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Fossil Homolidae (Crustacea; Decapoda)

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Abstract

An historical introduction to the family Homolidae from the palaeontological point of view is followed by detailed analyses of the 11 genera presently concerned and a review of their stratigraphic and geographic occurrences. A new genus, *Lignihomola*, is introduced to contain *Pithonoton etheridgei* Woodward, 1892.

Key words: Crustacea, Decapoda, Homolidae, review, *Lignihomola* gen, nov.

1. The family, a historical account

Various authors have been credited with the introduction of the family Homolidae; in neontological literature it has been attributed to Henderson, 1888, although it had previously been applied by White, 1847 and for some time Bell, 1863 was given the credit among palaeontologists, but Williams & Moffitt (1991) point out that the name was first used by de Haan (1839) (ICZN, 1989). *Homola* Leach, 1815 was conserved by the International commission for Zoological Nomenclature (opinion 522) against *Thelxiope* Rafinesque-Schmaltz, 1814, and, although recognised at least as late as 1990 by Takeda, Rathbun's (1937) change of the family name to Thelxiopeidae is invalid.

Whether or not the family Latreilliidae Stimpson, 1858 should be included in the Homolidae has long provided cause for debate, particularly among neontologists (Williams & Moffitt, 1991). However, the accepted relationship between the two families was considered by Wright & Collins (1972) to be based on no more than a few primitive features shared also by various extinct genera of Prosopidae. The essential character that distinguishes Homolidae from other Dromiacea, the dorsal *lineae homolicae*, is not found in *Latreillia* or *Heeia* Wright & Collins (1972), an Upper Cretaceous genus included in the Latreilliidae. For this reason Wright & Collins (1972) did not follow Gordon (1950) and Ihle (1913), who remarked (p. 54) that in *Latreillia* the *lineae homolicae* had disappeared; these authors, combined the two families on the ground that there is a continuous range in the number of gills and epipodites, features much used in the diagnosis of extant genera of the two families ; similarly, there is no clear dividing line between the two families in the insignificant matter of the relative length of the basal and sections of the eyestalks, while *Homola* and *Latreillia* stand at each end of a more or less continuous range of carapace shapes, from rectangular to an acute-angled isosceles triangle. None of these features is as significant as the presence or absence of dorsal *lineae homolicae* and the two families have probably been independent stocks since late Jurassic times, albeit developing to some extent in parallel.

Although comparatively rare as fossils, homolids have had an extensive geological history with gener-

ally accepted origins among the prosoponids in the Upper Jurassic. The fossil record, however, extends only to the Oligocene, the lack of evidence thereafter being attributed to an adaptation to the deeper water life style favoured by Recent members of the family. With geographical roots in central Europe specific development and distribution was fairly rapid, with forms reaching southern England and Japan by the early Cretaceous and Australia, Greenland, North America by the late Cretaceous.

In his observations on *Homolopsis edwardsii*, Bell (1863) stated, "The affinity of this species to *Homola* was first noted by, Mr Carter, of Cambridge, who had applied to it in his own cabinet the generic name which I have adopted." Curiously, while Bell provided a sound formula for others to follow, he made no mention of the *lineae homolicae* in either his diagnosis or description, despite their being clearly evident in the figured specimen which came from the Gault (Albian) of Folkestone, Kent.

The first allusion to the *lineae homolicae* was made by Carter (1898) in a supplementary description of *Homolopsis edwardsii*, when he remarked, "As usually found most specimens have a fracture on one or both sides, extending from the orbit to the posterior border, probably the result of pressure upon the highly-vaulted carapace; not unfrequently the lateral portions are completely broken away." Also in this work Carter described *Homolopsis depressa* from the Upper Albian Cambridge Greensand.

Although it may be said that *Homolopsis edwardsii* was the first fossil homolid to be described as such, some Jurassic species described by von Meyer as far back as 1847 belonged to the family, but were not wholly accepted until 1980 ! *Homolopsis* remained the sole fossil genus until 1926 when Rathbun described *Palehomola gorrelli* from the Oligocene of North America. A new genus, *Zygastrocarcinus*, was introduced by Bishop (1983) and contains a small group of North American species, to which Bishop added (1992) *Prosopon* [=*Homolopsis*] *etheridgei* Woodward, 1892, an Albian species from Queensland - herein assigned to the new genus *Lignihomola* (see 2.5).

A significant contribution, which was to have widespread repercussions regarding the appreciation of the family, was made by Patrulius (1966) when he not only confirmed Glaessner's (1933) tentative assignment of *Tithonohomola*, but perspicaciously referred *Laeviprosopon* - genera erected by Glaessner (1933) to contain Upper Jurassic prosoponid crabs - to the Homolidae. Glaessner (1969), however, was either unaware of Patrulius's (1966) work or remained sceptical, because he maintained his original opinions regarding the position of both genera. Patrulius's views were supported by Wright & Collins (1972), who considered that *Laeviprosopon* not only foreshadows the smooth Cretaceous species of *Homolopsis*, but also seemed to be near the rootstock of the family.

Important additions to our knowledge of homolids from the southern hemisphere were made by Jenkins (1977) with the publication of an Oligocene species of the extant genus *Paromola* Wood Mason & Alcock, 1891 from southeastern Australia, and by Förster & Stinnesbeck (1987) with the description of the remarkably well preserved *Homolopsis chilensis* from the Maastrichtian of Chile.

Karasawa (1992) introduced *Prohomola* to contain the middle Eocene *Prohomola japonica* (Yokoyama, 1911) but, perhaps the most significant recent contribution to our knowledge of fossil homolids has been the discovery (Feldmann, Tucker & Berglund, 1991) of a species, *Homola* sp., in deep water deposits of the upper Eocene Hoko River Formation of Washington, U.S.A., which Tucker (*pers. comm.*) considers intermediate in position between *Eohomola* and those extant members of *Homola* - and in particular to *Homola barbata* Fabricius, 1793 - which have a bifid rostrum and a metabranchial ridge (q.v. Collins & Rasmussen, 1992).

Opinions regarding the evolution of the Homolidae have, in general, been confined to development within the family and its relationship to the Latreilliidae (Wright & Collins, 1972; Williams & Moffitt, 1991; Bishop, 1992, *et al.*). A concise scheme for the early evolution of the family, however, was put forward by Wehner (1988): from presumed origins in the Middle Triassic *Pseudopemphix albertii* (von Meyer, 1840) she envisaged a line of descent by way of *Eoprosopon klugi*

Table. 1. Family Homolidae de Haan, 1839: fossil species and their stratigraphic occurrence.

