

Clusters of shallow pits in gastropod shells from the type area of the Maastrichtian (Upper Cretaceous, the Netherlands)

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Close-set, shallow pits are preserved in external moulds of one species each of campanilid and aporrhaid gastropods from coquinas in the uppermost Maastrichtian Meerssen Member (subunit IVf-6) at the former Ankerpoort-Curfs quarry (Geulhem, southern Limburg, the Netherlands). These clustered pits are broad, dish-like, and rounded to polygonal where closely packed; a circular, sunken groove lies within the dish; and a central rounded dome has a central, rounded depression. The producing organism obviously pursued a gregarious lifestyle. These structures are referred to a new ichnotaxon, *Salsariichnus collinsi* igen. et isp. nov., which is considered to belong to the ethological class of domichnia. It differs in several respects from attachment scars (ichnogenus *Lacrimichnus*) and deeper embedment structures such as *Oichnus excavatus* that are known from coeval levels. • Key words: Maastricht Formation, Meerssen Member, *Salsariichnus*, domichnia.

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Gastropods and, particularly, their shells are amongst the wonders of the natural world, but perhaps they are so familiar as to be rather taken for granted. Most pertinent to the present study is the fact that gastropod shells may be used as hard substrates for encrusting and boring organisms to inhabit or foul. In life, the external surfaces of gastropod shells of (particularly) marine snails may be host to a wide variety of episkeletozoans (*sensu* Taylor & Wilson 2002). An empty snail shell in a marine setting is a valuable substrate; a genuine benthic island (compare with Tapanila & Ebbestad 2008, Belaústegui *et al.* 2013), being available for attachment and invasion both internally and externally (Pickerill & Donovan 1997). Indeed, empty conchs may be of such value that even extinct species are recycled and utilised by extant hermit crabs (Gould 1980).

Herein, we examine trace fossils associated with natural external moulds (the internal moulds were not found in association) of three medium- to large-sized gastropod shells from the type area of the Maastrichtian Stage (Upper Cretaceous). These shells provided substrates for infestation after death; each of them has been densely infested by unknown organisms that left behind close-packed, shallow, discoidal pits. These cannot be

ascribed to *Oichnus* Bromley, 1981, already well known from all members of the Maastricht Formation and often densely infesting their benthic islands, commonly the holasteroid echinoid *Hemipneustes striatoradiatus* Leske, 1778 (see, for example, Donovan & Jagt 2002, 2013, in press; Donovan *et al.* 2018) or ostreid bivalves (Jagt & Deckers 2014). Rather, they are interpreted as a morphologically distinct, new ichnogenus of domicile trace fossils (ethological class: domichnia). All specimens are deposited in the collections of the Natuurhistorisch Museum Maastricht, the Netherlands (prefix NHMM PK).

Locality and horizon

The present examples, NHMM PK M2643-1, PK M3083 and MK M3094, all originate from the former Ankerpoort-Curfs quarry [outcrop 62A-13, coordinates 182.000/320.120; now a nature reserve of Stichting ‘Het Limburgs Landschap’], near Geulhem, southern Limburg, the Netherlands (Fig. 1; for a more detailed map, see Felder & Bosch 2000, fig. 3.49). At this locality, the uppermost metre or so of the Nekum Member and the entire Meerssen Member

