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A Synopsis of the Biostratigraphic Distribution of the Crab Genera (Crustacea, Decapoda) of the Danian (Palaeocene) of Denmark and Sweden

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Abstract

The relationship of the fifteen genera of crabs presently recognised from the Danian (Lower Palaeocene) of Denmark and Sweden to stratigraphic and biogeographic occurrences of similar genera elsewhere is discussed, with particular reference given to those genera passing through the KT Boundary.

Key words: Crustacea, Decapoda, Danian (Palaeocene), Denmark, Sweden, stratigraphic distribution, palaeoenvironment.

Introduction

The first definitive work on the decapod crustaceans from the Danian (Lower Palaeocene) of Denmark and Sweden was that of Segerberg (1900) who described twenty species attributed to eleven genera. In the following year, Woodward (1901) published an accurate English translation of the descriptions of those species from Faxe (*sic*) brought to England by Miss Caroline Birley and Miss L. Copeland, which are now deposited in the Palaeontological Department of the Natural History Museum, London. The original collection of Segerberg and a vast accumulation of material since amassed is currently being assessed by the present authors.

Of the fifteen decapod genera now known from the Danian of Denmark and Sweden ten make their appearance in the Cretaceous and of these, three do not extend beyond the Danian, three continue to the Tertiary and/or Quarternary, three give rise to

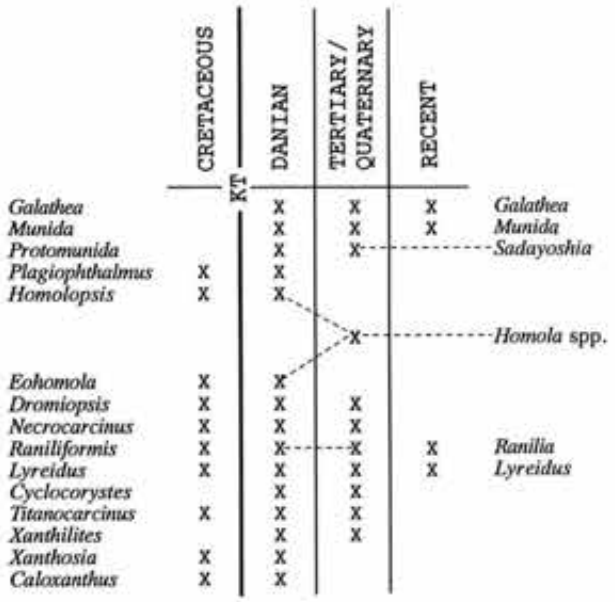


Fig. 1. Broad outline of stratigraphic occurrences of Danish/Swedish Danian crab genera in relation to the KT boundary and subsequent events.

Recent forms and one continues to the Recent. Two of the genera making their appearance in the Danian do not extend beyond the Tertiary, two are extant and one gives rise to a Recent form (Fig. 1).

Stratigraphic Appraisal of the Danian

The type Danian stage as exposed in Denmark and Sweden is a complex formation comprising numerous lithological units. Formerly the division was based on primary spines of the echinoid genus *Tylocidaris* Pomel, 1883 and although this system is still widely recognised (Gravesen, 1993) from a macrofaunal point of view, other studies based on microfauna — e. g. dinoflagellates, Hansen (1977); coccoliths, Perch-Nielsen (1979a, 1979b) etc. —have shown these organisms to be more reliable as subdivisional indicators.

Broadly speaking, however, the formation is divided into Early, Middle and Late Danian and crabs occur to a greater or lesser degree in all of these units.



Fig. 2. Map showing the crab-bearing Danian localities in Denmark and southern Sweden. 1, Bagenkop, Langeland Island; 2, Fakse quarry, southern Zealand; 3, Type-section at Stevns Klint, southern Zealand; 4, various outcrops in neighbourhood of Copenhagen; 5, Limhamn quarry, Scania, southern Sweden.

The Early Danian as exposed at the type section at Stevns Klint, southern Zealand (Fig. 2) is a bryozoan-rich, biohermal limestone which, "typically consists of numerous skeletal fragments of benthic biota, mostly bryzoans in a micritic matrix" (Gravesen, 1993) and here includes the hardground horizons, 'Krabbelag' of Nielsen (1917), which contains crabs, but not in such numbers as are met with in the coral-bryzoan limestone in the section of the Middle Danian at Fakse, southern Zealand (Fig. 2).

