Crab zoeae and brachyuran classification: a re-appraisal

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Introduction

In a recent paper (Rice, 1980a) I reviewed the available information on crab zoeal morphology and attempted to assess its bearing on the classification of the Brachyura. Although zoeal evidence had already been employed several times to try to elucidate specific problems of crab relationships, there had been no previous attempt to relate a general classification based on the larval stages to that based on the adults. The reasoning behind the study was founded on the hope that since the zoeal stages are all adapted for a mid-water existence any classification based on them would be largely free from the problems associated with the convergent and divergent adaptations of the adults to their varied life styles. Using a variety of zoeal features, including details of the appendage setation, I was able to demonstrate, at least to my own satisfaction, a high degree of agreement with the traditional adult classification at the family level, but much less congruence at higher levels. For example, the zoeal stages of the constituent families of the Oxystomata are so distinct from one another that they confirm the doubts about the validity of this grouping which have been expressed by several students of adult crabs. Not only are there no zoeal grounds for grouping the dorippids, leucosiids and calappids together, but there is no support for their separation, either collectively or individually, from the Brachyrhyncha. Similarly, the clear differences between the zoeae of the parthenopids, hymenosomatids and majids argue strongly against their inclusion in a separate oxyrhynchous group, for the former two families, like the oxystomes, clearly seem to belong to the Brachyrhyncha. The majids, on the other hand, did seem to warrant separation from the majority of crabs, for their zoeae exhibit a number of distinctive features which indicate an early divergence and the adoption of a different developmental strategy from that of the rest of the Brachyura.

In dividing up the Brachyrhyncha the zoeal stages seemed to be much less helpful. Only two major groups were recognized; first a collection of families with relatively primitive larvae corresponding roughly with Milne Edwards' Cyclometopa or Guinot's (1978) Heterotremata, and a second group with more advanced larvae which corresponds fairly closely with Milne Edwards' Catometopa or Guinot's Thoracotremata. Such a division, however, seemed to be very artificial since it grouped the families according to their general evolutionary level rather than into phylogenetic lineages. Moreover, there were some important discrepancies between the larval divisions and those suggested by Guinot based on the morphology of the sexual organs in the adults. In particular, the Leucosiidae, which Guinot placed in her Heterotremata because at least some members of this family have coxal male sexual openings, have very advanced zoeal stages which seemed to ally them to the catometopous families which Guinot placed in her Thoracotremata.

During recent months the debate on brachyuran relationships has progressed somewhat, for in two most interesting notes Saint-Laurent (1980a & b) has generally supported Guinot's division of the Brachyura into the Podotremata, Heterotremata and Thoracotremata, but has disagreed fundamentally in her interpretation of the relationships between them.

The main diagnostic differences between Guinot's suggested groups are the positions of the male and female sexual openings: in the Podotremata both the male and female openings are coxal; in the Heterotremata the female openings are all sternal, but at least some species in

Bull. Br. Mus. nat. Hist. (Zool.) **40** (5) : 287–296

Issued 30 July 1981

each family have the male openings on the coxa; in the Thoracotremata both the male and female openings are consistently sternal. Guinot suggested that during brachyuran evolution there has been a strong tendency for the sexual openings to move from the primitive decapodan coxal position onto the sternum and that her three sections therefore represent successive stages in this migration.

Saint-Laurent, on the other hand, sees great difficulty in deriving these groups from one another. She points out (1980a, p. 1266) that the female genital apparatus in the Podotremata is comparable with that in many other decapodan groups in which the spermatophores are deposited with the aid of the male sexual pleopods into a receptacle, the thelycum, formed from an intersegmentary fold of the integument and without any connection with the oviducts. Fertilization in these forms is external and takes place after egg-laying. Within the Sternitremen crabs (that is the Heterotremata and Thoracotremata together, or the Eubrachyura in Saint-Laurent's terminology) the spermatic mass is deposited, again via the sexual pleopods, in an internal seminal chamber formed by a dilation of the oviduct, within which fertilization takes place. Saint-Laurent finds it difficult to envisage the intermediate stages between one situation and the other involving, as it would, not only the loss of the thelycum but also a change in the orientation of the male sexual pleopods from the thelycum towards the oviducts. Instead, she suggests that the separation between the Podotremata, on the one hand, and the Heterotremata and Thoracotremata, on the other, is cladistic and not simply a difference of evolutionary level. Whether the Eubrachyura were derived from ancestors with or without a thelycum, Saint-Laurent concludes that they represent an independent branch which became separated at an early stage from the primitive brachyuran line.

