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New raninid crabs (Crustacea, Decapoda, Brachyura) from the late Maastrichtian of the Netherlands

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Abstract

Three new raninid crabs, *Lyreidina pyriformis* gen. n., sp. n., *Raniliformis chevrona* sp. n., and *Raniliformis prebaltica* sp. n., are described from the Maastrichtian type area (SE Netherlands). The new genus *Lyreidina* is the third member within the subfamily Lyreidinae Guinot 1993, and the first anterolateral-spines-lacking representative from the Cretaceous. The evolutionary development of the genus *Raniliformis* Jagt, Collins & Fraaye (1993) seems to include a continuous lineage *occlusa-prebaltica-baltica. R. chevrona* is considered as an offshoot.

Introduction

The Raninidae or frog crabs, which first appeared in the Early Cretaceous with forms similar to Recent genera, flourished during the Late Cretaceous and Early Cenozoic (e.g. Guinot 1993; R.H.B. Fraaye, unpublished data). Guinot (1993) subdivided the Raninidae into six subfamilies. Prior to the present study the subfamily Lyreidinae comprised two genera, *Lyreidus* de Haan 1841 and *Lysirude* Goeke 1985, to which six extant and twelve extinct species were assigned (Guinot 1993).

Feldmann & Zinsmeister (1984) referred the ten lyreidine species then known to three groups based on the number of lateral spines. In recent years, Feldmann & Wilson (1988), Feldmann & Maxwell (1990), Feldmann (1992) and Collins & Rasmussen (1992) have described eight new fossil species of the genus *Lyreidus*.

Of the fossil representatives known to date, only two have been recorded from the Late Cretaceous: *Lyreidus succedanus* (Collins & Rasmussen 1992) of early Campanian to Maastrichtian, and *L. rosenkrantzi* (Collins & Rasmussen 1992) of Maastrichtian age, both from west Greenland (Collins & Rasmussen 1992). These two species, together with *L. bispinulatus* (Collins & Rasmussen 1992), *Lyreidus* sp. (Collins & Rasmussen 1992; Collins & Jakobsen 1994) and *Lyreidus* sp. nov. (Collins & Jakobsen 1994), all of Palaeocene age, and the three new species here described are all from the northern hemisphere. They yield new data regarding the earliest evolutionary and palaeogeographic distribution patterns of this group of frog crabs as reconstructed by Feldmann (1990, 1992).

The genus *Raniliformis* was erected by Jagt, Collins & Fraaye (1993) for *Raninella baltica* Segerberg 1900 from the middle Danian of Denmark and Sweden and from the early Danian of the Netherlands. Survival of this species into the late Danian was reported by Collins & Jakobsen (1994). The second species assigned to this genus was *Raniliformis occlusa* Collins, Fraaye & Jagt (1995) from the late Maastrichtian of Belgium and the Netherlands.

With the three new species described herein the total number of raninids from the Maastrichtian type area comes to eight; thus being the most diverse Mesozoic raninid fauna known to date. Within this group of back-burrowing crabs, the carapace morphology (ornamentation and convexity) and succession of population blooms are related to the change of the substrate. Crabs are suitable for documenting evolutionary relationships within the often reworked sediments of the Maastrichtian stratotype area because their fragile carapaces rule out reworking (R.H.B. Fraaye, unpublished data).

Systematic description

Section Podotremata Guinot 1977
Superfamily Raninoidea de Haan 1841
Family Raninidae de Haan 1841
Subfamily Lyreidinae Guinot 1993

Lyreidina gen. n.

Derivation of name: Indicating a member of the subfamily.
Diagnosis: Carapace pyriform, widest in posterior half; stout rounded-triangular and ridged rostrum; tube-like very narrow front; width of orbitofrontal margin smaller than width of posterior margin; no orbital or anterolateral spines; raised cardiac region; terraced intestinal region.