Because of its size and relatively easy access, the quarry at Fakse is probably the best known exposure of the Middle Danian. The coral/bryozoa banks, according to Floris (1980) consist of some 35 species of scleractinian and 12-15 of octocorals, found together with beds of autochtonous bryzoans-the whole forming a complex series of subfacies. This environment supported a mixed and abundant invertebrate assemblage, elements of which have received the attention of many authors.

The palaeobathymetric position of the Middle Danian coral/bryozoa banks of Fakse has been under debate for many years. Various levels of deeper marine environments as well as shallow ones have been considered. The first historical account of that debate was given by Asgaard (1968).

Rasmussen (1973) assumed a shallow water environment for the coral banks of Fakse based on his discovery of scelerosponges (stromatoporids) comparable to Recent forms within the photic zone (? 50 m) of Jamaica. Based on observation of corals, Floris (1980) postulated a high energy environment with depths of 50 m and a temperature of 18℃.

According to Clausen (1982), the presence of the calcareous sponge *Wienbergia* Clausen, 1982 suggested a habitat comparable with that of the closely similar Recent *Noecoelia crypta* which occurs on the outer slope of coral reefs in water depths of 15-38 m.

A more recent historical account has been published by Bernecker & Wiedlich (1990) in which these authors suggested a bathymetric range extending below the photic zone—probably 200 m-300 m. Recently, however, Floris (1992) stated that the

coral/bryozoan bank complex could have been above and below the photic range at the same time. The presence of an abundant fauna of gastropods, including many presumed algae grazing forms and therefore light dependent, indicates a water depth of no more than 80 m.

Generally speaking, all of the crab genera now known from Fakse are represented in earlier or later environments of essentially shallow water deposition; four, however, have Recent representatives with a preference for deeper water, but all have species with overlapping depth-range tolerances and there is every indication that the migration to deeper bottoms began during the Eocene (Feldmann, Tucker & Berglund, 1991). The crabs, therefore, also support a shallow water environment inferred for Fakse from studies of other faunas by Rasmussen (1973) and Floris (1980, 1992).

The complete stratigraphy of Limhamn quarry (Annetorp of earlier authors), in Scania, southern Sweden (Fig. 2) is fully discussed in a field guide prepared by Holland & Gabrielson (1979) who considered the quarry to be the principle exposure of the Danian Stage in Scandinavia. The small section of the Maastrichtian/Danian boundary mentioned by these authors no longer exists. Some 15 m of the lower part of the Early Danian, followed by about 50 m of the Middle Danian are exposed; the lower 20 m of this section are not present at Fakse. Eight to ten meters of the Late Danian of this section are present in the south wall of the quarry. Unfortunately, Holland & Gabrielson (1979) did not include a fauna list and no stratigraphic records for crabs from the locality have been kept; these authors, however, refer to highly fossiliferous ahermatypic coral thickets in the uppermost Middle Danian, and it is probable that the majority of crab specimens available for study came from this part of the section.

More reliable data, however, is available (Bertelsen, 1962) concerning temporary exposures of the Sandy Limestone facies of Late Danian in the neighbourhood of Copenhagen and crab-bearing glacial erractics are found over a large part of Denmark. The age of some these erractics is probably Late Danian, others, however, may be Middle Danian in origin.

Synopsis of Danian Crab Genera

Genera appearing in the Cretaceous

Ten Danian crab genera have their origins in the Cretaceous: *Plagiophthalmus, Homolopsis, Eohomola, Dromiopsis, Necrocarcinus, Raniliformis, Lyreidus, Xanthosia, Titanocarcinus* and *Caloxanthus.*

Plagiophthalmus (Pl. 10, Fig. 4)

Outside Denmark, *Plagiophthalmus* is represented by six species, the earliest of which occurs in the Calcaire à Spatangues (Barremian) of France. The earliest known British species comes from the Lower Albian Carstone *Douvilleiceras mammillatum* Superzone of the Isle of Wight. The genus occurs in the Albian of France, but it is unknown from the Gault of England where it makes its next appearance in the Cenomanian *Mantelliceras mantelli* and *Acanthoceras rhotomagense* Zones of Devonshire; it occurs also in the Cenomanian of Spain (Wright & Collins, 1972). It is known from Campanian deposits of North America (Bishop, 1988, Bishop & Brannen, 1992) and in the Upper Cretaceous of Antarctica, in deposits considered to have been "laid down below storm-wave base in mid to outer shelf depths." (Feldmann, Tshudy & Thomson, 1993; Crame, Pirie, Riding & Thomson, 1991).