Genus *Eohomola* Collins & Rasmussen, 1992	
E. adelphina Collins & Rasmussen, 1992	U. Campanian-Maastrichtian
E. dispar (Roberts, 1962)	L. Campanian
E. affinis Jakobsen & Collins, 1996	Danian
Genus *Homolopsis* Bell, 1863	
H. brightoni Wright & Collins, 1972	Albian-Cenomanian
H. chilensis Förster & Stinnesbeck, 1987	Maastrichtian
H. declinata Collins, Jagt & Fraaye, 1995	Maastrichtian
H. edwardsii Bell, 1863	Albian
H. glabra Wright & Collins, 1972	U. Aptian-Cenomanian
H. hachiyai Takeda & Fujiyama, 1983	L. Aptian
H. pikeae Bishop & Brannen, 1992	Cenomanian
H. schlueteri Beurlen, 1928	Santonian
H?. schlueteri (Stolley, 1924)	Neocomian
H. spiniga Jakobsen & Collins, 1996	Danian
H?. spinulosa Glaessner, 1980	Cenomanian
H. transiens Segerberg, 1900	Danian
H. tuberculata van Straelen, 1936	Neocomian
H. williamsi Bishop, 1992	Turonian
H. sp. (Zululand)	Santonian
H. sp. Via Boada, 1981	Cenomanian
H. sp. Ludvigsen & Beard, 1994	L. Maastrichtian
Genus *Gastrodorus* von Meyer, 1864	
G. neuhausensis von Meyer, 1864	Kimmeridgian
Genus *Hoplitocarcinus* Beurlen, 1928	
H. atlanticus (Roberts, 1962)	L. Campanian
H. brevis (Collins, Kanie & Karasawa, 1993)	Turonian
H. centurialis (Bishop, 1992)	L. Campanian
H. gibbosus (Schlüter, 1879)	Coniacian-Santonian
H. punctatus (Rathbun, 1917)	U. Campanian-Maastrichtian
H. shapiroi (Bishop, 1988)	Maastrichtian
Genus *Lignihomola* gen. nov.	
L. etheridgei (Woodward, 1892)	Albian
Genus *Laeviprosopon* Glaessner, 1933	
L. fraasi (Möricke, 1889)	Neocomian
L. laevis (von Meyer, 1860)	Oxfordian-Neocomian
L. sublaeve (von Meyer, 1860)	Neocomian
Genus *Homola* Leach, 1815	
H?. sp. (Feldmann, Tucker & Berglund, 1991)	Late Eocene
Genus *Paromola* Wood Mason & Alcock, 1891	
P. pritchardi Jenkins, 1977	Oligocene
Genus *Palehomola* Rathbun, 1926	
P. gorrelli Rathbun, 1926	Oligocene
P. richardsoni (Woodward, 1896)	L. Cretaceous
Genus *Prohomola* Karasawa, 1992	
P. japonica (Yokoyama, 1911)	M. Eocene
P. katunai Blow & Manning, 1996	M. Eocene
Genus *Tithonohomola* Glaessner, 1933	
T. armata (Blaschke, 1911)	Tithonian
T. echinora (Collins, 1985)	Oxfordian
T. longa (Möricke, 1889)	Tithonian
Genus *Zygastrocarcinus* Bishop, 1983	
Z. cardsmithi Bishop, 1986	L. Campanian
Z. griesi Bishop, 1983	L. Campanian
Z. mendryki (Bishop, 1982)	Maastrichtian

Table. 2. Synonymy of fossil species assigned to the Homolidae.

Species	Synonomy	Present genus
adelphina	*Eohomola*	*Eohomola*
affinis	*Eohomola*	*Eohomola*
armata	*Oxythyreus*	*Tithonohomola*
atlanticus	*Homolopsis*	*Hoplitocarcinus*
	Metahomola	
brevis	*Metahomola*	*Hoplitocarcinus*
brightoni	*Homolopsis*	*Homolopsis*
cardsmithi	*Zygastrocarcinus*	*Zygastrocarcinus*
centurialis	*Homolopsis*	*Hoplitocarcinus*
chilensis	*Homolopsis*	*Homolopsis*
dawsonensis	*Homolopsis*	*Dioratiopus**
	Glaeessnerella	
declinata	*Homolopsis*	*Homolopsis*
depressa	*Homolopsis*	*Dioratiopus**
	Glaessneria	
	Glaeessnerella	
dispar	*Homolopsis*	*Eohomola*
edwardsii	*Homolopsis*	*Homolopsis*
echinora	*Nodoprosopon*	*Tithonohomola*
etheridgei	*Prosopon*	*Lignihomola*
	Homolopsis	
	Zygastrocarcinus	
fraasi	*Prosopon*	*Laeviprosopon*
glabra	*Homolopsis*	*Homolopsis*
gibbosus	*Dromiopsis*	*Hoplitocarcinus*
	Homolopsis	
	Metahomola	
gorrelli	*Palehomola*	*Palehomola*
	Zygastrocarcinus	
griesi	*Zygastrocarcinus*	*Zygastrocarcinus*
hachiyai	*Homolopsis*	*Homolopsis*
icaunensis (= *fraasi*)	*Prosopon*	*Laeviprosopon*
japonica	*Homolopsis*	*Prohomola*
	Parahomola	
	Oncinopus	
	Zygastrocarcinus	
johannesboehmi (= *gibbosa*)	*Hoplitocarcinus*	*Hoplitocarcinus*
katunai	*Prohomola*	*Prohomola*
laeve	*Prosopon*	*Laeviprosopon*
laeve punctatum	*Prosopon*	*Prosopon**
	Laeviprosopon	
longa	*Prosopon*	*Tithonohomola*
	Avihomola	
mammillatum (of Förster, 1985) (= *laeve*)	*Prosopon*	*Laeviprosopon*
mendryki	*Homolopsis*	*Zygastrocarcinus*
neuhausensis	*Prosopon*	*Gastrodorus*
	(*Gastrodorus*)	
	Eopagurus	
obesa	*Homolopsis*	*Rathbunopon**
pikeae	*Homolopsis*	*Homolopsis*
planum	*Pithonoton*	*Foersteria**
	Homolopsis	
pritchardi	*Paramola*	*Paramola*
punctata	*Homolopsis*	*Hoplitocarcinus*
	Metahomola	
richardsoni	*Homolopsis*	*Palehomola*
	Zygastrocarcinus	
rostratus	*Homolopsis*	*Homologenus**
shapiroi	*Latheticocarcinus*	*Hoplitocarcinus*
schlueteri	*Homolopsis*	*Homolopsis*
schneideri	*Prosopon*	? *Homolopsis*
spiniga	*Homolopsis*	*Homolopsis*
spinosa	*Homolopsis*	*Dioratiopus**
spinulosa	*Homolopsis*	? *Homolopsis*
sublaeve	*Prosopon*	*Laeviprosopon*
transiens	*Homolopsis*	*Homolopsis*
tuberculata	*Homolopsis*	*Homolopsis*
williamsi	*Homolopsis*	*Homolopsis*
sp. (*Homola* ?)	? *Homola*	? *Homola*
sp. 1; sp. 2; sp. 3 (*Homolopsis*)	*Homolopsis*	*Homolopsis*

*Genera not included in Homolidae.

Förster, 1986 (Upper Lias) to *Prosopon mammillatum* Woodward, 1868 (Bathonian), thence to *Laeviprosopon sublaeve* (von Meyer, 1860) in the Tithonian. An alternative, though seemingly less acceptable route, was suggested through *Prosopon punctatum* von Meyer, 1860 – contemporary of *L. sublaeve* and a later offshoot of *P. mammillatum*.

