



Fig. 8. *Palehomola*. *P. richardsoni* (Woodward), holotype, GSMC, $\times 1.5$, middle Cretaceous, Queen Charlotte Island, British Columbia.

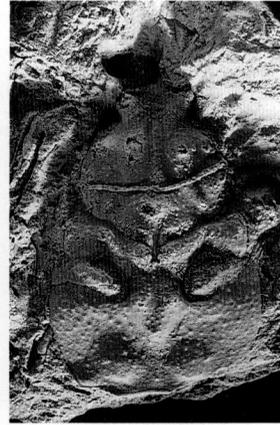


Fig. 9. *Prohomola*. 1, *P. japonica* (Yokoyama), KMNH IvP 300,010, $\times 3.0$, Middle Eocene, Kyushu, Japan; 2, *P. japonica* (Yokoyama), 5988, $\times 3.0$, Middle Eocene, Kyushu, Japan.

ked these eminently diagnostic characters when she erected *Palehomola* for *Palehomola gorrelli* - a species essentially similar to *H. richardsoni* - particularly when she stated in her description that the front was "furnished with two short, curved (concave inwards) horns", and yet retained *richardsoni* - clearly eligible for inclusion in *Palehomola* - in *Homolopsis*. The presence of a bifid rostrum further distinguishes this genus from *Zygastrocarcinus*.

Whereas Woodward (1896) referred to similarities with *Latreillia*, Roger (1953) included *Palehomola* in the Latreilliidae. Rathbun (1926), on the other hand, refers to *Latreillioopsis* Henderson, 1888 and also to the rostral horns of the Jurassic "*Homolus* (= *Palaeoinachus*) *longipes* Woodward, 1866" = *Foersteria audini* (Eudes-Deslongchamps, 1835) (Wehner, 1988), but apart from that feature, there are few likenesses other than general prosoponid propensities.

2.8. *Prohomola* Karasawa, 1992 (Fig. 9)

Type species: By monotypy *Homolopsis japonica* Yokoyama, 1911 - a species previously placed in *Paromola* Jenkins (1977) (*non Paromola japonica* Parisi, 1915); *Oncinopus*? by Tomita, Ishibashi & Hara, 1992 and *Zygastrocarcinus* by Bishop & Brannen, 1992.

The type species, *Prohomola japonica* (Yokoyama, 1911), comes from the Kattachi Formation, Manda Group of late Middle Eocene age of Japan. It has a

longitudinally ovate carapace tapering anteriorly, the dorsal surface is flattened and granulated without spines; the rostrum is simple and downturned, there is a pair of short, triangular, dorsally projecting pseudo-rostral spines not over-reaching the rostrum; the mesogastric lobe has a median tubercle. These characters were considered by Karasawa (1992) sufficient to distinguish *Prohomola* from *Paromola*. Earlier, Jenkins (1977), who had only the type of *Homolopsis japonica* Yokoyama available to him, had noted only the presence of, "a distinct transverse ridge over the anterior part of each metabranchial region," and several additional spines to distinguish that species from *Paromola*. These differences, he thought, were minor and indicative of slow evolutionary change. That *Prohomola* is close to *Paromola* is unequivocal, but whatever the degree of overlapping characters, it would be prudent to maintain *Prohomola* if only to protect the status of *Paromola japonica* Parisi, 1915 as noted above. The only other known species, *Prohomola katunai* Blow & Manning, 1996, described from a partial carapace between the *lineae homolicae*, comes from the Middle Eocene Santee Limestone of South Carolina. It differs from *P. japonica* in having a spine on the hepatic region, a more prominent mesogastric tubercle and coarser, sparser surface ornament.

According to Karasawa (1992) the presence of a bifid rostrum serves to separate *Palehomola*, whereas

the pseudorostral spines and single mesogastric tubercle distinguish *Prohomola* from *Homolopsis*. An internal cast figured by Karasawa (1992) shows a metabranchial ridge extending from the cardiac region, reminiscent of *Hoplitocarcinus*, but this feature is evidently absorbed by shell thickness, for it is not present in an accompanying figure of a plaster cast of an external mould.

2.9. *Gastrodorus* von Meyer, 1864

Type species: By monotypy *Prosopon* (*Gastrodorus*) *neuhausensis* von Meyer, 1864 [*Eopagurus* Beurlen, 1925 (obj.)].

Range: Tithonian.

Notice of the transference of *Gastrodorus* to the Homolidae was given by Glaessner (1929a) in the 'Fossilium Catalogus' and evaluation appeared more or less at the same time in his 'Dekapodenstudien' (1929b).