Three of the genera, *Homolopsis, Necrocarcinus* and *Xanthosia*, that pass through the KT Boundary into the Danian occur in the limestone lenticles of the Upper Aptian Shenley Limestone (*Leymereilla tardefurcata* Zone) deposited, "between piles of broken iron pan on current-swept shellbanks." (Wright & Collins, 1972) and are found, to a greater or lesser degree, throughout the Gault. This, essentially clayey, sequence embodies habitats ranging from sandy-clays and variable amounts of glauconite, phosphate, calcium and iron in the succeeding deposits.

The three genera pass into the sandy deposits of the Lower Cenomanian of southern England and occur together in fine-grained calcareous deposits of the Miyako Group (Upper Albian) of Japan (Takeda & Fujiyama, 1983). *Necrocarcinus* and *Xanthosia* occur with *Eohomola* in the mid- early Campanian Mer-

chantville Formation of New Jersey (Bishop, 1986a; Collins & Rasmussen, 1992) which is composed of "black, glauconitic, micaceous and occasionally sandy clay." (Richards, 1958) and again in the sandy deposits of the Maastrichtian of Limberg Province (Collins, Fraaye & Jagt, in press).

Homolopsis and *Eohomola* (Pl. 10, Figs. 5, 6)

Homolopsis, first known from the Hauterivian of France (Wright & Collins, 1972) is known elsewhere in Europe from deposits of Albian, Lower Campanian and Maastrichtian age, and world wide distribution was fairly rapid, the genus reaching Japan by the Lower Aptian (Takeda & Fujiyama, 1983); it was established in the Western Inferior of North America by the Lower Turonian (Bishop, 1992) and is present in the Maastrichtian of Chile (Förster & Stinnesbeck, 1987). The generic status of a species described by Glaessner (1980) from the Lower Cenomanian of Australia is questionable.

The Danian species, *Homolopsis transiens* Segerberg, 1900 was considered by Wright & Collins (1972) probably to be related to the Lower Albian *Douvilleiceras mammillatum* Superzone species *Homolopsis brightoni* Wright & Collins, 1972, especially when compared with the specimen figured by Segerberg (1900, pl. 2, fig. 8). But, recently collected material has allowed determination of a second Danian species in which that particular figured specimen of Segerberg is included (Collins & Jakobsen, in press).

Eohomola—a genus first occurring in the Lower Campanian of North America (Collins & Rasmussen, 1992)—is closely related to *Homolopsis* from which it probably diverged in the middle Cretaceous and *Eohomola adelphina* Collins & Rasmussen, 1992 has been described from the Upper Campanian and Maastrichtian of West Greenland. A new species, closely related to the Greenland one, recently found in the Middle Danian of Fakse, Denmark (Collins & Jakobsen, in press), is the only known European member of the genus.

There are few, if any morphological characters distinguishing *Homolopsis* and *Eohomola* from their Recent analogues in species presently assigned to *Homola*; the former in the Group of *Homola mieensis* Sakai, 1979 and the latter in the Group of *Homola barbata* (Fabricius, 1793) (Collins & Rasmussen, 1992). An undescribed species of *Homola* has been recorded from turbidite sequences of the Late Eocene Hoko River Formation of Washington, U. S. A. by Feldmann, Tucker & Berglund (1991) who interpreted the sequence as confirming deeper marine conditions, with the reservation that some of the included species could have been transported from shallower water environments. A transgression to deeper water could account for the virtual absence of homolids in later Tertiary and Quaternary deposits. The Recent *Homola barbata* is found in the Mediterranean in depths of 40-100 m (Zaraiquiey Alvarez, 1946) and Guinot & Richer de Forges (1981) record 25-120 m for specimens taken off Madagascar. Rapid and powerful swimming activity has been observed in this species by Hartnoll (1970). The deepest depth (?) 1000 m recorded by Guinot & Richer de Forges (1981) is for *H. mieensis* Sakai, 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 was effected by, or about Late Eocene times.

