

With respect to the lateral carapacial carinae I, 10.8% (18/166) of the specimens have five teeth on both sides. Other aberrant conditions found in this species are that two specimens have 6 dorsal teeth and another specimen has four dorsal teeth on the carapace, and in one specimen there are four teeth on the lateral carapacial carina II of one side.

The specimens from Zanzibar reported by BALSS (1925) and CALMAN (1939) as "*P. andamanensis*" and "*P. bengalensis*" respectively seem to have fewer teeth on the lateral carapace and probably belong to the present species instead.

EVOLUTION

Morphology. — The 21 species in the present study appear to show a continuum in the morphological characters. The intermediate position of the species of *Aegaeon* between *Parapontocaris* and *Pontocaris* has long been noticed by many authors (eg. KEMP, 1916; DE MAN, 1920; CHACE, 1984). From *Parapontocaris* to *Pontocaris*, the similarities of the five species of *Aegaeon* to these two genera can probably be arranged in the order: *A. boschii*, *A. rathbuni*, *A. orientalis*, *A. lacazei* and *A. cataphractus*. The degree of development of the hepatic groove in these five species fits well with this order. At first glance it seems that the interruption by the hepatic groove caused the second anterior tooth of the lateral carapacial carina II to move upwards. However, the lateral carina II is likely to have been originally on the same level as the antennal spine as in *Parapontocaris* and *A. boschii*. It only later moved down to the level of the branchiostegal spine as in *Pontocaris* and *A. cataphractus*. Thus, the development of the hepatic groove actually caused the anteriormost tooth of lateral carina II to move gradually from the level of the antennal spine down to the branchiostegal spine, beginning in *A. rathbuni* (with only the anteriormost tooth moved very slightly downwards, the second anterior tooth without any deviation), more so in *A. orientalis*, and finally becoming level with the branchiostegal spine in *A. lacazei* and *A. cataphractus*. However, the second anterior tooth of lateral carina II is still directed towards the antennal spine, but is compressed by the hepatic groove and finally reduced to a tubercle, as in some *Pontocaris* species.

It appears likely that the enlarged branchiostegal spine in *Pontocaris* resulted from the fusion of this spine with the anteriormost tooth of the lateral carapacial carina III, as suggested by their corresponding positions in *A. lacazei* and *A. cataphractus*. Furthermore, the single tooth on the anterior part of lateral carina II in *A. cataphractus* was later split into two teeth, as in *Pontocaris*. Alternatively there is the possibility that the enlarged branchiostegal spine pushed the anteriormost teeth of lateral carinae III, and II backwards (i.e. of the two teeth on the anterior part of lateral carina II in *Pontocaris*, the anterior one originated on lateral carina III, the posterior one on lateral carina II). However, the positions and sizes of these teeth in the species of *Aegaeon* seem to lend more support to the former hypothesis. It is worth noting that the second anterior tooth of the lateral carina III is positioned slightly upward in *A. boschii*. However, it is highly unlikely that the two teeth on the anterior part of lateral carina II in *Pontocaris* both originated from the anterior teeth of lateral carina III, since no such upward movement is observed in any of the other four *Aegaeon* species. The enlargement of the branchiostegal spine pushed the lateral carina III closer to the ventral carapace and the spine eventually reached the level of the pterygostomial spine. On the other hand, the presence of only one tooth on the anterior part of the lateral carina II in some *Pontocaris* species is probably secondary, due to the degeneration of the second tooth, since the armature and sculpturing on the body of these species are generally less developed.

With respect to the number of spines on the posterior margin of abdominal pleuron V, there are two spines (distal one smaller) in *Parapontocaris*, but only one distal spine or sharp tubercle is present at most in *Pontocaris*. In *A. rathbuni* there are two subequal spines on the posterior margin of abdominal pleuron, while only the posterodistal spine is present in *A. orientalis*, *A. lacazei* and *A. cataphractus*. Only the posterobasal spine is distinct on abdominal pleuron V in the geographically isolated *A. boschii*.

