

Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area

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Abstract

The result of some twenty years of intensive collecting from strata in the Maastrichtian type area is a collection of more than 1,200 generally small-sized anomuran and brachyuran remains. The stratigraphical ranges of the thirty-one species known to date from the Maastricht Formation (Late Maastrichtian) are shown and five successive decapod assemblages are discussed. For the first time, decapod crustacean remains now turn out to be useful biostratigraphic tools on a local to regional scale.

Introduction

Brachyurans utilize a broad array of feeding types, including deposit feeding, filter feeding, seaweed grazing, scavenging and predation. They have been a major component of many marine communities from the Late Jurassic onwards and probably have played an important role in the evolution of marine ecosystems. Unfortunately, they are only rarely described by paleontologists and are also frequently overlooked by biologists in Recent marine communities, especially in the tropics where crabs reach their highest diversity (Zipser & Vermeij, 1978). Apart from paleoecological factors and possible destruction after death, their apparent scarcity in paleontological collections is probably often due to their relatively small sizes, and therefore the chance of being overlooked in the field (Bishop, 1986; Plotnick et al., 1990). The average size of anomuran and brachyuran crab remains in the fine-grained sediments of the Maastrichtian type area is less than 10 mm. Almost all decapod crustacean species from the Maastricht Formation described

prior to 1987 by various authors (Bosquet, 1854; van Binkhorst, 1857; Binkhorst van den Binkhorst, 1861; Noetling, 1881; Pelseneer, 1886; Forir, 1887a-c, 1889; Mulder, 1981) suffer from a lack of stratigraphic control. A taxonomic revision of most of these species was carried out by Collins et al. (1995). Since 1987, new species from the Maastrichtian type area were described and discussed by Fraaye & Collins (1987), Feldmann et al. (1990), Jagt et al. (1991, 1993), Collins et al. (1995), Fraaye (1996 a-c, 2002), Fraaye & van Bakel (1998) and Jagt et al. (2000).

Rigid collecting from six key sections (see Collins et al. 1995, p. 168, fig. 1) during the past two decades has resulted in an extensive, stratigraphically well-documented, decapod, crustacean collection containing over 1,200 specimens and housed at the Oertijdmuseum de Groene Poort, Boxtel (the Netherlands).

Carapace size and morphology through time

Crab size is thought to be related to predation pressure (Vermeij, 1978). The relatively small size of the majority of Mesozoic crabs was probably controlled by predation pressure of simultaneously evolving reef teleost fish (Vermeij, 1978) and co-occurring cephalopods. Apart from size selection, predation pressure can also lead to avoidance strategies, i.e., strategies devised to minimize the risks of being predated upon. For crabs, we may envisage four strategies that play a continuous role during their evolution: 1 – to hide and live in crevices;

2 – camouflage their carapace; 3 – burrow into loose sediments; 4 – swim in open waters.

Carapace morphology in the first group is generally quadratic or somewhat elongate. Such crabs have been successful from the Late Jurassic onwards and have consistently retained a relatively small size. The vast area of shelf seas with an expansion of redundant bioherms after the Callovian transgression offered various new ecological niches and led to the rapid diversification of prosopids (Förster, 1985). The other three strategies, which probably evolved during the Cretaceous, are characterized by a considerable size increase through time. The strongly elongate and burrowing Raninidae (frog crabs) are examples of the third group. They appear in the Early Cretaceous and show an increase in size and diversity through time, with maxima during the Late Cretaceous (Feldmann et al., 1996) and Eocene (Förster & Mundlos, 1982). The Raninidae predominantly lived in shallow-water environments during the Mesozoic but today are, probably due to strong competition during the Cenozoic, mainly deep-water organisms.