In an extensive revision of living Homolidae Guinot & Richer de Forges (1995) dealt with 57 species in 14 genera. To date, the Homolidae contains ten fossil genera : *Eohomola* Collins & Rasmussen, 1992 ; *Gastrodorus* von Meyer, 1864 ; *Homolopsis* Bell, 1863 ; *Hoplitocarcinus* Beurlen, 1928 ; *Laeviprosopon* Glaessner, 1933 ; *Lignihomola* gen. nov. ; *Palehomola* Rathbun, 1926 ; *Prohomola* Karasawa, 1993 ; *Tithonohomola* Glaessner, 1993 and *Zygastrocarcinus* Bishop, 1983. A fossil species has also been assigned to the extant genus *Paromola* Wood Mason & Alcock, 1891, and another, tentatively, to *Homola* Leach, 1815.

Williams & Moffitt (1991) recorded 38 species of living homolids. Fifty two fossil taxa (including 4 unnamed) have been included in Homolidae, although of these, some have subsequently been placed in synonymy with other species within the family, others

have been relegated to different genera within the Homolidae and a few to other families. Forty three fossil members of the family are recognised herein (Tables 1 and 2).

The figured specimens are deposited in the Natural History Museum, London (BM), the Geological Survey Museum, Nottinghamshire, U.K. (GSM), the Geological Survey Museum, Canada, Ottawa (GSMC), the Institute of Geology, University of Warsaw (IPGU), the Kitakyushu Museum of Natural History, Japan (KMNH), the GeoCentrum Brabant Collections, Boxtel (MAB), the Mizunami Fossil Museum (MFM), the Geological Museum, Copenhagen (MGUH), the Sedgwick Museum, Cambridge (SM), the Museum of Geology, South Dakota School of Mines and Technology (SDSM), and the Yokosuka City Museum, Japan (YCM).

2. Genera

2.1. *Laeviprosopon*, Glaessner, 1933 and *Tithonohomola* Glaessner, 1933.

Range: Upper Jurassic–Lower Cretaceous.

Glaessner (1933) erected *Laeviprosopon* and *Tithonohomola* to contain five species formerly placed in the Prosopidae; *Prosopon laeve* von Meyer 1860, *Prosopon sublaeve* von Meyer, 1860 and *Prosopon fraasi* Möricke, 1889 were assigned to *Laeviprosopon*, while *Oxythyreus armatus* Blaschke, 1911 and *Prosopon longa* Möricke, 1889 were placed in *Tithonohomola*.

Patrulius (1966) confirmed the status of *Tithonohomola* in the Homolidae and from structural details of the front of a well preserved specimens of *Laeviprosopon laeve*, together with *lineae homolicae* preserved on specimens of *L. fraasi*, he concluded that *Laeviprosopon* should also be included in the Homolidae instead of the Prosopidae.

2.1.1. *Laeviprosopon* (Fig. 1)

Type species: By original designation, *Prosopon laeve* von Meyer, 1860 from the Tithonian of Moravia.

The carapace has a rectangular outline, about one third longer than wide, flatly arched in longitudinal and transverse sections with the sides turned almost vertically down; the pointed, slightly sulcate rostrum is downturned; the regions are well defined, although the hepatic regions are not completely isolated from the protogastric lobes and the dorsal surface is devoid

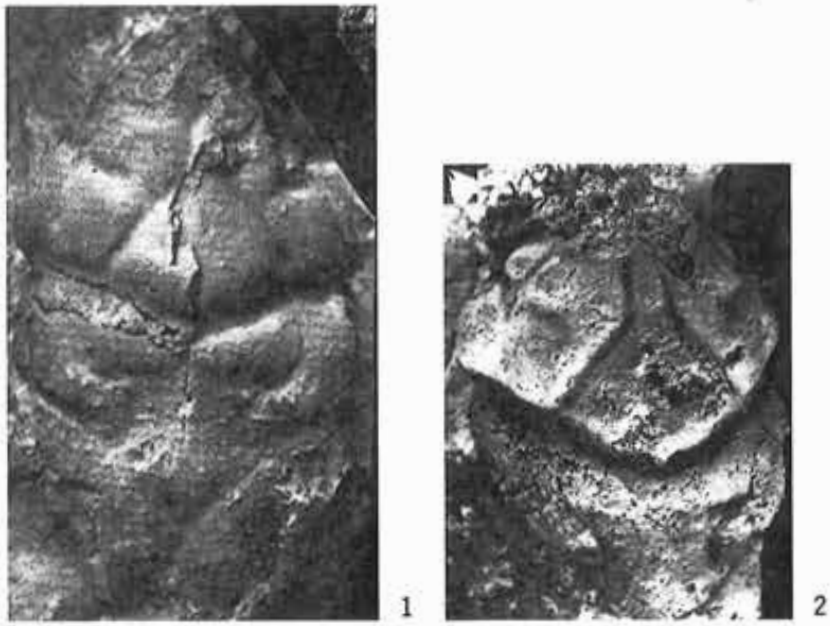


Fig. 1. *Laeviprosopon*. 1, *L. laeve* (von Meyer), IGUP/C/1/128, ×3.75, U. Oxfordian, Udiniki at Częstochowa, Poland; 2, *L. laeve* (von Meyer), IGUP/C/1/129, ×3.75, U. Oxfordian, Niwiska Dolne, Poland.



Fig. 2. *Tithonohomola. T. echinora* (Collins), Holotype IGUP/C/1/6, ×5.0, U. Oxfordian, Niwiska Dolne, Poland.

of ornament.

The subspecies *Laeviprosopon laeve punctatum* (von Meyer, 1860) of Glaessner (1929) is not recognised as a homolid by Wehner (1988), who presented a succinct taxonomic survey of the Prosopidae, and so reverts to *Prosopon punctatum* von Meyer. Wehner (1988) recognised complete conformity of the type of *Prosopon icaunensis* Van Straelen, 1936 (no. 801 Auxerre Museum), although much damaged, to the type of *L. fraasi* and included Van Straelen's species as a junior synonym of *L. fraasi*. The range of *L. fraasi* was thereby extended to the Hauterivian. Wehner (1988) further opined that the specimen figured by Förster (1985) as *Prosopon mammillatum* Woodward, 1868 retains sufficient characters to be placed with *L. laeve*.

2.1.2. *Tithonohomola* (Fig. 2)

Type species: By original designation, *Oxythyreus armatus* Blaschke, 1911 from the Tithonian of Moravia.

The lateral parts outside the *lineae homolicae* of the elongate carapace are unknown, the carapace is inflated and tuberculate anteriorly and the flattened, triangular rostrum has supraorbital projections; cervical and branchiocardiac furrows are distinct.

The placing of *Tithonohomola* in the Homolidae was questioned by Glaessner (1969) who opined that the genus could be included in the Latreilliidae. However, the genus was accepted into the Homolidae by Wehner (1988) who included in it *Nodoprosopon echinora* Collins, 1985, the only known specimen of which comes from an Upper Oxfordian megasponge facies of Poland, and *Prosopon longum* (Möricke, 1881), which, coming as it does from the Portlandian (of Moravia), is the youngest known member of the genus.

2.2. *Homolopsis* Bell, 1863 (Fig. 3)

non Homolopsis Bonaparte, 1831 (an invalid emendation of *Homalopsis* Kuhl & Hassett, 1822); *non Homolopsis* A. Milne Edwards, 1880 = *Homologenus* A. Milne Edwards *in* Henderson, 1888.