It can be easily assumed that *Parapontocaris* is the oldest of the three genera (see also CHRISTOFFERSEN, 1988). Although crangonids are generally considered to be rather advanced among the carideans (e.g. ORTMANN, 1895), species of *Parapontocaris* still have pointed rostrums and the telsons bearing both dorsolateral and terminal spines.

Their slender body, narrow scaphocerite and abdominal sculpturing composed of only ridges and carinae are common to many other carideans. However, species of *Pontocaris* appear to possess many "advanced" characters, even though ORTMANN (1895) considered this genus to be the most primitive in the Crangonidae. Other than the modification of the pereopods in spawning females, which is probably unique in Caridea, the broadened and hardened body, the interlocked thoracic sternum and carapace, cleft rostrum, wing-like branchiostegal spine, widened scaphocerite, spineless telson and the lobular abdominal sculpturing of *Pontocaris* also differ from most carideans. The presence of distinct median spines on the abdominal sternites, and the ventral margins of the abdominal pleura being even sharper in spawning females of *Pontocaris*, are in contrast to the situation in most, if not all, other carideans. It is reasonable to believe that the above mentioned characteristics of *Pontocaris* are in a rather advance state, as some of them (such as the hard integument, interlocked thoracic sternum and carapace, broadened scaphocerite, enlarged branchiostegal spine, lobular abdominal sculpturing, spiny abdominal pleura and spineless telson) are also present in Glyphocrangonidae, which is generally supposed to be the most advanced caridean family [though CHRISTOFFERSEN (1987, 1988) suggested that the Glyphocrangonidae is older than the Crangonidae].

The characteristics of the species of *Aegaeon* are intermediate between those of *Parapontocaris* and *Pontocaris*. Therefore, there is little hesitation to assume that this genus forms a natural link between the other two genera. The tip of the rostrum is simple in *Parapontocaris* but reduced and finally lost, as shown by the tri- and bifurcate rostrum in the species of *Aegaeon* (see also CHRISTOFFERSEN, 1988). The bifurcate rostrum, however, is gradually fused and becomes pointed again in *Pontocaris*. The fact that there is one *A. lacazei* and one *A. cataphractus* specimen in the present study having the bifurcation of the rostrum weaker and in appearance cleft further supports the above interpretation. Furthermore, the posterior thoracic sternites are slightly expanded laterally in *A. lacazei* and *A. cataphractus*, with the spines on the telson of the latter sometimes being rather obscure. Although still distinct, the median spines on the abdominal sternites in most of the species of *Aegaeon* are often rather small on the posterior somites and may even diminish to tubercles in females.

Within *Pontocaris*, *P. hilarula* appears to be more closely related to the genus *Aegaeon* by the anterior end of the lateral carapacial carina III being quite close to the branchiostegal spine, the branchiostegal spine relatively smaller (sometimes only extending to half of the outer margin of the laterally extended scaphocerite), the lateral sinuous ridges of abdominal tergite III interrupted near the lateral ends, and the telson occasionally having four long terminal setae. The dactylus of pereopod V is strongly modified in the spawning females of *P. hilarula*. This suggests that the lengthening of the carpus of pereopod II in spawning females probably represents a more advanced adaptation than the modification of the dactylus on pereopod V in *Pontocaris*, though both kinds of pereopod modification are found together in the Red Sea species. The cleft rostrum appears to have originated from the bifurcate rostrum of *Aegaeon* and only later changed back to being entire. This is probably shown in *P. sibogae* and *P. major* where the rostrums of the juveniles are mainly cleft but become microscopically cleft or entire in adults. As already mentioned, the reduction to only one tooth on the anterior part of the lateral carapacial carina II as well as the loss of the posteromedian spine on abdominal somite IV, are probably secondary and result from the reduction in the sculpturing of the body. Other than the above, however, little can be concluded at present about the evolutionary relationships amongst the species of *Pontocaris*. *Parapontocaris* also poses similar problems, though the fewer teeth on the carapace and fewer ridges at the abdomen probably represent a more ancestral state in this genus.