The ancestors of the Recent swimming crabs possess carapaces that are wider than long and with antero-lateral spines. They appeared in the latest Cretaceous (Fraaye, 1996a). During the Eocene, the largest swimming crabs quadrupled their carapace size in comparison to their probable Maastrichtian ancestors. It is not mere coincidence that periods of increase in size and diversity of crabs are linked with global sea level high stands (Haq et al., 1987). Major explosive adaptive radiations among crabs occurred during the Late Jurassic, the Albian-Cenomanian, the Campanian-Maastrichtian, and during the Eocene and Miocene transgressions. These periods are characterized by high stands leading to many shallow, more or less isolated, seas. Consequently, more ecospace and new niches for crabs came into existence. In isolated seas, rapid diversification of clades was probably very common. The monophyletic clades produced by this type of event have recently been referred to as 'species flocks' (Yacobucci, 1996). After sea level fall, newly evolved crab populations were forced to retreat and mixing led to strong competition, in turn possibly leading to extinction and faunal turnovers (Fraaye, 1996b). This was followed by periods of stasis,

during which a slower and stabilized evolutionary pattern dominated. This model with pulses of rapid diversification, mixing and more stable periods, in roughly 30 million year cycles, perfectly matches the polyphyletic origin of such groups as the swimming crabs. After each period, however, more and more ecological niches were successfully filled, leading to the recent, most diverse (in size, morphology and feeding strategy) decapod crustacean fauna ever seen on earth.

Cretaceous/Cenozoic decapod crustacean evolution

The Late Cretaceous diversification of crabs coincides with two similar radiations in other predatory groups, teleost fish and gastropods (Taylor, 1981). These groups also seem to have thrived during periods of transgression with maximum (semi-isolated) shallow-water habitats. The rapid evolution of these predatory groups and others probably had profound effects upon the structure of all benthic communities, and thus also affected crab evolution. To put the evolutionary patterns of decapod crustaceans in the type Maastrichtian in some perspective, faunal data for five other well-studied regions and ages are summarized in Fig. 1. As the majority of the type Maastrichtian decapods is linked with reef-associated carbonates all decapod crustacean faunas compared are from similar environments. Further, all faunas represent the most diverse of their age as presently known. Studies used are Bishop (1983, 1986: Lower Albian, Texas), Müller & Collins (1991: Upper Eocene, Hungary), Müller (1984: Middle Miocene, Hungary and Austria), Guinot (1985: Recent, French Polynesia) and personal observations (Lower Kimmeridgian, southern Germany).

Brachyuran crab diversity increased in time (Fig. 1), implying a strong evolutionary radiation from the Late Jurassic onwards. It is also clear that certain brachyuran groups played a more prominent role in the shallow marine ecosystems than they do currently. For instance, the Dynomenidae and Raninidae first appeared during the Late Jurassic and Early Cretaceous, respectively. After a rapid evolutionary radiation during the Late Cretaceous,