Lyreidina pyriformis sp. n.
Figures 1A, 2A
Holotype: Geo Centrum Brabant Collections, MAK k. 2251 (ex Van Bakel Collection).
Type horizon and locality: Maastricht Formation (Fm), middle part (IVf3 or IVf4) of Meerssen Member (Mbr), late Maastrichtian, *Belemnitella junior* Zone; ENCI Nederland BV quarry, Maastricht, the Netherlands.
Derivation of name: Referring to the pear shape of the carapace.
Material: Holotype only.
Diagnosis: As for genus.
Description: Moderately small raninid, pear-shaped carapace twice as long as broad, strongly convex transversely, almost flat longitudinally. Orbitofrontal margin very narrow, almost circular in cross-section, about one third of carapace width. Orbital margin with two fissures, outer lobe half the size of inner lobes. Broad and rounded triangular rostrum with prominent ridge bounded by two wide grooves shallowing to the gastric region. Anterolateral margins long, slightly sinuous and lacking spines. Posterolateral margins are convex and bear a well-defined rim covered with coarse tubercles. Rim continues on the almost straight and smooth posterior margin. Posterior margin slightly wider than orbitofrontal margin.

Hepatic and anterior gastric regions covered with numerous pits becoming smaller along the anterolateral margin. Posterior gastric region smooth except for two relatively large pits. Slightly raised and smooth heart-shaped cardiac region separated from branchial regions by faint grooves. Intestinal region covered with terraced incisions running parallel to the posterior margin. Terraced incisions continue on branchial regions and vanish towards widest part of carapace.
Discussion: The genus *Lyreidus* de Haan 1841 is currently found in the western North Atlantic and the central western Indo-Pacific (Feldmann 1990, 1992; Goeke 1985; Griffin 1970). Until 1992, the oldest documented occurrence of *Lyreidus* was in the Eocene of the southern hemisphere (Chile, Antarctica and New Zealand; Feldmann 1990, 1992; Feldmann & Chirino-Galvez 1991). A few younger species are known from the northern USA (Feldmann 1989), Japan (Karasawa 1993) and Europe (Feldmann 1992). Based on these occurrences the earliest evolutionary history of this genus was considered to be confined to the southern hemisphere. Feldmann (1990) suggested an early and rapid evolution of two morphologically distinct groups within the genus; one arising in the New Zealand region and radiating first into the northeast Pacific and later into the North Atlantic and Europe. The second group arose in the high-latitude part of the southern hemisphere and radiated into the western Pacific as far north as Japan and Hawaii.

These suggested palaeogeographic patterns have to be reconsidered with the discovery of early species of *Lyreidus* in Greenland (Collins & Rasmussen 1992) and Denmark (Collins & Jakobsen 1994) and of the new genus from the Netherlands here described.

The genus most closely resembling *Lyreidina pyriformis* in carapace outline is the prosopid crab *Oonoton* Glaessner 1980 from the upper Albian of Australia. This similarity is an example of convergence in the fossil crab record.

Lyreidina differs from other genera of Lyreidinae in having a ridged rostrum, pyriform outline of the carapace (widest carapace at c. 75% from front), raised cardiac region, ornamentation of carapace (strongest on hepatic and intestinal areas), and absence of orbital and/or anterolateral spines.

Morphologically, the extant *Lyreidus stenops* Wood-Mason 1887, and the early Eocene *Lyreidus lebuensis* Feldmann 1992 are closest to *Lyreidina pyriformis* in having no anterolateral spines, the largest width at 50 to 60% distance from the front, and a narrow tube-like front.

Subfamily Notopodinae Serène & Umali 1972
Genus *Raniliformis* Jagt, Collins & Fraaye 1993