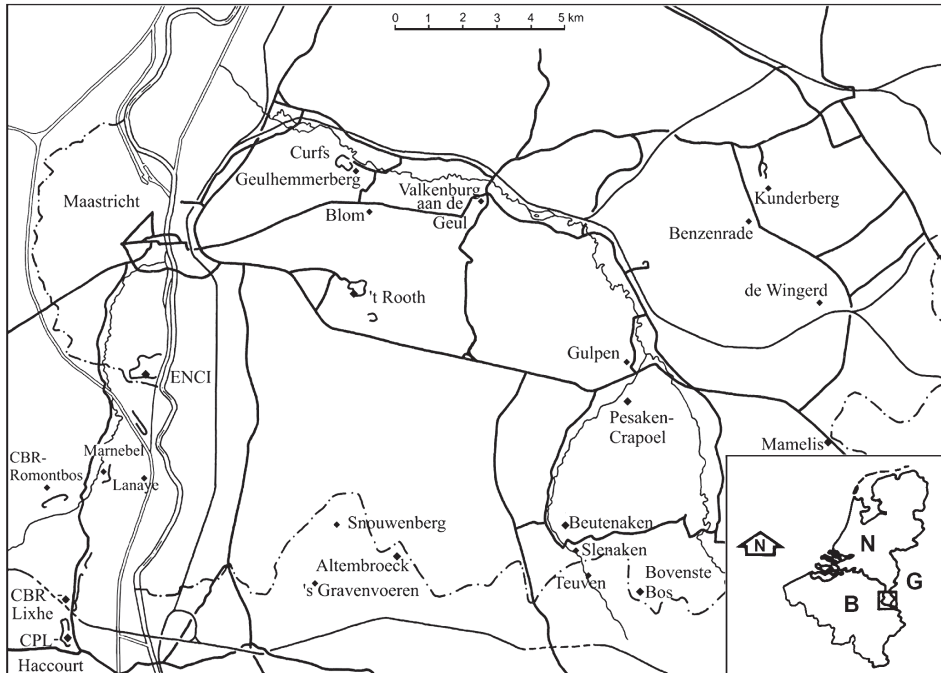


Figure 1. Map of southern Limburg, the Netherlands, and contiguous areas in northeast Belgium (Voerstreek, provinces of Limburg and Liège) and western Germany (Aachen area), showing the most important localities [(temporary) outcrops and quarries] in the type area of the Maastrichtian Stage (after Jagt & Jagt-Zayzkova 2012, fig. 1). The position of the former Ankerpoort-Curfs quarry, which yielded the specimens described herein, is in the upper part of the map and left of centre. The inset map of northern Europe (B = Belgium; G = Germany; N = Netherlands) shows the position of the main map (box).

(subunits IVf-1 to IV-7) of the Maastricht Formation (upper Maastrichtian), as well as the overlying lower Palaeocene Geulhem Member (Houthem Formation), were formerly exposed (Herngreen & Wong 2007, p. 142, fig. 18; Jagt & Jagt-Zayzkova 2012, fig. 5, tab. 1; Jagt *et al.* 2013, fig. 2a). The upper 20 cm or so of subunit IVf-6 comprised laterally discontinuous coquinas or lumachelles from which molluscan material was collected already in the second half of the nineteenth century (Binkhorst van den Binkhorst 1861–1862, Ubaghs 1879, Kaunhowen 1898). These shell beds have yielded hundreds of close-packed specimens (predominantly internal and external moulds, except for ostreids and neritids) of gastropods, bivalves, scaphopods, nautiloids and ammonites, in association with scleractinian corals, echinoids, and rare decapod crustaceans and belemnittellid coleoids. On cephalopod evidence, the upper part (subunits IVf-4 to -6) of Meerssen Member can be dated as latest Maastrichtian, within the zones of the belemnittellid species, *Belemnella (Neobelemnella) kazimiroviensis* (Skołozdrówna, 1932) and *B. (N.) skolozdrownae* Kongiel, 1962 (see Keutgen *et al.* 2017), and the final one million years of the Cretaceous (Keutgen 2018, fig. 4).

Systematic ichnology

Ichnogenus *Salsariichnus* nov.

Type species. – *Salsariichnus collinsi* igen. nov., isp. nov., the only ichnospecies known.

Etymology. – From the Latin *salsarium*, saucer (Brown 1993, p. 2693).

Diagnosis. – Clustered shallow pits; gregarious; pits broad, dish-like, rounded to polygonal where closely packed; circular, sunken groove within dish; central rounded dome with a central, rounded depression.