Biogeography. — The abundant material from many localities in the present study enables a rough interpretation of the distribution and evolution of these three, closely-related crangonid genera. The genus *Parapontocaris* has a typical Tethys distribution and, except for *P. andamanicus*, the species are widely distributed (fig. 21). Furthermore, *P. aspera* with *P. levigata* and *P. caribbea* with *P. vicina* always occur together in the Indo-West Pacific and in the Caribbean, respectively. The distribution of *Aegaeon* is the widest amongst the three genera, with all the species widely dispersed (fig. 19). The fact that four of the five species are found in the Indo-West Pacific suggests that this genus originated there and only later spread into the Mediterranean and Atlantic. However, it is possible that *A. cataphractus* evolved in the Atlantic, since not a single specimen of this common Atlantic species has been found in the West Pacific by the many large expeditions in this area (the previous record

from New Zealand is incorrect, see "Remarks" under this species). Furthermore, the rather different pattern of abdominal sculpturing and the unique presence of intermediate tubercles on the carapace in *A. cataphractus* also suggest that it may be phylogenetically isolated. If the above is true, then the *A. lacazei* line would logically have given rise to *Pontocaris* in the Indo-Pacific. On the other hand, the occurrence of *A. boschii* in the southwestern Atlantic probably represents dispersion of the genus from the other side of the Atlantic, instead of a relict of a former Caribbean/S. Atlantic distribution, since no other species of the genus is found in the West Atlantic, even though the entire coast of West Africa is populated by *Aegaeon* species. The close resemblance of *A. boschii* with *Parapontocaris* may suggest that the geographical isolation of the former resulted in its being more similar to the common ancestor of *Aegaeon*, which is no longer extant in the Indo-West-Pacific.