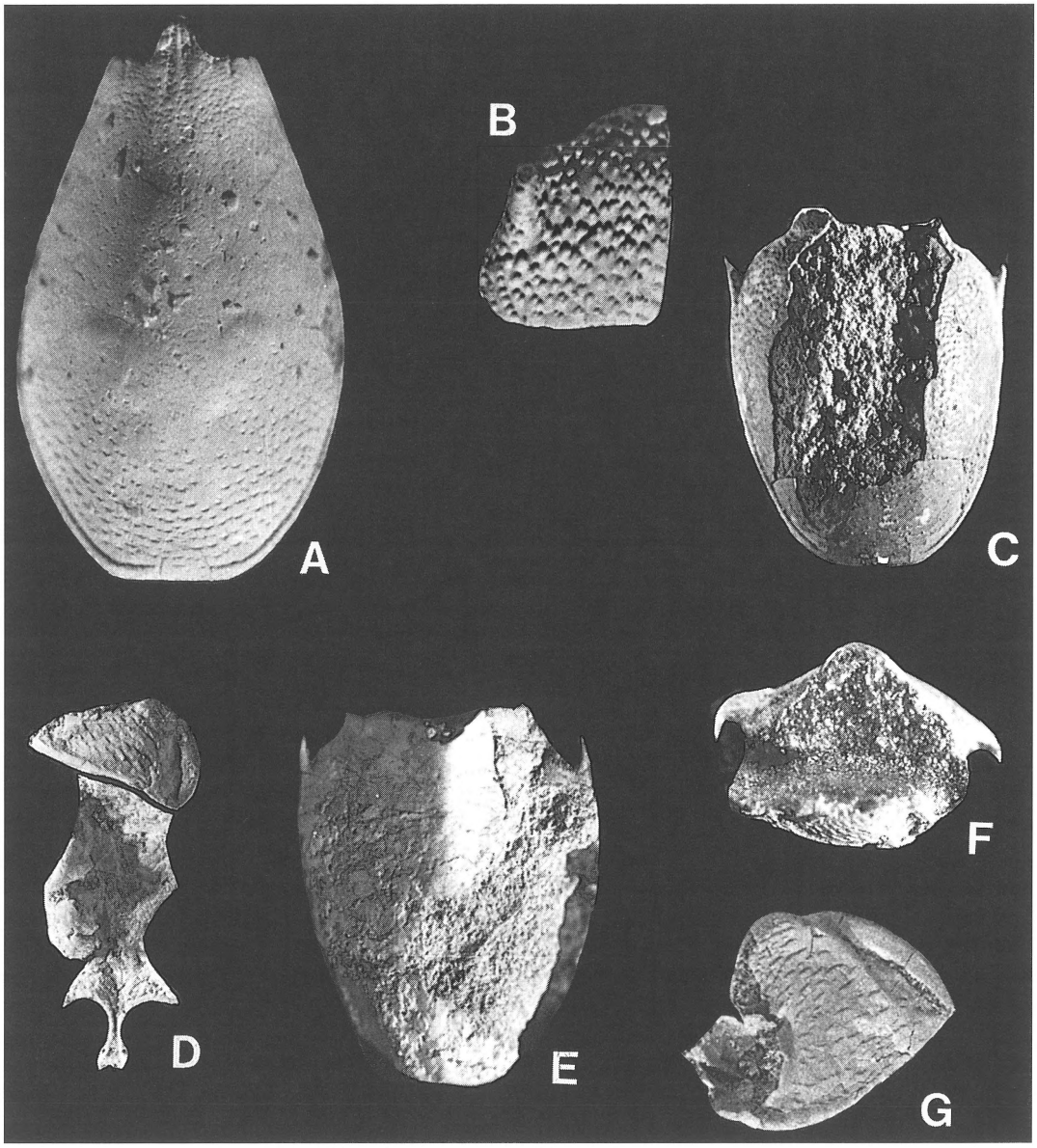

Figure 1. A–C) Dorsal views: *A*) *Lyreidina pyriformis* sp. n., holotype MAB k. 2251, × 5.5; *B, C*) *Raniliformis prebaltica* sp. n.: *B*) paratype MAB k. 2276, left frontal part, × 5; *C*) holotype NHMM 005986, × 2. *D-G*) *Raniliformis chevrona* sp. n.: *D–F*) holotype MAB k., 2252, × 3: *D*) sternal plates and right chela; *E*) dorsal view; *F*) frontal view; *G*) paratype MAB k. 2276, left chela, × 5.

Raniliformis prebaltica sp. n.
Figures 1B, C, 2B, 3B
Holotype: Natuurhistorisch Museum Maastricht Collections, no. NHMM 005986, a carapace with damaged orbitofrontal and central regions.
Type horizon and locality: Maastricht Fm, provenance unknown. Most probably Nekum Mbr or lower part of Meerssen Mbr, late Maastrichtian, *Belemnitella junior* Zone; Maastricht region.
Derivation of name: Referring to the precursor of *R. baltica*.
Material: Paratypes; in the Geo Centrum Brabant Collections: no. MAB k. 2243 left frontal part of carapace, (ex Van den Engel Collection); no. MAB k. 2277 right frontal part of carapace (ex Van Bakel Collection). Both paratypes from middle part of Meerssen Mbr, ENCI Nederland BV quarry, Maastricht.
Diagnosis: A *Raniliformis* with long transverse tuber-

