TYPE-MAASTRICHTIAN GASTROPOD FAUNAS SHOW RAPID ECOSYSTEM RECOVERY FOLLOWING THE CRETACEOUS–PALAEOGENE BOUNDARY CATASTROPHE

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Abstract: The study of the global mass extinction event at the Cretaceous–Palaeogene (K/Pg) boundary can aid in understanding patterns of selective extinction, and survival and dynamics of ecosystem recovery. Outcrops in the Maastrichtian type area (south-east Netherlands, north-east Belgium) comprise a stratigraphically expanded K/Pg boundary succession that offers a unique opportunity to study marine ecosystem recovery within the first few thousand years following the mass extinction event. A quantitative analysis was performed on systematically sampled macrofossils of the topmost Maastrichtian and lowermost Danian strata at the former Ankerpoort-Curfs quarry (Geulhem), which represent 'snapshots' of the latest Cretaceous and earliest Palaeogene marine ecosystems, respectively. Molluscs in particular are diverse and abundant in the studied succession. Regional ecosystem changes across the K/Pg boundary are relatively minor, showing a decline in suspension feeders, accompanied by an ecological shift to endobenthic molluscs. The earliest Paleocene gastropod assemblage retains many 'Maastrichtian' features and documents a fauna that temporarily survived into the Danian. The shallow, oligotrophic carbonate platform in this area was inhabited by taxa that were adapted to low nutrient levels and resistant to starvation. As a result, the local taxa were less affected by the short-lived detrimental conditions related to K/Pg boundary perturbations, such as darkness, cooling, starvation and ocean acidification. This resulted in relatively high survival rates, which enabled rapid recolonization and recovery of marine faunas in the Maastrichtian type area.

Key words: gastropods, Cretaceous–Palaeogene boundary, extinction, recovery, Maastrichtian type area.

PRESENT-DAY marine biotas are increasingly subjected to invasive species and anthropogenically forced extinctions (Harnik *et al.* 2012; McCauley *et al.* 2015). The study of global extinction events throughout geological history can further our understanding of patterns of selective extinction and survival and dynamics of ecosystem recovery (McKinney 1997; Erwin 2001; Harnik *et al.* 2012; Aberhan & Kiessling 2014). One of the most abrupt mass extinction events marks the Cretaceous–Palaeogene (K/Pg) boundary, dated *c.* 66.04 Ma (Alvarez *et al.* 1980; Schulte *et al.* 2010; Renne *et al.* 2013). The catastrophe at this boundary, triggered by the Chicxulub bolide impact (Schulte *et al.* 2010), ranks amongst the best-studied

Phanerozoic bioevents (Bambach 2006). Yet, most palaeontological studies of mass extinction events have focused on long-term, evolutionary recovery, over geological time scales (Aberhan & Kiessling 2014, 2015). As a result, our understanding of the worldwide ecological recovery and diversity dynamics in the direct aftermath of the K/Pg boundary mass extinction event is still rather limited (D'Hondt 2005).

Compared to most other K/Pg boundary sites, the outcrops in the Maastrichtian type area (south-east Netherlands, north-east Belgium) comprise a rarely stratigraphically expanded K/Pg boundary sequence (Smit & Brinkhuis 1996; Herngreen *et al.* 1998). The K/Pg

boundary occurs within the Meerssen Member of the Maastricht Formation; exposed at the former Ankerpoort-Curfs quarry (Geulhem) and in the adjacent Geulhemmerberg subterranean galleries (Felder 1975; Jagt *et al.* 1996, 2013; Smit & Brinkhuis, 1996; Herngreen *et al.* 1998; Felder & Bosch 2000; Robaszynski *et al.* 2001; Jagt & Jagt-Yazykova 2012; see Fig. 1).The Meerssen Member was subdivided into units IVf-1 to IVf-7 by Felder (1975) and Felder & Bosch (2000). The topmost Maastrichtian unit IVf-6 comprises in its upper part a coquina, or lumachelle, rich in a range of macrofossils, including gastropods, bivalves, cephalopods, scleractinian corals, echinoids and polychaete annelids (Jagt & Jagt-Yazykova 2012).This unit is capped by a prominent hardground, the Berg en Terblijt Horizon (Herngreen *et al.* 1998; Felder & Bosch 2000), which equates with the K/Pg boundary in the region (Smit & Brinkhuis 1996; Herngreen *et al.* 1998). The overlying, that is lowermost Danian, unit IVf-7 consists of a biocalcarenite, up to 4 m thick at the former Ankerpoort-Curfs quarry, with a thin
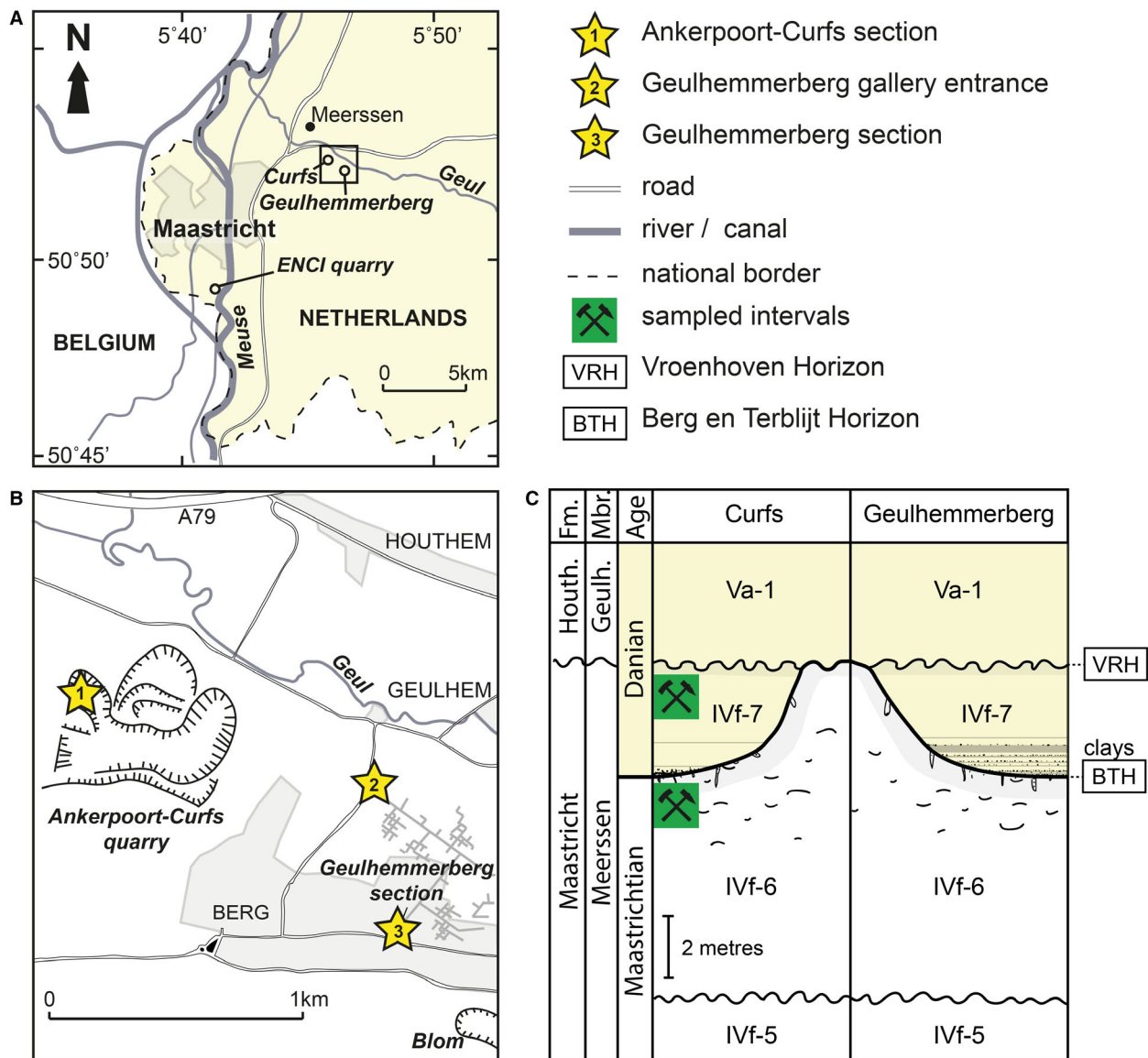

FIG. 1. A, map of the Maastricht area (southern Limburg, the Netherlands), showing the localities referred to in the text ('Curfs' is the former Ankerpoort-Curfs quarry); the boxed area is shown in B. B, detailed map of the Geulhem area, with the former Ankerpoort-Curfs quarry and the adjacent Geulhemmerberg K/Pg boundary sections in subterranean galleries. C, schematic stratigraphical context of the former Ankerpoort-Curfs quarry and adjacent Geulhemmerberg K/Pg boundary sections (note: vertical exaggeration is 10×). Colour online.

shell hash at its base (Jagt 1996; Felder & Bosch 2000). The lower 2 m of this unit comprise several discrete clay layers (Smit & Brinkhuis 1996; Jagt & Jagt-Yazykova 2012), which are best developed in the adjacent Geulhemmerberg subterranean galleries. Unit IVf-7 can be referred in its entirety to planktonic foraminiferal Zone P0 (Smit & Zachariasse 1996). Extensive sedimentological, micropalaeontological, palynological and geochemical studies on the sequences exposed at the former Ankerpoort-Curfs quarry and the adjacent Geulhemmerberg subterranean galleries all suggest that the deposition of unit IVf-7 was completed within a few hundreds to thousands of years after the Chicxulub bolide impact (Smit & Brinkhuis 1996; Herngreen *et al.* 1998).