Remarks. – Other rounded ‘scars’ have been recorded from the type Maastrichtian in recent years, but these all differ from *Salsariichnus collinsi* igen. nov., isp. nov. Best known is *Oichnus excavatus* Donovan & Jagt, 2002; these are non-penetrative, gently undercut pits with a central boss, much deeper than the new trace described herein. Although *O. excavatus* is confined to holasteroid echinoid substrates in the upper Maastrichtian of the study area, it has been recorded from a Miocene gastropod of Jamaica (Blissett & Pickerill 2003). *Lacrimichnus?* isp., as described by Jagt (2007), is a rounded groove, probably a gastropod homing scar (compare Santos *et al.* 2003, 2004); this lacks the complexity of *S. collinsi* igen. et isp. nov. Finally, *Oichnus halo* Neumann & Wisshak, 2009, now transferred to the ichnogenus *Loxolenichnus* Breton, Wisshak, Néraudeau & Morel, 2017 (see Wisshak *et al.* 2019, p. 24) and recorded from a test of the echinoid genus *Echinocorys*, differs in having in faint additional ring and in lacking a central depression (Jagt & Deckers 2014).

Occurrence. – Known only from the type locality at the former Ankerpoort-Curfs quarry, southern Limburg, the Netherlands (Fig. 1); uppermost Meerssen Member

(subunit IVf-6), Maastricht Formation, uppermost Maastrichtian (Upper Cretaceous).

***Salsariichnus collinsi* igen. et isp. nov.**

Types. – Holotype, NHMM PK M2634-1, specimen at top of Fig. 3E. Paratypes, all other specimens on NHMM PK M2634-1 as well as all examples on NHMM PK M3093 and NHMM PK M3094. Specimens are preserved on external moulds of gastropods; the substrate is a medium- to coarse-grained biocalcarenite that does not favour definition of fine details.

Type horizon and locality. – Former Ankerpoort-Curfs quarry, near Geulhem, southern Limburg, the Netherlands (Fig. 1); uppermost Meerssen Member (subunit IVf-6), Maastricht Formation, of latest Maastrichtian (Late Cretaceous) age.

Etymology. – In memory of our late colleague, Mr. J.S.H. Collins (1927–2019), a noted expert on fossil barnacles and decapod crustaceans.

Diagnosis. – As for the ichnogenus.

Description. – Pits on external moulds are all clustered and arrayed as a column along the long axes of high-turreted gastropod shells (Figs 2A–C, 3A–C). Pits are broad, dish-like depressions, with a rounded to polygonal outline where they are closely packed. Within this dish is a circular, shallow, sunken groove, of variable section, but commonly semi-circular. The central raised area is rounded in outline, domed; in turn, this dome has a central, rounded depression. Pits are commonly rounded, but closely packed, either in lateral contact or leaving only a small gap between pits, commonly resulting in a more polygonal outline.

Figure 2. The trace fossil *Salsariichnus collinsi* igen. nov., isp. nov., infesting campanilid (A, C, D) and aporrhaid (B) gastropods from the former Ankerpoort-Curfs quarry, southern Limburg, the Netherlands; uppermost Meerssen Member (subunit IVf-6), Maastricht Formation, latest Maastrichtian [zone of the belemnitellids, *Belemnella* (*Neobelemnella*) *kazimiroviensis* and *B. (N.) skolozdrownae*]. All three are natural external moulds; the accompanying internal moulds could not be recognised after blasting when the quarry was still in operation. All trace fossils are paratypes unless stated otherwise. • A, D – NHMM PK M2634-1, in ‘*Cerithium*’ *tuberculiferum* Binkhorst van den Binkhorst, 1861; A – note that pits are densely packed on the right in the top half of the specimen, but over the full width of the shell near the bottom; holotype in the centre, just above mid-height (compare with Fig. 3C, E); D – detail of pits in lower half of gastropod mould. • B – NHMM PK M3093, in *Alaria binkhorsti* Ubaghs, 1879; pits are clustered more or less in a row in the top half of the shell. • C – NHMM PK M3094, in ‘*Cerithium*’ *tuberculiferum*; pits forming a broad, densely packed band in the centre of the specimen. Specimens uncoated. All scale bars equal 10 mm.