Similarly, Saint-Laurent believes that the distinction between the coxal and sternal position of the male orifice is a fundamental one, indicating that the Heterotremata and Thoracotremata diverged at a very early stage in brachyuran evolution (see Fig. 1). She redefines the Heterotremata as eubrachyurans in which the male genital ducts always pass via the coxae of the fifth legs before opening to the exterior, either on the coxa itself or on the sternum. In the Thoracotremata the ducts always open to the exterior directly through the sternum without passing via the coxae. Guinot had suggested that some heterotrematous groups, such as the Goneplacidae and Leucosiidae, in which the male orifices are, in her terms, sometimes coxo-sternal, represent an intermediate stage towards the thoraco-trematous condition. Saint-Laurent, on the other hand, sees these groups as being truly heterotrematous since the male orifice only *appears* to be sternal because the tubular pro-longation of the male duct, that is the penis, becomes encapsulated after it leaves the coxa within an integumentary canal at the boundary between sternites seven and eight, to emerge finally in a sternal position. The tendency of the male orifices to move towards the mid-line in both the Heterotremata and the Thoracotremata is seen by Saint-Laurent as a response to the relative narrowing of the anterior abdominal somites compared with the posterior cephalothorax, and the need to bring the orifices close to the bases of the sexual pleopods to ensure successful sperm transer. But she considers the mechanisms by which this has been achieved in the two groups as totally distinct.

Consequently, Saint-Laurent's view of brachyuran phylogeny (see Fig. 1) is rather different from that put forward by most authors in the past and implied by Guinot. For while most authors have derived the higher Brachyura from within the Podotremata, Saint-Laurent does not identify ancestors for either the podotrematous groups or the Eubrachyura, but she suggests that they diverged at a very early stage. Similarly, although she indicates that the Heterotremata and the Thoracotremata had a common ancestor, she maintains that the Heterotremata diverged very early on, possibly via more than one line, and that the ancestors of the Thoracotremata are not to be found amongst the extant Heterotremata or their immediate predecessors. Finally, she suggests that the assumption of the thoracotrematous condition, in which the posterior thoracic appendages are freed from any involvement in reproduction, may have allowed the development of highly perfected locomotory mechanisms and enabled this group to colonize a variety of terrestrial habitats.
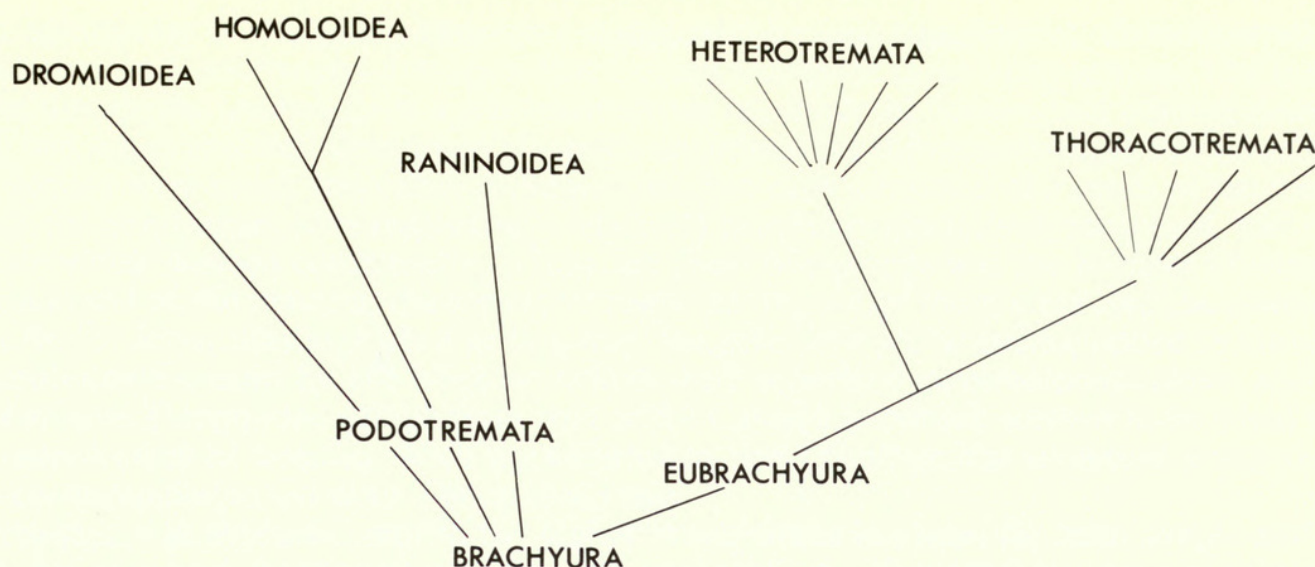
Fig. 1 Summary of the phylogenetic relationships of the main brachyuran groups according to Saint-Laurent (modified from Saint-Laurent 1980*b*).