Dromiopsis (Pl. 10, Figs. 7, 8)

Glaessner (1969, R419) envisaged development of *Dromiopsis* from *Prosopon mammillatum* Woodward, 1868, but a more convincing line of descent from the Upper Jurassic *Pithonoton serratum* (Beurlen, 1929)—or perhaps, *Pithonoton bidentatum* von Meyer, 1847—is strongly suggested by an unnamed *Dromiopsis* figured by Via (1988) from the Aptian of Spain which appears to be the earliest known member of the genus. Förster (1975) retained Forir's 1887 Cenomanian species *gigas* in *Dromiopsis*, but well preserved specimens in the Institut royal des Sciences naturelles de Belgique, Brussels, examined by us have characters not in accordance with other *Dromiopsis* species and its generic position is therefore equivocal. The records of earlier authors (e. g. Pelseneer, 1886) for *Dromiopsis elegans* Reuss, 1859 occurring in the Maastrichtian have been dispelled (Collins, Fraaye & Jagt, in press) after examination of a carapace retaining the original

label, also in the Institute, Brussels, proved it to belong to a new species. A Cenomanian species has been described by Secretan (1964) from Madagascar (although this species has little in common with other members of the genus) and Förster (1975) confirmed the presence of a form comparable with the abundant Danian *Dromiopsis rugosa* (von Schlotheim, 1820) from the Campanian of Germany. The genus has since been described from the Campanian Bearpaw Shale of North America (Bishop, 1986b); it is also known from the Maastrichtian of West Greenland (Collins & Rasmussen, 1992) and Holland (Collins, Fraaye & Jagt., in press). The genus also occurs in the Palaeocene, Vincentown Formation of North America (Roberts, 1956).

Without doubt, the greatest known concentration—both in species (four) and individuals—of *Dromiopsis* occurs in the Middle Danian of Denmark and Sweden and the striking difference between the smooth and rugose forms of the Danian species, together with the intermediate development encountered in Upper Cretaceous species, clearly indicates the presence of two phyletic lines with the divergence from one of the presumed ancestral forms taking place in early Cretaceous times. The Danian *Dromiopsis laevior* Reuss, 1859 suggests strong phyletic ties with several Recent dromiid genera.

Perhaps it is because of the large numbers of *D. rugosa* available for study that instances of taphonomy appear to be more obvious in this species than in any other decapods in the assemblage. Pre-fossil carapace fractures are frequently met with; internal moulds show evidence of burrowing activity, while dorsal surfaces with sponge-borings and others encrusted with bryozoa and/or worm tubes are not uncommon.

Necrocarcinus (Pl. 10, Fig. 11)

Necrocarcinus tricarinatus Bell, 1863 from the Upper Aptian is the earliest known member of a genus that became numerous and widespread in the Middle and Upper Cretaceous; species have been described from Europe, North America, Sudan (Bishop, 1991), Japan (Takeda & Fujiyama, 1983), Antarctica (Feldmann, Tshudy & Thomson, 1993) and an undescribed species is tentatively recorded from India (Stoliczka, 1871).

North American Cretaceous species have been described by (Bishop, 1991, 1992), who opined that the North American necrocarcinids, "either crawled close appressed to the bottom or, more likely, sheltered in the muddy bottom (much like calappid analogues do today.)". It is possible that a similar mode of life would have suited those species inhabiting conditions prevailing in the calcareous sands of the Cenomanian and Maastrichtian.

Well preserved specimens clearly indicate that the Danian species *Necrocarcinus insignis* Segerberg (1900) from the Middle and Late Danian is but a junior synonym of *Necrocarcinus senonensis* Schlüter, 1879. The apparent differences being due to ontogeny and preservation.

Rathbun (1926) records the genus from the Eocene of California, but the geologically youngest known member of *Necrocarcinus*, together with *Homola*, an extant genus, is recorded by Feldmann, Tucker & Berglund (1991) from the Upper Eocene Hoko River Formation. Recent calappids, however, occur in tolerably shallow water and it is possible that this recording represents one of the 'included species' provisioned for by those authors.

Xanthosia (Pl. 10, Fig. 14)

Xanthosia, first described from the Lower Aptian (*Xanthosia jacksoni* Wright & Collins, 1972), is found among the more prominent Cretaceous decapod assemblages of Europe and North America, where, as remarked above, it is frequently found in company with *Homolopsis* and / or *Necrocarcinus*. It occurs also in the Cenomanian and Lower Campanian of Madagascar (Secretan, 1964), but is not known above the Danian where it is represented by an, as yet, unnamed species.

