

Why the spermathecal openings are so displaced forward in the Podotremata (Decapoda: Brachyura)? Ontogenetic changes and phylogenetic implications

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Introduction

The Podotremata Guinot, 1977 is a group of basal Brachyura, which encompasses three subsections: (i) Dromiacea De Haan, 1833, with three families: Homolodromiidae Alcock, 1900, Dromiidae de Haan, 1833, and Dynomenidae Ortmann, 1892; (ii) Homolidea De Haan, 1839, with three families: Homolidae de Haan, 1839, Latreilliidae Stimpson, 1858, and Poupiniidae Guinot, 1991; and (iii) Archaeobrachyura Guinot, 1977, with three families: Cyclodorippidae Ortmann, 1892, Cymonomidae Bouvier, 1897, and Phyllotymolinidae Tavares, 1998, and the superfamily Raninoidea De Haan, 1839 (Guinot and Tavares, 2003: 45).

All 89 genera of recent Podotremata, totaling about 350 known species, as well as the Cretaceous genera *Etyus* Leach in Mantell, 1822, and *Dakoticancer* Rathbun, 1917, are provided with paired spermathecae at the distal end of the sternal suture 7/8. This is a general rule, never contradicted so far (Guinot and Tavares, 2001: 522). The basic anatomical organization of the spermathecae is also invariable throughout the Podotremata: it is always derived from two adjacent thoracic segments, that is, a split between the plates of the intersegmental phragmae 7/8 (figure 1A-D). One of the plates of the phragma 7/8 is derived from sternite 8, whereas the other is derived from sternite 7 (figure 1A). The paired spermatheca of the Podotremata always involves these two segments (Gordon, 1950; Hartnoll, 1979; Tavares and Secretan, 1993: 135).

The unusual female thoracic sternum of the Podotremata, with its thoracic sternal sutures 7/8 and paired spermatheca, attracted attention very soon. De Haan (1839: 105) described the long thoracic sternal sutures 7/8 of *Dromia* Weber, 1795, and mentioned that they end in a “tubercula perforata” (spermathecal openings). He also recognized that both structures were related with mating: “styli in sulco sterni feminei inserti ut fulcrum inservire in copulationis actu” (see Guinot and Quenette, in press). Alcock (1901: 29) remarked that “... the sternum thoracic of the female [Dromiidae] is traversed in more or less of its extent by two obliquely-longitudinal grooves or furrows [sternal sutures 7/8]...” (see also Ihle, 1913: 12-18).

The sutures 7/8 and the spermathecal openings have been described in some detail in a number of families of recent and fossil Podotremata (see for example Gordon, 1950; 1963; 1966; Hartnoll, 1973; 1979; Guinot, 1993; 1995; Guinot and Richer de Forges, 1995; Guinot and Tavares, 2001; Tavares, 1993; 1998). In the Podotremata the spermathecal openings are placed far forward, at the distal end of an usually long thoracic sternal suture 7/8. This unusual position of the podotreme spermathecae attracted Gordon's (1950: 251) attention: “Why should the spermathecal openings (if such they are) be so far forward in the Dromiidea? [currently Dromiacea]”. Her query, however, has remained overlooked since then. Actually, the spermathecal openings are displaced forward as a result of the movement in a forward direction, during ontogeny, of the thoracic sternal suture 7/8. Information in the literature on the ontogenetic changes of the thoracic sternal suture 7/8 is extremely scarce and the observations

available are limited to the Dromiidae. "Les observations sur les sillons sternaux sont rares et nous connaissons mal les aspects variés qui peuvent correspondre à des stades de croissance". This quote from Monod (1956: 75) is just as valid today, 48 years later. Lewinsohn (1984: 93, 94) remarked that in *Dromia intermedia* Laurie, 1906, "...the end of the sternal grooves of the female during growth moves in a forward direction."; Manning and Holthuis (1981: 21) noticed that in *Sternodromia spinirostris* (Miers, 1881) "...the arrangement of the sternal grooves changes drastically when sexual maturity is reached." Based on three females of different sizes McLay (1993: 194) reported ontogenetic changes in the length of the thoracic sternal suture 7/8 in *Cryptodromiopsis unidentata* (Rüppell, 1830), currently *Lewindromia unidentata* (Rüppell, 1830) (see Guinot and Tavares, 2003).

