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Provenance, systematics and palaeoecology of Mississippian (Lower Carboniferous) corals (subclasses Rugosa, Tabulata) preserved in an urban environment, Leiden, the Netherlands

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Abstract

There are few sites in The Netherlands where the pre-Pleistocene rock and fossil records can be examined *in situ*. In the city of Leiden, Mississippian (Lower Carboniferous) limestones used as building stones expose diverse invertebrate fossils, principally brachiopods, fenestrate bryozoans, crinoid columnals, molluscs and corals. This study focuses on the corals, which belong to the subclasses Rugosa and Tabulata. The aim of the research was to determine the biodiversity of fossil corals in the city of Leiden and any associated palaeoecological signals. Two street surveys were made through Leiden and a database of pictures was built up. The corals were then identified using published keys and literature. Research and identification revealed four genera, namely *Michelinia*, *Syringopora*, *Zaphrentites* and *Siphonodendron*. Most were common, but *Siphonodendron* was only encountered once in this study, and may be from a different locality and horizon from the other corals. The other genera were compared with literature on coral faunas and it is concluded that the limestones are from the Late Tournaisian Ourthe Formation in Belgium.

Key words: *Michelinia*, *Syringopora*, *Zaphrentites*, *Siphonodendron*, Tournaisian, Ourthe Formation

Introduction

In the Netherlands, there are few sites where the macropalaeontology of the pre-Pleistocene can be examined. The number of *in situ* localities in this country is limited, but supplemented by various building stones in major cities, and specimens reworked by fluvial or glacial action (*e.g.*, Reumer, 2016; Donovan, 2016; Donovan *et al.*, 2016). Sedimentary rocks have been imported and used as building stones in the major cities in the Netherlands for hundreds of years. Fossils from the Upper Palaeozoic are locally common in buildings in, for example, Amsterdam (van Roekel, 2007; Reumer, 2016), Leiden (Donovan, 2016), Utrecht (Donovan & Wyse Jackson, in press) and Maastricht (Donovan *et al.*, 2017). The diversity of the identifiable fossils enclosed in the limestones is limited, and consists mainly of articulated brachiopods, fenestrate bryozoans, crinoid columnals, molluscs and corals.

Unlike many other macrofossil groups, corals can be identified to, at least, generic level from cut and polished section using published keys (*e.g.*, Anonymous, 1969; Mitchell, 2003). That makes the corals the most suitable subject for systematic determination in these rocks, even though standard study techniques such as petrographic thin sections are precluded from the investigation. A preliminary survey at the Rapenburg, Leiden, revealed that there are at least four genera to be found in the building stones (see below).

The aim of this research was to determine the systematic and palaeoecological signals of these fossils. This was initiated by making a preliminary index of the diversity in the corals (not reproduced herein) and identifying the various taxa. The solitary rugose corals were particularly hard to identify. By comparing a large suite of specimens, each apparent as a two-dimensional section and found in varied orientations, it was possible to make distinctions between several genera and so increase the known diversity of taxa in these limestones. The palaeoecological signal was then determined by comparing the results with related research on coral faunas.

A preliminary comment is considered necessary to

explain why we think that this study on exotic blocks of limestone, far removed from their area of outcrop and not available for destructive sampling, is a worthwhile study for palaeontologists. We recognise three principal benefits contributing to and benefitting from our research on the Leiden coral fauna.

1. Local history: The building stones of old Leiden are diverse, but their provenance is poorly known. For example, in the Rapenburg, apart from Mississippian limestones, there are sandstones (Pennsylvanian?), Maastrichtian? limestones (Donovan, research in progress), variegated marbles and larvikite. These are currently being examined with a view to producing either an information board or field guide (or both) for the non-specialist.
2. An aid for teaching: These limestones have been a focus for laboratory classes from the University of Leiden, and led by S.K.D., for many years. These are an important resource in a locale where the nearest *in situ*, fossil bearing rocks are 3 hours' drive away, and giving life science majors with little background in geology a feel for some of the problems of systematic palaeontology in the field, such as cut effect.
3. A faunistic study: These exercises have already lead to papers on the classification of the included molluscs (Donovan, 2016; Donovan & Madern, 2016). Brachiopods, fenestrate bryozoans and crinoids are currently under study (Donovan, research in progress). Eventually, a comprehensive faunal list will be produced.

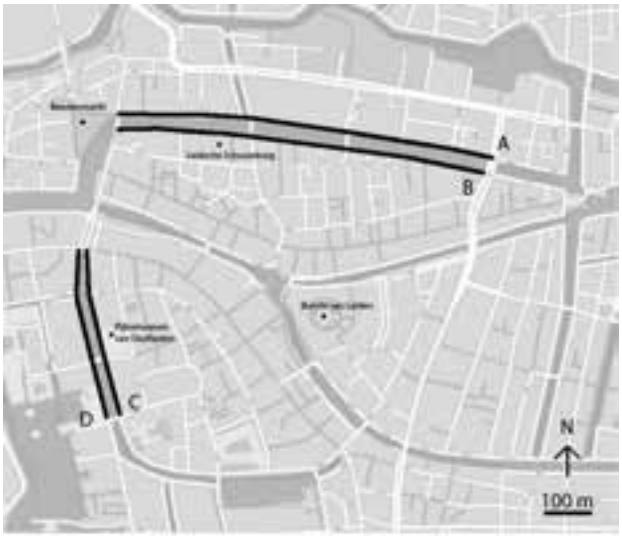


Fig. 1. Map of the centre of Leiden. Indicated lines are the streets included in this paper.
(A) Oude Singel. (B) Oude Vest. (C) Rapenburg, even-numbered side. (D) Rapenburg, uneven-numbered side. Redrawn from Google Maps using Photoshop.

Materials and methods

The coral fossils are imbedded in limestones used as building, paving and decorative stones. To enhance the contrast between fossil and rock, a thin layer of water is spread over the dry fossils. The limestone became darker, while the coral, which consists of crystalline calcium carbonate, stayed white and stood out; that is, the contrast between rock and fossils was enhanced. After that, selected fossils were photographed next to a standard scale in cm (Figs 2–6). The database was organized based on the road name and ordered after the house number. All photographs were taken with a Canon Powershot G11 digital camera.

