

spines a rounded, barely elevated suborbital ridge bearing three equidistant spines curves to the postcervical notch. The lateral wall of the ridge is steep, and somewhat concave. The postcervical furrow is wide and deep with the posterior wall sloping steeply back throughout its length; it is broadly curved at the midline and obtusely V-shaped to the suborbital ridge. The carapace behind the postcervical furrow is incomplete. The part preserved has a median carina with three spines reducing in size posteriorly; the distance between the first and second spines is about equal to the basal length of the second and third spines together. On either side of the foremost of these two spines is an enlarged granule. There are five spines reducing in size and distance apart on the lateral margins and the surface between the lateral margins and median ridge is regularly concave.

Apart from the bases of the postcervical furrow and the groove between the hindmost of the median paired spines the entire surface is covered with rounded granules of several diameters generally well separated, but crowding the spines and ridges; on the branchial region they tend to form longitudinal rows.

Discussion. *Linuparus (P.) spinosus* is similar to *L. (P.) africanus* Glaessner, 1932, *L. (P.) schluteri* (Tribolet, 1874), *L. (P.) grimmeri* Stenzel, 1945, *L. (P.) watkinsi* Stenzel, 1945, and *L. (P.) eocenicus* Woods, 1925, in its tuberculate surface and in the general pattern of spines, but in *L. (P.) spinosus* the spines are much stouter and the two pairs of spines between the suborbital ridges, and postcervical furrow are closer to the midline. Furthermore it differs from *L. (P.) africanus* and *L. (P.) grimmeri* in having two median spines and a stronger ornament on the anterior part of the carapace; from *L. (P.) schluteri*, *L. (P.) grimmeri* and *L. (P.) watkinsi* it differs in having only three spines along the suborbital ridge. The supraorbital spines of *L. (P.) eocenicus* are united by a ridge and the suborbital ridge has 3–5 spines, there is, however, only a single elongate median tubercle set between the postorbital spines.

Infraorder Anomura H. Milne-Edwards, 1832
Superfamily Galattheoidea Samouelle, 1819
Family Galatheidæ Samouelle, 1819
Subfamily Galatheinae Samouelle, 1819

Genus *Galathea* Fabricius, 1793

Type species. *Cancer strigosus* Linné, 1761 by subsequent designation Latreille, 1810 [ICZN opinion 434].

Range. Lower Cretaceous to Recent.

Galathea cf. *G. strigifera* Fischer-Benzon 1866

Fig. 6

- 1866 *Galathea strigifera* Fischer-Benzon, p. 28, pl. 5, figs 4–6.
1900 *Galathea strigifera* Fischer-Benzon; Segerberg, p. 352, pl. 7, figs 1, 2?
1929 *Galathea strigifera* Fischer-Benzon; Glaessner, p. 173 (see also for other synonymies).

Range. Paleocene, Danian.

Material. A dorsal fragment of a carapace (MGUH 21.586) from the slightly consolidated sand of the 'Sonja lens' in the Agatdal Formation in Agatkløften, Nûgs-suaq.

Remarks. The carapace fragment is 6.0 mm in length and 5.0 mm in width; the rostrum and lateral margins are not preserved. From close behind the anterior margin to a little behind the cervical furrow the surface shows a pattern of undulating transverse ridges similar to the Middle Danian *G. strigifera* from Fakse, Denmark. The sharp edges of the transverse ridges show a fine and delicate crenulation and a row of very small setae pits on the steep anterior side. The posterior side of each ridge is smooth and flat, gently sloping. No spines are preserved on the dorsal surface and it is uncertain whether or not the frontal area was granulated.

