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PHYLOGENY AND EVOLUTION OF CRUSTACEA

# IV

# On the Relationship of Dromiacea, Tymolinae and Raninidae to the Brachyura

## By

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In 1950 I described in some detail the spermathecae of females belonging to species of the families Dromiidae and Thelxiopidae (= Homolidae), and showed how the male intromittent organs were adapted to suit these two kinds of spermathecae. I did not at that time discuss the relationship of the Dromiacea to the brachyuran crabs, because it was my intention to continue the study of other crab-like forms that are often referred to the Brachyura. This work, however, was delayed, partly because of other commitments, partly for lack of certain essential material. As mentioned by Balss (1957, p. 1616), I found in the Raninidae a special kind of unpaired female spermathecal opening or pit, quite different from the paired ones of Dromiidae or Thelxiopidae. Quite recently I obtained some material of the so-called Tymolinae which enabled me to examine the sternal furrows in the female, structures that are absent in females of the supposedly related subfamily Dorippinae. I hope ere long to publish a detailed account of these spermathecae; here I can only deal with some of them briefly.

# TYMOLINAE

In Figure 10A the thoracic sternum of a female of Tymolus japonicus Stimpson is represented, tilted so that the almost vertical posterior sternites are seen. In true ventral aspect, most of the sternum behind the ridges (r) on sternites 5 is not visible. In the tilted position, however, the sternal furrows are obvious; they resemble rather closely those of the family Dromiidae. But the large spermatophores, or spermatophoral masses, visible through the thin sternal wall, are situated near the spermathecal openings (Fig. 10A, f, o and s). As in Dromia, these sternal furrows in the female are just the 7/8 sutures carried forwards and anteriorly modified; the papillae on which the spermathecal openings are placed are situated on a level with the sockets for peraeopods 2 and thus well in front of the genital openings on the coxae of peraeopods 3. In this tilted position, the coxae of peraeopods 4 and 5 are also visible (Fig. 10A, p4 and p5). I have been able to confirm the presence of very similar sternal furrows in the now fragmentary female syntype of Xeinostoma eucheir Stebbing. In the genus

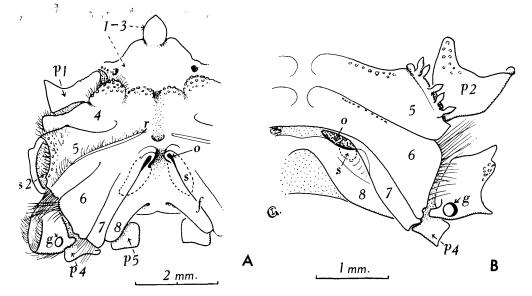


FIG. 10. A. *Tymolus japonicus* Stimpson,  $\mathcal{Q}$  from Manazuru, Japan; thoracic sternites tilted to show the almost vertical posterior ones and the sternal furrow (f) ending distally in the spermathecal opening (o). B. *Cymonomus granulatus* Norman, left thoracic sternites of  $\mathcal{Q}$ , slightly tilted, to show oval area (o) at the spermathecal opening. Abbreviations: 1-8, thoracic sternites; g, genital opening on coxa of peraeopod 3; r, ridge on sternite 5; p1-p5, coxae of peraeopods 1 to 5; s2, socket for peraeopod 2; s, indicates position of the spermatophore.

Cymonomus, on the other hand, the thoracic sternum is bent much less abruptly than in Tymolus and the large oval areas that indicate the spermathecal openings are visible in ventral aspect. In Figure 10B, however, the specimen is tilted so that sternites 7 and 8 are seen more completely. Here the 6/7 suture runs across the full width of the thorax; thus the 7/8suture is shorter than in Tymolus, ending opposite the coxa of peraeopod 3, but still in front of the genital opening on that coxa. Only the distal half of the 7/8suture forms the spermatheca, the position of which is indicated by a distinct bulge on sternite 8; the sutural margin of sternite 8 overlaps that of sternite 7, as shown in Figure 10B. The spindle shaped area (o) presumably belongs to sternite 7 and the entrance to the spermatheca is along its posterior edge. The

position of the relatively small spermatophoral mass is indicated by a broken line (s, Fig. 10B). This type of spermatheca is reminiscent of that found in the Thelxiopidae.