The publication of this new approach to brachyuran phylogenetics has prompted me to re-examine the zoeal evidence for crab inter-relationships and, in a later publication, to consider also the megalopa stage.

PODOTREMATA

Guinot's Podotremata contains the dromiids, homolids, raninids and tymolids, the last three groups being placed together in the subsection Archaeobrachyura.

After discussing the zoeal evidence at some length (Rice, 1980*a*, p. 289 *et seq*.) I supported Williamson's (1965, 1976) view that the Dromioidea are more closely related to some of the anomuran groups than to the brachyurans and should accordingly not be included in the latter. This conclusion was based on a number of generally anomuran features of dromioid zoeae, but particularly on the presence of the hair-like second telson seta in all known dromiid zoeae, and in the anomurans and thalassinids, but its absence from all higher brachyurans. Knowledge of dromioid larvae was at that time limited to those of the Dromiidae, and Williamson (1976, p. 407) had suggested that larvae of the families Homolodromiidae and Dynomenidae might be much more homolid (that is brachyuran). No homolodromiid larvae have yet been described, but an examination of the late embryos of the dynomenid *Acanthodromia erinacea* H. Milne Edwards (Rice, in press) has demonstrated that the zoea is very similar to known dromiids, including the presence of a hair-like second seta. Thus, there is still no larval evidence of a more brachyuran branch of the Dromioidea and I therefore remain convinced that they should not be included within the Brachyura.

In establishing her Archaeobrachyura, Guinot (1978) recognized that it was not a natural group since, she maintained (p. 232), 'ils comportent à la fois des espèces primitives, qui sont sans doute à l'origine des autres sections (les "vrais Crabes"), et des espèces apomorphes avec des caractéristiques spéciales aux trois super-familles.' From the zoeal evidence I also concluded that this grouping is not natural in the strictly cladistic sense since I believed that the raninids became separated from the primitive brachyuran line at a later stage than that which gave rise to the ancestral lineage of the extant homolids. Thus, I suggested (Rice, 1980*a*, Fig. 9) that the raninids and the higher brachyurans share a more recent common ancestor than either group does with the homolids. I nevertheless felt that the archae-obrachyuran concept is a useful one since it indicates that although the higher crabs originated from an ancestor within it, they have attained a significantly higher evolutionary

