" was assigned to

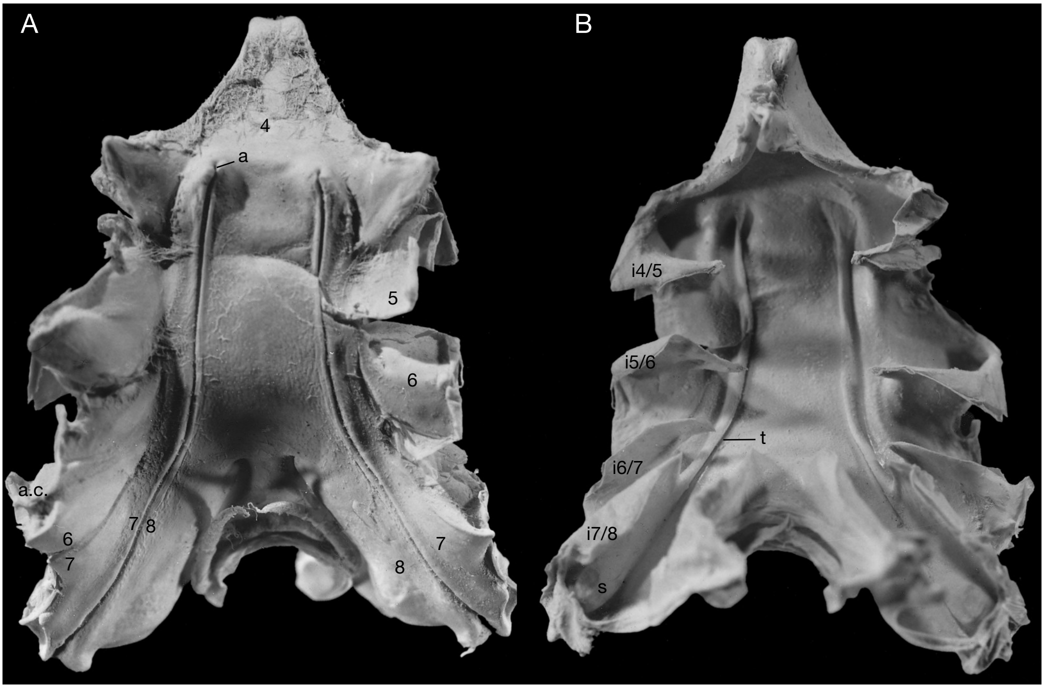

FIG. 1. — Modified thoracic sternum and long sutures 7/8 of the female of an unidentified dromiid (probably *Lauridromia* sp.) (Dromiidae, Dromiinae) (MNHN) (see Tavares 1994: fig. 37C, D); **A**, external view, with spermathecal aperture at level of P1; **B**, internal view, most of interosternites 4/5-7/8 removed, showing internally closed tube. Abbreviations: **a**, aperture of the spermatheca at extremity of sternal suture 7/8; **a.c.**, arthrodial cavity of P3; **i4/5-i7/8**, interosternites 4/5-7/8; **s**, location of the spermathecal pocket or chamber; **t**, spermathecal tube; **4-8**, sternites 4-8; **6/7**, **7/8**, thoracic sternal sutures 6/7, 7/8. (Courtesy of S. Secretan and M. Tavares).

these two different orifices. Previously, H. Milne-Edwards (1832: 304, 305, 326) had clearly separated the (true) Brachyura, characterized by the sternal vulvae (continued by a copulatory pocket; in French “poche copulatrice”), from the forms (*Dromia*, *Homola*, *Ranina*) with crab-like facies and with the genital orifices (so-called vulvae) positioned on the P3 coxa, and for that very reason assigned by this author to the Anomura.

In the Brachyura the term vulva is currently restricted to the female opening on the sternite 6, with a dual role role in copulation and release of eggs, and therefore concerns only the Eubrachyura (i.e. the non-Podotremata). All other Decapoda share with the Podotremata a genital, oviductal, opening on the third pereopod.

De Haan (1839: 105) was the first to observe the podotreme spermatheca and to define the podotreme organization. In *Dromia*, De Haan continued to name vulva the female gonopore on P3 coxa but, at the same time, he described in the anterior part of the sternum two “perforated tubercles” (“*tubercula perforata*”) in the prolongation of their very elongated “*sulci*” and lying beyond the female gonopores of the legs (“*Illa tubercula, a parte interior sunt clausa, et sulci ibidem plicis vel carinis duabus respondent*”). These perforations clearly correspond to the apertures of the spermathecae at the extremities of the sutures 7/8. Most certainly, De Haan had dissected a female dromiid and seen the internal anatomy, namely a structure which was closed on the internal side and formed by two careen-shaped infoldings (careen in the sense of shell of ship “coque d’un bateau”, or walnut husk “coque de noix”). De Haan (1839: 105) also remarked the differences with the males, in evoking the styliform male G2 inserted in the female furrows for mating (“*styli in sulco sterni feminei inserti ut fulcrum inservire in copulationis actu*”).

Thus, it was a long time before Ihle (1913: 12) that De Haan (1839) has first suggested the special sexual function of the female "*sulci*". Ihle (1913: 12-18) has discussed the significance of the "female furrows", observing their part modified in a special area and found only in females.

Stimpson (1858: 225, 226) erected five new genera besides *Dromia*, which at that time almost monopolised the family Dromiidae. Stimpson's subdivision was based chiefly on the disposition of female sutures 7/8, i.e. the level attained by their extremities and their termination apart or together, and accompanied or not by tubercles. Thus, from that date, the "sternal furrows" of the earlier authors were considered to be diagnostic characters by Alcock (1900a), Borradaile (1903a, b) and Ihle (1913).

The female thoracic sternum changes dramatically during ontogeny in the Dromiidae, with a drastic change in the development of the sutures 7/8, which move in a forward direction (Gordon 1950: fig. 23; Forest 1974: 75, 83; Lewinsohn 1977: 94; Manning & Holthuis 1981: fig. 3; Tavares 1994: 214-219), and passing through peculiar decalcified areas during growth (Franco 1998: figs 24, 25) (Fig. 1). Such a structure was considered to be a character with limited value (McLay 1993: 122, 150). But, just because a character or a character complex changes during ontogeny is not, in itself, an argument for not using it to separate genera. For Manning & Holthuis (1981: 21) it was "debatable whether the sole character of the placement of the female sternal grooves is sufficient to distinguish genera", and currently, authors place reliance on the disposition of the females sutures 7/8 (Forest 1974; McLay 2001a-c, 2002; Guinot & Tavares 2003). It is evident that morphological comparisons should only be made between fully developed individuals. The female genital morphology is only known due to the studies of Gordon (1949, 1950) and Hartnoll (1975). In the recent arrangement of the Dromiidae by Guinot & Tavares (2003), the generic condition of spermathecae does not detract their usefulness and, on the contrary, the detailed study of the thoracic sternum, including female sutures 7/8 (as the maintaining of the abdomen in males), makes hopeful a comprehensive view of the group.

In the recent years, the thoracic sternum has been described for a number of podotreme families.

The female sutures 7/8 of the Dynomenidae were described only recently by McLay (1999), but no detailed illustrations have been published since the interesting figures given by A. Milne-Edwards (1879: pl. 14, fig. 25). The female sutures 7/8 and the shape of the spermathecal apertures of the Homolodromiidae were studied in all known species by Guinot (1995). In the Homolodromiidae, as in the Dromiidae and Dynomenidae, the other sutures are only lateral. McLay's assertion (1999: 455) that, according to Guinot (1995), "only the sutures 7/8 and traces of 6/7 are visible", is erroneous.

With regard to the Homoloidea, De Haan (1839: 105) correctly observed that the female posterior sternal furrows form two ovate areas, which are covered by a membrane and are absent in the males ("*Sterni sectio postrema in feminis offert duas plagas ovatas, membrana obductas, quae in maribus desunt*"). Ihle (1913: 59, 60) had not realized the great importance of sutures 7/8 and the different patterns shown by homoloid species. The spermathecae have been carefully described and drawn (Gordon 1950; Hartnoll 1975) and may be used in the systematics of the group (see for example Lewinsohn 1977, 1979, 1984). The morphology of the spermathecae was unfortunately not employed by Guinot & Richer de Forges (1995).

The peculiar condition of the spermathecae of the Raninidae was investigated by Gordon (1950, 1963, 1966), Hartnoll (1975), Guinot (1993b), and their phyletic implications discussed by Hartnoll (1979). It was not taken into account in the revision by Tucker (1998).

A pattern with female sutures 7/8 in an anterior location is also encountered in derived podotreme families, i.e. in the Cyclodorippidae Ortmann, 1892 (in *Corycodus decorus* Tavares, 1993: see Tavares 1993: fig. 9b; specially extended in *Neocorycodus* Tavares, 1993, see Tavares 1994: fig. 22D; 1996: fig. 23D), the Cymonomidae Bouvier, 1897, and in the Phyllotymolinidae Tavares, 1998 (see Tavares 1994) (Fig. 28).

The first observation of orifices at the extremity of the sutures 7/8 in fossil crabs was published by Guinot (1993a: 1229, figs 7, 8) in the Cretaceous genus *Dakoticancer* Rathbun, 1917, even if they were clearly visible (and gonopores on the P3 coxae as well) in the photographs by Bishop (1974). The second case of a fossil with spermathecae was observed in the Cretaceous *Etyus martini* Mantell, 1844 by Guinot & Tavares (2003: figs 2, 3, 10J), who erected a new family, the Etyidae, for *Etyus* Leach *in* Mantell, 1822 and *Xanthosia* Bell, 1863. This confirmed the accurate views of Glaessner (1929a, b, 1969) who suspected their position in the Dromiacea, perhaps in the Dynomenidae. The oblique, large apertures at the extremities of the sutures 7/8, unclear in the photographs of *Etyus martini* by Wright & Collins (1972: 102, pl. 21, fig. 6d, e), were considered orifices of oviducts (Schweitzer Hopkins *et al.* 1999).

It is evident that the lack of ventral parts in the fossil record does not allow a good understanding of the number of crabs with the podotreme condition. For example, in the numerous known Prosopidae von Meyer, 1860, the female sutures 7/8 remain unknown (Müller *et al.* 2000): we lack precise data, but we would predict that they are probably short. In other respects, different fossil genera and species previously attributed to Eubrachyura probably possess spermathecae and must be re-evaluated.

THE SPERMATHECAE OF EXTANT PODOTREMES

Section PODOTREMATA Guinot, 1977

Subsection DROMIACEA De Haan, 1833

In all the Dromiacea the thoracic sternum (sternal plate) forms in both sexes a relatively narrow shield, with all sternites almost completely fused together, except laterally where traces of the sutures are still visible near the condylar articulation of the coxae of the pereopods (Homolodromiidae: Figs 3A; 27A; Dromiidae: Figs 1A; 5; 8A; 10A; 11B; 12A; 13; 15; 16A). The sutures are sometimes so faint that they are hardly apparent (Dynomenidae: Fig. 4A, C). The second gonopods are very long, often longer than the first, always each with a needle-like flagellum (except for the enigmatic *Stebbingdromia* Guinot & Tavares, 2003).

A review of the morphology of the Dromiacea, considered monophyletic, had revealed the wealth of morphological patterns found in the Dromiidae (Guinot & Tavares 2003). A subfamilial division for the Dromiidae with three subfamilies, Dromiinae De Haan, 1833, Hypoconchinae Guinot & Tavares, 2003, and Sphaerodromiinae Guinot & Tavares, 2003, was proposed (Guinot & Tavares 2003).

The typical spermatheca of an adult dromiacean may be internally subdivided into two or three parts. After dissection, a female specimen *Dromia marmorea* Forest, 1974 (Dromiidae Dromiinae) showed three parts (Figs 2; 6): 1) at the posterior corner of the endosternite 7/8, a strongly calcified boss, the bulb; 2) a larger structure, a chamber, also named pocket, that corresponds to the main bulge of the endosternite 7/8, its size depending of the space left between the two sheets which form both external (endosternite 7) and inner (endosternite 8) walls; and 3) along the rest of the length of the suture 7/8, a long and calcified hollow tube, with a relatively small lumen, communicating with the exterior (see also Fig. 14). This channel is not found in all Dromiacea; it is absent in one dromiid subfamily (Sphaerodromiinae), in the Dynomenidae, and in all other Podotremata where the chamber directly communicates with the exterior.

Superfamily HOMOLODROMIOIDEA De Haan, 1833

Family HOMOLODROMIIDAE Alcock, 1900

The family Homolodromiidae, considered to be monophyletic, consists of only two genera, *Homolodromia* A. Milne-Edwards, 1880, and *Dicranodromia* A. Milne-Edwards, 1880, with

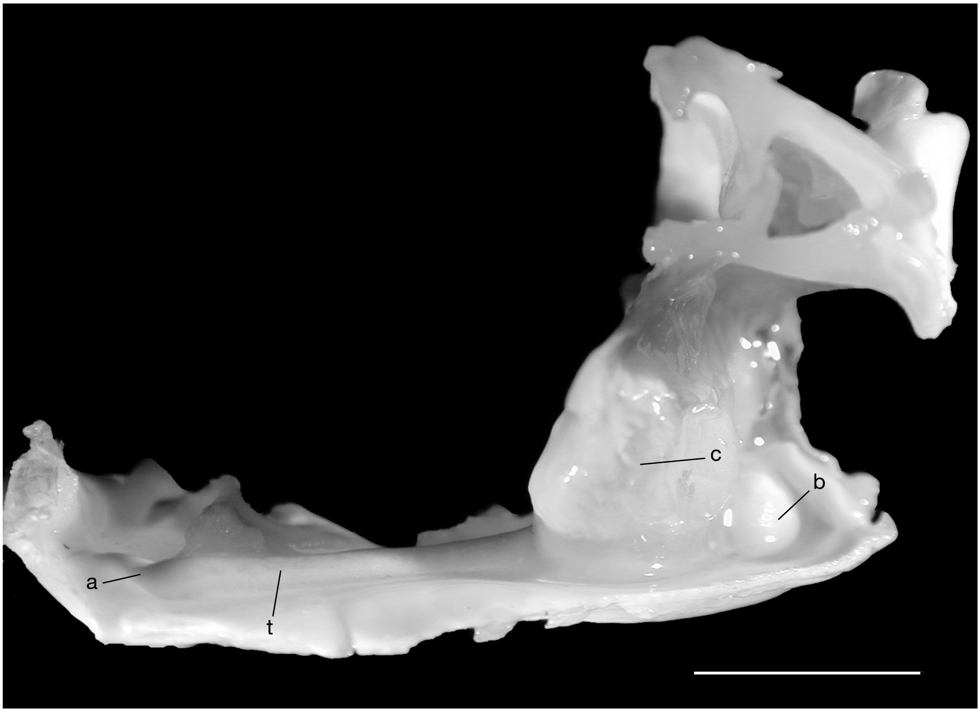

FIG. 2. — The three main internal parts of a typical dromiacean spermatheca, after the removal of the skeleton, median view, *Dromia marmorea* Forest, 1974 (Dromiidae, Dromiinae), female 57 × 72 mm, Azores (MNHN-B 21900). Abbreviations: **a**, communication with exterior by spermathecal aperture; **b**, bulb; **c**, chamber; **t**, spermathecal tube. Scale bar: 0.5 cm.

some 20 extant species, relatively rare but distributed in major oceans (Guinot 1993a, 1995: figs 39-41), including New Zealand waters (Dawson 2002). Numerous ancestral homolodromiids constitute the closely related, exclusively fossil family Prosopidae, known from the Early Jurassic (including *Eoprosopon klugi* Förster, 1986) but that disappeared at the early Palaeocene (Müller *et al.* 2000). The genus *Homolodromia* is known since the Upper Cretaceous of New Zealand (Feldmann 1993; Feldmann & McLay 1993).

Scholtz & Richter (1995) supported the primitive status of the Homolodromiidae but went so far as regarding homolodromiids as the sister-group of all other Brachyura. They have since, however, returned homolodromiids to the Dromiacea (Scholtz & Richter, oral statement in the 2nd European Crustacean Conference, Liège 1996). The extant homolodromiid representatives show a great number of plesiomorphic characters that supports the contention that the family probably contains the most primitive members of the Podotremata.

The male abdomen, which completely fills the sterno-abdominal depression, maintains vestigial pleopods and markedly extended abdominal pleurae. The thoracic sternum has its sternites distinctly layered, with exclusively lateral but visible sutures. Sutures 7/8 are more or less situated laterally along the species and are sometimes very convergent, as in *Dicranodromia foersteri* Guinot, 1993 (Guinot 1995: fig. 17d). They end either far back on the plate behind level of P3 coxae (*Homolodromia kai*; *H. robertsi* Garth, 1973; *Dicranodromia karubar* Guinot, 1993) or approximately at the level of the P3 coxae (*H. bouvieri* Doflein, 1904, see Fig. 27A; *D.* aff. *foersteri* Guinot, 1993; *D. nagaii* Guinot, 1995; *D. felderi*), or extend slightly beyond (notably

D. spinosa Martin, 1994) (Guinot 1995: 182, figs 6, 10C, 12C, 14b, 16C, 17d, 28b, 32c, d, 33, 37b-g). The spermathecal apertures are generally tiny, rounded or slightly ovate, and diversely (along the species) accompanied by a sternal tubercle or a thickening (Gordon 1950: fig. 1; Guinot 1995: 182). In a recently examined female of *D. spinulata* Guinot, 1995 from Fiji Islands (MNHN-B 28901), however, the terminal spermathecal apertures are each replaced by a long slit (about half the length of the suture 7/8) because of the two sheets of endosternites 7/8 that do not join in their subterminal parts.

It should be noted that *Homolodromia* species show relatively distinct patterns of the sutures 7/8. Sutures 7/8 are regularly curved to converge medially and their apertures are located, in the middle of a ring, posteriorly to the gonopores on the P3 coxae (as in *H. kai*; see Guinot 1995: fig. 10C; and Fig. 3A). Or they are oblique and open behind the females gonopores (as in *H. robertsi* Garth, 1973; see Guinot 1995: fig. 6), or they run along the margins of the sternum, being almost vertical, and open each on the summit of a strong tubercle at the level of the P3 gonopores (as in *H. bouvieri*; see Fig. 27A). Further investigations are needed to clarify the systematics of the genus *Homolodromia*.

In the family Homolodromiidae, the tip of a male second gonopod was found broken-off in the spermathecal apertures (on one side or on both sides) of some females (Guinot 1995: 178, 182, fig. 6), an indication that the long G2 enters the spermatheca and can be used for an internal insemination (see discussion below). In other species (for example in an ovigerous female of *Dicranodromia foersteri*, MNHN-B 24866) a small amount of brownish sperm protrudes from the two apertures.

In the homolodromiid axial skeleton (Fig. 3B, D), the connections still occur by interfingering, i.e. by simple digitations, a condition encountered in the Nephropidae (Drach 1959, 1971; Guinot 1979a; Secretan 1998; Secretan-Rey 2002) and in most Decapoda. Endosternites are not grouped in a single mass but join each other transversally metamere by metamere. All parts are regularly layered. A large intertagmal phragma (which links the tagma/thorax to the tagma/abdomen) extends toward the last endosternite and joins it.

A carrying behaviour of members of the family, similar to that of the Dromiinae and Sphaerodromiinae, is now documented, always with a sponge, in *Dicranodromia doederleini* Ortmann, 1892 (Ikeda 1998), in *D. felderi* Martin, 1990 (Martin & Zimmerman 2001) and in *Homolodromia kai* Guinot, 1993 (Ho & Ng 1999).

Genus *Homolodromia* A. Milne-Edwards, 1880

Homolodromia kai Guinot, 1993

Female 12.4 × 8.3 mm, Indonesia, Kai Islands, KARUBAR 1991, stn CC 21 (MNHN-B 22704).

On the thoracic sternum (Guinot 1995: fig. 10C), sutures 7/8 are relatively short, oblique and converge medially (Fig. 3A, C). They end in apertures situated behind the level of the female gonopores on the P3 coxae. The small spermathecal apertures open each in the center of a salient ring. The bulb of each spermatheca (Fig. 3B, D) is rather large but not swollen. The chamber has its two sheets nearly adjoining, without a marked space between them; its inner wall is membranous but not very soft, and unornamented. A basal thickening extends on whole length of the chamber; its entire visible surface is well calcified. A tube is clearly present, although it is not very long (corresponding to the rather short sutures 7/8), and it ends by a conspicuous terminal opening. The axial skeleton (Fig. 3B) conforms to the above description.

Homolodromia bouvieri Doflein, 1904

Ovigerous female 33 × 26 mm, Madagascar, trawling 123, 30.XI.1980, 800 m, Rudo von Cosel coll., A. Crosnier det. 2003 (MNHN-B 28940).

The sternal sutures 7/8 of this big female are marked and lined by a thickening at each spermathecal aperture, which is raised at the summit of a strong tubercule, at the level of the P3 coxae and very close to the wide female gonopores (Fig. 27A).

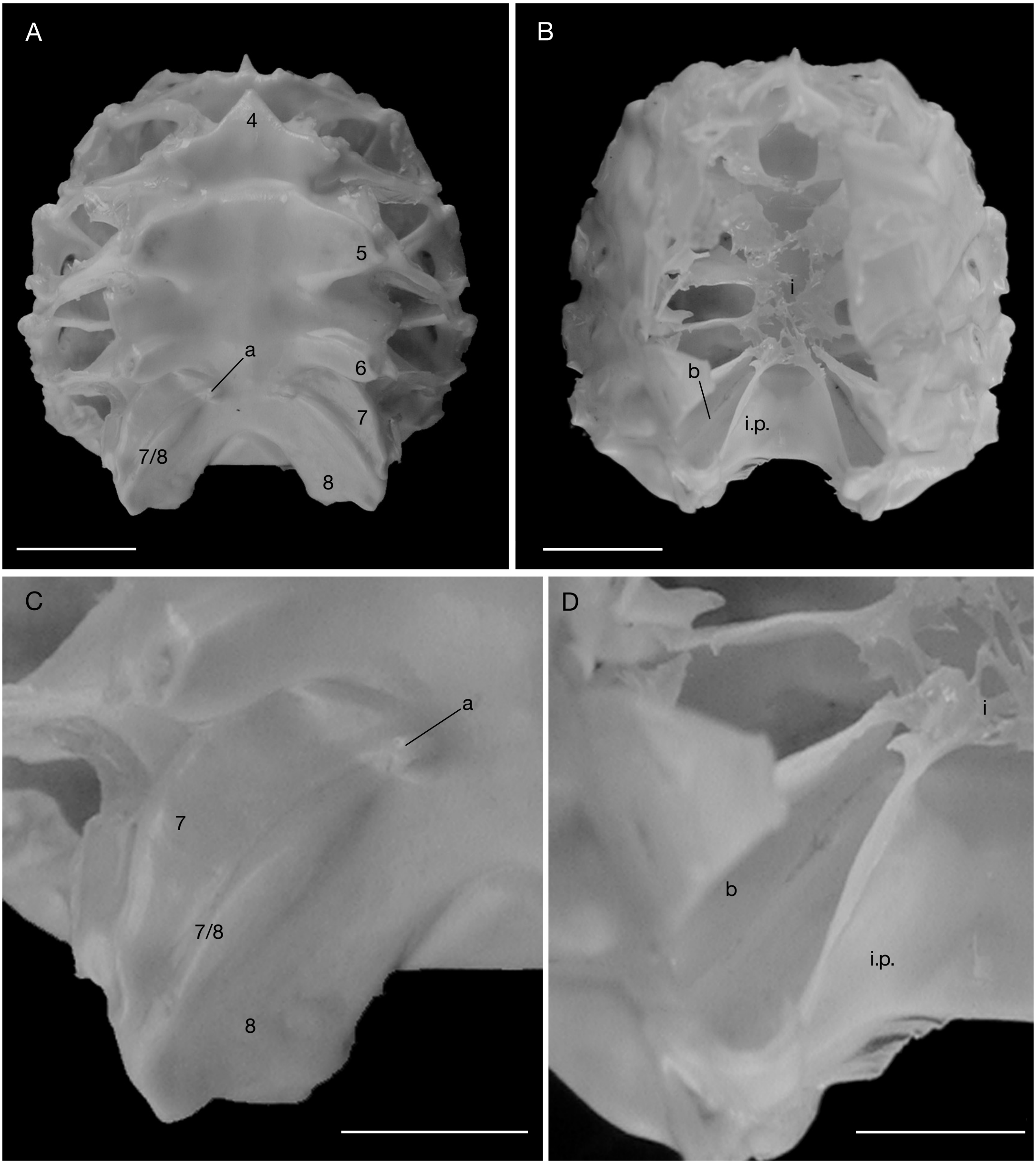

FIG. 3. — *Homolodromia kai* Guinot, 1993, female 12.4 × 8.3 mm, Indonesia, Kai Islands (MNHN-B 22704); **A**, thoracic sternum; **B**, axial skeleton, with spermathecal bulb visible but short spermathecal tube not discernible; **C**, detail of A, left posterior part; **D**, detail of B, left posterior part. Abbreviations: **a**, spermathecal aperture at extremity of sternal suture 7/8; **b**, bulb; **i**, connections by interfingering; **i.p.**, intertagmal phragma; **4-8**, sternites 4-8; **7/8**, thoracic sternal suture 7/8. Scale bars: A, B, 4 mm; C, D, 2 mm.

In this specimen a small sperm plug fills the two apertures. The pattern is the same as in the Dromiinae, for example *Lauridromia intermedia* (Laurie, 1906) (Fig. 13), except that in *Homolodromia* sutures 7/8 are shorter and spermathecal apertures opposite P3 coxae (while ending at the level of P1 coxae in *Lauridromia*). The specimen was not dissected.

Genus *Dicranodromia* A. Milne-Edwards, 1880

Dicranodromia doederleini Ortmann, 1892

Female 21.2 × 14 mm (partly dissected out by Bouvier), near Tokyo (MNHN-B 21683).

Sutures 7/8 of the thoracic sternum converge medially and end in apertures situated slightly behind the level of P3 coxae. Spermathecal apertures are tiny and each is surrounded by a salient transversal thickening (Guinot 1995: fig. 12C). The presence of a well visible spermathecal tube is confirmed, in accordance with the hypothesis of Gordon (1950: 25) who predicted the presence a very short tube in *Dicranodromia baffini* Alcock & Anderson, 1899. Skeletal connections occur by interfingering.

Superfamily DROMIOIDEA De Haan, 1833

Family DYNOMENIDAE Ortmann, 1892

The family Dynomenidae, reviewed by McLay (1999) and with recent new records (McLay 2001b), is worldwide in distribution but consists of only five genera and less than 20 described species, which are often associated with corals. The Dynomenidae are probably known from the Jurassic (Glaessner 1969), but Müller (1984: 64) wrote that *Dynomene* Guérin-Méneville, 1832 remained unrecognized in fossil form "because of the similarity of its carapace to some Xanthids".

We agree with Beschin *et al.* (2004: 113): the Eocene *Kromtitis tetratuberculatus* Beschin, Busulini, De Angeli & Tessier, 2002 (p. 12, fig. 7, pl. 2, figs 2, 3), originally referred to the family Dromiidae, shows close relationship with the living *Paradynomene* Sakai, 1963.

The dynomenid thoracic sternum is relatively broad, with all the sutures laterally located. The sternum clearly widens in some members of the family (Guinot & Bouchard 1998). In males the sterno-abdominal depression is not deeply hollowed (except for *Acanthodromia*), always with a well developed central flat surface, a great part of sternites 1-6 being fused in a single wide plate. Sternites 7 (narrow) and 8 do not markedly slope backwards, even in females (except for *Acanthodromia*). Sutures 4/5, 5/6 and 6/7 are faint, being completely lateral and concealed inside the sterno-coxal depressions. Female sutures 7/8 are short but marked, and generally lie close to the margins of the P3 coxae. The broad, flexible male abdomen is not closely held on the sternum, retains vestigial pleopods on segments 3-5 and may be involved in the locomotion (A. Milne-Edwards 1879: 4; McLay 1999: 456). In males the sternal plate is covered by a long abdomen that occupies its whole length (*Acanthodromia* A. Milne-Edwards, 1880), or the abdomen is shorter and leaves the anterior sternites uncovered (all other dynomenid genera). The sternum is either entirely covered laterally (*Acanthodromia*, *Metadynomene* McLay, 1999, *Paradynomene*) or partly visible on each external side (*Dynomene*, *Hirsutodynomene* McLay, 1999). The latter condition is considered the advanced one (Guinot & Bouchard 1998). Due to the shortness of sutures 7/8 the spermathecal apertures lie just below or slightly behind the female gonopores on the P3 coxae. They are ovate, small but deep, and always end apart, either beneath a curved over-hanging lip (*Acanthodromia*) or behind low tubercles (*Hirsutodynomene*, *Dynomene*) (McLay 1999: 455).

Junctions occur by fusion in the dynomenid axial skeleton, as in the Dromiidae, and the intertagmal phragma skirts the last endosternite to join the median mass from below. The skeletal system shows two distinct patterns in the two genera that were examined. In *Dynomene pilumnoides* Alcock, 1900 the transverse bridge is shorter and thicker (Fig. 4D) than in *Metadynomene tanensis* (Yokoya, 1933) (Fig. 4B), which corroborates the more advanced condition of *Dynomene*. A third pattern is represented by *Paradynomene* (Secretan 1998: figs 7, 8), in which the skeletal parts seem more layered, and the median fusion is longitudinally extended on a longer part.

Genus *Dynomene* Guérin-Méneville, 1832

Dynomene pilumnoides Alcock, 1900

Female 12.4 × 14.5 mm, Madagascar (MNHN-B 6913).

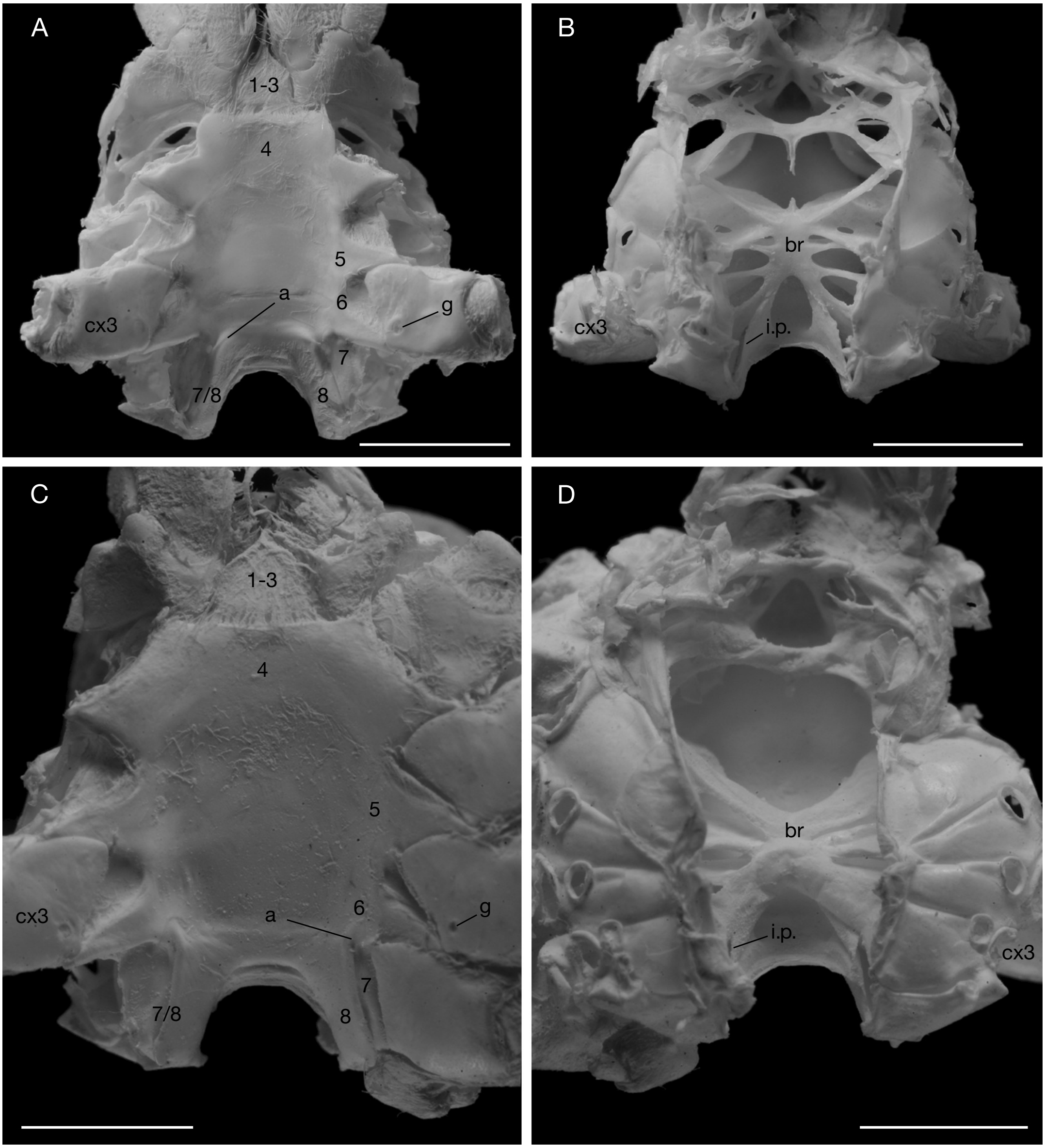

FIG. 4. — **A**, **B**, *Metadynomene tanensis* (Yokoya, 1933), female 20.5 × 21.9 mm, New Caledonia (MNHN-B 26576); **C**, **D**, *Dynomene pilumnoides* Alcock, 1900, female 12.4 × 14.5 mm, Madagascar (MNHN-B 6913); **A**, **C**, thoracic sternum; **B**, **D**, axial skeleton, with connections by fusion. Abbreviations: **a**, spermathecal aperture at extremity of sternal suture 7/8; **br**, transverse bridge; **cx3**, P3 coxae; **g**, female gonopore; **i.p.**, intertagmal phragma; **1-3**, sternites 1-3; **4-8**, sternites 4-8; **7/8**, thoracic sternal suture 7/8. Scale bars: 5 mm.

Sutures 7/8 lie at the limit of the hollows corresponding to the sterno-coxal depressions of the P4, and the apertures are not discernible (Fig. 4C). The spermathecal bulb is well developed. Each chamber has its two nearly adjoining sheets without a marked space between them. There is no tube, which means that the chamber itself ends by the small terminal opening.