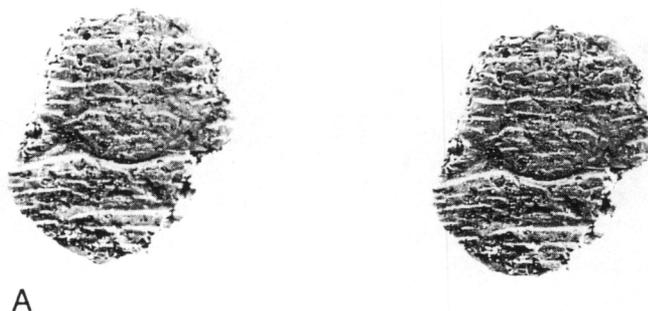


Fig. 6. *Galathea* cf. *G. strigifera* Fischer-Benzon from the Middle Paleocene at Agatkløft, 'Sonja lens', MGUH 21.586, dorsal view of carapace, $\times 1$.

Among fossil Galatheinae described the present specimen comes very close to *G. strigifera*, but the variation within species of *Galathea* is considerable and a safe determination of small fragments is not possible.

Infraorder Brachyura Latreille, 1803
Section Podotremata Guinot, 1977
Sub-section Dromiacea de Haan, 1833
Superfamily Dromioidea de Haan, 1833
Family Dynomenidae Ortmann, 1892

Genus *Dromiopsis* Reuss, 1859

Type species. *Brachyrites rugosus* von Schlotheim, 1820, by subsequent designation Beurlen, 1928.

Range. Upper Cretaceous to Paleocene.

Dromiopsis granulata sp. nov. Figs 7A-D

Derivation of name. With reference to the granulated surface of the median gastric region.

Diagnosis. – A *Dromiopsis* with rounded pentagonal outline; lateral edge sharp, forming a ridge with small, well separated spines. Cervical and branchiocardiac furrows distinct, the branchiocardiac furrows stopping at the conspicuously delimited cardiac region. Dorsal surface almost smooth with fine pores, and close granulation on the meso-urogastric region. The gastro-hepatic region is undifferentiated.

Material. Holotype, a carapace and associated chela (MGUH 21.587). In an Upper Cretaceous, Maastrichtian, concretion from the 'Oyster-ammonite conglomerate' on the west side of Agatdalen, 530 m above sea level. Paratype, a longitudinally compacted carapace (MGUH 21.588). 'Oyster-ammonite conglomerate', locality III at alt. 510 m on west side of Agatdalen.

Description. The carapace is rounded sub-pentagonal in outline, a little longer than wide, with the greatest width just anterior to the cervical furrow, regularly tumid transversely. In longitudinal section it is convex with the highest point more or less coincident with the greatest width. The front is damaged, but has most of one side preserved to indicate a triangular form. The orbitofrontal width occupies three fourths of the carapace width and the large, broadly elliptical orbits form an angle of about 85° to the midline. The upper orbital margin is raised with no indication of an outer orbital spine; the lower orbital margin extends a little beyond the upper orbital margin. The lateral edges are sharp, almost

ridge-like and the sides are moderately inclined inwards. There are three or four regularly placed spines on the short, broadly rounded anterolateral margins and three or four similar spines line the more gently rounded lateral margin between the furrows. The posterolateral margins are curved with a few granules close behind the branchiocardiac furrow; the edge is gently rounded and leads by bluntly rounded posterior angles to the posterior margin which is a little narrower than the front.