The senior author identified the images of the corals, and sorted them into the different taxa using published keys and relevant literature (*e.g.*, Hill, 1981). Contact with other researchers in this field of work was made to acquire necessary information on the subject. Most pertinently, these included Professor Julien Denayer (Université de Liège, Belgium), co-author of a most relevant article on the Rugosa from Belgium, which was used to determine the species of solitary corals herein (Denayer *et al.*, 2011). Identification to genus or species was not always possible, because of the various angles at which the fossils are sliced. A transverse section is the most optimal for identifying corals, but building stones do not always provide them in that way (Figs 2–6). A map of central Leiden with the roads where species were found is provided (Fig. 1).

The biodiversity of the corals was then compared with published research on Lower Carboniferous limestones. Finally, the palaeoecological signal was determined. This was done by comparing the results with other studies on this specific period of time and studies on the provenance of these limestones (*e.g.*, Dubois *et al.*, 2014). Terminology of the coral skeleton follows Hill (1981) and Clarkson (1998). In the text, specimens are associated with their road (OS = Oude Singel; OV = Oude Vest; R = Rapenburg) and house number. This is further clarified in the figure captions. As these taxa are all well-known with a detailed literature, only brief descriptions of principal features have been included.

Apart from research on the fossils, research on the history of Leiden was also necessary to determine the geographic origin of the limestones. Information on the building process of several buildings was sought to complete the survey. The source and age of the limestones is estimated based on both the biodiversity of corals and the building history.

Localities and lithologies

The fossil corals found in Mississippian building stones in Leiden were imaged from two different streets. Most of the fossils were found in the somewhat older streets of the city,

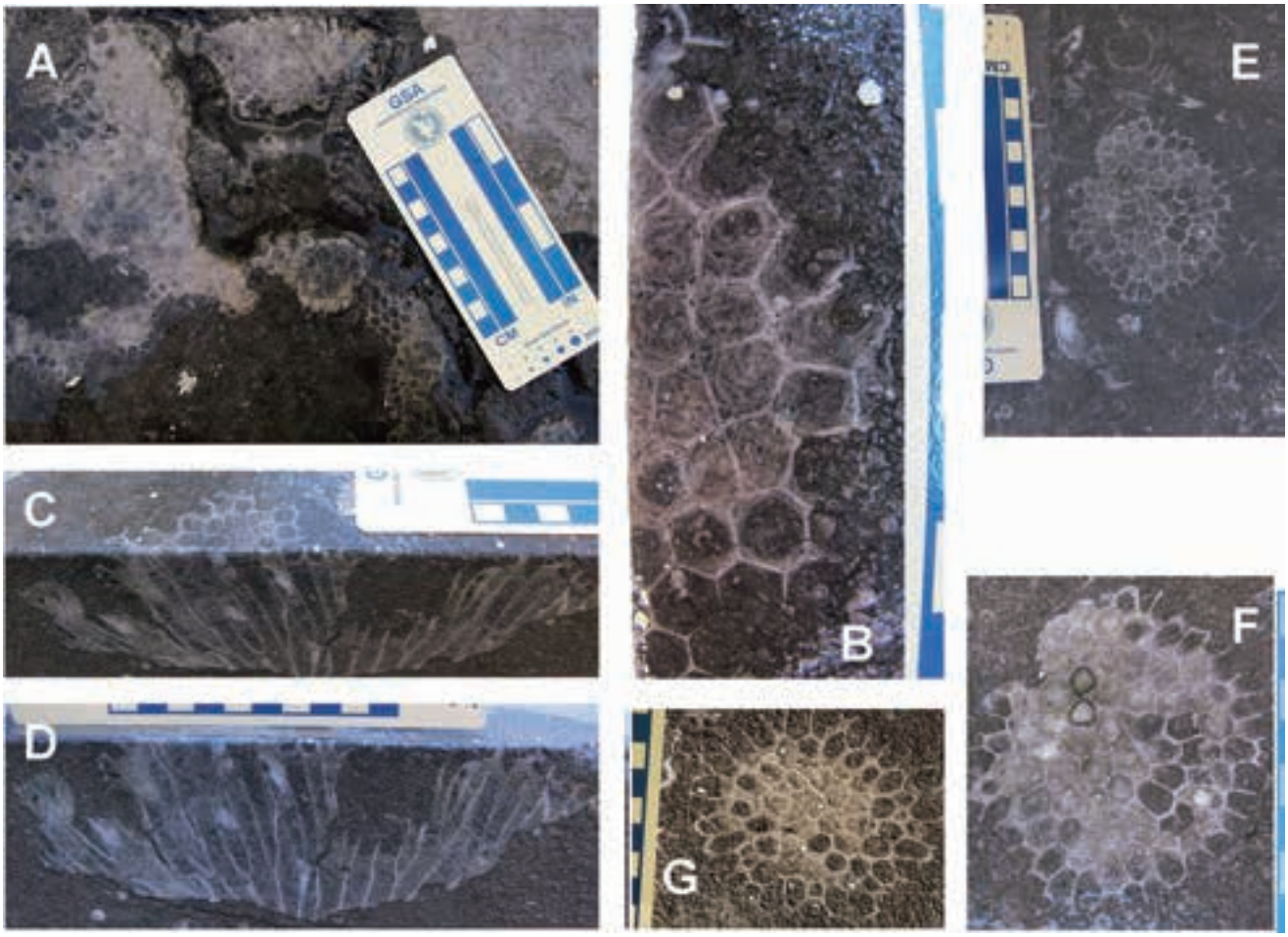


Fig. 2. Sections of colonies of the tabulate coral genus *Michelinia* sp. A, OS138_001, transverse section of a particularly large specimen found at the pavement of Oude Singel 138. B, C, D, three views of R71_001, a colony found in a windowsill of the University of Leiden at Rapenburg 71. B, transverse section. C, oblique view. D, longitudinal section. E, F, OS64_002, transverse section found in the pavement of Oude Singel 64. E, colony and other associated fossils, including solitary rugose corals. F, transverse section in detail. G, OS98_004, transverse section found in the façade of Oude Singel 98. All scale bars in cm.

namely the Rapenburg and the Oude Singel (Fig. 1). Limestones were used as building stones or as street decoration, in a period from the 16th Century until now (van Hees *et al*., 2008). Especially, the upper class could afford to use limestones as a building material and so somewhat enrich their houses (van Tussenbroek, 2013).

Most of the buildings that have limestone facades were built in the 16th Century and then renovated in late 19th Century (van Hees *et al*., 2008). The building history of Leiden is not entirely clear regarding imported limestones. It is evident that there was a 'trend' amongst the upper class house owners to enhance their dwellings with imported stone, a fashion necessitated by the lack of outcrop of well-lithified, pre-Pleistocene sedimentary rocks over much of the Netherlands. Some individual locations have a well-known and individual history, like, for example, the Sieboldhuis at Rapenburg 19.