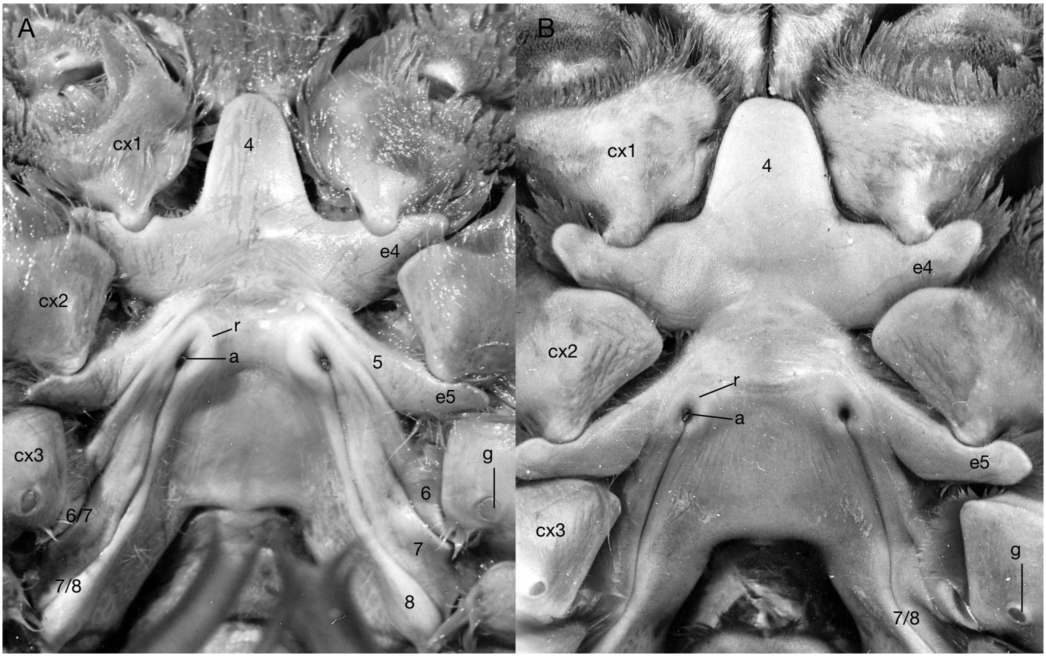

FIG. 5. — Thoracic sternum in two species of *Dromia* Weber, 1795 (Dromiidae, Dromiinae); **A**, *D. personata* (Linnaeus, 1758), female 47 × 58 mm, France, Island of Yeu (MNHN); **B**, *D. marmorea* Forest, 1974, female paratype 57 × 73 mm, near Dakar (MNHN) (Courtesy of J. Forest). Abbreviations: **a**, spermathecal aperture at extremity of sternal suture 7/8; **cx1**-**cx3**, P1-P3 coxae; **e4**, **e5**, episternites 4, 5; **g**, female gonopore; **r**, ring encircling spermathecal aperture; **4-8**, sternites 4-8; **6/7**-**7/8**, thoracic sternal sutures 6/7 to 7/8.

Genus *Metadynomene* McLay, 1999

Metadynomene tanensis (Yokoya, 1933)

Female 20.5 × 21.9 mm, New Caledonia, SMIB 8, stn DW 199 (MNHN-B 26576).

Suture 7/8 ends by a visible aperture (Fig. 4A). The spermathecal bulb, well developed and pear-shaped, extends along the whole length of each chamber, without a visible basal thickening. The chamber has its two sheets nearly adjoining, without a marked space between; the inner wall is relatively soft. There is no tube, and at its anterior part the chamber itself ends by a well marked terminal opening.

Family DROMIIDAE De Haan, 1833

The family Dromiidae, commonly referred to as "sponge crabs", was extensively revised by McLay (1993), and later augmented with several new genera and species (McLay 2001a-c, 2002; Guinot & Tavares 2003). It forms the largest family of primitive brachyuran crabs (more than 120 species in some 40 genera). The subfamilial system (Dromiinae, Hypoconchinae, and Sphaerodromiinae) proposed by Guinot & Tavares (2003) was largely based upon the organization of the thoracic sternum, including the female sternal sutures 7/8 and the apertures of the spermathecae at their extremities.

Subfamily DROMIINAE De Haan, 1833

The female thoracic sternites 7 and 8 are more or less strongly tilted backwards. In adult females, sternites 7 and 8 grow forward, encroaching the preceding sternites (6, 5, and even 4), and sutures 7/8

FIG. 6. — Details of the spermatheca of *Dromia marmorea* Forest, 1974 (Dromiidae, Dromiinae), female 57 × 72 mm, Azores (MNHN-B 21900); **A**, posterior part of axial skeleton in median view to show spermatheca *in situ*; **B**, details of foldings at level of the spermathecal bulb; **C**, lateral view, skeletal parts removed; **D**, vertical view of spermathecal chamber, cut to show sperm inside. Abbreviations: **a**, communication of the spermatheca with exterior; **b**, bulb; **c**, chamber, uneven surface of inner wall; **e5**, episternite 5; **en 6/7**, endopleurite 6/7; **is 6/7**, interosternite 6/7; **t**, spermathecal tube. Scale bars: A, C, 1 cm.

advance far forward, sometimes so far that sternites 7 and 8 occupy much of the ventral surface of the cephalothorax (Fig. 1). Additionally, in many dromiids the female sternal surface becomes more complex, owing to the fact that the apertures of the spermathecae often end apart on (or beneath) two more or less prominent tubercules, or more or less together on (or beneath) a unique tubercle (Forest 1974: fig. 6b, c, pl. 6, figs 1, 2). Dromiine females consequently show a completely distorted thoracic sternum. From the observations and figures given by Gordon (1950: 244, figs 23-25, pl. 1, fig. B, as *Dromia vulgaris*) it is clear that the dromiid spermatheca constitutes a differentiated complex structure. The present study expands the results of Guinot & Tavares (2003) and confirms the characters of dromiine spermatheca as a generic one. The axial skeleton of the Dromiinae, figured here for several species (Figs 7; 10B; 11A; 12B), typically shows the following organization: connections between the phragmae effected by fusion; endopleurites of each lateral part remaining on the sides, the two sides being connected by a wide transverse bridge; intertagmal phragma exclusively fused with the endosternal part of the skeleton; and absence of a sella turcica (Secretan 1998: 1758, figs 9-11). Endosternite 7/8 is completely modified, notably by presence of the spermathecal tube.

Genus *Cryptodromia* Stimpson, 1858

Cryptodromia tuberculata Stimpson, 1858

Ovigerous female 9 × 10 mm, New Caledonia, Karembé, McLay det. (MNHN-B 26387) (not dissected).
Sutures 7/8 are long and end between P2 and P1 in terminal apertures that stand apart on two strong tubercles. The phragmal sheets, which are distinctly raised, are disjoined along a more or less long distance and form wide opened slits, leaving visible the bottom of the spermathecal tube (Fig. 27B).

Genus *Dromia* Weber, 1795 *s.l.*

Examination of the species assigned to *Dromia* sensu McLay, 1993 has shown that the genus was not monophyletic, which necessitated to establish two new genera for two Indo-Pacific species, viz. for [*Dromia*] *dormia* (Linnaeus, 1763) and [*Dromia*] *wilsoni* (Fulton & Grant, 1902) (Guinot unpubl. data).

Dromia marmorea Forest, 1974

– Female 57 × 72 mm, Azores, BIAÇORES, stn P.34 (MNHN-B 21900).
The sternal sutures 7/8 open anteriorly between the P2 and each ends apart in the middle of a very weak and circular prominence, by an aperture consisting of terminal rounded opening (Figs 2; 5B; 6). The bulb of each spermatheca is posterior only, without extending on basis of the chamber, but it prolonges by a marked basal thickening; the bulb is globular, prominent, not tapering, its surface is uneven, and a small pointed prominence is visible anteriorly. The dissection of the bulb showed the presence of sperm inside. The chamber is much inflated and filled with sperm mass; the inner wall is membranous and well ornamented. The tube is very thick, ending in a terminal opening, corresponding to each spermathecal aperture positioned between the P2.
– Female 12 mm length, Azores, BIAÇORES 1971 (MNHN-B 12746).
The sternal sutures 7/8 only end at the level of the P3, beyond the level of gonopores on the P3 coxae, however.

Dromia personata (Linnaeus, 1758)

– Female 64.2 × 77.1 mm, French coasts (MNHN-B 21971).
The female sternal sutures 7/8 open anteriorly at the level of the P2 and end apart inside a prominent ring; the spermathecal apertures are terminal and rounded (Fig. 5A). The bulb of each spermatheca is well defined and prominent, with uneven surface and with a pointed anterior prominence. The chamber (Fig. 7B) consists of two parts: inferior part, larger and inflated, superior one more flattened. The inner wall (endosternite 8) is flexible and bears a few scattered calcifications, resulting in a wrinkled texture; the outer wall (endosternite 7) is rigid and its surface smoother. The basal thickening is well marked. The tube is very thick, with terminal orifice. The details conform to the disposition that was already described and figured by Gordon (1950: 244, figs 23, 25, as *Dromia vulgaris*) and Hartnoll (1979: 667, fig. 6).

– Female, approximately 36 mm width (MNHN; skeleton prepared by Sylvie Secretan).
The aspect is similar. The chamber contains sperm mass. In smaller immature females the two walls of the chamber are joined.

– Male 58.7 × 74.9 mm, Quiberon(?), Bourdon coll. (MNHN-B 21981).
The sternal plate of the males is characterized by the presence, on its median fused part and at the level of episternites 5, of an unpaired setiferous boss to which corresponds an internal concavity. Suture 7/8 is not in any way modified and ends almost at the level of suture 6/7 and opposite the P3 coxae. As in the immature females, there is no pocket between the two sheets of interosternites 7/8; a basal thickening is not present; the tube is absent. There is a relief, which probably corresponds only to a reinforcement, at the same place as the female's bulb.

Dromia bollorei Forest, 1974

Dromia bollorei differs from *D. personata* by the sutures 7/8 that converge medially and end together (instead of being separate); the apertures of the spermathecae are located together on two well discernible, coalescent tubercles forming a transverse prominence (Forest 1974: fig. 6a, pl. 6, fig. 1).

[***Dromia***] ***dormia*** (Linnaeus, 1763)

Female, 107 mm carapace length, New Caledonia, Tabu Recif, Laboute coll. (MNHN-B 26439). A new genus to be erected (Guinot unpubl. data).
The very long female sternal sutures 7/8 (total length about 50 mm) converge gradually but diverge slightly near the end at the level of the chelipeds. They end together in the middle of sternite 4, being only separated by a smooth ridge. Each suture 7/8 opens in a pit, which is ovate (length about 10 mm) and unperforated, with very thin external and internal edges, not so calcified as the median part, which corresponds internally to the spermathecal tube (Guinot unpubl. data). The pit corresponds to the level

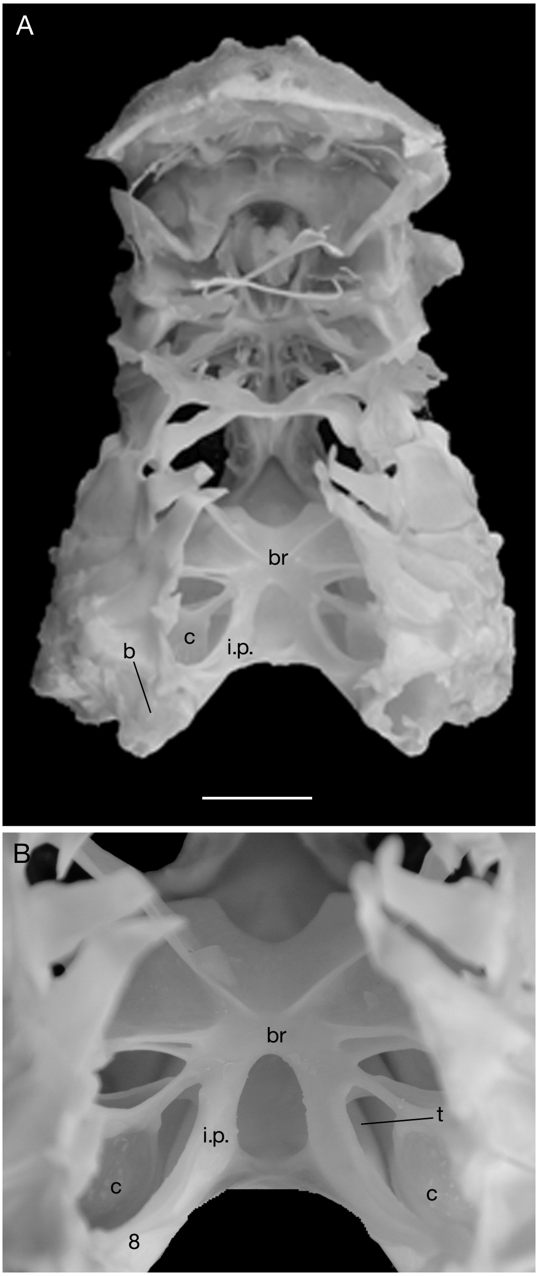

FIG. 7. — *Dromia personata* (Linnaeus, 1758), female 64.2 × 77.1 mm, France (MNHN-B 21971); **A**, axial skeleton, dorsoventral view, spermathecae *in situ*, bulb and chamber visible; **B**, posterior part enlarged, tube discernible on the bottom. Abbreviations: **b**, bulb; **br**, transverse bridge; **c**, spermathecal chamber; **i.p.**, intertagmal phragma; **t**, spermathecal tube; **8**, sternite 8. (See Secretan 1998: fig. 11). Scale bar: A, 1 cm.

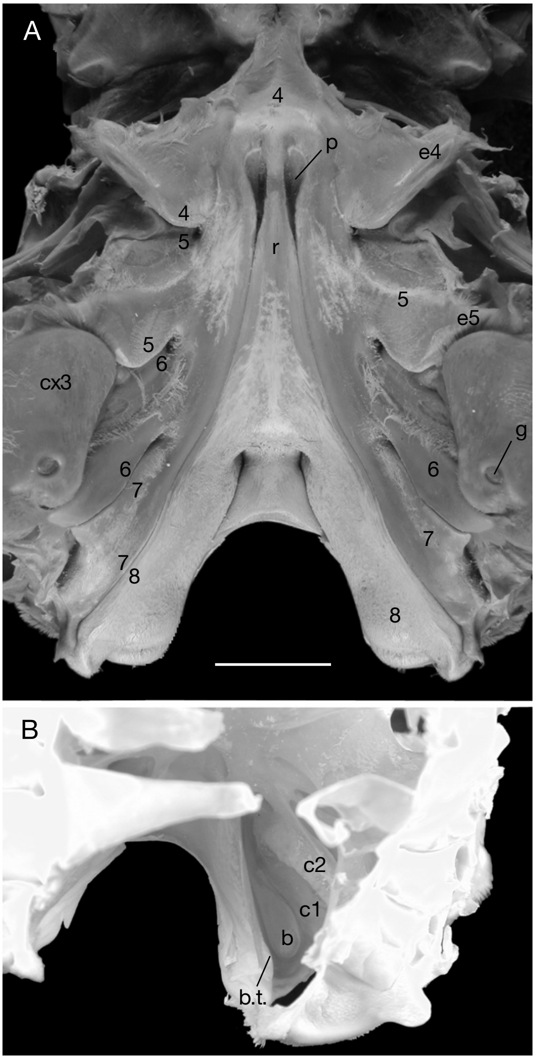

FIG. 8. — [*Dromia*] *dormia* (Linnaeus, 1763), female 107 mm carapace length, New Caledonia (MNHN-B 26439); **A**, thoracic sternum; **B**, detailed part view of spermatheca, skeletal parts removed. Abbreviations: **b**, bulb; **b.t.**, basal thickening; **c1**, soft part of spermathecal chamber; **c2**, rigid part of spermathecal chamber; **cx3**, P3 coxa; **e4**, **e5**, episternites 4, 5; **g**, female gonopore; **p**, pit; **r**, ridge between the two pits; **4**-**8**, sternites 4-8; **4/5**-**7/8**, thoracic sternal sutures 4/5 to 7/8. Scale bar: A, 1 cm.

where phragma 7/8 rises to the surface (Figs 8A; 9). As a result, the spermatheca is devoid of the terminal circular aperture found in the species of *Dromia*. The whole sternal part that bears these pits slopes backwards and upwards at an angle of about 45°, while the anterior part of the sternite 4 is horizontal. Since only extremely large individuals of [*Dromia*] *dormia* were examined, there is some doubt about the structure shown by small sized adult individuals (Guinot unpubl. data).

The bulb of the spermatheca (Fig. 8B) is elongated, not very globular, and shows a raised part that forms a flat area in the posterior corner; it bears a small anterior prominence. The inner wall of the chamber has a soft inferior part, while the superior one is more rigid. The remains of sperm are visible inside the chamber. The basal thickening is marked. The tube is long (as long as the suture 7/8 which is about 50 mm length), thick, and its extremity raises progressively, with two weakly calcified zones on each side at the level of the external pit (Fig. 9). The tube is not perforated at its end but is opened in its terminal length, the phragma 7/8 itself becoming exposed and constituting the aperture of the spermatheca.

[***Dromia***] ***wilsoni*** (Fulton & Grant, 1902)

Female 35 × 47.8 mm, French Polynesia, Marquesas Islands, Tahuata (MNHN-B 26480). A new genus to be erected (Guinot unpubl. data). The whole thoracic sternum is short and enlarged, rather flat, without a marked posterior curvature; the sterno-abdominal depression is wide. The female sternal sutures 7/8 are relatively short, reaching only the level of the episternites 5, remain lateral and end apart; the spermathecal apertures are terminal and rounded (Fig. 10A). The bulb of the spermatheca is weakly prominent, prolonged by basal thickening on half of the chamber. This chamber is rather small, not very high. The tube is very narrow on its whole length, tapering, and with terminal orifice. The thoracic skeleton (Fig. 10B) is characterized by the concentration of the phragmae.

Genus *Dromidiopsis* Borradaile, 1900

Dromidiopsis indica (Gray, 1831) n. comb.

Female 59 × 58 mm, Nhatrang, McLay det. *Lauridromia indica* (MNHN-B 12758) (not dissected).

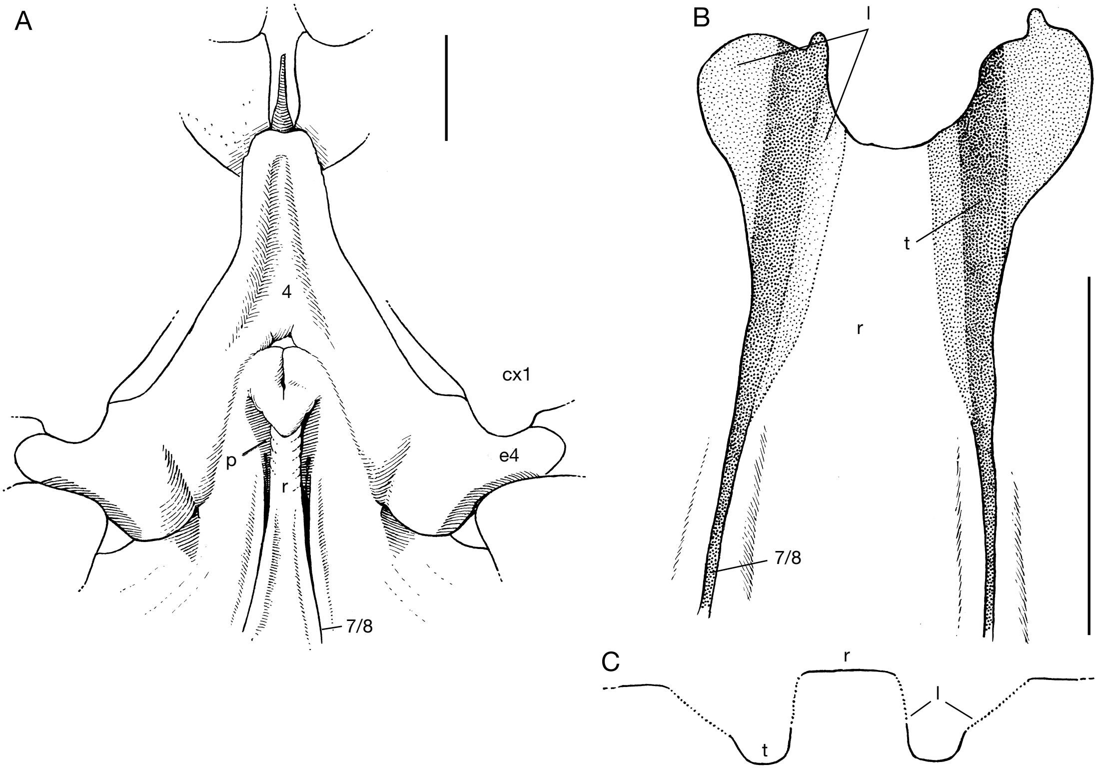

FIG. 9. — [*Dromia*] *dormia* (Linnaeus, 1763), female 88 × 105.8 mm, New Caledonia (MNHN-B 26438); **A**, anterior part of thoracic sternum (see Fig. 8A), showing terminal part of sutures 7/8 forming two pits; **B**, detailed view of pits; **C**, schematic section at level of the pits. Abbreviations: **cx1**, P1 coxa; **e4**, episternite 4; **l**, weakly calcified lateral parts of the pits; **p**, pit; **r**, ridge between the two pits; **t**, location of spermathecal tube; **4**, sternite 4; **7/8**, thoracic sternal suture 7/8. Scale bars: 5 mm.

In the revision of McLay (1993) *Dromia indica* Gray, 1831 was assigned to *Lauridromia* McLay, 1993, and the same way was followed later with a detailed description based on an abundant material (McLay 2001c: 823). But this species does not conform to the two other species of the genus, *L. intermedia* (Laurie, 1906), the type species, and *L. dehaani* (Rathbun, 1923). *D. indica* must be referred to *Dromidiopsis* (see Guinot & Tavares 2003: 61) because of the following characters: abdominal segments 5 and 6 almost totally fused (a character shared by *Dromidiopsis* and *Lauridromia*); external borders of abdominal segment 6 deeply excavated and thickened on the edges; telson long and ovate; male uropods oriented obliquely; anterior margin of sternite 4 bluntly truncate; female sternal sutures 7/8 gradually convergent, then getting abruptly close to each other and remaining parallel along the distal half of their lengths; spermathecal apertures located just between the P1, together at the summit of two coalescent tubercles; P4 with one distal propodal spine opposing the dactylus and, additionally, presence of two small outer propodal spines concealed by the setae (not signaled in the diagnosis given by Guinot & Tavares 2003); P5 with two unequal distal propodal spines opposing the dactylus, one outer propodal spine and one outer dactylus spine. In fact, *Dromidiopsis* and *Lauridromia* distinguish only by a very few characters, and the differences between *D. intermedia* (Gray, 1831) n. comb. and the other species of *Dromidiopsis* need to be re-evaluated (Guinot unpubl. data).

Lauridromia indica has the two sheets of the phragma 7/8 not completely joined; traces of

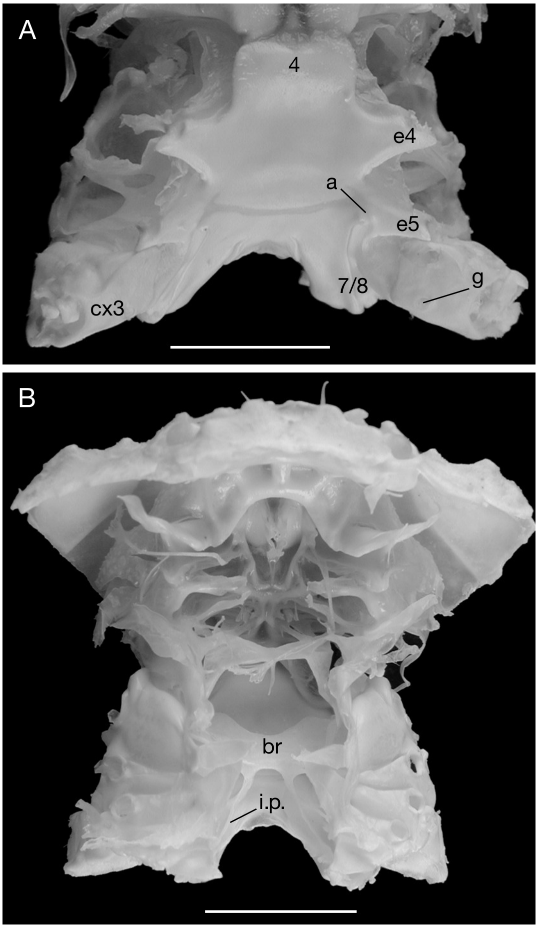

Fig. 10. — [*Dromia*] *wilsoni* (Fulton & Grant, 1902), female 35 × 47.8 mm, Marquesas Islands (MNHN-B 26480); **A**, thoracic sternum; **B**, axial skeleton, dorsoventral view, spermathecae not visible. Abbreviations: **a**, spermathecal aperture; **br**, transverse bridge; **cx3**, P3 coxa; **e4**, **e5**, episternites 4, 5; **g**, female gonopore; **i.p.**, intertagmal phragma; **4**, sternite 4; **7/8**, thoracic sternal sutures 7/8. Scale bars: 1 cm.

sperm in the space between the sheets are visible on both sides of the specimen.

Genus *Epigodromia* McLay, 1993

Epigodromia areolata (Ihle, 1913)

Female 12.2 × 13.3 mm, New Caledonia, MUSORSTOM 8, stn CP 1018 (MNHN-B 26336).

The thoracic sternum is broad, rather flattened, the sterno-abdominal depression is wide. The female sternal sutures 7/8 are relatively short, reaching only the level of the episternite 5; they remain lateral, and end wide apart; the spermathecal aperture is terminal and rounded, located in the middle of a small prominence (Fig. 11B). The bulb of the spermatheca is reduced. The chamber has its two sheets not well separated. The tube is very narrow and relatively short, with terminal opening. The thoracic axial skeleton is flattened and widened.

Genus *Frodromia* McLay, 1993

Frodromia is dealt herein in the Dromiinae, despite some sphaerodromiine characters and its uncertain status (Guinot & Tavares 2003: 108, figs 25, 26). The thoracic sternum (Fig. 12A) is rather wide, with a developed flat bottom. The suture 7/8 is rather short and almost longitudinal. Spermathecal aperture lies not very far from the P3 coxae, but slightly behind the level of female gonopore, and is raised on a tubercule and well visible. The location of the female gonopore is peculiar, being displaced very close to the anterior border of the coxa and at the summit of a tubular process, so that the P3 coxae are markedly dimorphic (Guinot & Tavares 2003: fig. 26). The axial skeleton (Fig. 12B) shows only one median bridge, a dromiine character, instead of the two transverse bridges characteristic of the Sphaerodromiinae (Fig. 17).

Frodromia* ? *atypica (Sakai, 1936)

Ovigerous female 10.6 × 9.9 mm, New Caledonia, Halipro 1, stn CP 868, McLay det. 1995 (MNHN-B 26360). The specific identification needs to be confirmed.

The bulb of the spermatheca is inflated, markedly calcified, and the chamber is small (Fig. 12B). Despite the shortness of suture 7/8, there is a tube, which is very narrow and oblique. This

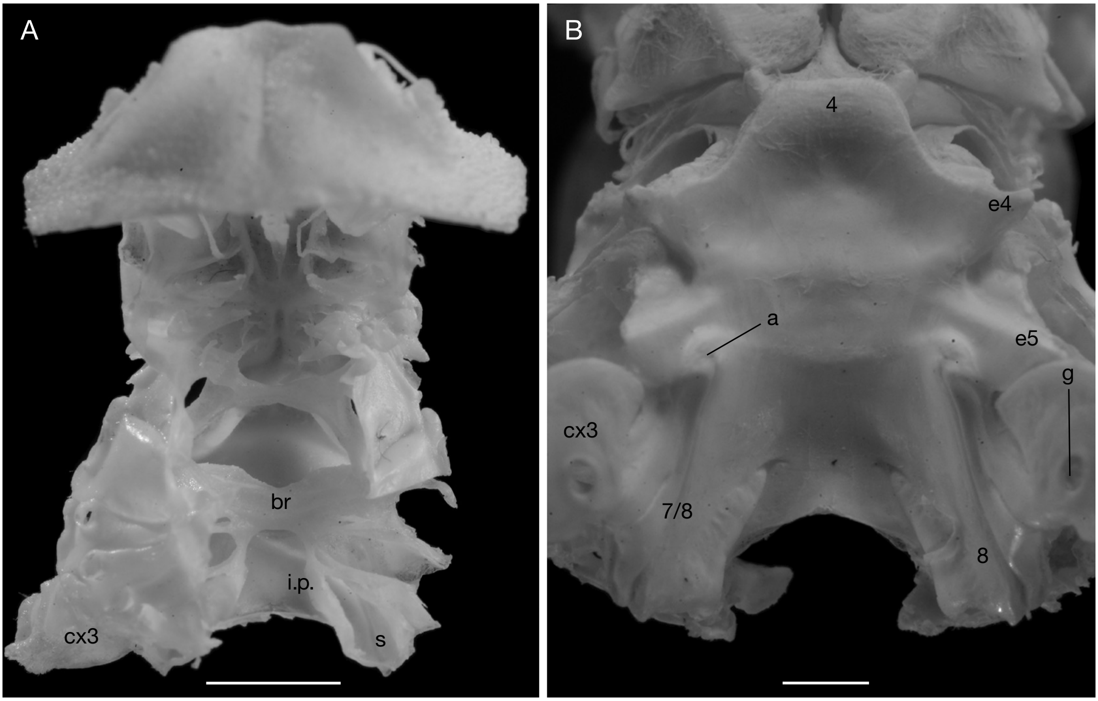

FIG. 11. — **A**, *Takedromia cristatipes* (Sakai, 1969), ovigerous female 19.8 × 21.6 mm, New Caledonia (MNHN-B 26420), axial skeleton; **B**, *Epigodromia areolata* (Ihle, 1913), female 12.2 × 13.3 mm, New Caledonia (MNHN-B 26336), thoracic sternum. Abbreviations: **a**, spermathecal aperture; **br**, transverse bridge; **cx3**, P3 coxa; **e4**, **e5**, episternites 4, 5; **g**, female gonopore; **i.p.**, intertagmal phragma; **s**, spermathecal chamber; **4**, **8**, sternites 4, 8; **7/8**, thoracic sternal suture 7/8. Scale bars: A, 4 mm; B, 1 mm.

arrangement is therefore similar to that of the Dromiinae.

Genus *Lauridromia* McLay, 1993

Lauridromia intermedia (Laurie, 1906)

Female 37.3 × 35.4 mm, New Caledonia, Canal Woodin (MNHN-B 26441) (not dissected).
On the relatively narrow thoracic sternum, the long, straight and lateral female sutures 7/8 (Fig. 13A) end apart, each at the summit of a markedly salient and long tubercle, at the level of sternite 4. The two sheets of the phragma 7/8 are not completely joined in a more or less long terminal part; a large true terminal aperture exists however (Fig. 13B, C). A sperm plug is present on one of the tubercles and traces of sperm are discernible on one side in the opened part of the suture 7/8 (Fig. 13A).

Lauridromia dehaani (Rathbun, 1923)

– Female 52 mm length, Madagascar, A. Crosnier coll. (MNHN-B 6868).
As in *L. intermedia*, female sternal sutures 7/8 are long, straight, roughly parallel and remain lateral; apertures of the spermathecae end apart, each at the summit of a strong tubercle, just behind the P1. The bulb of the spermatheca is tapering and is prolonged by the basal thickening; in the posterior corner a raised part forms a flat area; a small prominence is visible anteriorly. The chamber has a membranous, transluscent inner wall; it contains a sperm mass in the anterior part. The basal thickening is well marked and well califled on its whole length. The long tube (Fig. 14) gets

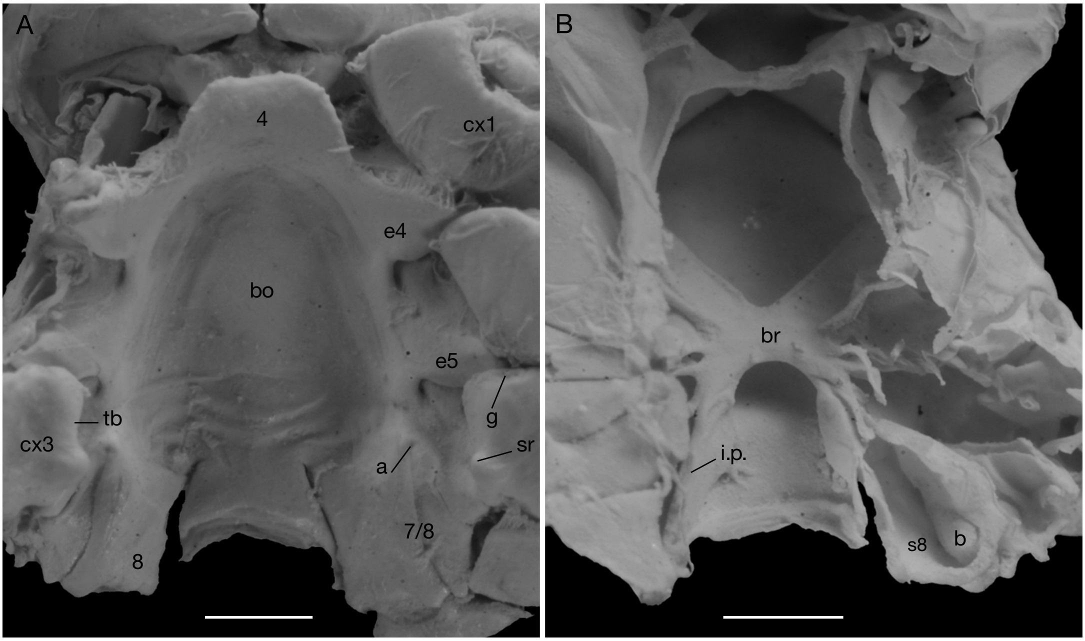

FIG. 12. — *Frodromia* ? *atypica* (Sakai, 1936), ovigerous female 10.6 × 9.9 mm, New Caledonia, McLay det. (MNHN-B 26360); **A**, thoracic sternum; **B**, thoracic axial skeleton, with endopleurites cut away at left to expose spermatheca. Abbreviations: **a**, spermathecal aperture at extremity of sternal suture 7/8; **b**, bulb; **bo**, flat bottom of the sterno-abdominal depression; **br**, transverse bridge; **cx1**, **cx3**, P1, P5 coxae; **e4**, **e5**, episternites 4, 5; **g**, female gonopore; **i.p.**, intertagmal phragma; **sr**, spur on P3 coxa; **s8**, internal surface of sternite 8; **tb**, tubular process on P3 coxa; **4**, **8**, sternites 4, 8; **7/8**, thoracic sternal suture 7/8. Scale bars: 1 mm.

thicker at the level where it changes direction and it ends in a terminal, raised tubercle before the external opening.

– Male 72 mm length, Madagasdar, FAO 26 coll. (MNHN-B 6923).

The phragma 7/8 has practically the same development as in the female, but the two sheets are adjacent and calcified (there is no convexity of the inner wall); there is no basal thickening, and the tube is absent.

Genus *Lewindromia* Guinot & Tavares, 2003

Lewindromia unidentata (Rüppell, 1830)

Female without dorsal surface of the carapace, Perim, Jousseaume coll. (MNHN-B 6940).

Sternites 7 and 8 are tilted, being almost perpendicular in relation to the precedent ones. The sternal sutures 7/8 are wide apart posteriorly, get abruptly close to each other at the level of the P3, where they are marked by a thick ridge; the rounded apertures of the spermathecae end together on a slight prominence between the P2 coxae. The bulb of the spermatheca is tapering and prolongs in the form of a basal thickening; its dorsal surface has a raised part forming a flat, well defined and circular area; no anterior visible prominence. The chamber has its two sheets lacking a marked space between them; its walls are weakly ornamented. The narrow tube shows an abrupt change of direction and is only sligthly widened distally.

Genus *Moreiradromia* Guinot & Tavares, 2003

The sutures 7/8 are extremely long, getting progressively close to each other as they run forward over the thoracic sternites (M. Tavares pers.