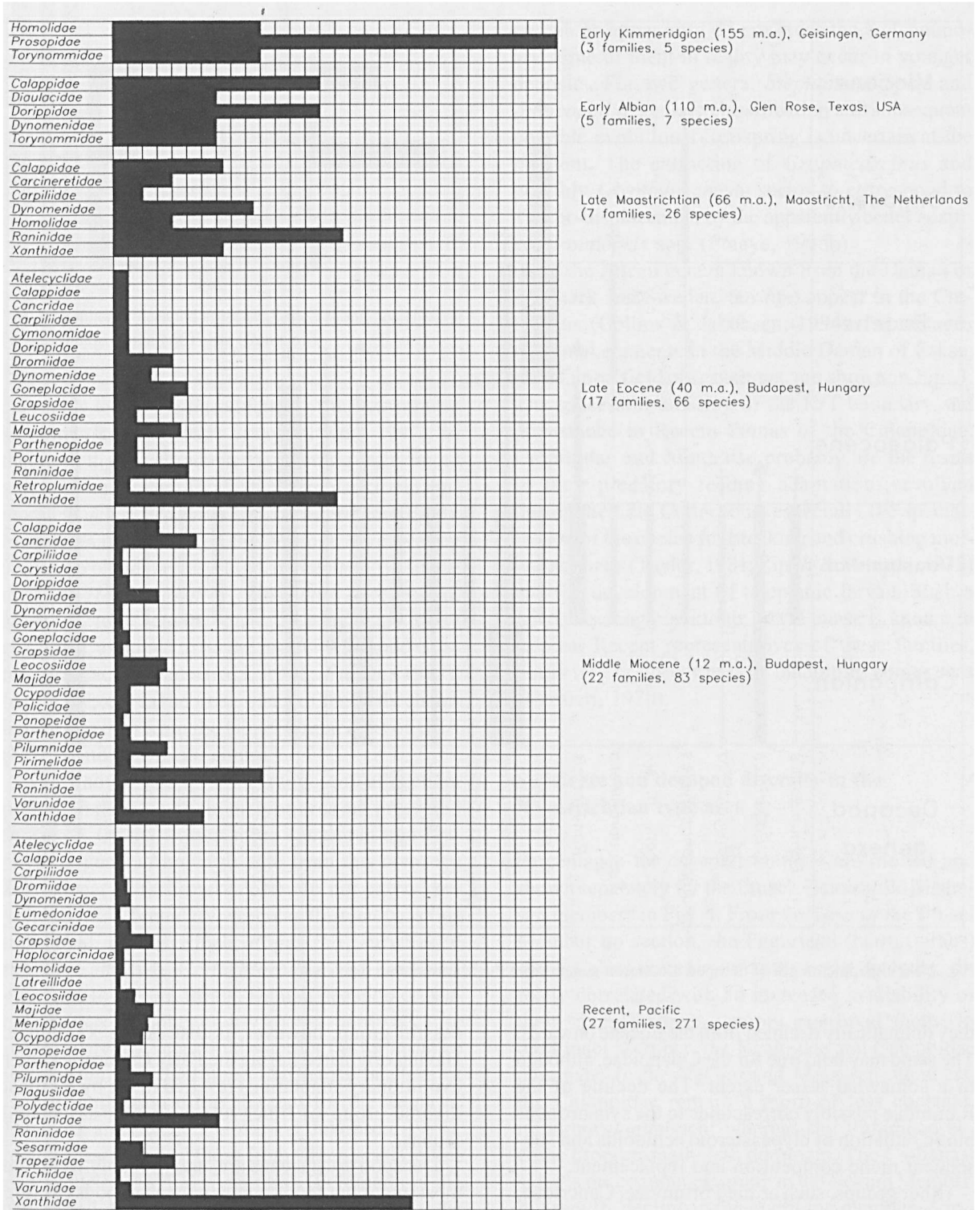


Fig. 1. Reef-associated decapod crustacean faunas through time.