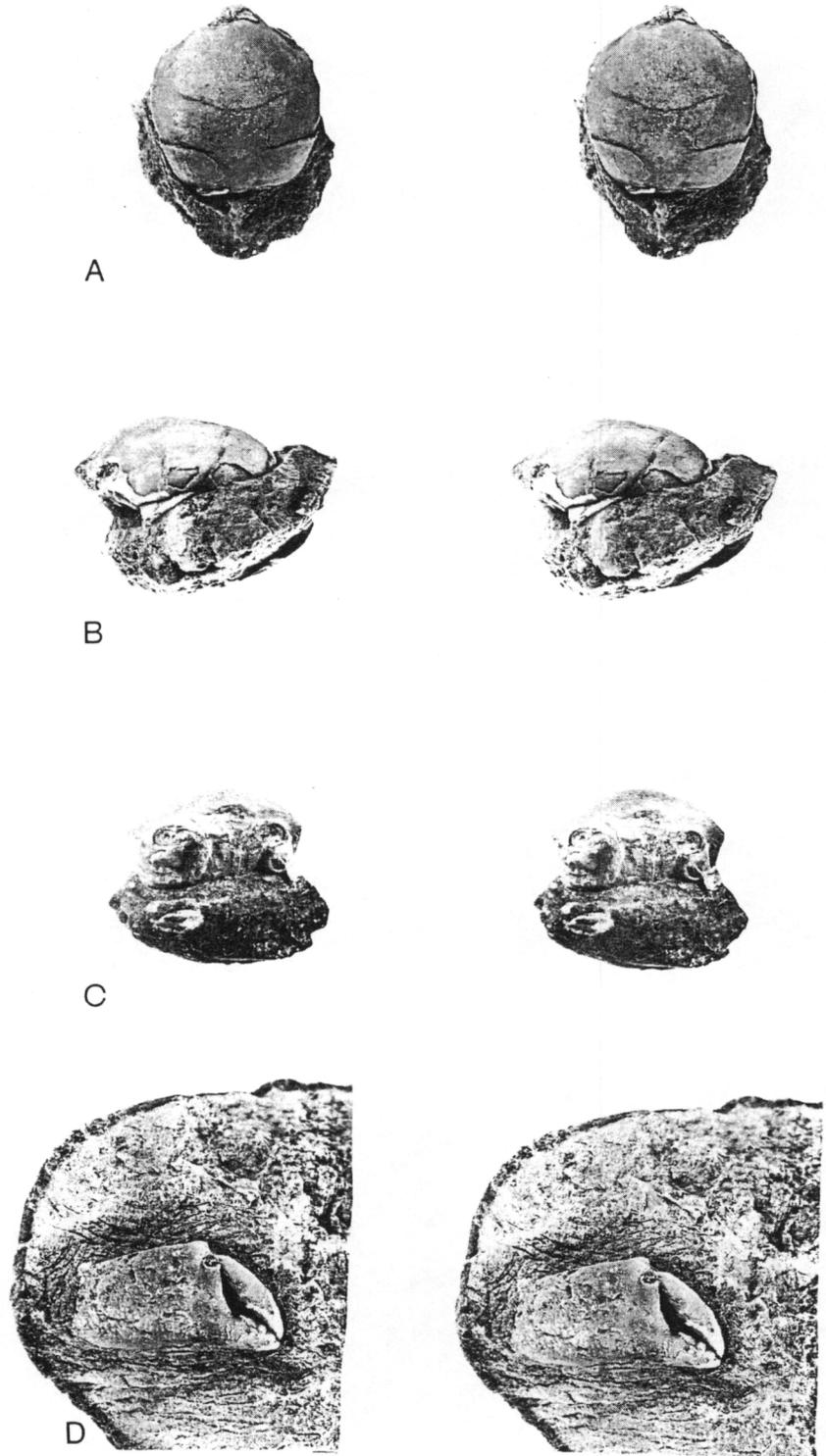
The cervical and branchiocardiac furrows are well defined; the cervical crosses the midline in a shallow curve a little more than half the distance from the front, then runs forwards and outwards in a gentle curve to the lateral margin; crossing the margin it curves back to join the branchiocardiac furrow. The branchiocardiac furrow is bordered behind by a low ridge and terminates at the margin of the elongate-pentagonal, slightly tumid cardiac region clearly defined by a thin groove. The post-cervical furrow, separating the epi- and mesobranchial lobes (well developed in, e.g. *D. rugosa* Schlotheim) is reduced to a short V-shaped spur off the cardiac furrow and serves to delimit the posterior margin of an otherwise undifferentiated urogastric lobe. There is evidence of very faint epigastric nodes at the base of the front and two or three pits mark the sides of an otherwise undefined mesogastric lobe.

The dorsal surface is minutely and closely pitted and there is a scattering of fine granules over the median area of the gastric region; similar sized granules on the cardiac region are loosely arranged in a circle.