The Sieboldhuis is now a museum dedicated to the imported curiosities of Philip Franz von Siebold (1796–1866), a collector of Japanese flora and fauna. The museum is located in a 16th Century house amalgamated from four 15th Century buildings. It has had various owners since then and minor changes to the building were made. In the second half of the 18th Century, a wealthy merchant renovated the facade to the current state with the pavement and stairs in limestone (Japanmuseum Sieboldhuis, 2016). However, there is no clear reference as to the provenance of the limestones.

More information is provided by the rocks themselves. Without knowing the exact source, it is clear from the evidence of both lithology and palaeontology that the limestones are Mississippian (Lower Carboniferous). The suite of fossils – rugose and tabulate corals, crinoids, brachiopods and rostroconchs – is typical of the Upper Devonian to Mississippian; in particular, many of the corals are recognised Mississippian biostratigraphic markers (compare with Mitchell, 2003). The fine-grained, dark-coloured limestones are typical of the Upper Devonian

and Mississippian, particularly of the Ardennes region of Belgium. It is most likely that the stones came from a quarry in the Ardennes. Professor Denayer suggested two possibilities as to the place of origin of the limestones (written comm. to D.M.v.R.). Mississippian building stones in Belgium are mainly 'petit granit' from the Late Tournaisian Ourthe Formation and 'calcaire de meuse' from the Middle Visean Lives Formation. These limestones were used in buildings in Belgium from the 15th Century and were exported to the Netherlands from the 17th Century (Pereira *et al*., 2015). The black-grey limestones from the Tournaisian are more common than the pale silver-grey stones from the Visean in buildings (Engering, 2008).

Performing field palaeontology in the city is a challenge in itself; you have to be lucky to find the right sections in accessible locations. Stonemasons do not take the fossils into account when they cut slices of limestone into blocks and slabs for use in buildings, pavements and decorative pillars. That is how fossils came to be cut in various orientations and oblique sections. Thus, different sections are seen in the same taxon of coral. The solitary rugose corals appear in longitudinal and transverse sections, and every angle that is in between those limits. For identification of these corals to genus or species, only transverse sections were truly useful, displaying clearly the pattern of septal insertion. Further, identifications had to be made without the benefit of thin sections or hand specimens. In many tabulate corals, microstructures in the walls are important features in determination of specific identity. In consequence, tabulate corals were left in open nomenclature.

The Mississippian closely followed the Late Devonian (Frasnian-Famennian) extinction event. Global temperatures dropped significantly during the crisis interval (Brand, 1989). This led to the reduction in diversity of tropical reef ecosystems and of warm water shallow faunas, which were the main habitats for corals Rugose and tabulate taxa were thinned out, and many families went extinct (Stearn, 1987; McGhee, 1989, pp. 140–142; Clarkson, 1998, pp. 118, 126).

In consequence, all the surviving rugose corals were members of the order Stauriida. This, however, gave the chance to other coral taxa to flourish during the Tournaisian, such as octocorals (Clarkson, 1998, p. 108). Solitary rugose corals with dissepiments arose in shallow waters, where corals without dissepiments grew primarily in deep waters. Taxa that went extinct were mostly shallow-water species, as deep-water corals are less affected by climate fluctuations. Therefore, the shallow water corals in the Carboniferous are most likely to be evolved from the surviving deep water corals. These rugose coral taxa were scarce at the beginning of the Carboniferous and radiated in time. Further, reefs were abundant in the Devonian, yet in the Mississippian they were scarce (Geys, 1993).

Systematic palaeontology

Remarks: After two detailed surveys through the streets of Leiden and other spot visits, the total number of specimens recorded and imaged was 74. Although at least four to five times as many specimens were observed in these urban traverses, many were insufficiently well preserved for this investigation and thus not imaged. The identification of the images recognized four genera. Many solitary rugose corals were exposed in oblique section, which made them difficult to identify. If they were preserved in transverse section, the characteristics had to be clear enough to distinguish them from other species.

There are similar problems in separating the tabulate corals to the level of species, although the genera are easier to differentiate. Despite having many specimens with distinctive characteristics, both tabulate genera *Michelinia* and *Syringopora* are in need of a detailed systematic revision (Professor J. Denayer, written comm. to D.M.v.R., April 11th, 2016).

Phylum Cnidaria Hatschek
Class Anthozoa Ehrenberg
Subclass Tabulata Milne-Edwards & Haime
Order Favositida Wedekind
Family Micheliniidae Waagen & Wentzel

Genus *Michelinia* De Koninck, 1841

Type species: *Calamopora tenuiseptata* Phillips, 1836, p. 201, by the subsequent designation of Milne-Edwards & Haime (1850, p. lx; Hill, 1981, p. F561).

Diagnosis: (After Hill, 1981, p. F561.) "Corallum cerioid with strong holotheca; corallites large and moderately rounded in section to small and polygonal; walls thin to moderately thick with median suture and projecting short septal trabeculae (may be holocanthine); mural pores large, tunnel-like and sparse; tabulae commonly incomplete, somewhat globose, and not forming regular pattern of inclination, some thickened and some carrying septal spinules on upper surface."

Remarks: The genus *Michelinia* is in need of comprehensive revision. Most descriptions of species are found in literature from the early 20th Century or before. Some species were described later, but the probability is that they are junior synonyms. In consequence, *Michelinia* from Leiden has been left in open nomenclature herein. The genus is distinguished from other colonial corals by their ceroid corallum.

Range: Lower to Middle Devonian, north Africa-North America; Carboniferous to Permian, cosmopolitan, except for South America (Hill, 1981, p. F561).