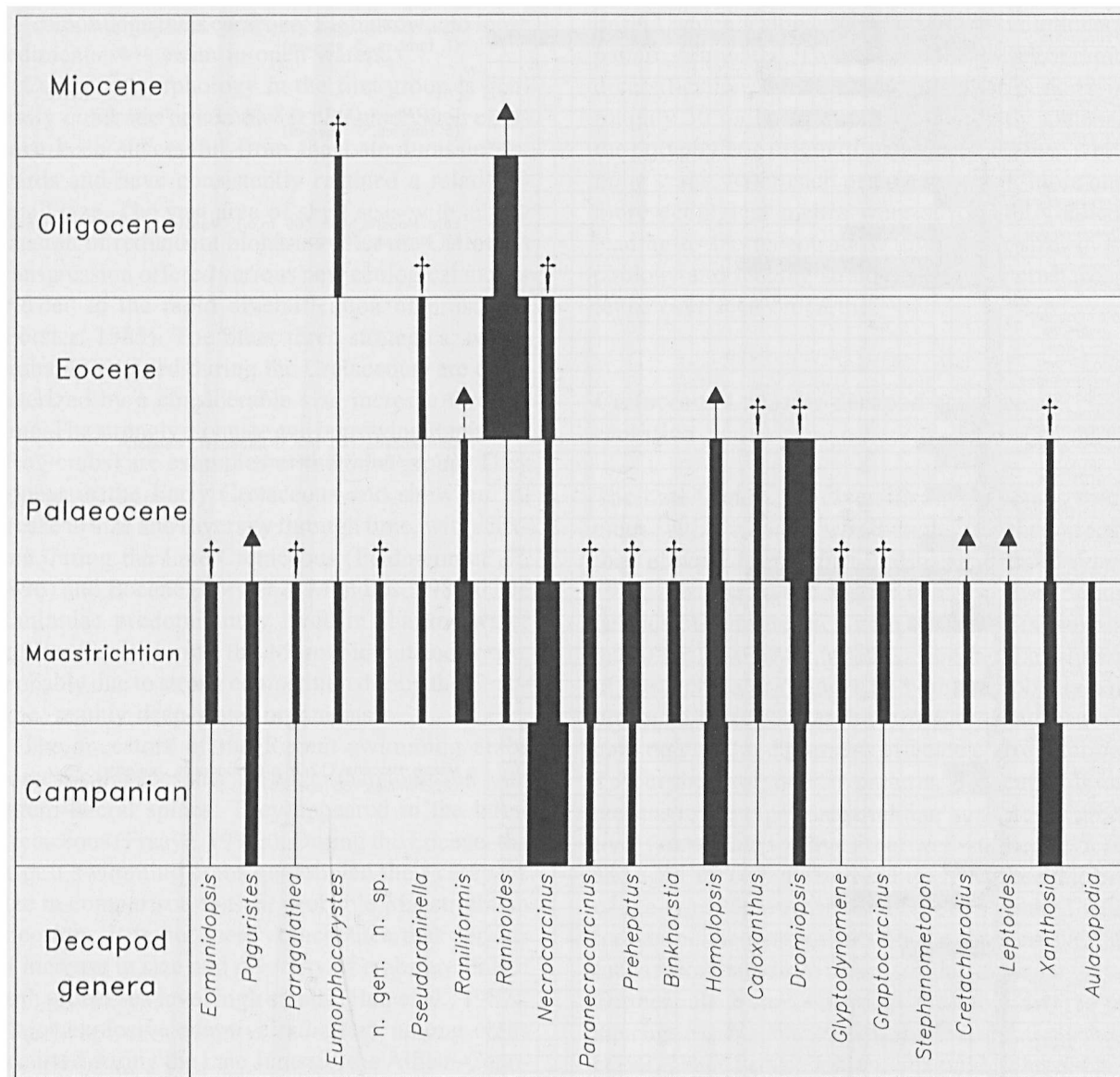


Fig. 2. Stratigraphic ranges of decapod crustacean genera from the Maastrichtian type area.

they dramatically declined from the Eocene onwards. The same may hold true for the Calappidae, although to a somewhat lesser extent. The decline of the Raninidae possibly corresponds to the synchronous biotic radiation of clypeasteroid echinoids and subsequent niche competition and replacement.

Other groups, such as the Portunidae, Cancridae, Majidae, Leucosiidae, Parthenopidae and Grapsidae, however, display a rapid evolutionary radiation in post-Eocene times, as do the Ocypodidae and Pilumnidae from the Miocene onwards. The most suc-

cessful group, however, is that of the Xanthidae. Having originated during the Early Cretaceous, their evolutionary adaptations resulted in the by far most diverse group of brachyurans in reef-associated faunas.

Decapod crustaceans are, and probably were, the most important food source for cephalopods (Fraaye & Jäger, 1996; Jäger & Fraaye, 1997). The predation pressure on crabs by relatively fast swimming and hunting ammonites such as *Placenticer* and *Sphenodiscus* in the Campanian and Maastrichtian

	Number of species	Percentages of total crab fauna
Galatheididae		
Calappidae		
Carpiliidae		
Dynomenidae		
Homolidae		
Prosopidae		
Raninidae		
Xanthidae		

Fig. 3. Number of decapod crustacean species and percentages for the Middle Danian of Fakse (Denmark).

may have led to the introduction of the swimming xanthids (Bishop, 1991; Fraaye, 1996a, 1997). In their turn these well-adapted swimming crabs found a new and abundant food source in planktonic ammonites such as *Scaphites* spp. (Westermann, 1996). In the Maastrichtian of the Vistula River valley (central Poland) a very high percentage of specimens of *Hoploscaphites constrictus* have paired, more or less regular punctures in their body chambers, assumed to be the result of decapod crustacean attacks (Radwański, 1996; Fraaye, 1997). Identical holes in the same place of the body chambers are known from the Upper Cretaceous of USA (N.H. Landman, pers. comm.).

