Sabellids and serpulids (Polychaeta sedentaria) from the type Maastrichtian, the Netherlands and Belgium

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Key words – Sabellidae, Serpulidae, Late Cretaceous, Maastrichtian, the Netherlands, Belgium, systematics.
Calcareous tubes of the sabellid genus *Glomerula* and of the family Serpulidae (subfamilies Serpulinae and Spirorbinae) rank amongst the commoner, highly diverse biota of the type Maastrichtian strata. These cover the sequence from the upper Beutenaken Member (Gulpen Formation) up to and including the Meerssen Member (Maastricht Formation). Of the 40+ taxa of calcareous worm tubes found in this interval, the commonest ones are described and illustrated in the present paper, which also comprises a revision of data published in 2005.

Contents

Introduction

Calcareous worm tubes are found either loose (free-lying) in sedimentary rocks or fixed to a solid substrate. The latter includes both biotic (e.g., echinoid tests, belemnite guards and oyster shells) and abiotic substrates, in particular, hardgrounds and walls of burrows or borings therein. Calcareous tubes found loose either belong to a minority of species that did not attach permanently to a substrate (obligate encrusters) or represent specimens that were originally fixed to substrates such as algae, sea grass or aragonitic molluscan shells, that have now dissolved, or constitute individuals that became separated from their substrates by mechanical means. The operculum is occasionally found of some species.

In the type Maastrichtian, many sabellids and serpulids possess a sturdy and well-preserved calcitic tube. However, a few taxa had aragonitic tubes which are preserved either as a mould in the host rock or as a negative imprint on the attachment area of epibionts (e.g., oysters) which settled over the serpulids and bioimmured them in this way. In other, rare cases, tubes are silicified. Some species, such as those of the subgenus *Pyrgopolon* (*Pyrgopolon*), have both calcitic (inner and outer tube layers) and aragonitic parts ('middle' tube layer and operculum).

Serpulid tubes occur in nearly rock-building frequencies at some intervals within the Nekum and Meerssen members, with one species, *Pyrgopolon mosae*, predominating.

Stratigraphic units in which serpulids are both common and diverse include the lower portion of interval 6 of the Vijlen Member, the Lanaye Member, and, best of all, the lower portion of the Meerssen Member with burrows into hardgrounds and their infills. In these natural shelters, even the most fragile serpulid tubes were protected from abrasion.

Pyrgopolon mosae was the first serpulid to be described and illustrated in 1808 by de Montfort, from levels which subsequently formed part of the definition of the type Maastrichtian, while Goldfuss (1831, 1841) erected numerous new species of serpulids, including a few from that area. Around the same time, Defrance (1827), J. de C. Sowerby (1829), Dujardin (1837), von Hagenow (1840) and Roemer (1841) described species from France, England and Germany, some of which were later recognised by Müller (1847, 1851) and subsequent authors to occur in the type Maastrichtian as well. Some serpulids recorded in the first half of the nineteenth century, especially those which currently are contained in the subgenus *Pyrgopolon* (*Pyrgopolon*), were considered to be scaphopods or other invertebrates (see Donovan & Jagt, 2012). De Ryckholt (1852) was among the first to interpret them correctly as serpulids; he also erected a few additional species.

The second half of the nineteenth century, and the first half of the twentieth, brought few new data on serpulids from the type Maastrichtian. Species appeared mostly in extensive faunal lists in works which focused on regional stratigraphy. There are two notable exceptions to this. First, there are the small illustrations in Voigt's seminal paper of 1929, and secondly, Umbgrove (1925, 1956) provided descriptions and illustrations of a curious taxon which is now known as *Dorsoserpula* (*Pegmaticula*) *turpificata*. This 'gap' of one hundred years is all the more remarkable, because in other regions research on fossil serpulids continued unabated.

The modern phase of scientific work on serpulids began in the 1950s. The opercula of *Pyrgopolon* were described by Wrigley (1952) and, later and in more detail, by Cupedo (1980a, b). Regenhardt's (1961) monograph was a milestone in the taxonomic assessment of Cretaceous serpulids from central Europe, although it was incomplete and the systematics proposed subsequently raised criticism. Regenhardt introduced several new species from the type Maastrichtian, on the basis of a unique collection of well-preserved mesofauna collected by the late Ehrhard Voigt.