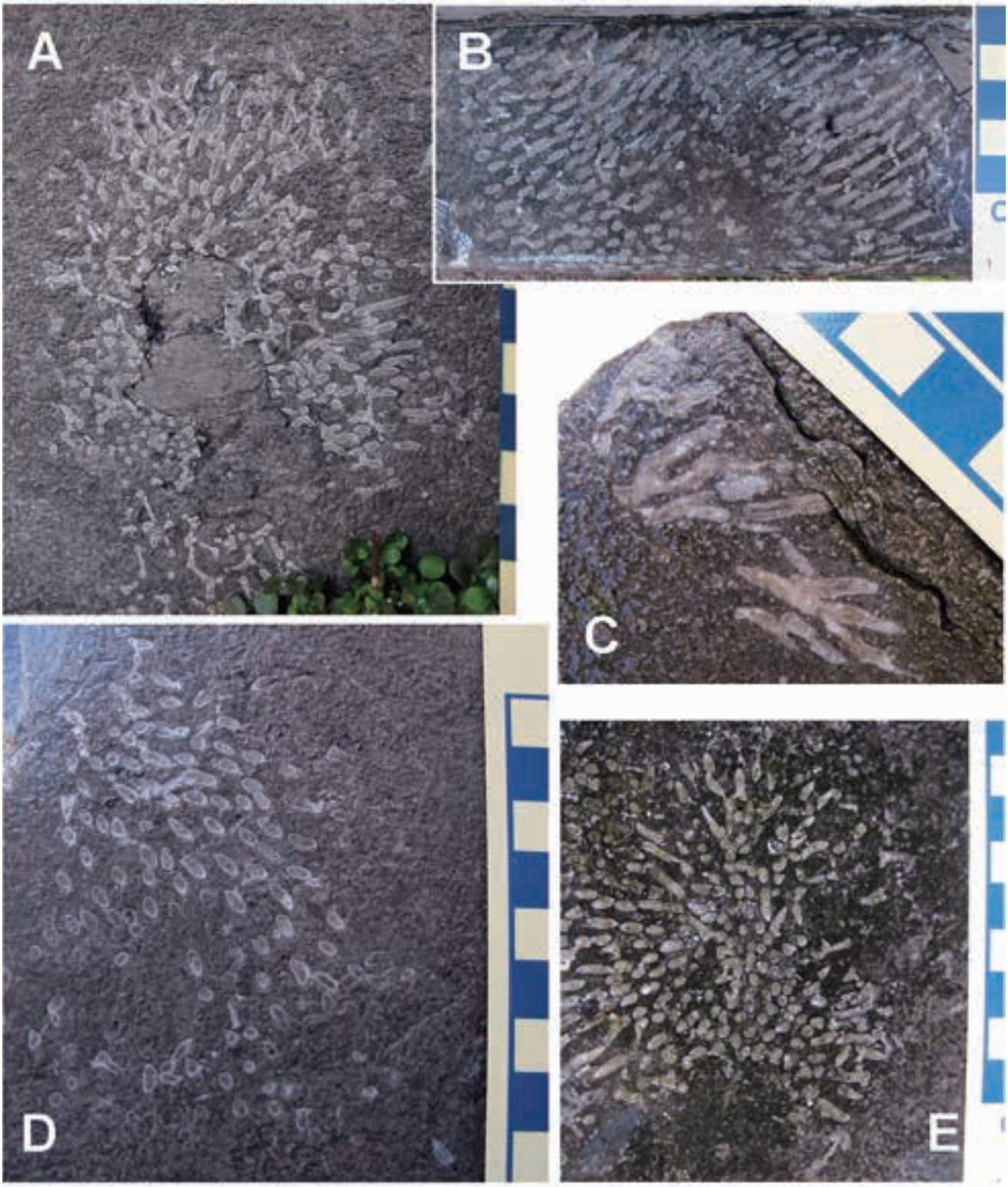


Fig. 3. Sections of colonies of the tabulate coral *Syringopora* sp. or spp. A, R16_001, transverse section in the plinth of Rapenburg 16. B, R65_004, transverse to longitudinal section in a curbstone at Rapenburg 65. C, OS138_003, small longitudinal section showing branching in a keystone at Oude Singel 138. D, R2_004, transverse section in the pavement of Rapenburg 2. E, R22_006, transverse section in the pavement of Rapenburg 22. All scale bars in cm.

Michelinia sp.

(Fig. 2)

2016 *Michelinia*; Reumer, pp. 80–82, figs 79–84.

Material: Longitudinal and transverse sections from Rapenburg 16, 22, 65, 71, Oude Singel 64, 68, 98, 138, 160, Korte Mare 34 and Oude Vest 91 (Fig. 2).

Brief description: Colonial corals with ceroid corallum. Corallite diameter about 8–10 mm; corallum diameter commonly about 70–90 mm, except, notably, for specimen OS138_001 (Fig. 2A).

Remarks: Specimen OS138_001 (Fig. 2A) is unusually big, but is nonetheless a single colony, albeit poorly preserved. There is a 'hole' in the middle of the colony, suggesting it grew on an uneven topographic surface, and the angle of the section is not equal over the whole specimen. R71_001 (Fig. 2B–D) was found in a windowsill, which was ideal because both the transverse and the longitudinal section were clearly visible. The longitudinal section shows that the corallites are not branched, but are all individual tubes. Specimens OS64_002 (Fig. 2E, F) and OS98_004 (Fig. 2G) both have corallites filled by calcite spar, a feature that is seen in other colonies (not figured). From the available images, there were no gross characteristics which suggested that more than one species of *Michelinia* was present.

Order Auloporida Sokolov

Superfamily Syringoporicae de Fromentel

Family Syringoporidae de Fromentel

Genus *Syringopora* Goldfuss, 1826

Type species: *Syringopora ramulosa* Goldfuss, 1826, p. 75, by the subsequent designation of Milne-Edwards & Haime (1850, pp. lxii, p. 251; Hill, 1981, p. F645).

Diagnosis: (After Hill, 1981, p. F647.) "Corallum fasciculate; corallites cylindrical, moderately thick-walled, connected by tubuli without regularity of orientation; septa represented by longitudinal rows of spinules or ?absent; tabulae infundibuliform, forming axial syrinx in many corallites; increase lateral or from connecting tubuli."

Remarks: Like *Michelinia*, *Syringopora* is also in need of systematic revision. The literature on this genus is old and there is no clear, modern overview. Many nominal species are regarded as junior synonyms in the literature. Herein, it is consequently left in open nomenclature. *Syringopora* is distinguished from other colonial corals in these limestones by the fasciculate corallum and cylindrical corallites without visible septa.

Range: Upper Ordovician, Europe; Lower Silurian to Upper(?) Carboniferous, cosmopolitan; Lower(?) Permian (Wolfcampian), North America (Hill, 1981, p. F647.).