Crucially, while many marine K/Pg boundary records are characterized by an earliest Paleocene 'dead zone' (Hansen *et al.* 1993; Håkansson & Thomsen 1999), the upper part of the lowermost Danian unit IVf-7 is rich in autochthonous macrofossils, including gastropods, bivalves, cephalopods and echinoids (Jagt *et al.* 1996, 2013). Amongst cephalopods from this biocalcarenite we note the ammonites *Eubaculites carinatus*, *Baculites* spp. and *Hoploscaphites constrictus johnjagti* (Landman *et al.* 2014). The ammonite assemblage from unit IVf-7 differs substantially in species composition and abundance of taxa from that of underlying units of the Meerssen Member (Jagt *et al.* 2003, 2013; Landman *et al.* 2014). Interestingly, most of the baculitid ammonites from unit IVf-7 are preserved with their apertures intact, showing that they were embedded without significant reworking or transport, which would have otherwise destroyed their delicate shells (Landman *et al.* 2014). Thus, ammonites from unit IVf-7 are considered to be earliest Danian survivors (Jagt *et al.* 2003, 2013; Machalski *et al.* 2009; Jagt & Jagt-Yazykova 2012), similar to records from eastern Denmark and New Jersey, USA (Machalski & Heinberg 2005; Landman *et al.* 2014). The earliest Danian ammonites from the Netherlands, Denmark and New Jersey may be considered as extreme examples of 'Dead Clade Walking' (*sensu* Jablonski 2002); a biological clade that temporarily survives a mass extinction, only to become extinct in its direct aftermath. Bivalves from the upper part of the IVf-7 biocalcarenite are often preserved in life or 'butterfly' position (Jagt *et al.* 2013), indicating that they are not reworked either. Many of the molluscs contain incompletely filled chambers/shells, with voids left after aragonite dissolution (Jagt *et al.* 2003, 2013), implying that they were buried without complete infilling (Landman *et al.* 2014). All of this suggests that the majority of macrofossils from the upper part of unit IVf-7 (i.e. above the basal shell hash and clay layers) are autochthonous and earliest Paleocene in age, and do not constitute reworked latest Cretaceous material (Jagt *et al.* 2003, 2013; Machalski *et al.* 2009; Goolaerts 2010; Jagt & Jagt-Yazykova 2012; Landman *et al.* 2014). Hence, the biocalcarenite of unit IVf-7 provides a 'snapshot' of the earliest Danian shallow marine ecosystem. Together with the coquina at the top of unit IVf-6, deposited during the very latest Maastrichtian, this succession thus offers an exceptional opportunity to study marine ecosystems just prior to, and directly following the Chicxulub impact, providing insights into the recovery within the first thousands of years following the K/Pg boundary catastrophe (Smit & Brinkhuis 1996).

Therefore, extensive, systematic bulk sampling of macrofossils was carried out on the coquina at the top of unit IVf-6 and the upper part of unit IVf-7 at the former Ankerpoort-Curfs quarry, to assess marine biotas in the latest Maastrichtian and earliest Danian, respectively. The emphasis was on the macroinvertebrate groups of Gastropoda, Bivalvia, Cephalopoda, Anthozoa and Polychaeta, some of the most abundant faunal groups in the type Maastrichtian strata. The K/Pg boundary interval within the Meerssen Member is particularly rich in molluscs, especially gastropods (Jagt *et al.* 2013). Importantly, gastropod assemblages constitute a key trophic component in shallow-marine food webs (Smith 2005), are considered useful indicators of marine biodiversity and ecosystem health (Gladstone 2002; Smith 2005; Chapman & Underwood 2008; Amin *et al.* 2009) and are comparatively well represented in the fossil record. For this reason, in the present study we have focused on changes in gastropod faunas across the K/Pg boundary in the Maastrichtian type area. To generate a more complete overview of gastropod turnover in this area, our quantitative analyses are complemented by qualitative data from the literature, the collections of the Natuurhistorisch Museum Maastricht (NHMM) and more than 20 years of collecting and taxonomic research by one of us (PVK).

STRATIGRAPHY

The former Ankerpoort-Curfs quarry (50°52′7″N, 5°46′E), is situated about 6 km north-east of the city of Maastricht in the type area of the Maastrichtian Stage (Fig. 1). As quarrying ended in late 2008, this site is currently a nature reserve, 'Stichting Het Limburgs Landschap'. Foraminiferal, nannoplankton and dinoflagellate biostratigraphy of the section exposed at the former Ankerpoort-Curfs quarry were discussed in detail by Herngreen *et al.* (1998). With both the Maastricht and Houthem formations being quarried, it was the only open pit allowing large-scale access to a well-preserved and stratigraphically expanded K/Pg boundary interval in the type Maastrichtian. The sequence exposed at this quarry is closely similar to that in the Geulhemmerberg subterranean galleries, *c.* 1 km to the east. The sedimentology,

geochemistry and biostratigraphy of the Geulhemmerberg sections have been described in detail in a special issue of the journal *Geologie en Mijnbouw*, which provides a wealth of data on the K/Pg boundary succession in the Maastrichtian type area (Smit & Brinkhuis 1996).

The Maastrichtian type area K/Pg boundary succession is situated within the Meerssen Member of the Maastricht Formation, as defined by Felder (1975). This member is capped by the Vroenhoven Horizon (Felder & Bosch 1998), a prominent hardground. The Vroenhoven Horizon can be traced over much of the area (Jagt & Janssen 1988) and marks the base of the overlying lower Danian Geulhem Member of the Houthem Formation (Felder 1975; Jagt *et al.* 1996; Robaszynski *et al.* 2001). Originally, the Vroenhoven Horizon was considered to equate with the K/Pg boundary in the area (see historical perspective in Jagt *et al.* 1996). However, on the basis of extensive sedimentological, geochemical and biostratigraphical studies (Brinkhuis & Schiøler 1996; Jagt 1996; Kuhnt 1996; Roep & Smit 1996; Romein *et al.* 1996; Smit & Zachariasse 1996; Vonhof & Smit 1996; Willems 1996; Witte & Schuurman 1996; Zijlstra *et al.* 1996; Herngreen *et al.* 1998), it was concluded that the Berg en Terblijt Horizon, a few metres below the Vroenhoven Horizon, represents the K/Pg boundary (Smit & Brinkhuis 1996; Herngreen *et al.* 1998). A typical planktonic foraminiferal 'disaster' assemblage (Smit & Zachariasse 1996), the presence of the earliest Paleocene dinocyst marker taxon *Senoniasphaera inornata* (see Brinkhuis & Schiøler 1996; Herngreen *et al.* 1998) and $^{87}Sr/^{86}Sr$ analyses of well-preserved foraminifera from the clay layers of the Geulhemmerberg underground galleries (Vonhof & Smit 1996) have all demonstrated that unit IVf-7 is of earliest Paleocene age, inferring that the Berg en Terblijt Horizon represents the K/Pg boundary.

The K/Pg boundary in the area, i.e. the hardground surface of the Berg en Terblijt Horizon, represents a submarine condensation level. The irregular surface and palaeorelief with knolls and depressions is inferred to be the result of bioerosion and current activity in relatively shallow (<40 m) waters (Roep & Smit 1996). The basal part of the overlying unit IVf-7 (i.e. the lowermost Danian) consists of a thin fossil hash (Roep & Smit 1996), succeeded by a biocalcarenite that is intercalated by several discrete clay layers. At the former Ankerpoort-Curfs quarry, these clay layers are few in number and very thin, often no more than clay films or wisps, whereas in the Geulhemmerberg galleries more and thicker clay layers are recorded. Microfacies distribution has shown that the calcarenitic Geulhemmerberg sediment was deposited under somewhat higher hydrodynamic energy conditions than coeval sediments at the Ankerpoort-Curfs quarry, explaining the sedimentological differences between these adjacent sites (Zijlstra *et al.*

1996). The succession of shell hash levels and clay layers in the basal part of IVf-7 biostratigraphically correlates to the basalmost part of planktonic foraminiferal Zone P0, with a planktonic foraminiferal assemblage dominated by survival taxa such as *Heterohelix globulosa* and *Guembelitria cretacea* (Smit & Zachariasse 1996) and dinocyst marker taxa also characteristic of the basalmost part of Zone P0 (Brinkhuis & Schiøler 1996; Herngreen *et al.* 1998). This succession of shell hash levels and clay layers is interpreted as reflecting a sequence of events that took place within days to decades after the K/Pg boundary impact: high-energy events (i.e. impact-triggered storms or seismites) that removed the loose sediments on the contemporary sea floor, including ejecta deposits overlying the Berg en Terblijt hardground, followed by storm-induced infill of palaeodepressions in the upper Maastrichtian palaeorelief by biocalcarenites and K/Pg boundary clays during times of decreasing storm intensity (Smit & Brinkhuis 1996). While it is likely that some of the topmost Maastrichtian sediments were removed during the K/Pg boundary event, the missing strata represent limited time, because accumulation rates of the upper Maastricht Formation were high (5–10 cm/kyr; Vonhof & Smit 1996; Zijlstra *et al.* 1996; Gras & Geluk 1999; Vonhof *et al.* 2011; Keutgen 2018). Indeed, the chemo- and biostratigraphy of the upper Maastricht Formation suggest that the uppermost Maastrichtian is still relatively complete, with unit IVf-6 representing the last tens of thousands of years of the Cretaceous Period (Smit & Brinkhuis 1996; Vonhof & Smit 1996; Keutgen 2018).

The succession of shell hash levels and clay layers in the basal part of unit IVf-7 is overlain by biocalcarenites, representing the upper part of IVf-7, the interval sampled for the present study. This upper part of IVf-7 reflects a return to normal conditions and a resumption of normal sedimentation, probably within the first millennia after the K/Pg boundary Chicxulub bolide impact (Smit & Brinkhuis 1996; Herngreen *et al.* 1998). Biostratigraphically, the upper part of IVf-7 also comprises planktonic foraminiferal (Smit & Zachariasse 1996; Herngreen *et al.* 1998) and dinocyst (Brinkhuis & Schiøler 1996; Herngreen *et al.* 1998) marker taxa characteristic of the basal part of P0 (survival planktonic foraminiferal taxa such as *H. globulosa* and *G. cretacea* and the dinocyst marker taxon *S. inornata*), without any markers for the upper part of Zone P0 or overlying zones Pα or P1a (such as the planktonic foraminifer *Parvularugoglobigerina eugubina* or the dinocyst marker taxa *Danea californica* and *Carpatella cornuta*). This constrains the age of the sampled interval (the upper part of IVf-7) to the first thousands of years after the Chicxulub impact.