This small, monotypic genus, barely reaching 5 mm in length, is known only from the median part of the carapace; it is widest anteriorly and has a markedly concave posterior margin. A median spine on the rostrum is continued as a prominent ridge to the cervical furrow which is posterior to mid-length. The well defined lobes are tumid and the metabranchial lobes are well separated by the cardiac region. Although lacking in prominent tubercles the dorsal surface is covered in flattened granules which become less crowded, but larger and steep-fronted on the metabranchial lobes. The median ridge and elongate cardiac region are unique among other known homolids.

Like others in the family, *Gastrodorus*, which apparently did not survive beyond the Jurassic, was earlier placed in the Prosopidae and, for a short time (1925-1929), was included in the Paguridae.

3. Palaeogeography & Biostratigraphy

In a summary of the palaeogeography and biostratigraphy of *Homolopsis*, Bishop (1992) referred to *Tithonohomola* as a possible Jurassic ancestor, and in citing Wright & Collins's (1972) suggestion that *Pithonoton* (= *Foersteria*) *planum* and *Pithonoton*

schneideri were close ancestral forms for *Homolopsis*, he overlooked those authors' reference (1972: 43) to the similarity of *Laeviprosopon* to *Homolopsis*, in particular, to the smooth, Cretaceous species *Homolopsis glabra* Wright & Collins, 1972. The similarity between *L. laevis*, *H. glabra* and *H. chilensis* is readily apparent. Wright & Collins (1972) were also of the opinion that the tuberculate forms comprise a series of offshoots from a continuing smooth stock. If this be the case, such offshoots were firmly established in the Lower Cretaceous Hauterivian by the strongly tuberculate *Homolopsis hachiyai* Takeda & Fujiyama and *H. tuberculata* van Straelen.

In principle, however, Bishop's scheme for the palaeogeographic and biostratigraphic distribution is sound and lends itself readily to a re-evaluation of fossil homolids in the light of recent events.

From presumed Jurassic prosoponid ancestors, *H. ? schneideri* and *H. tuberculata* were present in the shallow waters of the Northern Tethys covering France and Switzerland by the Neocomian. *Homolopsis hachiyai*, a tuberculate species, reached Japan by the Aptian, while *H. glabra*, continuing the presumed smooth ancestral line, is found in the Upper Aptian through to the Middle Cenomanian of southern England where it is found in almost equal numbers with *H. brightoni* - a tuberculate form becoming smoother as growth advances - which makes its appearance in the Middle Albian. The highly individualistic *H. edwardsii* is confined to the Albian of southern England and France (Van Straelen, 1936) and *Homolopsis declinata* Collins, Fraaye & Jagt, 1995 is known from the Maastrichtian of Belgium and Holland.

Two genera, *Homolopsis* and *Eohomola*, are among ten decapod genera recorded from the Danian (Palaeocene) of Denmark and Sweden known to have crossed the K/T boundary (Collins & Jakobsen, 1994; Jakobsen & Collins, 1997). *Homolopsis* is represented in the Danian by two species, *H. transiens* and *H. spiniga*. The genus appears to have an essentially Northern Tethys distribution, for apart from the Japanese *H. hachiyai*, only three other species - with the exception of the Australian species *H. ? spinulosa* which is found in deposits laid down in a shallow

epicontinental sea (Woods, 1953) - *H. pikeae* and *H. williamsi* from the Cenomanian and Turonian respectively of the Western Interior seas of North America and the South American Maastrichtian *H. chilensis* (the associated fauna, particularly, the *Ophiomorpha* dominated ichnofauna, of which suggests a shallow water environment (Förster & Stinnesbeck, 1987)) are known to occur outside the European region.

Bishop (1992) was of the opinion that three distinct lineages of homolid crabs, those assignable to *Homolopsis*, to *Zygastrorcarinus*, and the aberrant *Homolopsis? spinulosa*, were derived from early forms by the Albian. To these must surely be added *Palehomola* with a triangular-acircular carapace and bifid rostrum, firmly established in North America by the Lower Cretaceous, and the characters distinguishing *Lignihomola* were also well developed by the Albian, *Prohomola* with its elongate ovoid carapace, single rostrum and distinct postrostral spines could be said to form yet another group. The genus was said by Karasawa (1992) to be endemic among other Manda Group decapods which are related to western and central European Tethyan forms, but a second species, *P. katunai*, has since been described by Blow & Manning (1996) from the Santee Limestone of South Carolina. This, rather earlier occurrence, raises questions of dispersal; although Blow & Manning (1996) considered that the crabs of the Santee/Castle Hayne Limestones as a whole had greater affinities with European decapod faunas, extreme migration of *Prohomola* to Japan along this route must remain speculative.

As remarked above, an evolutionary development in *Homolopsis* occurred in the Santonian of Germany - again, between Northern Tethys and Boreal waters - with the appearance of *Hoplitocarcinus gibbosa*. The genus had reached Japan, through *Hoplitocarcinus brevis*, by the Turonian and *Hoplitocarcinus atlanticus* occurs in the Lower Campanian of the Atlantic Coastal Plain more or less coincident with the appearance of *Hoplitocarcinus centurialis* in the Western Interior of North America where the genus is continued into the Upper Campanian and Maastrichtian by *Hoplitocarcinus punctatus*.