A critical revision of Regenhardt's systematics was initiated by Lommerzheim (1979) and continued by Jäger (1983). However, both these papers focused primarily on serpulids from Germany; material from the type Maastrichtian was considered only in passing. Later, Pillai (1993) described the internal tube structures of *Spiraserpula*, while Keutgen (1996) presented detailed stratigraphic data of serpulids of early Maastrichtian age in the Aachen area and direct environs. Numerous specimens from the borehole Thermae 2000 at Valkenburg aan de Geul (the Netherlands) were illustrated by Jäger (1987), who also (1988) presented a detailed overview of serpulid biostratigraphy around the boundary between the Gulpen and Maastricht formations.

A second phase of revisions began with Jäger (1993), who considered only species from the early-middle Danian Houthem Formation in southern Limburg and the Belgian province of Limburg. Subsequently, Jäger (1998) illustrated material from the ENCI-Heidelberg Cement Group quarry (Maastricht) and a list of species occurring at several intervals of the Vijlen Member at Altembroeck (Voer, northeast Belgium) was provided by Jäger *in* Jagt *et al*. (1995), who also discussed the stratigraphic value of *Nogrobs*

(*Tetraditrupa*) *canteriata* and *Conorca trochiformis*. Lastly, Jäger (2005) published a monograph in which several new species from the type Maastrichtian were described and illustrated. Since then, a few name changes have proved necessary.

Systematic palaeontology

Class Polychaeta Grube, 1850
Subclass Canalipalpata Rouse & Fauchald, 1997
Order Sabellida Fauchald, 1977
Family Sabellidae Latreille, 1825
Subfamily Sabellinae Latreille, 1825 (*nom. transl.* Chamberlin, 1919)
Genus *Glomerula* Brünnich Nielsen, 1931

Description – *Glomerula* forms a simple tube which closely adheres either to a substrate or to previously constructed tube portions; however, attachment is only weak. In compensation, lengthwise tube growth is rapid and the potential to regenerate after breakage is great. Some specimens reveal special features on the inside of the tube with which the animal is anchored. Tubes are long and increase in diameter slowly; they are strongly curved in many specimens, with the newly constructed portions growing thigmotaxically along older portions, thereby forming meanders, irregular spirals or, highly characteristic, chaotic knots. On softgrounds, in the absence of larger solid objects, a small substrate is required only by juveniles. More or less straight tube portions, either attached wholly to or growing vertically away from the substrate, may occur between the meanders, spirals or knots, and at the anterior end. Many erect tube portions are broken at the top; regeneration shows up as a successive smaller tube growing out of the old one. The new tube, after a sharp curve, may either enwrap the old stump more or less regularly or is curved irregularly.

The tube surface is somewhat rough, but lacks regular ornament. The base of the tube is slightly deformed as a result of close contact to the substrate, but, in contrast to most serpulids, is not widened by a border. The tube wall consists of the cylinder layer only, which is composed of many single layers arranged in either a concentric or eccentric pattern. Between the single layers free space, crescent-shaped in cross section, may be left. Uncommonly, the small innermost layer may wind like a corkscrew within the lumen. The thickness of the tube wall and the diameter of the central lumen vary widely. A characteristic feature of Cretaceous and Paleogene species of *Glomerula*, although seen only in few specimens in any population, is the local trilobate narrowing of the tube lumen for anchorage of the animal inside its tube.

Remarks – Formerly, *Glomerula* was considered to be a serpulid. However, close examination of the Recent *Calcisabella piloseta* Perkins, 1991, which is the sole extant species of the family Sabellidae to construct a calcareous tube, shows that its tube is similar to that of fossil *Glomerula*. Thus, *Calcisabella* is considered to be a junior synonym of *Glomerula*, as is *Cycloserpula*. *Glomerula* is one of the commonest, stratigraphically most long-ranging, and geographically and ecologically most widely distributed polychaete worms. It is difficult to separate species due to the simple shape and wide range of tube variation.

***Glomerula serpentina* (Goldfuss, 1831)**
Pl. 1, figs. 1, 3.

Description – See generic description above; the tube may attain diameters in excess of 3 mm, but usually is less than 2 mm.