A right-hand chela is present in the nodule with the carapace. By and large it agrees with the chelae of other *Dromiopsis* and may be considered to belong to the present species. The propodus is subcylindrical with the inner side flattened, without a sharp upper or lower margin; on the tumid outer surface are six or seven longitudinal rows of granules with a very faint pattern of short and irregular lines or depressions in between. The fixed finger is about one third the length of the propodus; it is directed a little downwards and inwards and has a constriction proximally. A smooth concavity at the proximal end of the opposing margin is followed by three or four blunt cusps decreasing in size distally.

Discussion. In its general outline and conspicuous furrows *D. granulata* rather resembles the Danian *D. rugosa* (Schlotheim); it differs in having poorly defined gastric lobes, a prominent intestinal lobe and in being much less granulate. A weaker cervical furrow, absence of granular ornament, a flattened cardiac region and large rugose or pitted areas at the base of the mesogastric lobe serve to distinguish *D. laevior* Reuss, 1859.

Fig. 7. *Dromiopsis granulata* sp. nov. from the Maastrichtian at Agatkløft. A-C: holotype, MGUH 21.587, A: dorsal view; B: side view, C: frontal view, $\times 2$; D: paratype, MGUH 21.588, outer surface of right chela, $\times 3$.



D. elegans Reuss, 1859 may be readily distinguished from *D. granulata* by its transversely ovate carapace. *Dromiopsis americana* Roberts, 1956, Paleocene, Vincentown Formation of New Jersey has a prominent intestinal lobe, but the cervical furrow is weaker and does not extend to the lateral margins; it differs further in having marginal spines placed only between the cervical and branchiocardiac furrows, in having rather conspicuous epi- and mesogastric lobes, and a poorly defined cardiac region.

Roberts (1956, p. 8) stated that the trend in *Dromiopsis* (from *Dromiopsis gigas* Forir, 1887) was towards a smooth carapace and a progressive reduction in the number and conspicuousness of the furrows. In this, he considered *D. americana* to be the culmination of the development begun by the Middle Maastrichtian *D. elegans* (which continues into the Danian) and continued through *D. laevior*, while *D. rugosa* formed a granulose and markedly furrowed line.

The present authors were not able to verify the presence of *D. elegans* in the Maastrichtian, but certainly, Danian adult forms of that species normally have weak grooves and a smooth surface. *Dromiopsis granulata* has a decidedly weaker cervical furrow than either *D. gigas* or *D. rugosa* and the surface granulation is finer, almost restricted to the gastric region. These characters together suggest that *D. granulata* forms a Maastrichtian member of Roberts's (1956) *D. americana* line.

Sub-section Archaeobrachyura Guinot, 1977
Superfamily Homoloidea White, 1847
Family Homolidae White, 1847

Genus *Eohomola* gen. nov.

Derivation of name. Eos (early) + Homola.

Type species. *Eohomola adelphina* sp. nov.

Diagnosis. The carapace is longer than wide, quadrangular, dorsal surface more or less flat, spinose or tubercular. The rostrum is bifid and there is a transverse metabranchial ridge extending from the widest part of the cardiac region towards the lateral margin. Orbital arrangement as in *Homolopsis*.

Range. Upper Cretaceous.

Discussion. The only significant character distinguishing *Homola* from the fossil genus *Homolopsis* is, according to Wright & Collins (1972, p. 44), the single bluntly pointed and downturned rostrum in *Homolopsis*, as opposed to a bifid rostrum in *Homola*. In having a bifid rostrum with well developed horns, the new genus is