It would appear that *Eohomola* had its origin in *E.*

dispar, in the Lower Campanian waters of the Atlantic Coastal Plain, from whence the genus made a northeasterly progression to West Greenland where it is represented in the Upper Campanian and Maastrichtian by *E. adelphina*. Continuing its easterly spread the genus next occurs in the late and middle Danian coral/Bryozoa banks of Denmark (*Eohomola affinis*) and generic characters are found in Recent species of *Homola*.

There seems little doubt that the rectangular carapace, juxtaposition of the furrows, regions and ornament of *Zygastrorcarinus* clearly foreshadows that of *Paromola*, some species of which differ little more than in development of spines, particularly about the frontal region, and strongly suggests that *Zygastrorcarinus* provided the ancestral stock. Even the larger size of *Zygastrorcarinus* compared with contemporary homolids, would seem to presage the greater size obtained by *Paromola*. There is also a degree of agreement in the cheliped of *Zygastrorcarinus* figured by Bishop (1983), although given the material, the strange representation of the joints in the reconstruction of his fig. 2 would seem to require justification.

Bishop (1986) considered that two evolutionary lineages of *Zygastrorcarinus* developed, one with a triangular carapace (= *Palehomola*) on the Pacific Slope, and one with a rectangular carapace (= *Zygastrorcarinus*) in the Western Interior of the United States. A possible line of descent from *Tithonohomola* for *Zygastrorcarinus* is discussed above and a Pacific association of *Palehomola* and *Lignihomola* is feasible.

Paromola is a widely distributed extant genus ranging from as far North as the Shetland Isles and West Coast of Norway to the Mediterranean Sea, Indo-Pacific Ocean and Pacific coast of America (Rathbun, 1937; Jenkins, 1977). Species would appear to tolerate greater depths than those common to *Homola*, for apart from an individual occurrence of *P. cowieri* found in a rock pool (Gordon, 1956) that species normally occurs in depths of between 180-1320 m, while specimens of *Paromola petterdi* (Grant, 1908) have been taken from depths of 91-1460 m. Overall, however, the average depths from which species are most frequently recorded are, according to Jenkins (1977), in the region of 100-500 m. Generally speaking,

individuals of *Paromola* attain the largest size known among the Homolidae.

The specimens of *P. pritchardi* were found in the upper member of the Gambier Limestone and from studies of the associated fauna, especially the foraminiferans and bryozoans, together with a scarcity of terrigenous detritus Jenkins (1977) deduced an open marine, clear water environment similar to that prevailing in present day seas of South Australia at depths of 90–229 m. Since these conditions are favourable to extant species of *Paromola*, Jenkins (1977) concluded that *P. pritchardi* lived in similar conditions.

As presently known, *Gastrodorus* appears to have been the least successful genus among the homolids, apparently confined to the Upper Jurassic of Central Europe, its origins are obscure and there are no known descendants attributable to it.

Homolids cannot be said to form a dominant part of any fossil decapod assemblage; frequently occurring with the crab genera *Necrocarcinus* and/or *Xanthosia* and raninids of several genera, they inhabited reasonably shallow seas during the Cretaceous and readily adapted to diverse, more or less, soft bottomed environments. A shallow water environment, for instance, was suggested by Bishop (1992) for *H. centurialis* as indicated by the associated fauna and in particular the dominance of *Ophiomorpha* among the ichnofauna. The Dutch/Belgian Maastrichtian species, *H. declinata*, and its associated fauna substantiates this view. This mode of life is in sharp contrast to that of the Palaeocene *Homolopsis* and, rarer, *Eohomola* in the Danian coral/bryozoan limestone of Denmark and Sweden. There is a tendency for a deep water environment among Recent homolids; the carapace of *Homola* sp. from the Hoko River Formation was found in a concretion within a turbidite sequence, interpreted by Feldmann, Tucker & Berglund (1991) as deepening marine conditions (with the reservation that some of the included species could have been transported from shallow water environments. The Recent *Homola barbata*, associated with *Homola?* sp. by Tucker, is found in the Mediterranean in depths of 40–100 m (Zariquiey Alvarez, 1946) and Guinot & Richer de Forges (1981) recorded 25–125 m for speci-

mens taken off Madagascar. The deepest depth (?) 1000 m, recorded by Guinot & Richer de Forges (1981), is for *Homola mieensis* Sakai, 1979, taken off the Iles Loyaute, New Caledonia. It would appear, therefore, that adaptation towards a deep water habitat commenced during the late Palaeocene/early Eocene, and present habitat transition – for some, if not all genera – was effected by or about Upper Eocene times.

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