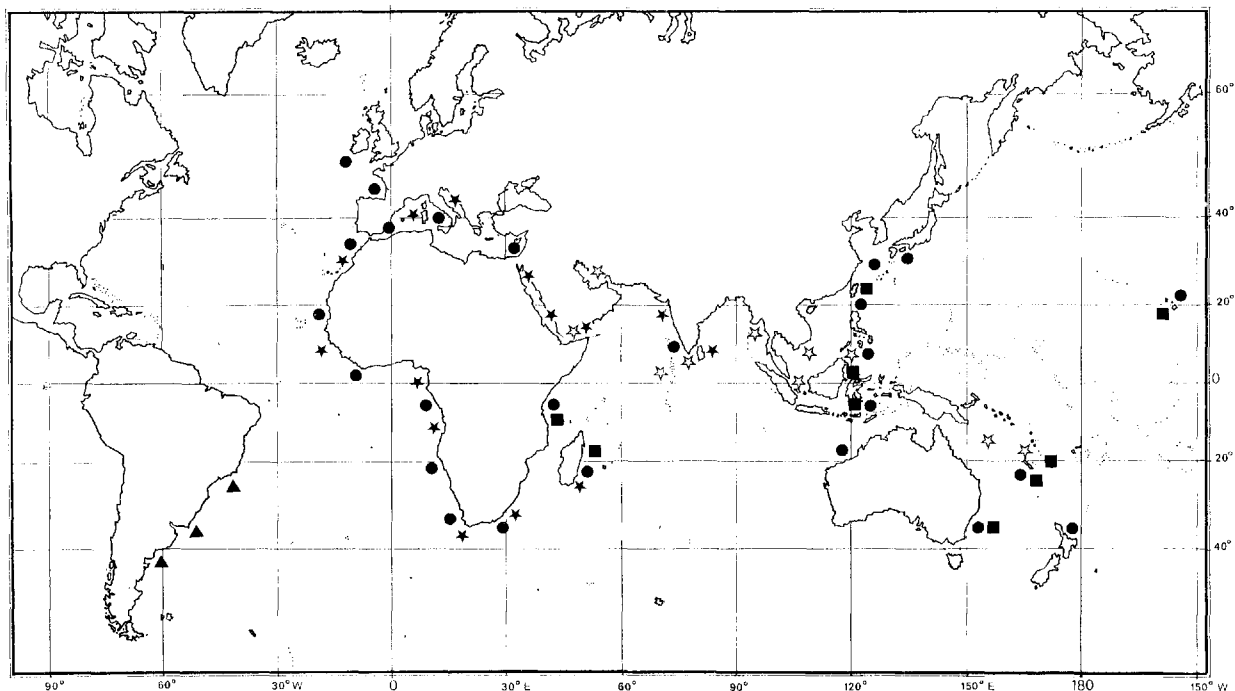


FIG. 19. — Geographical distribution of the species of the genus *Aegaeon*: ★, *A. cataphractus*; ●, *A. lacazei*; ■, *A. rathbuni*; ✱, *A. orientalis*; ▲, *A. boschii*.

Of the 10 species known in *Pontocaris*, 8 are found in the Philippine Indonesian area (fig. 20), three of which apparently have very restricted distributions (i.e. *P. laurentae* occurs only in Makassar, *P. spinifera* in the Flores Sea and *P. major* in the northeastern Philippines). Northwards only two species, namely *P. sibogae* and *P. pennata*, are found in Japan and Taiwan. On the other hand, only three species, *P. propensalata*, *P. sibogae* and *P. hilarula*, have dispersed south to New Caledonia (*P. propensalata* may also occur in southeast Australia). The entire Indian Ocean has only two species, with *P. affinis affinis* found scattered in this region and *P. propensalata* just across the Strait of Malacca into the Andaman Sea, or perhaps Bay of Bengal. In the Red Sea (including the Gulf of Aden), a subspecies of *P. affinis* is found with another endemic species *P. profundior*. The occurrence of both kinds of pereiopod modifications in the spawning females of these two endemic forms further suggests that the Red Sea is a rather distinct zoogeographical subregion. The above distribution pattern matches quite well with EKMAN's (1953) zoogeographical theory that the Indo-Malay region is a species center. Thus, it seems likely that *Pontocaris* originated in the Indo-Malay region in relatively recent times and is still actively evolving.

The Tethys distribution of *Parapontocaris* suggests that it is the most ancient of the three genera. The genus *Aegaeon* probably evolved from a *Parapontocaris* ancestor in the Indo-West Pacific and only later migrated to the Mediterranean and Atlantic. The considerably fewer species but much wider distribution of *Aegaeon* indicate that it