Because the movement forward of both the suture 7/8 and spermathecal openings during ontogeny is poorly understood, and in order to address Gordon's (1950) question, we studied the ontogenetic transformations of the thoracic sternum suture 7/8 and spermatheca in *Moreiradromia antillensis* (Stimpson, 1858) (Dromiidae), from the megalopa to the female adult age. The phylogenetic implications of both the displacement forward of the thoracic sternum suture 7/8 and the modifications of the intersegmental phragma 7/8 to form the spermathecal bulb are also addressed in this paper.

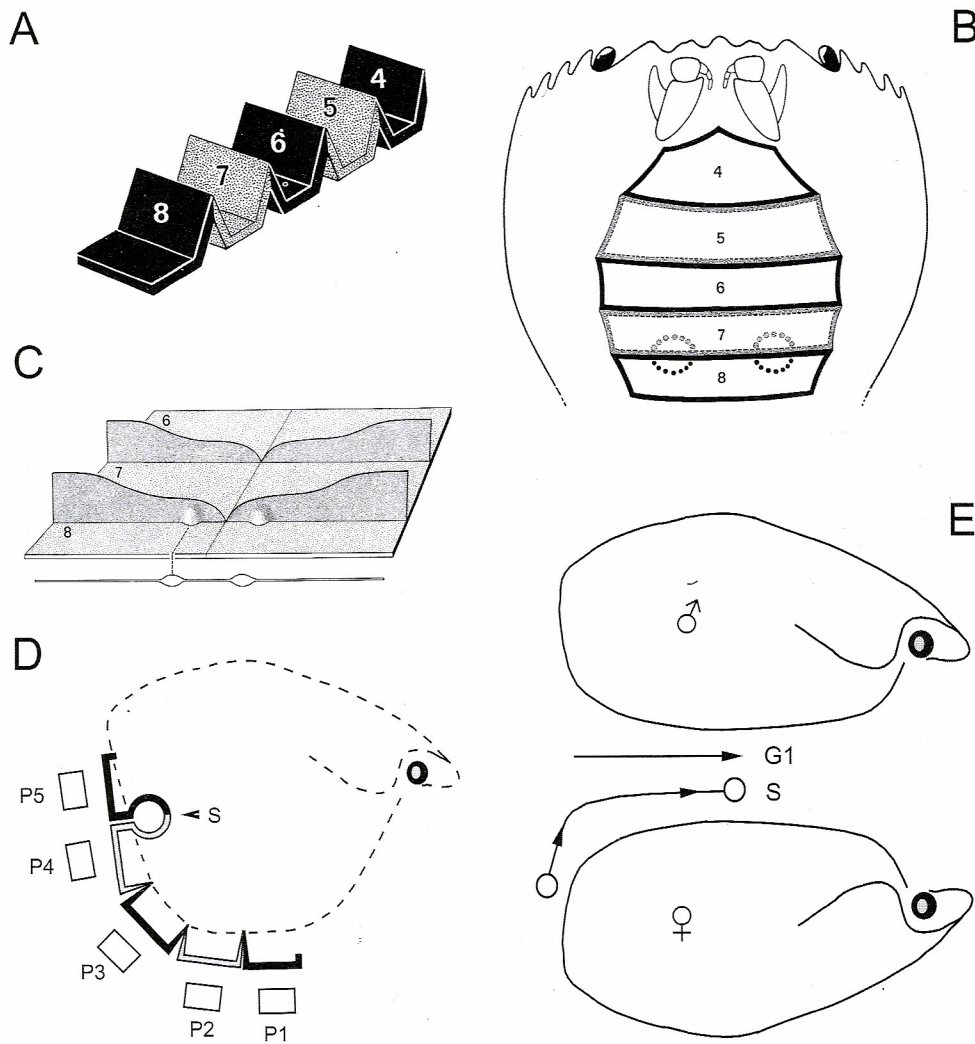


Figure 1: A-D, diagrammatic representations. A, relative position of the thoracic sternites 4-8 and their interosternites. B-C, paired spermathecae of the Podotremata. D, lateral view of a female Podotremata (S = spermatheca). E, Podotremata crabs in the mating position. G1, first gonopod directed forward. S, spermathecal apertures. Notice in D the thoracic sternites 6-8 almost perpendicular to the precedent ones; in B,D the unsuitable position of the spermathecae to be attained by G1; and in E the movement forward of the suture 7/8 bringing the opening of the spermathecae near to the tip of G1.

Material and Methods

We studied 50 megalopae and 35 female individuals of *Moreiradromia antillensis* (Stimpson, 1858). The specimens illustrated herein are listed below.

Material.- *Moreiradromia antillensis*. Brazil, Amapá, R. V. Almirante Saldanha, 28.xi.1968: megalopa cl 7.2 mm, cw 6.0 mm (MNRJ). Paraíba, Projeto Algas st. 30, 01.iv.1981: female cl 8.4 mm x 8.8 mm (MZUSP 5905). Abrolhos, Bahia, GEOMAR 18: female cl 4.8 mm, cw 4.4 mm (UFRJ). Espírito Santo, 20.v.1967: female cl 8.3, cw 8.4 mm (MZUSP 6058). Bacia de Campos, Rio de Janeiro, PETROBRAS st. 32: female cl 5.4 mm, cw 5.4 mm (MZUSP 11919).

Dromia sp. France: female cl 6.5 mm x 7.5 mm (MNHN).

The studied material has been deposited in the collections of the Museu de Zoologia, Universidade de São Paulo (MZUSP), Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), reference collection of the Departamento de Zoologia, Universidade Federal do Rio de Janeiro (UFRJ), and the Muséum national d'Histoire naturelle, Paris (MNHN). Measurements are given in millimeters (mm), as carapace length (cl) and carapace width (cw). Abbreviations: P1-P5, pereopods 1 to 5; G1, first gonopod. Individuals are referred to by carapace width.