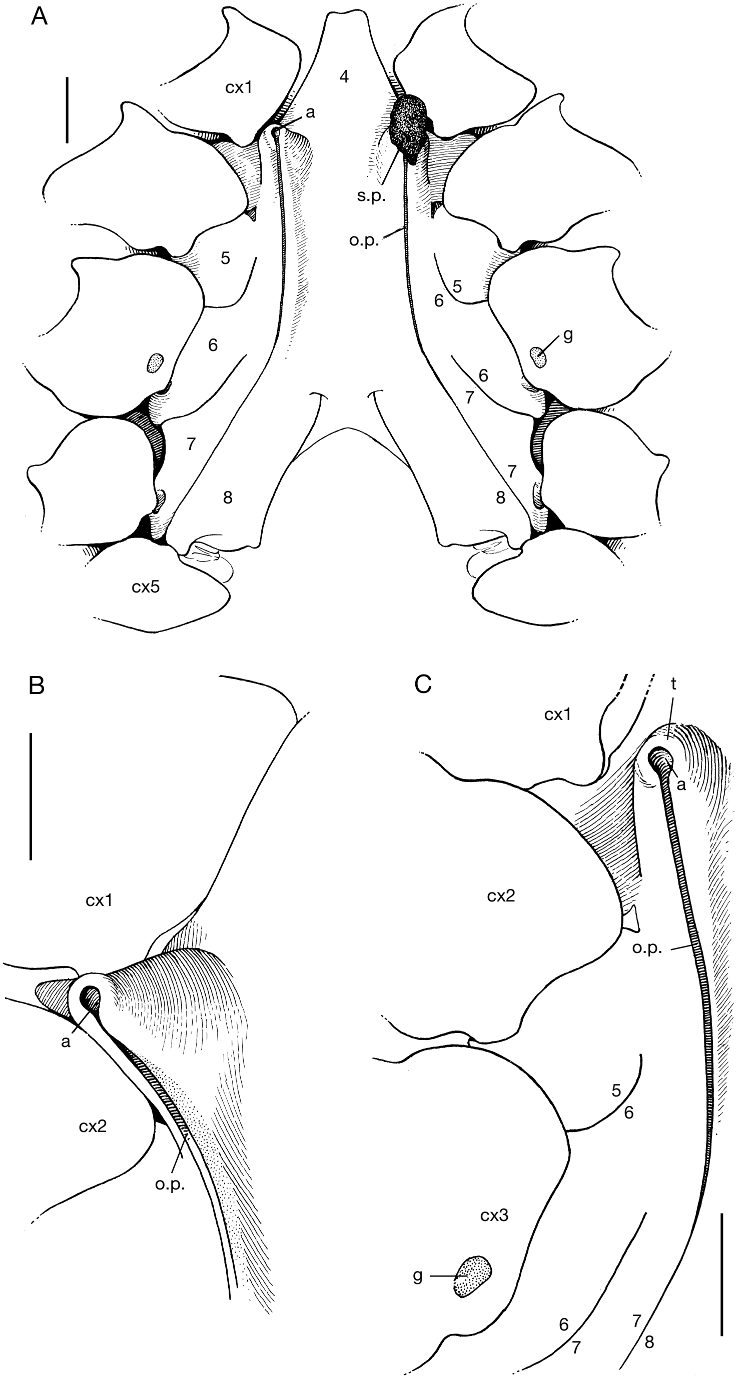

Fig. 13. — *Lauridromia intermedia* (Laurie, 1906), female 37.3 × 35.4 mm, New Caledonia (MNHN-B 26441); **A**, thoracic sternum; **B**, **C**, two views of the tubercle bearing spermathecal aperture (notice that the two sheets of the phragma 7/8 are not completely joined in their terminal parts). Abbreviations: **a**, spermathecal aperture; **cx1**-**cx3**, **cx5**, P1, P2, P3, P5 coxae; **g**, female gonopore; **o.p.**, opened part of the phragma 7/8; **s.p.**, sperm plug; **t**, tubercle; **4**-**8**, sternites 4-8; **5/6**-**7/8**, thoracic sternal sutures 5/6 to 7/8. Scale bars: A, C, 2.5 mm; B, 5 mm.

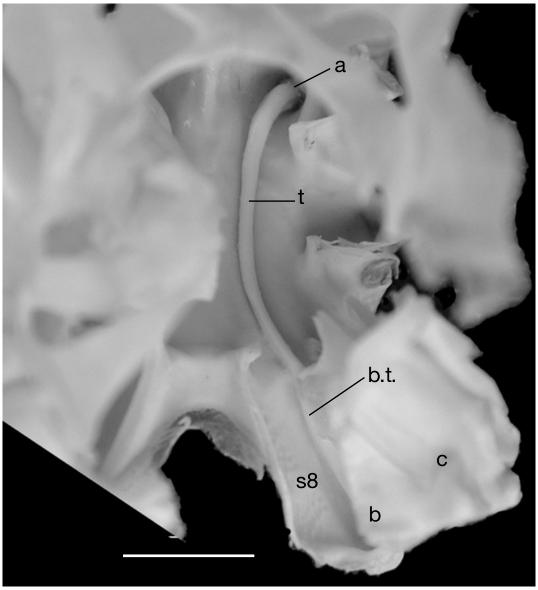

FIG. 14. — *Lauridromia dehaani* (Rathbun, 1923), female 52 mm length, Madagascar (MNHN-B 6868), spermatheca in lateral view, skeletal parts removed. Abbreviations: **a**, location of the spermathecal aperture on sternum; **b**, bulb; **b.t.**, basal thickening; **c**, spermathecal chamber; **s8**, internal surface of sternite 8; **t**, spermathecal tube. Scale bar: 1 mm.

comm.). The spermathecal apertures, situated together, are situated far forward on the anterior part of of sternite 4 (i.e. beyond the articular condyles of the chelipeds).

Moreiradromia sarraburei (Rathbun, 1910)

(not *larraburei* in Schmitt 1921; see Boyko 1998: 234)
– Female 21.5 × 22.2 mm, Baja of California, San Juan Island, Diguet coll. (MNHN-B 12761). The bulb of the spermatheca is globular and pear-shaped, without the small anterior prominence visible in *Dromia*, *Sternodromia* and *Lauridromia.* The chamber has its two sheets nearly adjacent to each other; its walls are membranous. There is a marked basal thickening. The tube is narrow and very long.
– Immature female 8.1 × 7.9 mm, same data (MNHN-B 12761). Suture 7/8 is short and hardly extends beyond the level of the P3 coxae, where the gonopore is not opened, and spermathecal aperture is not visible. The two sheets of phragma 7/8 are joined and a delimited tube is not yet discernible at this small size.

Genus *Stebbingdromia* Guinot & Tavares, 2003

Because of the poorly avalaible material of *S. plumosa* (Lewinsohn, 1984), it was unfortunately not possible to prepare the skeleton and observe the spermathecae. This genus is peculiar among the Dromiinae because it possesses short female sutures 7/8, with apertures ending apart on very slight prominences between the P3 (even in mature females, McLay, 2001a: 85, 86), i.e. not far from gonopores on the P3. In the two females that were examined these apertures were hidden beneath sperm plugs, so that their precise shape is unknown (Guinot & Tavares, 2003: 92, 94, fig. 17C).

Genus *Sternodromia* Forest, 1974

Sternodromia was not recognized by most of the authors (Manning & Holthuis 1981; McLay 1993; Davie 2002). We have resurrected it as a valid genus (Guinot & Tavares 2003: 49), with *S. spinirostris* (Miers, 1881) as its type species, and a second species, *Dromia monodi* Forest & Guinot, 1966, is added herein. The axial skeleton of *Sternodromia* shows a more developed partitioning than *Dromia* (Fig. 7A), as well as a different shape of the transverse bridge, which confirms the establishment of the genus by Forest (1974).

Sternodromia spinirostris (Miers, 1881)

Female 45 × 53 mm, Ivory coast, Guinean Trawling Survey (MNHN-B 24117); female 58 × 69 mm, Congo, off Pointe-Noire (MNHN-B 7862); female 40 × 41 mm, Gulf of Guinea (MNHN-B 22052).

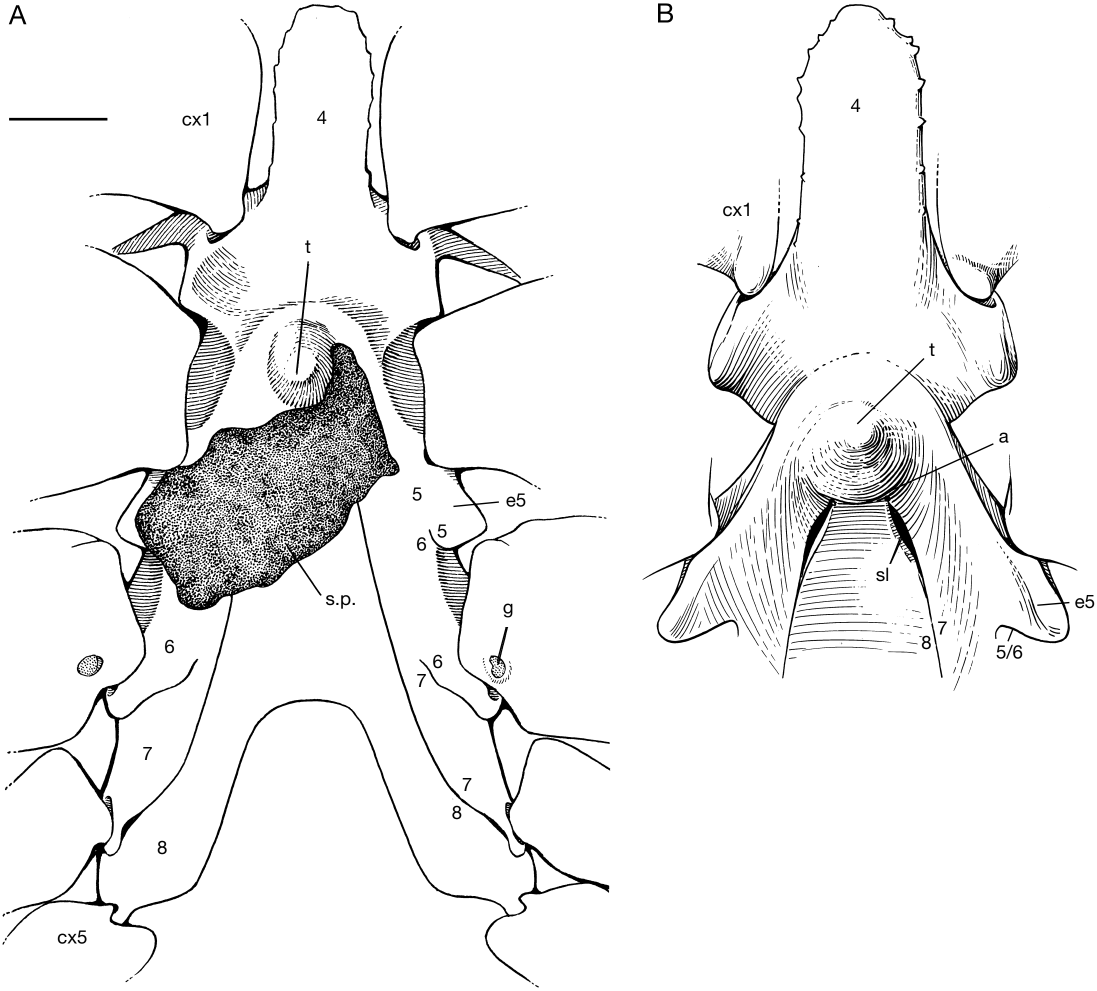

FIG. 15. — *Sternodromia spinirostris* (Miers, 1881); **A**, female 40 × 41 mm, Gulf of Guinea (MNHN-B 22052), thoracic sternum showing sperm plug around slits of the spermathecae; **B**, female 34 × 37.2 mm, Gulf of Guinea (MNHN), detailed view of anterior sternal plate. Abbreviations: **a**, spermathecal aperture; **cx1**, **cx5**, P1, P5 coxae; **e5**, episternite 5; **g**, female gonopore; **sl**, slit; **s.p.**, sperm plug; **t**, tubercle; **4-8**, sternites 4-8; **5/6-7/8**, thoracic sternal sutures 5/6 to 7/8. Scale bar: A, 2.5 mm.

The thoracic sternum (Fig. 15) is rather narrow; sternite 4 forms an elongated plate, with external borders parallel and anterior margin truncated, in contact with the mxp3 coxae. The female sternal sutures 7/8 gradually converge anteriorly and end at the level of P2. Their subterminal part forms a very narrow and long slit; these slits taper near their extremity where there is only a tiny terminal perforation (Fig. 15B). A marked tubercle surrounds the extremity of sutures 7/8; internally, it corresponds to a marked hollow. The bottom of the slit that is not externally closed and corresponds to a slight separation of the two sheets of the phragma 7/8, may serve as aperture of the spermatheca, since we have seen several individuals with sperm inside and around it. Sperm can therefore penetrate in the underlying channel that corresponds to the open part of endosternite 7/8. In a female (MNHN-B 22052) a hardened brown (partly yellowish) sperm plug was seen glued to the sternum, surrounding the half terminal part of the sutures 7/8 and including these slits (Fig. 15A). In another female (MNHN-B 7862), small fragments of male seminal material protruding from the slits were observed.

The bulb of the spermatheca is well defined and globular (and may be extremely salient in some other individuals), not tapering; anteriorly, a small prominence is well visible. The chamber is well dilated, filled by sperm; inner wall is soft, markedly ornamented; the outer wall is more calcified. There is no distinct basal thickening. The tube is thick but becomes flatter at the level of the subterminal slit, which connects the underlying spermathecal channel and the exterior.

Sternodromia monodi (Forest & Guinot, 1966)

In *S. monodi* the sternal plate is roughly similar to that of *S. spinirostris*, but in *S. monodi* the tubercle surrounding the extremities of the two slits is absent, and sternite 4 and epsisternites 4, 5 have a different shape; additionally, the subterminal slits are shorter in *S. monodi*.

– Immature female 20.3 × 23.5 mm, Senegambia, *Calypso* (MNHN-B 7841), with gonopores on the P3 coxae not yet perforated. Sutures 7/8 are shorter, ending behind the level of the episternite 5 only. The bulb of the spermatheca is very small. The tube is narrow but quite distinct, and the subterminal slit is not yet opened.

– Male 58 × 71 mm, Congo, off Pointe-Noire, A. Crosnier coll. (MNHN-B 7883). There is no chamber between the two adjacent sheets, no distinct basal thickening; the tube is absent.

Genus *Takedromia* McLay, 1993

Takedromia cristatipes (Sakai, 1969)

Ovigerous female 19.8 × 21.6 mm, New Caledonia, BATHUS 4, stn DW 931 (MNHN-B 26420).

The axial skeleton is flattened and widened (Fig. 11A). Thoracic sternum is very broad and the sterno-abdominal depression rather wide. Female sternal sutures 7/8 are relatively short, reaching only level of the episternites 5, only lateral, not converging, and end wide apart, each on a weak prominence. The spermathecal apertures are terminal and very small (Guinot & Tavares 2003: fig. 19A). The bulb of the spermatheca is pear-shaped. The chamber is weakly developed, with adjacent sheets; the inner wall is soft, ornamented. The tube is markedly narrow, with terminal opening.

Subfamily HYPOCONCHINAE
Guinot & Tavares, 2003

The members of the subfamily Hypoconchinae are characterized by several peculiar features. They are obligate shell-carriers, always a valve of lamellibranch mollusk carried by the last two pairs of pereopods, which are morphologically quite different from those of the other dromiids, with a particular method of grapsing (Guinot & Tavares 2000, 2003). The uniqueness of *Hypoconcha* led several workers to doubt of their belonging to the Dromiidae (McLay 1993: 229). Guinot & Tavares (2003) erected the subfamily Hypoconchinae within the Dromiidae for the genus *Hypoconcha*.

The female thoracic sternites 6, 7 and 8 are tilted drastically, almost perpendicular in relation to the preceding thoracic sternites. The posterior sternal sutures are localized on this inclined part. The sutures 7/8 are not so extended forward as in the Dromiinae; the apertures of the spermathecae are located beyond the level of the P3, not very far from the female gonopores, however. The thoracic axial skeleton (Fig. 16C) has a single transverse bridge, as in the Dromiinae.

Genus *Hypoconcha* Guérin-Méneville, 1854

Hypoconcha panamensis Smith, 1869

Female approximately 30 mm wide, Mexico, Cabo San Miguel, CORTES 1 (MNHN-B 20865).

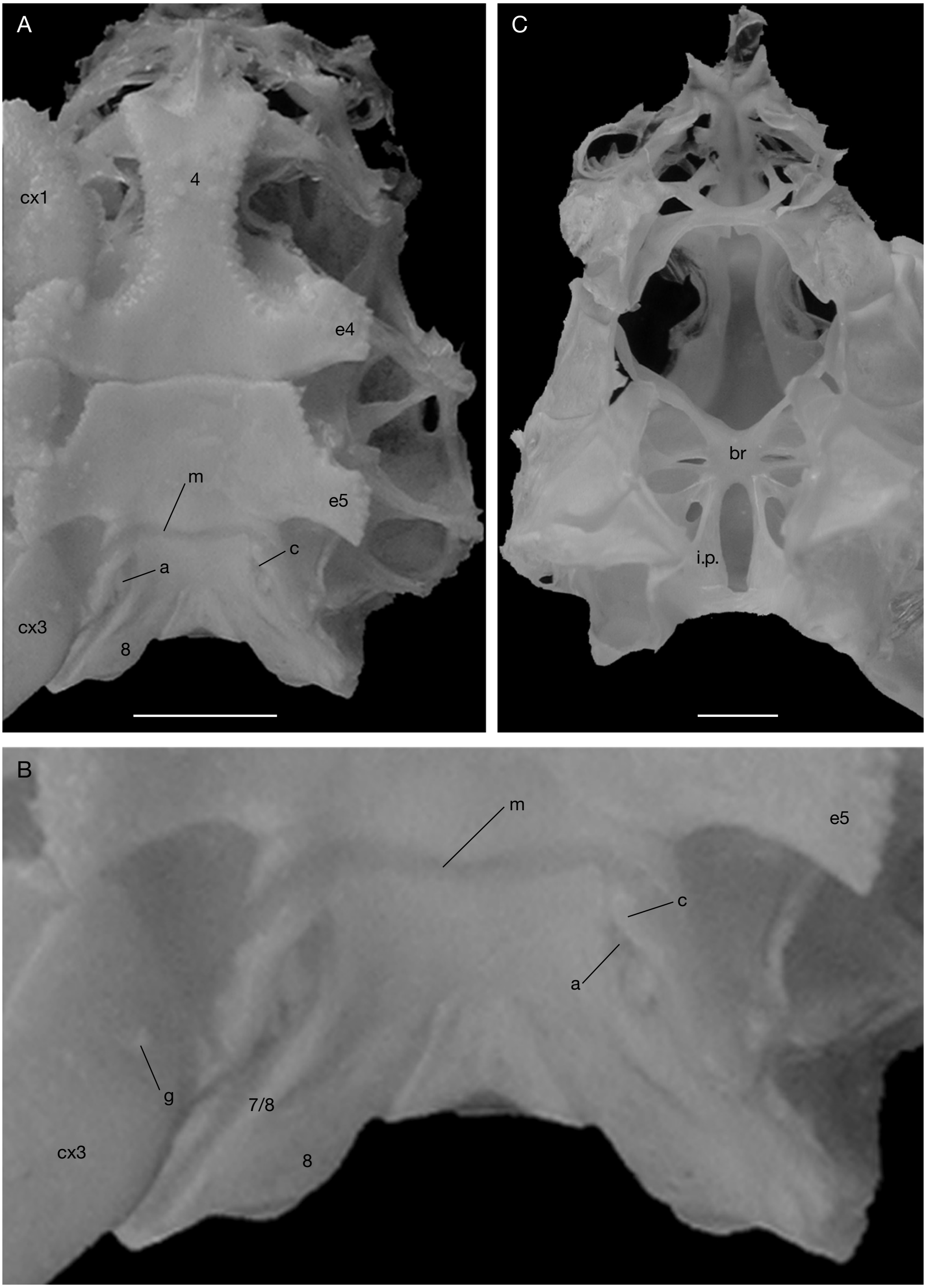

FIG. 16. — *Hypoconcha panamensis* Smith, 1869, female approximately 30 mm width, Mexico, Cabo San Miguel (MNHN-B 20865); **A**, thoracic sternum; **B**, detail of posterior part; **C**, axial skeleton, not dissected so that spermathecae are not visible. Abbreviations: **a**, spermathecal aperture; **br**, transverse bridge; **c**, crest surrounding spermathecal aperture; **cx1**, **cx3**, P1, P3 coxae; **e4**, **e5**, episternites 4, 5; **g**, female gonopore; **i.p.**, intertagmal phragma; **m**, membranous zone separating the flat anterior sternal part from tilted last sternites; **4**, **8**, sternites 4, 8; **7/8**, thoracic sternal suture 7/8. Scale bars: A, C, 4 mm.

The thoracic sternum (Fig. 16A) is peculiar in that the anterior sternites 4 and 5 form a horizontal plate, sternites 6-8 are bent at right angles and are perpendicular to the preceding ones. The sterno-abdominal depression is located posteriorly. Female sutures 7/8 are relatively short, only present on bent surface of posterior sternites, and end apart. Apertures of spermathecae are located only slightly beyond the level of P3, not very far from female gonopores on P3, and are surrounded by a crest (Fig. 16B). The opening is slightly larger than in the Dromiinae and shows as an ovate membranous area. The bulb of the spermatheca is rather large but weakly globular. The chamber has its two sheets that are nearly close to each other, without a marked space between them; the basal thickening is not well marked. A tube is present, although short and relatively narrow, and it is situated laterally; there is a weakly calcified area at the level where it communicates with the exterior.

Subfamily SPHAERODROMIINAE
Guinot & Tavares, 2003

The genera *Sphaerodromia* Alcock, 1899 and *Eodromia* McLay, 1993 share a number of characters unique among the Dromiidae that led the recent distinction of the subfamily Sphaerodromiinae (Guinot & Tavares 2003). Some of these characters are not found in *Frodromia* McLay, 1993, the single one genus which, for the moment, has a status apart.

In the subfamily Sphaerodromiinae, the thoracic sternum is narrow, quite flattened, without a marked posterior curvature. The female sternal sutures 7/8 are short, oblique and lie laterally; they end wide apart. The spermathecal apertures are situated far back on the thoracic sternum, behind the level of the female gonopores on the P3 coxae; they are terminal and located laterally, small and more or less rounded. In some *Sphaerodromia* species (such as *S. lamellata* Crosnier, 1994) and in *Eodromia*, short sutures 7/8 end in completely exposed apertures. In other species, such as *S. ducoussoi* McLay, 1991 (see Guinot & Tavares 2003: fig. 21C) or *S. kendalli* (Alcock & Anderson, 1894) sutures 7/8 are sligthly longer and the apertures are concealed under a lateral heightening and fold of the sternite 8.

In the Sphaerodromiinae, the axial skeleton (Fig. 17) shows the dromiine condition (i.e. connections between phragmae by fusion), but the thoracic axial skeleton is more partitioned than in the Dromiinae, and the two sides are connected by two transverse bridges (instead of only one in the dromiine pattern, Figs 7; 10B; 11A; 12B), which supports the plesiomorphic condition of the Sphaerodromiinae within the Dromiidae. It is possible that sphaerodromiines prove to have been referred to dynomenids in the fossil record because of their similar carapace outline and shape of fronto-orbital region.

Genus *Sphaerodromia* Alcock, 1899

Sphaerodromia lamellata Crosnier, 1994

Ovigerous female 36.4 × 36.2 mm, New Caledonia, Norfolk Ridge, stn CP 813 (MNHN-B 28389).

The suture 7/8 is extremely short, so that the spermathecal aperture lies posteriorly and is completely exposed; the opening is tiny. The bulb of the spermatheca is very developed, inflated and well calcified in the posterior corner and membranous in its anterior part, which contains sperm mass. The chamber is not large, its two sheets being nearly adjoined and without a marked space between, and does not contain any sperm; the inner wall is soft. The tube is absent, which corresponds to the shortness of suture 7/8. As a result, the chamber itself directly ends on the exterior. The skeleton shows two transverse bridges (Fig. 17).

Sphaerodromia kendalli
(Alcock & Anderson, 1894)

Ovigerous female 36.4 × 36.2 mm, Philippines, MUSORSTOM 3, CP 143 (MNHN-B 22543).

The axial skeleton, with two transverse bridges similarly to that of *S. lamellata*, was not completely dissected, but it was possible to partially examine the endosternite 7/8. Spermathecal apertures are concealed. Despite that suture 7/8 is slightly longer than in *S. lamellata*, a tube does not exist, however.

CONCLUSIONS FOR THE DROMIACEA

In all the Dromiacea that were examined, the spermatheca consisted of a bulb, which is formed by infoldings of the phragma 7/8, and a sort of pocket, herein called "chamber", which corresponds to delamination of the two laminae of the endosternite 7/8, one belonging to the segment 7, the other to the segment 8. Another structure may be present along a part of the suture 7/8: an internal, closed tube, completely calcified, hollow and, in very most cases, perforated at its extremity, namely the spermathecal aperture. This tube is the forward prolongation of the chamber and continues well beyond it, sometimes along a great length of the suture 7/8 (in [*Dromia*] *dormia*, the tube is as long as the suture 7/8 of about 50 mm length). The tube, which is "doubtless formed by infoldings of sternites 7 and 8 along their sutural margins" (Gordon 1950: 248), is the result of the fusion, on a short space, of the two laminae of the phragma 7/8. Its lumen forms a channel leading to the spermathecal aperture, which is generally terminal. Thus, the spermathecal tube corresponds to an entirely modified and elaborate structure: it is the result of a specialization. It is found only in the females. In dromiine males, the suture 7/8 is short, and the endosternite 7/8 is only a thin double septum, consisting of two coalescent sheets, not modified and without any prolongation. Gordon (1950: 245) observed that, in a small female *Dromia* "*already* the anterior third of the suture 7/8 is wider and more conspicuous than it ever is in the male". For Hartnoll (1979: 82) "the dromiid structure has been elaborated by the development of spermathecal canals along the line of suture 7/8 to link the openings with the spermathecae".

Considering the material available in the MNHN collections that was used to prepare the skeletons,

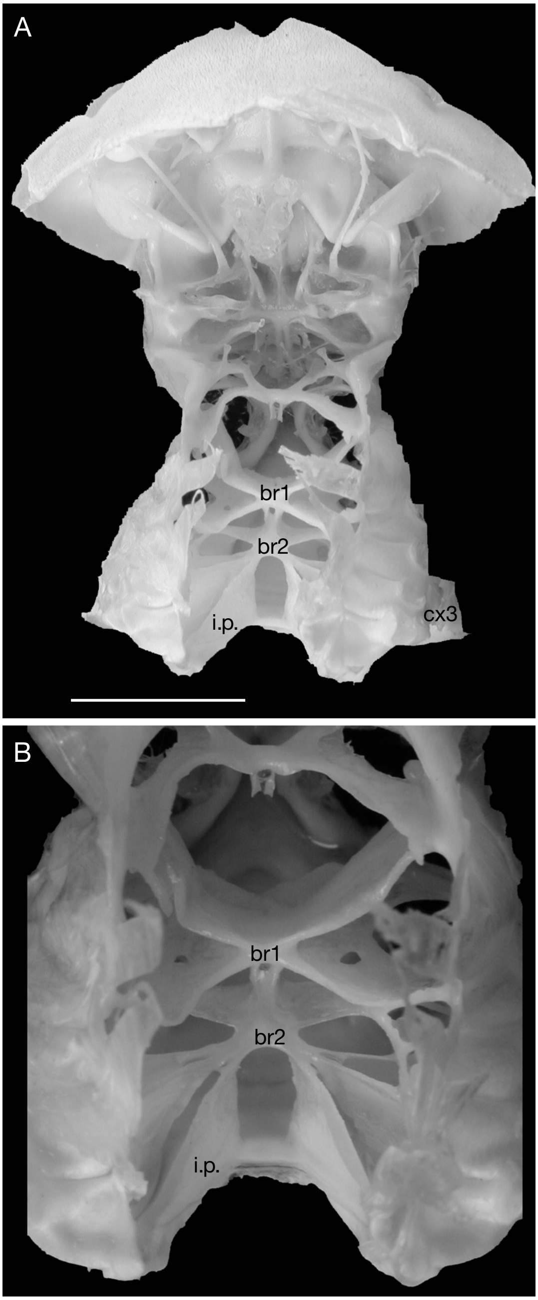

FIG. 17. — *Sphaerodromia lamellata* Crosnier, 1994, ovigerous female 36.4 × 36.2 mm, New Caledonia, Norfolk Ridge (MNHN-B 28389). See Guinot & Tavares (2003: fig. 21C as *S. ducoussoi* McLay, 1991) for the peculiar location of the spermathecae; **A**, axial skeleton, with connections by fusion; **B**, detailed view of posterior part. Abbreviations: **br1**, anterior transverse bridge; **br2**, posterior transverse bridge; **cx3**, P3 coxae; **i.p.**, intertagmal phragma. Scale bar: A, 1 cm.

the Dromiacea exhibit two main patterns concerning the spermathecal tube: 1) the tube is absent and the chamber communicates directly with the exterior through a spermathecal aperture: Dynomenidae (Fig. 4) and Sphaerodromiinae (Fig. 17); or 2) a more or less long tube is present and leads to an external aperture: Homolodromiidae (Fig. 3), Dromiinae (Figs 1; 2; 6-11; 13-15), Hypoconchinae (Fig. 16), and the enigmatic genus *Frodromia* (Fig. 12).

The visible but short tube is present even in the pattern with short sutures 7/8 (Homolodromiidae). Gordon's (1950: 250, fig. 1) hypothesis about *Dicranodromia baffini*, a suture 7/8 of the dromiid type and "in all probability" a very short "channel leading to the spermathecal pit", is thus verified.

The Homolodromiidae, which shows a unique combination of plesiomorphic morphological characters (pediform mxp3, abdominal pleurae, exopod present on G2, uropods showing as ventral lobes, elongated coxae of P5, skeletal connections by interfingering), exhibits the same spermathecal tube pattern as in the Dromiinae, in contrast to the Sphaerodromiinae (at least in the only ovigerous dissected female, *Sphaerodromia lamellata*). If we consider the tube a more advanced condition, it corroborates the basal place of the Sphaerodromiinae within the Dromiidae, as previously pointed out (Guinot & Tavares 2003). The presence of a (short but well visible) tube in the Hypoconchinae supports the placement of this subfamily in the Dromiidae. The specialized *Hypoconcha* is perhaps not as primitive as indicated until now.

The absence of a spermathecal tube in the Dynomenidae is of particular interest. The Dynomenidae shares several characters with the Dromiidae (dorsal uropods, skeletal junctions occuring by fusion), but it shows a peculiar mix of characters. Plesiomorphic are notably the presence of vestigial pleopods on the somites 3-5 as (generally) biramous vestiges, and elongated male coxae of P5. Apomorphic are a widened thoracic sternum and innovation in some genera (*Dynomene*, *Hirsutodynomene*) of a sternal differentiation on the thoracic somite 5 (corresponding to P2) for the holding (although not efficient, see Guinot & Bouchard 1998) of the abdomen.

To examine phylogenetic relationships between Homolodromiidae, Dromiidae and the Dynomenidae, spermatological characters (exemplified by *Homolodromia kai*, *Sphaerodromia lamellata*, and *Metadynomene tanensis*, respectively) were used. They strongly endorse monophyly of the Dromioidea, but without a clear recognition of the three families (Guinot *et al.* 1998).

In addition to features of the carapace during the course of this investigation, the Homolodromiidae, Dynomenidae and the Sphaerodromiinae share the following features, considered plesiomorphic: 1) male pleopodal formula complete or nearly complete (vestigial pleopods on abdominal somites 3-5, biramous in the Sphaerodromiinae and most Dynomenidae, uniramous in the Homolodromiidae) (the Hypoconchinae maintains various vestiges of these pleopods, while most Dromiinae lack male Pl3-Pl5; see Guinot & Tavares 2003: table 1); 2) exopod present on G2 (in the Sphaerodromiinae, present only in the genus *Sphaerodromia*, probably absent in *Eodromia*); G2 exopod absent in the Dromiinae and Hypoconchinae; and 3) a totally modified male P5 coxa, which assumes the shape of a hard and elongated extension, resulting in a dimorphic male P5 coxa (the Dromiinae and the Hypoconchinae share a never dimorphic P5 coxa, bearing in males a long movable, "articulated", sclerotized tube, the penial tube; see Guinot & Tavares 2003: 115, fig. 28).

The enigmatic genus *Frodromia* combines dromiine and sphaerodromiine characters, and its status remains uncertain (Guinot & Tavares 2003: 110). Its sphaerodromiine features include short female sternal sutures 7/8 and spermathecal apertures lying close to the female gonopores on the P3 coxae. The present study permits to add two dromiine features to *Frodromia*: the presence of a spermathecal tube and skeleton with only one transverse bridge. The most important features which still conflict with the inclusion of *Frodromia* in the Dromiinae are the elongated male P5 coxa and the absence of a mobile penial tube.

All the Dromiacea, either basal (Homolodromiidae, Dynomenidae, Spharodromiinae) or more advanced (Dromiinae, Hypoconchinae), share a similar spermathecal aperture, that is generally a small orifice. For the moment, only five cases differ from the typical condition.

1) In the Homolodromiidae, only one species, *Dicranodromia spinulata* Guinot, 1995, shows suture 7/8 occupied by a long subterminal slit, while other homolodromiids have rounded or ovate terminal apertures.

2) The dromiine genus *Sternodromia* (Fig. 15) shows very tiny terminal apertures but they are replaced (or complemented) by subterminal slits, long (*S. spinirostris*) or shorter (*S. monodi*), the bottom of the tube being partly exposed and opened along its subterminal part so that the underlying spermathecal channel is connected with the exterior (Guinot unpubl. data).

3) The dromiine species [*Dromia*] *dormia* (a species that belongs to a different genus [Guinot unpubl. data]) is devoid of the usual circular terminal spermathecal aperture (Figs 8A; 9). Each suture 7/8 opens in a partly decalcified and unperforated pit; at its extremity, the thick spermathecal tube is no longer closed, and the bottom of the phragma 7/8 itself is opened and becomes exposed at the sternal surface to form an ovate pit, which is the spermathecal aperture.

4) In *Lauridromia* the two sheets of the phragma 7/8 are not completely joined subdistally, but it does not prevent the presence of a terminal aperture; sperm may penetrate in the space between the two separated sheets (Fig. 13).

5) In the genus *Cryptodromia* Stimpson, 1858 *sensu lato*, the two phragmae of the endosternite 7/8 do not join, being sometimes significantly opened in their half distal part. In *C. tuberculata* Stimpson, 1858 (Fig. 27B), the margins of the suture 7/8 are distinctly raised, there is a wide, long slit, and the rounded aperture is located on the summit of a strong tubercle.

In the Dromiacea, due to the shortness or the lengthening of sutures 7/8, the spermathecal apertures are situated either just below or slightly behind the female gonopores on the P3 coxae (Homolodromiidae *pro parte*, Dynomenidae) or approximately opposite the P3 coxae (Sphaerodromiinae, *Stebbingdromia* and *Frodromia*). Or they extend slightly beyond and are not very far from the female gonopores (Homolodromiidae *pro parte*, Hypoconchinae) or extend far forward in leaving a great gap between the spermathecal apertures and the female gonopores and also the storage chambers (most Dromiinae).

Subsection HOMOLIDEA De Haan, 1839

Superfamily HOMOLOIDEA De Haan, 1839

The superfamily Homoloidea has long been associated with the Dromiacea (De Haan 1839; Bouvier 1896), and different authors continue to subordinate them to the Dromiacea (Gordon 1950; Glaessner 1969; Hartnoll 1975; Števčić 1981; Bishop 1986; Dawson 2002). The classification of Martin & Davis (2001: 49-51, 112) similarly proposes the alliance of the Homoloidea with the Dromioidea, within the Dromiacea. But morphological and spermatological data support the proposition that Homoloidea should be removed from the Dromiacea and form a separate group (Drach 1971; Guinot 1978). Our view is to distinguish the two subsections Dromiacea and Homolidea to be included in a high-level group, the section Podotremata (Guinot *et al.* 1994; Guinot & Richer de Forges 1995; Guinot & Bouchard 1998). The Homolidea should be considered a main podotreme lineage, apart from the dromiacean lineage (Guinot & Tavares 2001: 531, fig. 16). Dromiacea and Homolidea are basal in the Podotremeta, opposing the Archaeobrachyura (including the Cymonomidae, Cyclodorippidae, Phyllotymolinidae, and Raninoidea).