Type species: By monotypy *Homolopsis edwardsii* Bell, 1863, from the Gault (Albian) of Folkestone, Kent.

Range: Cretaceous (Neocomian) - Palaeocene (Danian).

The exact relationship of *Tithonohomola* to *Homolopsis* is not clear, but the system of furrows and tubercles in, for example *Tithonohomola longa* (which shows only the central part of the carapace), is not far from that of *H. edwardsii*. *Laeviprosopon*, however, not only foreshadows the smooth Cretaceous species of *Homolopsis*, but also seems to be near the rootstock of the family. It appears probable that the tuberculate forms comprise a series of offshoots from a continuing smooth stock. From the earlier *Laeviprosopon* species, *Homolopsis* is distinguished by its more rectangular carapace, a flatter upper surface and more complex system of furrows and lobes.

The carapace of *Homolopsis* is generally more or less rectangular, ranging from much longer than wide to slightly wider than long; the sides may converge to or diverge from the front. The upper surface is more or less flat and the sides deep and vertical or even undercut. The furrows are well developed and the regions often tumid, with or without large areolar tubercles or spines. The rostrum is bluntly pointed and turned down. There are no true orbits but a groove for the narrow eyestalk leads to a deep notch in the frontal margin in which the eyestalk could rest when

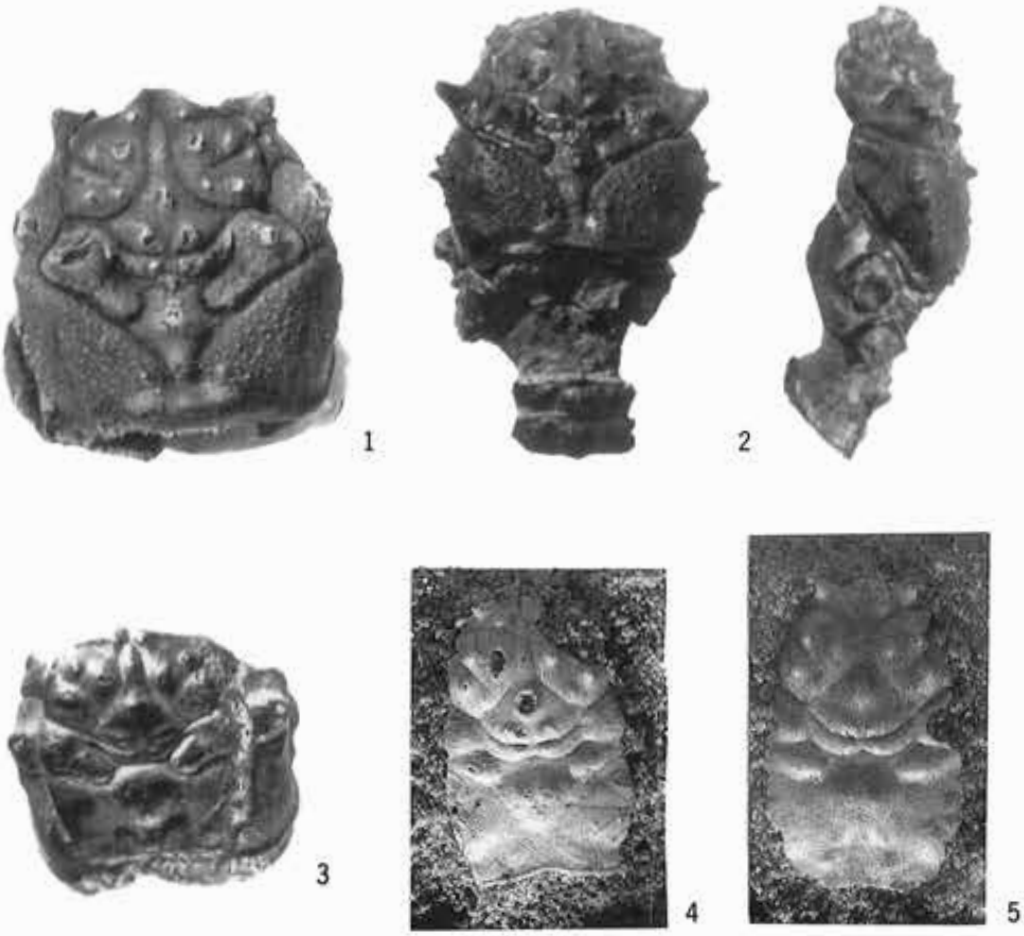


Fig. 3. *Homolopsis*. 1, *H. edwardsii* Bell, Lectotype, SM 26302, ×2.0, Gault (Albian), Folkestone, England; 2, *H. edwardsii* Bell, BM In 60132, ×2.0, top and side view, Gault (Albian), Folkestone, England; 3, *H. bringhtoni* Wright & Collins, paratype, SM B23202, ×2.0, Cambridge Greensand (Albian), Cambridge, England; 4, *H. declinata* Collins, Fraaye & Jagt, holotype, MAB k. 1005, ?male, ×5.0, Maastrichtian, Maastricht, The Netherlands; 5, *H. declinata* Collins, Fraaye & Jagt, paratype, MAB k. 1006, ?female, ×5.0, Maastrichtian, Maastricht, The Netherlands.

retracted; in this position, at least in some species, the eye itself probably rested against a smooth depressed area on the hepatic lobe, oblique in horizontal and vertical axes, on the anterior border behind the external spine or tumidity (Wright & Collins, 1972, text figs. 8a, b). The abdominal somites are tuberculate in the more highly ornamented species.

A description of the limbs (of *H. edwardsii*) was given by Carter (1898) and enlarged upon by Wright & Collins (1972); the merus is generally as long as the carapace, longitudinally sulcate and slightly granulate, the carpus is cuboid; the propodus is as long as the width of the orbitofrontal margin, the manus twice as long as wide and oval in section. The ambulatory legs are long and slender; the meri are angular in section. granulated and spinous on both borders. Two distinct forms of isolated left and right chelae – the one, long, slender ovate in section and tuberculate along the margins, the other more squat, circular and smooth are known to occur in the Cenomanian of southern England, they are comparable in shape and relative size to those found among Recent *Homola* species and may safely be ascribed either to *Homolopsis brightoni* Wright & Collins, 1972, or *Homolopsis glabra* Wright & Collins, 1972 described from the same locality.

Hartnoll (1970) drew attention to the absence of special morphological adaptation of the walking legs,

as found in some swimming crabs, when describing observations of rapid and powerful swimming activity among captive specimens of *Homola barbata* Fabricius, 1793. According to Hartnoll (1970) the 2nd-4th limbs are employed in swimming while the chelipeds are, 'held flexed against the ventral side of the body' and the 5th pair are, 'kept flat against the dorsal surface'. The crabs were seen swimming forwards and, in one instance, sideways with the form of the leg movement basically the same for either direction.

Because of the dorsal position of the *lineae homolicae* it is usually the case that only that part of the carapace between them is found, and a number of descriptions are based solely on that part. Isolated side parts - or walls - are rare, although several, attributable to two *Homolopsis* species, have recently been recognised (Jakobsen & Collins, 1997) from the Danian (Palaeocene) coral/bryozoan limestone of Denmark and Sweden.