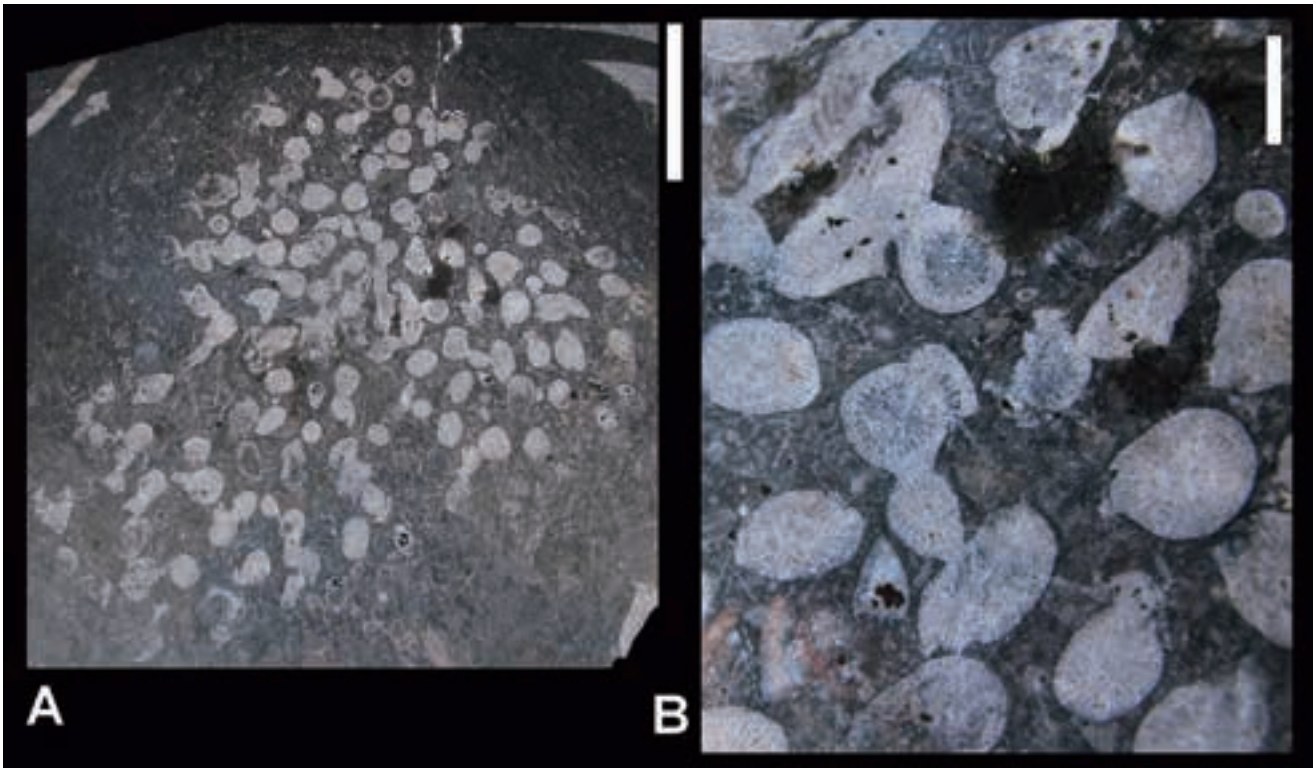


Fig. 4. R19_001, transverse section of *Siphonodendron martini* Milne-Edwards & Haime, 1850, found in the doorstep of Rapenburg 25. A, general view of the colony. Scale bar represents 50 mm. B, detail of some corallites showing the septa and dissepiments. Scale bar represents 10 mm.