The known stratigraphic ranges of all genera present in the Maastrichtian type area are presented in Fig. 2. Of the twenty-three anomuran and brachyuran genera known to date from this area, ten first appear in this interval, ten do not extend beyond the K/T boundary, whereas thirteen pass this unscathed, one of which, *Paguristes*, survives to this day, and two, *Cretachlorodius* and *Leptoides* gave rise to Recent forms. Danian decapod crustacean faunas are rather poorly known, partly because of relatively few accessible outcrops (as for instance in the region studied here) and partly because of lack of collection effort. Except for the fauna of Denmark and Sweden (Collins & Jakobsen, 1994), and to a lesser degree those from Greenland (Collins & Rasmussen, 1992), Argentina (Feldmann et al., 1995) and Antarctica (Feldmann et al., 1993), the decapod crustacean data base for the Danian is rather meager, with overall poor biostratigraphic control. Therefore, it is to be expected that of the ten gen-

era which apparently do not cross the K/T boundary some of them in reality may occur in younger deposits. For two genera, *Stephanometopon* and *Aulacopodia*, generic classification and subsequent possible evolutionary offspring is uncertain at the moment. The extinction of *Graptocarcinus* and possibly *Glyptodynamene* seems to correspond to a niche-displacement by the apparently better adapted *Dromiopsis* spp. (Fraaye, 1996b).

Of the fifteen genera known from the Danian of Denmark and Sweden, ten first appear in the Cretaceous (Collins & Jakobsen, 1994). Percentages of faunal elements in the Middle Danian of Fakse, based upon field observations, are shown in Fig. 3. The successful crossing of the K/T boundary and persistence in Recent faunas of the Calappidae, Carpiliidae and Xanthidae probably are the result of their predatory feeding adaptations, evolved during the Late Cretaceous, especially the specialization of the chelae for breaking and crushing molluscan shells (Taylor, 1981; Zipser & Vermeij, 1978) and the development of teleplanic larvae. Such a relatively long planktonic larval phase is known in tropical Recent representatives of these families, but is rare or absent in taxa inhabiting cooler seas (Vermeij, 1978).

Substrate and decapod diversity in the Maastrichtian type area

Percentages for decapod families are plotted and shown separately for the Emael, Nekum and Meerssen members in Fig. 4. From the base of the Emael Member up section, the Paguridae (hermit crabs) show a clear increase in number and diversity, directly correlated with an increased availability of their 'mobile homes', empty gastropod shells. In the Emael Member, the Raninidae and Calappidae dominate. In the Nekum and Meerssen members, the Calappidae remain a more or less constant, important component whereas the Raninidae become proportionally less dominant. The Callinassidae is the commonest group in the Nekum Member, but rapidly decline in the overlying member. Torynomids reached their acme in the Nekum Member and rapidly declined in the lower Meerssen Member, probably as a result of competition with

	Emael	Nekum	Meerssen
Paguroidea			
Galatheidæ			
Calappidæ			
Carcineretidæ			
Carpiliidæ			
Dynomenidæ			
Homolidæ			
Raninidæ			
Xanthidæ			

Fig. 4. Percentages for decapod crustacean families in the three highest members of the Maastricht Formation in the type area.

the presumably more efficient swimmers amongst the Xanthidae (Fraaye, 1997); some of these latter represent Tethyan invaders (Fraaye, 1996a). The Dynomenidae and Homolidæ display the same trend as pagurids going up-section from the Nekum to the Meerssen members. The Galatheidæ and Carpiliidæ make their first appearance in the Meerssen Member (Fig. 5), but are far outnumbered by other families. Within the interval studied, five successive decapod assemblages may be recognised, as follows (in ascending order):

- (I) raninid
- (II) raninid/diogenid/calappid
- (III) callianassid/calappid/torynommid
- (IV) calappid/xanthid/raninid
- (V) calappid/dynomenid

The diversity increase between the Emael and Meerssen members is intimately linked with an increase of substrate diversity (Fig. 6). Accumulations of dead shell material grew markedly up section. The entire spectrum of live/dead interactions (ecological consequences of shell accumulation) in benthic communities was referred to as 'taphonomic feedback' by Kidwell & Jablonski (1983). The change from a predominantly soft-bottom dwelling community in the lower Emael Member (and underlying members), to the firm ground and shell-gravel dwelling communities in the Nekum and Meerssen members, was probably triggered by the mass oc-