There seem to be, within the so-called Tymolinae, two different kinds of spermathecae. When the intromittent organs of the male are examined (Figs. 11A and 11B), they differ chiefly as regards the apex of pleopod 2. In Cymonomus and in Tymolus there is a large penial projection on the coxa of peraeopod 5; the terminal segment of pleopod 1 (= the endopod) is a hollow, folded, leaf-like structure; pleopod 2 is large in both. But the apex of the last segment (= the endopod) resembles a hypodermic needle in Tymolus (2a, Fig. 11A); in Cymonomus it is like the sole of a boot (apex of 2, Fig. 11B). In Tymolus only the needle-like tip of

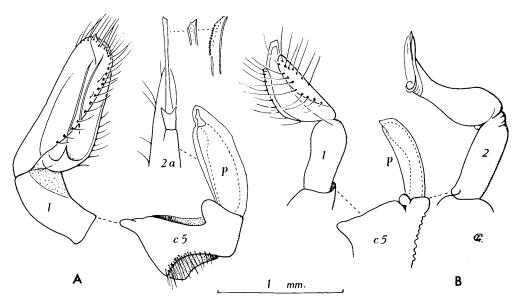


FIG. 11. Intromittent organs of 3 of: A. *Tymolus japonicus* Stimpson and B. *Cymonomus granulatus* Norman. Abbreviations: 1, pleopod 1; 2, pleopod 2; 2a, apical part of pleopod 2; c5, coxa of peraeopod 5; p, penis.

pleopod 2 probably enters the small opening of the female spermatheca and the seminal fluid is probably poured into the spermathecal sac. In *Cymonomus*, pleopod 2 probably acts as a sort of piston, the "sole" pushing aside the spindle-like flap to place a spermatophore in the spermathecal pocket. At least that is how I interpret these structures. This fits in nicely with Ihle's subdivision of the "Tymolinae" into two tribes Cyclodorippae and Cymonomae (Ihle, 1916, p. 154). Since *Cyclodorippe* is a synonym of *Tymolus* the tribe should be called Tymolae.

# RANINIDAE

In the Raninidae the thoracic sternites are specially modified, presumably in connection with their burrowing habits. Figure 12A represents the thoracic sternites of a very immature female of *Ranina ranina* (L.), carapace length 63 mm. Owing to the fact that the sternum bends abruptly

upwards, at an angle of nearly  $90^{\circ}$ , in the region of the genital or sixth somite, the posterior part is foreshortened. Sternites 8 are not visible because the last pair of peraeopods are dorsal and somewhat anterior to peraeopods 4. The separate figure of sternites 7, at the same scale, gives a better idea of their length although the portion behind the articulation of peraeopods 4 is still foreshortened. Even at this immature stage sternites 7 can be distinguished from those of a male because of the median depression in the anterior half, which indicates an incipient spermathecal opening. In the adult female this single spermathecal pit is very conspicuous (Fig. 12B). It is situated in the anterior half of sternites 7 behind the small genital openings on the coxae of peraeopods 3.

The single spermathecal opening is even more conspicuous in the much smaller species *Notopoides latus* Henderson (Fig.

