

SYSTEMATIC POSITION AND STATUS OF THE HOMOLODROMIIDS (CRUSTACEA, DECAPODA, BRACHYURA)

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SUMMARY. The systematic position as well as the systematic status of the homolodromiids and some related taxa has been considered. By comparison with other Dromiacean taxa it has been established that homolodromiids form a separate family Homolodromiidae, which cannot be included either in Homoloides or Dromioidea. The Homolodromiidae are most closely related to the fossil families Eocarcinidae and Prosopidae with which they should form a separate superfamily Prosoipoidea. This superfamily is the most primitive one within the Dromiacea, therefore it has to be retained at the beginning of the system of the Brachyura.

Although the homolodromiid crabs have been much investigated (1, 5, 11, 13, 16) their systematic position and status, as with most brachyuran taxa, have been variously considered and conclusions have varied from author to author. At first both homolodromiid genera *Homolodromia* and *Dicranodromia* were described in 1880 by A. Milne Edwards (13) as members of the family Dromiidae. Alcock (1) placed these two genera in a separate family Homolodromiidae, as a part of the superfamily Dromioidea. Such a classification was accepted by Borradaile (4), Gordon (11), Gurney (12) and Rathbun (18), while some authors, such as Beurlen (3) Monod (15) and Serène (19), treated them only as a family of the Dromiacea. Glaessner (9, 10) included these genera in the family Prosopidae as the subfamily Homolodromiinae, but in the superfamily Dromio-

idea. A. Milne Edwards and Bouvier (6, 14) considered them only as genera of the subfamily Dromiinae. Balss (2), although giving a systematic review of the primitive Dromiacea according to Glaessner (9), treated them nevertheless as a separate family. Finally, Pichod-Viale (17) considered both homolodromiid genera to be a part of the family Homolidae.

As is obvious from this historical review, these two homolodromiid genera have had various treatments regarding their status, i.e. from genera to family, as well as their systematic position, being included in the Dromiidae, Prosopidae or Homolidae. As a consequence of such diversity of opinions, two questions could be posed: what is the systematic position of the homolodromiids in the Brachyura, and what is the systematic status of this taxon? It is noteworthy that for these con-

siderations, only comparative morphological evidence from adults can be used, because in these two genera free swimming larvae are not known and their development is probably direct (7, 12).

The first point in considering the systematic position is to stress that the genera *Homolodromia* and *Dicranodromia* are very similar and form a natural taxon clearly delimited from other brachyuran taxa, which we have named conditionally homolodromiids. In order to establish the systematic position of the homolodromida it is necessary to establish the next higher taxon in which they can be included. In spite of the fact that many authors hold widely differing opinions on this taxon, they mostly agree that homolodromiids are the most primitive living crabs and they are placed among the Dromiacea at the beginning of the Brachyuran system. The homolodromiids correspond indeed to the Dromiacea in all diagnostic characters (antennal segments not fused; front narrow; seminal ducts perforate coxae of the fifth pereopods; oviducts open in coxae of the third pereopods; greater number of branchiae; the first pleopod present in females; epipodites on the first three pereopods; the fourth and fifth pereopods usually in dorsal position and sometimes subchelate). However, the principal problem is their position within the Dromiacea and their relationships with other dromiid taxa. Before this consideration it is necessary to point out that the homolodromiids are the only crabs to possess such primitive characters as rudimentary antennal scalae and trichobranchs.

Considering the relationships with other Dromiacean taxa, we shall first examine the relationships between homolodromiids and the superfamily Dromioidea, which is composed of Dromiidae and Dynomenidae. Between these two taxa there are several similarities, e.g.: linea dromica; abdomen incompletely folded against cephalothorax; epipodites on the first pereopod; sternal furrows present; rudiments of uropods present. On the other

hand there are many differences, because the homolodromiids have an elongate and cylindrical cephalothorax; their third maxilliped is pediform; 21 branchiae on each side; epipodites on the second and third pereopods; sternal furrow very short; endoskeleton is discontinued (8) and the head is not condensed, i.e. the ocular segment is not invaginated into the antennular one (17), so that there are neither orbits nor orbital and antennular grooves. Because of these great differences in important and distinctive characters it is not possible to include the homolodromiids into the superfamily Dromioidea.

Comparing homolodromiids with Homoloidea, which include two families Homolidae and Latreillidae, one can see that these two taxa have several characters in common: the endoskeleton is discontinued, the head is not condensed; the third maxilliped is pediform; the cephalothorax is elongate; the fifth pair of pereopods is dorsal and subchelate. The differences are, however, also considerable: homolids do not possess sternal furrows; rudiments of uropods are absent; phylobranchs are present and the linea homolica is present. Because of these considerable differences the homolodromiids cannot be included into the superfamily Homoloidea.