distinct from *Homolopsis*. However, in addition to the bifid rostrum *Eohomola* has a transverse metabranchial ridge extending from the widest part of the cardiac region to the lateral margin. This ridge is absent from six, at least, of the eight European members of *Homolopsis* recognised by Wright & Collins, 1972 (the exceptions being *H. gibbosa* (Schlüter, 1879) and *H. tuberculata* Van Straelen, 1936, the latter known only from the anterior portion of the carapace), but present in the North American species *H. punctata* Rathbun, 1917, and *H. atlantica* Roberts, 1962 (the latter placed in synonymy with *H. punctata* by Wright and Collins, 1972). While describing his species *Homolopsis dispar* Roberts (1962, p. 180) included a description of a bifid rostrum, "freed from the matrix after the plate figure has been prepared", and this feature is clearly discernible on (a plaster cast of) the specimen (made available to J. S. H. C.). Roberts also drew attention to a metabranchial ridge fused laterally to the cardiac region and this is seen to extend slightly concave to the lateral margin. In having these two eminently diagnostic characters in common with *Eohomola adelphina*, *dispar* (considered by Wright & Collins, 1972 to be synonymous with *Homolopsis punctata*) fulfils the requirements for *Eohomola* and is here transferred to that genus.

Eohomola adelphina sp. nov.

Figs 8A-C

1970 *Homolopsis* sp.; Rasmussen in Rosenkrantz, p. 425, 426.

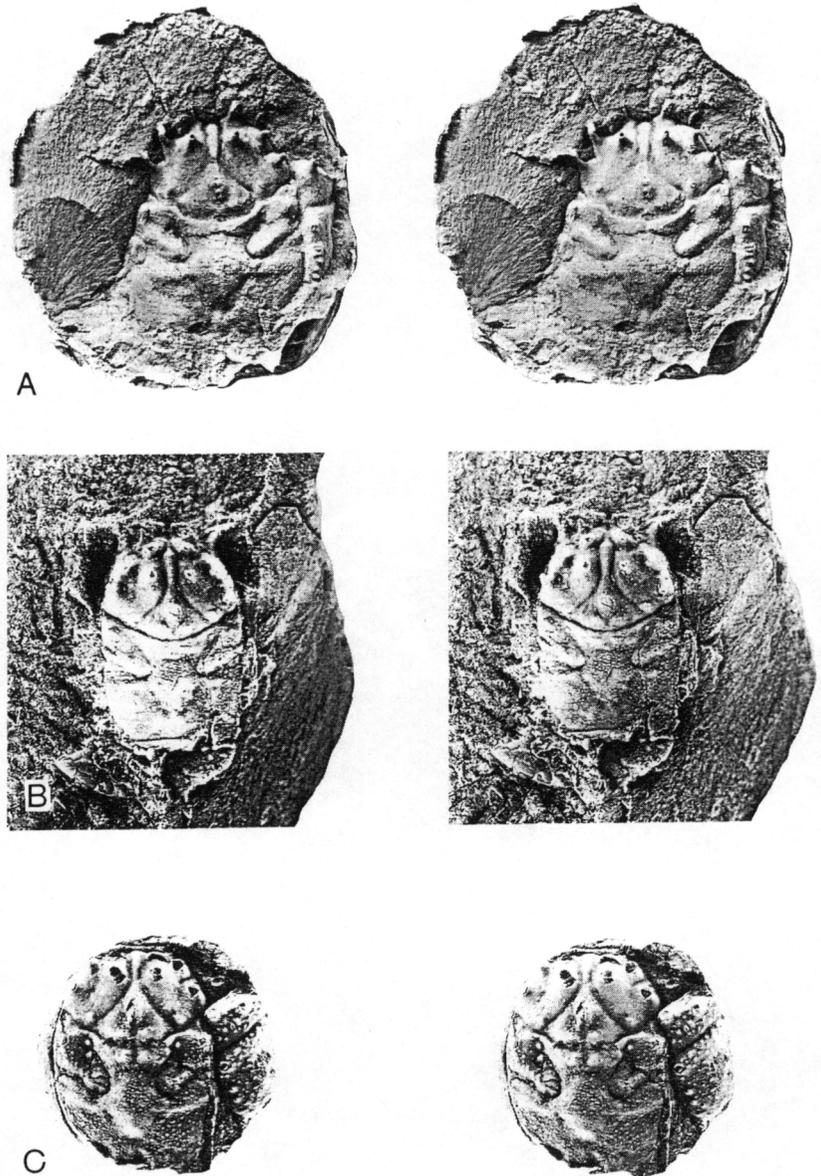
Derivation of name. Brotherly – with reference to the relationship with *Homola*.