currence of seagrass fields during deposition of the uppermost Emael, Nekum and lower Meerssen members (Liebau, 1978; Felder et al., 1980; Voigt, 1981). The sea grasses enabled the colonisation of small epizoans such as bryozoans (Voigt, 1981), foraminifera (Sprechmann, 1981) and calcareous algae (Brasier, 1975). Sediments which accumulate around sea grass communities are distinctive and, if they escape channeling and other forms of associated erosion within the biotope, they stand a high chance of preservation (Brasier, 1975). Sea grass is notable for its ability to influence the character of the sediment substrate. The dense plant growth probably reduced current velocities, whereas the rhizomes stabilised the accumulated sediments. Infaunal filter feeders, e.g., *Protocallianassa faujasi*, thrived in the nutrient-enriched sediments around sea grasses, making use of things such as decaying plant material (Sven et al., 2001). The accumulated dead hard parts of the sea grass-epibionts facilitated the colonization of other epizoans such as fungi, sponges, corals, brachiopods, serpulids, lunulitiform bryozoans, boring and encrusting bivalves, sessile gastropods and cirripedes. In the lower Meerssen Member (units IVf-1 to -4) this colonization finally led to the development of small-sized bioherms, vertically and laterally alternating with hard grounds (Voigt, 1974; van den Elsen, 1985) and relief infillings (Zijlstra, 1995). Cavities in hardgrounds