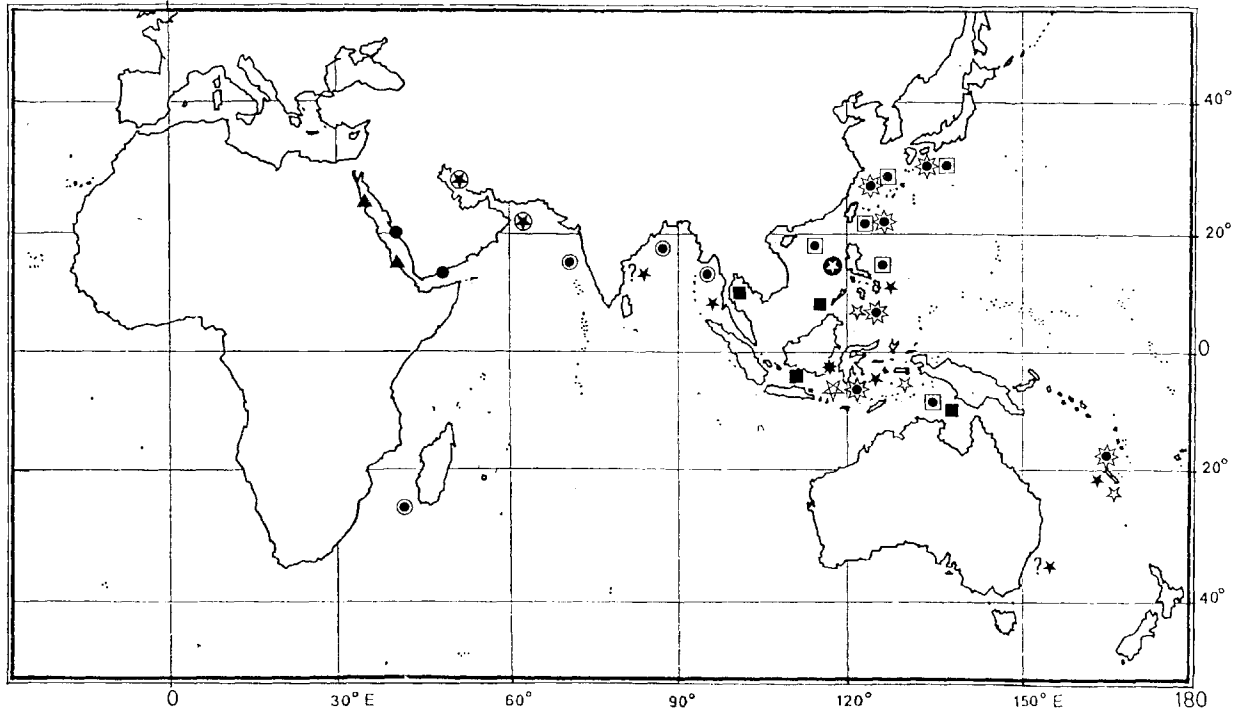


FIG. 20. — Geographical distribution of the species of the genus *Pontocaris*: ★, *P. propensalata*; ●, *P. profundior*; ■, *P. arafurae*; ☆, *P. hilarula*; ⊙, *P. affinis affinis*; ▲, *P. affinis allodactylus*; ⊕, *P. major*; ✱, *P. laurentae*; ✨, *P. sibogae*; ◻, *P. pennata*; ☆, *P. spinifera*; ⊕, *P. affinis affinis* or *P. affinis allodactylus*; ?, exact identity still uncertain.