HOMOLOIDEA   RANINOIDEA   EUBRACHYURA

A
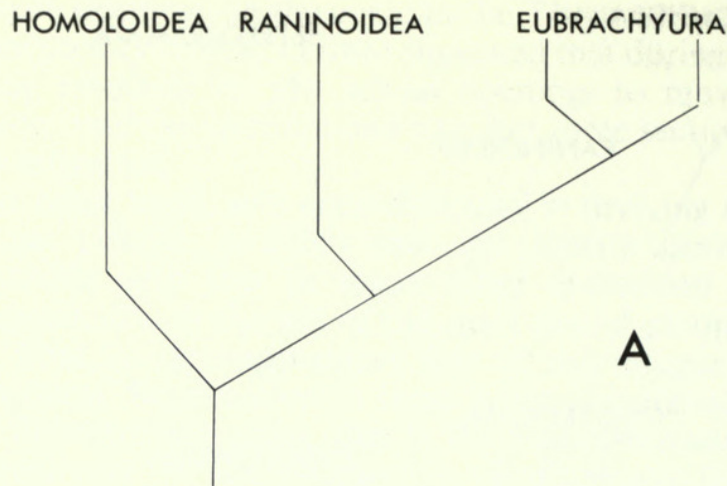
HOMOLOIDEA   RANINOIDEA   EUBRACHYURA
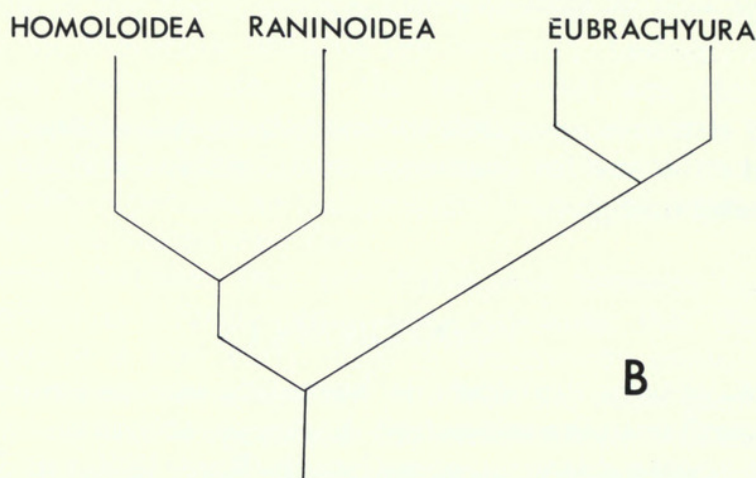
B

Fig. 2 Alternative phylograms showing the relationships of the homolids, raninids and eubrachyurans (see text).

level so that their separation from the raninids in terms of evolutionary change is much greater than that between the homolids and raninids.

Saint-Laurent did not give details of her opinion of the origin of the brachyuran groups. However, since she considers the divergence between the Podotremata and the Eubrachyura to be cladistic, she would presumably favour a phylogram for the homolids, raninids and eubrachyurans like Fig. 2B rather than 2A, that is with the homolids and raninids having a more recent common ancestor than the raninids and the eubrachyurans. It seems to me that the apomorphic characters shared by the zoeae of the raninids and the Eubrachyura, but not by the homolids, argue strongly against this and I would therefore still contend that the homolids became separated from the primitive brachyuran line at an earlier stage than the raninids.

EUBRACHYURA (HETEROTREMATA & THORACOTREMATA)

Guinot's Heterotremata consists of the superfamilies Dorippoidea, Calappoidea, Corystoidea, Portunoidea, Xanthoidea, Majoidea, Parthenopoidea, Bellioidea and Leucosioidea. It therefore corresponds to Milne Edwards' Cyclometopa with the addition of the dorippids (excluding the tymolids), the calappids and the leucosiids from the Oxystomata, and the majids and parthenopids from the Oxyrhyncha. The Thoracotremata contains all the remaining higher crabs and therefore corresponds to Milne Edwards' Catometopa with the addition of the hymenosomatids.

In attempting to categorize the zoeal stages, and having, like Guinot, dismembered the oxystomes and oxyrhynchs, I thought that I could recognize three main groups. The first of these, the majids, seemed to be a well-defined one in which the zoeal phase is abbreviated to only two stages and well-developed pleopods are present in the second stage. The remaining two groups were much less easily distinguished, but each consisted of a series of families in which the zoeal stages were respectively relatively primitive or relatively advanced. The only feature which seemed consistently to separate these two groups was the number of setae on the endopod of the maxilla, the primitive zoeae having six or more setae and the advanced ones five or fewer. Distinguished in this way, the primitive group corresponded to Guinot's Heterotremata except for the Majidae, which were separated as mentioned above, and the Leucosiidae, Dorippidae and perhaps part of the Calappidae which seemed to be allied with the more advanced families. With the addition of these families, the advanced group therefore corresponded to Guinot's Thoracotremata.