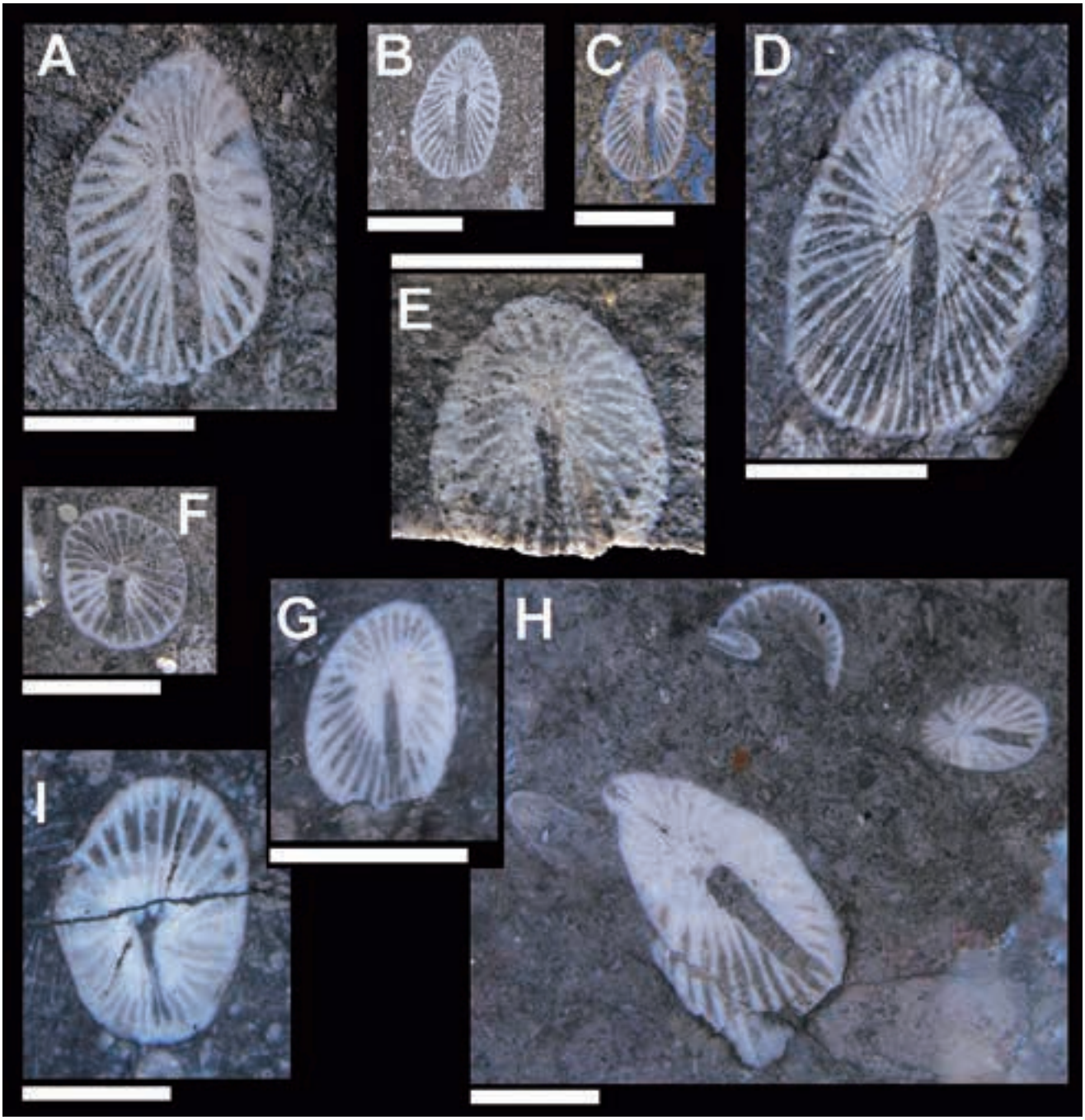


Fig. 5. Transverse sections through the solitary rugose coral *Zaphrentites delanouei* Milne-Edwards & Haime, 1851. A, OS64_001, found at Oude Singel 64. B, OS64_003, found at Oude Singel 64. C, OS68_001, found at Oude Singel 68. D, OV91_003, found at Oude Vest 91. E, R6_001, found in the windowsill of Rapenburg 6. F, R2_013, found at Rapenburg 2. G, R2_007, found at Rapenburg 2. H, R2_006, assemblage with two specimens of *Z. delanouei*; other fossilized corals are visible. Found at Rapenburg 2. I, R2_005, found at Rapenburg 2. All scale bars represent 10 mm.

Syringopora sp. or spp.

(Figs 3, 7)

2016 *Syringopora* sp.; Donovan, pp. 45–46, fig. 1.

2016 *Syringopora*; Reumer, p. 77, figs 75–78.

Material: Transverse sections from Rapenburg 2, 16, 22 and 65, and Oude Singel 138 (Fig. 3).

Brief description: Colonial coral with fasciculate corallum. Corallites are branching; corallite diameter 3-5 mm.

Remarks: Specimen R16_001 (Fig. 3A) contains a blemish in the middle of the specimen. It seems like the paving stone has been broken and later repaired with concrete. Specimen OS138_003 (Fig. 3C) shows a small longitudinal section. Although small, it is evident that the corallites are branching. Specimen R2_004 (Fig. 3D) shows a clear transverse section. In this specimen, the walls are easy to distinguish from the sedimentary fill of the corallite. The absence of septa in all these images is readily apparent. Specimen R65_004 (Fig. 3B) shows a transverse to longitudinal

section found in a curb stone. The left side of the picture shows more transverse sections, the right side more longitudinal sections. Overall, the section is oblique. Specimen R22_006 (Fig. 3E) shows a transverse section found in the pavement of Rapenburg 22. The corallum is complete and has a diameter of approximately 100 mm.

For completeness, we mention the only fossil coral hitherto described from these rocks (Donovan, 2016; Fig. 7 herein). A large gastropod, *Straparollus* sp., or a cephalopod (Reumer, 2016, pp. 64–66, considered such shells to be goniatites) provides a substrate for encrustation by *Syringopora* sp. This is evidence of biotic interactions rarely seen in the imported Upper Palaeozoic limestones of the Netherlands. *Syringopora* typically attached to firm/hard substrates (Adams, 1984); although locally common in limestones in the Rapenburg, no other evidence of attachment has been noted. They are most commonly an indicator of shallow water deposition (Sando, 1980).

Subclass Rugosa Milne-Edwards & Haime
Order Stauriida Verrill
Suborder Lithostrotionina Spasski & Kachanov
Family Lithostrotionidae d'Orbigny

Genus *Siphonodendron* McCoy, 1849

Type species: *Siphonodendron aggregatum* McCoy, 1851, p. 108, by the subsequent designation of Chi (1931, p. 26; Hill, 1981, p. F381).

Diagnosis: (After Hill, 1981, p. F381.) "Fasciculate; increase predominantly lateral; corallites with columella thinly lenticular in transverse section, continuous with both counter and cardinal septa or with counter septum only; major septa may be connected with columella by crests on upper surfaces of tabulae; minor septa short to long; tabular floors conical, tabulae complete or incomplete when tabellae are commonly in only indistinctly bounded axial and periaxial zones; dissepimentarium normally concentric; diphymorphic corallites in which columella fails and tabulae become domed or nearly flat may occur within normal corolla; cardinal fossula not distinct."

Remarks: *Siphonodendron* is distinguished from colonial tabulate corals in these building stones, like the smaller and more gracile *Syringopora* by having bigger corallites which contain radiate septa.

Range: Lower to Upper Carboniferous, Europe-North Africa-Asia-Australia; Upper Mississippian, North America; Upper Carboniferous, Europe-Asia (Hill, 1981, p. F381).

***Siphonodendron martini* Milne-Edwards & Haime, 1850**

(Fig. 4)

2016 *Siphonodendron*; Reumer, pp. 74, 77, figs 72–74.

Material: Transverse section found at Rapenburg 25 (Figure 4), 'Bibliotheca Thysiana'.

Brief description: Colonial coral with fasciculate corallum. Corallite diameter about 8-12 mm. Corallites contain septa, as well as a dissepiment zone.

Remarks: Only one specimen of this species was found in the centre of Leiden. This transverse section is well preserved and many characteristics are clearly visible.

Suborder Stereolasmatina Hill
Family Hapsiphyllidae Grabau
Subfamily Hapsiphyllinae Grabau

Genus *Zaphrentites* Hudson, 1941

Type species: *Zaphrentis parallela* Carruthers, 1910, p. 533, by original designation (Hudson, 1941, p. 309; Hill, 1981, p. F316).

Diagnosis: (After Hill, 1981, pp. F316–317.) "Small, conical, slightly curved, with strong longitudinal ribbing; cardinal fossula on concave side; in early forms and early stages cardinal fossula closed, expanding adaxially, and major septa pinnately arranged with respect to cardinal and alar fossulae; in later forms and later stages cardinal septum shortened and septa withdrawn from fossula, first in cardinal quadrants, then in counter quadrants, so that radial arrangement supercedes pinnate arrangement; minor septa very short or immersed in wall; tabulae incomplete, floors conical, with highest point at inner edge of fossula."

Remarks: The nominal species of the genus *Zaphrentites* are based upon certain misconceptions and require revision. The genus has not been reviewed since it was first described. Distinction between species is greatly facilitated by Denayer *et al*. (2011) on the rugose corals from southern Belgium.