Lyreidus (Pl. 10, Fig. 10)

Perhaps the most successful of the genera occurring in the Danian is *Lyreidus* (and for the purpose of this report, the closely allied subgenus, *Lysirude* Goeke, 1985). It dates from the Lower Campanian of West Greenland (*Lyreidus succedanus* Collins & Ras-

mussen, 1992), where it occurs in deposits made up of undifferentiated shales, to the present day. *Lyreidus bispinulatus* Collins & Rasmussen, 1992, first described from more or less contemporaneous deposits of West Greenland is now known to occur in the Upper Danian Sandy Limestone of Copenhagen (Fig. 2). A carapace from northern Germany, found in a Danian erratic of uncertain age, formerly described by Gripp (1969) as *Pseudoraninella* sp. was assigned to *Lyreidus* sp. by Collins & Rasmussen (1992). Another, unnamed, Palaeogene species was recorded by Jenkins (1977) from southeastern Australia.

The genus has been described (Feldmann & Chirino-Galvez, 1991) from fine-grained sandstone deposits of Eocene age of Chile and, concerning its occurrence in the Eocene of Antarctica, Feldmann & Wilson (1988) considered the conditions to have been laid down in, "a variety of deposits of nearshore shallow water, wave and tidally dominated habitats interpreted to represent a deltaic complex.". Despite the first known occurrence to be from West Greenland the majority of the species assigned to the genus are of Eocene age and distributed in the Southern Hemisphere, although Oligocene species are well documented from Hungary and Washington, U.S.A.; the youngest fossil recording was made by Karasawa (1993) for an unnamed species from sandy siltstone of the Kawabara Formation, Lower Pliocene of Japan. The genus is also known (without data) from Italy.

Lyreidus is presently distributed in the western Pacific and western Atlantic oceans. Like *Homola*, it is a genus whose members have, by and large progressed to deeper water, Recent species having been recorded from 27–1,030 m (Goeke, 1985).

Raniliformis (Pl. 10, Fig. 9)

Raniliformis, a genus first known as an unpublished species from the Maastrichtian of Holland (Collins, Fraaye & Jagt, in press) probably gave rise to the Danian *Raniliformis baltica* (Segerberg, 1900; Jagt, Collins & Fraaye, 1993). It is not one of the commoner species in the Middle Danian of Fakse and only one specimen is known from the Late Danian Sandy Limestone found as an erratic on Langeland Island, Denmark (Fig. 2).

The surface ornament on well preserved specimens of *R. baltica*, which is also known from biocalcenerites of early Palaeocene age (Houthem Formation, Geulthem Member) in the neightbourhood of Maastricht, The Netherlands (Jagt, Collins & Fraaye, 1993), consists of a fine granulation composed into transverse cuticular terraces extending the length of the carapace. A function of these terraces is to secure firm lodgement for back-burrowing crabs within their burrows, or for crabs that wedge themselves in rock crevices (Savazzi, 1985); it would seem, therefore, that *R. baltica* was well adapted both for a probable burrowing mode of life or for life among the interstices of a coral/bryozoa environment.

The nearest congener of *Raniliformis* appears to be *Ranilia punctulata* Beschin, Busulini, Angeli & Tessier, 1988 from the Middle Eocene of Italy; it is the only known fossil species of this extant genus.

Titanocarcinus (Pl. 10, Fig. 15)

With but few exceptions *Titanocarcinus* is essentially an European genus. A species described by Secretan, 1961 from the Senonian (?) of Morocco is questioned by Förster, 1970. The genotype, *Titanocarcinus serratifrons* A. Milne Edwards, 1864 is known from the Upper Maastrichtian of Belgium, but *Titanocarcinus reisi* Böhm, 1891 which makes its appearance in the Lower Maastrichtian of Bavaria and continues to the Palaeocene of Haunsburg, near Salzburg (Förster, 1970) is closer to *Titanocarcinus subellipticus* (Segerberg, 1900), a fairly common Danian species, formerly placed in *Panopeus*. The species makes its first appearance in the Middle Danian and is succeeded by Lutetian forms from Hungary and Germany; a Middle Eocene species has been described from Texas (Förster, 1970). The only other known coral-associated species, *Titanocarcinus kochi* Lőrenthey, 1898, is found in the Upper Eocene Priabonian Szépvölgy Formation of Hungary (Müller & Collins, 1991), and this species is also found in Pliocene deposits of Italy (Ristori, 1889). The genus also occurs in the Miocene Tortonian of Austria, France, Germany and Italy.