I realized that evolution within the higher brachyurans has been far from simple and has probably involved many separate lines. Nevertheless, the apparent existence of these two large groups of crabs with seemingly primitive and advanced zoeae respectively, together with Guinot's recently published thesis, encouraged me to hope that phylogenetic lines might be discernible from one group to the other. In fact, this hope was not realized, for although I was able tentatively to identify some possible phylogenetic lines within the primitive zoeal groups, I was unable to extend these into the more advanced families because many of them seemed to have a confusing mixture of advanced and primitive features which precluded their derivation from any of the extant groups with generally more primitive zoeae.

Adopting the view of eubrachyuran phylogeny suggested by Saint-Laurent, many of these difficulties disappear. For according to this view the Heterotremata and Thoracotremata should be considered as quite distinct taxa with no phylogenetic links between them. On the other hand, this approach poses new problems, for although the zoeae of the Heterotremata are certainly generally more primitive than those of the Thoracotremata, there is much more overlap than I had thought. The distinction between the two groups based on the setation of the endopod of the zoeal maxilla is clearly invalid, for the leucosiids and dorippids are simply highly evolved Heterotremata in which the zoeal morphology has advanced beyond the general level for this group and in a number of features, including the maxilla setation, has approached the thoracotrematous condition. The same is true of the most advanced majids, but in this case a single family, if indeed it is to be regarded as such, contains a whole range of zoeal forms from the relatively primitive oregoninids to the very advanced inachinids.

Having eliminated the maxillary endopod setation as a distinction between the heterotrematous and thoracotrematous zoeae, I can find no other single feature or combination of features which will consistently separate the two groups. This seems rather surprising if, as Saint-Laurent has suggested, the Heterotremata and Thoracotremata have had separate evolutionary histories from a very early stage. However, the key difference between the two groups, that is whether or not the coxae of the fifth legs are involved with the male reproductive apparatus, would not directly affect the larval stages at all. For although this difference may have resulted in the adults evolving along very diverse adaptive lines, the Heterotremata retaining the benthic habit or becoming at least partly pelagic while several of the thoracotrematous groups have invaded the terrestrial environment, the zoeal stages of both groups have retained the primitive planktonic dispersive role. Under these circumstances, while the selective pressures operating on the adults might be expected to cause the two groups to diverge in features not directly related to the primary distinction between them, adaptation by their larval stages to the same life-style would presumably result in convergence.

Assuming that my interpretation of primitive and advanced zoeal characters is correct (Rice, 1980a, p. 299 et seq.), such convergence indeed seems to have occurred. Thus, although the most primitive zoeae of the Thoracotremata have a much simpler appendage

setation than most zoeae of the Heterotremata, the same trends are apparent in both groups. In both cases the armature of the carapace and abdomen tends to become reduced, the separation of the sixth abdominal somite from the telson tends to become delayed, the setation of the cephalic appendages tends to become simplified, and there is some fusion of segments, particularly of the endopods of the maxillule and the third maxilliped. As a result of these trends, both sections of the Eubrachyura contain families with at least some representatives having zoeae in which some or all of the carapace spines are absent, the antennae are greatly reduced, the setation of the endopods of the maxillule and maxilla are greatly simplified, the segments of the endopod of the third maxilliped are partly fused and the sixth abdominal somite is fused with the telson throughout the zoeal phase. These conditions are found in the Leucosiidae amongst the Heterotremata and the Pinnotheridae amongst the Thoracotremata, producing a general resemblance between the two which led me to believe that they are closely related (Rice, 1980b). The same trends are apparent in a rather less extreme form in the advanced spider crabs (Inachinae) and the Dorippidae amongst the Heterotremata, and in the Hymenosomatidae amongst the Thoracotremata.

However, apart from the advanced features which they share, these groups are all very distinct, four of them, for instance, having the most characteristic telson structures of any of the brachyurans, quite different both from each other and from those found in any other families. They each appear to represent the end point of a different phylogenetic line and suggest that the evolution of each of the sections of the Eubrachyura has involved several of these lines, though not all of them, perhaps, have produced such advanced zoeae. Using only the zoeal characters, in my earlier paper I attempted to trace these lineages amongst the forms which I then considered to be the cyclometopous families, that is the Heterotremata excluding the Leucosiidae and the Dorippidae. Although the philosophy behind this attempt was incorrect in that I hoped to be able to extend the lines into the more advanced zoeal groups, the general conclusions, summarized here in somewhat simplified form in Fig. 3, are still probably valid.