Unit IVf-7 of the Meerssen Member is capped by the Vroenhoven Horizon, a hardground surface that marks a

sharp lithological transition to the glauconitic calcarenites of the lower Danian Geulhem Member of the Houthem Formation. Regionally, the Vroenhoven Horizon cuts into the underlying strata of the Meerssen Member, with the topmost unit of the Meerssen Member, unit IVf-7, only preserved in palaeodepressions. Biostratigraphically, the basalmost part of the Geulhem Member comprises a nannofossil assemblage that is characteristic of Zone NP1, and dinoflagellate marker taxa typical of planktonic foraminiferal zones P1a to P1b (*D. californica*; *C. cornuta* and *Xenicodinium rugulatum*; Herngreen *et al.* 1998). The NP1/NP2 zonal boundary, which has been dated at 65.47 Ma (Vandenberghe *et al.* 2012), occurs within 20 cm above the Vroenhoven Horizon (Herngreen *et al.* 1998). According to Jagt & Janssen (1988) the Geulhem Member comprises *Parasubbotina pseudobulloides* and *Globoconusa daubjergensis*, planktonic foraminiferal taxa characteristic of Zone P1b. The Geulhem Member therefore appears to represent a time equivalent of the Korsnaeb Member of the Stevns Klint Formation at Stevns Klint, Denmark (Surlyk *et al.* 2006) and lower Danian unit G in the Polish K/Pg boundary records (Machalski *et al.* 2016). As the upper part of unit IVf-7 of the Meerssen Member was laid down during the first thousands of years after the Chicxulub impact, and the basalmost part of the overlying Geulhem Member comprises the NP1/NP2 zonal boundary, the Vroenhoven Horizon probably represents a hiatus of *c.* 0.5 million years (Herngreen *et al.* 1998).

DEPOSITIONAL SETTING

At the time of deposition of the Maastricht Formation exposed in the former Ankerpoort-Curfs quarry, a shallow, inner-shelf sea flooded the study area. The type-Maastrichtian epicontinental sea was bordered by the Central European Massif in the east, inverted blocks of the Ruhrgraben in the north and the Brabant Massif in the west and south-west (Bless 1991). Based on sedimentology and benthic foraminiferal assemblages (Roep & Smit 1996; Witte & Schuurman 1996), the water depth during deposition of the Meerssen Member is interpreted to have been 20–40 m. Bulk rock and benthic foraminiferal oxygen isotope records and assemblages of benthic foraminifera, calcareous nannofossils and organic-walled dinoflagellate cysts in the studied area are characteristic of shallow but fully marine conditions (Brinkhuis & Schiøler 1996; Schmitz & Speijer 1996; Herngreen *et al.* 1998). Deposition occurred under hydrodynamically high-energy conditions with episodic storm activity, as indicated by local fossil hashes, biocalcarenites and sporadic clay layers (Roep & Smit 1996).

SAMPLING AND MATERIAL

An extensive, systematic bulk sampling of macrofossils was performed at two levels within the Meerssen Member of the Maastricht Formation at the former Ankerpoort-Curfs quarry: (1) the coquina in the top of unit IVf-6, this is 0–50 cm below the Berg en Terblijt Horizon; and (2) the partly indurated upper part of unit IVf-7, just below the Vroenhoven Horizon. No fossils were collected from the basalmost part of the latter unit, because the thin and discontinuous fossil hash here comprises fossils that are clearly reworked (Jagt 1996; Roep & Smit 1996), making it difficult to establish which fossils are of definite Danian age and which are reworked from the underlying upper Maastrichtian.

Due to the quarrying conditions at the time of sampling, only a limited number of large blocks from the IVf-6 coquina could be collected *in situ*. However, this level has a very characteristic texture and colour; for example, with many white spots representing larger benthic foraminifera, making them readily recognizable, allowing them to be hand-picked from a debris pile in front of a recently blasted quarry wall. The IVf-7 calcarenite was sampled *in situ*, with large blocks being extracted from the quarry face. These blocks were subsequently processed in the field into smaller fragments of 5–50 cm diameter, after which their macrofossil content was quantitatively examined in the laboratory. Samples of the biocalcarenite of unit IVf-7 were impregnated with a *c.* 1/10 solution of Elmer glue to consolidate fossil material for easier handling. The IVf-6 coquina is slightly firmer than the IVf-7 calcarenite and was therefore not impregnated.

For a basic assessment of marine ecosystems just prior to (i.e. unit IVf-6) and directly following the K/Pg boundary catastrophe (i.e. unit IVf-7), all macrofossils encountered were identified at class/order level. Following standard procedures (Patzkowsky & Holland 2007; Aberhan & Kiessling 2014), the number of bivalve individuals was determined as the sum of articulated specimens plus the larger number of right or left valves of disarticulated shells plus one half the number of fragments which could not be assigned to either right or left valves, but which make up more than 50% of a valve. Gastropods were counted when more than 50% of the specimen was preserved. Macrofossils were counted up to a minimum of 700 specimens per unit. Gastropods encountered were identified as precisely as possible, often to species level, predominantly on the basis of Binkhorst van den Binkhorst (1861–1862) and Kaunhowen (1898), with later nomenclatural emendations considered (Vellekoop *et al.* 2019, table S1). Specimens which could not be identified confidently to genus level, were solely attributed to a

'form group', based on general morphology (Vellekoop et al. 2019, table S1). For ecological classification or interpretation, only identified specimens were used. To enable a comparison of gastropod assemblages between units IVf-6 and IVf-7, similar numbers of gastropod individuals for both units were obtained. To this end, after reaching 708 macrofossils for unit IVf-6, the count of gastropods was continued until a minimum of 300 gastropods was obtained. The remainder of the collected blocks were scanned for additional rare taxa. Standard quantitative diversity metrics Shannon H diversity index and Dominance (D) were applied following Hayek & Buzas (2013), on the quantitative counts of gastropod specimen, including only specimens identified up to genus and/or species level. All material studied is catalogued and stored in the collections of the Natuurhistorisch Museum Maastricht (NHMM).

Following Sessa et al. (2012) and Aberhan & Kiessling (2015), we have applied an ecological classification of benthic molluscs (bivalves and gastropods), in which taxa are classified with respect to three variables: tiering, mobility and feeding mechanism, using the 'theoretical ecospace' scheme of Bush et al. (2007). Extinct taxa are assigned to specific modes of life (MOL) by comparison with extant relatives and analogues, following Sessa et al. (2012) and Aberhan & Kiessling (2015). For this assignment of MOLs, we have assumed that MOLs are often similar within genera (Sessa et al. 2012), allowing us to apply the MOLs proposed for these genera by Aberhan & Kiessling (2015). We have classified gastropods in feeding strategies following Sessa et al. (2012), for example, carnivorous predator (active, fast moving carnivores), carnivorous browser (carnivores feeding on sedentary animals), suspension feeder (feeding on suspended particles), herbivorous grazers (microalgivores, macroalgivores) and surface deposit feeders (microphages, detritivores). An ecological classification of benthic molluscs allows for the identification of different modes of life, yielding insights into the ecological

dynamics of the extinction and subsequent recovery (Aberhan & Kiessling 2015).

RESULTS

Total macroinvertebrates

Both the topmost Maastrichtian coquina (unit IVf-6) and the biocalcarenite of unit IVf-7 are rich in macrofossils, such as gastropods, bivalves, cephalopods, corals, echinoids and polychaete annelids (serpulids). Generally only calcitic shells are preserved, while all aragonitic parts are dissolved post-burial. For all originally aragonitic taxa, representing the majority of fossils encountered, the original shell form is inferred from the internal and external moulds.

From the IVf-6 coquina, 708 macrofossils were counted in total, 40% (n = 283) of which are bivalves, 23% (n = 165) are gastropods, 20% (n = 139) are corals, 4% (n = 27) are polychaetes and 3% (n = 19) are cephalopods (Fig. 2; Vellekoop et al. 2019, table S2). Cephalopods from IVf-6 comprise mainly baculitids (*Baculites vertebralis* and *B. anceps*) and several other ammonite taxa (*Hoploscaphites constrictus johnjagti* and *Sphenodiscus binckhorsti*). Scleractinian corals include *Diploctenium cordatum* (74%) and solitary species such as *Cunnolites cancellata* and *Micrabacia* sp. (23%). From the IVf-7 biocalcarenite, 704 macrofossils were identified, of which nearly 67% (n = 469) are gastropods and about 24% (n = 166) bivalves, 4% (n = 31) scleractinian corals, 1.7% (n = 12) cephalopods and 0.4% (n = 3) polychaetes (Fig. 2). Cephalopods are represented by at least two (maybe three) species of baculitid (90%) and with a handful of *Hoploscaphites constrictus johnjagti*. All encountered corals were solitary forms, such as *Micrabacia* sp.