Caloxanthus (Pl. 10, Fig. 16)

The earliest known member of this genus, *Caloxanthus americanus* Rathbun, 1935, was first described from the uppermost Albian Paw Paw shale of Texas. Later, Wright & Collins (1972) described it from the sandy limestone of the Cenomanian of Devon and included in the genus *Creticarcinus purleyensis* Withers, 1928 from the Coniacian *Micraster cortestudinarium* Zone of Surrey, England. One other species comes from the Santonian of Montée des Crontets, France, but *C. americanus* is the probable ancestor of the Danian *Caloxanthus ornatus* (von Fischer Benson, 1866). This species is the commonest crab found in the Bryozoan/micritic Limestone of the Early Danian in the section at Stevns Klint and occurs frequently in the coral/bryozoa sequence of the Middle Danian.

Genera appearing in the Danian

Cyclocorystes, Xanthilites, Protomunida, Galathea and *Munida*, make their appearance in the Danian and of those the two latter species extend to the Recent.

Cyclocorystes (Pl. 10, Fig. 13)

The not so common Danian species *Cyclocorystes incertus* (Segerberg, 1900) compares favourably with the genotype *Cyclocorystes pulchellus* Bell, 1858 from the Lower Eocene London Clay of England which species also occurs in the Lower Eocene Lillebæld Formation of Denmark. The only other record for the genus is from the Late Palaeocene of the USA (Squires, 1980).

Xanthilites (Pl. 10, Fig. 12)

Glaessner (1969) indicated that the earliest record for *Xanthilites* lay in the Palaeocene, but queried an Upper Cretaceous age for the Argentinian species *Xanthilites gerthi* Glaessner, 1930. Although this opinion was followed by Via (1969), Artel & Via, 1989 were firm in their opinion of a Danian age for the species. The genus occurs in Danian deposits of West Greenland (Collins & Rasmussen, 1992) and is known from the Palaeocene of Germany (Förster, 1970). The Japanese Eocene species, *Xanthilites pentagonalis* Yokoyama, 1911 was assigned to *Branchioplax* Rathbun, 1906 by Karasawa (1992). It is considered, however, to be essentially an Eocene genus and occurs in the London Clay (Ypresian) of England. By the Upper Eocene the genus was established in Europe, Jamaica and the USA (Via, 1969). The youngest known occurrence is from the Oligocene of northwest USA and British Colombia (Artel & Via, 1989). Bell (1958) considered that the most obvious relation of *Xanthilites* is to *Xantho* Leach, 1814—a Recent genus extending from the Upper Miocene. The long-term inclusion of the Danian in the Cretaceous is reflected in the name of the Danian species, *Xanthilites cretacea* Segerberg, 1900.

Galathea (Pl. 10, Fig. 3)

Specimens of the Danian species *Galathea strigifera* (von Fischer Benson, 1866) occur rarely in the Early Danian of Stevns Klint, but are abundant in the coral/bryozoan limestones of the Middle Danian and the species is also tentatively recorded from the Middle Palaeocene of West Greenland (Collins & Rasmussen, 1992). Several species formerly described as *Galathea* have been subsequently assigned to other genera and the restricted genus is not too common in the fossil record which nonetheless has a widespread geographic distribution. A Middle Miocene species has been recorded from coral facies constituting the Megami Formation, Japan (Karasawa, 1993); the genus is well known from an Upper Badenian Porites layer at Rákos, Hungary (Müller, 1984a); and the same species has been recorded by Müller (1984b) from Messinian near-shore reefs of Greece and from deposits of similar age in Spain (Via, 1988). A Pliocene species has been described from Italy (Ristori, 1886) and recently Feldmann & Keyes (1992) listed an undescribed species recorded from the Pliocene of New Zealand. Rare instances of bopyriform infestation have been found in carapaces from Fakse. Recent species are cosmopolitan in distribution.

Protomunida (Pl. 10, Fig. 1)

The carapace of this genus has characters in common with both *Galathea* and *Munida* and Segerberg (1900) drew particular attention to the rostrum

of *Protomunida munidoides* (Segerberg, 1900) regarding it as an, "interesting form between the genera *Galathea* and *Munida*" (*vide* Woodward, 1901). *P. munidoides* occurs frequently in the Middle Danian of Fakse, and the genus, also known from the Upper Eocene Coral Limestone of Hungary, has been compared with the Recent coral associated genus *Sadayoshia* (Müller & Collins, 1991).