Results

Ontogenetic changes in the sternal suture 7/8 in *M. antillensis*

In the 6.0mm megalopae of *M. antillensis* the thoracic sternal sutures 7/8, 6/7, 5/6, and 4/5 are poorly developed and visible laterally only. The suture 7/8 is about as long as the remaining sternal sutures and possesses no visible trace of spermathecal opening at its end. Also, there is no trace of suture in the middle of the thoracic sternum nor a trace of gonopore on the coxa of P3 or P5 (figure 2A). In the megalopa the thoracic sternites 6-8 are already twisted, leading to the formation of a thoracic arch posteriorly. During ontogeny, while the female suture 7/8 starts growing in length in a forward direction (figure 2 B-E), the sternal sutures 6/7, 5/6, and 4/5 remain poorly developed. Thus, in the 4.4 mm female the suture 7/8 does not reach the level of the female gonopore on the coxa of P3 (figure 2 B); in the 5.4 mm female the suture 7/8 achieves well beyond the female gonopore (figures 2 C, 3 A); in the 8.4 mm female the suture 7/8 ends at the level of P2 (figures 2 D, 3 B); and in the 8.8 mm female the suture 7/8 reaches as far as the level of P1 (figures 2 E, 3 D). The sternal sutures 7/8 and the spermathecal openings undergo a dramatic change in size and shape. The female sternal sutures 7/8 become longer and increasingly convergent as they move forward. While in the earlier ontogenetic stages the ends of the sutures 7/8 are widely separated (figures 2 B, 3 A), in the full mature female the sternal suture 7/8 is about five times as long as the suture 7/6 and the spermathecal openings are placed closed together (figures 2 D-E, 3 B, D). Accordingly, the male second gonopods are long (almost attaining the level of P1), styliiform, and convergent terminally. The spermathecal pores do not open (figures 3 B-C) until the sternal suture 7/8 is fully developed and attain the level of P1 (figure 2 E, 3 D). A direct consequence is that no mating seems possible before the spermathecal openings are in the right forward position (figures 1 E, 2 E, 3 D). Because such ontogenetic changes in the sutures 7/8 are related with the possession of a spermatheca, the male sutures 7/8 do not undergo major changes during ontogeny. In adult males of *M. antillensis* the sternal suture 7/8 is inclined forward, but never beyond the level of P3.