Remarks. – These traces represent most likely the attachment scars of a gregarious, sessile organism rather than the homing scars of vagile benthos. The close-packed nature of these scars has modified the rounded outlines into polygonal shapes. A vagile organism would only be able to adapt to this if either it could easily change the outline of its shell to fit or it lacked a hard shell. The former seems rather draconian, necessitating a constant race to adjust its shape to fit a changing outline as neighbouring shells grew, encroaching on its space. The latter seems unlikely, homing scars being the mark of cap-like gastropods such as limpets, hipponicids and platyceratids (Vermeij 1998; Bromley 2004, p. 463; Donovan & Webster 2013).



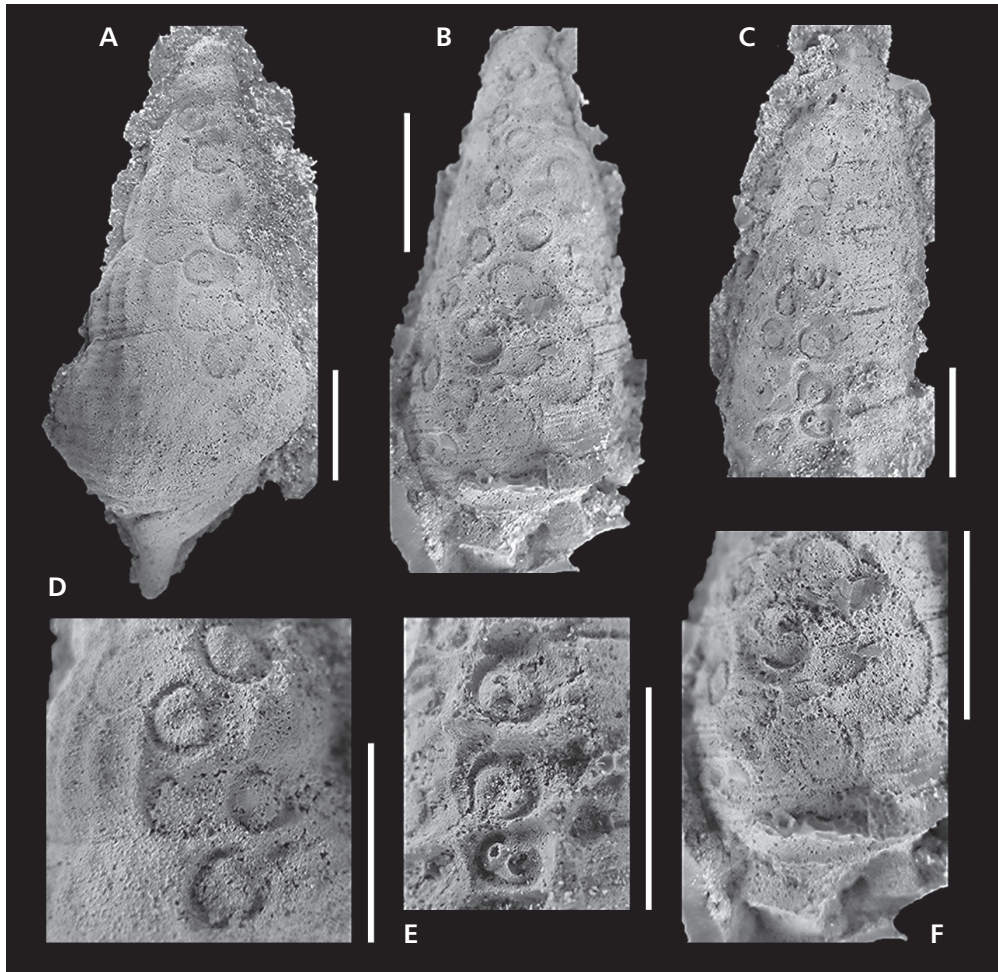


Figure 3. The trace fossil, *Salsariichnus collinsi* igen. nov., isp. nov., infesting campanilid (B, C, E, F) and aporrhaid (A, D) gastropods from the former Ankerpoort-Curfis quarry, southern Limburg, the Netherlands; uppermost Meerssen Member (subunit IVf-6), Maastricht Formation, latest Maastrichtian (see Fig. 2). Latex casts. All trace fossils are paratypes unless stated otherwise. • A, D – NHMM PK M3093 in *Alaria binkhorsti*; A – clustering of pits on the shell; D – details of several pits. • B, F – NHMM PK M3094 in *Cerithium tuberculiferum*; B – shell with numerous pits; F – pits in the lower half of the shell. • C, E – NHMM PK M2634-1 in *Cerithium tuberculiferum*; C – upper part of the shell, pitted on the left; holotype just below the centre; E – detail of the linear array of pits; holotype at the top. Specimens coated with ammonium chloride prior to photography. All scale bars equal 10mm.

Discussion

These scars were produced by a gregarious, sessile invertebrate. The specimens are all about the same size on any given shelly substrate, suggesting that each represents a single spatfall. These criteria immediately suggest that *S. collinsi* igen. nov., isp. nov. was the spoor of a barnacle or barnacle-like organism. The earliest balanomorphs were of Late Cretaceous age (Newman *et al.* 1969, p. R283; Gale & Sørensen 2014), so it is at least possible. However, to date only asymmetrical verrucomorphs have been recorded from the highest levels of the Maastricht Formation (Jagt 2011, Gale 2014). In view of the fact that representatives of either cirripede group have calcareous valves, their shells should be preserved *in situ*. Further, *S. collinsi* igen. nov., isp. nov. differs markedly from the attachment scars and basal plates associated