The homoloid thoracic sternum is relatively broad, not much hollowed; in males the sterno-abdominal depression is completely covered (at least longitudinally, generally across) by a wide and long abdomen (Guinot & Bouchard 1998: figs 8, 9). The anterior sternites form a narrow shield between the mxp3; sternites 1-6 are fused together, except laterally where traces of the sutures are still visible near the condylar articulations of the coxae of the pereopods (Figs 19; 20). In females the posterior part (sternites 7-8) is variously inclined. Sternites 7, which are fused medially, form a wide, low arch that encloses sternite 8. In both sexes, suture 6/7 is always complete, observed as a continuous, horizontal line, and dividing transversally the thoracic sternum into two main parts (Gordon 1950: 232, figs 13, 16, 18, 20, 21, 22A; Hartnoll 1975: figs 2A, 7A; Guinot & Bouchard 1998: fig. 9C). Internally, this corresponds to a short invagination of the phragma 6/7, leading to the formation of a strong tubular ridge which crosses medially the sternal surface (never present in the Dromiacea); laterally, the usual vertical walls are present. The dissection has shown the very weak port of this ridge 6/7, its weak lumen. Sutures 7/8 are markedly convergent, oblique, and end always apart, approximately at the level of the female gonopores on the P3 coxae, being more or less distinct throughout their course. The suture 7/8 may be not continuous and replaced medially by a weak thickening, to which does not correspond any invagination.

Sternite 8 is folded twice. As in the Dromiacea, there is a dorsal folding but, additionally, sternite 8 doubles up with regard to the median axis of the thorax, which corresponds to a median invagination. Consequently, a longitudinal furrow (median line), visible on the sternal plate of the crab, may divide medially the sternite 8 (along a more or less long distance). Thus, the median line (when present) corresponds to the median junction of the two symmetrical parts of sternite 8. These two parts are in contact, either entirely (*Homola* Leach, 1815, *Paromola* Wood-Mason *in* Wood-Mason & Alcock, 1891, *Moloha* Barnard, 1947; Fig. 19) or weakly (*Homolomannia* Ihle, 1912). When sternite 8 is completely separated into two parts, however, the median line is absent (*Latreillia* Roux, 1830, *Eplumula* Williams, 1982; see Castro *et al.* 2003), and the abdomen is inserted in the resulting space, that is, the sterno-abdominal notch. There is only a very short median line and a deep sterno-abdominal notch in the Poupiniidae (Fig. 20). Scholtz & Richter (1995: 304, 316, fig. 1), who included the Brachyura into a new taxon Fractosternalia Scholtz & Richter, 1995 (but the fracosterne has been lost in several groups, including the Brachyura, see Dixon *et al.* [2003: 957, 969] who established a new group, the Eurysternalia Dixon, Ahyong & Schram, 2003), indicated that homolids and homolodromiids show an incomplete fusion of lateral parts of the last sternites. Sternite 8 may be variously divided in the Homolidea, sometimes at a large extent, while only a short, posterior median line exists in the Homolodromiidae, which never shows a sterno-abdominal notch and thus has an organization similar to that of the Dromiidae.

In the Homolidea, part of the sternum situated around the suture 7/8 is differently modified to form the external part of the spermatheca. Gordon (1950: 232-244, figs 13-22, pl. 1, fig. C, as Thelxiopidae) extensively studied and figured the spermatheca in a number of homoloid genera, and named its different components. Hartnoll (1975: fig. 7) described and figured the spermathecae of *Homola barbata* (Fabricius, 1793).

The spermatheca lies in the endosternite 7/8. There is a space between the two sheets of the phragma 7/8 in the posterior part, while the rest of the phragma has its vertical sheets joined and calcified. The spermathecal chamber is relatively small, generally with a flexible inner wall and a more rigid external wall (as in the Dromiacea). It communicates directly with the exterior by an aperture surrounded or lined by membranous areas, which varies among the genera and species. The opening is visible as a slit, or it is obscured by membraneous areas.

The skeletal junctions occur by interfingering (Secretan 1983). In *Moloha* Barnard, 1947 and *Paromola* the intertagmal phragma is extended and reaches transverse bridge as in *Homola* Leach, 1815 (Secretan 1998: figs 5, 6) (Fig. 18). A peculiar skeletal arrangement is exhibited by the Poupiniidae (see below).

Family HOMOLIDAE De Haan, 1839

The family Homolidae consists approximately of some 50 species distributed in 14 genera.

Homola ranunculus
Guinot & Richer de Forges, 1995

Female 41.4 × 38.1 mm, New Caledonia, stn CC1 (MNHN-B 19869).
Sternite 8 shows a relatively long median line, and the sterno-abdominal notch is not very deep. The spermatheca occupies about half of the suture 7/8. A wide membranous area, which belongs to sternite 7, is followed by a long slit along suture 7/8; another membranous area, belonging to sternite 8, is more internal and oblique inside the slit. The aperture is slit-like and concealed. The inner wall of the chamber is soft and slightly wrinkled; the external wall is not so flexible. The skeleton (Fig. 18) shows the connections by interfingering, typical for homoloids.

Paromola bathyalis
Guinot & Richer de Forges, 1995

Ovigerous female 75 × 57 mm, New Caledonia, Chalcal II, stn CH 7 (MNHN-B 19900).
Sternite 8 shows a median line. The spermathecal aperture is slit-like and narrow. The chamber of the spermatheca is inflated and contains sperm; rest of the phragma consists of an oblique wall.

Moloha majora (Kubo, 1936)

Ovigerous female 43.8 × 38.6 mm, Sagami Bay, off Jogashima, 180-200 m, H. Ikeda coll. and det. *Paromola alcoki* (Stebbing, 1920) (MNHN-B 24798).
This individual was not dissected. Sternal plate (Fig. 19) shows the typical complete and transversal suture 6/7 (corresponding to short invagination of the phragma 6/7), which forms on each side (at the level of the vertical phragmae) a denticulate process overlapping sternite 6. Anterior median part of sternite 7, just below the nearly horizontal course of suture 6/7, is poorly calcified. Sternite 8 shows a short longitudinal median line (not visible in our figure), and the sterno-abdominal notch is developed. External part of the spermatheca consists of a conspicuous membranous region.

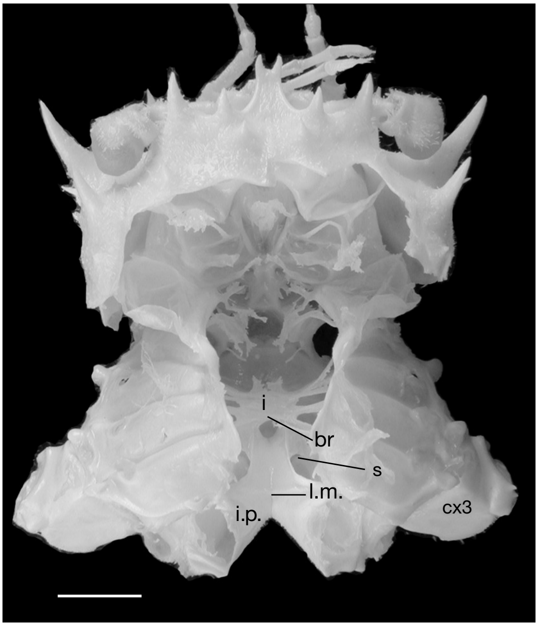

FIG. 18. — *Homola ranunculus* Guinot & Richer de Forges, 1995, female 41.4 × 38.1 mm, New Caledonia (MNHN-B 19869), axial skeleton. Abbreviations: **br**, transverse bridge; **cx3**, P3 coxae; **i**, connections by interfingering; **i.p.**, intertagmal phragma; **l.m.**, median line; **s**, location of the spermathecal chamber. Scale bar: 1 cm.

Moloha aff. *majora* (Kubo, 1936)

Ovigerous female 47 × 42.3 mm, New Caledonia, BIOCAL, stn CP 105 (MNHN-B 13807).
The external part of the spermatheca is markedly conspicuous (Fig. 19); the slit-like aperture, between the two membranous parts of sternites 7 and 8 respectively, is very deep. It internally corresponds to a large chamber.

Homolomannia sibogae Ihle, 1912

Female 40.7 × 30 mm, Philippines, MUSORSTOM 2, stn CP 67 (MNHN-B 13893).
The well delimited chamber seems to contain sperm.

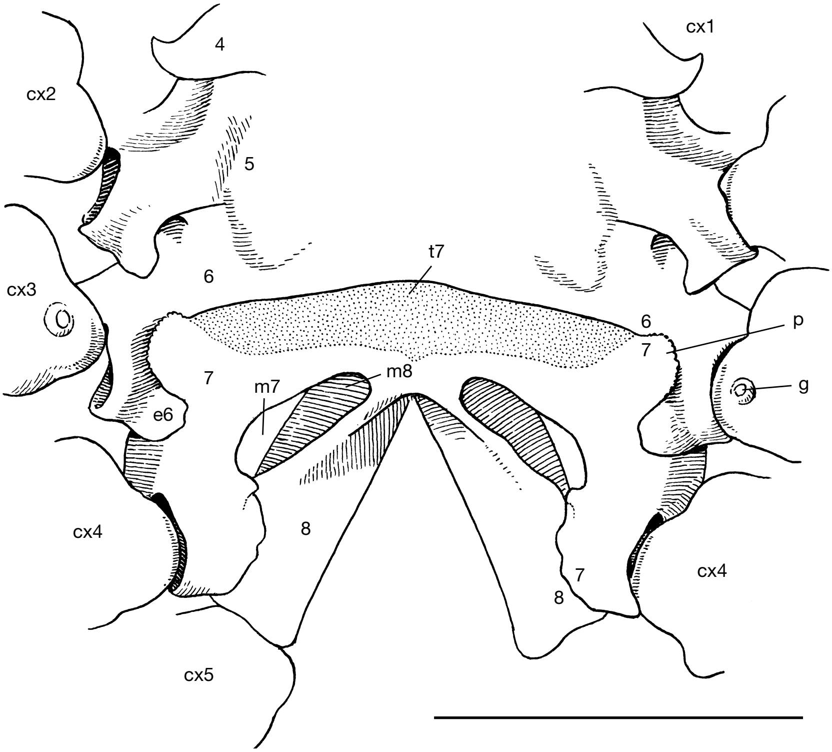

FIG. 19. — *Moloha majora* (Kubo, 1936), ovigerous female 43.8 × 38.6 mm, Japan, Sagami Bay (MNHN-B 24798), thoracic sternum (median junction of the two symmetrical parts of sternite 8 not visible). Abbreviations: **cx1**-**cx5**, coxae of P1-P5; **e6**, episternites 6; **g**, female gonopore; **m7**, poorly calcified part belonging to sternite 7; **m8**, membranous part of inclined sternite 8; **p**, denticulate process of lateral part of suture 6/7; **t7**, thinly calcified anteromedian part of sternite 7; **4-8**, thoracic sternites 4-8; **4/5-7/8**, sternal sutures 4/5 to 7/8. Scale bar: 1 cm.

Family LATREILLIIDAE Stimpson, 1858

The family Latreilliidae consists of seven species distributed among two genera (Castro *et al.* 2003). In the latreilliids the male thoracic sternum is variously broadened and not completely covered by the abdomen (Guinot & Bouchard 1998: 638, fig. 9D).
The available material for dissection was insufficient to give good figures of the spermatheca.

Latreillia valida De Haan, 1839

Female, approximately 8 mm wide, New Caledonia, BATHUS 1, stn CP710 (MNHN-B 28031).
We agree with Gordon (1950: 243, fig. 22B) in that the spermatheca is set obliquely and partially concealed by sternite 7.

Family POUPINIIDAE Guinot, 1991

The family Poupiniidae is monogeneric, with *Poupinia* Guinot, 1991, and monospecific.

Poupinia hirsuta Guinot, 1991

Female 54 × 41 mm, allotype, French Polynesia, Raiatea (MNHN-B 24346).
It was possible to observe partly the skeleton and the spermatheca of this female without immersion in a bath of potassium hydroxyde. Its carapace was partly detached from the rest of the body, and the spermatheca was visible only on one side. The thoracic sternum (Fig. 20) is relatively wide, medially with a large, flat, and translucid horizontal area. All sutures are lateral, except for

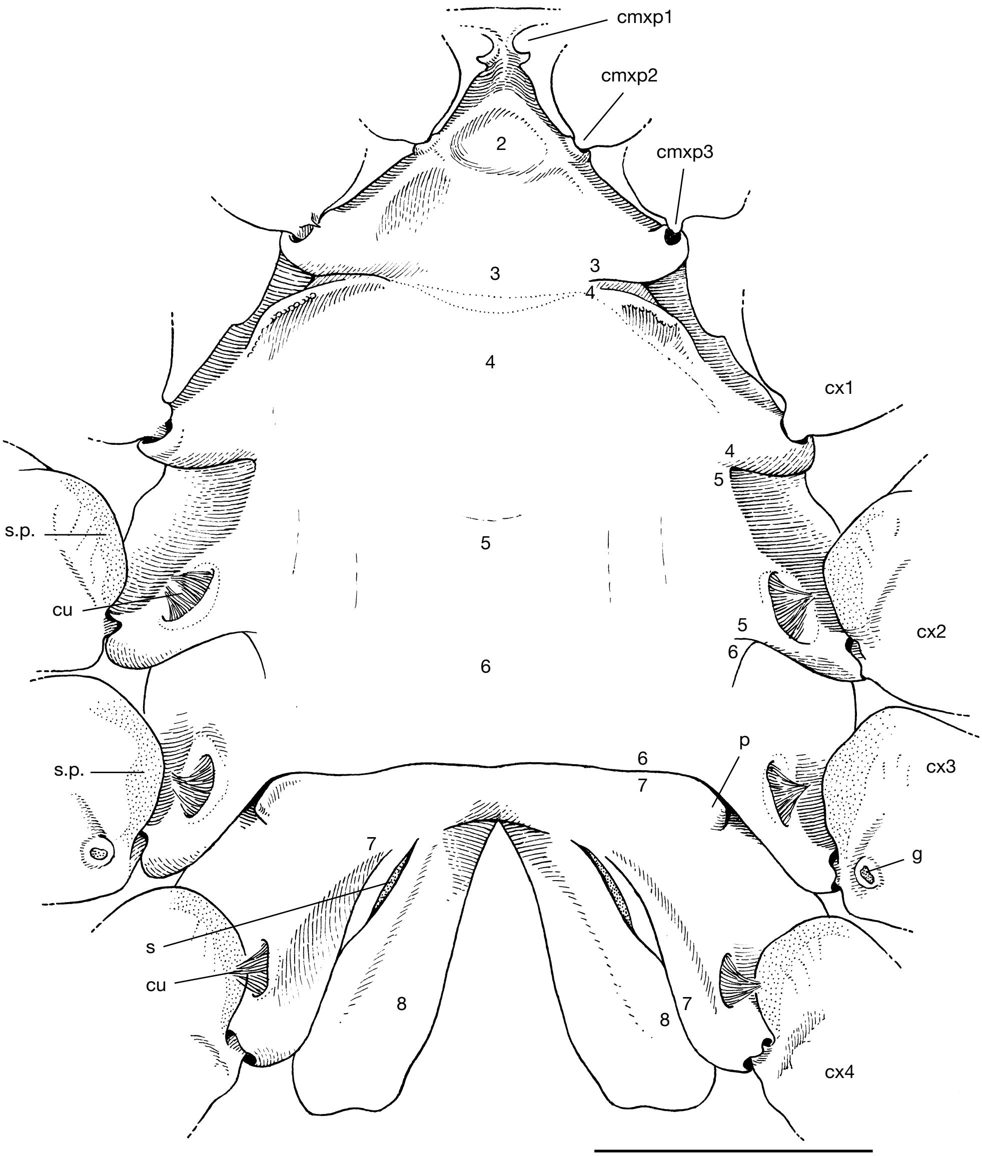

FIG. 20. — *Poupinia hirsuta* Guinot, 1991, female 54 × 41 mm, allotype, French Polynesia (MNHN-B 24346), thoracic sternum. Abbreviations: **cmxp1**-**mxp3**, articular condyles of mxp1-mxp3; **cu**, cupule; **cx1**-**cx4**, coxae of P1-P4; **g**, female gonopore; **s**, spermathecal membranous part; **p**, prominence on each side of suture 6/7; **s.p.**, inflated supra-condylar area of the coxa; **2**-**8**, thoracic sternites 2-8; **3/4**-**7/8**, sternal sutures 3/4 to 7/8. Scale bar: 1 cm.

suture 6/7, which forms a transverse ridge throughout most of its course, but bends sharply backwards and slightly inwards at the level of the P3 coxae (Guinot 1991: pl. 3F). At each extremity of its horizontal course, suture 6/7 shows a marked spine in the male, while there is only a prominence in the female. Sternite 8 is longitudinally divided by a very short median line, and the sterno-abdominal notch is deep. As in the Homolidae, the sternal plate bears large and well delimited sterno-coxal depressions at the level of the P2, P3 and P4 (sterno-coxal depressions 5, 6, 7).

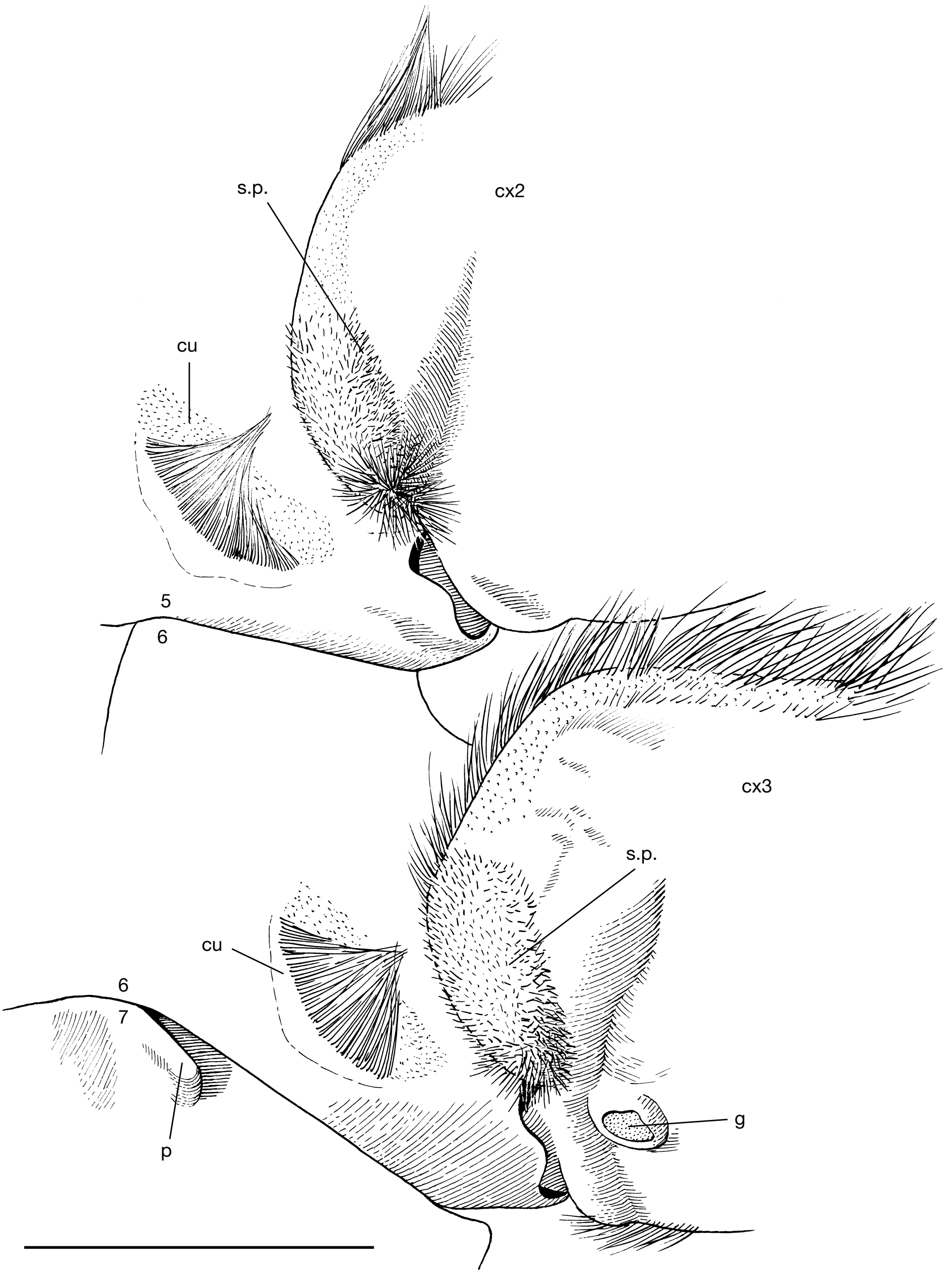

FIG. 21. — *Poupinia hirsuta* Guinot, 1991, female 54 × 41 mm, allotype, French Polynesia (MNHN-B 24346), detail of sternal cupules and supra-condylar areas of corresponding coxae. Abbreviations: **cu**, cupule; **cx2**-**cx3**, coxae of P2, P3; **g**, female gonopore; **p**, prominence on each side of suture 6/7; **s.p.**, inflated supra-condylar area of the coxa; **5/6**, **6/7**, sternal sutures 5/6, 6/7. Scale bar: 5 mm.

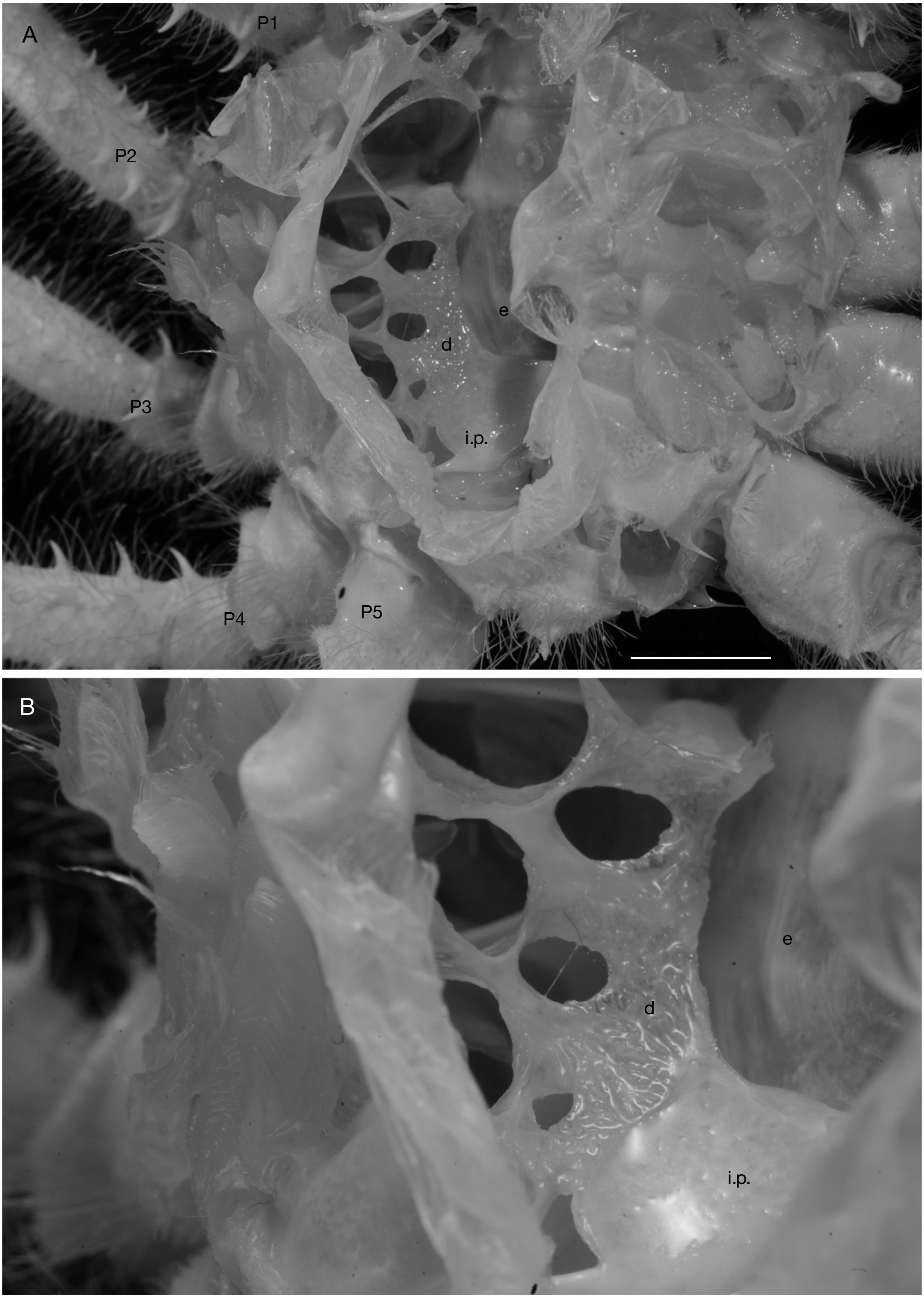

FIG. 22. — *Poupinia hirsuta* Guinot, 1991, female 54 × 41 mm, allotype, French Polynesia (MNHN-B 24346); **A**, thoracic axial skeleton, oblique view to show exclusively lateral location of phragmae; **B**, detailed view to show surface of endopleurites covered by digitations. Abbreviations: **d**, digitations; **e**, empty part of the body, without median connections; **i.p.**, intertagmal phragma; **P1**-**P5**, pereopods P1-P5. Scale bar: A, 1 cm.

Sternites 5, 6 and 7 of *Poupinia hirsuta* bear paired formations looking like setiferous cupules (Figs 20; 21). Each cupule (small cup) comes in contact with the basal region of the corresponding coxa, specifically with its inflated supra-condylar part, which shows a different texture and is covered by a very short, worn tomentum, mixed with longer setae along the margins. These cupules exist only in the female, while they are absent in the male, which shows similar P2-P4 coxae, with inflated and tomentose supra-condylar areas.

The axial skeleton of *Poupinia* is very peculiar, and such a disposition had never been described. There is a wide and short intertagmal phragma (in contrast to longitudinally extended in *Homola ranunculus*, Fig. 18), but the center of the body is empty (Fig. 22). This means that the short endopleurites and endosternites exclusively join laterally and do not present the median connections (by interfingering) seen in the other Homolidea. *Poupinia* lacks the median mass that constitutes the transverse binding between the two lateral endopleural parts, either by interfingering (Homolodromiidae, Homolidae, Latreilliidae) or by fusion (Dromiidae, Dynomenidae, Cyclodorippoidea, Raninoidea, all Eubrachyura). Nevertheless, careful examination revealed that the external surface of the lateral endosternites were covered by irregular elongated structures, contrasting with the smooth surface of the intertagmal phragma (Fig. 22B). These structures actually correspond to the digitations (presumably corresponding to extremities of interosternites) that normally constitute the transverse, median binding by interfingering in the Homolidea. Here they are displaced to the sides so that *Poupinia*, as in the other Homolidea, actually presents interdigitations, but in a different location. We speculate that these digitations will ultimately fuse with endopleurites in another evolutionary stage. The original condition of the Poupiniidae is now completed by this unusual skeletal organization. The skeletal data support the views pointed out by Guinot (1995) that Poupiniidae is unique to the Podotremata. However, if placement of the family Poupiniidae in the Homolidea remains unquestioned, this newly presented character does not permit to surely interpret it as a basal or advanced condition in this subsection. We will have to wait pending a more thorough investigation into the skeletal morphology and diversity in the Anomura, the Astacidea Latreille, 1802, and the Palinura Latreille, 1802. It is true that the relationships of the Archaeobrachyura (as a whole or partly) remain debatable.

Externally, the spermatheca occupies approximately the two-thirds of suture 7/8 and lies far from transversal suture 6/7. There is an extended aperture corresponding to the wole membranous area, which is relatively simple (Fig. 20). Internally, the chamber is very inflated on its inner side and is filled by sperm.

CONCLUSIONS FOR THE HOMOLIDEA

In the Homolidea the sternum around the sutures 7/8 is modified to form the external part of the spermathecae, with distinct membranous areas belonging either to sternite 7, or to sternite 8, or to both. The relatively large spermathecal apertures are always situated on a level with female gonopores on the P3 coxae. The internal organization is rather similar among the genera and species, always with a chamber never far from the aperture and directly opening on the exterior.

Subsection ARCHAEOBRACHYURA
Guinot, 1977

Archaeobrachyura (Cyclodorippoidea and Raninoidea) essentially differs from the two subclades Dromiacea and Homolidea by the absence of uropods on abdominal somite 6, even if a socket (that is, a modification of the uropod; see Guinot & Bouchard 1998) exists in the Lyreidinae Guinot, 1993. Cyclodorippidae, Phyllotymolinidae and Cymonomidae, regrouped as the superfamily Cyclodorippoidea (a suprafamilial name used only *for convenience*; Guinot & Bouchard 1998: 640), were not considered podotreme crabs in the classification of Martin & Davis (2001: 74) and were attributed, with the Raninoidea De Haan, 1839, to the subsection Raninoida.

The total number of the archaeobrachyuran crabs is about some 100 species distributed in approximately 30 genera.

The current number of the konwn Cyclodorippoidea is a little more than 50 species distributed in approximately 18 genera (M. Tavares pers. comm.). Dissections of members in the three cyclodorippoid families are difficult because of the very small size of the individuals.

Family CYCLODORIPPIDAE Ortmann, 1892

In contrast to the preceding families, there is a wide thoracic sternum, with the last sternites (at least sternite 8) more or less abruptly tilted. A deep but small and posterior sterno-abdominal cavity is present. As in the other Podotremata, the thoracic sternal sutures are generally incomplete, diversely interrupted and only lateral; suture 4/5 even seems to be absent, as in the genus *Corycodus* A. Milne-Edwards, 1880 (*C. bouvieri* Ihle, 1916 and *C. merweae* Tavares, 1993 in Tavares 1993: figs 7c, 8c; *C. bullatus* A. Milne-Edwards, 1880 in Tavares 1993: fig. 6b; 1996: fig. 10B).

Suture 6/7 is complete in the female Cyclodorippinae: in *Cyclodorippe* A. Milne-Edwards, 1880 (*Cyclodorippe antennaria* A. Milne-Edwards, 1880, in Tavares 1991a: fig. 5B) and in *Tymolus* Stimpson, 1858, at least in *T. brucei* Tavares, 1991 (Tavares 1991b: 451); for *T. japonicus* Stimpson, 1858 (Tavares 1991a: fig. 5A) a verification is needed. In *Clythrocerus* A. Milne-Edwards & Bouvier, 1899 suture 6/7 is long and probably complete, and in *Deilocerus* Tavares, 1993 as well (M. Tavares pers. comm.). Suture 6/7 was figured incomplete in *Corycodus* (*C. bullatus* in Tavares 1996: fig. 10B; *C. decorus* Tavares, 1993 in Tavares 1993: 280, fig. 9b) and *Neocorycodus* Tavares, 1993, as in *N. stimpsoni* (Rathbun, 1937) (Fig. 28), but a new examination is necessary. Among the Xeinostomatinae Tavares, 1992, suture 6/7 is complete in *Ketamia* Tavares, 1992 (*K. depressa* (Ihle, 1916) in Tavares 1993: fig. 16c; *K. limatula* Tavares, 1993 in Tavares 1993: fig. 18c) and in *Krangalangia* Tavares, 1992, as in *K. spinosa* (Zarenkow, 1970) (Fig. 23C) and *K. orstom* Tavares, 1993 (Tavares 1994: fig 37B). The suture 6/7 is complete in the Cymonomidae Bouvier, 1897.

It is possible that the suture 6/7 is complete in all the Cyclodorippoidea (perhaps only very few exceptions).

In females, either sutures 4/5-7/8 or 5/6-7/8 may be situated in the tilted posterior part of the sternum, as in the cyclodorippine *Corycodus bullatus*, *C. bouvieri* and *C. merweae* (Tavares 1993: figs 6b, 7c, 8c), or all sternal sutures project forward and are pushed on the lateral sides of the sternal plate, as in the cyclodorippine *Neocorycodus stimpsoni* (Rathbun, 1937) (Tavares 1994: fig. 22D; 1996: fig. 23D) (Fig. 28).

There are paired spermathecae, formed by the forwardly carried and anteriorly modified sutures 7/8. Sutures 7/8, which end apart or together, extend variously forward and thus the apertures are more or less far from the female gonopores on the P3 coxae. In the cyclodorippine *Neocorycodus stimpsoni* sutures 7/8 project so much forward that they reach the anterior part of the sternal plate; they end closely together but are not contiguous. The apertures show as narrow oblique slits beneath a characteristic unpaired bump (Tavares 1996: 286, fig. 23D) (Fig. 28).

The axial skeleton is figured herein for the first time. Connections are made by fusion, endopleurites are located only on the sides, there is a transverse bridge that is markedly narrow (*Tymolus*, Fig. 23B) or wider (*Krangalangia*), and the intertagmal phragma is very reduced.

Subfamily CYCLODORIPPINAE Ortmann, 1892

(Senior synonym of Tymolinae Alcock, 1896).

Tymolus daviei Tavares, 1997

Female 8 × 8 mm, paratype, Vanuatu Archipelago, BATHUS 2 (MNHN-B 28946).