In the thoracic sternum of the immature females a membranous area is generally clearly visible just ahead of the sternal suture 7/8, transversally relative to the body axis (figures 2 B-C). It is apparent that these membranous areas correspond to a pronounced decalcification of the skeleton. These membranous areas have been noticed by a number of authors. Gordon (1950: 245, fig. 23) clearly indicated them in the drawings of both a very young and an immature female of *Dromia vulgaris* H. Milne Edwards, 1837, currently *Dromia personata* (Linnaeus, 1758) (see Guinot and Tavares, 2003). Manning and Holthuis (1981: 16, figs 3a-c) illustrated the thoracic sternum of three young females of *Dromia monodi* Forest & Guinot, 1966, of different sizes in which a membranous area is well discernible just ahead of the sutures 7/8. The movement of the suture 7/8 in a forward direction is the result of the growth, during molting, of the thoracic sternites 7 and 8 as well as the correspondent parts of the axial skeleton, namely the intersegmental phragma 7/8 (Gordon, 1950: 246, fig. 24 B; Tavares, 1994: 217, fig. 37 C-D). The role played by these decalcified areas placed just ahead the suture 7/8 is unknown. Membranous areas are generally absent or only weakly perceptible in adult females.

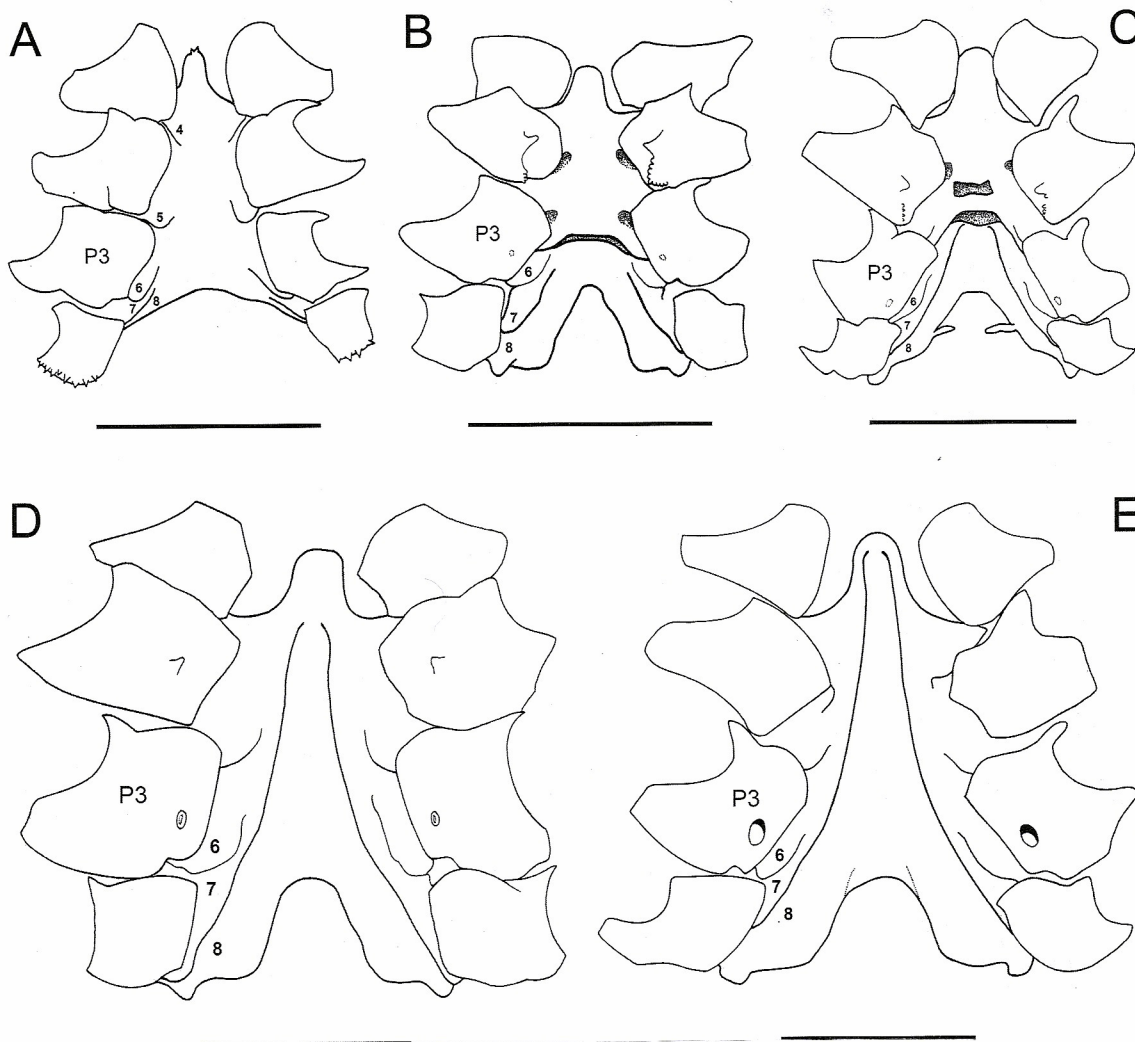


Figure 2: A-E, thoracic sternum in *Moreiradromia antillensis* (Stimpson, 1858). A, megalopa cw 6.0 mm (MNRJ) with the sternal suture 7/8 almost as long as the remaining sutures. B, female cw 4.4mm (UFRJ) with suture 7/8 ending before the gonopore on the coxa of P3. C, female cw 5.4 mm (MZUSP 11919) with suture 7/8 well beyond the gonopore on the coxa of P3. D, female cw 8.4 mm (MZUSP 6058) with the suture 7/8 ending at the level of P1. E, female cw 8.8 mm (MZUSP 5905) with the suture 7/8 fully developed. Notice in B-C the membranous area placed ahead of the suture 7/8. Bar scales 2 mm.