Range: Middle Devonian, Europe; Lower to Upper Carboniferous, Europe-Asia; Lower Mississippian to Lower Pennsylvanian, North America (Hill, 1981, p. F317).

***Zaphrentites delanouei* Milne-Edwards & Haime, 1851**

(Fig. 5)

2016 *Zaphrentis*; Reumer, p. 72, figs 64–66.

Material: Transverse sections from Rapenburg 2, 6, Oude Singel 64, 68, and Oude Vest 91 (Fig. 5).

Brief description: Horn-shaped solitary coral; diameter about 10–13 mm; 33 major septa; long cardinal fossula with a short cardinal septa; alar fossula well-developed.

Remarks: *Zaphrentites delanouei* is distinguished from other species in this genus by the well-developed alar fossula, which is far less adaxially developed in *Z. crassus* (Denayer *et al.*, 2011). The similarities between the specimens are readily apparent (Fig. 5). Although specimen

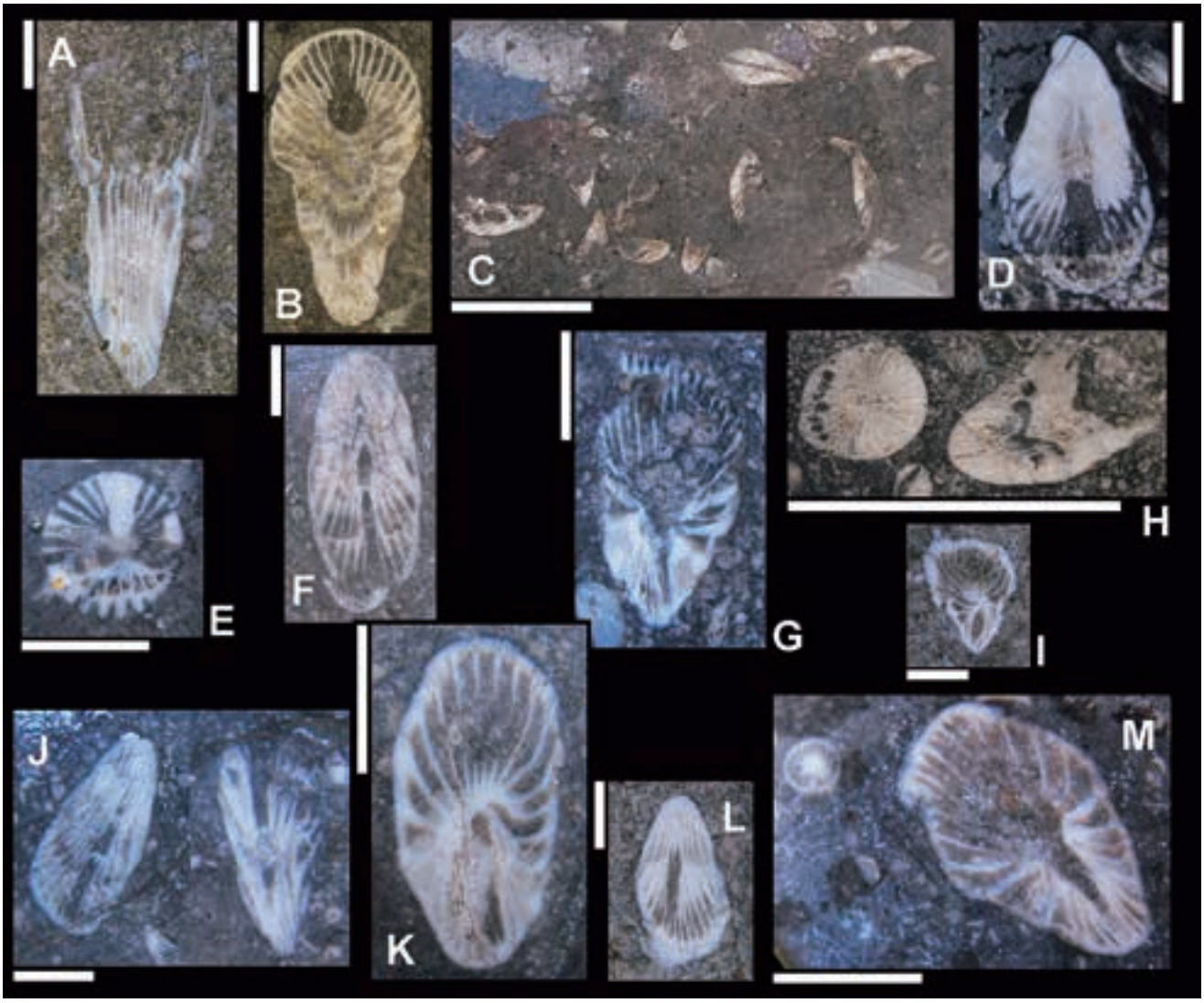


Fig. 6. Various sections and assemblages of Rugosa *incerti ordinis*, although at least some may be *Z. delanouei*. A, OS132_001, longitudinal section found at Oude Singel 132; note bowl-like calice. B, OS68_003, transverse to longitudinal section found at Oude Singel 68. C, OS78_004, assemblage of solitary corals found in the pavement of Oude Singel 78. Scale bar represents 50 mm. D, R28_001, oblique section found at Rapenburg 28. E, R2_011, transverse section found in the pavement of Rapenburg 2. F, R2_012, oblique section found at Rapenburg 2. G, R2_010, oblique section found at Rapenburg 2. H, OS84_001, two solitary corals found at Oude Singel 84. Scale bar represents 50 mm. I, R2_002, oblique section found at Rapenburg 2. J, R2_014, assemblage of solitary corals in oblique section found at Rapenburg 2. K, R4_002, oblique section found at Rapenburg 4. L, R2_003, another oblique section found at Rapenburg 2. M, R28_002, oblique section found at Rapenburg 28. Scale bars represent 10 mm except where stated otherwise.

R2_006 (Fig. 5H) is cut at a slightly oblique angle, the septa and alar fossula are still clear enough to see that it is *Z. delanouei*. Specimen R2_013 (Fig. 5F) is also different from the rest of the specimens of this species; the septa seem relatively thinner, but the number of septa and the structure of the alar fossula are consistent.

Rugosa *incerti ordinis*

(Fig. 6)

Remarks: There are many specimens of solitary rugose corals which could not be identified to genus with confidence (Fig. 6), although at least some are likely to be *Z. delanouei*. In many of these corals, such as specimens OS132_001 (Fig. 6A) and OS68_003 (Fig. 6B), the section is oblique, precluding confident identification (see also Figure 6D, F, G, I, J–M).