Invertebrate assemblages from IVf-6 and IVf-7 differ, both in numbers and composition (Fig. 2). The bivalves
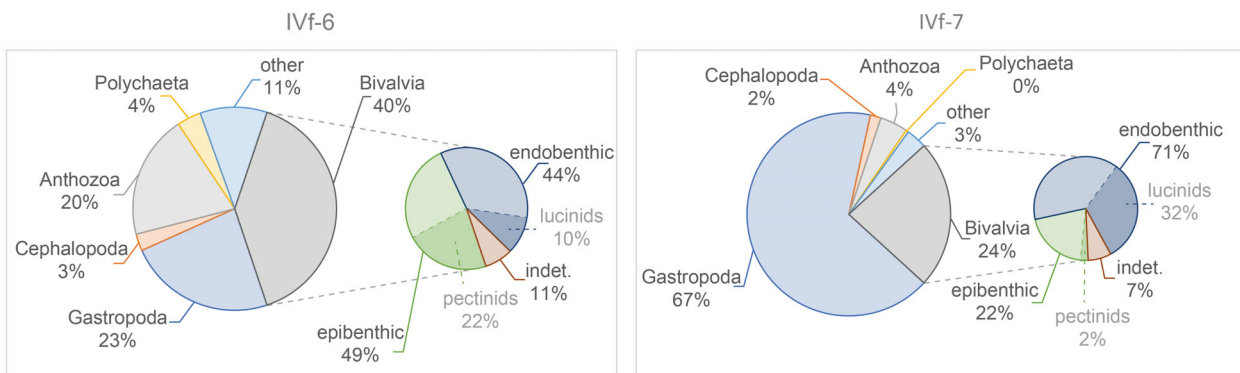

FIG. 2. Relative contributions of the various macroinvertebrate groups in faunal assemblages from Meerssen Member units IVf-6 (latest Maastrichtian) and IVf-7 (earliest Paleocene). Colour online.

decrease from 40% to 24% of the total macroinvertebrate assemblages. In IVf-6, 49% of bivalves are epibenthic, 44% endobenthic, while 11% could not be assigned to life habit. In IVf-7, percentages change to 71% endobenthic bivalves vs 22% epibenthic bivalves and 7% unassigned. Changes in bivalve assemblages across the K/Pg boundary are mostly due to a drop in pectinoids such as *Entolium* and *Syncyclonema* (from 22% to 2%) and an increase in lucinids (from 10% to 32%). Cephalopods decrease from 3% to 1.7%, while polychaetes drop from 4% to 0.4% and corals from 20% to 4%. A qualitative assessment of the sampled rock material showed that larger benthic foraminifera, such as species of *Orbitoides*, *Lepidorbitoides* and *Siderolites*, disappear completely across the K/Pg boundary. The sole group to increase in relative abundance is gastropods, which rise from 23% to 67% of the assemblage.

Gastropods

In total, 302 gastropod specimens were counted from unit IVf-6, of which about 57% (n = 172) could be identified to genus and/or species level, whilst 480 specimens were counted from IVf-7, of which about 55% (n = 264) could be assigned generically or specifically. In both IVf-6 and IVf-7, gastropods belonging to the aporrhaids are dominant (see Vellekoop *et al.* 2019, table S3). The gastropod assemblage from IVf-6 is dominated by *Aporrhais limburgensis* (21% of the total number counted and 37% of specifically identified gastropods). *Turritella* sp. and *Otostoma retzii* (*auctorum*, *non* Nilsson) each comprise 9% of the specimens identified. Various naticids, *Cerithium* (*s.l.*) spp. and *Cerithium alternatum* each account for 8% of the identified gastropod specimens. The 13 other taxa account for the remaining 22%. The gastropod fauna in unit IVf-7 is dominated by *Arrhoges* (*Latiala*) *pelecyphora*, representing at least 16% of the assemblage, and 51% of the identified gastropods from this unit. *Arrhoges* (*Latiala*) *pelecyphora* was not encountered in unit IVf-6 during sampling for the present study. Other abundant taxa are *Xenophora nilssoni* (11% of identified specimens), followed by *Hippochrenes binkhorsti* (8%), *Natica* spp. (6%), *Turritella* (*s.l.*) spp. (6%) and *Cerithium* (*s.l.*) spp. (5%). All other taxa belong to the remaining 20% of taxa identified. In both the top Maastrichtian and the basal-most Paleocene, neogastropod taxa such as *Cancellaria*; *Columbarium*, *Fusus* and *Popenoeum* are rare, representing *c.* 2% of identified specimens. This suggests that neogastropods were minor players in the type-Maastrichtian ecosystem.
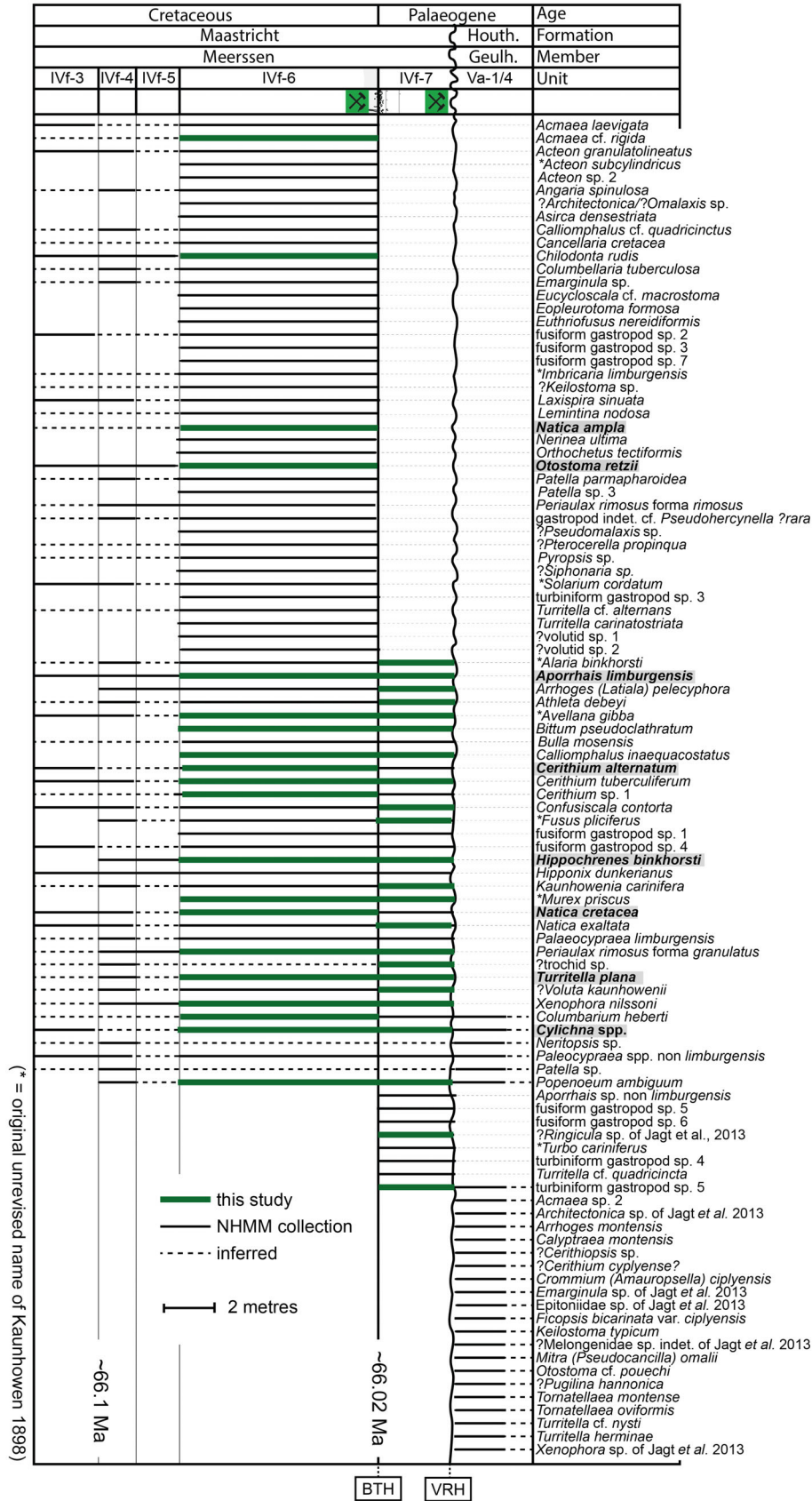
Gastropod faunas document a shift across the K/Pg boundary, with diversity decreasing between IVf-6 to IVf-7 (Vellekoop *et al.* 2019, table S1), as for example

indicated by the Shannon H index (2.2–1.9). The Dominance (D) index of gastropods is slightly higher in unit IVf-7 (0.27) compared to unit IVf-6 (0.21). *Aporrhais limburgensis*, predominant in unit IVf-6 (21%), strongly drops in unit IVf-7 (2%). In unit IVf-7, *Arrhoges* (*Latiala*) *pelecyphora* becomes dominant (27%). Taxa such as *Turritella* (*s.l.*) spp., *Natica* spp., *Cerithium* (*s.l.*) spp., *Cylichna* spp., *Aporrhais* spp. and *Periaulax rimosus* also dwindle in numbers, while *Otostoma retzii* and *Cerithium alternatum*, accounting for 9 and 8% of the IVf-6 assemblage, disappear in unit IVf-7. When the quantitative analyses performed in the present study are complemented by qualitative data from previously literature sources and the NHMM collections, results show that of the 74 gastropod taxa that are known from the uppermost Maastrichtian of the type area (unit IVf-6), 41 (*c.* 55%) are not found above the Berg en Terblijt Horizon (Fig. 3; Vellekoop *et al.* 2019, table S4). A total of eight taxa first occur in unit IVf-7, representing the earliest truly Paleocene taxa in this region. All the 'new' Paleocene taxa have close relatives in the Cretaceous, suggesting a role for incumbency, which may have been a significant factor in the survival and phased recovery of marine fauna following the K–Pg catastrophe (Sessa *et al.* 2012). At the Vroenhoven Horizon, which marks the hiatus between the Maastricht and Houthem formations, 34 taxa disappear, representing >82% of the gastropod taxa that survived the Chicxulub impact. In total, 21 taxa make their first appearance in the Geulhem Member, above the Vroenhoven Horizon. For apparent speciation and extinction rates throughout the Meerssen and Geulhem members, reference is made to Vellekoop *et al.* (2019, appendix S1).

Gastropods in units IVf-6 and IVf-7 are mainly slow motile shallow infaunal surface deposit feeders, representing 75–80% of identified gastropod specimen. Suspension feeders decrease slightly across the K/Pg boundary, from 9% to 6% of gastropod specimens identified (Vellekoop *et al.* 2019, table S3). The most notable change across the boundary is thus an increase in soft-substrate herbivores (semi- and shallow infaunal microaglivores, macroalgivores, microphages and detritivores), from 40% in unit IVf-6 to 63% in IVf-7 (Vellekoop *et al.* 2019, appendix S1).