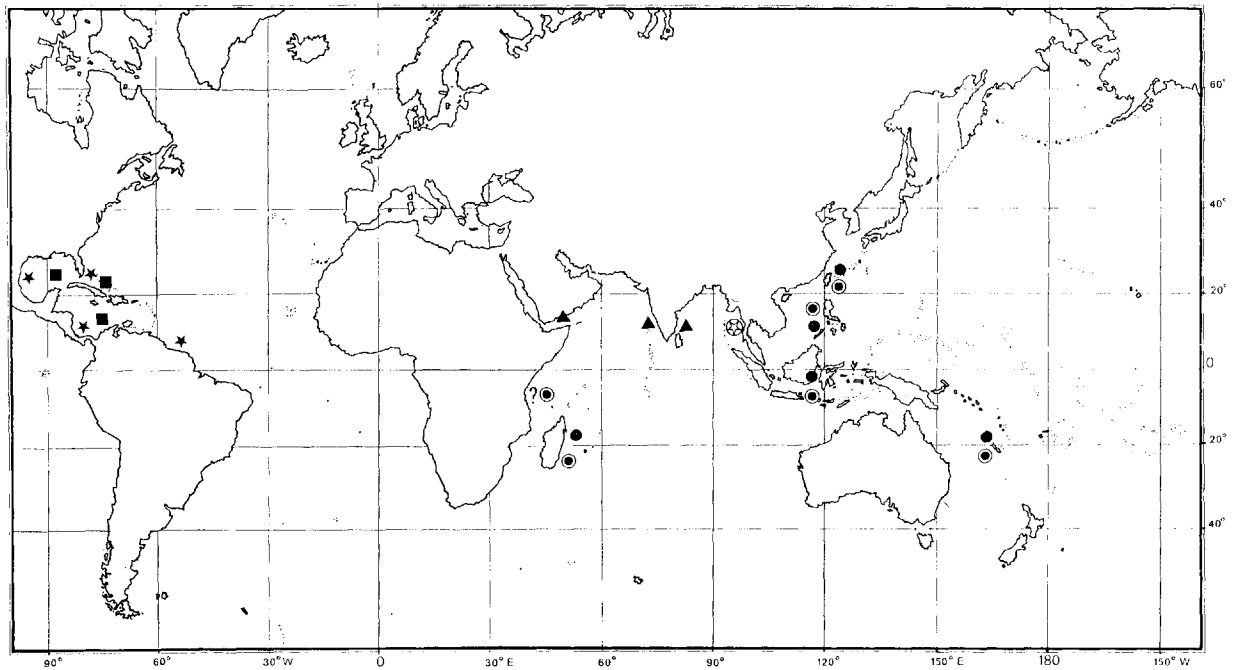


FIG. 21. — Geographical distribution of the species of the genus *Parapontocaris*: ★, *P. caribbaea*; ●, *P. aspera*; ■, *P. vicina*; ⊕, *P. andamanensis*; ▲, *P. bengalensis*; ⊙, *P. levigata*; ?, exact identity still uncertain.

has a longer history than *Pontocaris*. The latter probably originated in the Indo-Malay region and is still actively evolving there.

Both the morphological evidence and the distribution patterns show that the three genera defined in the present study may truly represent "natural" discontinuities. More details on the distribution of the living species and of possible fossils, as well as biochemical or phylogenetic analyses, may perhaps provide more information on the phylogenetic relationships of the species in these three closely related groups.

ACKNOWLEDGEMENTS

Grateful acknowledgement is extended to : M. DE SAINT LAURENT of the Muséum national d'Histoire naturelle, Paris, for generously providing the author with her personal notes and drawings of part of the material used in the present study, and kindly sparing a lot of valuable time to discuss many details with the author, though not all of her suggestions have been followed; A. CROSNIER of the Institut français de Recherche scientifique pour le Développement en Coopération, Paris, for providing the opportunity to study these interesting groups and arranging most of the loans, helping with the final checking of the station data and editing the manuscript, as well as for his warm hospitality to the author in Paris; F.A. CHACE, Jr. of the National Museum of Natural History, Washington, D.C., for kindly allowing the author to examine the "*Albatross*" material during a stay in the USNM in 1990 and reviewing the manuscript; L. B. HOLTHUIS of the Nationaal Natuurhistorisch Museum, Leiden, for reviewing the manuscript, discussing the proper generic names pertinent to the present study and providing the author with his manuscript on the recent genera of caridean and stenopodidean shrimps.

I also sincerely thank J. FOREST of the Muséum national d'Histoire naturelle, Paris, for help in various ways; M. GAILLARD, formerly of the Muséum national d'Histoire naturelle, Paris, now retired, for agreeing to execute the drawings; K.-I. HAYASHI of the Shimonoseki University of Fisheries, Shimonoseki, for providing Japanese *Pontocaris* specimens and photographs; M.L. CHRISTOFFERSEN of the Universidade Federal da Paraíba, Paraíba, for donating some paratypes of *A. boschii* and providing his notes on the phylogenetic relationships of the present groups; and ORSTOM (Institut français de Recherche scientifique pour le Développement en Coopération) for providing a short-term research grant to the author to study at the Muséum national d'Histoire naturelle, Paris, and thereby making the present work possible.

I am greatly indebted to the following scientists for sending me material on loan : A.J. BRUCE, Northern Territory Museum of Arts and Science, Darwin; P. CLARK, The Natural History Museum, London; C.H.J.M. FRANSEN, Nationaal Natuurhistorisch Museum, Leiden; R.B. MANNING, National Museum of Natural History, Washington; S. PINKSTER, Zoologisch Museum, Amsterdam; R.C. PREECE, University Museum of Zoology, Cambridge; L. TIEFENBACHER, Zoologische Sammlung des bayerischen Staates, München; M. TÜRKAY, Forschungsinstitut Senckenberg, Frankfurt.

My thanks are also due to M. JUDSON for correcting my English.

This study is a contribution from a research grant on the Decapod Crustacea of Taiwan, supported by the National Science Council, R.O.C. (NSC 83-0409-B-019-011).

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