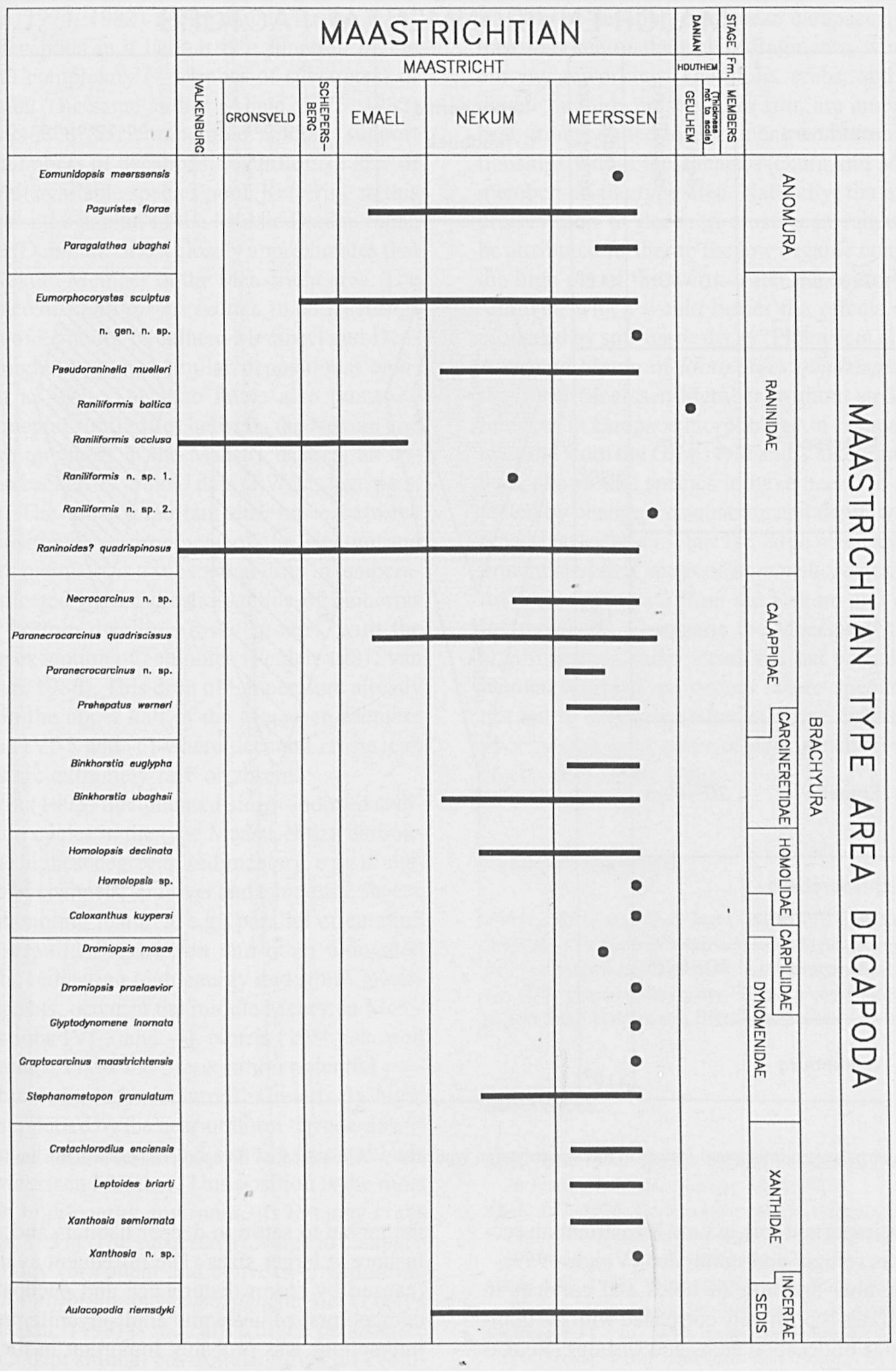


Fig. 5. Decapod crustacean species range chart in the Maastrichtian type area.

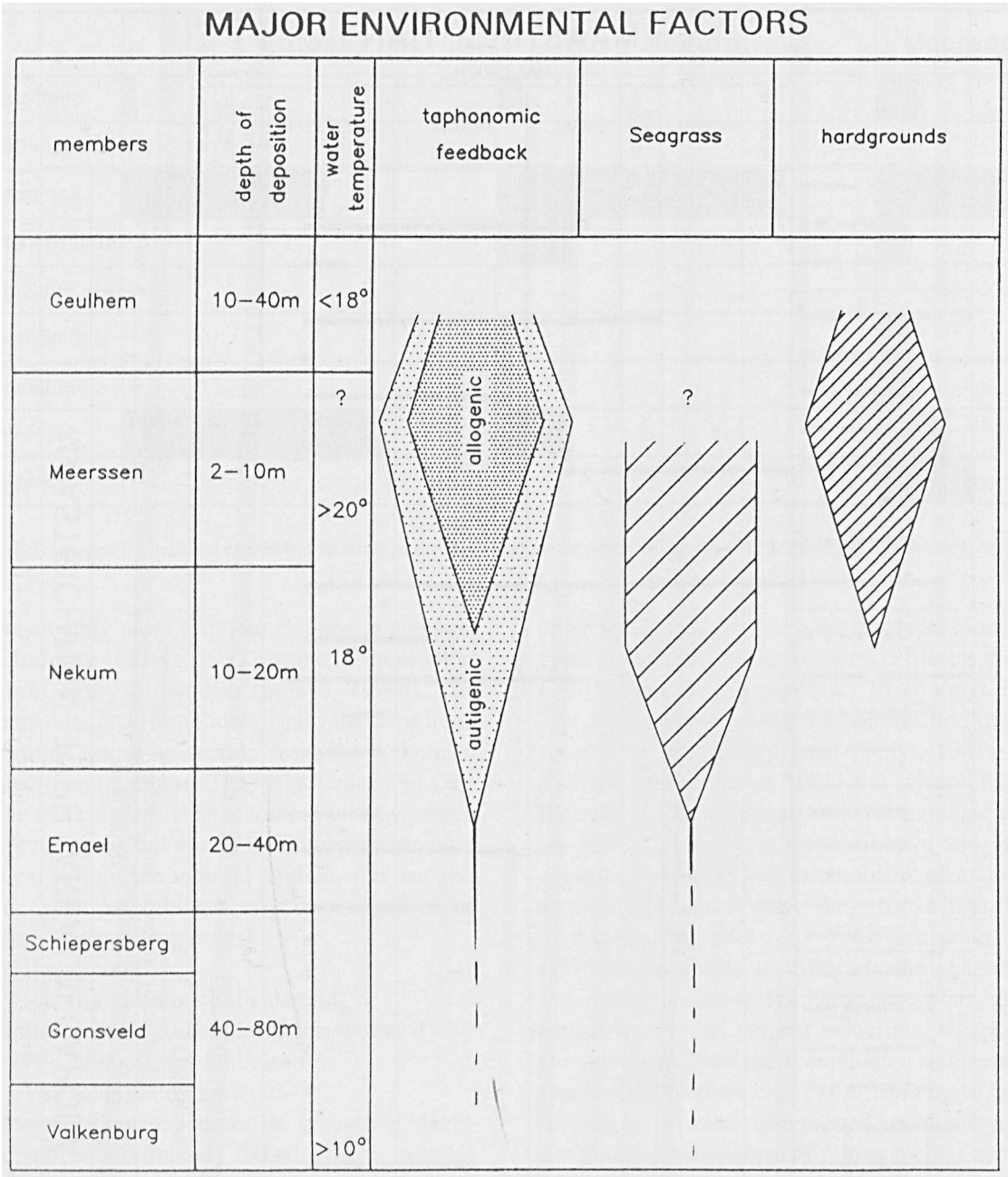


Fig. 6. Major palaeoenvironmental factors in the Maastrichtian type area which influenced decapod crustacean communities.