Diagnosis. *Eohomola* with the rostral horns long, widely divergent and upturned; the transverse metabranchial ridge is straight and extends to the lateral margin.

Range. Upper Campanian to Maastrichtian.

Material. Nine carapaces. Holotype, a carapace (MGUH 21.589) from a calcareous concretion found in a boulder in the 'Oyster-ammonite conglomerate' on the western side of Agatdalen, 510 m above sea level in central Nûgssuaq. Most of the boulders in this conglomerate are of Maastrichtian age, but a few Upper Campanian fossils are also recorded, and this age is more in agreement with the occurrence of two carapaces from Ikorfat on the north coast of Nûgssuaq. Additional specimens, four carapaces from the 'Oyster-ammonite

Fig. 8. *Eohomola adelphina* sp. nov.
 A: holotype, MGUH 21.589, from the Maastrichtian at Agatkløft, dorsal view of silicone rubber cast of the carapace, $\times 2$; B: paratype, MGUH 21.590, from the Upper Campanian–Maastrichtian, dorsal view, $\times 1.5$; C: paratype, MGUH 21.591, from the Upper Campanian–Maastrichtian at Ikorfat, dorsal view, $\times 3$.



conglomerate' in Agatkløften (405–410 m): two from the Upper Campanian black shales of Brudkløft (625 m) at Ikorfat; a single carapace of uncertain age from Saviarqat between Niaqornat and Ikorfat; and a small carapace lacking any information regarding age or locality.

Description. The carapace is subquadrate in outline, almost as wide as long (excluding the rostrum) with convex sides widest at the anterior part of the branchial region. Between the prominent *line homolica* the length is about one and one third to one and a half times the width. In section it is nearly flat longitudinally with the front only slightly downturned; it is slightly arched

transversely, smoothly rounded at the lateral margins with deep sides inclined a little inwards. The orbitofrontal margin occupies about 60–66% of the carapace width. The rostrum is very prominent and forms a broad moderate to deeply grooved projection continuing the downward slope of the front. It is widely bifurcated with two long, upwardly directed pointed spines. The upper orbital margin is ridged and has a stout forwardly directed median spine, a longer one at the outer angle and a fine spinule at the lower outer angle. The obtusely angular cervical furrow is deep and distinct, unbroken at the midline and continuing to the margin with almost no undulation round the meso- and protogastric lobes; below the margin it curves back to join the branchiocar-

diac furrow below the somewhat bulbous epibranchial lobe. The branchiocardiac furrow runs almost parallel to the cervical as far as the *linea homolica* where it turns abruptly forward for a short distance before resuming its original course.

The triangular mesogastric lobe carries a large median tubercle which may be either elongated or double-pointed, behind this is a pair of small transversely expanded tubercles. The anterior mesogastric process is devoid of tubercles; it terminates in a point between small rounded epigastric lobes each of which has a small spiny tubercle, and is constricted behind by the base of a large forwardly hooked spine forming the inner of two rising from each protogastric lobe; there is also a low tubercle close to the angle of the mesogastric lobe and cervical furrow. The hepatic furrow is deep at the margin where it curves round the outer protogastric spine when it becomes shallower and sometimes obsolete as it curves round the inner spine. The hepatic lobe has a similar spine to those on the protogastric lobe with one or two granules near its lateral base, and there is another spine on the epibranchial lobe. The very short urogastric lobe, divided by a median furrow, is tumid, almost ridged and sometimes has a few granules near the midline; it tapers rapidly as it curves round the base of the mesogastric lobe. A deep depression separates the urogastric lobe from the ridged extension of the mesobranchial lobe and there is a mesobranchial spine close to the cervical furrow. The broad tongue-shaped cardiac region has three indistinct to obsolete tubercles in an inverted triangle; from its widest part a low ridge extends almost transversely across the anterior part of the metabranchial lobe to the margin. Posteriorly a shallow depression separates the cardiac region from the almost flat metabranchial lobes and ovate intestinal region.