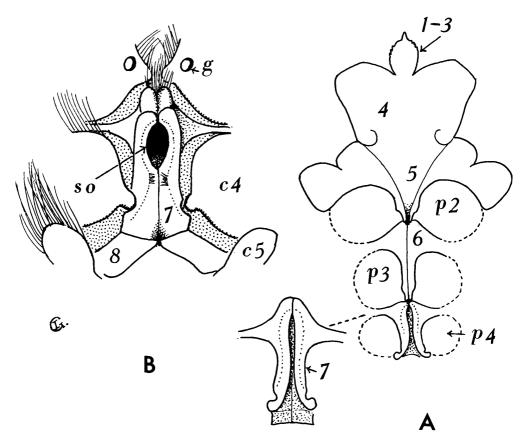


FIG. 12. Ranina ranina (L.),  $\Im$ . A. Thoracic sternum of a very immature specimen (carapace length = 63 mm.). B. Thoracic sternites 7 and 8 of an adult (carapace length = 138 mm.), to show the large spermathecal opening (so). Abbreviations: 1-8, thoracic sternites 1 to 8; c4, c5, coxae of peraeopods 4 and 5;  $p^{2}-p^{4}$ , sockets for peraeopods 2 to 4; g, genital opening on third coxa.

13A). On dissection, I found that the spermathecal pit leads obliquely backwards and inwards to a spermathecal pocket (s) enclosed in part of the endophragmal skeleton. The endophragmal system of a raninid differs strikingly from that of a typical brachyuran crab such as *Maja squinado* (Herbst)—compare Figures 13B and 14B. One of the peculiarities of *Notopoides* is the very high median apodeme arising from the median suture of sternites 6 and 7, respectively. In a male of *Notopoides* the apodeme

arising from sternites 7 is similar to that arising from sternites 6 (see Bourne, 1922, pl. 4, fig. 9 of *Ranina*); in the female, however, part of apodeme 7m is modified to form the spermathecal pocket and the passage leading to it (*s*, *so*, Fig. 13B). The male intromittent organs are also modified in a special way, pleopods 1 being fused basally and the free portions being relatively slender and closely apposed so that both can enter the single spermathecal opening.

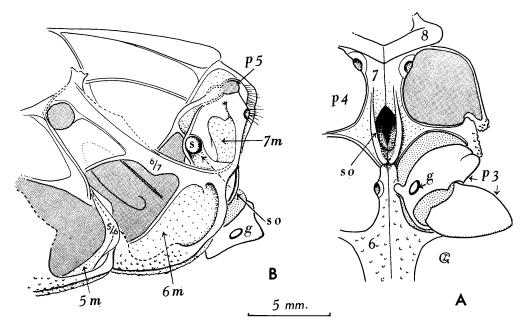


FIG. 13. Notopoides latus Henderson,  $\varphi$  syntype. A. Posterior almost vertical portion of thoracic sternum, to show the large spermathecal opening (so) on sternites 7. B. Posterior part of endophragmal system of same, in median aspect. Abbreviations: g, genital opening of coxa on peraeopod 3; p4, p5, sockets for peraeopods 4 and 5; 5m-7m, median apodeme from sternites 5 to 7; s, spermathecal pocket.

## BRACHYURA

Maja squinado (Herbst): This common spider-crab may be taken as an example of a typical brachyuran crab. The endophragmal system has been described and figured by Drach (1939, pp. 369-373). The thoracic sternites of the female are much broader than those of the male and all are visible in ventral aspect (Fig. 14A). The genital opening is sternal, situated on sternite 6 just behind the 5/6suture line. The posterior part of the endophragmal system of the same female is represented in median aspect in Figure 14B. The sella turcica or turkish saddle (ts) with its wing-like extension (w), and the way in which the five posterior endopleurites above and the four posterior endosternites below (4/5-7/8) are all

conjoined, give great strength to the whole. The vagina lies in the space between endosternites 5/6 and 6/7 but it and its spermathecal portion (s) are quite free, not incorporated in any part of the endoskeleton.

#### DISCUSSION

The division of one family Dorippidae into "Dorippidae sternitremen" (Dorip-"Dorippidae peditremen" pinae) and has always seemed odd (Tymolinae) to me. Because, if the Decapoda are all the Natantia taken as a whole,<sup>1</sup> Reptantia and many of the are "peditremen" (with genital opening coxal in the female). It is only in the Brachyura

<sup>&</sup>lt;sup>1</sup> The classification in Balss (1957) may be taken as the latest, though Balss was ultra conservative in places.