Remarks – In nearshore settings, only a single species of *Glomerula* appears to have been present, which is here identified as *G. serpentina*. However, from offshore chalk or marly limestone facies, a small-sized congener, *G. lombricus*, has been recorded. This distinction differs slightly from the interpretation favoured by Jäger (2005), who included also small-sized specimens from nearshore biotopes in *G. lombricus*.

Distribution – Known from all members (Beutenaken to Meerssen); common. The total known range is late Valanginian (Early Cretaceous) to late Priabonian (Late Eocene).

***Glomerula lombricus* (Defrance, 1827)**
Pl. 1, fig. 2.

Description – See generic description above; tube diameter usually is less than 1 mm.

Remarks – This small species is only in offshore chalk facies (see above).

Distribution – Ranging from the Beutenaken to the Lanaye members. The total known range is late Valanginian to latest Maastrichtian.

Family Serpulidae Rafinesque, 1815
Subfamily Serpulinae Rafinesque, 1815
Genus *Filograna* Oken, 1815
***Filograna filosa* (Dujardin, 1837)**
Pl. 1, fig. 4.

Description – Tube small, 0.25-0.50 mm in diameter; diameter increasing very slowly. Many tubes are found attached more or less parallel to each other, thus forming bundle-shaped aggregates. The bundles may ramify and unite to form a mesh-like plaiting. Commonly, the tubes lack any ornament. The tube wall is thin, so that not only the outline, but occasionally also the lumen may be deformed polygonally. In contrast to *Glomerula*, *Filograna* never shows a trilobate narrowing of the lumen.

Remarks – *Filograna filosa* may be confused with worn cyclostome bryozoans and with constructions made by the polychaete *Dodecaceria* (family Cirratulidae).

Distribution – Meerssen Member, principally in the upper part of section IVf-6, mostly in the Geulhem/Berg en Terblijt area (the Netherlands). The total known range of this species is Late Jurassic to latest Maastrichtian; common, extant species of *Filograna* are widespread and similar to *F. filosa*.

Genus *Josephella* Caullery & Mesnil, 1896
***Josephella subanulata* Regenhardt, 1961**
Pl. 2, fig. 9.

Description – The diameter of the tube is small, maximum *c.* 1 mm. Both fixed and free tube portions are present, as are relatively large annular peristomes. No other ornament seen.

Remarks – In the near-total absence of any characteristic morphological features, it is difficult to distinguish these small tubes from juveniles of other genera.

This species was referred to previously as '*Proliserpula*? sp.' (Jäger, 1983, 1987, 1988).

Distribution – Lanaye to Valkenburg members; Gronsveld Member(?); Emael to Meerssen members. The total known range is earliest Cenomanian to latest Maastrichtian.

Genus *Nogrobs* de Montfort, 1808
Subgenus *Nogrobs* (*Tetraditrupa*) Regenhardt, 1961

Description – The fixed tube portion is normally not preserved. Members of this subgenus constructed a large 'effective base' to prevent the free, loose-lying tube from sinking into the soft, muddy sea floor and from being toppled by vagile animals. This base was made by forming an open, loose spiral shaped like a watch spring, of which usually only fragments are found. This free tube portion is long, and generally consists of an open spiral of three-quarters to one and a half turns. The main portion of the spiral is more or less low, but, in the posterior portion and near the aperture, tube growth may be obliquely upwards. The cross section is rounded squarish to near-circular. The surface usually is white, but dull. While the outer and inner parable layer often are distinct, the cylinder layer being very thin.

Remarks – *Nogrobs* is well known, as *Tetraserpula* Parsch, 1956 (a synonym), from the Jurassic, and perhaps it continues to the present day under the name of *Bathyditrupa* Kupriyanova, 1993.

***Nogrobs* (*Tetraditrupa*) *canteriata* (von Hagenow, 1840)**
Pl. 1, figs. 5, 6.

Description – Medium sized; cross section rounded squarish. Between the rounded edges, all four sides are slightly concave. Large specimens often display a characteristic chevron-shaped pattern at the edges. At the aperture, the diameter is somewhat reduced. The tube wall is thick at the edges, but moderately thin between these.