For the spermatheca we follow the terminology given by Gordon (1963: 51, fig. 10A) for *Tymolus*

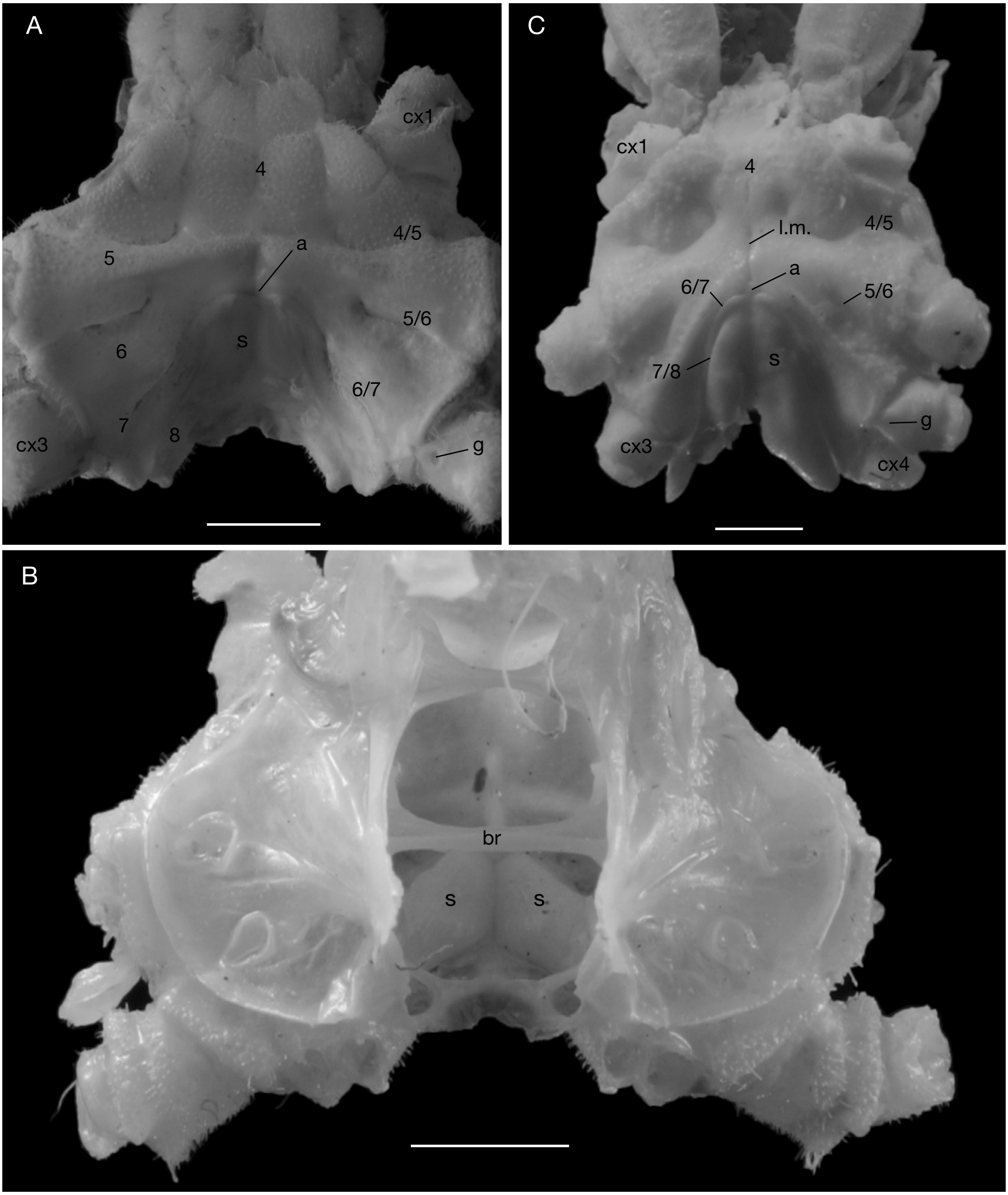

FIG. 23. — **A**, **B**, *Tymolus daviei* Tavares, 1997 (Cyclodorippidae, Cyclodorippinae), female 8 × 8 mm, paratype, Vanuatu (MNHN-B 28946); **C**, *Krangalangia spinosa* (Zarenkow, 1970) (Cyclodorippidae, Xeinostomatinae), female 7.1 × 6.5 mm, New Caledonia (MNHN); **A**, **C**, thoracic sternum; **B**, thoracic axial skeleton. Abbreviations: **a**, spermathecal aperture; **br**, transverse bridge; **cx1**-**cx4**, P1-P3 coxae; **g**, female gonopore; **l.m.**, median line; **s**, spermatheca; **4-8**, thoracic sternites 4-8; **4/5**-**7/8**, sternal sutures 4/5 to 7/8. Scale bars: A, 2 mm; B, 10 mm; C, 1 mm.

japonicus Stimpson, 1858. Sutures 7/8 converge medially and end on two small papillae. The terminal apertures are not clearly visible, showing only as two poorly calcified subterminal areas situated at the level of P2, thus anterior to the female gonopores (Fig. 23A). We assume that they correspond to slits, to a place where the two sheets of the endosternites 7/8 are not joined. The spermatheca consists of a developed pocket (the chamber) with an enlarged, inflated anterior part, that occupies large part of sternite 8, and a narrow posterior one that corresponds to a shorter invagination of endosternite 7/8. The two chambers are largely in contact with the sternal surface but are not fused to it (they may be easily detached) since they are invaginations of the phragma 7/8. The two pockets are almost contiguous, clearly visible through the thin sternal wall, and are filled with a whitish material, probably sperm masses (Fig. 23B). The apex of G2 resembles a needle (Gordon 1963: 52, fig. 11A for *T. japonicus* Stimpson, 1858), that corresponds to the small spermathecal opening.

The spermatheca was figured in another cyclodorippine, *Corycodus decorus* Tavares, 1993 (Tavares 1993: fig. 9b; see also Guinot & Tavares 2003: fig. 10I): only narrow slits are present.

Subfamily XEINOSTOMATINAE Tavares, 1992

Krangalangia spinosa (Zarenkow, 1970)

Female 7.1 × 6.5 mm, New Caledonia, MUSORSTOM 5, stn 023 (MNHN).

Sutures 6/7 and 7/8 greatly converge medially, forming a marked curvature, and both end very close together at the level of P2 coxae (Fig. 23C). Suture 6/7 is more marked than suture 7/8, may be considered continuous, and forms a subterminal ridge surounding the two tiny spermathecal apertures at the extremities of the sutures 7/8. As a result, the nearly contiguous apertures (filled with sperm in this individual) are situated just posteriorly to extremities of sutures 6/7. The internal shape of the spermathecal pocket is not discernible in this individual.

Krangalangia orstom Tavares, 1993

The posterior part of the thoracic sternum, figured by Tavares (1994: fig 37B) for the female of *Krangalangia orstom*, shows the same arrangement.

Family PHYLLOTYMOLINIDAE Tavares, 1998

Sternites 7 and 8 are bent perpendiculary to the sternites 4-6 and are contiguous (Tavares 1998); suture 6/7 is complete (M. Tavares pers. comm.). It was not possible to prepare the skeleton of a phyllotymolinid. But the key of the phyllotymolinid genera given by Tavares (1998: 118) was partly based on the location of the spermathecae. Their apertures are either nearly contiguous (genus *Lonchodactylus* Tavares & Lemaitre, 1996) or very apart, being indicated by a well defined bump (genera *Phyllotymolinum* Tavares, 1993 and *Genkaia* Miyake & Takeda, 1970). In a preceding work, Tavares (1994: 219, fig. 56) considered close spermathecae the apomorphic condition.

Family CYMONOMIDAE Bouvier, 1897

The thoracic sternum remains hitherto poorly known, despite the photograph of the ventral view of a male of *Curupironomus agassizi* (A. Milne-Edwards & Bouvier, 1899) given by Rathbun (1937: pl. 31, fig 2, as *Cymopolus agassizii*). A description of the spermatheca of *Cymonomus granulatus* (Norman *in* Wyville Thomson, 1873) was provided by Gordon (1963: 51, fig. 10B). Suture 6/7 runs accross the full width of the thorax, thus is complete. The position of the spermatheca is indicated by a distinct bulge on sternite 8, the spermatophoral mass seems rather small, and the aperture is spindle-shaped. Sternite 8 may partly overlap the sternite 7 in providing a kind of pocket at the extremity of the suture 7/8 (see also Tavares 1994: fig. 37A, as *Cymonomus* sp.). The apex of G2 is like the sole of a boot (Gordon 1963: 52, fig. 11B), which corresponds to the ovate spermathecal opening.

According to Gordon (1963: 52), the *Cymonomus* type of spermatheca is reminiscent of that found in the Homolidae.

Superfamily RANINOIDEA De Haan, 1839

The superfamily Raninoidea De Haan, 1839, which contains the single family Raninidae or frog crabs, and assigned to the Podotremata by Guinot (1978, 1979a), was subdivided into six Recent subfamilies (Ranininae De Haan, 1839, Raninoidinae Lörenthey & Beurlen, 1929, Notopinae Serène & Umali, 1972, Symethinae Goeke, 1981, Cyrtorhininae Guinot, 1993, Lyreidinae Guinot, 1993), principally based on morphology of the thoracic sternum (Guinot 1993b: figs 1-6). Dawson & Yaldwyn (2000) adopted these views. Tucker (1998) also followed Guinot (1993b) but elevated the Symethinae to familial rank, and recognized the exclusively fossil subfamily Palaeocorystinae Lörenthey & Beurlen, 1929, which ranged from the Lower Albian to the Cenomanian and is supposed to represent the rootstock of the Raninidae.

The superfamily consists currently of less than 50 extant species, distributed in 12 genera. Basal relationship of raninoids to the heterotreme-thoracotreme assemblage, indicated by some morphological features, spermatological analysis of *Ranina ranina* (Linnaeus, 1758) (Jamieson 1989) and molecular sequences (Spears *et al.* 1992), was partly refuted by further spermatozoal studies (Jamieson 1994; Jamieson *et al.* 1994). Nevertheless, subsection Raninoida, with the two superfamilies Raninoidea and Cyclodorippoidea, was recently attributed to the Eubrachyura (Martin & Davis 2001). This change in the classification of the Raninoidea was made mostly on the basis of arguable molecular evidence while rejecting morphology and functional morphology, in particular that related to the female genital condition. It is nevertheless possible that the Archaeobrachyura may eventually prove to be an "interim" scheme, between the basal Podotremata (Dromiacea and Homolidea) and the Eubrachyura. Cladistic analysis and the study of molecular sequences are in progress to critically examine the phylogenetic relationships of the Archaeobrachyura (Guinot unpubl. data). The distinctive morphology of the raninoids seems to reflect a high degree of specialization for burrowing, which has characterized the group throughout its long geologic history since its apparition in the Early Albian.

In raninid crabs the abdomens are only weakly sexually dimorphic, with all the somites that are not folded down in males. The sterno-abdominal depression is small, only posterior, and a single subfamily, the Lyreidinae, shows an efficient holding of the abdomen (Guinot & Bouchard 1998; Bouchard 2000). The posterior part of the sternum shows an acute dorsal flexion and, in ventral aspect, only the anterior sternites form a flat shield. Posterior sternites are narrower, sometimes linear; sternite 8 is variously reduced. The spermathecae, which are generally small and medially located, lie in a depression and are more or less recessed to the bottom or sides of the pit-like depression (Fig. 24), so that they are not immediately obvious or even not visible at all. In order to see their paired apertures, it is necessary to bend the crab and examine the bottom of the depression and its more or less steep opposite sides.

The axial skeleton of the raninoids is very peculiar (Bourne 1922), the extreme dorsal flexion of last sternites resulting in a marked modification of the axial skeleton in that region. Posterior sternites are separated medially and to a variable extent by a high longitudinal wall ("median apodeme" of Gordon 1963 and Hartnoll 1979), marked externally by the median line that is present at least on sternites 7 and 8, and often also on sternite 6 and a part of sternite 5. Each spermatheca, with its aperture occluded by a membranous area, is only composed by a chamber that is enclosed on each side of this wall. As a result, the spermathecae are variously placed together, that led Gordon (1966) to suppose a single, unpaired spermatheca. The paired spermathecal structure was remarkably determined by Hartnoll (1979), the gonopods described by Minagawa (1993), and the reproductive biology studied by Minagawa *et al.* (1993, 1994).

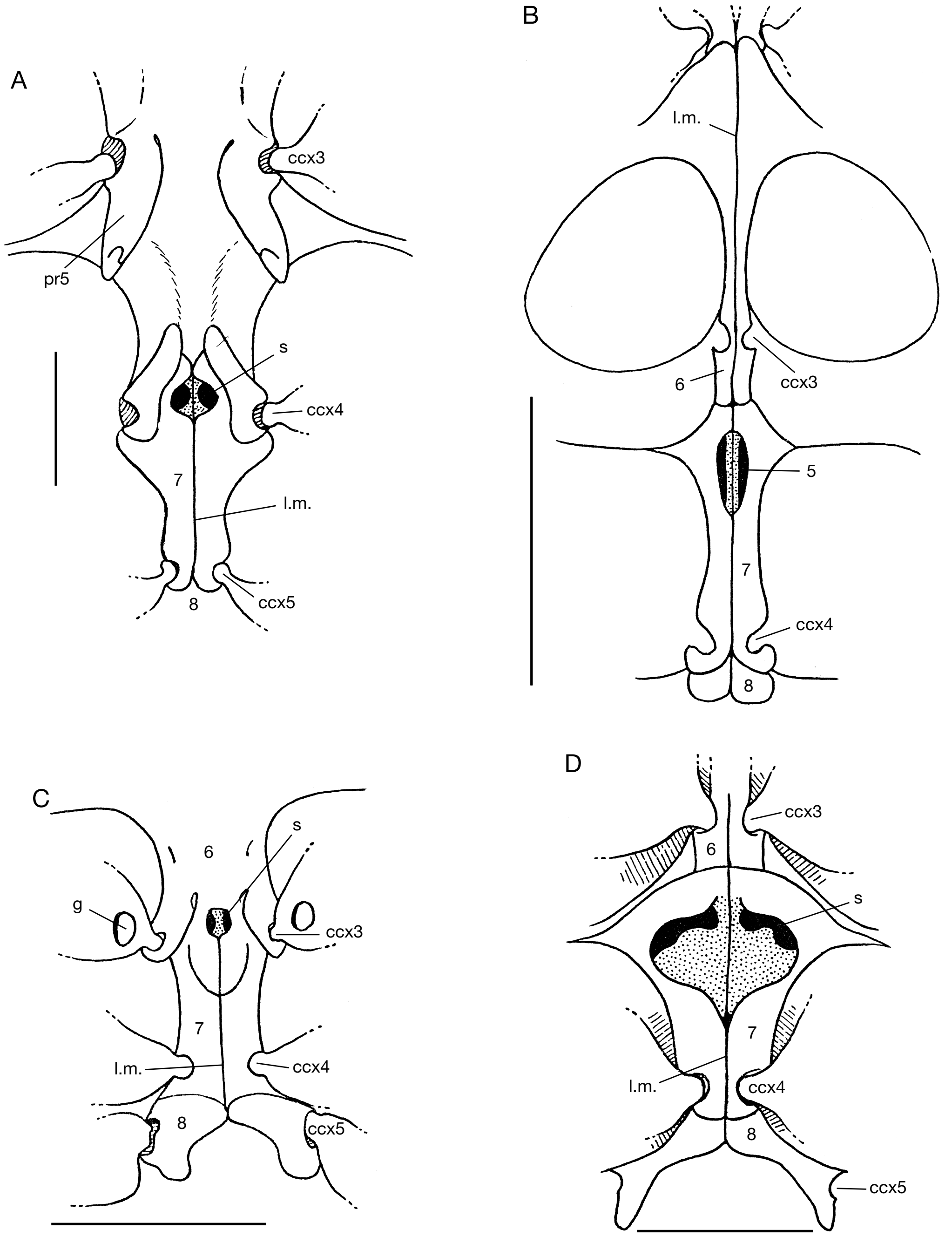

Fig. 24. — Posterior part of thoracic sternum in four Raninoidea; **A**, *Lyreidus tridentatus* De Haan, 1841 (Lyreidinae); **B**, *Ranina ranina* (Linnaeus, 1758) (Ranininae); **C**, *Cosmonotus grayii* White, 1847 (Notopodinae); **D**, *Symethis corallica* Davie, 1989 (Symethinae). Abbreviations: **ccx3**-**ccx5**, articular condyles of P3-P5; **g**, female gonopore; **l.m.**, median line; **pr5**, projection from sternite 5 for abdominal maintaining; **s**, spermatheca; **6**-**8**, thoracic sternites 6-8. Scale bars: A, C, D, 2.5 mm; B, 1 cm.

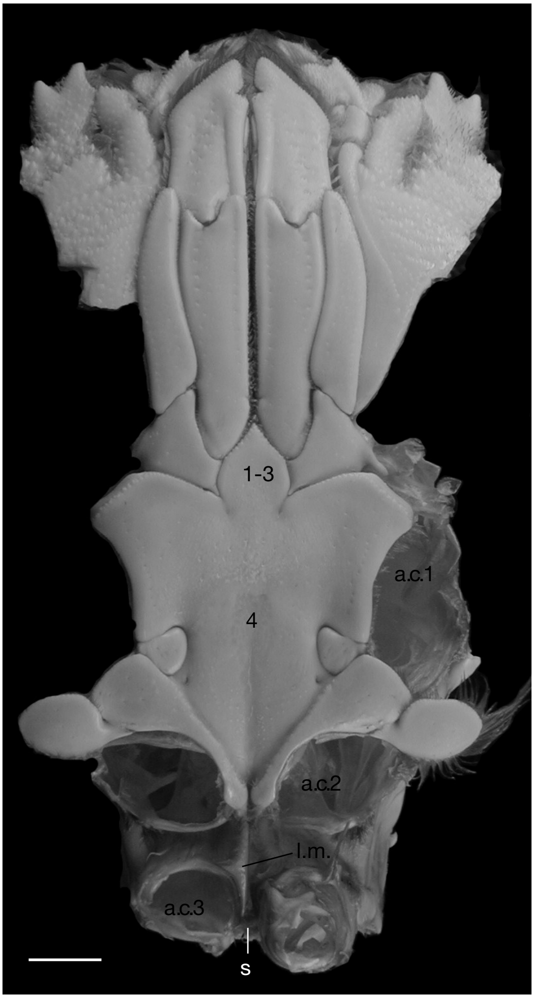

FIG. 25. — *Ranina ranina* (Linnaeus, 1758) (Raninniae), female approximately 80 mm width, New Caledonia, Nouméa (MNHN-B 17716), thoracic sternum, with only sternite 4 well developed, sternites 6 and 7 linear. Abbreviations: **a.c.1-3**, arthrodial cavities of P1-P3; **l.m.**, median line; **s**, approximate location of the paired spermathecae; **1-3**, thoracic sternites 1-3; **4**, thoracic sternite 4. Scale bar: 1 cm.

Family RANINIDAE De Haan, 1839

Subfamily LYREIDINAE Guinot, 1993

Lyreidus tridentatus De Haan, 1841

Female, 17 mm wide, Philippines, MUSORSTOM 2, stn 30 (MNHN).

The complete sternite 7 is trough-like; it slightly widens anteriorly and becomes deeper to form a depression (Guinot 1993b: fig. 4; Hartnoll 1979: 76, 80, figs 1-3). The two small spermathecae face each other on opposite sides of this depression and are separated by the vertical median wall, marked externally by the median line (Fig. 24A). "A rather indistinct suture crosses it [median line] to link the two openings: this is where the endosternites 7/8 fuse with the median apodeme and the seventh sternite" (Hartnoll 1979: 77, 78). Each spermathecal aperture is occluded by a membranous area and opens close to the female gonopore on P3 coxa. Because of the distortion of the posterior axial skeleton, "it is possible for the spermathecae to lie in endosternites 7/8, yet at the same time to open anteriorly well away from the sternal suture 7/8" (Hartnoll 1979: 78).

Subfamily RANININAE De Haan, 1839

Ranina ranina (Linnaeus, 1758)

Female, approximately 80 mm wide, New Caledonia, Nouméa (MNHN-B 17716).
Anterior part of sternite 7 shows an elongated, very deep, steep-sided median depression. The two apertures, located behind the gonopores on the P3 coxae, lie facing each other on either sides at the bottom of this depression, and are occluded by a flexible membrane (Gordon 1963: fig. 12; Hartnoll 1979: fig. 4; Guinot 1993b: fig. 2) (Figs 24B; 25). The chamber, which is relatively small compared to the size of the animal, is inflated, shows a flexible outer wall, and is filled by a sperm mass.

Subfamily RANINOIDINAE Lörenthey & Beurlen, 1929

Raninoides bouvieri Capart, 1951

Female, approximately 17 mm width, Senegambia, *Calypso* 1956, stn 4 (MNHN-B 16179). Sternites 4-6 form a flat shield, whereas posterior part of sternites 6 and 7 is narrower; sternite 8

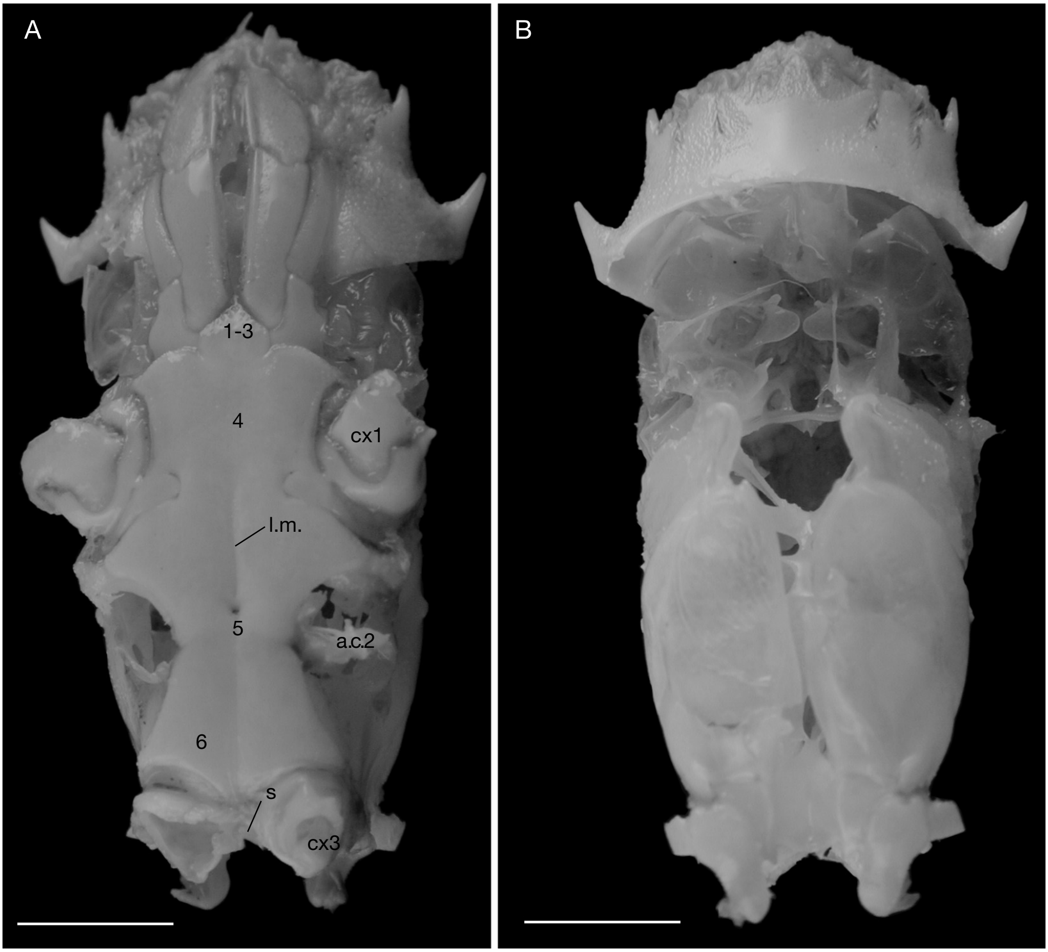

Fig. 26. — *Raninoides bouvieri* (Capart, 1951) (Raninoidinae), female approximately 17 mm width, Senegambia (MNHN-B 16179); **A**, thoracic sternum; **B**, axial skeleton. Abbreviations: **a.c.2**, arthrodial cavity of P2; **cx1**, **cx3**, P1, P3 coxae; **l.m.**, median line; **s**, approximate location of the paired spermathecae; **1-3**, thoracic sternites 1-3; **4-6**, thoracic sternites 4-6. Scale bars: 5 mm.

is horseshoe-shaped (Fig. 26A). Median line longitudinally divides sternites 5 to 8. The small spermathecae are located in the tilted posterior part of the sternal plate and lie at the bottom of the deep pit-like depression, so that they are not obvious. The axial skeleton shows the typical and unique arrangement of the raninoids (Fig. 26B).

Raninoides sp.

Female approximately 10 mm width, Brazil (MNHN).

Sternite 7 is very narrow and shows anteriorly a narrow, deep and steep sided median depression. Since the small paired spermathecae are located on the opposite sides of this depression, they are not visible externally and cannnot be seen without dissection. The two spermathecal apertures are located behind the female gonopores on the P3 coxae.

Notopoides latus Henderson, 1888

Female, approximately 29 × 22 mm Philippines, MUSORSTOM 2, stn 57 (MNHN-B 11556).

There is an oval and a very deep median depression in the anterior part of sternite 7, which is wider and more elongated than in *Raninoides*. The apertures are located on opposite sides of this depression. The pocket seems very small.

THE SPERMATHECAE IN THE FOSSIL PODOTREME FAMILIES

The spermathecal apertures have been positively identified in two fossil families, both from the Cretaceous.

Family DAKOTICANCRIDAE Rathbun, 1917

Genus *Dakoticancer* Rathbun, 1917

The American Cretaceous genus *Dakoticancer* shows female gonopores on the P3 coxae. On the developed sternal plate sutures 7/8 end in large, rounded orifices, which are considered homologous to spermathecal apertures (Guinot 1993a: 1229, figs 7, 8; Guinot & Tavares 2003: fig. 10H). Maastrichtian Mexican specimens of *D. australis* Rathbun, 1917, notably showing dislocation of sternal plates, were found associated with burrows, suggesting that these crabs molted in burrows to seek haven (Vega & Feldmann 1991).

The diagnosis of the family Dakoticancridae Rathbun, 1917 by Bishop *et al.* (1998) must be corrected to: "sternum of females with longitudinal grooves constituted by sutures 7/8" [instead of "without"] and, additionally, it must indicate the presence of the large orifices which are homologous to the spermathecal apertures.

Family ETYIDAE Guinot & Tavares, 2003

Etyus martini Mantell, 1844

In *Etyus martini*, from the European Cretaceous, two oblique and relatively large slits at the extremities of the sutures 7/8 (Wright & Collins 1972: 102, pl. 21, fig. 6d, e) were considered homologous to spermathecal apertures by Guinot & Tavares (2003: figs 2, 3, 10J).

THE AXIAL SKELETON IN THE PODOTREME GROUPS

The axial skeleton is a relatively poorly studied structure. The condition of the spermatheca, directly linked with the axial skeletal organization, specially in its posterior part, and always initially lying within endosternite 7/8, provides some interesting information. In the Brachyura phragmal organization proves to be consistent with the phylogeny, showing different evolutionary stages (Drach 1950, 1959, 1971; Secretan 1983, 1998). The different patterns are briefly presented herein.

The Homolodromiidae (Fig. 3B, D) shows a regularly layered, partitioned skeleton, and a binding of the endopleurites effecting transversally in the median axis, metamere by metamere, with several median connections by interfingering. This certainly represents the most primitive organization of the Recent crabs. Short endopleurites join together longitudinally, but the last endopleurite, which is shorter, has no contact with other phragmae, while the large intertagmal phragma extends towards the last endosternite and joins it (Secretan 1998: 1758, figs 12, 13).

The pattern in Dromiidae and the Dynomenidae markedly differs from that of the Homolodromiidae. Endopleurites of each lateral part join together longitudinally and remain on the sides; the two sides are connected by wide transverse connections constituted by the grouped endosternites. The connections occur by fusion, such as in the advanced Brachyura. The intertagmal phragma extends and fuses with endosternal part of the skeleton. There is no sella turcica (Drach 1971: 290; Secretan 1998: 1758, figs 7-11).

For the first time the axial skeleton in the Sphaerodromiinae (Fig. 17) and the Hypoconchinae (Fig. 16C) is observed and described herein. Dissections have shown a layered skeletal organization and the presence of two transverse bridges in the Sphaerodromiinae (considered the plesiomorphic condition), in contrast to a more complete median concentration and only one transverse bridge in the Dynomenidae (Fig. 4B, D), Hypoconchinae (Fig. 16C) and Dromiinae (Figs 7; 10B; 11A; 12B) (apomorphic condition). The Dromiinae, which has elaborated a long, calcified spermathecal tube in the females and have modified uropods in dorsal plates that allow the holding of the abdomen in males, now proves to be markedly specialized crabs. In the dynomenid axial skeleton, at least three distinct patterns (probably four, when the primitive *Acanthodromia* A. Milne-Edwards, 1880 is dissected) are present, with the following polarity: *Paradynomene* (probably plesiomorphic condition), *Metadynomene* (Fig. 4B), *Dynomene* (Fig. 4D), that corroborates the more advanced condition of *Dynomene* already pointed out (Guinot & Bouchard 1998). The Dynomenidae, known since the Jurassic, was perhaps confused with the Sphaerodromiinae in fossil record, because they share similar carapace outline, shape of fronto-orbital region, antennules and antennae.

In certain respects the Homolidea, with a less marked convergence of skeletal parts and junction by interdigitation (interfingering) (Fig. 18), retains a more ancestral condition of the axial skeleton than the Dromiidae. Nevertheless, in contrast to *Nephrops norvegicus* (Linnaeus, 1758) (see Secretan-Rey 2002), the pleurites are in an oblique position (vertical in *Nephrops*) and the endopleurites do not reach the median axis (versus stretching out toward median axis in *Nephrops*). In the numerous homoloid genera that were examined, the intertagmal phragma lengthens toward the median endosternites-bridge, to which it joins partially without any contact with the endopleurites. The Homolidea, which exhibits a skeletal pattern somewhat intermediate between the astacidean and eubrachyuran patterns (Secretan 1983: fig. 1; 1998: fig. 16), forms a lineage different from that of the Dromiacea. The spermathecal chamber is relatively simple and directly opens to the exterior, there are no specialized uropods, and abdominal maintaining is made by using the coxae of pereopods but adding the "homoloid" press button. The Homolidea is, with the Homolodromiidae, the most ancient podotreme group, known since the Jurassic (Wehner 1988; Müller *et al.* 2000).

In the family Poupiniidae, *Poupinia hirsuta* shows a peculiar skeletal disposition (Fig. 22), with a general organization similar to the homolid one, but there is no median junction, and digitations (which form the median binding in the other Homolidea) completely cover dorsally the endopleurites. An analogous case of laterally shifted digitations is observed in the "carcinized" anomuran crab *Lomis hirta* (Lamarck, 1818) (Lomisidae Bouvier, 1895), where the median axis is devoid of a central bridge, the digitations are only at the extremities of the endopleurites and also partly covering them. The taxonomic placement of *Lomis* is controversial (Tudge 1997; McLaughlin & Lemaitre 1997; see discussion in Martin & Davis 2001: 48). Further studies about this peculiar skeletal pattern found (homoplasically) in the Poupiniidae and in the Lomisidae may help in the interpretation about their questioned basal or advanced position in their respective groups, Brachyura Homolidea and Anomura.

To our knowledge, the Homolodromioidea and the Homolidea are the only cases in the Brachyura where phragmae, instead of connections by fusion, join by interfingering (Secretan 1998: figs 12, 13). It does not mean a close relationship, however, only a plesiomorphic condition.

The axial skeleton was not known in the Cyclodorippoidea. In the two cyclodorippids that were examined in this study, *Tymolus* (Cyclodorippinae) (Fig. 23B) and *Krangalangia* (Xeinostomatinae), the narrow transverse bridge shows connections by fusion, there is a strict lateral location of the endopleurites, and the intertagmal phragma is reduced.

The skeletal organization of the Raninoidea (Fig. 26B), which is strongly modified, with distortion and particularly extreme dorsal flexion of the rear part but showing distinct patterns in the different subfamilies, constitutes a separate investigation by itself, one that is out of the scope of the present one.

Thus, the podotreme crabs show different evolutionary stages of their median connections and in the fusion of their intertagmal phragma with other skeletal parts. Some Podotremata (Homolodromiidae, Homolidea) show the same kind of connections by interfingering as the other Decapoda (such as *Nephrops norvegicus*), instead of connections by fusion (Dynomenidae, Dromiidae, Cyclodorippoidea, Raninoidea) as the Eubrachyura. In the Eubrachyura the intertagmal phragma has become the sella turcica for it is always fused to both endosternal and endopleural phragmae, the median binding(s) has(ve) disappeared and the phragmal structures have been separated into two lateral parts (Secretan 2002). In the primitive Eubrachyura these lateral parts are close to the median axis (narrow thoracic sternum with sutures 4/5 to 7/8 parallel and continuous), and in the advanced ones (wider thoracic sternum with sutures 4/5 to 7/8 variously interrupted) the phragmae are widely separated and isolated on each side. Another structure, the junction plate (fused to sella turcica) transversally connects the lateral phragmae, reinforces the skeletal system and ensures its cohesion. These different steps may be considered "transformations" and "progression" (terms used by Secretan 1998) from a primitive ground plan to reach the carcinized condition by means of fusion, new junctions and compartmentation. This "progression" does not involve a phylogenetic conclusion, but the general skeletal scheme permits to consider a podotreme group combined with the eubrachyuran one.

GENERAL DISCUSSION

THORACIC STERNUM AND SUTURES

A regular feature among all the Podotremata is the more or less abrupt dorsal flexion of the posterior part of the thoracic sternum, sometimes so much that last sternites may be almost perpendicular to the preceding somites. Arthrodial cavities of the last pereopods (P4 and P5, or P5 alone) become dorsal, and the concerned legs are modified and reduced, being very often used for carrying behaviour (Guinot *et al.* 1995). The female sutures 7/8 completely lie in a tilted posterior sternal part, except when they project forward on the sternal plate, so that at least sternite 8 becomes partly anterior (see discussion below).

In the Dromiacea the complete thoracic sternum in both sexes forms a single piece, where all the sutures are only lateral. Sutures are only partially apparent in the Dynomenidae, so that they seem to have "very derived sterna" (McLay 1999: 455). In fact, however, sutures are lateral and concealed in the relatively wider and flat sternum. In this matter dynomenids are rather similar to dromiids and homolodromiids, with only lateral sutures 4/5 to 6/7 and the thoracic sternum showing as an undivided plate. Only sutures 7/8 may be very long and project forward in (most) dromiine females. We agree with McLay (1999) in regarding the short sutures 7/8 as the plesiomorphic condition while the long and specialized sutures 7/8 represent derived condition.

Sutures 4/5, 5/6 and 7/8 are lateral in all the Homolidea. Suture 6/7 is continuous and completely crosses the sternal floor in both sexes, however. Thus, the thoracic sternum is divided transversally into two parts by a complete suture, a condition never present in the Dromiacea. Internally, suture 6/7 corresponds to a short invagination of the phragma 6/7 that forms a tubular ridge that completely crosses the internal sternal floor. After dissection, this tubular ridge shows a very weak port, indication of its very small lumen. In the Homolidae sternite 8 consists of two more or less joined parts, the presence of a median line corresponding to a median invagination. As a result, the sternal plate in both sexes may be divided twice, by the transversal suture 6/7 and by the longitudinal median line. In the Poupiniidae, sternite 8 is longitudinally divided by a very short median line, while the sterno-abdominal notch is deep. In the Latreilliidae sternite 8 is completely separated into two parts, so that the median line is absent and the abdomen is inserted into sterno-abdominal notch.

Members of the three families of Cyclodorippoidea (term used *for convenience* to group Phyllotymolinidae, Cymonomidae and Cyclodorippidae) show a wide sternal plate and have acquired a true sterno-abdominal cavity (although small and generally posteriorly located), that markedly contrasts with the Dromiacea and Homolidea where a longer male abdomen fills completely each side of the sterno-abdominal depression (or more or less completely in some dynomenids and in all latreilliids). But, as in the other Podotremata, most sternal sutures are interrupted in various extent. In fact, female sutures 4/5-7/8 show different patterns along the three cyclodorippoid families. Suture 6/7 is very often (if not always) complete, as in the Homolidea. A more or less long and discontinuous median line is very often present. As in the Dromiinae, suture 7/8 is very oblique and may extend much forward to the gonopores on the P3 coxae, sometimes reaching the anterior part of the sternal plate, at a level even to P1. Sutures 4/5-7/8 or 5/6-7/8 may be all situated in a tilted posterior part of the sternum (as in the cyclodorippine genus *Corycodus*, see Tavares 1993: figs 6b, 7c, 8c). Another pattern, with all sternal sutures projecting forward and pushed on the lateral sides of the sternal plate, is also observed, as in the cyclodorippine *Neocorycodus stimpsoni* (see Tavares 1994: fig. 22D; 1996: fig. 23D) (Fig. 28).

The pattern is quite different in the Raninoidea. The posterior part of the sternal plate is narrow, sometimes linear, and the generally incompletely folded abdomen fills a reduced, posterior space between the last pereopods (Fig. 24). The courses of the sutures 4/5-7/8 are very different from those of the preceding families. Posterior sternites are divided by median line corresponding to a high vertical wall.