Following Bell's publication, a crude, somewhat stylized figure of *H. edwardsii* was depicted by Salter & Woodward, 1865 and in 1877 the species - as *Homolopsis Edwardsi* [sic] - made its appearance in a systematic catalogue of fossil Crustacea compiled by Woodward, who like Bell before him, included it among the Anomura. Thirty three years were to pass, however, before Woodward (1896) made known the second fossil species, *Homolopsis richardsoni*, which comes from the Middle Cretaceous of British Columbia. Meanwhile, A. Milne Edwards (1880) had applied the name *Homolopsis rostrata* to a Recent species, later transferred to *Homologenus* (A. Milne Edwards *in* Henderson, 1888). By the turn of the century, two more European species, *Homolopsis depressa* Carter, 1898 and the first non Cretaceous species, *Homolopsis transiens* Segerberg, 1900 had been described; Segerberg (1900) also assigned *Dromiopsis gibbosa* Schlüter, 1879 to *Homolopsis*. The geographical range of the genus was considerably extended by Van Straelen (1928) when he assigned *Prosopon etheridgei* Woodward, 1892 to the genus.

Glaessner (1929) included references to the foregoing species; he also included *Homolopsis schlueteri* Beurlen, 1928 and *Hoplitocarcinus johannesboehmi* Beurlen, 1928 and considered *Homolopsis japonica* Yokoyama, 1911 should be transferred to the Latreilliidae. Beurlen (1928) made it clear that *H. richardsoni* and *H. japonica* did not belong in *Homolopsis*, but took no further steps.

Van Straelen (1936, 1944) provided a description of *Pithonoton planum* and placed three species, *tuberculata, spinosa* and *obesa* in *Homolopsis*, but of these, the two latter were to become assigned to other families. *Hoplitocarcinus johannesboehmi* was relegated to junior synonymy of *Homolopsis gibbosa*, in a critical revision of that species by Mertin (1941).

Prior to the publication of the major review of the genus by Wright & Collins (1972) all English species of *Homolopsis* had automatically been referred to *Homolopsis edwardsii*. However, during preparation of the monograph, a number of specimens ranging from the Upper Aptian Shenley Limestone *Leymeriella tardefurcata* Zone to the Cenomanian *Mantelliceras mantelli* Zone had become available for study and these, together with the original material, convinced Wright & Collins that there were three distinct species of British Cretaceous *Homolopsis*. The characters of these species (among the limited material) had confused the earlier authors. Altogether, Wright & Collins (1972) recognised the following ten species:

H. tuberculata Van Straelen, 1936 Hauterivian, France

H. planum (Van Straelen, 1936) Hauterivian, France

H.? schneideri (Stolley, 1924) Hauterivian, Switzerland

H. glabra Wright & Collins, 1972 Upper Aptian to Cenomanian, England

H. brightoni Wright & Collins, 1972 Albian to Cenomanian, England

H. edwardsii Bell, 1863 Albian, England

H. etheridgei Woodward, 1892 Albian, Queensland

H. gibbosa (Schlüter, 1879) Santonian, Germany

H. punctata Rathbun, 1917 Campanian to Maastrichtian, U.S.A. (=*H. dispar* Roberts, 1962 & *H. atlantica* Roberts, 1962)

H. transiens Segerberg, 1900 ? Campanian-Danian (?=*H. schlueteri* Beurlen, 1928)

Van Straelen's species, *Homolopsis obesa*, 1944 was

assigned to *Rathbunopon* Stenzel, 1945, and his *H. spinosa* and *Homolopsis depressa* Carter to a new genus *Glaessneria* Wright & Collins, 1972 (type species *Homolopsis spinosa* Van Straelen, 1936: 83) *non Glaessneria* Takeda & Miyake, 1969. To replace the homonym, Wright & Collins (1975) proposed *Glaessnerella*, but this genus, together with the Maastrichtian *Homolopsis dawsonensis* Bishop, 1973, was transferred to *Dioratiopus* Woods, 1953 by Glaessner (1980), *Homolopsis plana* (formerly *Pithonoton*) was subsequently transferred by Wehner (1988) to *Foersteria* Wehner, 1988 and reinstated in the Prosopidae.

Glaessner (1980) also described a poorly preserved Cenomanian species, *Homolopsis spinulosa*, from Australia and drew attention to differences in ornament from other known species of *Homolopsis*. In the same work he remarked upon characters of *Homolopsis etheridgei* differing from other members of the genus and suggested that subgeneric status might be appropriate.

Despite the poor condition of the only known specimen of *H. spinulosa* Glaessner provided a clear reconstruction, showing the juxtaposition of the spinules, from the associated external mould. By and large tubercular ornament, when developed, is not only rather variable among *Homolopsis* species, but in some, also during ontogeny. The major difference in the ornament of *H. spinulosa* would seem to be the three additional 'tubercles' on the metabranchial lobes and even these may be accounted for in other *Homolopsis* species by the presence of (single) 'intestinal' tubercles set in similar position. Sharing Glaessner's opinion on *H. spinulosa*, Bishop and Brannen (1992) referred to its status as *Homolopsis? spinulosa -an adequate distinction until better preserved specimens come to light - and suggested that the species probably represented a lineage of homolopsid evolution which apparently rapidly became extinct.*

Homolopsis mendryki from North America was made known by Bishop (1982) and this was shortly followed by the description of a Lower Aptian Japanese species, *Homolopsis hachiyai* Takeda & Fujiyama, 1983.

Roberts's (1962) hesitation on whether or not to keep *dispar* in *Homolopsis* becomes apparent in remarks following his description of that species when he said, "I have placed this species in the genus *Homolopsis* even though the rostrum is bifid.", the tip and rostral horns of which, "were freed from the matrix after the plate of the figure had been prepared." (Features clearly evident in a plaster cast kindly sent by Roberts to the present author.)

Recognising characters in common between *H. dispar* and a new species from West Greenland, Collins & Rasmussen (1992) acted upon Roberts's train of thought *Homolopsis* and divided into three genera on the presence of a single or bifid rostrum and carapaces with or without a metabranchial ridge issuing from the widest part of the cardiac region. This development apparently emerges in the Upper Cretaceous. If, as Wright & Collins (1972) suggest, *Laeviprosopon*, with a single rostrum and smooth metabranchial lobes, is near the rootstock of *Homolopsis*, then the single rostrum/smooth metabranchial lobe forms would seem to be natural ancestors and these forms were retained in *Homolopsis*. Those with a single rostrum and metabranchial ridge were placed in *Metahomola*, and *Eohomola* was erected to contain those species with a bifid rostrum and metabranchial ridge.

Unfortunately, when including *Homolopsis gibbosa* in *Metahomola*, the significance of Mertin's (1941) act of synonymising the (then) junior taxon, *Hoplitocarcinus johannesboehmi*, with *Homolopsis gibbosa* was overlooked. Consequently *Metahomola* becomes a junior synonym of *Hoplitocarcinus* with *Homolopsis gibbosa* as the type species.