Modes of life

Amongst the benthic molluscs of the type-Maastrichtian K/Pg boundary succession, a total of 15 unique modes of life could be identified. While none of the modes of life was lost across the K/Pg boundary (see Fig. 4), there are distinct shifts in tiering, mobility and feeding mechanism (Fig. 5; Vellekoop *et al.* 2019, table S5). Particularly, epibenthic taxa decrease in relative abundance (from 47%

							Age
Cretaceous					Palaeogene		
Maastricht						Houth.	Formation
Meerssen						Geulh.	Member
IVf-3	IVf-4	IVf-5	IVf-6		IVf-7	Va-1/4	Unit

Species ranges (left to right stratigraphic units; green = this study, solid black = NHMM collection, dashed = inferred):

- Acmaea laevigata
- Acmaea cf. rigida
- Acteon granulatolineatus
- *Acteon subcylindricus
- Acteon sp. 2
- Angaria spinulosa
- ?Architectonica/?Omalaxis sp.
- Asirca densestriata
- Calliomphalus cf. quadricinctus
- Cancellaria cretacea
- Chilodonta rudis
- Columbellaria tuberculosa
- Emarginula sp.
- Eucycloscala cf. macrostoma
- Eopleurotoma formosa
- Euthriofusus nereidiformis
- fusiform gastropod sp. 2
- fusiform gastropod sp. 3
- fusiform gastropod sp. 7
- *Imbricaria limburgensis
- ?Keilostoma sp.
- Laxispira sinuata
- Lemintina nodosa
- **Natica ampla**
- Nerinea ultima
- Orthochetus tectiformis
- **Otostoma retzii**
- Patella parmapharoidea
- Patella sp. 3
- Periaulax rimosus forma rimosus
- gastropod indet. cf. Pseudohercynella ?rara
- ?Pseudomalaxis sp.
- ?Pterocerella propinqua
- Pyropsis sp.
- ?Siphonaria sp.
- *Solarium cordatum
- turbiniform gastropod sp. 3
- Turritella cf. alternans
- Turritella carinatostriata
- ?volutid sp. 1
- ?volutid sp. 2
- *Alaria binkhorsti
- **Aporrhais limburgensis**
- Arrhoges (Latiala) pelecyphora
- Athleta debeyi
- *Avellana gibba
- Bittum pseudoclathratum
- Bulla mosensis
- Calliomphalus inaequacostatus
- **Cerithium alternatum**
- Cerithium tuberculiferum
- Cerithium sp. 1
- Confusiscala contorta
- *Fusus pliciferus
- fusiform gastropod sp. 1
- fusiform gastropod sp. 4
- **Hippochrenes binkhorsti**
- Hipponix dunkerianus
- Kaunhowenia carinifera
- *Murex priscus
- **Natica cretacea**
- Natica exaltata
- Palaeocypraea limburgensis
- Periaulax rimosus forma granulatus
- ?trochid sp.
- **Turritella plana**
- ?Voluta kaunhowenii
- Xenophora nilssoni
- Columbarium heberti
- **Cylichna spp.**
- Neritopsis sp.
- Paleocypraea spp. non limburgensis
- Patella sp.
- Popenoeum ambiguum
- Aporrhais sp. non limburgensis
- fusiform gastropod sp. 5
- fusiform gastropod sp. 6
- ?Ringicula sp. of Jagt et al., 2013
- *Turbo carniferus
- turbiniform gastropod sp. 4
- Turritella cf. quadricincta
- turbiniform gastropod sp. 5
- Acmaea sp. 2
- Architectonica sp. of Jagt et al. 2013
- Arrhoges montensis
- Calyptraea montensis
- ?Cerithiopsis sp.
- ?Cerithium cyplyense?
- Crommium (Amauropsella) ciplyensis
- Emarginula sp. of Jagt et al. 2013
- Epitoniidae sp. of Jagt et al. 2013
- Ficopsis bicarinata var. ciplyensis
- Keilostoma typicum
- ?Melongenidae sp. indet. of Jagt et al. 2013
- Mitra (Pseudocancilla) omalii
- Otostoma cf. pouechi
- ?Pugilina hannonica
- Tornatellaea montense
- Tornatellaea oviformis
- Turritella cf. nysti
- Turritella herminae
- Xenophora sp. of Jagt et al. 2013

Legend:
- this study
- NHMM collection
- inferred
- 2 metres

~66.1 Ma

~66.02 Ma

(* = original unrevised name of Kaunhowen 1898)

BTH   VRH

to 27%), while shallow endobenthic taxa increase (from 23% to 41% of benthic molluscs). In terms of mobility, motile taxa increase from 32% to 55%. Across the K/Pg boundary, surface deposit feeders increase in relative abundance (form 21% to 34%), at the expense of suspension feeders, which decrease in relative abundance, from 41% to 13% of the benthic molluscan assemblage. These shifts in tiering, mobility and feeding mechanism result in changes in the proportional abundance of modes of life of the marine molluscan assemblages of the type-Maastrichtian. Most notably, epibenthic suspension feeders (MOLs 1 and 2) decrease in relative abundance (with minus 13% in relative abundance each), whilst shallow endobenthic, motile, surface deposit feeders (MOL 4) increases by 17% in relative abundance.

DISCUSSION

Taphonomy

There are several taphonomic differences between units IVf-6 and IVf-7. The IVf-6 coquina is slightly more lithified than the IVf-7 biocalcarenite, requiring a different approach in sample handling and preparation. Preservation of the external ornament of molluscan fossils is slightly better in the IVf-6 coquina, which is more consolidated than the IVf-7 biocalcarenite (Figs 6–8). The latter contains a relatively larger proportion of sediment relative to the more or less randomly distributed fossils. In the IVf-6 coquina the fossils are preserved in great number and are closely stacked. However, in both units preservation is sufficient to allow for *c.* 55% of the encountered gastropods to be identified to species or genus level. In view of these similar numbers, we conclude that the taphonomic differences between these units are such that they allow for a palaeoecological comparison of the fossil assemblages from these levels.

Environmental change across the K/Pg boundary

The dense packing of fossils and numerous disarticulated bivalve valves in the uppermost Cretaceous IVf-6 coquina are indicative of relatively high current and
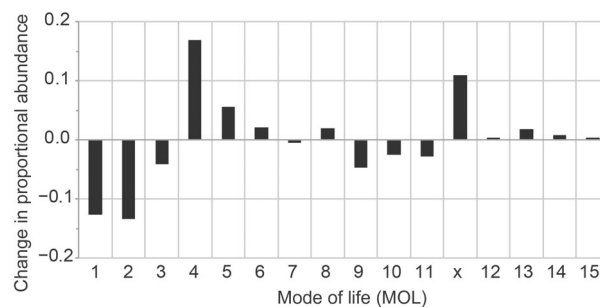

FIG. 4. Changes in the proportional abundance of modes of life (MOLs 1–15) represented in marine molluscan assemblages across the Cretaceous–Palaeogene boundary of the type-Maastrichtian. Modes of Life are rank ordered according to latest Maastrichtian abundance, decreasing from left to right. Negative values indicate proportionally declining modes of life and positive values, expanding modes of life across the K/Pg boundary. 1, epibenthic, stationary, byssate, suspension feeders; 2, epibenthic, facultatively motile, unattached or byssate, suspension feeders; 3, deep endobenthic, facultatively motile, surface deposit feeders; 4, shallow endobenthic, motile, surface deposit feeders; 5, epibenthic, motile, carnivores; 6, deep endobenthic, facultatively motile, chemosymbiotic; 7, shallow endobenthic, motile, suspension feeders; 8, epibenthic, motile, herbivores; 9, endobenthic bivalves, unassigned; 10, shallow endobenthic, facultatively motile, unattached, suspension feeders; 11, unassigned bivalves; 12, epibenthic, facultatively motile, herbivores; 13, shallow endobenthic, motile, carnivores; 14, epibenthic, stationary, cemented, suspension feeders; 15, epibenthic bivalves, unassigned; x, unknown MOL.

wave activity. In view of the fact that unit IVf-6 is capped by a hardground, it is likely that that the sediments were already becoming indurated during deposition of the top part of this unit. This synsedimentary cementation can also be concluded on the basis of encrustations and bioturbation traces (Roep & Smit 1996). In contrast, the upper part of the lowermost Paleocene unit IVf-7 comprises more fine-grained calcareous sediment and more bivalves preserved *in situ* than unit IVf-6, suggesting softer substrates and decreased current activity during the deposition of this part of the unit. Consistent with this sedimentological evidence, soft substrate herbivorous gastropods are more abundant in assemblages from unit IVf-7 (see Vellekoop *et al.* 2019, table S3). There are no indications of changing water depths between IVf-6 and IVf-7.