Among the Podotremata, the sternum shows all sutures that are incomplete in all the Dromiacea and in all Homoloida and Cyclodorippoidea, except for suture 6/7 which is complete in the last two groups (perhaps, with very few exceptions in the Cyclodorippinae).

THE DROMIACEAN SPERMATHECAE

A strong modification characterizes the sutures 7/8 of females. The spermatheca of the Podotremata is an example of a modification of the axial skeleton (i.e. of one intermetameric septum) in response to functional necessities of the regions of the body that the phragmae partition off. This corresponds to a secondary and dimorphic feature of the skeletal organization, for a reproductive function. The fact that the podotreme spermatheca results from a split between the two plates of the female phragmal invagination that separates the two last thoracic segments (endophragma 7/8) demonstrates that the two sheets of a phragma may be not joined (Secretan 1982). The podotreme spermatheca is a paired, intersegmental or intertagmal structure. The paired spermatheca that characterizes the Podotremata is internalized: it always corresponds to two pockets (the chambers), inside invaginations of the phragmae 7/8.

Among the Dromiacea, the spermathecal chamber opens either directly by an anteroventral aperture (Sphaerodromiinae, Dynomenidae) or is prolonged by a calcified tube (Homolodromiidae, Dromiinae, Hypoconchinae). The tube, very short in the Homolodromiidae, becomes very long in most Dromiinae, so that the spermathecal aperture becomes remote from the chamber. This corresponds, during ontogenetic development, to the growth forward and to the expansion of the thoracic sternites 7 and 8, which encroach on preceding sternites, namely sternites 6, 5, and even 4 (Fig. 1). Consequently, limits between the sternites are difficult to evaluate, becoming difficult to determine if sternites 6, 5, and 4 are only crossed by the sutures 7/8 or if they are pushed away? (In the cyclodorippine *Neocorycodus stimpsoni*, with all sternal sutures projecting forward on the wide sternal plate, it is evident that sutures 5/6 at least are pushed to the sides of the sternum [Fig. 28]).

The first pattern (without tube: Sphaerodromiinae, Dynomenidae) is considered plesiomorphic, suggesting that the Sphaerodromiinae is basal to the Hypoconchinae + Dromiinae and that the Dynomenidae is basal to the remaining dromiacean families (Guinot & Tavares 2003). The Hypoconchinae shares apomorphically a tube (although rather short) with the Dromiinae.

It should be stressed that the presence of a spermathecal tube is not necessarily linked with long sutures 7/8 since such a tube is present even in species where sutures 7/8 do not extend beyond the level of female gonopores on the P3 coxae. Such a condition characterizes the Homolodromiidae, in which a tube is present in species with spermathecal apertures lying back on the sternum (*Homolodromia kai*, Fig. 3A, C; *Dicranodromia doederleini*), the dromiine *Frodromia* (Fig. 12A), in which spermathecal apertures lie slightly behind gonopores on the P3 coxae, and the subfamily Hypoconchinae (Fig. 16A, B), in which they are located only slightly beyond the level of the P3. The arrangement is not known in the enigmatic genus *Stebbingdromia*, in which sutures 7/8 end between the P3 (Guinot & Tavares 2003: fig. 17C). On the other hand, the tube seems to be absent in all the Dynomenidae (Fig. 4), in which spermathecal apertures lie just below or slightly behind the female gonopores, and in the Sphaerodromiinae, similarly with short sutures 7/8 (Guinot & Tavares 2003: fig. 21C).

The spermathecal tube corresponds to an elaborate structure, a new character, and seems to be the result of a specialized organization, implying that the Dromiidae (Sphaerodromiinae excepted) is less "primitive" than supposed.

THE DROMIACEAN APERTURES

In the Homolodromiidae and the Dynomenidae the apertures of the spermathecae lie just below or behind the level of the gonopores on the P3 coxae or about their vicinity. In the Sphaerodromiinae, the more basal dromiids, due to the shortness of the sutures 7/8, the spermathecal apertures are situated far back on the thoracic sternum in the vicinity of the female gonopores. In the more advanced dromiids, Dromiinae and Hypoconchinae, lengthening of the sutures 7/8 (internally corresponding to calcified tubes) displaces the spermathecal apertures far from the female gonopores.

The selective advantage of having the spermathecal apertures situated so far forward, in front of the female gonopores, poses an interesting question. According to Gordon (1950: 251), due to the dromiid globular carapace, this position is perhaps more efficient for the reception of the male gonopods during mating (M. Tavares pers. comm.). Position of spermathecal apertures at the summit of an ornament (for example two rings in *Dromia*, Fig. 5, two high tubercles in *Lauridromia*, Fig. 13) supports this hypothesis. In *Moreiradromia sarraburei*, a relatively small but globose species, apertures lie at the level of the chelipeds. However, even in flat dromiids, the apertures lie forward, and in the Sphaerodromiinae, all with a globose carapace, the female sutures 7/8 are short. Nevertheless, the presence of apertures situated so far forward is likely related to the formation of two closed spermathecal tubes and corresponds to an elaborate organization. The carcinization phenomenon produces new condition and perhaps explains the podotreme evolutionary pathways and the relationships with the Eubrachyura (see below).

Externally, apart from the fact that sutures 7/8 are more or less long and end separately or together with different ornamentation, the organization is similar among the (adult) Dromiacea, nearly all having small terminal apertures, that are not occluded by membranous areas (at least in mature individuals). The pattern is different in only a few cases: long terminal slits (homolodromiine *Dicranodromia spinulata*), that correspond to areas where the two sheets of endosternites 7/8 are not completely joined; presence of subterminal slits (dromiine genus *Sternodromia*, Fig. 15) (Guinot unpubl. data); wide and long slits (dromiine genus *Cryptodromia*, Fig. 27B), the two phragmae of the endosternites 7/8 do not joining along a more or less long distance and being significantly opened; or partly decalcified and unperforated terminal pits ([*Dromia*] *dormia* Figs 8; 9; Guinot unpubl. data) that correspond to areas where the bottom of the phragma 7/8 itself becomes exposed at the sternal surface.

Gordon (1950: 204, fig. 1) referred to which sternite(s) may belong the ornaments often associated with the extremities of suture 7/8: the spermathecal apertures at the summit of two tubercles in *Lauridromia intermedia* (Fig. 13) or

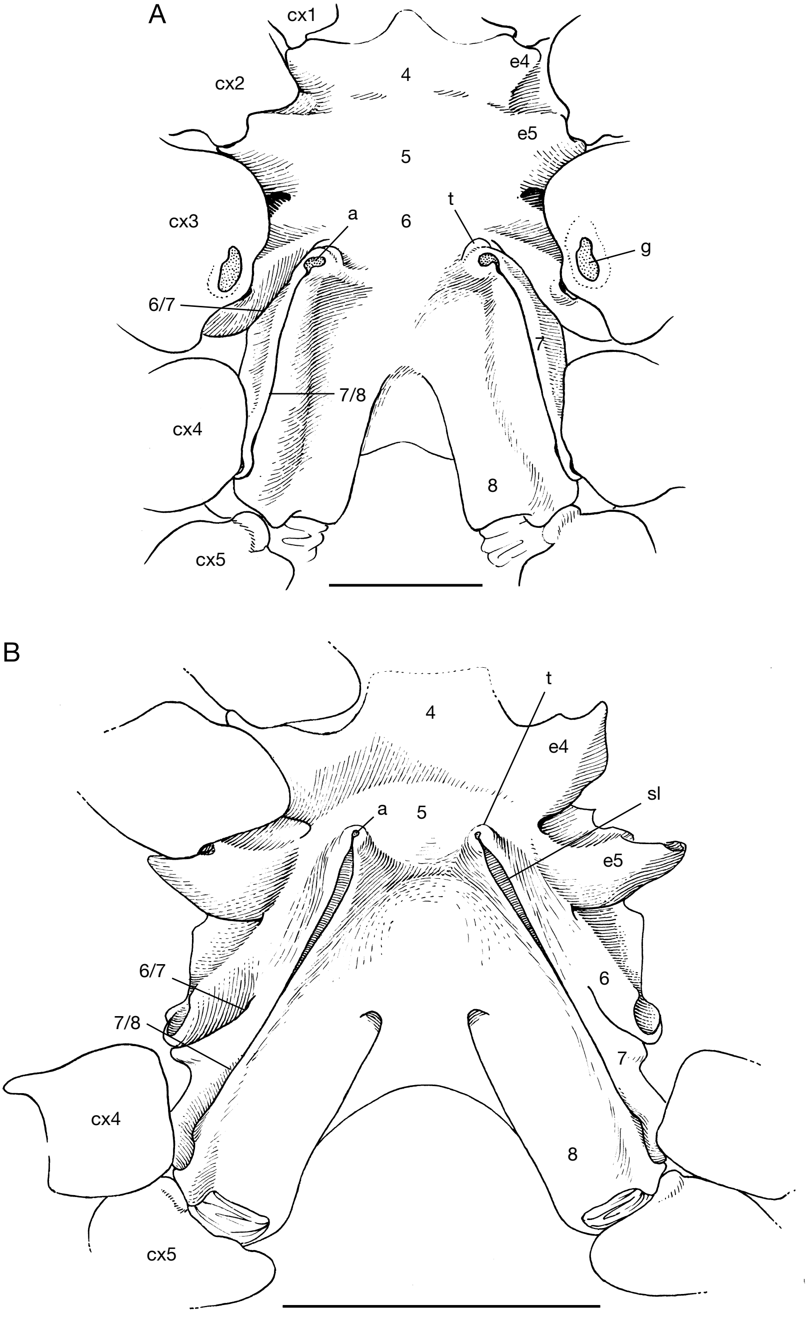

FIG. 27. — **A**, *Homolodromia bouvieri* Doflein, 1904 (Homolodromiidae), ovigerous female 33 × 26 mm, Madagascar (MNHN-B 28940), thoracic sternum (sternites 1-3 not drawn); **B**, *Cryptodromia tuberculata* Stimpson, 1858 (Dromiidae), ovigerous female 9 × 10 mm (with large eggs), New Caledonia, Karembé, McLay det. (MNHN-B 26387), spermathecal apertures as long opened slits. Abbreviations: **a**, spermathecal aperture; **cx1**-**cx5**, P1-P5 coxae; **e4**, **e5**, episternites 4, 5; **g**, female gonopore; **sl**, slit; **t**, tubercule; **4**-**8**, sternites 4-8; **6/7**, **7/8**, thoracic sternal sutures 6/7, 7/8. Scale bar: A, 5 mm; B, 2.5 mm.

in *Mclaydromia* (Guinot & Tavares 2003: fig. 12B), the ring encircling each aperture in *Dromia personata* and *D. marmorea* (Fig. 5A, B), or the single tubercle or prominence surrounding or bearing the two apertures or slits placed together in *Sternodromia spinirostris* (Fig. 15).

The raising of spermathecal apertures is not exclusive to the Dromiinae. In a large homolodromiid ovigerous female (*Homolodromia bouvieri*) (Fig. 27A), sternal sutures 7/8 were raised at the summit of two strong tubercules, as in a dromiine such as *Lauridromia* (Fig. 13), the only difference being the closeness between spermathecal apertures and female gonopores in *Homolodromia*. Regarding *Dicranodromia baffini* Alcock & Anderson, 1899, Gordon concluded that the tubercle near the junction of sternites 6 and 7 may be formed partly by both or may have only belonged to sternite 7. The presence of these ornaments often leads to the fact that spermathecal apertures are raised, perhaps to be more accessible for insemination. Gordon (1950: 251) and Hartnoll (1979: 82) have brought to attention how the forward position of the spermathecal apertures shown by advanced Dromiinae bears a resemblance to the vulvae of the Eubrachyura (see General discussion). The eubrachyuran vulvae are always situated in approximately the middle of the thoracic sternum (in the area corresponding to sternite 6), and the male gonopods are inserted inside them.

THE ROLE OF THE GONOPODS IN THE DROMIACEA

The arrangement of the two gonopods with the G2 passing through the G1, "the two forming collectively a single gonopod" (Dixon *et al.* 2003: 952, 966), is a synapomorphy of Brachyura, since the two gonopods never interact in this way in other decapods. In *Nephrops norvegicus*, the two gonopods of each side are combined together and function as a single apparatus (see Guinot 1979a: 224, figs 57-59A, B), with the difference that they transfer sperm to an unpaired spermatheca. In contrast, the Podotremata is characterized by a paired spermatheca, and the Eubrachyura possesses a unique sternal orifice, the vulva. The G1 of the Podotremata are incompletely folded, thus partially opened, even in advanced Cyclodorippoidea, as the phyllotymolinid *Clythrocerus nitidus* (A. Milne-Edwards, 1880) (see Tavares 1998: 117, fig. 7B-D) and the cymonomid *Cymopolus asper* A. Milne-Edwards, 1880 (see Guinot 1979a: 236, fig. 61A, C). They show a more or less large aperture, which can be lateral or proximal and is provided with a distinct, well delimited single basal foramen for the introduction of both penis and G2. The podotreme G2 is always well developed, often longer than the G1, and is introduced into base of G1 or inserted laterally along the slit of G1. In contrast, there are two basal foramina in the Eubrachyura, and their G1 are tubular, completely closed; their G2, which also show tubulation, may be long (see Brandis *et al.* 1999: 164) but more generally are very short.

Similarly in both Podotremata and Eubrachyura the two gonopods and penes interact together.

The tubulation of the G1 among the Dromiacea is often far from being complete, and the G2 is always long and, with the exception of *Stebbingdromia* Guinot & Tavares, 2003, ends in a styliform, needle-like appendix masculina.

The role of the gonopods in sperm transfer in the Dynomenidae was discussed in detail by McLay (1999: 456, figs 2f-i, 12, 13). The exopod of the G2 plays an important role in channelling the sperm into the base of G1, and the action of the spines arranged on the needle-like part of G2 may propel the sperm into G1. Spermatophores are delivered through the setose tip of G1 into the female spermatheca, with the medial plate of G1 acting to guide the sperm. According to McLay (1999: 459), the exopod of G2 in the Dynomenidae does not appear to be vestigial and it may be involved in the delivery of the sperm.

Similarly, the Sphaerodromiinae has a medial soft plate on G1 (McLay & Crosnier 1991: fig. 3b, c, for *Sphaerodromi brizops* McLay & Crosnier, 1991; Crosnier 1994: 345, fig. 3b, c, for *S. lamellata* Crosnier, 1994). The G2 has an exopod and its shaft bears spines. Conversely, these structures are absent in the other Dromiidae (McLay 2001c: 850, fig. 10). The plesiomorphic condition of both gonopods in Dynomenidae and in the

Sphaerodromiinae may be linked to their short sutures 7/8. The angle of the gonopods, during mating, would have to be greater due to the more posterior placement of the spermathecal apertures. The plate of the G1 and the spines on the G2 "may ensure better sperm transfer to prevent leakage" (McLay 2001c: 851, 852). On the other hand, close proximity between spermathecal apertures and the female gonopores characterizing the Homolodromiidae, Dynomenidae and the Sphaerodromiinae ensures an easier fertilization of the eggs when they are laid. McLay (2001c: 852) concluded that Homolodromiidae, in which lack a medial plate on G1 and spines on G2, retains ancestral condition, while the ancestor of the dynomenids + dromiids evolved these new structures, nevertheless secondarily lost in the more advanced dromiids (i.e. the Dromiinae). We agree that the dromiine condition is probably the derived one, which is proved by the formation of an elaborate spermathecal tube.

The shape of the penis, which in the Podotremata penetrates by a unique basal foramen at the base of G1 and along a more or less long distance inside G1, probably plays an important role in the reproductive strategies. The developed, mobile male penial tube present on the P5 coxa in all the Dromiinae (*Frodromia* excepted) and in the Hypoconchinae cannot have the same functioning than the modified, elongated P5 coxa of the Homolodromiidae and Dynomenidae, and of the Sphaerodromiinae as well (Guinot & Tavares 2003: 115, figs 18A, 20A, 23A, 25D, 28).

The possibility of an internal insemination was questioned in the Homolodromiidae, in which broken-off tips of G2 were found inside spermathecal apertures in several females, sometimes in a symmetrical manner (Guinot 1995: 177, figs 4C, 6B). It is not known, however, if it was the result of an accident (the case was observed in three species at least) and to what extent it may have injured the male individuals. A similar phenomenon was not observed in any other members of the Dromiacea examined during the present study.

The mechanism of sperm delivery and transfer remains poorly understood, even if the role of G2 was referred to by several authors (Gordon 1950; Guinot 1995; McLay 1999, 2001a). In the Dromiacea, the styliform G2 are always longer than G1 and most of them have an acute tip. This tip was observed as sclerotized and hardened in large [*Dromia*] *dormia* males (McLay 2001a: 98). When G2 is inserted inside G1, its tip can more or less extend out the G1 opening and comes in contact with the female. Potentially, it may enter into the spermathecal aperture, which is generally so small that insemination by G2, or with help of G2, seems easier than with the large tip of G1 (see Brandis *et al.* 1999).

The question remains as to how does the sperm in the Dromiinae reaches the spermathecal chamber and bulb, which are situated at the posterior extremity of a long tube, after it has been deposited in the spermathecal apertures. The present study has confirmed the frequent presence of sperm in these two structures. It is easy to see the sperm mass inside the chamber, specially through its transparent inner wall (endosternite 8). Because it is flexible, the inner wall may bulge at copulation to accommodate seminal material received from the male. Hartnoll (1975: 667, fig. 6) has described the contents of the spermathecal chamber, which consist of a complex of sperm and secretions issued from different parts of the male vas deferens. The bulb, which is more calcified, may also contain sperm: the presence of male material was observed inside the bulb after dissection in *Dromia marmorea* (Fig. 6D). In the three close genera *Dromia*, *Sternodromia* and *Lauridromia*, a small prominence is similarly visible anteriorly at the surface of the bulb; its role is unknown.

Another important question is how the sperm mass gets out again, how it is squeezed out from the bulb and expelled from the spermathecal chamber to make the inverse course to be pushed through the tube's lumen and reach the external surface for fertilization. The precise function of the bulb and chamber respectively and their role during the discharge of the sperm mass are unknown. In *Dromia personata* copulation is an extended process. This is explained by Hartnoll (1975: 675) by the weakness of the musculature of the vas deferens and the ejaculatory duct, in contrast to the "Astacura" (namely *Nephrops*) in which the thick musculature ensures rapid expulsion of the spermatophores, and copulation is very fast. Hence the question by Hartnoll (1975: 675) as to why the Dromiacea has abandoned "the efficient mechanism of the Astacura" which pass sperm also in integumental spermatheca. It is likely that in dromiids a musculature (perhaps from the last pereopod) acts on the flexible inner wall of the chamber to ensure entrance and expulsion of the sperm.

When the spermathecal aperture is present so much forward as in most Dromiinae, a long distance separates it from the female gonopore, which releases the eggs. In our large [*Dromia*] *dormia* (107 mm carapace length) this distance is approximately 35 mm. If the anterior position of the spermathecae facilitates mating, it seems that it perhaps complicates the fertilization process.

The question of fertilization was asked by McLay (2001a: 98). In an ovigerous female of [*Dromia*] *dormia* (cw 137.3 mm, thus similar to the female in Figs 8A; 9), the length of suture 7/8 was about 50 mm, the last 8 mm of the suture was blocked by transparent and soft material, and posterior to the blockage about 4 mm of the suture remained "open". This ovigerous female must have mated and fertilized her eggs, but it is not known if the blockage was formed after mating or after fertilization. If the material blocking the female apertures forms after mating, how does the sperm get out and fertilize the eggs? In the precise case of [*Dromia*] *dormia*, the distal part of the sutures 7/8 remains "open" and permits the release of sperm. But we have observed several dromiines in which a yellowish and hardened seminal material completely covers the sutures, including the round apertures or slits (such as in *Sternodromia spinirostris*, Fig. 15, *Lauridromia intermedia*, Fig. 13). Hartnoll (1975: 667-669, fig. 6) observed the plaques of hardened secretions around the spermathecal apertures in many dromiine females which have yet to lay eggs, which means that they are formed during copulation rather than fertilization. Assuming that females mate immediately after ecdysis and have soft and flexible integuments, Hartnoll observed that in a few females particularly copious spermathecal contents may extend "beyond the normal limits of the chamber by forcing apart" endosternites 7/8 so that they are exposed between P4 and P5.

Hartnoll (1975: 670-671) has shown the important role of ecdysis in *Dromia personata*. Copulation occurs after a pre-ovigerous moult, and females either mate immediately before their integuments are hardened, or they may do so after they have hardened. The entire contents of the spermathecae are shed with the cast shell at the post-ovigerous moult. In a female mating in captivity, there were no secretions on the female sternum before mating, but afterwards each spermathecal aperture "was surrounded by a plaque of hardened secretions pierced by only a small opening leading to the canal" (i.e. the spermathecal tube). It is not known to what corresponds this "small opening" on the sperm plug. Perhaps to a trace left by G2.

Plaques of hardened male secretions covering the two spermathecal apertures were observed in females of *Austrodromidia octodentata* (Haswell, 1882) (Guinot & Tavares 2003: fig. 2C). They were found only on one side in *Lauridromia intermedia* (Fig. 13A). The large apertures of spermathecae at the level of P3 were concealed by sperm plug in *Stebbingdromia plumosa* (Lewinsohn, 1984) (Guinot & Tavares 2003: fig. 17C). A single big mass may recover most part of the sutures 7/8 in *Sternodromia spinirostris* (Fig. 15A) and *Pseudodromia latens* Stimpson, 1858 from South Africa (unpublished figure). A rounded mass occluded each spermathecal aperture in *Homalodromia* ? *coppingeri* Miers, 1884 (Guinot & Tavares 2003: fig. 9B).

In the few female Sphaerodromiinae that were examined plaques of hardened secretions were not found around the spermathecal apertures, but this result is not necessarily significant. A sperm plug was never observed in any of the dynomenid females examined by McLay (1999: 455) or by us, a fact probably linked with the presence of spermathecal apertures close to the female gonopores. This implies a distinct reproductive modality.

We can now answer Gordon's (1950: 250) question on how the male sexual pleopod of *Dromia* fits into the sternal suture 7/8 and whether "the male secretions are simply poured in and around the opening to form the blotches found in certain females, or (much more probable) whether the sac [pocket or chamber] in endosternites 7/8 does indeed act as a spermatheca". We have very often observed the chamber filled with a yellowish, hardened matter, similar to the brown secretions glued to the sternum in many females (i.e. sperm mass) (Figs 13; 15).

Internal organization is similar among the Dromiacea, always with a chamber and a bulb, and it has been found filled with a sperm mass in the numerous female individuals of Dromiinae that were examined. The only difference concerns the absence or presence of the spermathecal tube. When the tube is absent, the result is the direct communication of the chamber itself to the exterior.

THE SPERMATHECA AND THE ROLE OF THE GONOPODS IN OTHER PODOTREMES

The spermathecal apertures of the Homolidea essentially differ in the size and shape of their various membranous areas, the spermathecae occupying a variable length of sutures 7/8. Spermathecal apertures are relatively large and elongate, always situated far back on the thoracic sternum, on a level with the female gonopores on the P3 coxae. Internal organization is rather similar along the genera and species, always with a chamber close to the aperture, which is situated at the extreme anterior end of the spermatheca, and directly opening to the exterior. More or less conspicuous membranous areas of the spermathecae have their external part belonging either to sternite 7, or to sternite 8, or to both. When sternite 8 is sunk below the level of sternite 7, the spermathecal apertures may be concealed. The spermathecae always form an anteroventral and hood-like bulge on both sides of endosternites 7/8 which contains the chamber, and nearly a great part of suture 7/8 is involved. The chamber may contain brownish and irregular masses of sperm. In *Homola barbata* dissected by Hartnoll (1975: 669), it consisted entirely of the material evacuated from the vas deferens of the male. To our knowledge, mating behaviour is not known in the Homolidea. For Hartnoll (1975: 674, 675), in *Homola barbata* (such as in *Dromia personata*) the spermatophores have a single sperm mass surrounded by secretions, without trace of subdivisions, and the weakness of the musculature of the vas deferens and ejaculatory duct suggests that copulation is an extended process.

In the Homolidea the G1 shows a more developed tubulation than in the Dromiacea, and its rather elaborated apex may fit with the spermathecal aperture. The G2 is short, rather stout and cylindrical, the endopodite being probably fused to the appendix masculina, and ends in a flat, cushion-like apex. Note that a G2 comprising a terminal "filamentous part" (character 59 of the Brachyura in Dixon *et al.* 2003: 953) does not characterize the Homolidea. The G2 may be interlocked with the G1 but without projecting beyond it (Gordon 1950: fig. 26B-D; Hartnoll 1975: fig. 2C, D; Guinot 1979a: fig. 61D, E; Guinot & Richer de Forges 1981: figs 5, 6; 1995: fig. 10). In the Dromiacea, when the two G1 and G2 are interlocked, the long needle-like G2 projects well beyond the apex of G1 and may penetrate into the generally small spermathecal aperture, without the possibility to reach the remote chamber in the Dromiinae. In the Homolidea, the coupled G1-G2 presumably enter the aperture and deposit the spermatophore in the chamber. The penis, which is always rather small, emerges from a non-modified coxa (Guinot 1979a: figs 43D-F, 61E). This differs markedly from the Dromiacea, in which the P5 coxa is either modified (elongated) or bears a separate, mobile and long penis.

Female sternal sutures 7/8 extend more or less forward in the Cyclodorippidae, sometimes projecting so much that they reach the extreme anterior part of the sternal plate, as in most Dromiinae. In *Neocorycodus* (Tavares 1994: fig. 22D; 1996: fig. 23D), the nearly contiguous spermathecal slits open at the level of the chelipeds (Fig. 28). In the Cymonomidae, sutures 7/8 end only slightly in front of female gonopores. The external shape

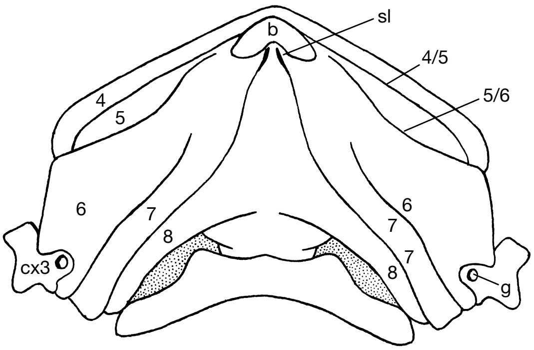

FIG. 28. — *Neocorycodus stimpsoni* (Rathbun, 1937) (Cyclodorippidae, Cyclodorippinae), ovigerous female 3.5 × 5 mm, holotype, thoracic sternum, with all sutures extended anteriorly and spermathecal slits at level of P1 coxae (redrawn from Tavares 1994: fig. 22D; 1996: fig. 23D). Abbreviations: **b**, unpaired bump; **cx3**, P3 coxa; **g**, female gonopore; **sl**, slit; **4-8**, sternites 4-8; **4/5-7/8**, thoracic sternal sutures 4/5 to 7/8. Notice that the suture 6/7 is perhaps longer and even complete.

of the spermathecae is variable in the Cyclodorippoidea, having at least two dispositions, but presumably more. The internal structure of the spermatheca seems rather simple. The apertures are small and show as rounded orifices, or are more extended and show as narrow slits; they may be situated apart or together, being sometimes nearly contiguous. Nevertheless, a constant feature is that the spermathecae are formed by invaginations of the sutures 7/8.

In the *Tymolus daviei* that was dissected, the two chambers show as inflated and almost contiguous whitish areas (probably filled with sperm masses) clearly visible through the thin sternal wall and running along suture 7/8. Internally, the spermatheca seems to consist of two parts: an anterior one corresponding to the inflated area already described, detached from the sternal surface (whitish area indicated as s on the Figure 23A, B), and a posterior one, cylindrical, tapering, and lighter, that is linked with the posterior part of the phragma 7/8. In contrast to the Dromiinae, the largest volume of the spermatheca (i.e. the chamber) is advanced forward. The trend of the migration of the apertures in the anterior part of the sternum is therefore encountered in the Cyclodorippoidea (Fig. 28), but the new development is that the chamber itself moves forward, while the posterior part remains fixed in its original position. It was difficult in this case (no sufficient available material and small size of the individuals) to determine the relationship between the chamber and the spermathecal aperture.

Such as in the other podotreme groups, the morphologies of G1 and G2 in the Cyclodorippoidea are modified in relation to their role in insemination. Gordon (1963) hypothesized that different kinds of spermathecae found in the cyclodorippids were linked to the shape of the male intromittent organs.

The spermathecae of the cymonomid *Cymonomus granulatus* (Norman *in* Wyville Thomson, 1873) were described and drawn by Gordon (1963: 52, fig. 10B), and the male gonopods figured by Hartnoll (1975: fig. 3A, B). The posterior part of the thoracic sternum is much less abruptly bent compared to that of *Tymolus daviei* (Fig. 23A). Sutures 6/7 are complete, and sutures 7/8 roughly end opposite P3 coxae, nevertheless in front of the female gonopores. Only the distal half of sutures 7/8 forms the spermatheca, which is shown by a distinct bulge in sternite 8 and contains a relatively small spermatophoral mass. Suture 7/8 ends by an oval, spindle-shaped area, presumably belonging to sternite 7, and the aperture is along its posterior edge. The apex of G2 of *Cymonomus*, looking as the sole of a boot, pushes aside the spindle-like area to place a spermatophore inside the spermathecal chamber. Conversely, in *Tymolus* the elongate needle-like apex of G2 probably enters the small aperture to pour the seminal fluid into the chamber (Gordon 1963: fig. 11A). The interpretations concerning shape of the spermathecal aperture and role of G2 were discussed by Guinot (1979a: 236, fig. 61A-C) who figured the spatulate G2 of another cymonomid, *Cymopolus asper*.

We stress that the tubulation of G1 in the Cyclodorippoidea, with its only barely rolled up endopodite, is not developed, a condition similar to that of the Dromiacea and remote from that of the Eubrachyura. Another resemblance to the Dromiacea is the needle-like apex of G2 found in *Tymolus*, in contrast to *Cymonomus*, in which the endopodite seems fused to the appendix masculina, as in the Homolidea. Very little, if nothing, is known about the biology and reproductive strategies of the small Cyclodorippoidea.

The spermathecal apertures are small and close in the Raninoidea, except in the Symethinae in which they are relatively larger. They are located either close to the female gonopores on the P3 coxae in the Notopodinae (*Notopus*; *Cosmonotus* White, 1847; Fig. 24C) or behind P3 coxae in the Ranininae (*Ranina*, Fig. 24B), in the Lyreidinae (*Lyreidus*, Fig. 24A) and the Raninoidinae (*Raninoides*) that were examined, and in the Symethidae (Fig. 24D) (Guinot 1993b: figs 1-5). The raninoid spermathecae are cryptic since they generally lie in a deep area of the sternum; their apertures are occluded by membranes; the chamber directly communicates with the exterior. Although in the Raninoidea spermathecae open anteriorly on sternite 7 rather than on sternal sutures 7/8 (Hartnoll 1979), the spermathecal chamber is still formed by the separation of the two laminae composing endosternite 7/8, however. In the female *Ranina* that was dissected, sperm mass filled the inflated pocket.

The reproductive biology of *Ranina ranina* is known from the studies of Minagawa (1993) and Minagawa *et al.* (1993, 1994). *Ranina* does not produce multiple sperm masses like other brachyuran crabs. The sperms are surrounded by a capsule in a portion of the vas deferens; muscles fibers of the ejaculatory duct and striated muscles in the penis are supposed to assist with the transfer of the spermatophore to the gonopod. In *Ranina* the tubulation of G1 is more developed than in the Dromiacea but less marked than in the Eubrachyura, and G2 endopodite is fused to the appendix masculina. The two G1 are closely apposed and act together; nevertheless their apices, which are not in contact medially, may inseminate the two closely placed spermathecal apertures The sperm, ejaculated from the penis to the base of G1 and picked up by the spoon-like structure of G2 to be placed in the distal part of G1, is transferred through G1 ejaculatory canal into spermathecae. Apical region of G1 forms a bent cuticular plate, the role of which is probably to stabilize the insertion into the spermathecae. It must be pointed out that the dromiacean Dynomenidae and Sphaerodromiinae similarly have a medial plate on G1 (see above). In *Ranina* setae on the ventromedian region of G1 "would work as sensors of the contact of females abdomen and spermathecae"; thus, the structure of both G1 and G2 "is modified to fit the copulation and spermathecal structures" (Minagawa 1993: 52, 53). A small spermatophore has been observed near the exit of the spermatheca in Japanese *R. ranina*, in which mating occurs between hard-shelled males and hard-shelled females without any ecdysis during the spawning season. The G1 is inserted shallowly inside the spermatheca since it must be firm for mating with hard shell females (Minagawa 1993; Minagawa *et al.* 1993, 1994).

The spermathecae of *Symethis* are peculiar: apertures are large, widely separate and overhanged by two calcified, arched, hoods. There is a decalcified flap below the hood "in such a manner as to make them approachable only from the posterior" (Goeke 1981: 976, fig. 2B; see also Davie 1989: fig. 1c). Females of *S. variolosa* (Fabricius, 1793) from the Gulf of Mexico were often (60% of the adult females) collected with their apertures completely occluded by a plug of hardened material that recovered large part of sternal area between P3 and P4. A similar condition was found among females of *S. garthi* Goeke, 1981 from the Pacific coast (Goeke 1981: 976). The plug, which sealed off the pits, may have been the result of the packing of spermathecae with sperm by the male after mating, and was supposed to prevent the female from mating with a second male. Similarly, a plug was found covering spermathecal apertures of the female holotype of *S. corallica* Davie, 1989 (Davie 1989: 430).

Gonopods of other raninoid subfamilies and families were figured for the type genera as follows: Raninoidinae (*Notopoides* Henderson, 1888; Gordon 1966: fig. 4), Lyreidinae (*Lyreidus*; Hartnoll 1975: fig. 3C, D), Notopodinae (*Ranilia* H. Milne-Edwards, 1837; Guinot 1979a: fig. 62E-H); Cyrtorhininae (*Cyrtorhina*; Monod 1956: figs 30, 31); Symethidae (*Symethis*;

Goeke 1981: fig. 3A, B; Davie 1989: fig. 1b). Tubulation of G1 is variously marked, the appendix masculina of G2 varies from relatively elongated to short and thus being fused with the endopodite, but the mutual functioning of the two gonopods is probaly analogous to that of *Ranina*. The only exception probably concerns *Symethis*, in which the laterally compressed G1 bear abundant tufts of setae and end in an acuminate tip, while the spermathecal apertures are large.

It appears that structure and function of the gonopods in all the Podotremata are adapted to ensure accurate positioning of spermatophores. The complex interaction of female gonopores, spermathecae, gonopods and spermatophores guarantees a safe sperm transfer.

PODOTREME CRABS VERSUS STERNITREME CRABS

Bauer (1986, 1991, 1994) has investigated among the Decapoda the various sets of genitalia that consist of open or closed thelycum and unpaired or paired cuticular invaginations in the cephalothorax. In their extensive revision of penaeoids and sergestoids, Pérez Farfante & Kensley (1997) distinguished the open thelycum from the closed thelycum, in which there are associated "seminal receptacles". These seminal receptacles are unpaired or paired, non-invaginated or invaginated in the cephalothoracic cavity, and open by exposed or protected slits. In certain respects the podotreme morphology shows analogies with female dispositions found in other Decapoda in which modifications concern also posterior sternites (generally 7 and 8, sometimes also 6), the genital area being diversely modified and involved with the deposit of the spermatophore and/or in its storage.