Specimen OS84_001 (Fig. 6H) has a calcite fill between septa, making the characteristics unclear. The left section is transverse and the septa are visible, but it appears different than *Zaphrentites* as it lacks the well-developed alar fossula.

Specimen OS78_004 (Fig. 6C) shows a typical assemblage of solitary corals, which are all in oblique section. However, the corals do show similarities in characteristics like the septa and cardinal fossula. There is also variation in coral diameter. Although these could indicate that the corals were in different stage of life, most likely they simply represent different levels at which the corallum was cut.

Specimen R2_011 (Fig. 6E) shows a transverse section of a solitary coral that appears to have been preserved 'inside out', that is, the walls and septa are not calcified, as is the inside of the coral. This has only been encountered once, which makes this specimen notable. The structure of the coral is recognizable and the thick bead on the top seems to be the cardinal fossula. However, with this preservation, identification was not possible.

Discussion

A preliminary survey of the diversity of the fossil corals in Leiden demonstrated that three colonial genera were present, namely *Michelinia*, *Syringopora* and rare *Siphonodendron*. Further, solitary corals were found to be abundant, some identified as *Zaphrentites*. The final number of fossil coral genera in building stones found in Leiden is four. In every street, the same genera were encountered by the author, except for *Siphonodendron*, which was only found once.

The limestones are from the Belgian Ardennes. The two formations that are the source for building stones in that region are the Late Tournaisian Ourthe Formation and the Middle Visean Lives Formation. The rare *Siphonodendron* is the only coral taxon with dissepiments and, therefore, is probably is Visean. The doorstep with the colonial coral is part of the 17th Century building 'Bibliotheca Thysiana'. It is most likely that the limestone was in place earlier than most of the other limestones in Leiden, as the building has never been renovated (Leiden University, 2014). This explains why the stone is the only one with *Siphonodendron*; it most likely derived from a different horizon or even formation and is of uncertain provenance.

The limestones with *Michelinia*, *Syringopora* and *Zaphrentites* were most likely from the upper Tournaisian Ourthe Formation (Denayer *et al*., 2011, fig. 1). The question of whether all coral taxa lived in the same environment is uncertain, but at least likely; they may be found together, two or more coral genera occurring in one limestone slab (*e.g*., Fig. 2E). Solitary rugose corals are commonly preserved in gregarious accumulations (Fig. 6C), probably the result of hydrodynamic sorting. For solitary corals in the Tournaisian, it is known that corals without dissepiments only appear in deep-water facies (Geys, 1993; such as *Zaphrentites*); it is thus probable that all three genera were to be found in deeper waters.

However, when comparing the literature on Carboniferous coral faunas, it was apparent that an assemblage like the one described herein has not been reported from Belgium. Mitchell (1980) considered the distribution of Mississippian coral faunas, and divided the Tournaisian and early Visean in Britain into different biozones based on their coral assemblages. One of the biozones is described as the *Zaphrentites delanouei* Assemblage Biozone (Mitchell, 1980, p. 580). This biozone contains *Zaphrentites delanouei*, *Michelinia favosa*, *Syringopora vaughani*, *Fasciculophyllum omaliusi* and *Sychnoelasma clevedonensis*. This shows an undoubted similarity with the fauna documented herein. The two last-named species are both solitary rugose corals; they may be hidden within the Rugosa *incerti ordinis*. That would mean that the faunas are similar and the building stones are likely derived from the same assemblage biozone. Mitchell (1980) also mentioned that detailed correlation between the Welsh and Belgian coral faunas has not been attempted, but is suggested based on the evidence of the conodont fauna. The *Zaphrentites* Biozone would be Tournasian, upper Hastarian to Ivorian (Mitchell, 1980, fig. 1), which agrees with the middle Ivorian position of the Ourthe Formation (Denayer *et al*., 2011, fig. 1). The Carboniferous formations in Britain and Belgium are both part of the same Wales-London-Brabant Massif. However, *Zaphrentites delanouei* is not mentioned by Poty, who divided the Belgium Tournaisian and Visean into rugose coral biozones (Poty, 1985).

Fedorowski (1981) suggested that the region of Belgium was the origin of the Tournaisian coral fauna. First appearances of many coral species reported in the Mississippian of the British Isles are younger than in Belgium. So, species arose in the Belgian area and would then migrate to the British area. This would mean that the regions are correlated, but not necessarily precisely identical in palaeoenvironment. The Tournaisian was an age of recovery after the Frasnian-Famennian mass extinction. *Michelinia*, *Syringopora* and *Zaphrentites* became widely distributed, and many species became cosmopolitan (Hill, 1981). That the coral biodiversity is similar wherever we looked in Leiden probably means that most limestones are from the same region and perhaps even from the same quarry. This could indicate that a lot of limestones were imported in the same period, supporting the suggestion that embedding limestones in buildings was a trend in the 19th Century.

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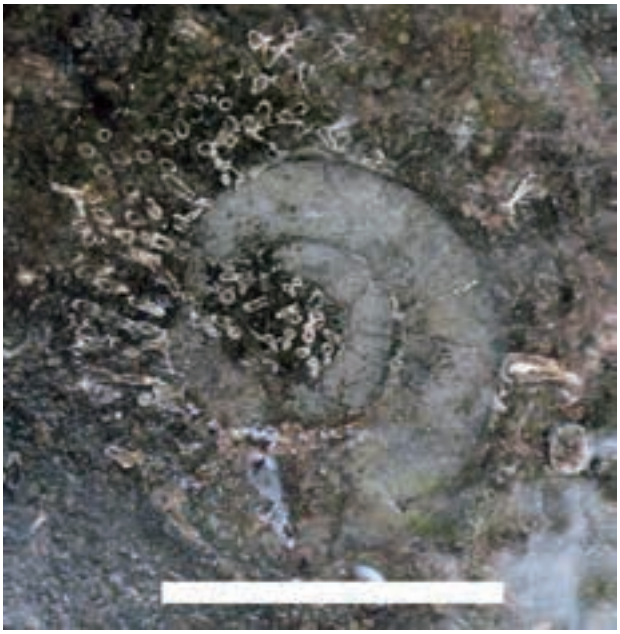


Fig. 7. The gastropod *Straparollus*(?) sp. in a paving slab at Rapenburg 22, encrusted by *Syringopora* sp. (after Donovan, 2016, fig. 1). Specimen contrast enhanced with water. Scale bar represents 50 mm.

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