Distribution – Uppermost part of the Beutenaken Member and Vijlen Member. A single specimen from the Kunrade limestone facies (equivalent of the Schiepersberg or Emael Member, Maastricht Formation) near Kunrade (the Netherlands) probably represents a remanié specimen from the Vijlen Member. The total known range is earliest

Maastrichtian to early late Maastrichtian (lower part of *tegulatus/junior* Zone), possibly extending to the latest Maastrichtian.

***Nogrobs* (*Tetraditrupa*) *superiora* (Jäger, 1983)**
Pl. 1, fig. 7.

Description – Medium sized; edges well rounded and sides convex, which explains why the cross section is nearly circular. A chevron-shaped pattern is seen only in few large-sized specimens. Some individuals reveal a sharp longitudinal furrow on three of the four sides. The tube wall is thick.

Distribution – Glauconitic lower part of the Vijlen Member. The total known range is early Maastrichtian (upper *sumensis* Zone), early late Maastrichtian (upper *tegulatus/junior* Zone) to latest Maastrichtian.

Genus *Vermiliopsis* de Saint-Joseph, 1894
***Vermiliopsis fluctuata* (J. de C. Sowerby, 1829)**
Pl. 1, figs. 8-10.

Description – Medium sized; maximum tube diameter is 3 mm. The tube increases rapidly in diameter and is fixed to a substrate for nearly the whole of its length, often strongly and irregularly curved or forming a loop. Usually five undulating keels and two, commonly similarly-shaped border lines at the base, making in total seven keels, situated in more or less equal distances from each other. The diameter of the tube enlarges at the aperture to form a flared or trumpet-shaped peristome, which may be constructed repeatedly at irregular distances. At the sides, the peristomes and incremental lines run somewhat obliquely, being curved anteriorly near the upper side.

Remarks – Atypical specimens with only five keels were noted by Jäger (1983, p. 64), but no additional material of such configuration has been collected since.

Distribution – Vijlen to Lanaye members; Gronsveld Member; Schiepersberg Member(?), Emael to Meerssen members. Common in the Meerssen Member. The total known range is middle Turonian to early Santonian(?); middle Santonian to latest Maastrichtian.

Genus *Metavermilia* Bush, 1904 (emend. Zibrowius, 1971)
Subgenus *Metavermilia* (*Vepreculina*) Regenhardt, 1961
***Metavermilia* (*Vepreculina*) *tuberculifera* (Brünnich Nielsen, 1931)**
Pl. 1, fig. 11.

Description – Tube long, but small sized, maximum diameter less than 2 mm. The tube diameter increases slowly; the tube is fixed to the substrate for nearly the whole of its length, except for a short free tube portion that may occur. Up to seven longitudinal rows of spines. Annular peristomes. The cross section usually near-circular or tunnel-shaped, less often triangular.

Distribution – Vijlen Member. The total known range is earliest late Campanian to early late Maastrichtian (*argentea/junior* Zone).

***Metavermilia* (*Vepreculina*) *schulzi* Jäger, 2005**
Pl. 1, fig. 12.

Description – Small sized; maximum tube diameter *c.* 1 mm. Both fixed and free tube portions occur, and commonly with seven narrow, sharp keels, which occasionally may form tall crests; wrinkled transverse incremental lines. Often small granules occur at the junctions of longitudinal and transverse elements of ornament. The cross section is near circular, the tube wall being thin.

Distribution – Meerssen Member; rare.

Genus *Filogranula* Langerhans, 1884
***Filogranula cincta* (Goldfuss, 1831)**
Pl. 1, figs. 13, 14.

Description – Medium sized; maximum tube diameter 3 mm. The tube increases slowly to moderately in diameter, the fixed tube portion having three keels and two, often similar, border lines at the base, making a total of five keels. The free tube portion is similar to the fixed one, and also has five keels. Keels commonly are undulose, sometimes enlarged to form frayed-out combs. Some specimens have longitudinal rows of granules rather than keels. Peristomes are either annular or stellate with five spines.