The dorsal surface is without pores, but anteriorly has a scattering of moderately sized well spaced granules with smaller ones intermingled; they become more densely crowded posteriorly and on tumid areas, while those on the cardiac region tend to become transversely linear.

The fragments of walking limbs preserved are long, slender elliptical in section and stoutly spinous.

The carapace length ranges from 10.0 mm to 15.0 mm and there are no structural differences among specimens from the several localities in Nügssuaq.

Discussion. The dorsal surface of *E. dispar*, which comes from the Campanian of New Jersey, is somewhat worn causing the ornament – which could well have been spinose – to appear tubercular; it differs from *E.*

adelphina in having less well developed rostral horns, the cervical furrow is shallower at the midline and the hepatic regions are more triangular, more deeply separated from the protogastric lobes causing the basal protogastric tubercle to appear as if on the hepatic region.

The arrangement of the principle spines on the dorsal surface of *Homolopsis*, *Eohomola* and *Homola* is essentially similar, differing little more than in strength of development and juxtaposition.

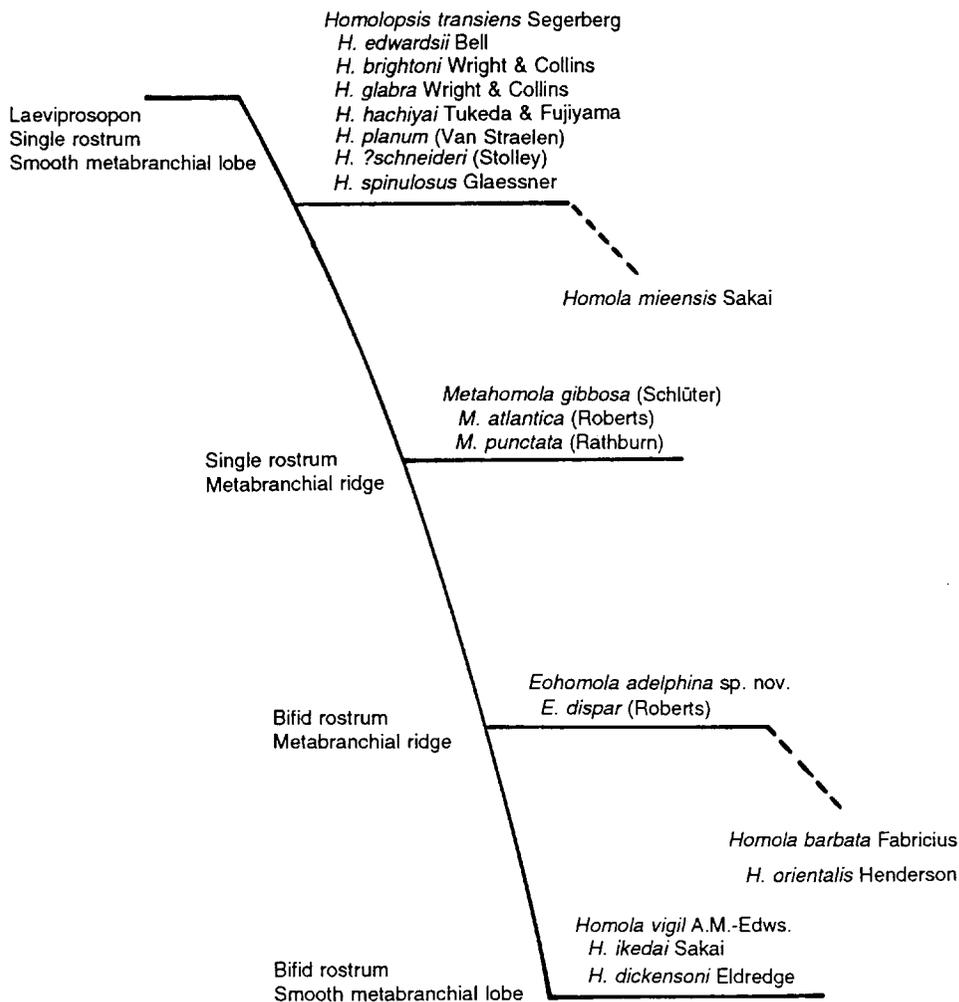
Remarks. The problem of homolids with a single or bifid rostrum/with or without a metabranchial ridge apparently emerges in the Campanian. If, as Wright & Collins (1972) suggest, *Laevihomola* – with a single rostrum and smooth metabranchial lobes – is near the root stock to *Homolopsis*, then the single rostrum/smooth metabranchial lobe forms would seem to be natural successors, but by Campanian times *H. punctata* and *H. atlantica* with a single rostrum had developed a metabranchial ridge (albeit weakly developed) and were followed by the strongly ridged European species *H. gibbosa* (Schlüter, 1879) in the Santonian.