From an ancestral form with a zoea similar to the most primitive of the extant xanthids, two major lines are envisaged, one leading to the Portunidae and Geryonidae and thence to the Parthenopidae, and the other to the Corystidae, Cancridae and part of the Atelecyclidae (that is the Corystoidea of Guinot) possibly via the Calappidae. A third major line, comprising the Majidae, is suggested as having separated from the ancestral stock at a level preceding that represented by the most primitive extant xanthids.

Apart from the Leucosiidae and the Dorippidae, these three major lines together account for most of the Heterotremata. However, several groups of known zoeae do not fit readily into this simple pattern and indicate the existence of a number of subsidiary evolutionary lines. First, anagenesis in several families has resulted in sub-families with zoeal features which suggest that they are offshoots from the main lines. This seems to be true of the Carcininae and Portuninae within the Portunidae, and of the Pilumninae and Xanthinae within the Xanthidae. Within the Cancridae, two distinctly different types of larvae are found in the single genus *Cancer* and, according to the criteria I applied, the Corystidae could have been derived only from the more primitive of these. Secondly, some whole families appear to represent short side-branches; the Geryonidae seem to be an off-shoot from a polybiinid ancestor, while the Goneplacidae seem to be very closely allied to the Pilumninae. Thirdly, some heterotrematous zoeae are so unusual that I can only assume that they represent separate, independent lines. One such group is the Bellidae, regarded as a subfamily of the Atelecyclidae by Balss (1957), but completely separated from the Corystoidea by several authors and given superfamily status by Guinot (1978). In my review I discussed only the larvae of *Corystoides* and *Heterozius,* for at that time I was unaware of the excellent descriptions of the larvae of *Acanthocyclus gayi* Milne Edwards and Lucas by Fagetti & Campodonico (1970) and *Acanthocyclus albatrossis* Rathbun by Campodonico & Guzman (1973). These zoeae resemble those of *Corystoides* in all essential details, including the very unusual setation of the endopod of the second maxilliped, and confirm the necessity of separating the group totally from the Atelecyclidae. Two other genera which
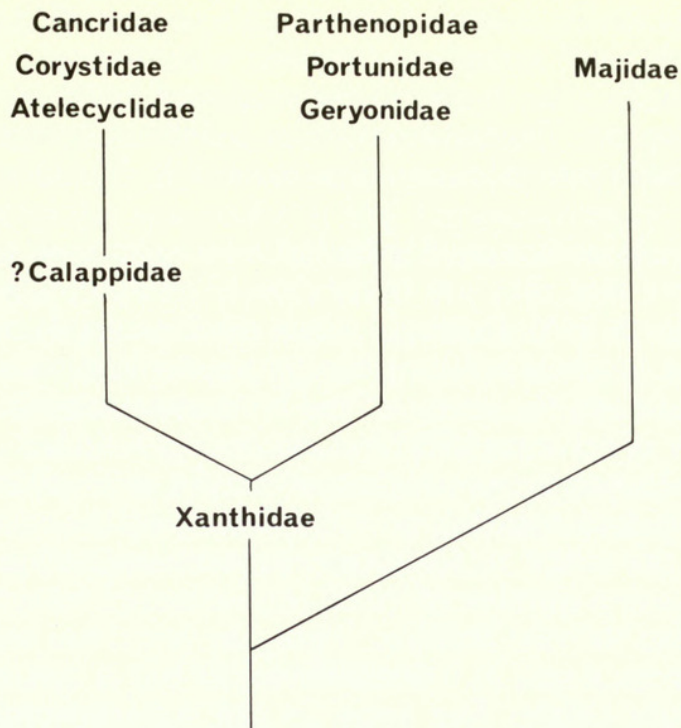
Cancridae   Parthenopidae

Corystidae   Portunidae   Majidae

Atelecyclidae   Geryonidae

? Calappidae

Xanthidae

Fig. 3   Main suggested phylogenetic lines within the Heterotremata.