Remarks – This species differs from the closely similar *Vermiliopsis fluctuata* by having five, rather than seven, longitudinal keels, and by the shape of the peristomes, which are perpendicular, not oblique, to the longitudinal axis of the tube and not funnel shaped. Some specimens are fixed tightly to large objects such as shells or pebbles, others only at several minute spots to small substrates like algae or sea grass.

Distribution – Beutenaken to Gronsveld members; Schiepersberg Member(?); Emael Member. The total known range is early Hauterivian to latest Maastrichtian.

Genus *Neovermilia* Day, 1961
***Neovermilia ampullacea* (J. de C. Sowerby, 1829)**
Pl. 2, figs. 1-3.

Description – Medium to large sized, *c.* 3-10 mm in diameter. The fixed tube portion is either curved irregularly or may form a more or less regular spiral. A long free tube portion may be present and either one keel or crest or none at all. Characteristic specimens show a fine transverse ornament of granules, minute crests or wrinkles. Weak to strong annular peristomes may be present. The cross section may be triangular, especially in the posterior portion of the tube, but is more commonly circular or tunnel-shaped. The tube surface is usually bright brownish or yellowish, the tube wall commonly being thin. The base of the tube generally is cellular, the cells being distinct and short. However, nearly all features may vary considerably.

Remarks – There is a similarity between '*Serpula*' *ampullacea* J. de C. Sowerby, 1829, which is the commonest species of the genus *Proliserpula*, and some members of the extant genus *Neovermilia*. Several of the species formerly assigned to *Proliserpula* are now considered to belong to *Neovermilia*.

Distribution – Vijlen to Gronsveld and Emael to Meerssen members. The total known range is late Albian to late Danian.

***Neovermilia*? *hemmoorensis* (Jäger, 1983)**
Pl. 2, figs. 5, 6.

Description – Small to medium sized, maximum tube diameter 3 mm at the peristomes and 2 mm in between. Both fixed and free tube portions occur. Three small, sharp keels or, more commonly, three longitudinal lines of granules on the upper side. Commonly, one weak, narrow furrow is seen, as a result of an interruption of the transverse ornament on each lateral side. Transverse ornament consists of numerous fine (but sharper than in *N. ampullacea*), commonly slightly undulose, ledges. Strong, but short, rarely somewhat longer annular peristomes occur. Some specimens may lack all or some of these types of ornament. The cross section is circular, while the base of the tube usually is cellular or, less commonly, not so.

Remarks – This species displays a wider range of variation than hitherto thought. Some of the specimens identified as '*Janita*? sp.' and '*Proliserpula ampullacea*' by Jäger (for example, 1987, pl. 1, figs. 29, 30; pl. 2, fig. 24) more correctly belong to *N.*? *hemmoorensis*.

Distribution – Lanaye to Nekum members. Relatively common in the Lanaye Member. The total known range is late early Maastrichtian (*cimbrica* Zone) to late late Maastrichtian (*baltica/danica* Zone).

Genus *Serpula* Linnaeus, 1758
***Serpula*? *trilineata* Roemer, 1841**
Pl. 2, fig. 4.

Description – Medium sized; only with the fixed tube portion present. Three weak, smooth or undulating keels, fine transverse wrinkles, but no peristomes. The cross section is tunnel-shaped. On each side of the tube base is a longitudinal cavity.

Remarks – In the palaeontological literature, the name '*Serpula*' has often been used as an artificial conglomerate, meaning 'a species of the family Serpulidae, genus unknown'. In neontological studies, however, *Serpula* has been shown to be a well-defined genus by its soft-part anatomy and operculum, but, unfortunately, the tube possesses no features that could characterise the genus. Therefore, it may be difficult to distinguish tubes of extinct species of *Serpula* from other genera and, therefore, each pre-Neogene *Serpula* can only be listed in open nomenclature.

Serpula? *trilineata* seems to be the correct name for tubes which formerly, but erroneously, were thought to belong to *Janita* (Jäger, 1983, 1987 [pl. 1, figs. 27, 28 only], 1988). Extant *Janita* has much stronger and more undulose keels.

Distribution – Gronsveld Member; Schiepersberg Member(?); Emael Member; Meerssen Member(?). The total known range is late Santonian to latest Maastrichtian.