FIG. 3. Stratigraphical distribution of gastropod taxa across the K/Pg boundary in the Maastrichtian type area; age estimates are based on Herngreen *et al.* (1998) and Keutgen (2018). Taxa indicated in bold with grey shadow each represent >2% in relative abundance of the latest Maastrichtian gastropod assemblage. This overview has been compiled from data gleaned from NHMM collections and from material collected for the present study at the former Ankerpoort-Curfs quarry. Note: only taxa that reached the K/Pg boundary are indicated. For the complete data set, refer to Vellekoop *et al.* (2019). In the present compilation, several forms could not be assigned to previously named species; these may constitute undescribed taxa. For the time being, they are here listed in open nomenclature (e.g. 'sp. 1', 'sp. 2') awaiting formal description at a later date. *Abbreviations*: BTH, Berg en Terblijt Horizon; VRH, Vroenhoven Horizon. Colour online.
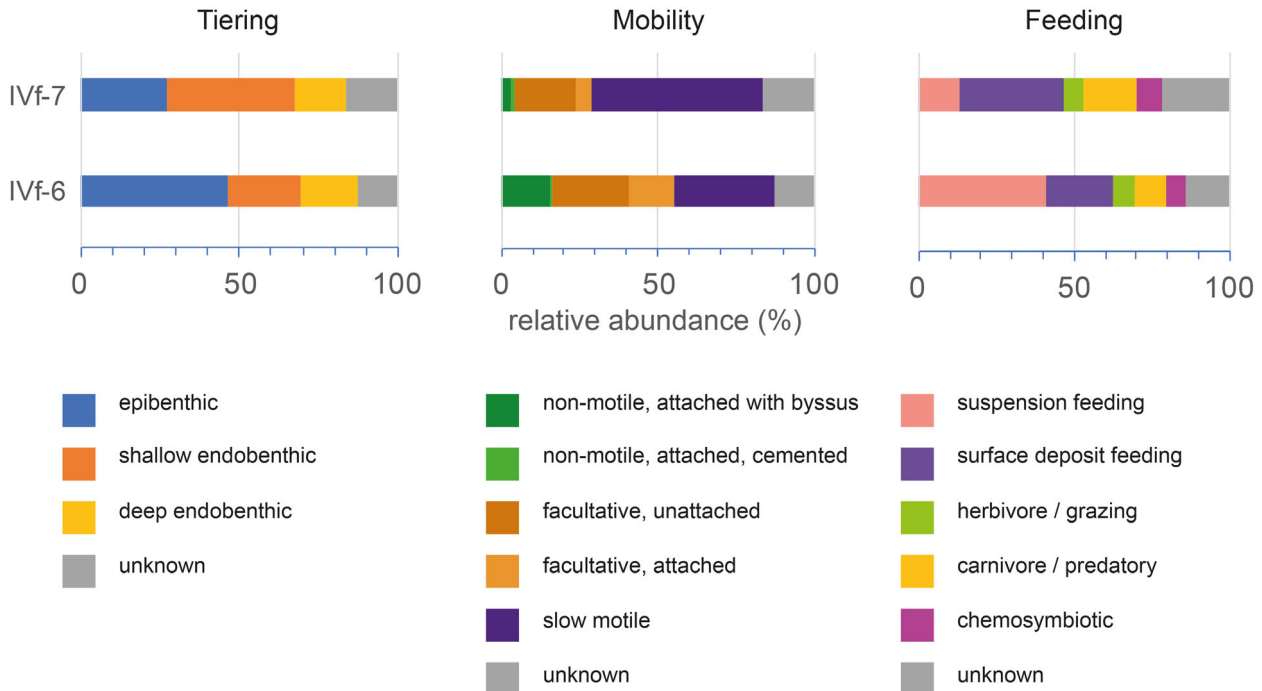
FIG. 5. Proportional taxonomic abundance based on specimen numbers, for tiering, motility and feeding categories of unit IVf-6 and unit IVf-7.

Gastropod faunal change at the K/Pg boundary?

Approximately 55% of gastropod taxa occurring in the topmost Maastrichtian unit IVf-6 are not encountered in the lowermost Danian, suggesting that the K/Pg boundary catastrophe marks a sharp transition in local gastropod assemblages. Yet, as unit IVf-6 is both thicker than unit IVf-7, and more widely exposed in the type-Maastrichtian region, this apparent extinction could partly be a consequence of a difference in sampling intensity between the two units, resulting in an overrepresentation of rare taxa in the assemblage of IVF-6, compared to unit IVf-7 (see Fig. 3). Remarkably, while the K/Pg boundary extinction appears as a major drop in diversity in numerous gastropod records across the globe (Hansen *et al.* 1993), our record from the type Maastrichtian merely shows a minor decrease in gastropod diversity, from 2.2 to 1.9 in Shannon H index, as most of the common taxa survived the boundary perturbations. This means that, although many

rare taxa appear to become extinct, the gastropod fauna of unit IVf-7 does not differ much from that of unit IVf-6. This is in contrast to, for example, the molluscan records from Seymour Island, Antarctica, where many of the dominant taxa become extinct at the K/Pg boundary (Witts *et al.* 2016). The most significant changes in the studied assemblage is a shift in dominant taxa. While the aporrhaid *Aporrhais limburgensis* is dominant in unit IVf-6, *Arrhoges* (*Latiala*) *pelecyphora* is the most common gastropod in unit IVf-7. Intriguingly, the macrobenthos of the immediate post-extinction level of Seymour Island, Antarctica, is also dominated by aporrhaid gastropods, suggesting that this group could embody opportunistic taxa, 'blooming' in the direct aftermath of the K/Pg boundary catastrophe (Witts *et al.* 2016). *Arrhoges* (*Latiala*) *pelecyphora* does occur in underlying units of the Meerssen Member (Fig. 3), but is invariably rare. The earliest Palaeogene assemblages show a strong preponderance of surviving lineages, which change in relative