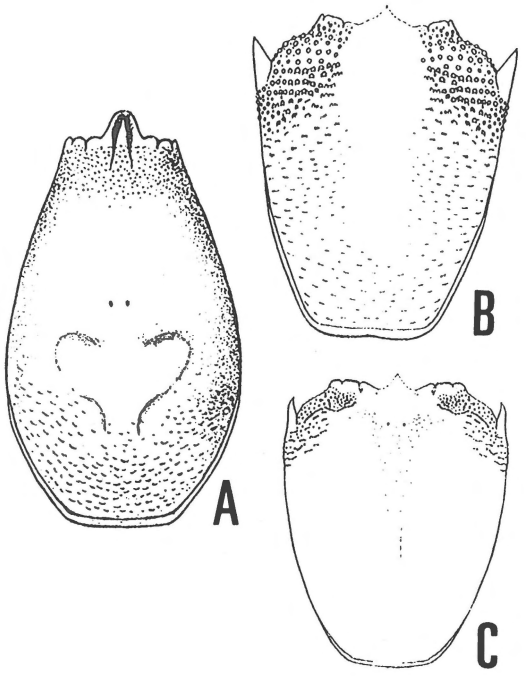

Figure 2. Carapaces in dorsal view. *A* = *Lyreidina pyriformis* sp. n., × 4.0, *B* = *Raniliformis prebaltica* sp. n., × 1.8, *C* = *Raniliformis chevrona* sp. n., × 2.0.

culate terraces on hepatic region, most prominent on widest part of the carapace, and a long prominent posterolateral rim.

Description: Ovate carapace, convex in transverse section, slightly arched in longitudinal section. Orbitofrontal margin half the carapace width, incised by two short fissures. Outer part of orbital margin one fifth of the inner lobe. Anterolateral margin straight from upper orbital margin and concave towards the narrow triangular anterolateral spine. Anterolateral spine more forwardly than outwardly directed. Anterior hepatic region covered with granules and tubercles; posterior part covered with three parallel transversely tuberculate terraces. Towards branchial regions tuberculation changes gradually into transversely orientated cuticule incisions. A slightly convex posterolateral margin bears a rim extending from half the length of the carapace to the slightly concave posterior margin.

Discussion: R. prebaltica most closely resembles *R. baltica* but differs in having narrower, more inwardly directed orbits, a more convex and less elongated anterolateral margin, a less convex carapace, a smoother posterior part of the carapace, less outwardly directed anterolateral spines, longer transverse cuticular terraces and a straighter posterior margin.

Occurrence: Maastricht Fm, upper part of Nekum Mbr to middle part of Meerssen Mbr, ENCI Nederland BV quarry, Maastricht.

Raniliformis chevrona sp. n.
Figures 1D–G, 2C, 3C

Holotype: Geo Centrum Brabant Collections, MAB k. 2252 (ex Van Bakel Collection).

Type horizon and locality: Maastricht Fm, upper part of Meerssen Mbr, latest Maastrichtian, *Belemnella kazimiroviensis* Zone; ENCI Nederland BV quarry, Maastricht.

Derivation of name: In allusion to the angular transverse section of the carapace.

Material: One additional specimen in the Van Bakel Collection.

Diagnosis: A *Raniliformis* with a longitudinally ridged and sharply curved carapace. Deep and strongly inclined ovate orbits, orbitofrontal margin more than half the carapace width.

Description: Ovate carapace, width three fourths of length, widest about one fourth distant from front, strongly curved longitudinally, V-shaped in transverse section over total length with sharpest angle anteriorly, almost flat in longitudinal section, smooth broad ridge extending from rostrum to posterior margin. Orbitofrontal margin slightly more than half the carapace width, divided by two short fissures into three almost equal parts. Deep ovate orbits steeply inclined (c. 60°). Rostrum apparently narrowly triangular. Short convex anterolateral margins terminating in forwardly directed, narrow, sharp spines with tips slightly curved towards the rostrum. Anterolateral spines placed one-fifth distant from the front. Rostral area smooth, with fine evenly distributed granules lining the middle and outer orbitofrontal margins, becoming larger and more densely packed towards the anterolateral spines. The ornamentation is most pronounced close to the anterolateral spines. Densely crowded tubercles form several short terraces. Terraces run parallel to a line from the anterolateral spine to the rostrum and are present from widest part of carapace to outer orbital notch. Median ridge is ornamented from smooth central rostral area to posterior margin with very fine and numerous pits. Pits decrease in size and number towards the posterior margin. All sternal plates covered with coarse pustules, arrangement and morphology of plates as in *R. occlusa*.