***Serpula*? *klaumanni* Lommerzheim, 1979**
Pl. 3, fig. 4.

Description – Small to medium sized; usually with a single narrow, low keel. The fine transverse ornament consists of sharp granules and short ledges, which are faintly curved anteriorly at the keel. Weak, short or, more often, long and bulge-shaped annular peristomes. The tube wall is thin and the base barely widened.

Distribution – Meerssen Member. The total known range is earliest Cenomanian and latest Maastrichtian.

Subgenus *Serpula* (*Cementula*) Regenhardt, 1961
***Serpula* (*Cementula*) *sphaerica* Brünnich Nielsen, 1931**
Pl. 2, figs. 7, 8.

Description – Tube small, slowly increasing in diameter, forming one (rarely more) regular or knot-shaped spiral. The outer tube layer forms a broad and flat base, fuses the whorls and, like sugar coating, fills up the depressions between the whorls, thus obscuring the sutures. Commonly, the spiral is strikingly low when attached to a large flat substrate, but hemispherical to globular when wrapped around a minute substrate. The umbilicus usually is lacking, but is present in rare specimens; in contrast to the similarly-shaped genus *Spiraserpula*, there are no internal tube structures.

A free tube portion is rare; it is more or less straight, occasionally possessing sharp, quadripartite peristomes consisting of rounded, birdwing-like 'alae' on the upper side and two pointed processes on the underside.

Remarks – In the type Maastrichtian, the group of *Cementula*, *Spiraserpula* and *Laquoserpula* needs more detailed examination. Rare specimens belonging either to *Cementula* or *Spiraserpula* occur in the Vijlen Member and in the Kunrade limestone facies (equivalent of the Gronsveld Member). In the Meerssen Member, one or several insufficiently known species exist, some specimens resembling *Cementula*, others *Laqueoserpula*. Some individuals have three keels, the central one protruding anteriorly.

Distribution – Emael and Nekum members(?); Meerssen Member. The total known range is middle Santonian to latest Maastrichtian.

Genus *Spiraserpula* Regenhardt, 1961
***Spiraserpula scrupea* Regenhardt, 1961**
Pl. 2, figs. 9-11.

Description – Tube medium sized, slowly increasing in diameter, forming several spirals, either stacked on one another or in close proximity. A strong attachment to the substrate is achieved by construction of more or less low spirals with a wide base. Between the spirals, non-spiral tube portions may be present. As in *Cementula*, the outer tube layer is like sugar coating, obscuring the sutures. Commonly, an umbilicus is present and the anterior portion of the tube has a keel. Widely spaced birdwing-like peristomes ('alae') may occur. On the inner surface of the posterior portion of the tube there are internal structures for anchorage of the animal. These consist of three keels situated at approximately equal distances from each other and protruding into the lumen. In Recent species of *Spiraserpula*, the animal can be drawn out of its aperture only by tearing it to pieces. A free tube portion may occur rarely and may bear quadripartite peristomes similar to those in *Cementula*.

Remarks – Specimens from the type Maastrichtian were described as *Spiraserpula* sp. 1 by Pillai (1993). It is possible that *S. scrupea* and *S. versipellis* Regenhardt, 1961, from the chalk facies of northern Germany, are conspecific. The only remarkable difference is the lack of granulation in the former.

Distribution – Emael and Nekum members(?); Meerssen Member.

Genus *Laqueoserpula* Lommerzheim, 1979
***Laqueoserpula schmidwallisi* Jäger, 2005**
Pl. 3, figs. 2, 3.

Description – Small to medium sized. The tube increases slowly in diameter. Commonly, several specimens are fused, the fixed portion(s) forming irregular loops and spirals growing upon each other. An indistinct longitudinal edge is commonly present. In contrast to *Spiraserpula*, there are no internal tube structures. The tube wall is thin. Tubes are often infested by the symbiont *Protulophila gestroi* Rovereto, 1901. The free tube portion is pentagonal, with three keels, of which the central one is the strongest.

Distribution – Meerssen Member; rare.

Genus *Protectoconorca* Jäger, 1983
***Protectoconorca senonensis* Jäger, 1983**
Pl. 3, fig. 1.