The Maastrichtian species, *Homolopsis chilensis*, not only compares favourably with *H. glabra*, as noted by Förster & Stinnesbeck (1987), but the deeply incised furrows and flattened, featureless lobes, bear a striking similarity to the basic primitive characters of *Laeviprosopon laeve*. *Homolopsis chilensis* is known only from the exceptionally well preserved type specimen; the natural position of the pereiopods is quite undisturbed and clearly shows the extreme posterior attachment of the 4th and 5th pairs, with the 4th set opposite the posterior angle of the carapace, and the fifth lodged between a shallow coxigeal embayment and the margin of the narrow first abdominal somite –

the abdomen, that of a female, being entirely preserved. As figured by Förster & Stinnesbeck (1987) the probable reduced size of the 5th limb is anticipated in the smaller diameter of the basiopodite. Tucker (*per. comm.*), however, considers that because of differences in ornament from the norm among *Homolopsis* spp. *H. chilensis* may represent a new genus.

A Maastrichtian species, *Homolopsis declinata* Collins *et al.*, 1995, from Belgium and the Netherlands is eccentric in being rather more steeply arched in longitudinal section than normally encountered and in having its greatest width (between the *lineae homolicae*) some four fifths distant from the front. Two specimens show a remarkable difference in the width of the posterior margin; the one (? female) occupying almost the entire carapace width, while the other (? male) takes up about a half. The carapace outline and tuberculate dorsal surface is vaguely similar to *H. edwardsii* (whose characteristic spines occur on the carapace sides), but in that species the longitudinal section is only gently rounded and the greatest width occurs about three fourths distant from the front.

The tuberculate line of *Homolopsis* is probably continued into the Danian, Palaeocene by way of *H. brightoni*, but of the three specimens upon which Segerberg (1900, pl. 8, figs. 6–8) founded *H. transiens* two are tuberculate and the other is a relatively smooth form, a difference considered by Wright & Collins (1972) to be one where tuberculation is prominent among middle growth stages but becoming smoother with age. Recent intensive collecting from the Middle Danian coral/bryozoan limestone of Fakse, Denmark, however, has yielded a number of carapaces which, while generally smaller than Segerberg's specimens, have among them tuberculate and smooth forms of similar growth stages – almost assuredly indicating the presence of two distinct species. *Homolopsis transiens* was selected as the tuberculate form (Jakobsen & Collins, 1997) and the smooth one described as *Homolopsis spiniga* Jakobsen & Collins, 1997. Thus, while the statement by Wright & Collins (1972) that *Homolopsis* probably survived into the Danian by way of *H. brightoni* to [*H. transiens*], Segerberg's pl. 8, fig. 7, to which Wright & Collins drew attention for comparison, remains effective, it can also be said that *H. spiniga* continues, the smooth line into the Danian by way of *H. glabra*. Also, by comparison with the new material it can be seen that *Homolopsis schlueteri*, tentatively placed in synonymy with *H. transiens* by Wright & Collins (1972) differs from that species in having a longer carapace in relation to its width, in having the cervical and branchiocardiac furrows set further from the front and interrupted at the midline, and the presence of a mesogastric tubercle. The lack of surface ornament on the new Danian species, at once distinguishes it from *H. schlueteri*.

While the publication of Collins & Rasmussen (1992) was in press, three more North American Upper Cretaceous species: *Homolopsis pikeae* Bishop & Brannen, 1992; *Homolopsis williamsi* Bishop, 1992 and *Homolopsis centurialis* Bishop, 1992 were made known. The Lower Turonian *H. centurialis*, however, has a metabranchial ridge as prominent as that seen on *Hoplitocarcinus atlanticus* and *H. punctatus* – particular similarity to which latter species was noted by Bishop (1992) – and *H. centurialis* should be included in *Hoplitocarcinus*.

A *Homolopsis* sp. was listed by Via Boada (1981) from the Cenomanian of Navarre, but doesn't seem to have been described. An undescribed *Homolopsis* in the Department of Palaeontology of the Natural History Museum, London, comes from the Santonian of Zululand, South Africa.

With the removal of *Homolopsis richardsoni* to *Palehomola* (see 2.7.), *Homolopsis* is re-established in British Columbia by an, as yet undescribed, species from the Lower Maastrichtian Lambert Formation of Hornby island (Ludvigsen & Beard, 1994).

The homolopsid line with a single rostrum and without a metabranchial ridge continues to the present day in species of *Homola*.

2.3. *Eohomola* Collins & Rasmussen, 1992 and *Hoplitocarcinus* Beurlen, 1928

2.3.1. *Eohomola* (Fig. 4)

Type species: By original designation *Eohomola adelphina* Collins & Rasmussen, 1992 from the Upper



Fig. 4. *Eohomola. E. adelphina* Collins & Rasmussen, holotype, MGUH 21,589,×2.0, Upper Campanian, central Nûgssuaq, West Greenland.

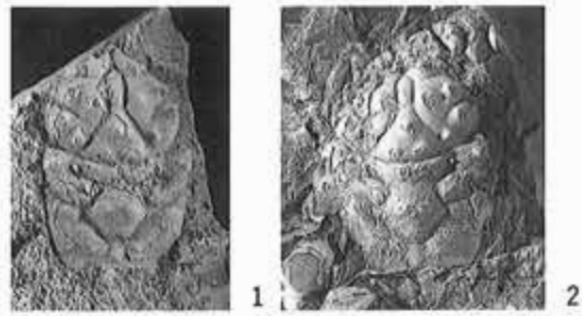


Fig. 5. *Hoplitocarcinus.* 1, *H. brevis* Collins, Kanie & Karasawa, holotype, YCM-G P854,×3.0, Santonian, Hokkaido, Japan; 2, *H. brevis* Collins, Kanie & Karasawa, paratype, MFM247,002,×3.0, Santonian, Hokkaido, Japan.

Campanian of West Greenland.

Range: Cretaceous Upper Campanian–Palaeocene late Danian.

The group of homolopsid species with a bifid rostrum and metabranchial ridge first appears with *Eohomola dispar* from the Lower Campanian of New Jersey, from whence it migrated rapidly northwards to reach West Greenland by the Upper Campanian where it is known by *Eohomola adelphina* Collins & Rasmussen, 1992 which ranges to the Maastrichtian of West Greenland. The genus also occurs in the middle and late Danian of Denmark where it is known by *Eohomola affinis* Jakobsen & Collins, 1997 – a species close to the Greenland form.

On recognising the proximity of *E. adelphina* and *E. dispar* and of those species retained in *Homolopsis* to some Recent species of *Homola*, Collins & Rasmussen (1992) considered that without knowledge of internal anatomy, external sexual characters etc., essential to neontological views on taxonomy it would be advisable to maintain the genus *Homola* as envisaged by Guinot & Richer de Forges (1981).

2.3.2. *Hoplitocarcinus* (Fig. 5)

Type species: *Homolopsis gibbosa* Schlüter, 1879 (= *Hoplitocarcinus johannesboehmi* Beurlen, 1928) from the Lower Santonian of North Germany, by original designation.

Range: Lower Santonian–Maastrichtian.