have usually been placed in the Atelecyclidae, *Telmessus* and *Erimacrus,* also have some unusual zoeal features which seem to separate them quite clearly from the remainder of the Corystoidea, but do not obviously ally them with any other group. These features include the appearance of the 'exopod' seta on the maxillule in the first stage, the unusually large number of scaphognathite setae in this stage and the presence of lateral setae on the endopod of the first maxilliped. I was, and am, unable to say where these genera belong, but can only suggest that since some of their zoeal characters indicate that they may have abbreviated a longer ancestral series of zoeal stages, they may have evolved from close to the stock which gave rise to the majids by a similar change in developmental strategy. Finally, the zoeae of the monotypic genus *Orithyia* possess a combination of features quite unlike that of any other known crab. The genus was placed with some doubt in the Calappidae by Ihle (1918) while Guinot (1978) gave it separate family status in her Calappoidea. There is certainly no feature of the zoeae of *Orithyia* which would rule out the possibility of it being derived from the more primitive calappid zoeae such as those of *Calappa* or *Hepatus.* On the other hand, the two groups have little in common which would positively indicate such a relationship. Instead, as I pointed out in the earlier paper, *Orithyia* zoeae have a superficial resemblance to the dorippids in having very long spinulose dorsal and rostral carapace spines and extended telson forks. *Orithyia* and dorippid zoeae also share with the higher majids the rather unusual feature of only three medial setae on the basis of the second maxilliped, while the first zoeal stage in both *Orithyia* and in the spider crabs has rather more marginal setae on the scaphognathite than is usual in the Brachyura. I have linked this last character with the abbreviated development of the majids, and since *Orithyia* passes through only three zoeal stages the same may be true here. However, none of these features indicate any clear relationship for *Orithyia* and I am therefore quite unable to suggest where it belongs.

I am similarly unable to place the Leucosiidae and Dorippidae into this scheme. Their zoeae are generally much more advanced than those of most other heterotrematous families and their specialized features, particularly their telsons, indicate that they occupy rather isolated positions at the ends of heterotrematous evolutionary lines. Since dorippid zoeae consistently have three setae on the basal segment of the endopod of the first maxilliped they presumably could not have been derived from the portunid-parthenopid branch which have only two setae in this position. Otherwise, however, both dorippid and leucosiid zoeae could have evolved from those of any of the heterotrematous groups.

As noted above, in my earlier review I was unable to identify any possible phylogenetic lines within those brachyuran groups with relatively advanced zoeae. This was partly because I had expected to be able to extend the suggested heterotrematous lineages into the Thoracotremata. Treating the Thoracotremata as a distinct group, as I am here, it is still difficult to identify possible evolutionary lines within it, but some general points can be made.

First, the Hymenosomatidae have a number of very advanced zoeal characters which in the past led me to believe that they are fairly closely related to the Pinnotheridae and the Leucosiidae (Rice, 1980a, p. 315). However, since the Leucosiidae are here considered to be advanced Heterotremata, a close relationship between them and the hymenosomatids is precluded. Similarly, although the zoeae of the Hymenosomatidae share with those of the Pinnotheridae a number of advanced features, including reduced carapace spines with the laterals, where present, close to the ventro-lateral margin, reduced antennal exopod, reduced setation of the maxillule and maxilla, and the failure of the sixth abdominal somite to become separated from the telson in all known hymenosomatids and several pinnotherids, the Hymenosomatidae have a number of much less advanced features which argue against a close relationship between the two families. Thus, the proximal segment of the endopod of the maxillule always carries a seta in hymenosomatids but is unarmed in pinnotherids, the endopod of the maxillule carries five setae in the hymenosomatids but only three in the pinnotherids, the endopod of the second maxilliped consists of three segments in the hymenosomatids but only two in the pinnotherids, and the basal segment of the endopod of the first maxilliped carries three setae in the hymenosomatids compared with two in the pinnotherids. In this last feature the Hymenosomatidae are unique amongst the Thoracotremata, suggesting that they could not have evolved from any of the extant groups. On the other hand, hymenosomatids have several very specialized features, particularly the reduced coxal endite on the maxilla, the failure to develop pleopods during the zoeal phase and a total absence of a megalopa stage, which indicate that they could not have been ancestral to any of the other extant groups either. I assume, therefore, that the hymeno-somatids are the sole extant representatives of a thoracotrematous evolutionary line which separated from the remainder at a very early stage.