Munida (Pl. 10, Fig. 2)

Munida is an extant genus with a preference for deep water and *Munida primaeva* Segerberg, 1900, which occurs very rarely in the Middle Danian, may have been carried onto the reef from the seaward side, rather than being an inhabitant of it. The genus is not common in the fossil record, but has been recorded (with *Homola*) from the Upper Eocene Hoko River Formation of Washington, U. S. A. (Feldmann, Tucker & Berglund, 1991) and a Palaeogene species is recorded from South Australia (Jenkins, 1977). An undescribed species is known from the Lower Miocene of Japan and *Munida nishioi* Karasawa, 1993, a Japanese Middle Miocene species, is considered by Karasawa (1993) to have lived in a subtropical, high energy, muddy bottomed lower sublittoral-upper bathyal environment.

Summary

Not only is it remarkable that 66 % of the known genera and two species of crabs: *Dromiopsis rugosa* and *Necrocarcinus senonensis*, of the Danish and Swedish Danian fauna pass through the KT Boundary, but all the genera involved have adapted from a relatively shallow, soft clayey or sandy bottomed environ to that of a coral/bryozoa bank complex and, with few exceptions, reverted to similar conditions. There are clear indications for a west-east migration route for *Eohomola* and *Caloxanthus*. For the most part, early history and development of the Danian galatheids remains obscure and the origins of *Cyclocorystes* and *Xanthilites* are not at all clear. The probability, therefore, of more or less direct ancestral roots of those species that first make their appearance in the Danian coming to light in the Cretaceous is an extremely high one.

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デンマーク・スウェーデンのダニアン階（暁新世）産十脚甲殻類の生層序学的分布

J. S. H. Collins and S. L. Jakobsen

要　　旨

デンマーク・スエーデンのダニアン階（暁新統下部）産十脚甲殻類15属の層序学的・古生物地理学的分布を議論する．これらの属の内10属は白亜紀に起源があり，KT境界を越えて生存する．*Eohomola*・*Caloxanthus* 属は白亜紀に北アメリカに出現し，それ以後ヨーロッパへ移動したことが明らかとなった．

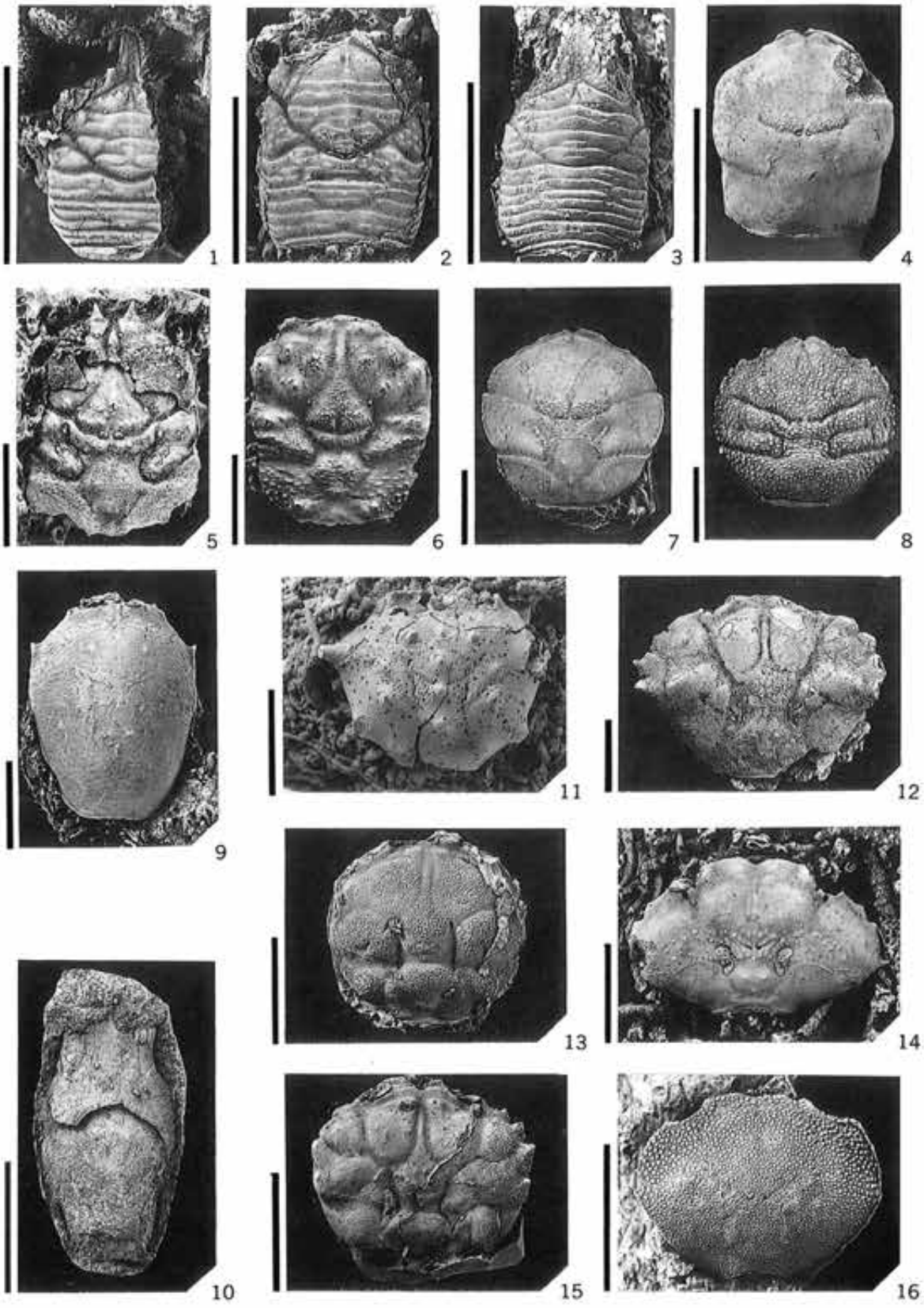
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Plate

