

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

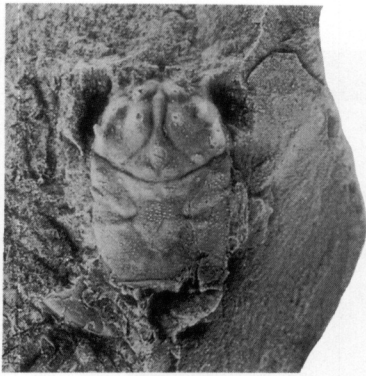


Fig. 4. *Eohomola E. adelphina* Collins & Rasmussen, holotype, MGUH 21,589,  $\times 2.0$ , Upper Campanian, central Nûgssuaq, West Greenland.

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

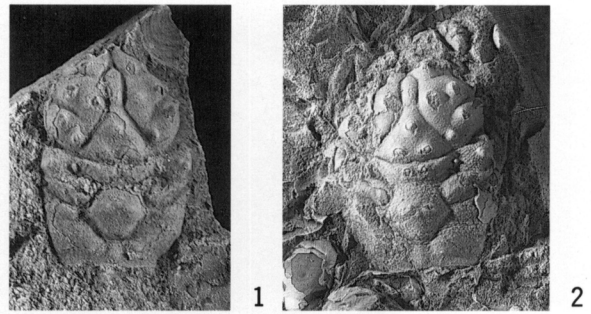


Fig. 5. *Hoplitocarcinus*. 1, *H. brevis* Collins, Kanie & Karasawa, holotype, YCM-G P854,  $\times 3.0$ , Santonian, Hokkaido, Japan; 2, *H. brevis* Collins, Kanie & Karasawa, paratype, MFM247,002,  $\times 3.0$ , Santonian, Hokkaido, Japan.

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 Interior, in which province the geological range of the genus is extended into the Upper Campanian/Maastrichtian by *Hoplitocarcinus punctatus*. Some development through ontogeny 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 shapiroï* 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. shapiroï* 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. shapiroï* 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. shapiroï* at species level rather than

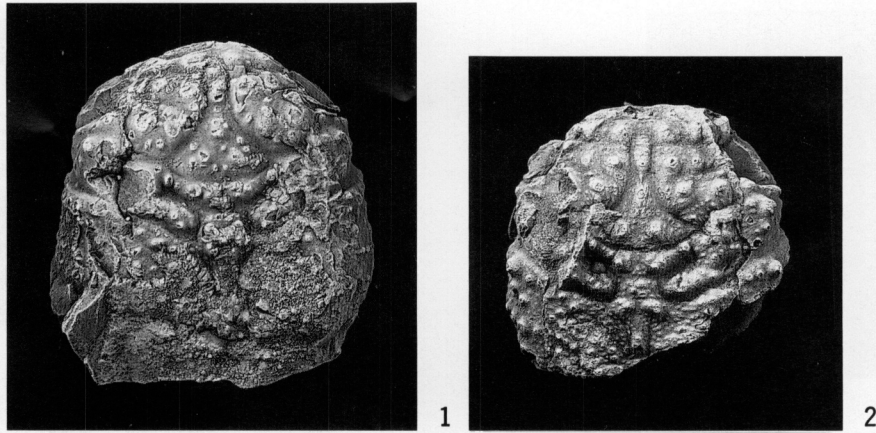


Fig. 6. *Zygastrocarcinus*. 1, *Z. griesi* Bishop, holotype, SDSM 10,004,  $\times 1.0$ , late Campanian, Montana, U.S.A.; 2, *Z. mendryki* (Bishop), holotype, SDSM 10,001,  $\times 1.5$ , Maastrichtian, South Dakota, U.S.A. (Both from plaster casts supplied by G. A. Bishop)

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,  $\times 1.5$ , 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 *Latreillia*, 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 homonymy.

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. cuvieri* 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-