The case of *Nephrops norvegicus* is interesting because, as in the Podotremata, genital female modification concerns the interphragmal plate 7/8, and genital structure (which is not a thelycum) consists of an unpaired spermatheca. But its sternite 8 is modified to form a triangular flap, occluding or exposing the opening which results from the scission of the sclerite of the sternite 7. Thus, in *Nephrops*, another type of functional modification arises: creation of functional articulations on the sclerites and splitting into two parts of a sclerite which was originally unpaired (Secretan-Rey 2002: 102, fig. 25). There is penetration of gonopods to force a spermatophore into the unpaired spermatheca (Farmer 1974).

If the term spermatheca is retained in its general sense, i.e. for "any enclosed space related to extended storage of sperm or spermatophores" (Bauer 1994: 720), it is convenient for the two conditions encountered in the Brachyura. Taking homology into account in Brachyura, Tavares & Secretan (1993) decided to use the term spermatheca (instead of thelycum) for the primitive Brachyura and clearly distinguished the podotreme condition from the eubrachyuran ones. Consequently, the name thelycum *sensu stricto* became restricted to a sternal modification concerning a single segment, thus unisegmentar. In the present paper the spermatheca of the Podotremeta has been reviewed in 10-11 extant families and two fossil families. The female genital modification involves always the sternal suture 7/8, and the spermatheca is always derived from a skeletic, sternal modification between two adjacent segments, i.e. between the two plates of the intersegmental phragma 7/8, and resulting in an internalized, closed pocket. The paired spermatheca proves to be a synapomorphy of the Podotremata (Guinot & Tavares 2001).

The podotreme condition is linked with a deposit and storage of sperm at the surface of the sternal surface and also inside. Many dromiids show at the same time a spermatophoric mass adhering to the female's ventral cephalothorax and also deposited inside the chamber located in the posterior part of the body. No such external male substances have been seen by us or reported for the Homolidea or Cyclodorippoidea. In Raninoidea, however, sperm plugs were found in *Ranina* and in *Symethis* (see above).

It is probable, as suggested by Hartnoll (1969: 176), that in the ancestral Brachyura the sperm were not deposited into the oviducts but glued to the sternum or deposited in spermathecae as in the extant primitive Brachyura.

The podotremes crabs possess two different reproductive areas, one for egg laying (the genital pore on P3), and one distinct (the spermatheca) for spermatophore laying. They strongly contrast to the sternitreme crabs (hetrotreme/thoracotreme assemblage) which have a single genital duct, the vulva being united with the oviduct and constituting the sole orifice used for egg laying, intromission of male pleopods, and storage of the spermatozoids (Guinot 1977, 1979a). The coxal positions of male and female gonopores and the spermathecae that are not associated with the ovary, implying external fertilization, are referred to as symplesiomorphies. With respect to the non-homology of the podotreme/sternitreme structures and the "highly modified system" of the Eubrachyura (Bauer 1986: 322), we prefer to restrict the term spermatheca to the condition found in the Podotremata and to call "seminal receptacle" the eubrachyuran type. The eubrachyuran transfer, insemination, fertilization and storage (Adiyodi & Subramaniam 1983; Adiyodi & Anilkumar 1988) stand apart from the other Decapoda. The insemination is always internal in the Eubrachyura. The eubrachyuran vulva, leading directly to the oviduct, was considered the strongest synapomorphy of the non-podotreme crabs (Guinot *et al.* 1994: fig. 7; Guinot & Tavares 2001: fig. 16) (see below).

PALEONTOLOGICAL DATA

In an attempt to use the paleontological data within this context, it was important to verify the female condition in the fossil record, whenever the ventral part was preserved. A spermatheca was found in two Cretaceous primitive families, the Dakoticancridae Rathbun, 1917, in which sutures 7/8 end in large, rounded apertures and P3 coxae bear distinct female gonopores (Guinot 1993a), and in the Etyidae for which, in *Etyus martini*, two large, oblique structures were observed at the extremities of sutures 7/8, thus representing spermathecae (Guinot & Tavares 2001).

The earliest occurences of the Podotremata are from the Jurassic (Prosopidae, Dynomenidae, Homolidae, Diaulacidae Wright & Collins, 1972), a period during which, as far as is currently known, all crabs were podotreme (Glaessner 1969). More precisely, they may date from the Early Jurassic if the inclusion of *Eoprosopon* Förster, 1986 (Prosopinae von Meyer, 1860) is correct. Podotreme crabs, still rare in the Early Cretaceous, begin to be better documented during the Cretaceous, when they exhibited their first expansion (Schram 1986). Some ventral features have become known in a few podotreme families (Dakoticancridae, Etyidae, Homolidae, Raninidae), and the presence of spermathecal apertures is now confirmed in the Dakoticancridae and Etyidae, two families that became extinct in the Late Cretaceous (Guinot & Tavares 2001; Feldmann 2003). A rich crab fauna occurs in the Cretaceous, and non-podotreme forms appear, unexpectedly, with a wide body, notably a broad thoracic sternum and other "modern" characters. That suggests an earlier diversification, already during Jurassic time. Paleontological data must be cautiously analysed when determining which eubrachyuran representatives are reliably known before the Tertiary.

In the exclusively fossil genus *Necrocarcinus* Bell, 1863, *N. siouxensis* Feldmann, Awuota & Welshenbaugh, 1976, from the Maastrichtian of North Dakota probably belongs to the Podotremata. It exhibits very large orbits, pediform mxp3, and a well preserved thoracic sternum with lateral and non-visible sutures except the transversal one. This evident suture seems to be similar to the homoloid transversal suture 6/7 (Guinot & Bouchard 1998: fig. 9C) (Figs 19; 20) except that the horizontal suture appears to be more anterior in *N. siouxensis*. Another interpretation is that the figure given by Feldmann *et al.* (1976: pl. 1, fig. 5) does not show the sternum but a wide and long abdomen, that completely fills the sterno-abdominal depression, reaches the mxp3 and is maintained by the pereopods as in homoloids. *N. siouxensis*, not referable to *Necrocarcinus* Bell, 1863 for Bishop & Williams (1991) and of uncertain position for Fraaye (1994: 264), was tentatively assigned to the necrocarcinid *Cenomanocarcinus* Van Straelen, 1936 by Schweitzer *et al.* (2003: 36, 37, 38, 39, table 1). Another species of *Cenomanocarcinus*, the Cretaceous *C. vanstraeleni* Stenzel, 1945 (p. 447, fig. 15, pl. 44) shows similar characters (same carapace outline, dorsal ridges, pediform mxp3) and a reduced P5 ("there is room only for a small leg", see Stenzel 1945: 448). The specimen, with the well preserved abdomen (Stenzel 1945: pl. 44), which was interpreted as a female probably because it completely fills the sterno-abdominal depression, likely is a male as in the case of *C. siouxensis*. The presence of reduced and dorsal P4 and P5 (or only P5) in *C. vanstraeleni* is not sufficient to absolutely assume that it is a podotreme crab since dorippoids offer the same disposition. In any case, *C. vanstraeleni* does not represent a condition observed in extant Calappoidea De Haan, 1833 and Dorippoidea MacLeay, 1838. The shape of abdomen and the mxp3 are typically podotreme. *C. siouxensis* and *C. vanstraeleni* as well as perhaps other necrocarcinid species must therefore be referred, after verification, to a new genus, perhaps a podotreme representative.

The family Necrocarcinidae Förster, 1968, first considered a member of the Calappoidea (Stenzel 1945; Förster 1968; Wright & Collins 1972; Schweitzer & Feldmann 2000a), has been associated with the Dorippoidea (Schweitzer *et al.* 2003: 31, 32). Its placement nevertheless remains difficult (Jagt *et al.* 2000: 40), and the hypothesis that certain of necrocarcinid members may actually prove to be non-eubrachyuran was already suggested by Larghi (2004: 529, 530), who questionably placed at least part of the family Necrocarcinidae in the Podotremata. It is quite possible that other *Necrocarcinus* or allied genera may actually prove to be non-eubrachyuran. It is difficult to assert without more complete, preserved ventral parts, characters that have historically been insufficiently considered and evaluated by the carcinologists. When ventral parts exist in fossil records and have been cleared from the matrix, the dimensionial relations between the male abdomen and the thoracic sternum are fundamental, the rule being that a basal podotreme crab is characterized by its sternum completely covered by the male abdomen, which is in contact with the coxae of pereopods (Guinot & Tavares 2001).

Other problems are the actual first occurence of the Dromiidae, which only appears in the Tertiary, according to Glaessner (1969: fig. 251), paleontological data on authentic Dynomenidae, and the possible relationships of the Torynommatidae Glaessner, 1980 (p. 180, sternum figured fig. 20) with the Cyclodorippoidea for instance. In other respects, the resemblance of the thoracic sternum and male abdomen between the Maastrichtian genus *Binkhorstia* Noetling, 1891 (Van Bakel *et al.* 2003: 85, fig. 1.5), included in the Torynommatidae (see Guinot & Tavares 2001: 539; Collins 2002: 85), and the Retroplumidae Gill, 1894 should be investigated (see below). Only the presence of coxal female gonopores and of the spermathecal apertures at the extremity of sutures 7/8 would be significant.

Thus, the rule of a paired spermatheca always concerning the same phragma 7/8 (versus vulvae) and separated from the ovary has never been contradicted, even if the shape and localisation of the spermathecal apertures on the sternal surface show varying modalities among the Podotremata (Guinot & Tavares 2001: fig. 10). The fact that the major brachyuran clades (Podotremata and Eubrachyura) are very distinct is not inconsistent with the idea of a monophyletic group Brachyura (Podotremata + Heterotremata + Thoracotremata). Instead of the hypothesis of multiple independent evolutions in several groups, the spermatheca perhaps originated once and was inherited by the whole Podotremata (Homolodromiidae, Dromiidae, Dynomenidae, Homolidae, Latreilliidae, Poupiniidae, Cymonomidae, Cyclodorippidae, Phyllotymolinidae, Raninoidea, Dakoticancridae, Etyidae) (Guinot & Tavares 2001: fig. 16). It is quite probable that spermathecae will be found in female individuals of the Prosopidae, after clearing and studying their ventral surfaces.

SPERMATHECAE, VULVAE AND CARCINIZATION

Hartnoll (1979: 82, fig. 5) has already proposed "a common spermathecal structure for all early Brachyura", including the Raninoidea. Regarding the raninoid spermatheca as having evolved beyond the condition found in the other primitive Brachyura, he suggested different ways by which "the dromiid condition could have evolved into the raninid one". The primitive spermatheca lying posteriorly within endosternite 7/8 might acquire a new condition, such as in raninoids. The spermathecal tubes of the Dromiidae and the secondary openings in the Raninoidea are presumed to serve the same purpose, that is, improving the efficiency of fertilization. We agree with Hartnoll that it is difficult to postulate a process whereby raninoid spermathecae with secondary openings on sternite 7 came to open on sternite 6 and become vulvae, as in the Eubrachyura. There is no evidence for such a sequence (see below), and the raninoid spermatheca is not relevant to the origin of the eubrachyuran seminal receptacle. On the other hand, the peculiar raninoid spermatheca may be considered as the result of strong modifications concerning the whole body (for example leading to the large exposure of thoracic pleurites in these crabs that were named "Gymnopleura" by Bourne 1922), in connection with early adaptation for burrowing. The specialized group Raninoidea, very diverse during and after the Cretaceous, but now in a stage of decline (Glaessner 1969), appears not to be on the direct line leading to the Eubrachyura, but its inclusion within the Podotremata (versus Heterotremata) needs to be confirmed.

The gap between the podotreme condition (10-11 extant families, approximately 320 known species distributed in about 92 genera) and the sternitreme condition (approximately 54 families, more than 6000 species), without known transitional dispositions, is not solved by the study of the thoracic sternum in general or of the spermatheca in particular. While it is reasonable to suppose an evolutionary sequence between the genital structures of the other Decapoda and that of the Podotremata, the origin of the eubrachyuran organization remains problematical.

In the classification of Martin & Davis (2001) two main podotreme characters (male and female gonopores on the pereopods, presence of spermathecae) are ignored, and the subsection Raninoida (including Cyclodorippoidea and Raninoidea) is included basally in the Eubrachyura. If this is correct, the presence of paired spermathecae and female gonopores on the P3 coxae does not exclusively characterize the Podotremata, and the presence of vulvae cannot be considered a strong synapomorphy for the Eubrachyura. In all other respects, it is true that it is difficult to reconcile the organization of Cyclodorippoidea and Raninoidea with that of the basal Podotremata (Dromiacea, Homoloida). In particular, the wide sternal plate of the Cyclodorippoidea, with a true sterno-abdominal cavity, contrasts with the simple sterno-abdominal depression which is completely filled (or nearly filled) laterally by the abdomen in the Dromiacea and in the Homolidea.

Carcinization (see McLaughlin & Lemaitre 1997), an evolutionary phenomenon leading to a crab-like body form and including the broadening of the thoracic sternum, has rarely been evoked for the Podotremata. The change in the adult carapace shape is already evident in the Dromiidae and Dynomenidae and is accompanied by a relatively advanced skeletal organization (in contrast to the elongated body and partitioned axial skeleton of the Homolodromiidae). In addition, a widening of the sternal plate is already evident in a part of the Dynomenidae and in all members of the Latreilliidae. In specializing the brachyuran model, the evolutionary process provides an abdomen that becomes removed from the coxae of the pereopods. This results in a "migration" of abdominal retaining structures onto the thoracic sternum, and particularly from P2 coxa onto sternite 5 (a transformation series found within the family Dynomenidae). The transformation of the narrow thoracic sternum of the basal Podotremata to the wide sternal plate of the Cyclodorippoidea, with the excavation of a cavity to receive the abdomen, constitutes another evolutionary step of carcinization. By the acquisition of sternal (instead of coxal) devices to retain the abdomen (Guinot & Bouchard 1998: 673-675, 680), crabs were provided greatly enhanced mobility.

Because of the widening of the body, the female openings on the P3 coxae become far apart from each other, resulting in too great a distance between them to satisfy the different reproductive requirements, a hypothesis previously formulated by Duvernoy (1853: 144). Carcinization has included, as a possible outcome, their migration to a more central location (on sternite 6). It has been already shown that the male openings of a part of the Eubrachyura left their primitive coxal position on P5 for a sternal location (Guinot 1979a: fig. 55), with different modalities, either coxo-sternal or truly sternal. On the other hand, pathways of change for the female condition are unknown, and there is no evidence for a transition between the podotreme and eubrachyuran organization (representatives of the Belliidae Dana, 1852 and Cheiragonidae Ortmann, 1893 must be re-examined, see Guinot 1976: 53, fig. 12A-C; 1978: 259; 1979a: 177, fig. 39A-C, pl. 25, figs 1-3; Guinot & Bouchard 1998: 646, fig. 13C).

We are not aware of any early authors that have attributed the lengthening of the sutures 7/8 and the anterior location of the spermathecal apertures (in front of the female gonopores on the P3 coxae) to the widening of the body, in particular between the P3 coxae. When the spermathecae acquire "new" apertures in front of the sixth sternite, they appear to be in position to "capture" the oviducts which pass through that segment. This concept, suggested by Hartnoll (1979: 82) in the conclusion of his study of the Raninidae, could explain a sequence showing how the spermathecal apertures can be replaced by the vulvae. Such a process is hypothetical, and, as noted above, we consider it difficult to postulate a process by which the podotreme condition could have evolved into the eubrachyuran one.

Nevertheless, in this context, support can be found in the answer to another puzzling question. How could the Brachyura, which had not advanced beyond the podotreme level of organization during the Jurassic, be represented already during the Cretaceous by well established eubrachyuran families? A list was provided by Forir (1887: 191-195, table) and new data were provided by Schweitzer *et al.* (2002) and Fraaije (2003). During the Cretaceous, the Retroplumidae Gill, 1894 was represented by the Costacopluminae Beschin, Busulini, De Angeli & Teissier, 1996 (this name was proposed conditionally by Saint Laurent 1989: 149, and thereby not made available, ICZN 1999: art. 15.1.) including *Costacopluma* Collins & Morris, 1975 (Collins & Morris 1975; Vega-Vera & Perrilliat 1989; Vega & Feldmann 1992; Vega *et al.* 1994, 1995; Beschin *et al.* 1996), with perfectly preserved ventral parts. The Hexapodidae Miers, 1886 was represented by the Maastrichtian *Goniocypoda* Woodward, 1867 (Remy & Tessier 1954; see Schweitzer & Feldmann 2001). The characters of these fossils, in particular those of the thoracic sternum and abdomen, are similar to those seen in the recent representatives. The living Hexapodidae (see Manning & Holthuis 1981) are known to be highly modified for commensalism in polychaete tubes and the body cavities of hydrozoans, and their zoeal stages show both primitive and advanced characters (Pereyra Lago 1988).

Special attention has therefore been paid to the condition of the vulvae in these two ancestral families, which proves to be quite particular. The vulvae of the recent Retroplumidae are not positioned in the middle of sternite 6 (or approximately), as is usual in the Eubrachyura, but instead open at the extremities of the sutures 5/6, as figured earlier (Guinot 1979a: 114, fig. 30E; Guinot & Bouchard 1998: fig. 17C) (Fig. 29A), an arrangement that was not described or discussed in the revision of the family by Saint Laurent (1989: 113). These terminal vulvae, connected with the sutures 5/6, are in a position similar to that of the podotreme spermathecal apertures at the extremities of the sutures 7/8. The examination of the internal sternal surface of *Retropluma planiforma* Kensley, 1969, after the removal of the soft tissues, shows the calcified and still preserved distal parts of the oviducts situated just below the terminal parts of the sutures 5/6.

In the Retroplumidae the wide thoracic sternum shows unexpected, parallel, equidistant sutures 4/5-6/7 (versus medially converging in wide eubrachyurans), as confirmed by the transversally partitioned axial skeleton. The well developed penis arises from the salient condyle of the P5 coxa (Guinot 1979a: fig. 54F, G, showing *Retropluma planiforma*), in a way rather similar to that found in the Dorippinae (Guinot 1979b: fig. 2A). Possible relationships should be investigated between the Maastrichtian genus *Binkhorstia* Noetling, 1891 (currently included in the Torynommatidae; see Van Bakel *et al.* 2003) and the Recent Cyclodorippoidea, as well as the Retroplumidae.

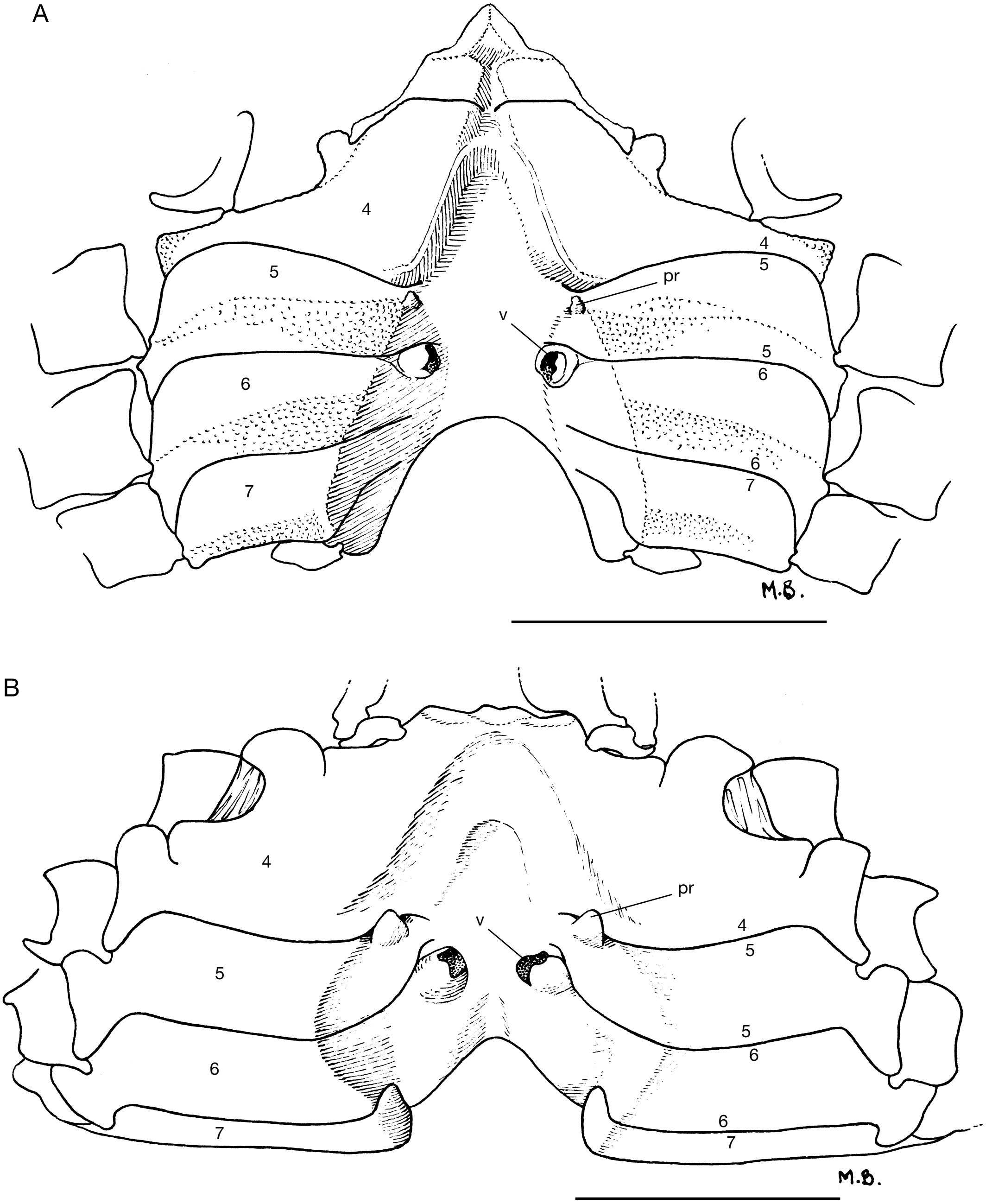

Fig. 29. — **A**, *Bathypluma forficula* Saint Laurent, 1989 (Retroplumidae), female 12 × 14 mm, Makassar Strait, Corindon Expedition (MNHN-B 11229), vulvae at the extremities of sutures 5/6; **B**, *Hexapus* ? *sexpes* (Fabricius, 1798) (Hexapodidae), female 10.5 × 18 mm, Persian Gulf (MNHN-B 10209), vulvae just below the extremities of sutures 5/6. Abbreviations: **pr**, projection from sternite 5 for abdominal maintaining, still present in mature females; **v**, vulva; **4-7**, sternites 4-7; **4/5-6/7**, thoracic sternal sutures 4/5 to 6/7. Scale bars: 5 mm.

The vulvae of the Hexapodidae (for their sternum, see Gordon 1971) are more or less close to the sutures 5/6 (Guinot 1979a: 114, figs 32, 33C-E, pl. 24, fig. 6; Guinot & Bouchard 1998: fig. 17E). In *Hexaplax megalops* Doflein, 1904, the vulvae open at the extremities of the sutures 5/6 (as in the Retroplumidae, Fig. 29A) and, in an internal view of the sternum, the calcified, preserved distal parts of the oviducts are located just at the extremities of the endosternites 5/6. In an unidentified West African hexapodid, the sternum shows externally two oblique, inflated, symmetrical areas close to the large vulvae, below the extremities of the sutures 5/6. There is a similar inflated but smaller area in the West African *Thaumastoplax anomalipes* Miers, 1881, and a less marked area in *Hexapus* ? *sexpes* (Fabricius, 1798), from the Persian Gulf (Fig. 29B). In the Hexapodidae the sutures 4/5-6/7 are parallel and equidistant (except in their terminal parts), as in the Retroplumidae.

Additionally, it should be noted that, in the members of Retroplumidae and Hexapodidae, the sternal prominences for maintaining the abdomen may persist in the adult (even ovigerous) females in the proximity of the vulvae, which is exceptional in the Brachyura (Guinot & Bouchard 1998: 650, 660, fig. 17C, E).

Relationships between the Retroplumidae and the Hexapodidae were suggested by Alcock (1900b: 297, as Ptenoplacidae Alcock, 1899), but finally rejected by Saint Laurent (1989: 156). The Retroplumidae was placed, with reservation, in the proximity of the Dorippidae and Palicidae (Guinot 1978: 214, 249, 251, 284). The Hexapodidae, after a provisional placement in the Thoracotremata, was transferred to the Heterotremata (Guinot & Richer de Forges 1997: 496, table 1), but their affinities remain enigmatic. Their relationships with the Dorippidae MacLeay, 1838, known by the Cretaceous *Eodorippe* Glaessner, 1980, merit re-evaluation. Evidently, the Retroplumidae and the Hexapodidae are far from being podotreme crabs! Further investigations of these families are needed to understand the process whereby the paired eubrachyuran vulvae could have evolved.

The Palicidae Bouvier, 1898 exhibits a different pattern. Their vulvae are displaced to the anterior of the thoracic sternum in its undivided median part, close to the sutures 4/5. The dissection of the nervous system by Hartnoll (1968: 296, fig. 14C) has shown that these vulvae "must be regarded as belonging not to the fifth segment, but to the sixth as in other Brachyura" (see also Guinot 1979a: 113, figs 30G, 31, pl. 24, fig. 9; Castro 2000: 444). A non-functional scar may persist in ovigerous females of *Palicus caroni* (Roux, 1830) (Guinot & Bouchard 1998: 653) and more than likely in other species. Interestingly, the Eocene fossil palicid *Spinipalicus* Beschin & De Angeli, 2003 (p. 7-12, figs 2-4) seems to show similarities with the Cretaceous *Archaeopus* Rathbun, 1908 (p. 346, pl. 47, figs 4-7, pls 48, 49, figs 2-4), considered either to belong in, or to be closely allied to, the Retroplumidae (Beurlen 1930; Vía Boada 1969; Collins & Morris 1975; Vega & Feldmann 1992; Beschin & De Angeli 2003), even perhaps representing the more ancestral retroplumid morphology (Bishop 1983), or to be removed from the Retroplumidae (Saint Laurent 1989).

All these crabs (retroplumids, hexapodids, palicids) share a peculiar (may be dorsal) position of the fifth pereopods or, at least, of sternite 8, and a possible reduction of sternite 8. In the Retroplumidae the P5 are short, thin, "reduced to feather-like rudiments, arising close together, high up, almost on the back" (Alcock 1899: 79, as *Ptenoplax* Alcock & Anderson, 1894), and very different from the preceding pereopods. Among the Palicidae, the P5 are conspicuously reduced in the Palicinae Bouvier, 1898, in which they are filiform, oriented dorsally, and end in a curved, especially movable dactylus, but they are similar in shape and orientation to anterior walking legs in the Crossotonotinae Moosa & Serène, 1981 (Castro 2000: 445). The relationships of the Palicidae with the Dorippidae were suggested by several authors, in particular by Bourdillon-Casanova (1960); the Palicidae (with the Dorippidae and, some reservation, the Retroplumidae) were tentatively referred to the Dorippoidea by Guinot (1978: 214, 245, 249).

Among the Carcineretidae Beurlen, 1930, which became extinct by the end of the Cretaceous (Bishop 1988; Vega & Feldmann 1991; Vega *et al.* 1993; Schweitzer & Feldmann 2000b; Feldmann & Villamil 2002; Feldmann 2003), some genera (for instance the Maastrichtian *Mascaranada* Vega & Feldmann, 1991, with natatory P5 suggesting a portunid) are important for understanding the history of crabs. Other families allied to the Xanthoidea *sensu lato* or genera referred to the Goneplacidae are already known from the Cretaceous (Bishop 1988; Vega *et al.*, 2001; Schweitzer 2003a, b).

The links observed in studying structures such as the spermatheca in Recent species, compared to even fragmentary paleontological data, might help to refine views on the origin and evolution of crabs.

From what evolved the sternum with only lateral sutures, at least 4/5 and 5/6, and also 7/8 in the Dromiacea and Homoloida? Guinot (1979a) considered the presence of complete and parallel sternal sutures 4/5 to 7/8 on a narrow ventral plate of the Eubrachyura as the plesiomorphic condition, and their interruption as the derived one. In contrast, even the living Podotremata showing the narrowest sternum have obviously interrupted sutures 4/5, 5/6 (sometimes 6/7) and 7/8, which means somites all fused medially. Unfortunately, the complete thoracic sternum of the Prosopidae is unknown, although in rare records of the Middle Jurassic (Förster 1985) it looks like the same condition as the Recent homolodromiid species in having only lateral oblique sutures. If the podotreme group is considered monophyletic (Tavares 2003), from what is derived the Podotremata? And is the Brachyura, including Podotremata and Eubrachyura, monophyletic?

The structure of the spermatheca still remains unknown in several podotreme genera, notably in the Cyclodorippoidea, which is probably a "key" to understand the evolution of the derived Podotremata. The function of the spermatheca remains largely unknown, and we do not have sufficient data about the mechanics of mating and fertilization among all the Podotremata. Such morphological study unfortunately cannot be completed in the absence of living material. The habits of the podotreme crabs have been rarely observed, and only in captivity as in the case of Dembowska (1926), Fenizia (1935), Hartnoll (1975), Minagawa (1993), and Minagawa *et al.* (1993, 1994).

Illustration

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REFERENCES

Adiyodi K. G. & Anilkumar G. 1988. — Arthropoda-Crustacea, *in* Adiyodi K. G. & Adiyodi R. G. (eds), *Reproductive Biology of Invertebrates*, Vol. 3, *Accessory Sex Glands*. John Wiley & Sons, New York: 261-318.

Adiyodi K. G. & Subramoniam T. 1983. — Arthropoda-Crustacea, *in* Adiyodi K. G. & Adiyodi R. G. (eds), *Reproductive Biology of Invertebrates*, Vol. 1, *Oogenesis, Oviposition and Oosorption*. John Wiley & Sons, New York: 443-495.

Alcock A. 1899. — *An Account of the Deep-Sea Brachyura Collected by the Royal Indian Marine Survey Ship "Investigator"*. Trustees of the Indian Museum, Calcutta, 85 p.

Alcock A. 1900a. — Materials for a carcinological fauna of India. No. 5. The Brachyura Primigenia or Dromiacea. *Journal of the Asiatic Society of Bengal* 68 (2) 3: 123-169 (dated 1899, published 1900).

Alcock A. 1900b. — Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. *Journal of the Asiatic Society of Bengal* 69 (2) 3: 621-798.

Bauer R. T. 1986. — Phylogenetic trends in sperm transfer and storage complexity in decapod crustaceans. *Journal of Crustacean Biology* 6 (3): 313-325.

Bauer R. T. 1991. — Sperm transfer and storage structures in penaeoid shrimps: a functional and phylogenetic perspective, *in* Bauer R. T. & Martin J. W. (eds), *Crustacean Sexual Biology*, chap. 11. Columbia University Press, New York: 183-207.

Bauer R. T. 1994. — Usage of the terms thelycum and spermatheca in the reproductive morphology of the Decapoda, with special reference to the Penaeoidea. *Journal of Crustacean Biology* 14 (4): 715-721.

Beschin C., Busulini A., De Angeli A. & Tessier G. 1996. — Retroplumoidae (Crustacea, Brachyura) nel Terziaro del Vicentino (Italia settentrionale). *Lavori Societa Veneziana di Scienze Naturali* 21: 83-102.

Beschin C., Busulini A., De Angeli A. & Tessier G. 2002. — Aggiornamento ai Crostacei Eocenici di Cava "Main" di Arzignano (Vicenza-Italia settentrionale) (Crustacea Decapoda). *Studi e Ricerche, Associazone Amici del Museo-Museo Civico "G. Zannato" Montecchio Maggiore (Vicenza)*: 7-28.

Beschin C., Busulini A., De Angeli A. & Tessier G. 2004. — The Eocene decapod crustacean fauna of the "Main" quarry in Arzignano (Vicenza-NE Italy) with the description of a new species of Raninidae. *Lavori Societa Veneziana di Scienze Naturali* 29: 109-117.

Beschin C. & De Angeli A. 2003. — *Spinipalicus italicus*, nuovo genere e specie di Palicidae (Crustacea, Decapoda) dell'Eocene del Vicentino (Italia settentrionale). *Studi e Ricerche, Associazone Amici del Museo-Museo Civico "G. Zannato", Montecchio Maggiore (Vicenza)*: 7-12.

Beurlen K. 1930. — Vergleichende Stammesgeschichte. Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. *Fortschritte Geologie und Palaeontologie* 8 (26): i-viii + 317-586.

Bishop G. A. 1974. — A sexually aberrant Crab (*Dakoticancer overanus* Rathbun, 1917) from the Upper Cretaceous Pierre Shale of South Dakota. *Crustaceana* 26 (2): 212-218.

Bishop G. A. 1983. — Fossil decapod Crustacea from the Late Cretaceous Coon Creek Formation, Union County, Mississippi. *Journal of Crustacean Biology* 3 (3): 417-430.

Bishop G. A. 1986. — Occurrence, preservation and biogeography of the Cretaceous crabs of North America, *in* Heck K. L. Jr & Gore R. H. (eds), *Crustacean Issues*. Vol. 4, *Crustacean Biogeography*. A. A. Balkema, Rotterdam: 111-142.

Bishop G. A. 1988. — Two crabs, *Xandaros sternbergi* (Rathbun, 1926) n. gen., and *Icriocarcinus xestos* n. gen., n. sp., from the Late Cretaceous of San Diego County, California, USA, and Baja California Norte, Mexico. *Transactions of the San Diego Society of Natural History* 21: 245-257.

Bishop G. A., Feldmann R. M. & Vega F. 1998. — The Dakoticancridae (Decapoda, Brachyura) from the Late Cretaceous of North America and Mexico. *Contributions to Zoology* 67 (4): 237-255.

Bishop G. A. & Williams A. B. 1991. — *Necrocarcinus olsonorum*, new species, a crab (Decapoda: Calappidae) from the Cretaceous Carlile Shale (Turonian), Western Inferior United States. *Journal of Crustacean Biology* 11 (3): 451-459.

Borradaile L. A. 1903a. — On the genera of the Dromiidae. *Annals and Magazine of Natural History* 11 (7): 297-303.

Borradaile L. A. 1903b. — Marine Crustaceans. IX. The sponge-crabs (Dromiacea), *in* Gardiner J. S. (ed.), *The Fauna and Geography of the Maldive and Laccadive Archipelagoes* 2 (1). Cambridge University Press, Cambridge, UK: 574-578.

Bouchard J.-M. 2000. — *Morphologie fonctionelle des systèmes de rétention de l'abdomen chez les Brachyoures (Crustacea Decapoda). Microstructures ; implications phylogénétiques et systématiques*. Thèse de Doctorat du Muséum national d'Histoire naturelle, Paris, France, 694 p.

Bourdillon-Casanova L. 1960. — Les larves de Crustacés Décapodes, *in* Le méroplancton du Golfe de Marseille. *Recueil des Travaux de la Station marine d'Endoume* 30 (18): 1-286.

Bourne G. C. 1922. — The Raninidae: a study in carcinology. *Journal of the Linnean Society of London* 35 (231): 25-79.

Bouvier E.-L. 1896. — Sur l'origine homarienne des crabes : étude comparative des Dromiacés vivants et fossiles. *Bulletin de la Société philomatique*, Paris (8) 8 (2): 34-110 (1-77) (dated 1895, published 1896).

Boyko C. B. 1998. — The correct original spelling of *Cryptodromidiopsis sarraburei* (Rathbun, 1910) not *C. larraburei* (Schmitt, 1921) (Decapoda, Brachyura, Dromiidae). *Crustaceana* 71 (2): 234-235.

Brandis D., Storch V. & Türkay M. 1999. — Morphology and function of the copulatory system in freshwater crabs of the genus *Potamon*. *Journal of Morphology* 239: 157-166.