FIG. 6. Representative gastropod specimens of the former Ankerpoort-Curfs quarry. A, *Aporrhais limburgensis*, NHMM M3363, IVf-6 of the Meerssen Member, B, *Aporrhais limburgensis*, NHMM M3360, IVf-6 of the Meerssen Member, C–D, *Arrhoges* (*Latiala*) *pelecyphora*, NHMM M2284, IVf-7 of the Meerssen Member. E, *Aporrhais limburgensis*, NHMM M1354, IVf-7 of the Meerssen Member. F, *Acirsa densestriata*, NHMM GC3055, Meerssen Member. G–H, *Hippochrenes binkhorsti*, NHMM GC3419, IVf-6 of the Meerssen Member: G, external mould; H, internal mould; I–J, *Acteon granulatolineatus*, NHMM GC3340, IVf-6 of the Meerssen Member: I, external mould; J, internal mould, K, *Cylichna* sp., NHMM M2755, IVf-6 of the Meerssen Member. L–M, *Cylichna* sp., NHMM M2775, IVf-6 of the Meerssen Member: L, external mould; M, internal mould. N, *Bulla mosensis*, NHMM GC5585, Meerssen Member. Scale bar represents 20 mm. Colour online.
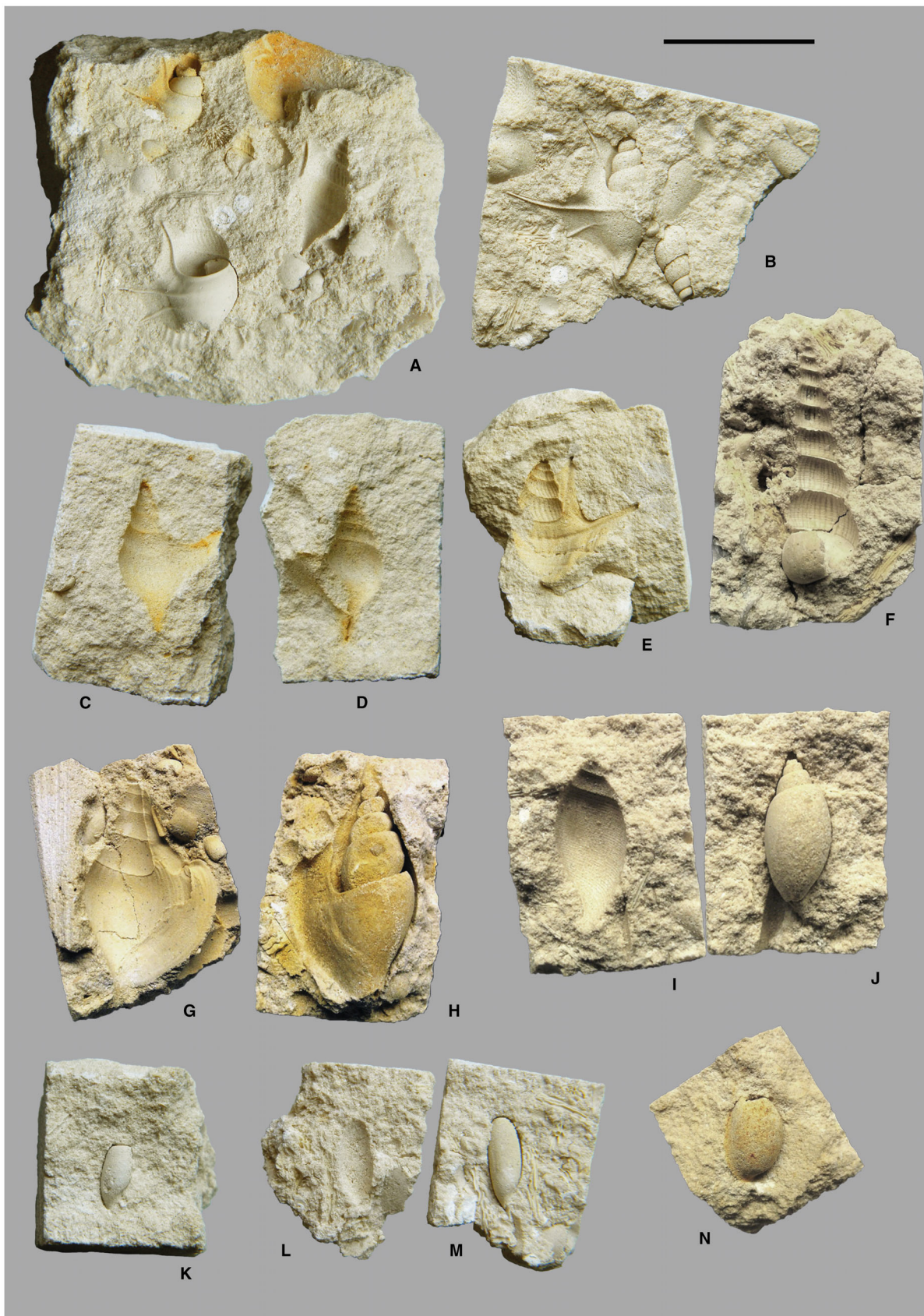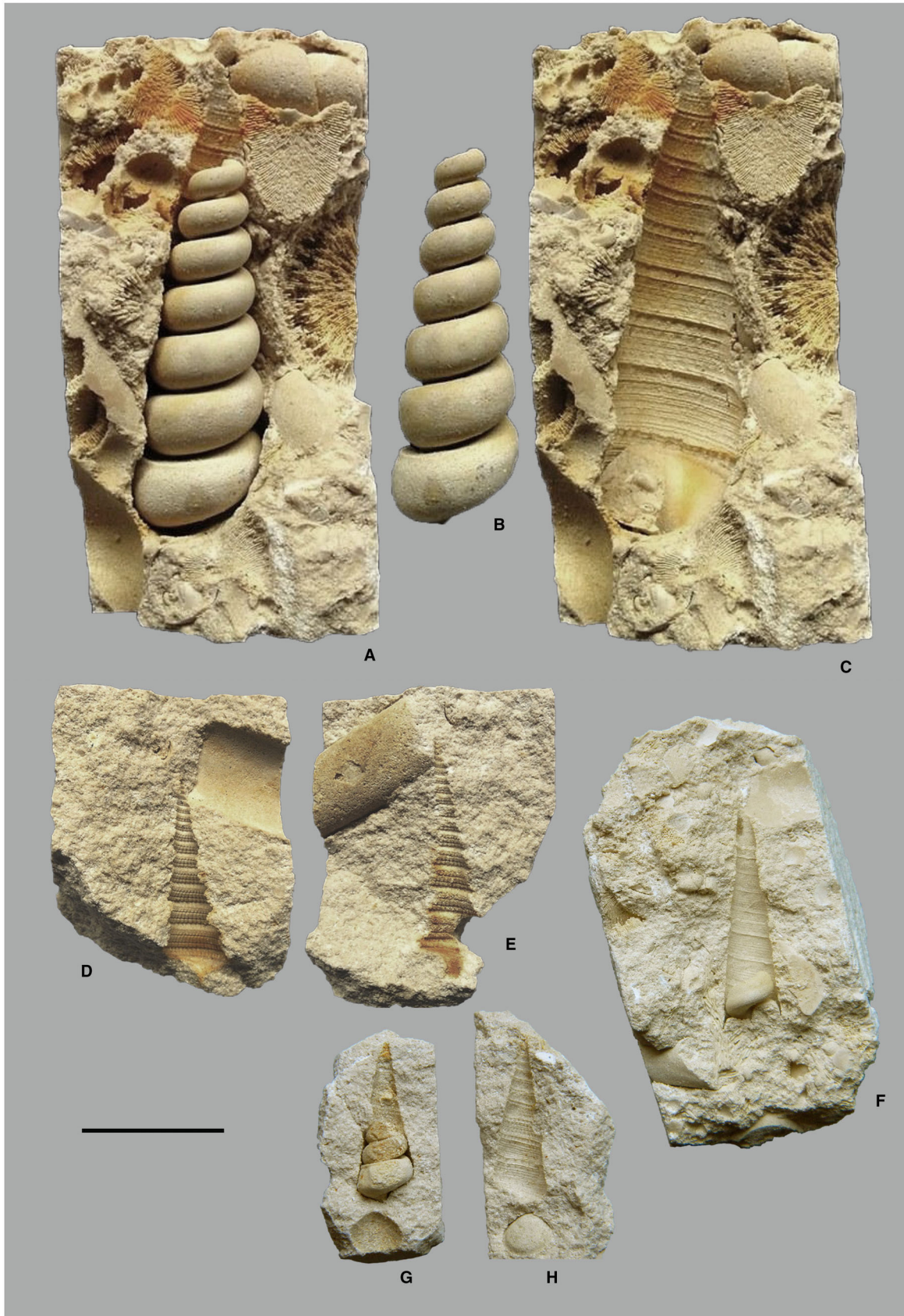
abundance from rare prior to the extinction event to predominant in the new assemblages. This seems to be a common signal in many post-K/Pg boundary records (Aberhan *et al.* 2007). Because both *Ar.* (L.) *pelecyphora* and *Ap. limburgensis* are aporrhaids, slow motile shallow infaunal surface deposit feeders (Yonge 1937; Perron 1978; Aberhan & Kiessling 2015), the former appears to be an ecological substitute of the latter, indicating that overall ecosystem functioning during the earliest Paleocene was quite similar to that during the latest Maastrichtian. Accordingly, while affected by extinction, the fauna from the lowermost Paleocene unit IVf-7 still has many 'Maastrichtian' features as well. As deposition of unit IVf-7 took place within an interval of a few thousands of years after the K/Pg boundary catastrophe (Smit & Brinkhuis 1996), it is possible that the associated gastropod fauna is part of a community that temporarily survived the K/Pg mass extinction. The presence of non-reworked ammonites in unit IVf-7 is consistent with this hypothesis. Only at the overlying Vroenhoven Horizon did many long-ranging, typical 'Maastrichtian' taxa effectively become extinct and did most of the typical Danian gastropod taxa make their first appearance. These data support the previously published view that, rather than the Berg en Terblijt Horizon (i.e. the K/Pg boundary), it is the Vroenhoven Horizon that marks the 'faunal break' amongst gastropod communities in the study area (Jagt *et al.* 2013), similar to many other biotic groups (Jagt *et al.* 1996). In a sense, the biological assemblage of unit IVf-7 represents a 'latest Maastrichtian' ecosystem that temporarily survived into the earliest Paleocene, only to disappear at the Vroenhoven Horizon: a 'Dead Ecosystem Walking', analogous of the 'Dead Clade Walking' phenomenon described by Jablonski (2002). Long-term biological and environmental changes across the K/Pg boundary, such as global trends in climate and large-scale evolutionary changes, will have eventually driven many of the initial survivors to extinction (Jablonski 2002), indicated by their disappearance across the hiatus represented by the Vroenhoven Horizon. The first 10–100 kyrs after the Chicxulub impact, encompassed by the hiatus of the Vroenhoven Horizon in the type Maastrichtian, was a period of considerable climatic, biotic and environmental change (D'Hondt 2005; Kring 2007; Vellekoop *et al.* 2017, 2018; Macleod *et al.* 2018). It is conceivable that this interplay of profound environmental and biotic changes eventually led to the demise of the last standing 'Maastrichtian' taxa. Accordingly, the transition from the classic 'Cretaceous' faunas to new, Paleocene assemblages in the Maastrichtian type area can be characterized as a two-step turnover that was initiated at the K/Pg boundary.

Ecosystem change across the K/Pg boundary

In the nearby Geulhemmerberg underground galleries, the lower part of the earliest Paleocene unit IVf-7 comprises benthic foraminiferal assemblages that are typical of food-limited environments in which much of the nutrient input was seasonally or erratically pulsed (Kuhnt 1996). A global comparison of ecological patterns suggests that an earliest Paleocene episode of reduced food supply was a controlling factor for extinctions amongst macrobenthic marine faunas (Aberhan *et al.* 2007). An additional selection amongst benthic invertebrates was probably linked to reproductive strategies, i.e. the differential survival of organisms with non-planktotrophic reproductive modes, such as sponges, corals, brachiopods and bryozoans while those with planktotrophic larval stages experienced reduction and/or extinction (Gallagher 2003). In the upper part unit IVf-7 in the Geulhemmerberg subterranean galleries, correlative with the interval of IVf-7 sampled in the present study, assemblages of benthic foraminifera and calcareous nannofossils indicate the initiation of marine ecosystem recovery after the short-lived disruption of the food web at the K/Pg boundary (Kuhnt 1996). The rapid resurgence of global marine productivity is likely to have occurred within 100 years after the K/Pg mass extinction (Sepulveda *et al.* 2009).

Studies of macroinvertebrate faunas at K/Pg boundary sites that have a predominantly siliciclastic sedimentation, such as New Jersey (Gallagher 1991, 2003) and the Gulf Coast in the USA (Hansen *et al.* 1993), Seymour Island (Antarctica; Witts *et al.* 2016) and Argentina (Aberhan *et al.* 2007) have identified large decreases in diversity, a major ecological shift towards deposit feeders, a strong increase in endobenthic taxa and an increase in mobility, immediately following the Chicxulub impact (Aberhan & Kiessling 2015). The benthic molluscan fauna of the Maastrichtian type area shows similar ecosystem changes; a decrease of suspension feeders and epibenthic taxa and an increase in motile taxa, in particular surface deposit feeders. Yet, the ecological shift across the K/Pg boundary in the type-Maastrichtian appears to be much less dramatic. Even though the time resolution of most K/Pg boundary records differs from that of the type-