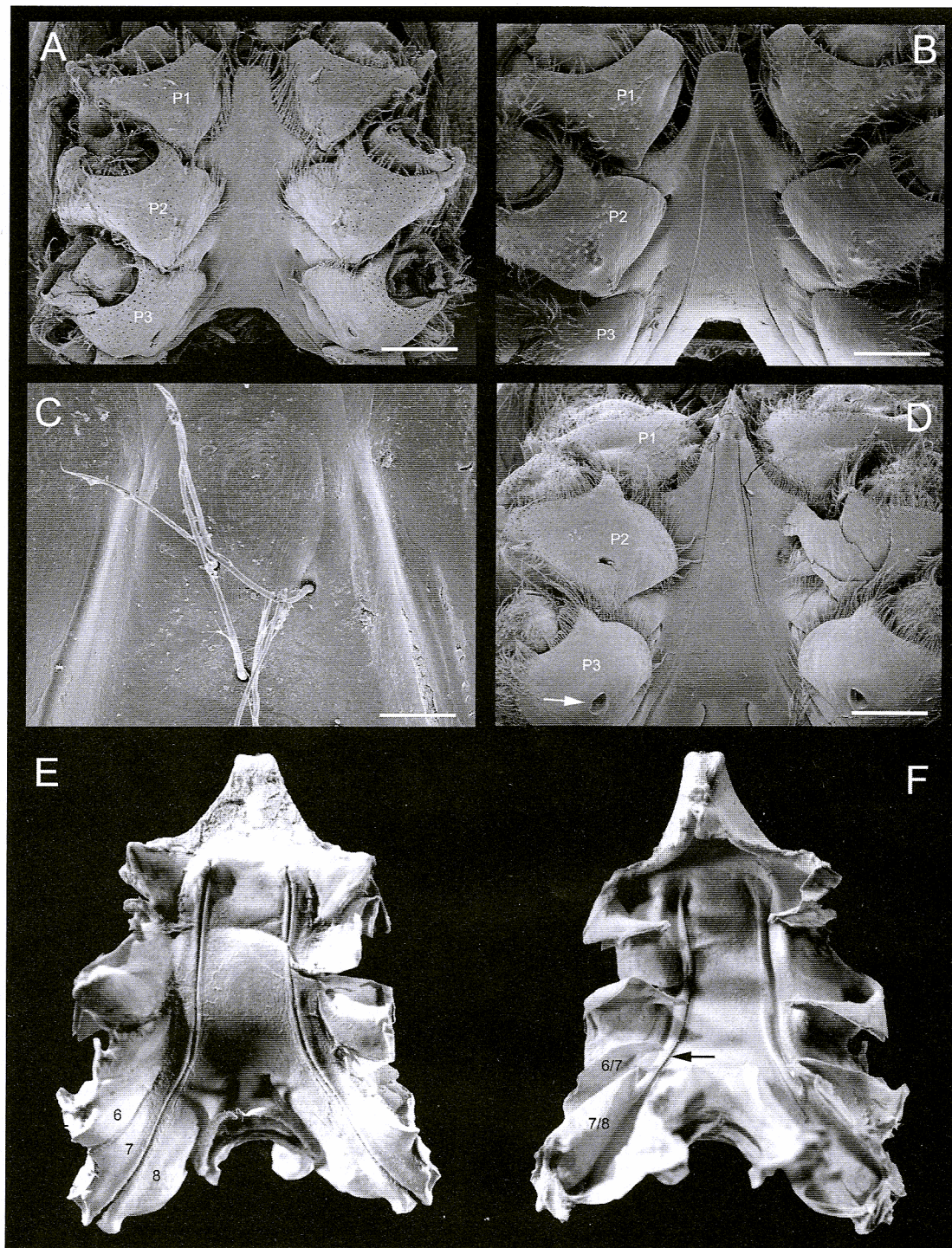


Figure 3: A-D, scanning electron micrographs of the thoracic sternum in *Moreiradromia antillensis* (Stimpson, 1858). A, female cw 5.4 mm (MZUSP 11919) with suture 7/8 well beyond the gonopore on the coxa of P3. B, female cw 8.4 mm (MZUSP 6058) with the suture 7/8 ending at the level of P1. C, detail of the terminal end of the suture 7/8 (female cw 8.4 mm MZUSP 6058). D, female cw 8.8 mm (MZUSP 5905) with the suture 7/8 fully developed. Notice in D the spermathecal openings at the terminal end of the suture 7/8 (not yet present in C) and the calcified hollowed tube in F. Bar scales 1 mm.

Discussion

Why the spermathecal openings are so forward displaced?