Elements of the first (right) pereiopod are either slender (carpus and merus) or flat (propodus and dactylus). Propodus with sharp, denticulate upper edge and

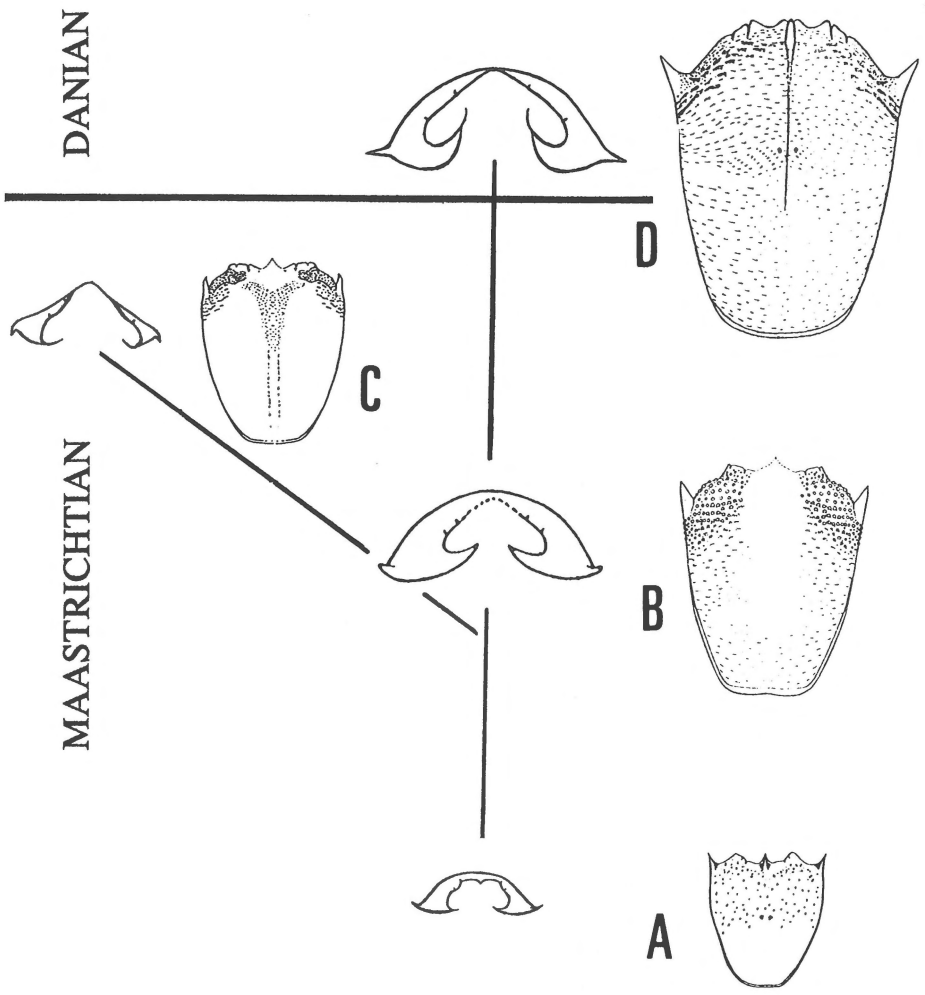

Figure 3. Carapace morphology and evolutionary relationship within the genus *Raniliformis* from the late Maastrichtian and early Danian of southern Limburg, the Netherlands. *A* = *R. occlusa*, × 1.3, *B* = *R. prebaltica*, × 1.3, *C* = *R. chevrona*, × 1.5, *D* = *R. baltica*, × 1.3.

very short fixed finger. Dactylus gently rounded with sinuous cutting edge. Outer propodus surface covered with oblique terraced elongated notches.