with fossil balanomorph (Miller & Brown 1979) and verrucomorph (Bromley & Martinell 1991) barnacles. Thus, our interpretation of the possible producing organism remains speculative.

The recently described etching trace, *Solealites ovalis* Uchman & Rattazzi, 2018, in lithic clasts from the Oligocene Savignone Conglomerate in northwest Italy, is superficially similar. This taxon comprises shallow, oval depressions with a flat, central elevation for which limpet gastropods (Patellogastropoda; homing scars), other snails or sea anemones have been suggested as possible producer. These lack the complexity of the present trace in gastropod shells (compare Bromley & Heinberg 2006, fig. 4). Finally, *Spirolites radwanskii* Uchman, Stachacz & Salamon, 2018, a depression in the form of an involute, smooth or annulated spiral, the width of which increases outwardly, differs in not being circular, dish-like and in

lacking the central rounded dome with a central depression of *S. collinsi*.

It has been assumed in the above discussions that infestation of the pit-former of *S. collinsi* was after the death of the gastropod. This seems most likely as the distinctive features of infestation are mainly linear associations of the new trace which occur along almost the entire extent of the shell in two of the three specimens (Figs 2A–C, 3A–C). This suggests that the shells were recumbent on the sea floor (post-mortem) rather than upright (pre-mortem). Attachment pre-mortem would most likely be towards the apex of the shell, raising the sessile producers of *S. collinsi* above the substrate and into clean water for feeding on plankton, the common sustenance of sessile zoobenthos, and distancing the infesters from the snail's radula. In contrast, a dead gastropod lying on the seafloor would provide only limited elevation along its whole length, suggesting the distribution of the new trace on these shells may have been on recumbent (dead) specimens.

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