played an important role in Late Maastrichtian ecosystems as refugia and domiciles (Voigt, 1959).
The number and size of holes and crevices in reef substrates is positively correlated with the number and size of decapod crabs and shrimps (Reaka-Kudla, 1990). These decapod crustaceans each prey on their own and each others' juveniles, forcing

the larvae to settle in deeper habitats and migrate inshore at larger sizes. The infrequent availability (caused by storm disturbance and occupation by competitors) of holes and adult-juvenile predatory interactions was probably important in the evolution of decapod crustaceans in reef communities over time.

Abele (1974, 1982) documented that the number of decapods in a habitat is a function of the structural complexity (= number of substrates) of that habitat. The same author (Abele, 1976, 1982) also concluded that comparable habitats support similar numbers of decapods, regardless of size of the overall available species pool. Referring to this hypothesis, the habitat of the Middle Danian fauna of Fakse (Denmark) most closely approximates that of the Nekum Member in the Maastricht area. The occurrence of *Raniliformis baltica* in both settings (Danian of Limburg [Geulhem Member] and Denmark) might suggest a similar depositional environment as well. The crab fauna also points to environmental similarities between the Nekum and Geulhem members in the Maastricht area, an observation backed by crinoid data (J.W.M. Jagt, pers. comm.). The most important difference between the depositional environment of the Nekum and Geulhem members is a substantial drop in temperature, indicated by the drastic decline of bioherms and all bottom-dwelling fossil groups, with the possible exception of echinoids (Felder, 1981; van den Elsen, 1986). This drop of temperature already started in the upper half of the Meerssen Member (sections IVf-5 and -6) where decapod crustacean remains are extremely rare or absent.

Zijlstra (1995) documented storm-induced sedimentation cycles in the type Maastrichtian carbonates. The highest degree of sedimentary, e.g., trough cross beds, channels, spillover and tempestite sheets, and taphonomic features, e.g., parallel orientation of the serpulid *Pyrgolopon* and other elongated bioclasts, indicating high energy and storm-generated deposits, occur in the middle Meerssen Member (sections IVf-3 and -4). Norris (1986) showed that amongst crabs the preservation potential produced by storm-induced burial is relatively high. This is supported by the near-uniform 'upside-down' position of carapaces in the storm-generated beds of the Meerssen Member. This position is the most stable in high-energy environments in many crabs (Schäfer, 1951). The successive change in carapace morphology (ornament and convexity) within the genera *Raniliformis* and *Eumorphocorystes* (Fraaye & van Bakel, 1998) is indicative of the persistence of such a depositional environment over an evolutionarily significant period of time. The extreme

fragility of decapod crustacean carapaces, in contrast to some of their claw fragments, would rule out any reworking. Therefore, crabs, and in particular raninids preserved *in situ*, are amongst the best groups suited to document evolutionary relationships within the Emael, Nekum and Meerssen members in the type area. Naturally, the excellent preservation of decapod crustacean remains may be attributed further to the low organic content and the high pH of the warm-water depositional environment, which would buffer the effects of acids produced by soft-tissue decay (Plotnick et al., 1988). A second bloom of *Raninoides quadrispinosus* in the lower Meerssen Member, without striking differences in carapace morphology in comparison to material from the Gronsvelt and Valkenburg members, shows this species to have been the least affected by changes in substrate and depth within the type Maastrichtian. Thus far, large-sized and highly ornamented specimens of *Eumorphocorystes sculptus* are only known from the Nekum and underlying members, whereas in the Meerssen Member a significantly smaller sized and but partially ornamented morphotype occurs. More specimens are needed to determine whether these different morphotypes are ontogenetic or phylogenetic (van Bakel et al., work under way).

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