FIG. 7. Representative gastropod specimens of the former Ankerpoort-Curfs quarry. A–C, *Cerithium tuberculiferum*, NHMM GC3080, IVf-6 of the Meerssen Member: A, external mould with internal mould; B, internal mould; C, external mould. D–E, *Orthochetus tectiformis*, NHMM GC2828, Meerssen Member. F, *Turritella plana*, NHMM M3547, IVf-6 of the Meerssen Member. G–H, *Cerithium alternatum*, NHMM M2184, IVf-6 of the Meerssen Member: G, external mould with internal mould; H, external mould. Scale bar represents 20 mm. Colour online.
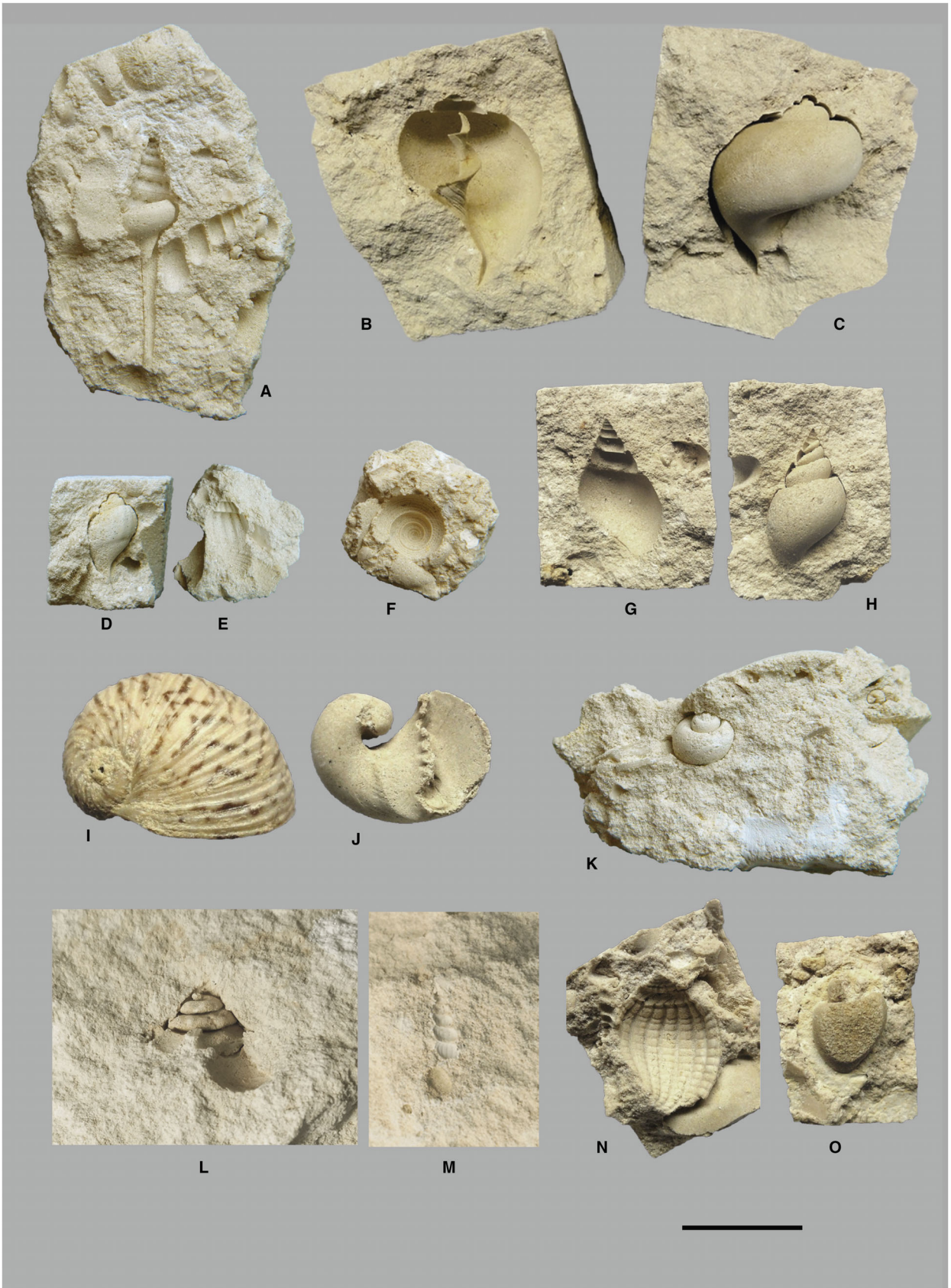
Maastrichtian are, the ecological changes documented here rather resemble those obtained for other K/Pg boundary sites with a predominance of carbonate sedimentation, such as Alabama (USA; Bryan & Jones 1989) and Denmark (Håkansson & Thomsen 1999). As oligotrophic carbonate shelf settings are generally characterized by the presence of benthic fauna adapted to low nutrient supply and more resistant to starvation (Aberhan *et al.* 2007), the effects of reduced productivity in the direct aftermath of the Chicxulub impact were more severe in siliciclastic environments that are generally characterized by relatively high nutrient conditions, in comparison to oligotrophic carbonate settings. The increase in relative abundance of lucinid bivalves across the K/Pg boundary in the study area (Fig. 2) could potentially also be related to the earliest Paleocene episode of reduced food supply. Lucinid bivalves harbour sulphide-oxidizing chemosymbiotic bacteria in their gills (Taylor & Glover 2000) and are both particulate and suspension feeders (Pennec *et al.* 1995; Duplessis *et al.* 2004). According to Aberhan *et al.* (2007), this could mean that they are less dependent on external food supply than most other bivalves, potentially making them more resilient against the earliest Paleocene primary productivity collapse. However, in modern-day oceans, lucinids usually occur in environments with high organic content (such as hydrocarbon seeps, mangroves etc.) a distribution that is difficult to reconcile with this proposed resistance to starvation. Heinberg (1999) and Aberhan *et al.* (2007) suggested that in oligotrophic carbonate settings such as the type Maastrichtian, Braggs (Alabama) and the Danish chalk at Stevns Klint, within-habitat ecological changes, like an increase of endobenthic suspension-feeding bivalves in the early Danian, could also be explained by changing sedimentological conditions, such as a lack of suitable substrates for epibenthic fauna. In the Maastrichtian type area, the ecological shift to endobenthic suspension feeders could, in part, have been triggered by the transition to softer substrates during deposition of the upper part of unit IV-f 7.

While most sites with predominant carbonate sedimentation are less severely affected by K/Pg boundary perturbations than sites with siliciclastic sedimentation, they are still characterized by an earliest Paleocene interval with reduced invertebrate diversity (Bryan & Jones 1989; Håkansson & Thomsen 1999). Remarkably, ecosystem changes across the boundary in the study area, representing the first step of the faunal turnover, appear to be moderate. This suggests that the local ecosystem was initially quite resilient against the environmental perturbations caused by the Chicxulub impact. This resilience is also highlighted by the fact that none of the 15 modes of life identified in the topmost Maastrichtian benthic mollusc community were lost across the K/Pg boundary (Fig. 4).

Ecosystem recovery following the K/Pg boundary catastrophe

Many earliest Paleocene marine records are characterized by impoverished micro and macrofaunas and suppressed productivity during several hundreds of thousands of years after the K/Pg boundary event (Hansen *et al.* 2004). In that respect, it is remarkable that a diverse, fully functioning gastropod community inhabited the study area, within thousands of years after the catastrophe. As the shallow-marine, oligotrophic carbonate settings were occupied by starvation-resistant, low nutrient-adapted taxa, the general impact of the short-lived detrimental effects of the K/Pg boundary catastrophe (i.e. short-lived darkness, cooling, starvation and ocean acidification; D'Hondt *et al.* 1994; Krings 2007; Vellekoop *et al.* 2014, 2016, 2017, 2018) appears to have been less severe in this region, resulting in relatively high survival rates. Indeed, the type Maastrichtian gastropod community is generally dominated by surface deposit feeders and herbivores, a group that is considered quite resilient against food starvation (Hansen *et al.* 1993), leading to high survival rates. It may be assumed that high survival rates enabled rapid recolonization and recovery of marine faunas in the type area of the Maastrichtian, once environmental conditions returned to normal. The post-impact reduction of primary productivity is assumed to have lasted less than a century; it was followed by a rapid resurgence of marine productivity and ecological reorganization (Sepulveda *et al.* 2009; Vellekoop *et al.* 2017; Lowery *et al.* 2018). As a result of the rapid recolonization and recovery, a new, fully functioning ecosystem could emerge within several thousands of years after the K/Pg boundary catastrophe. In view of the high survival rate, this new ecosystem was characterized by an

FIG. 8. Representative gastropod specimens of the former Ankerpoort-Curfs quarry. A, *Columbarium heberti*, NHMM M20071025, IVf-6 of the Meerssen Member. B–C, *Natica ampla*, NHMM GC2019, IVf-4 of the Meerssen Member: B, external mould with central spire placed back; C, internal mould. D–E, *Popenoeum ambiguum*, NHMM M2560, IVf-6 of the Meerssen Member: D, internal mould; E, external mould. F, *Periaulax rimosus* forma *granulatus*, NHMM M2728, IVf-6 of the Meerssen Member. G–H, *Natica exaltata*, NHMM GC3244, IVf-6 of the Meerssen Member: G, external mould; H, internal mould. I–J, *Otostoma retzii*, NHMM GC1312, IVf-6 of the Meerssen Member: I, original shell; J, internal mould. K, *Natica cretacea*, NHMM M3462, IVf-6 of the Meerssen Member. L, *Xenophora nilssoni*, NHMM KUL2006001, IVf-7 of the Meerssen Member. M, *Confusiscala contorta*, NHMM KUL1006002, IVf-7 of the Meerssen Member. N–O, *Cancellaria cretacea*, NHMM GC2769, Meerssen Member: N, external mould; O, internal mould. Scale bar represents 10 mm for (M) and 20 mm for all others. Colour online.

unusually high number of 'Cretaceous' forms, giving it 'Maastrichtian' features.

CONCLUSIONS

In the type-Maastrichtian area, the topmost Maastrichtian IVf-6 Meerssen Member coquina and the lowermost Danian IVf-7 calcarenite provide 'snapshots' of shallow-marine oligotrophic carbonate platform molluscan ecosystems in the millennia before and after the Chicxulub impact. Bulk sampling of both stratigraphic intervals reveal that the area was inhabited by taxa adapted to low nutrient settings, resistant to starvation. High survival rates of many common taxa resulted in the relatively limited community-level change across the K/Pg boundary. The latter corroborates well with earlier studies and exemplifies the different rate of survival of communities in carbonate and siliciclastic depositional environments. While no modes of life were lost, a decline in epibenthic suspension feeders was observed, accompanied by an ecological shift to more motile taxa. A remarkable species-level change is the shift from the dominant species of gastropod from one to another species of aporrhaid (*Ar.* (*L.*) *pelecyphora* – *Ap. limburgensis*). Even though the K/Pg boundary in the study area is marked by the species-level extinction of *c.* 55% of the gastropod assemblage and a drop of diversity and increase in dominance in faunas, the earliest Paleocene gastropod fauna still retains many 'Maastrichtian' features. Accordingly, the biota of the lowermost Paleocene unit IVf-7 represent a 'Cretaceous' ecosystem that temporarily survived into the earliest Paleocene. The high survival rate must have enabled a rapid recolonization and recovery of marine faunas in the area, as soon as environmental conditions returned to normal. As a result of this, a new, fully functioning ecosystem could emerge within several thousands of years after the Chicxulub impact, suggesting that the transition from the classic 'Cretaceous' faunas to new Paleocene assemblages in the Maastrichtian type area must have been a two-step turnover.

DATA ARCHIVING STATEMENT

Data and supporting information for the present study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.r7mh8sr

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