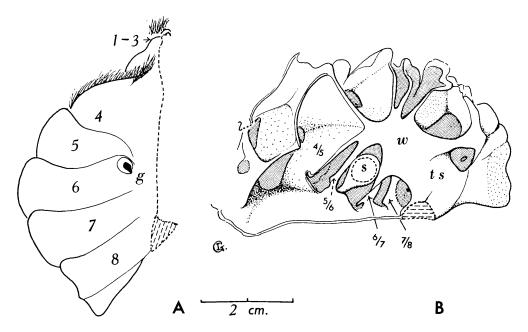


FIG. 14. Maja squinado (Herbst),  $\mathcal{Q}$ . A. Right thoracic sternites 1 to 8, with genital opening (g) on sixth sternite. B. Posterior part of endophragmal system of same, in median aspect. Abbreviations: 4/5-7/8, endosternites 4 to 7 arising from the sutures between the sternites indicated; s, spermathecal part of vagina; ts, sella turcica; w, wing of sella turcica.

that a few families and subfamilies are "peditremen," all the rest being "sternitremen," with the female genital opening sternal. The "peditremen" forms among the Brachyura are the Dromiacea, the Raninidae and the Tymolinae, and, as I have shown, it is these that possess various kinds of spermathecae in the formation of which the endophragmal system is involved. To me it seems logical to exclude all these from the true Brachyura, restricting the term to the vast majority of crabs with the female genital openings sternal (the "Decapoda sternitremen"). In 1922 Bourne made a careful study of various raninids and separated them from the Oxystomata, placing them in the new superfamily Gymnopleura. Previous workers like Boas, and Milne Edwards and Bouvier also thought the raninids were

not related to the Oxystomata. The discovery of a special, unpaired spermathecal pit leading to a spermathecal pocket in the endophragmal system, together with the specialisation of the male pleopods, fully supports Bourne's conclusion and justifies the term Gymnopleura. I do not know why Bourne missed the conspicuous spermathecal pit, but the abdomen and the pleopods have to be turned right back in order to see it. He happened to dissect a male *Ranina* for the endophragmal system (Bourne, 1922, pl. 4, fig. 9).

Certainly the so-called Tymolinae with sternal furrows and coxal genital pores should not be placed in the same family as the dorippids without sternal furrows and with the genital openings of the female sternal. The tymolids should at least be placed in a separate family, Tymolidae;

their true place in the classification is with or near the Dromiacea. All the females of Tymolidae that I have examined have been in poor condition and the endophragmal system is either poorly or not at all calcified, at least in the region of the spermathecae. The internal structure of the spermathecae has been studied as far as the imperfect condition of the material allowed, and will be described more fully elsewhere. If the "Tymolinae" are given family rank, then Ihle's two tribes become the subfamilies Tymolinae and Cymonominae. If the term Brachyura is restricted to the eminently successful "Decapoda sternitremen" and the Dromiacea, Gymnopleura and Tymolidae placed where they belong in the "Decapoda peditremen," the term Anomura will probably have to be abandoned. At present it is in Monod's words simply a "rag bag" into which is thrown an assortment of superfamilies and families that do not fit in anywhere else. Our knowledge of the endophragmal system of the Decapoda is still fragmentary and imperfect. Drach (1950) has pointed out that it is present in the Decapoda Natantia, contrary to what is generally supposed. He also thinks that

the Eryonidea should be excluded from the Palinura because their endophragmal system proves to be of a different kind, much more primitive. He also says that the homolids (Thelxiopidae), homolodromiids and "certain raninids" differ as regards endophragmal system from the rest of the Brachyura. Much work has still to be done before we can arrive at a satisfactory classification of the Decapoda.

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