During ontogeny the spermathecal openings are displaced forward as a result of the movement in a forward direction of the thoracic sternal suture 7/8. Tavares (1994) hypothesized

that the twist of the posterior thoracic sternites (figure 1 B, D) and the dramatic changes in the thoracic sternum during ontogeny are actually related. Because the spermatheca is derived from the intersegmental phragma 7/8, once the sternites 6, 7, and 8 are twisted and become perpendicular in relation to sternites 4 and 5, the spermathecae normally should be found in a higher position, that is, between P4 and P5 (figure 1 B, D), at the level of the sternites 7 and 8, almost in a subdorsal position (Tavares, 1994) and thereby not in a suitable location to be attained by the first gonopods (figure 1 D). This original position of the spermathecal apertures is dramatically modified as a result of the movement of the thoracic sternal sutures 7/8 in a forward direction: displaced forward on the thoracic sternum the spermathecal apertures can be more easily reached by the first gonopod (figure 1 E). Gordon (1950) remarked that the length of the female suture 7/8, and consequently the forward position of the spermathecal apertures, vary from one taxon to another. She noticed in the crabs she had at hands that the suture 7/8 was much longer in the dromiids than in the homolids and concluded that the length of the suture 7/8 could be correlated with the thickness of the body: "...may well be that the more globular is the carapace the farther forward are they [the spermathecal apertures] placed. The Thelxiopidae [currently Homolidae de Haan, 1839] are much flatter than are the majority of the Dromiids" (Gordon, 1950: 251). Our view is that the length of the suture 7/8 is actually correlated to the twist of the posterior thoracic sternites: the more the posterior thoracic sternites are twisted (sternites 6, 7, and 8 at most), the greater is the length of female the suture 7/8.

Monophyly of the Podotremata

The monophyletic status of the Podotremata is an open question since H. Milne Edwards (1832) transferred *Dromia* Weber, 1795, from the Brachyura to the Anomura (see Guinot and Tavares, 2003: 45-46). Tavares (2003) discussed in detail the assumptions related with the lingering uncertainties about the monophyly of the Podotremata. The monophyletic status of the Podotremata hold a central position in the debate on the monophyly of the Brachyura. It is apparent that no firm outline of the brachyuran tree history will emerge until the monophyletic status of the Podotremata is cleared. Guinot and Tavares (2001: 524) maintained that the Podotremata is a monophyletic group sharing synapomorphically paired spermathecal openings (versus single spermathecal openings). Actually, none of the synapomorphies postulated for the clade Brachyura (e.g., Scholtz and Richter, 1995) are so constant as the possession of paired spermathecae in the Podotremata. While the characters putted forward so far to advocate (e.g. Rice, 1980; 1981) for a closest relationships between Anomura and Podotremata (partially or collectively) should be discarded on the ground that they are shared plesiomorphies, evidences formally proposed to date to support the monophyly of the Podotremata are based on the presence of the paired spermathecal openings alone. Although poorly documented, the development in a forward direction of the thoracic sternal suture 7/8 leading to the forward displacement of the spermathecae is an attribute shared synapomorphically by all Podotremata, though the length of the suture 7/8 is taxa-dependent (Gordon, 1950: 251; Guinot and Tavares, 2001: 523, fig. 10; Guinot and Quenette, in press). The intersegmental phragma 7/8 modified to form the spermathecal bulb is another shared apomorphy exclusive of the Podotremata, while the spermathecal chamber also exist elsewhere (Secretan-Rey, 2002). Gordon (1950: 251) had already surmised the uniqueness of the female posterior axial skeleton: "...the Dromiacea [Podotremata] are unique in possessing the special modifications [spermathecal bulb and chamber] in the female endophragmal system and sternum...".

Additionally the intersegmental phragma 7/8 gives rise to a hollowed calcified low tube (figure 3 E-F), which provides communication between the spermathecal bulb and chamber,

and the spermathecal openings (Gordon, 1950: 248, fig. 24 B; Tavares, 1994: 217, fig. 37 C-D; Guinot and Quenette, in press). Guinot and Quenette (in press) showed, however, that the hollowed tube actually has a much more restrict level of generality (Nelson, 1978; Wiley, 1981: 126) as it is shared by the Homolodromiidae, Dromiinae, Hypoconchinae, and the genus *Frodromia* McLay, 1993 only, being absent from the remaining Podotremata including the Dynomenidae and Sphaerodromiinae.

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