During Lower Santonian times a line with a single rostrum and metabranchial ridge had emerged in the European species *Hoplitocarcinus gibbosa* and more or less contemporaneously with *Hoplitocarcinus brevis* (Collins, Kanie & Karasawa, 1993) in Japan. By the Lower Campanian the genus had reached the Atlantic Coastal Plain of North America, *Hoplitocarcinus atlanticus*, while *Hoplitocarcinus centurialis* penetrated into the Western Inferior, in which province the geological range of the genus is extended into the Upper Campanian/Maastrichtian by *Hoplitocarcinus punctatus*. Some development through ontogeney of the metabranchial ridge may be discerned in figures of *H. punctatus* from the early Maastrichtian of North Dakota (Tucker, Feldmann, Holland & Brinster, 1987, emended figs. 1–3). A sufficient quantity of specimens may reveal similar development in other species.

A very small carapace, c 4.5 mm – c 10.0 mm, from the Maastrichtian of South Dakota described by Bishop (1988) as *Latheticocarcinus shapiroi* and placed in the Dakoticancridae compare favourably with small specimens of *H. punctatus*, differing little more than in having a flatter, more diffuse ornament – indeed the description of *L. shapiroi* could as well be applied to *H. punctatus* except that the metabranchial ridge (described as a, 'narrow ridge almost continuous with the cardiac region') of *L. shapiroi* is transverse rather than postero-oblique as in *H. punctatus*.

This could be no more than an ontogenetic trait, but it would seem prudent, for the time being at least, to maintain *H. shapiroi* at species level rather than

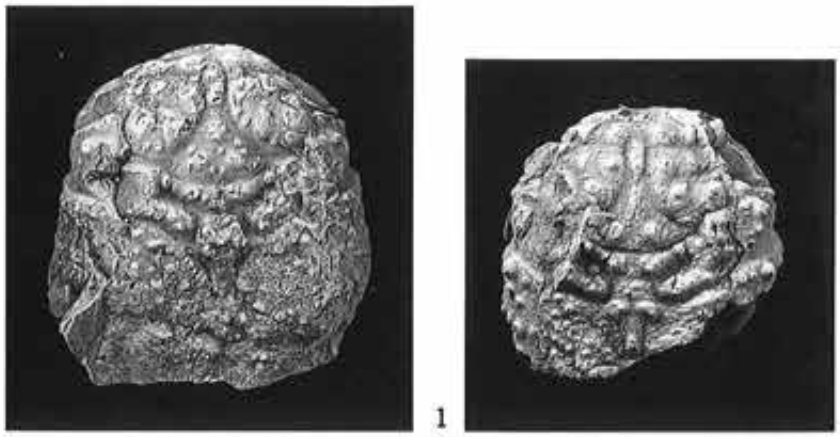


Fig. 6. *Zygastrocarcinus*. 1, *Z. griesi* Bishop, holotype, SDSM 10,004, ×1.0, late Campanian, Montana, U.S.A.; 2, *Z. mendryki* (Bishop), holotype, SDSM 10,001, ×1.5, Maastrichtian, South Dakota, U.S.A. (Both from plaster casts supplied by G. A. Bishop)

regard it as a junior synonym of *H. punctatus*.

Although diagnostic characters of this genus do not appear among extant species of *Homola*, Guinot & Richer de Forges (1995) drew attention to characters shared by the North American species of *Metahomola* [=*Hoplitocarcinus*] and the Recent genus *Hypsophrys* Williams, 1974, and in particular to *Hypsophrys noar* (Wood Mason *in* Wood Mason & Alcock, 1891), a species ranging from Florida to Guadaloupe.

2.4. *Zygastrocarcinus* Bishop, 1983 (Fig. 6)

Type species: By original designation *Zygastrocarcinus griesi* Bishop, 1983 from the Late Campanian Bearpaw Shale of Northern Montana.

Range: Middle Campanian-Maastrichtian.

Diagnosis: Carapace rectangular or slightly ovate, longer than wide, widest in posterior half, dorsal surface nearly level, laterally rounded, lateral margin nearly vertical, rostrum downturned. Carapace well differentiated by deep furrows, regions often developed into bosses or spines, surface ornamented with coarse tubercles. *Lineae homolicae* well developed, dorsal, parallel to lateral margins. Cheliped long (palm as long as carapace), slim and tuberculate. Pereiopods 2-4 long, slim, somewhat flattened with longitudinal dorsal and ventral grooves. (Bishop, 1983)

Zygastrocarcinus was introduced by Bishop (1983) to contain the Maastrichtian species *Homolopsis mendryki* Bishop, 1982 and Late Campanian *Zygastrocarcinus griesi*. The carapace is square to rectangular, dorsally flattened with well rounded margins leading to nearly vertical sides: the ocular arrangement, as observed by Bishop in *Z. griesi* (1983), is similar to that described for *Homolopsis* by Wright & Collins (1972) and the regions and lobes are well defined, with the major ornament moderately to strongly developed as bosses or spines, the secondary (dorsal surface) ornament is coarsely tuberculate. A left chela, safely associated with *Z. griesi*, relates to the elongate form attributed to *Homolopsis* and would, as depicted by Bishop (1983) almost certainly have been longer than the carapace. The genus differs from (the American species of) *Homolopsis* largely in the length/width proportions of the carapace and coarseness of the secondary ornament – and certainly, the latter is peculiar to *Zygastrocarcinus*. As Bishop (1983) also remarked, individuals of *Zygastrocarcinus* attain a much larger size than *Hoplitocarcinus punctatus* or *Hoplitocarcinus atlanticus*.

In 1986 Bishop described *Zygastrocarcinus cardsmithi*; at the same time he drew attention to the similarity of *Palehomola gorrelli* Rathbun, 1926 to *Zygastrocarcinus* and included it, together with *Homolopsis richardsoni*, in the genus. By so doing, he jeopardized the validity of *Zygastrocarcinus* by the seniority of *Palehomola*, 1926. As indicated below, however, in having structural differences inconsistent

with *Zygastrocarcinus, Palehomola* must be considered distinct and the question of synonymy is averted. Later, Bishop (1992) incorporated *Homolopsis etheridgei* and the taxonomic situation was further complicated (Bishop & Brannen, 1992) by the inclusion of *Homolopsis japonica* Yokoyama, 1911 which species had previously been transferred to *Paromola* by Jenkins (1977) – a move which threatened the status of the Recent *Paromola japonica* Parisi, 1915.

With the incorporation of *P. gorrelli* and *H. richardsoni* in *Zygastrocarcinus* Bishop (1986) opined that two evolutionary lineages within *Zygastrocarcinus* were present (one with a triangular carapace containing *Z. gorrelli* and *Z. richardsoni*, the other with a rectangular carapace with *Z. cardsmithi, Z. griesi* and *Z. mendryki* – with *Z. richardsoni* the oldest) which were distinguishable from one another and from *Homolopsis* by the Campanian. As seen below, however, there are morphological differences in *Palehomola* other than a triangular carapace which distinguishes that genus. With the removal of *Palehomola Z. cardsmithi* becomes the oldest known North American *Zygastrocarcinus*, which was pre-dated by the Albian *Z. etheridgei*.

The inclusion of *Homolopsis etheridgei* in *Zygastrocarcinus*, however, remains equivocal because it has characters not in accordance with the diagnosis of that genus as defined by Bishop (1986) and under the circumstances it may be appropriate to assign this species to a new genus, rather than to a subgenus of *Homolopsis* as suggested by Glaessner (1980) (see 2. 5).