The line of species with a single rostrum and smooth metabranchial lobe is carried into the Danian by way of *H. planum* (Van Straelen, 1936), *H. brightoni* Wright & Collins, 1972, etc., to *H. transiens* Segerberg, 1900, and may be said to be represented at the present day by *Homola mieensis* Sakai, 1979 (Indo-Pacific). The line with a bifid rostrum and a metabranchial ridge appears in the Campanian (*Eohomola dispar*); it is represented in the Campanian and Maastrichtian by *E. adelphina* and possibly represented at the present time by *Homola barbata* Fabricius and *H. orientalis* Henderson, 1888, s.l. – the metabranchial ridge being much reduced in the latter. This may be summarised as in Fig. 9.

From the above it becomes apparent that Section 2 is isolated from Section 1 (*Homolopsis sensu stricto*) and Section 3 (*Eohomola*) and should therefore constitute a separate genus for which the name *Metahomola*, containing *gibbosa*, *punctata* and *atlantica* is here proposed, with *punctata* selected as type-species.

While close to some species of *Homola*, *adelphina* and *dispar* cannot well be included in that genus without knowledge of internal anatomy, external sexual characters etc., essential to neontological views on taxonomy, but placed in *Eohomola* they stand as a possible stage in development between *Homolopsis* and *Homola*. Similarly, to avoid confusion between neontological and palaeontological demands, it is considered advisable to maintain the genus *Homola* as envisaged by Guinot & Richer de Forges (1981).

Fig. 9. Cladogram showing the relationship of homolid species with earliest taxa at the top.



Superfamily Raninoidea de Haan, 1841
Family Raninidae de Haan, 1839
Subfamily Raninidae de Haan, 1841

Genus *Hemioon* Bell, 1863

Type species. By monotypy; *Hemioon cunningtoni* Bell, 1863. [= *Raninella elongata* A. Milne Edwards, 1862]

Range. Upper Albian to Coniacian.

Hemioon eysunesensis sp. nov. Figs 10A-C

1970 Raninid, Rasmussen in Rosenkrantz, p. 425

Derivation of name. From Eysunes (Old Norse: smouldering promontory) a mediaeval Norse locality in the northernmost hunting district of West Greenland. Identified by Rosenkrantz (1967, p. 380) as Nûgssuaq, where bituminous black shale was locally set on fire and smoke was seen for several years. The red-burned shales from self combustible fires are seen at many points on the coast of Nûgssuaq.

Diagnosis. A *Hemioon* with a truncated elliptical carapace widest at base of the lateral spines; anterolateral margins rather long, converging towards the front which is less than two thirds the width. Rostrum bifid, the horns separated by an acute V-shaped cleft and slightly longer than the outer orbital spines. The lateral spines are much stronger than those on the anterolateral margin.