

## **Fossil Homolidae (Crustacea; Decapoda)**

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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 wide-

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

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

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

\* 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 *Paramola* 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 *Tith-*

*onohomola* 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*.

Patrullius (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

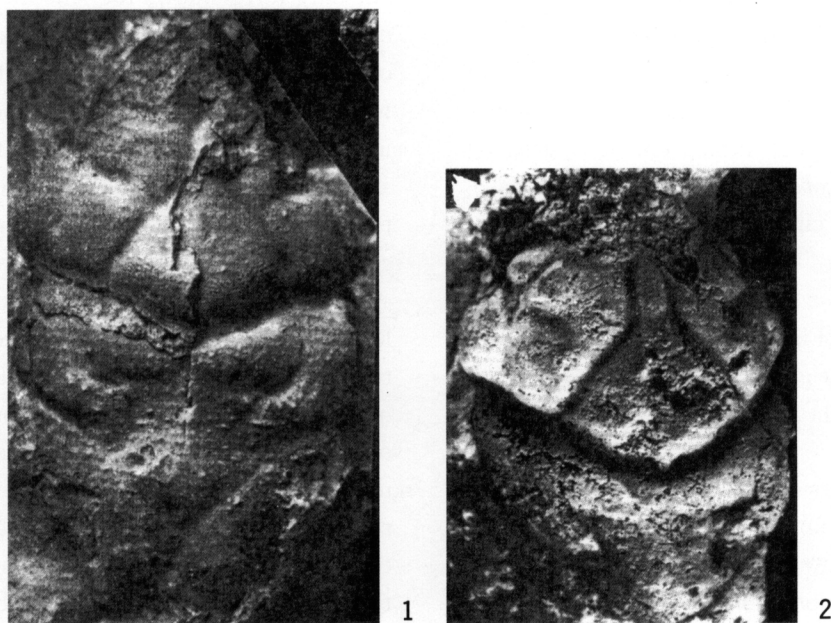


Fig. 1. *Laeviprosopon*. 1, *L. laeve* (von Meyer), IGUP/C/1/128,  $\times 3.75$ , U. Oxfordian, Udiniki at Czéstochowa, Poland; 2, *L. laeve* (von Meyer), IGUP/C/1/129,  $\times 3.75$ , U. Oxfordian, Niwiska Dolne, Poland.

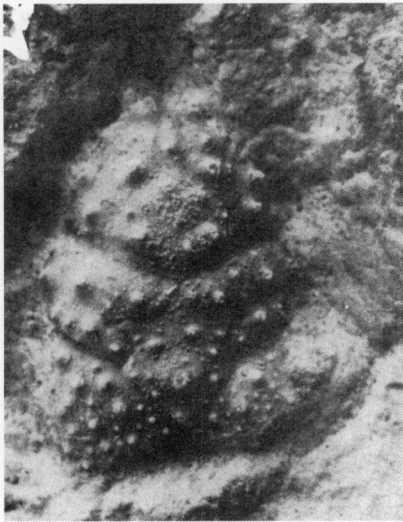


Fig. 2. *Tithonohomola T. echinora* (Collins), Holotype IGUP/C/1/6,  $\times 5.0$ , U. Oxfordian, Niwiska Dolne, Poland.

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* (Mörnicke, 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



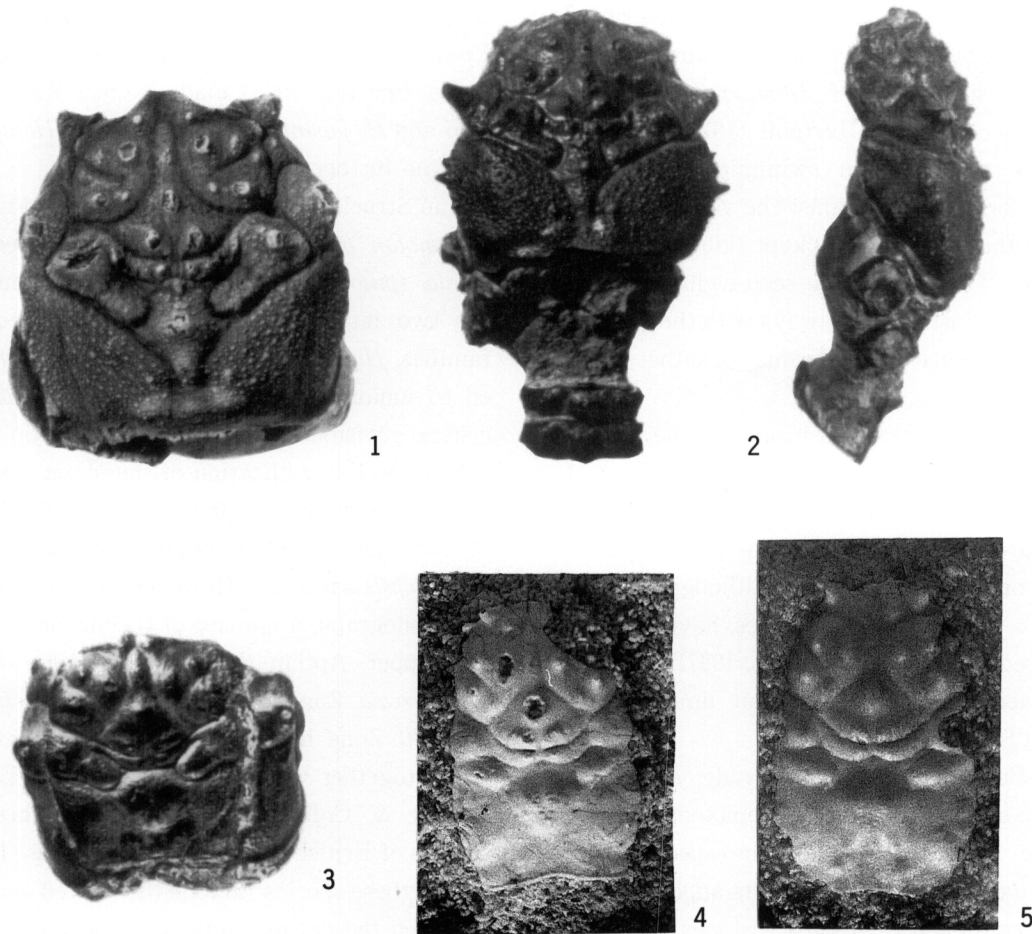


Fig. 3. *Homolopsis*. 1, *H. edwardsii* Bell, Lectotype, SM 26302,  $\times 2.0$ , Gault (Albian), Folkestone, England; 2, *H. edwardsii* Bell, BM In 60132,  $\times 2.0$ , top and side view, Gault (Albian), Folkestone, England; 3, *H. brightoni* Wright & Collins, paratype, SM B23202,  $\times 2.0$ ,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