Description – Medium sized. The tube forms a spiral which usually is sinistrally coiled. Not much more than the last whorl is visible in external view. Height and diameter of the spiral are more or less equal, or the diameter slightly exceeds the height. A strong keel protrudes horizontally or obliquely towards the centre of the spiral and narrows the umbilicus; nevertheless, the latter commonly remains relatively wide, less

often being narrow or nearly occluded. Often the tube wall is thickened at the aperture, which is rounded squarish.

Distribution – Kunrade limestone facies (equivalent of the Lanaye to Emael members); rare. The total known range is middle Turonian(?), middle Santonian to late Maastrichtian.

Genus *Dorsoserpula* Parsch, 1956

Description – Small to very large sized. Tube shape is variable. In the most characteristic specimens, one or several tubes together wind around a vertical cylindrical substrate, often a crinoid stem or the free portion of another serpulid tube, forming a spiral. A long free tube portion is commonly present. A small side tube, running more or less parallel to the main tube within its tube wall, may occur. At the surface of the main tube, the side tube resembles a rounded longitudinal edge. Additionally, one ordinary keel may be present or not. Otherwise, the surface is smooth except for weak bulges. The tube wall is moderately to very thick; in the large sized subgenus *D.* (*Pegmaticula*) it includes sponge-like layers.

Remarks – Formerly, *Dorsoserpula* was used a 'wastebasket' name for many different species possessing one keel and a triangular or circular cross section. Now, however, only species similar to the Jurassic type species, *Serpula delphinula* Goldfuss, 1831, are placed in *Dorsoserpula*. Unfortunately, the two most characteristic features, the side tube (seen only in *Dorsoserpula*), and the winding around a cylindrical substrate, are present only in a minority of specimens.

Umbgrove (1956) interpreted the large side tube of *D.* (*Pegmaticula*) *turpificata* as the tube of a sipunculid. This is unlikely, because in regular-sized species, such as *D. wegneri*, the corresponding side tube is much smaller than that of a regular sipunculid.

Dorsoserpula wegneri wegneri (Jäger, 1983)

Pl. 3, figs. 5, 6.

Description – Small to large sized, lacking a keel. The tube base is not cellular and the inner surface is smooth.

Distribution – Vijlen Member; Lanaye to Nekum members; Meerssen Member(?). The total known range is early Turonian to latest Maastrichtian.

Dorsoserpula wegneri maastrichtensis Jäger, 2005

Pl. 3, figs. 8-11.

Description – Small to large sized. Many specimens do not wind around a vertical cylindrical substrate. Usually there is but a single keel, at which the incremental lines are curved anteriorly; the tube base is cellular.

Remarks – This subspecies was named 'Maastricht-Variante', 'cf. *wegneri*' and 'n. sp. aff. *wegneri*' by Jäger (1983, 1987, 1988, respectively).

Distribution – Lanaye to Meerssen members, commoner than *D. w. wegneri*. The total known range is early late Maastrichtian to latest Maastrichtian. It is unknown if this subspecies occurred in the early Maastrichtian, because formerly (see Jäger, 1983) no distinction was made between the two subspecies.

Subgenus *Dorsoserpula* (*Pegmaticula*) Regenhardt, 1961
***Dorsoserpula* (*Pegmaticula*) *turpificata* (Regenhardt, 1961)**
Pl. 3, fig. 7; Pl. 4, fig. 2.

Description – Tube very large, up to 14 mm in diameter, the diameter of the side tube being *c*. 3 mm. The tube is irregularly curved, often forming a spiral or it (or several tubes together) forms a gall-shaped lump. The surface is smooth. The outer tube layer fuses the tube portions and, like sugar coating, fills the depressions between the whorls, thus obscuring the sutures. There is no ornament, except for the longitudinal edge formed by the side tube. The tube wall is up to 5 mm thick; in large specimens it consists of three to four layers, these being, from inside to outside, a relatively thin, compact layer; an irregular, sponge-like layer which is wide at the base and thin above this; and a layer which is compact where moderately thick, but sponge-like where thick. The sponge-like structure consists of hollow, wrinkled cylinders which are perpendicular to the tube surface.

Distribution – Meerssen Member, especially at its base, and apparently commonest in the Bemelen area (compare Jagt *et al*., 2009). The total known range is late Maastrichtian.