Like the Hymenosomatidae, the advanced Pinnotheridae have a number of specialized zoeal features, particularly the very characteristic telson, which suggest that no other extant group could have evolved from them. Moreover, all pinnotherid zoeae have the antennal exopod vestigial or absent, the basal segment of the endopod of the maxillule unarmed, only three setae on the endopod of the maxilla, and the endopod of the second maxilliped consisting of only two segments, the proximal being unarmed*. This combination of characters is more advanced than that of any thoracotrematous group and is approached only by the Ocypodinae in which, however, the antennal exopod is rarely rudimentary and the endopod of the second maxilliped always consists of three distinct segments. This resemblance does not, of course, necessarily indicate a close relationship, for there are considerable differences between ocypodinid and pinnotherid zoeae. Nevertheless, the appendage setation is so similar in the two groups that it seems likely that they both evolved from the same, or closely related, ancestors.

The zoeae of the other ocypodid sub-families, that is the Macrophthalminae and the Scopimerinae, are both somewhat less advanced than those of the Ocypodinae. While either of these more primitive sub-families could have given rise to the Ocypodinae, neither of them could apparently have evolved from the other (see Rice, 1980a, p. 344). Either or both of them must therefore be off the postulated line which led to the Ocypodinae and thence to the Pinnotheridae.

A similar situation exists in the Grapsidae from which the Ocypodidae were possibly derived. Here, the subfamily Grapsinae contains the most advanced zoeae, derivable from any of the other sub-families. But the Sesarminae, Plagusinae and Varuninae each have

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*When preparing the general review (Rice, 1980a) I was unaware of the description of the larvae of *Pinnixa rathbuni* Sakai by Sekiguchi (1978).

different combinations of advanced and primitive characters which suggest that they each represent a different evolutionary line within the family (see Rice, 1980*a*, p. 340).

Finally, the zoeae of the Gecarcinidae seem to be at an evolutionary level comparable with, or slightly below that of the less advanced sub-families of the Grapsidae and are therefore the most primitive of the known thoracotrematous forms. This does not mean that the gecarcinids are ancestral to the remainder of the Thoracotremata, but it certainly suggests that they separated from the other evolutionary lines before the zoeae of the latter had attained their present forms.

These suggested relationships between the zoeae of the Thoracotremata are far too vague to be formalized into any kind of phylogenetic diagram, even one as tentative as that produced above for the Heterotremata. Nevertheless, they do indicate relative evolutionary levels which may be useful in support of evidence from adult morphology and palaeontology. They also provide a framework to be strengthened or changed as each new piece of larval evidence is obtained, for like all larval studies, they are based on data from only a small proportion of the species known as adults.

Conclusion

Brachyuran zoeae can provide valuable insights into crab relationships at a variety of taxonomic levels. Since they are all adapted for a relatively similar pelagic existence rather than the very varied environments occupied by the adults stages, they may help to separate groups which have been classified together because of a superficial resemblance between the adults caused by convergence. At the highest level this is the case, for instance, of the Oxystomata and the Oxyrhyncha, while at a lower level the example of the Atelecyclidae sensu Balss (1957) might be cited.

However, assuming that Saint-Laurent is correct in her interpretation of the Heterotremata and Thoracotremata as having had quite distinct evolutionary histories, this re-examination of the zoeal data has convinced me of a potential danger in the uncritical use of larval information. For groupings based on the larvae, such as those which I thought were recognizable within the Eubrachyura, may be just as misleading as those based on the adults. A major divergence amongst the adult forms, such as the suggested one between the Heterotremata and the Thoracotremata, may not be reflected in the larval stages since parallel adaptation to the same pelagic life-style may cause the zoeae of advanced members of both branches to share apomorphous characters which have apparently been acquired independently, as in the Leucosiidae and the Pinnotheridae.

There remains the problem of explaining why the thoracotrematous zoeae are generally so much more advanced than those of most of the heterotrematous groups. One explanation might be that the early Thoracotremata, which presumably had zoeae at more or less the same evolutionary level as those of the bulk of the Heterotremata, have left no extant representatives. But this rather begs the question since it does not explain why these forms should have disappeared while the primitive Heterotremata survived.

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