Discussion: *R. chevrona* is easily distinguished from congeneric species by its longitudinally curved carapace, angular frontal view, broad orbitofrontal margin, and forwardly directed and inwardly curved anterolateral spines. A strongly curved and ridged carapace occurs also in the closely related genus *Notopella* Lórenthey 1929, from the Ecocene of Spain and Hungary (Vía 1969; Müller & Collins 1991).

R. chevrona differs from *Notopella vareolata* Lórenthey & Beurlen 1929 in having a non-spinose orbital margin, curved, forwardly directed spines, more concave lateral margins and a smaller rostrum.

The genus *Raniliformis* is the oldest representative of the Notopodinae and very close to, and most likely the precursor of, the genus *Ranilia* H. Milne Edwards 1837 (Collins & Jakobsen 1994). Another closely related Recent genus is *Umalia*, erected by Guinot (1993) for species assigned to aff. *Ranilia* by Serène & Umali (1972). A possible phylogeny of the Notopodinae is shown in Figure 4.

Collins, Fraaye & Jagt (1995) placed *Pseudoraninella muelleri* within the Notopodinae and *Eumorphocorystes sculptus* within the Raninidae on presumed differences in sternal plates only. A recently discovered *E. sculptus*, the first one with preserved sternal plates, revealed no such differences. Except for carapace ornamentation there are no other clear mor-

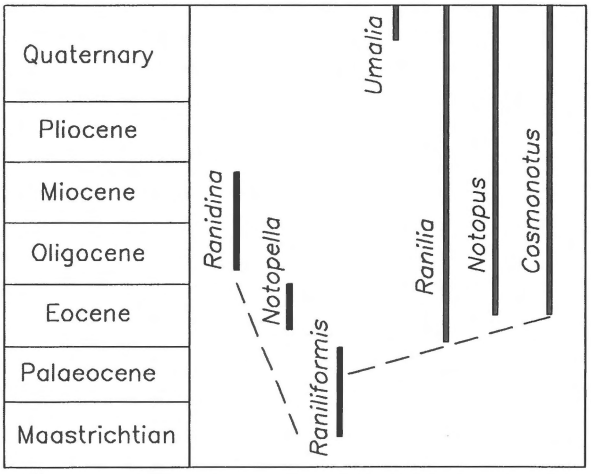

Figure 4. Range chart with possible phylogenetic relationships (dashed lines) of the subfamily Notopodinae.

phological differences between the two species, which is why we concur with Wright & Collins (1972, p. 78) in regarding *Pseudoraninella* as a junior synonym of *Eumorphocorystes*. *Eumorphocorystes* species in the type Maastrichtian have a carapace width/length proportion of 65 to 70%. Other differences with *Raniliformis* species were noted by Jagt, Collins & Fraaye (1993, pp. 178, 179).

In the Maastrichtian type area four species of *Raniliformis* are known so far. Three successive species show an obvious increase in size, elongation, ornamentation and convexity of the carapace and also an outwardly directed trend of the orbits, and are here regarded as a continuous lineage: *R. occlusa–prebaltica–baltica* (Figure 3). In this lineage the carapace width/length ratio is 87, 80, and 80%, respectively.

R. chevrona differs in having a width/length ratio of c. 76%, an extremely angular carapace in transverse section and curved, forwardly directed spines. It is interpreted as an offshoot representing the ancestral root of the genus *Notopella* Lórenthey 1929 (Figures 3, 4).

Like several other burrowing crabs (Seilacher 1961; Savazzi 1981, 1982), *Raniliformis* evolved a cuticular sculpture. Within the lineage *R. occlusa–prebaltica–baltica* there is a transition from randomly arranged, forwardly directed granules to tuberculate terraces especially on the frontal and widest parts of the carapace. There is a concomitant increase in carapace elongation and convexity. These changes are interpreted as adaptations to change of environment (R.H.B. Fraaye, unpublished data), in particular grain size and firmness of the substrate. From the Maastrichtian Emael Mbr upwards the size of the carbonate grains and the number of hardgrounds gradually increases. *Occurrence*: Apparently confined to the upper part of the Meerssen Mbr (Maastricht Fm, late Maastrichtian, *B. kazimiroviensis* Zone).

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