Similarities in carapace outline, surface characters, ocular arrangement and chelae between *Zygastrocarcinus* and *Homolopsis* appear too obvious to ignore and strongly suggest that *Zygastrocarcinus* is derived from early Cretaceous stock; migrating westwards, it became established in the Western Interior of the U.S.A.

On the other hand, there is no doubt that, as observed by Bishop (1983) *Zygastrocarcinus* is less closely related to *Homolopsis* than it is to the extant genus *Paromola* Wood Mason, 1891; indeed, the similarity was sufficient to inspire Bishop to adapt the vernacular name – box crab – applied to *Paromola*, for his new genus. while it is yet feasible that *Zygastrocarcinus* could have had its origins in homolopsid stock descending from *Laeviprosopon*, its rectangular carapace outline, the prominence, greater number, and distribution of tubercles, and dense secondary ornament is strongly reminiscent of *Tithonohomola*, which also has a rectangular carapace, longer than wide, with greatest width posterior to mid-length and, generally speaking similar ornament, particularly as displayed by its Oxfordian member, *T. echinora*. It would seem, therefore, that Bishop's (1983) mention of *Tithonohomola* in relation to *Homolopsis* could have more credence if applied to *Zygastrocarcinus*.

2.5. *Lignihomola* gen. nov. (Fig. 7)

Derivation of name: *Lignum* + familial root, thereby referring to H. Woodward and J. Woods, both of whom contributed so largely to Australian palaeocarcinology.

Type species: By monotypy *Prosopon etheridgei* Woodward, 1892.

Prosopon etheridgei Woodward, 1892, p. 303; Etheridge & Dun, 1902, p. 65; Etheridge, 1917, p. 5; Glaessner, 1929, p. 342.

Homolopsis etheridgei (Woodward); Van Straelen, 1928, p. 619; Woods, 1953, p. 50; Wright & Collins,



Fig. 7. *Lignihomola. L. etheridgei* (Woodward), JSHC Coll. 2391, ×1.5, Albian, Alaru Mudstone 10 miles north of Dartmouth. between Long Beach & Baracaldine, Queensland, Australia.

1972, p. 44; Glaessner, 1980, p. 173.

Zygastrocarcinus etheridgei (Woodward); Bishop, 1992, p. 62; Bishop & Brannen, 1992, p. 321.

Diagnosis: Carapace rounded-triangular with downturned, almost vertical, inflated sides and the margins converging towards the front, the obtuse rostrum is moderately downturned; dorsal surface convex with typical homolopsid areolar tubercles and the branchial region is densely tuberculate; the furrows are well developed.

Woodward's concise description was supplemented by Etheridge (1917) who, applying the sobriquet "man-faced" crab, paid particular attention to the position of the limbs associated with carapaces. Three of his figured (pl. 1) specimens are lightly compressed between the *lineae homolicae*, but the significance of this evidently escaped Etheridge because he retained the species in the Prosopidae. Further refinements were made by Woods (1953), who illustrated male and female abdominal and the sternal position of the limbs, and by Glaessner (1980).

The rounded-triangular carapace outline differs from the rectangular outline of North American species of *Zygastrocarcinus* and the significantly more convex carapace of *Lignihomola* certainly does not meet the, "upper surface nearly level" diagnostic requirement of Bishop (1986) for *Zygastrocarcinus*. Similarly, as Glaessner pointed out, the more convex carapace does not conform to the, "more or less flat" requirement for *Homolopsis* of Wright & Collins (1972).

In carapace outline, surface convexity and dorsal features *L. etheridgei* has an affinity to *Palehomola*, but lacks the bifid rostrum of that genus.

2.6. *Paromola* Wood Mason & Alcock, 1891

Type species: By monotypy *Dorippe cuvieri* Risso, 1816.

The only known fossil member of this extant genus, *Paromola pritchardi* Jenkins, 1977, was described from several specimens of late Early Oligocene age from southeastern Australia.

After drawing attention to confusion in the literature between *Paromola* and two other genera, *Homola* and *Latreilliopsis*, Jenkins (1977) succinctly tabulated distinguishing characters and listed ten extant species either previously described or referable to *Paromola* and included *Homolopsis japonica* Yokoyama, 1911 in its original spelling, *Homolopsis japonicus* Yokoyama, 1911. Guinot & Richer de Forges (1981) on the other hand, acknowledged only nine of the above species, added one other and a subspecies.

According to Jenkins (1977) *P. pritchardi* differs from *Paromola japonica* Yokoyama apparently in, "lacking a distinct transverse ridge over the anterior part of each mesobranchial region and in bearing several additional spines." With recently collected specimens to hand, however, Karasawa (1993) considered the Japanese species to be sufficiently distinct and assigned it to a new genus, *Prohomola*; thereby restoring the status of the otherwise junior *Paromola japonica* Parisi, 1915, threatened by misdeclined homonomy.

The specimens of *P. pritchardi* comprise the sides outside the *lineae homolicae* as well as the median part of the carapace, and the species, which belongs to the *P. couvieri* species-group, is considered by Jenkins (1977) to closely resemble *Paromola petterdi* and *Paromola alcocki* (Stebbing, 1920) and although *P. pritchardi* has a closer similarity to the former species, Jenkins (1977) considered the possibility of it being ancestral to both forms.

2.7. *Palehomola* Rathbun, 1926 (Fig. 8)

Type species: By monotypy *Palehomola gorrelli* Rathbun, 1926 from the Lower Oligocene of Oregon.

Range: Lower Cretaceous-Lower Oligocene.

The outline of the carapace is broadly ovate, from its broadest part at the middle of the branchial region its sides converge to a two horned rostrum: the branchial regions extend fully to mid-carapace length. The cervical and branchiocardiac furrows are more or less equally prominent, the latter sloping back to a median point behind the cardiac region. The chelipeds are stout and elongate.

In his description of *Homolopsis richardsoni* Woodward (1896) noted, the presence of, "Two small spines (or other appendages) project (as in the genus *Latreillia*) from the rostrum on either side." It seems incredible that Rathbun (1926) should have overloo-



Fig. 8. *Palehomola. P. richardsoni* (Woodward), holotype, GSMC, ×1.5, middle Cretaceous, Queen Charlote Island, British Colombia.



1



2

Fig. 9. *Prohomola*. 1, *P. japonica* (Yokoyama), KMNH IvP 300,010, ×3.0, Middle Eocene, Kyushu, Japan; 2, *P. japonica* (Yokoyama), 5988, ×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 *Latreilliopsis* 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 pseudorostral 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. tuberclulata* 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 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 *Zygastrocarcinus*, 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 Inferior 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 *Zygastrocarcinus* 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 *Zygastrocarcinus* provided the ancestral stock. Even the larger size of *Zygastrocarcinus* 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 *Zygastrocarcinus* 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 *Zygastrocarcinus* developed, one with a triangular carapace (=*Palehomola*) on the Pacific Slope, and one with a rectangular carapace (=*Zygastrocarcinus*) in the Western Interior of the United States. A possible line of descent from *Tithonohomola* for *Zygastrocarcinus* 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. couvieri* 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 know, *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 specimens 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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