The third attempt at the classification of homolodromiids placed them in the family Prosopidae as the subfamily Homolodromiinae, along with the subfamilies Prosopinae and Pithonotinae. Unfortunately the latter two taxa are known only as fossils and therefore a complete comparison is more difficult than with recent crabs. There are indeed similarities with both prosopid subfamilies. For instance, they correspond in having an elongate and cylindrical cephalothorax without orbits, antennal grooves or a distinct lateral margin, but with well developed cervical and branchiocardiac grooves. Yet, prosopids differ in having the fourth and fifth pairs of pereopods neither dorsally placed nor

subchelate in some examples; hepatic grooves are absent in homolodromiids; the rostrum projects in prosopids while in homolodromiids there are two long frontal spines. Also the sculpturing in the prosopids is very prominent, especially in the cervical and branchiocardiac furrows, the last of which is stronger. Moreover, in the Pithonotidae the fronto-orbital margin is wide, not very projecting, and there is an incomplete lateral margin in some forms. In spite of several similarities, homolodromiids cannot be classified together with these taxa in the Prosopidae.

Of the fossil Brachyuran families there is still the family Eocarcinidae, which is very similar to both the prosopids and to the homolodromiids. The homolodromiids and the eocarcinids have the following characters in common: elongated and cylindrical cephalothorax; orbits and lateral margins absent; cervical and branchiocardiac furrows well developed; last pair of pereopods in dorsal position. Differences are also present: in eocarcinids the intercalated lateral platelets between; the sixth and seventh somites (rudiments of uropods) are absent; the telson is small: the abdomen is not folded under the cephalothorax (unless it is an artefact of fossilization); the directions of the furrows on the carapace are different. So the homolodromiids cannot be included in this taxon.

Having considered all the possible relationships between the homolodromiids and other Dromioidean taxa it is obvious that they are most similar in form and structure to eocarcinids and prosopids, while they are less like the Homoloidea and Dromioidea. Moreover, the aforementioned evidence permits the inference that the homolodromiids, the eocarcinids and the prosopids are not only on the same organizational level, but also that they are related and therefore form a separate taxon on the level of a superfamily. This new superfamily could be named Prosopoidea because the genus *Prosopon* was

described the first. Since these three taxa are also mutually different in some details it is necessary to consider them as separate families. Thus, the homolodromiids should be regarded as the family Homolodromiidae, which with the Eocarcinidae and Prosopidae form the superfamily Prosopoidea. This superfamily, because of the most primitive organization, could be retained at the beginning of the Dromioidean system, as the most primitive taxon.

By way of a summary here is the definition and classification of the superfamily Prosopoidea including the subject of our consideration — the family Homolodromiidae. The definition of the superfamily runs as follows:

Prosopoidea superfam. nov.

Cephalothorax elongate and usually cylindrical; front mostly narrow; rostrum present; true orbits absent; orbital grooves present in some genera only: lateral margin usually absent; carapace frequently strongly sculptured; cervical and branchiocardiac grooves distinct; abdomen large in both sexes, with seven unfused somites; chelae small and equal and cannot be flexed against the carapace; fourth pair of pereopods sometimes reduced and dorsally placed: fifth pair of pereopods, excluding some genera of the Prosopidae, reduced and dorsally placed and subchelate. Predominantly fossil crabs. The Prosopoidea includes the following families: Eocarcinidae Withers, 1932; Prosopoidea, von Meyer, 1860 and Homolodromiidae, Alcock, 1899.

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SISTEMATSKI POLOŽAJ I STATUS HOMOLODROMIIDA

SAŽETAK. Položaj u sistemu i sistematski status homolodromiida različito su shvaćeni u prošlosti, a mišljenja karcinologa ni do danas nisu usklađena. Uvrštavali su ih u natporodice Homoloidea i Dromioidea i u porodicu Prosopidae, a status im je kolebao od razine roda do porodice. Da bi im ustanovili sistematski položaj i status, obavljena su posebna istraživanja sa sistematski najbližim svojcima (taxa) unutar Dromiacea. Ustanovljeno je da se homolodromiidi zbog svojih specifičnih i izrazito primitivnih svojstava ne mogu uvrštavati ni u jednu od spomenutih svojti, već da je riječ o posebnoj porodici Homolodromiidae, kao što je to već ranije utvrdio Alcock (1). Ta se porodica po svom ustrojstvu podudara s porodicama Prosopidae i Eocarcinidae, s kojima čini novu natporodicu Prosopoidea, koja je ovdje opisana. To je najprimitivnija svojta unutar Dromiacea te je stoga valja zadržati na početku sistema kratkorepaca (Decapoda, Brachyura).