Plate 10

Fig. 1. *Protomunida munidoides* (Segerberg, 1900). Lectotype; Segerberg, 1900, pl. 1, fig. 5. Middle Danian, Fakse quarry.
Fig. 2. *Munida primaeva* (Segerberg, 1900). Lectotype; Segerberg, 1900, pl. 1, fig. 6. Middle Danian, Fakse quarry.
Fig. 3. *Galathea strigifera* Steenstrup, 1863. Middle Danian, Fakse quarry. Silicone rubber cast showing surface ornament.
Fig. 4. *Plagiophthalmus depressus* (Segerberg, 1900). Lectotype; Segerberg, 1900, pl. 1, fig. 3. Middle Danian, Fakse quarry.
Fig. 5. *Eohomola* sp. nov. Middle Danian, Fakse quarry.
Fig. 6. *Homolopsis transiens* Segerberg, 1900. Lectotype; Segerberg, 1900, pl. 2, fig. 2. Middle Danian, Fakse quarry.
Fig. 7. *Dromiopsis laevior* Steenstrup, 1863. Middle Danian, Fakse quarry.
Fig. 8. *Dromiopsis rugosa* (von Schlotheim, 1820). Middle Danian, Fakse quarry. Silicone rubber cast showing surface ornament.
Fig. 9. *Raniliformis baltica* (Segerberg, 1900). Middle Danian, Fakse quarry.
Fig. 10. *Lyreidus* sp. nov. Late Danian, Knippelsbro, Copenhagen harbour.
Fig. 11. *Necrocarcinus senonensis* Schlüter, 1879. Middle Danian, Fakse quarry.
Fig. 12. *Xanthilites cretacea* Segerberg, 1900. Middle Danian, Fakse quarry.
Fig. 13. *Cyclocorystes incertus* (Segerberg, 1900). Middle Danian, Fakse quarry. Silicone rubber cast showing surface ornament.
Fig. 14. *Xanthosia* sp. nov. Middle Danian, Fakse quarry.
Fig. 15. *Titanocarcinus subellipticus* (Segerberg, 1900). Middle Danian, Fakse quarry. Siltstone rubber cast showing surface ornament.
Fig. 16. *Caloxanthus ornatus* (von Fischer Benzon, 1866). Middle Danian, Fakse quarry. Siltstone rubber cast showing surface ornament.

Figs. 1–4, 13, 14, 16 bar-scale=5.0 mm: Figs. 5–12, 15 bar-scale=10.0 mm
All specimens, with the exception of Figs. 9, 11, 15 which are in the collection of Alice Rasmussen, Fakse, are deposited in the Geological Museum, Copenhagen.


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