Broekhyusen G. J. 1936. — On development, growth and distribution of *Carcinides maenas* (L.). *Archives néerlandaises de Zoologie* 2: 257-399.

Castro P. 2000. — Crustacea Decapoda: a revision of the Indo-west Pacific species of palicid crabs (Brachyura Palicidae), *in* Crosnier A. (ed.), Résultats des campagnes MUSORSTOM, vol. 21. *Mémoires du Muséum national d'Histoire naturelle* 184: 437-610.

CASTRO P., WILLIAMS A. B. & COOPER L. L. 2003. — Revision of the family Latreilliidae Stimpson, 1858 (Crustacea, Decapoda, Brachyura). *Zoosystema* 25 (4): 601-634.

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, xiii + 597 p.

CHURCHILL E. P. 1919. — Life history of the blue crab. *Bulletin of the United States Bureau of Fisheries* 36: 91-128.

COLLINS J. S. H. 2002. — A taxonomic review of British decapod Crustacea. *Bulletin of the Mizunami Fossil Museum* (29): 81-92.

COLLINS J. S. H. & MORRIS S. F. 1975. — A new crab, *Costacopluma concava*, from the upper Cretaceous of Nigeria. *Palaeontology* 18 (4): 823-829.

CROSNIER A. 1994. — *Sphaerodromia lamellata*, espèce nouvelle de Nouvelle-Calédonie. *Crustaceana* 67 (3): 341-347.

DAVIE P. J. F. 1989. — *Smethis* [*sic*, for *Symethis*] *corallica* sp. nov. (Crustacea, Brachyura, Raninidae), the first member of the Smethinae [*sic*, for *Symethinae*] to be recorded from the Indo-West Pacific region. *Bulletin du Muséum national d'Histoire naturelle* 4^{e} sér., 11, A (2): 425-430.

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 Publ. Australia, Melbourne, xiv + 641 p.

DAWSON E. W. 2002. — First record of the primitive crab *Homolodromia* in New Zealand waters (Crustacea, Decapoda, Brachyura, Homolodromiidae), with a provisional new key to the extant species of *Homolodromia*. *The Hutton Fondation New Zealand*, special paper No. 1: 1-21.

DAWSON E. W. & YALDWYN J. C. 2000. — Description and ecological distribution of a new frog crab (Crustacea, Brachyura, Raninidae) from Northern New Zealand waters, with keys to recent raninid genera and *Notosceles* species. *Tuhinga* 11: 47-71.

DE HAAN W. 1833-1850. — Crustacea, *in* SIEBOLD P. F. VON (ed.), *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summun in India Batava Imperium Tenent, Suscepto, Annis 1823-1830 Collegit, Notis, Observationibus e Adumbrationibus Illustravit*. Lugduni-Batavorum (Leiden), fasc. 1-8: xvii + xxxi + 243 p. [1833, fasc. 1, Praemissa: ix, x; 1839, fasc. 4: 73-108; 1841, fasc. 5: 109-164)].

DEMBOWSKA W. S. 1926. — Study on the habits of the crab *Dromia vulgaris* M. E. *Biological Bulletin of the Marine Biological Laboratory*, Woods-Hole 50: 162-178.

DESMAREST A. G. 1825. — *Considérations générales sur la classe des Crustacés et description des espèces de ces animaux, qui vivent dans la mer, sur les côtes, ou dans les eaux douces de la France*. F. G. Levrault, Paris; Strasbourg, xix + 446 p.

DEUVE T., GUINOT D. & BOUCHARD J.-M. 2004. — Dromiidae Bonelli, 1810 (Insecta, Coleoptera, Caraboidea): proposed emendment of spelling to Dromiusidae to remove homonymy with Dromiidae De Haan, 1833 (Crustacea, Decapoda, Brachyura, Dromiacea). *Bulletin of Zoological Nomenclature* 61 (4): 225-231.

DIXON C. J., AHYONG S. T. & SCHRAM F. R. 2003. — A new hypothesis of decapod phylogeny. *Crustaceana* 76 (8): 935-975.

DRACH P. 1950. — Les étapes évolutives de l'endosquelette chez les Crustacés Décapodes. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* 231 (25): 1563-1565.

DRACH P. 1959. — *Groupes de tendances évolutives chez les Brachyoures*. XVth International Congress of Zoology, London 1958, sect. 2, paper 34: 158-160.

DRACH P. 1971. — Tendances évolutives et niveaux d'évolution chez les Crustacés Décapodes, *in* ALVARADO R., GADEA E. & HARO A. DE (eds), Actas del Simposio internacional de Zoofilogenia (Salamanca, 13-17 octobre 1969). *Acta Salamanticensia, Ciencias* 36: 283-292.

DUVERNOY G. L. 1853. — Des organes de génération de divers animaux. Deuxième fragment. Des organes extérieurs de fécondation dans les Crustacés décapodes. *Mémoires de l'Académie des Sciences* 23: 133-182.

FARMER A. S. D. 1974. — Reproduction of *Nephrops norvegicus* (L.) (Decapoda: Nephropsidae). *Journal of Zoology* 174: 161-183.

FELDMANN R. M. 1993. — Additions to the fossil decapod crustacean fauna of New Zealand. *New Zealand Journal of Geology and Geophysics* 36: 201-211.

FELDMANN R. M. 2003. — The Decapoda: new initiatives and novel approaches. *Journal of Paleontology* 77 (6): 1021-1039.

FELDMANN R. M., AWUOTA E. E. I. & WELSHENBAUGH J. 1976. — *Necrocarcinus siouxensis*, a new species of calappid crab (Crustacea: Decapoda) from the Fox Hills Formation (Cretaceous: Maastrichtian) of North Dakota. *Journal of Paleontology* 50 (5): 985-990.

FELDMANN R. M. & MCLAY C. L. 1993. — Geological history of brachyurans decapods from New Zealand. *Journal of Crustacean Biology* 13 (3): 443-455.

FELDMANN R. M. & VILLAMIL T. 2002. — A new carcineretid crab (Upper Turonian, Cretaceous) of Columbia. *Journal of Paleontology* 76 (4): 718-724.

FENIZIA G. 1935. — La *Dromia vulgaris* (M. Edw.) e le sue abitudini. *Archivio Zoologico Italiano* 21: 509-539.

FOREST J. 1974. — Les Dromies de l'Atlantique oriental. Description de *Sternodromia* gen. nov. et de deux espèces nouvelles du genre *Dromia* Weber (Crustacea Decapoda Dromiidae). *Annales de l'Institut océanographique*, Paris 50 (1): 71-123.

FORIR H. 1887. — Contribution à l'étude du système crétacé de la Belgique. III. Bibliographie et tableau des Thoracostracés crétacés décrits jusqu'à ce jour. *Annales de la Société géologique de Belgique, Mémoires* 14: 176-195.

FÖRSTER R. 1968. — *Paranecrocarcinus libanoticus* n. sp. (Decapoda) und die Entwicklung der Calappidae in der Kreide. *Mitteilungen Bayerische Staatsammlung Paläontologische historiche Geologie* 8: 167-195.

FÖRSTER R. 1985. — Frühe Anomuren und Brachyuren (Decapoda, Crustacea) aus dem mittleren Dogger. *Mitteilungen Bayerische Staatssammlung für Paläontologie und historische Geologie* 25: 45-60.

FRAAIJE R. H. B. 2003. — Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. *Contributions to Zoology* 72 (2-3): 119-130.

FRAAYE R. H. B. 1994. — Early Paleocene crabs (Crustacea, Decapoda) from the Middle Vistula Valley, Central Poland. *Acta Geologica Polonica* 44 (3-4): 261-266.

FRANCO G. M. DE O. 1998. — *Zoés, megalopa e estágios juvenis de* Cryptodromiopsis antillensis *(Simpson, 1858): impliçacões sobre a monofilia dos Dromiacea (Crustacea: Decapoda: Brachyura).* Master thesis, Rio de Janeiro, Brazil, 135 p.

FRANSEN C. H. J. M., HOLTHUIS L. B. & ADEMA J. P. H. M. 1997. — Type-catalogue of the Decapod Crustacea in the collections of the Nationaal Natuurhistorisch Museum, with appendices of pre-1900 collectors and material. *Zoologische Verhandlingen* (Leiden) (311), xvi, 344 p.

GLAESSNER M. F. 1929a. — *Crustacea Decapoda. Fossilium Catalogus*, pars 41. W. Junk, Berlin, 464 p.

GLAESSNER M. F. 1929b. — Decapodenstudien. *Neuen Jahrbuch für Mineralogie* 63 (B): 137-176.

GLAESSNER M. F. 1969. — Decapoda, *in* MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology,* Part R, *Arthropoda*, 4 (2). Geological Society of America, Boulder; University of Kansas Press, Lawrence: R399-R533, R626-R628.

GLAESSNER M. F. 1980. — New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. *Transactions of the Royal Society of South Australia* 104 (6): 171-192.

GOEKE G. D. 1981. — Symethinae, new subfamily, and *Symethis garthi*, new species, and the transfer of *Raninoides ecuadorensis* to *Notosceles* (Raninidae: Brachyura: Gymnopleura). *Proceedings of the Biological Society of Washington* 93 (4): 971-981 (dated 1980, published 1981).

GORDON I. 1949. — *The Presence of a Special Type of Spermatheca in the Dromiacea*, *in* XIII^{e} Congrès international de Zoologie, Paris, 21-27 juillet 1948. Abstract, 1 p.

GORDON I. 1950. — Crustacea Dromiacea. Part I: Systematic account of the Dromiacea collected by the "John Murray" Expedition. Part II. The morphology of the spermatheca in certain Dromiacea. *The John Murray Expedition 1933-34, Scientific Reports* 9 (3): 201-253.

GORDON I. 1963. — On the Relationship of Dromiacea, Tymolinae and Raninidae to the Brachyura, *in* WHITTINGTON H. B. & ROLFE W. D. I. (eds), Phylogeny and evolution of Crustacea. *Museum of Comparative Zoology*, Harvard, Special Publication: 51-57.

GORDON I. 1966. — On the spermatheca in the Raninidae (Crustacea: Decapoda), *in* BARNES H. (ed.), *Some Contemporary Studies in Marine Science.* Allen and Unwin, London: 343-354.

GORDON I. 1971. — On the thoracic sternum in the subfamily Hexapodinae (Brachyura, Goneplacidae). *Crustaceana* 21 (1): 106-110.

GUINOT D. 1976. — Constitution de quelques groupes naturels chez les Crustacés Décapodes Brachyoures. I. La superfamille des Bellioidea et trois sous-familles de Xanthidae (Polydectinae Dana, Trichiinae de Haan, Actaeinae Alcock). *Mémoires du Muséum national d'Histoire naturelle* (A) 97: 1-308.

GUINOT D. 1977. — Propositions pour une nouvelle classification des Crustacés Décapodes Brachyoures. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* (D) 285: 1049-1052.

GUINOT D. 1978. — Principes d'une classification évolutive des Crustacés Décapodes Brachyoures. *Bulletin biologique de la France et de la Belgique* n.s. 112 (3): 211-292.

GUINOT D. 1979a. — Données nouvelles sur la morphologie, la phylogenèse et la taxonomie des Crustacés Décapodes Brachyoures. *Mémoires du Muséum national d'Histoire naturelle* (A) 112: 1-354.

GUINOT D. 1979b. — Problème pratique [*sic* pour Problèmes pratiques] d'une classification cladistique des Crustacés Décapodes Brachyoures, *in* Actes de la VI^{e} Réunion des carcinologistes de langue française, Nabeul, Tunisie, 4-9 septembre 1979. *Bulletin de l'Office national des Pêches de Tunisie* 3 (1): 33-46.

GUINOT D. 1993a. — Données nouvelles sur les Crabes primitifs (Crustacea Decapoda Brachyura Podotremata). *Comptes rendus de l'Académie des Sciences* (III) 316 (10): 1225-1232.

GUINOT D. 1993b. — Données nouvelles sur les Raninoidea de Haan, 1841 (Crustacea Decapoda Brachyura Podotremata). *Comptes rendus de l'Académie des Sciences* (III) 316 (11): 1324-1331.

GUINOT D. 1995. — Crustacea Decapoda Brachyura: Révision de la famille des Homolodromiidae Alcock, 1900, *in* CROSNIER A. (ed.), Résultats des Campagnes MUSORSTOM, vol. 13. *Mémoires du Muséum national d'Histoire naturelle* 163: 155-282.

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., DOUMENC D. & CHINTIROGLOU C. 1995. — A review of the carrying behaviour in brachyuran crabs, with additional information on the symbioses with sea anemones. *Raffles Bulletin of Zoology* 43 (2): 377-416.

GUINOT D., JAMIESON B. G. M. & RICHER DE FORGES B. 1994. — Relationship of Homolidae and Dromiidae: evidence from spermatozoal ultrastructure (Crustacea: Decapoda). *Acta Zoologica*, Stockholm 75 (3): 255-267.

GUINOT D., JAMIESON B. G. M., RICHER DE FORGES B. & TUDGE C. C. 1998. — Comparative spermatozoal ultrastructure of the three dromiacean families exemplified by *Homolodromia kai* (Homolodromiidae), *Sphaerodromia lamellata* (Dromiidae) and *Dynomene tanensis* (Dynomenidae) (Podotremata: Brachyura). *Journal of Crustacean Biology* 18 (1): 78-94.

GUINOT D. & RICHER DE FORGES B. 1981. — Homolidae, rares ou nouveaux, de l'Indo-Pacifique (Crustacea, Decapoda, Brachyura). *Bulletin du Muséum national d'Histoire naturelle* (4) 3 (A) (2): 523-581.

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. 2000. — *Conchoedromia alcocki* Chopra, 1934: megalopa of *Conchoecetes artificiosa* (Fabricius, 1798) (Decapoda, Brachyura, Dromiidae). *Journal of Crustacean Biology* 20 (spec. number 2): 301-309.

GUINOT D. & TAVARES M. 2001. — Une nouvelle famille de Crabes du Crétacé, et la notion de Podotremata Guinot, 1977 (Crustacea, Decapoda, Brachyura). *Zoosystema* 23 (3): 507-546.

GUINOT D. & TAVARES M. 2003. — A new subfamilial arrangement for the Dromiidae de Haan, 1833, with diagnoses and descriptions of new genera and species. *Zoosystema* 25 (1): 43-129.

HARTNOLL R. G. 1968. — Morphology of the genital ducts in female crabs. *Journal of the Linnean Society* (Zool.) 47 (312): 279-300.

HARTNOLL R. G. 1969. — Mating in the Brachyura. *Crustaceana* 16 (2): 161-181.

HARTNOLL R. G. 1975. — Copulatory structures and function in the Dromiacea, and their bearing on the evolution of the Brachyura, *in* VIIIth European Marine Biology Symposium Sorrento (Naples) 1973. *Pubblicazioni della Stazione zoolologica di Napoli* 39 (Suppl.): 657-676.

HARTNOLL R. G. 1979. — The phyletic implications of spermathecal structure in the Raninidae (Decapoda: Brachyura). *Journal of Zoology*, London 187: 75-83.

HESS G. S. & BAUER R. T. 2002. — Spermatophore transfer in the hermit crab *Clibanarius vittatus* (Crustacea, Anomura, Diogenidae). *Journal of Morphology* 253: 166-175.

HO P. H. & NG P. K. L. 1999. — *Homolodromia kai* Guinot, 1993 (Decapoda, Brachyura, Homolodromiidae) from the South China Sea. *Crustaceana* 72 (9): 1123-1126.

ICZN 1999. — *International Code of Zoological Nomenclature*. 4th ed. The International Trust for Zoological Nomenclature, London, 306 p.

IHLE J. E. W. 1913. — Die Decapoda Brachyura der Siboga-Expedition. I. Dromiacea. *Siboga Expeditie*, Monogr. 39b, livr. 71: 1-96.

IKEDA H. 1998. — *The Deep-Sea Crabs of Sagami Bay*. Isshiki, Hayama Shiosai Museum, 180 p.

JAGT J. W. M., FRAAYE R. H. B. & VAN BAKEL B. W. M. 2000. — Late Cretaceous decapod crustacean faunas of northeast Belgium and the southeast Netherlands. *Studi e Ricerche, Associazione Amici del Museo-Museo Civico "G. Zannato", Montecchio Maggiore, Vicenza*: 37-42.

JAMIESON B. G. M. 1989. — Ultrastructural comparison of the spermatozoa of *Ranina ranina* (Oxystomata) and of other crabs exemplified by *Portunus pelagicus* (Brachygnatha) (Crustacea, Brachyura). *Zoomorphology* 109: 103-111.

JAMIESON B. G. M. 1994. — Phylogeny of the Brachyura with particular reference to the Podotremata: evidence from a review of spermatozoal ultrastructure (Crustacea, Decapoda). *Philosophical Transactions of the Royal Society* (B) 345: 373-393.

JAMIESON B. G. M., GUINOT D. & RICHER DE FORGES B. 1994. — Podotreme affinities of *Raninoides* sp. and *Lyreidus brevifrons*: evidence from spermatozoal ultrastructure (Crustacea, Decapoda, Raninoidea). *Marine Biology* 120: 239-249.

LARGHI C. 2004. — Brachyuran Decapod Crustacea from the Upper Cretaceous of Lebanon. *Journal of Paleontology* 78 (3): 528-541.

LEWINSOHN C. 1977. — Die Dromiidae des Roten Meeres (Crustacea Decapoda, Brachyura). *Zoologische Verhandelingen, uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden* (151): 1-41.

LEWINSOHN C. 1979. — Researches on the coast of Somalia. The shore and dune of Sar Uanle. 21. Dromiidae (Crustacea Decapoda Brachyura). *Monitore zoologico Italiano* (n. ser.) suppl. 12 (1): 1-15.

LEWINSOHN C. 1984. — Dromiidae (Crustacea, Decapoda, Brachyura) from Madagascar and the Seychelles. *Bulletin du Muséum national d'Histoire naturelle* (4) A 6 (1): 89-129.

MANJÓN-CABEZA M. E. & GARCÍA RASO J. E. 2000. — Reproductive aspects of females of the hermit crab *Diogenes pugilator* (Crustacea: Decapoda: Anomura) from southern Spain. *Journal of the Marine Biological Association of the United Kingdom* 80: 85-93.

MANNING R. B. & HOLTHUIS L. B. 1981. — West African Brachyuran Crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* 306: i-xii, 1-379.

MARTIN J. W. & DAVIS G. E. 2001. — An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Science Series* 39: 1-124.

MARTIN J. W. & ZIMMERMAN T. L. 2001. — Notes on three western Atlantic deep-sea crabs (Decapoda, Brachyura). *Crustaceana* 74 (4): 411-414.

MCLAUGHLIN P. A. & LEMAITRE R. 1997. — Carcinization in the Anomura - fact or fiction? I. Evidence from adult morphology. *Smithsonian Contributions to Zoology* 67 (2): 79-123.

MCLAY C. L. 1993. — Crustacea Decapoda: the sponge crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera, *in* CROSNIER A. (ed.), Résultats des campagnes MUSORSTOM, vol. 10. *Mémoires du Muséum national d'Histoire naturelle* 156: 111-251.

MCLAY C. L. 1999. — Crustacea Decapoda: revision of the family Dynomenidae, *in* CROSNIER A. (ed.), Résultats des campagnes MUSORSTOM, vol. 20. *Mémoires du Muséum national d'Histoire naturelle* 180: 427-569.

MCLAY C. L. 2001a. — The Dromiidae of French Polynesia and a new collection of crabs (Decapoda: Brachyura) from the Marquesas Islands. *Zoosystema* 23 (1): 77-100.

MCLAY C. L. 2001b. — A new genus and two new species of unusual dromiid crabs (Brachyura: Dromiidae) from Northern Australia. *Records of Australian Museum* 53: 1-8.

MCLAY C. L. 2001c. — Dynomenidae and Dromiidae crabs (Decapoda: Brachyura) from Guam, Philippines Islands, Tonga and Samoa. *Zoosystema* 23 (4): 807-856.

MCLAY C. L. 2002. — *Foredromia rostrata*, a new genus and species of sponge crab (Decapoda, Brachyura, Dromiidae) from Southeast Asia. *Crustaceana* 75 (3-4): 505-515.

MILNE-EDWARDS A. 1879. — Mémoire sur les Crustacés Décapodes du genre Dynomène. *Annales des Sciences naturelles* (Zool.), 6e sér., 8 (3): 1-11.

MILNE-EDWARDS H. 1832. — Recherches sur l'organisation et la classification naturelle des Crustacés Décapodes. *Annales des Sciences naturelles* 25: 298-332.

MILNE-EDWARDS H. 1834-1837. — *Histoire naturelle des Crustacés comprenant l'anatomie, la physiologie et la classification de ces animaux*. Librairie Encyclopédique de Roret, Paris, vol. 1, xxxv + 468 p.; vol. 2, 531 p.; atlas, 1837, 32 p., 42 pls.

MINAGAWA M. 1993. — Gonopods of the red frog crab *Ranina ranina* Linnaeus (Decapoda: Raninidae). *Crustacean Research* (22): 45-54.

MINAGAWA M., CHIU J.-R., KUDO M., ITO E. & TAKASHIMA F. 1993. — Female reproductive biology and oocyte development of the red frog crab, *Ranina ranina*, off Hachijojima, Izu Islands, Japan. *Marine Biology* 115: 613-623.

MINAGAWA M., CHIU J.-R., KUDO M. & TAKASHIMA F. 1994. — Male reproductive biology of the red frog, *Ranina ranina*, off Hachijojima, Izu Islands, Japan. *Marine Biology* 118: 393-401.

MONOD T. 1956. — Hippidea et Brachyura ouest-africains. *Mémoires de l'Institut français d'Afrique Noire* (45): 1-674.

MÜLLER P. 1984. — A bádeni emelet tízlábú rákjai [= Decapod Crustacea of the Badenian]. *Geologica Hungarica*, series Palaeontologica 42: 1-317 (in Hungarian).

MÜLLER P., KROBICKI M. & WEHNER G. 2000. — Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura) – their taxonomy, ecology and biogeography. *Annales Societatis Geologorum Poloniae* 70: 49-79.

PÉREZ FARFANTE I. & KENSLEY B. 1997. — Penaeoids and sergestoid shrimps and prawns of the World. Keys and diagnoses for the families and genera. *Mémoires du Muséum national d'Histoire naturelle* 175: 1-233.

PEREYRA LAGO R. 1988. — Larval development of *Spiroplax spiralis* (Barnard, 1950) (Brachyura Hexapodidae) in the laboratory; the systematic position of the family on the basis of larval morphology. *Journal of Crustacean Biology* 8 (4): 576-953.

PYLE R. & CRONIN E. 1950. — The general anatomy of the blue crab *Callinectes sapidus* Rathbun. *Chesapeake Biological Laboratory, Solomons* (87): 1-38.

RATHBUN M. J. 1908. — Descriptions of fossil crabs from California. *Proceedings of the United States National Museum* 35 (1647): 341-349.

RATHBUN M. J. 1937. — The oxystomatous and allied crabs of America. *Bulletin of the United States National Museum* 166: i-vi + 1-278.

REMY J.-M. & TESSIER F. 1954. — Décapodes nouveaux de la partie Ouest du Sénégal. *Bulletin de la Société géologique de France* 4 (6): 185-191.

RYAN E. P. 1967. — *Structure and Function of the Reproductive System of the Crab* Portunus sanguinolentus *(Herbst) (Brachyura: Portunidae)*. I. *The Male System*. II. *The Female System*. Proceedings of the Symposium on Crustacea, Ernakulam, 1965. Mandapam Camp, Marine Biological Association: 506-544.

SAINT LAURENT M. DE 1989. — La nouvelle super-famille des Retroplumoidea Gill, 1894 (Decapoda, Brachyura) : systématique, affinités et évolution, *in* FOREST J. (ed.), Résultats des campagnes MUSORSTOM, vol. 5. *Mémoires du Muséum national d'Histoire naturelle* (A) 144: 103-179.

SCELZO M. A., MANTELLATTO F. L. & TUDGE C. C. 2004. — Spermatophore morphology of the endemic crab *Loxopagurus loxochelis* (Anomura, Diogenidae) from the southwestern Atlantic-Brazil and Argentina. *Invertebrate Reproduction and Development* 46 (1): 1-9.

SCHMITT W. L. 1921. — The marine Decapod Crustacea of California with special reference to the Decapod Crustacea collected by the United States Bureau of Fisheries Steamer *Albatross* in connection with the Biological Survey of San Francisco Bay during the years 1912-1913. *University of California Publications in Zoology* 23: 1-469.

SCHOLTZ G. & RICHTER S. 1995. — Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zoological Journal of the Linnean Society* 113: 289-328.

SCHOLTZ G. & RICHTER S. 1996. — Phylogeny and evolution of decapod crustaceans. *Abstracts, 2nd European Conference*, September 2-6, 1996, Liège (Belgium): 14.

SCHRAM F. R. 1986. — *Crustacea*. Oxford University Press, Oxford, 606 p.

SCHWEITZER C. E. 2003a. — Progress on the fossil Xanthoidea MacLeay, 1838 (Decapoda, Brachyura). *Contributions to Zoology* 72 (2-3): 181-186.

SCHWEITZER C. E. 2003b. — Utility of proxy characters for classification of fossils: an example from the fossil Xanthoidea (Crustacea: Decapoda: Brachyura). *Journal of Paleontology* 77 (6): 1107-1128.

SCHWEITZER C. E. & FELDMANN R. M. 2000a. — New species of calappid crabs from western North America and new species of calappid crabs from Western North America and reconsideration of the Calappidae sensu lato. *Journal of Paleontology* 74 (2): 230-246.

SCHWEITZER C. E. & FELDMANN R. M. 2000b. — New fossil portunids from Washington, USA, and Argentina and a reevaluation of generic and family relationships within the Portunoidea Rafinesque (Decapoda: Brachyura). *Journal of Paleontology* 74 (4): 636-653.

SCHWEITZER C. E. & FELDMANN R. M. 2001. — Differentiating fossil Hexapodidae Miers (Decapoda: Brachyura) from similar forms. *Journal of Paleontology* 75: 330-345.

SCHWEITZER C. E., FELDMANN R. M., FAM J., HESSIN W. A., HETRICKS S. W., NYBORG T. G. & ROSS R. M. L. 2003. — *Cretaceous and Eocene Decapod Crustaceans from Southern Vancouver Island, British Columbia, Canada*. National Research Council Press, Ottawa, 66 p.

SCHWEITZER C. E., FELDMANN R. M., GONZÁLES-BARBA G. & VEGA F. J. 2002. — New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. *The Paleontological Society Memoir 76* (supplement to No. 6 of *Journal of Paleontology*): 1-43.

SCHWEITZER HOPKINS C., SALVA E. W. & FELDMANN R. M. 1999. — Re-evaluation of the genus *Xanthosia* Bell, 1863 (Decapoda: Brachyura: Xanthidae) and descriptions of two new species from the Cretaceous of Texas. *Journal of Paleontology* 73 (1): 77-90.

SECRETAN S. 1980. — Le plan de base du « squelette axial » d'un Crustacé décapode macroure et sa terminologie. *Comptes rendus hebdomadaires de l'Académie des Sciences* (D) 291: 877-880.

SECRETAN S. 1982. — Les modifications fonctionnelles des intercloisons du squelette axial d'un crustacé décapode macroure: *Nephrops*. *Bulletin de la Société zoologique de France* 107 (4): 551-556.

SECRETAN S. 1983. — Les caractères panchroniques de *Paromola*. *Bulletin de la Société zoologique de France* 108 (4): 580-585.

SECRETAN S. 1991. — Modifications fonctionnelles du sternite au niveau de la spermathèque de *Nephrops* et du métamère mandibulaire des crustacés décapodes. *Comptes rendus de l'Académie des Sciences* 312 (3): 335-341.

SECRETAN S. 1998. — The sella turcica of crabs and the endophragmal system of decapods, *in* Acta of the 6th Colloquium Crustacea Decapoda Mediterranea. *Journal of Natural History* 32: 1753-1767.

SECRETAN S. 2002. — La lame de jonction, base de l'organisation phragmale des Décapodes Brachyoures. *Crustaceana* 75 (3-4): 637-641.

SECRETAN-REY S. 2002. — Morphologie du squelette axial de *Nephrops norvegicus* (Linné, 1758). *Zoosystema* 24 (1): 81-176.

SERÈNE R. & UMALI A. F. 1972. — The family Raninidae and other new and rare species of brachyuran decapods from the Philippines and adjacent regions. *Philippine Journal of Science* 99 (1-2): 21-105 (dated 1970, published 1972).

SPEARS T., ABELE L. G. & KIM W. 1992. — The monophyly of brachyuran crabs: a phylogenetic study based on 18S rRNA. *Systematic Biology* 41 (4): 446-461.

STENZEL H. B. 1945. — Decapod crustaceans from the Cretaceous of Texas. *Texas University Publication* 4401: 401-416 (dated 1944, published 1945).

ŠTEVČIĆ Z. 1981. — Systematic position and status of the Homolids (Decapoda-Brachyura). *Arhiv Bioloskih Nauka* 33 (1-4): 83-91.

STIMPSON W. 1858. — Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit, Pars VII. Crustacea Anomoura. *Proceedings of the Academy of Natural Science of Philadelphia* 10 (4): 225-252.

SUBRAMONIAM T. 1977. — Aspects of sexual biology in the Anomuran Crab *Emerita asiatica*. *Marine Biology* 43: 369-377.

TAVARES M. 1991a. — Espèces nouvelles de Cyclodorippoidea Ortmann et remarques sur les genres *Tymolus* Stimpson et *Cyclodorippe* A. Milne-

Edwards (Crustacea, Decapoda, Brachyura). *Bulletin du Muséum national d'Histoire naturelle* (4) 12 (A) (3-4): 623-648 (dated 1990, published 1991).

TAVARES M. 1991b. — Révision préliminaire du genre *Tymolus* Stimpson, avec la description de *Tymolus brucei* sp. nov. d'Australie occidentale (Crustacea, Brachyura, Cyclodorippoidea). *Bulletin du Muséum national d'Histoire naturelle* (4) 13 (A) (3-4): 439-456.

TAVARES M. 1993. — Crustacea Decapoda : les Cyclodorippidae et Cymonomidae de l'Indo-Ouest-Pacifique à l'exclusion du genre *Cymonomus*, *in* CROSNIER A. (ed.), Résultats des campagnes MUSORSTOM, vol. 10. *Mémoires du Muséum national d'Histoire naturelle* 156: 253-313.

TAVARES M. 1994. — *Brachyoures bathyaux récoltés par le* Marion Dufresne *au large du Brésil. Systématique et phylogénie des Cyclodorippoidea mondiaux (Crustacea, Decapoda, Brachyura).* Thèse de Doctorat de l'Université Pierre et Marie Curie, Paris, France, 324 p.

TAVARES M. 1996. — Révision systématique des Cyclodorippidae américains (Crustacea, Decapoda, Brachyura). *Bulletin du Muséum national d'Histoire naturelle* (4) 18 (A) (1-2): 233-295.

TAVARES M. 1997. — Crustacea Decapoda : Cyclodorippidae récoltés dans l'archipel des Vanuatu (Brachyura), *in* CROSNIER A. (ed.), Résultats des campagnes MUSORSTOM, vol. 18. *Mémoires du Muséum national d'Histoire naturelle* 176: 261-271.

TAVARES M. 1998. — Phyllotymolinidae, nouvelle famille de Brachyoures Podotremata (Crustacea, Decapoda). *Zoosystema* 20 (1): 109-122.

TAVARES M. 2003. — A new theoretical approach for the study of monophyly of the Brachyura (Crustacea, Decapoda) and its impact on the Anomura. *Memoirs of the Museum Victoria* 60 (1): 145-149.

TAVARES M. S. & SECRETAN S. 1993. — La notion de thelycum et de spermathèque chez les Crustacés Décapodes. *Comptes rendus de l'Académie des Sciences* 316 (3): 133-138.

TUDGE C. C. 1997. — Spermatologic evidence supports the taxonomic placement of the Australian endemic hairy stone crab, *Lomis hirta* (Decapoda: Anomura: Lomidae). *Memoirs of the Museum of Victoria* 56: 235-244.

TUDGE C. C. 2003. — Endemic and enigmatic: the reproductive biology of *Aegla* (Crustacea: Anomura: Aeglidae) with observations on sperm structure. *Memoirs of the Museum of Victoria* 60 (1): 63-70.

TUDGE C. C. & LEMAITRE R. 2004. — Studies of male sexual tubes in hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea). I. Morphology of the sexual tube in *Micropagurus acantholepis* (Stimpson, 1858), with comments on function and evolution. *Journal of Morphology* 259: 106-118.

TUCKER A. B. 1998. — Systematics of the Raninidae (Crustacea: Decapoda: Brachyura), with accounts of three new genera and two new species. *Proceedings of the Biological Society of Washington* 111 (2): 320-371.

VAN BAKEL B. W. M., JAGT J. W. M., FRAAIJE R. H. B. & COOLE Y. 2003. — New data on the crab *Binkhorstia ubaghsii* (Late Maastrichtian; NE Belgium, SE Netherlands). *Contributions to Zoology* 72 (2-3): 85-89.

VEGA F. J. & FELDMANN R. M. 1991. — Fossil crabs (Crustacea Decapoda) from the Maastrichtian Difunta Group, Northeastern Mexico. *Annals of Carnegie Museum* 60 (2): 163-177.

VEGA F. J. & FELDMANN R. M. 1992. — Occurence of *Costacopluma* (Decapoda: Brachyura: Retroplumidae) in the Maastrichtian of southern Mexico and its paleobiogeographic implications. *Annals of Carnegie Museum* 61 (2): 133-152.

VEGA F. J., FELDMANN R. M. & DAVILA-ALCOCER V. M. 1994. — Cuticular structure in *Costacopluma mexicana* Vega and Perrilliat, from the Difunta Group (Maastrichtian) of northeastern Mexico, and its paleoenvironmental implications. *Journal of Paleontology* 68 (5): 1074-1081.

VEGA F. J., FELDMANN R. M., OCAMPO A. C. & POPE K. O. 1993. — A new species of Late Cretaceous carcineretid crab (Brachyura: Carcineretidae) from Albion Island, Belize. *Journal of Paleontology* 71 (4): 615-620.

VEGA F. J., FELDMANN R. M. & SOUR-TOVAR F. 1995. — Fossil crabs (Crustacea: Decapoda) from the Late Cretaceous Cardenas Formation, east-central Mexico. *Journal of Paleontology* 69 (2): 340-350.

VEGA F. J., FELDMANN R. M., GARCÍA-BARRERA P., FILKORN H., PIMENTEL F. & AVENDANO J. 2001. — Maastrichtian Crustacea (Brachyura: Decapoda) from the Ocozocuautla Formation in Chiapas, southeast Mexico. *Journal of Paleontology* 75 (2): 319-329.

VEGA-VERA F. J. & PERRILLIAT M. C. 1989. — Una especie nueva de cangrejo del género *Costapluma* (Decapoda: Brachyura: Retroplumidae) del Maastrichtiano del Estado de Nuevo León. *México, Universidad Nacional Autónoma, Instituto de Geología, Revista* 8 (1): 84-87.

VÍA BOADA L. 1969. — Crustáceos Decápodos del Eoceno español. *Pirineos* (91-94): 1-479.

WEHNER G. 1988. — *Über die Prosopiden (Crustacea, Decapoda) des Jura.* Inaugural-Dissertation zur Erlangung des Doktorgrades der Fakultät für Geowissenschaften der Ludwig-Maximilians-Universität. München, Germany, i-iv + 154 p.

WRIGHT C. W. & COLLINS J. S. H. 1972. — British Cretaceous crabs. *Palaeontographical Society* [*Monographs*] London: 1-114.

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