Genus *Pentaditrupa* Regenhardt, 1961
***Pentaditrupa subtorquata* (Münster *in* Goldfuss, 1831)**
Pl. 3, figs. 12, 13.

Description – The tube is regularly curved, having a small radius posteriorly and a large radius anteriorly. The shape is either like a released watch spring, but consisting of one-quarter to one and a quarter turns only, or like an elephant's tusk. Moreover, the tube may either lie in one plane or be slightly curved trochospirally, erecting the aperture obliquely over the substrate. As a consequence of the thick outer parable layer, the tube diameter is reduced at the aperture. Five rounded, longitudinal edges are situated at equal distances from each other, are relatively sharp near the posterior end and rounded near the aperture. In some specimens, these edges are weak or even totally absent. The cross section is either rounded pentagonal or circular. The circular specimens closely resemble species of *Ditrupa*. The surface smooth and shiny, usually not white, but somewhat brownish, pinkish or yellowish.

Remarks -- The present species ranks amongst the most typical soft-bottom dwelling serpulids. In fine-grained rocks it may occur in large numbers. It needs only a tiny object for initial fixation, or none at all, the tube lying free on the sea floor. In contrast to Jurassic species of the genus, no unequivocal fixed tube portion has ever been recognised for *P. subtorquata*. This species adopted the same strategy as did *Nogrobs* (see above) in forming a large 'effective base' by constructing an open, loose spiral like a

watch spring to prevent the tube from sinking into the mud and from being toppled by vagile animals. However, some specimens are curved less strongly and may actually have been lodged in mud like members of the genus *Ditrupa* Berkeley, 1835, the Cenozoic-Recent descendant of *Pentaditrupa.*

Distribution – Vijlen Member; Lixhe to Valkenburg members(?). A mass occurrence is known from the base of interval 6 of the Vijlen Member in the Haccourt-Lixhe area (CPL SA and CBR-Lixhe quarries). The total known range is late Albian to late Danian.

Genus *Mucroserpula* Regenhardt, 1961
'*Mucroserpula*' *felderi* Jäger, 2005
Pl. 4, figs. 1-4.

Description – Very large, tube diameter up to 16 mm; up to 19 mm at the widened base. The fixed tube portion is long; the free portion may reach 25 mm in length. The tube usually is curved and may form a loop or an irregular spiral. In the posterior portion, ornament is either weak or absent. In the anterior portion usually there is but a single keel. More rarely, two additional, albeit much weaker, longitudinal edges are situated on the upper side, but at a slightly lower level than the main keel. In the anterior tube portion, incremental lines usually are strong, wrinkled, bulging, some of them reaching the size of peristomes. Incremental lines curve anteriorly at the upper side, forming an obtuse spine protruding over the aperture. The cross section is rounded sub-squarish to circular. The tube wall, especially the outer parable layer, is thick, while the base of the tube is cellular, with very short cells.

Remarks – This species was originally introduced as a member of the genus *Mucroserpula* by Jäger (2005). However, the type of that genus is rather small, whereas '*M.*' *felderi* is large and thus may belong to a different genus.

Distribution – Confined to the Meerssen Member.

Genus *Placostegus* Philippi, 1844
***Placostegus aduncus* (Regenhardt, 1961)**
Pl. 4, figs. 5-9.

Description – Small to medium sized. The tube diameter increases slowly to moderately rapidly in the fixed portion, being constant or even slightly decreasing in the free portion. The fixed portion is either straight or curved, often forming an inwardly curved loop or a spiral. Usually there is one keel or a longitudinal row of granules. The free portion is long, straight or only slightly curved, usually erected obliquely or vertically, having three sharp or rounded longitudinal edges and thus a sharp or rounded triangular cross section.

Many transverse ribs follow in short, regular distances from each other. Some specimens instead have transverse striae or transverse ornament may be lacking altogether. Transverse ornament is curved anteriorly at the keel or edges. Thus, there is either one

spine protruding over the aperture in the fixed portion or three spines protruding around the aperture in the free portion.

Remarks – This species was named '*Eoplacostegus* sp.' by Jäger (1987, 1988). Although the material is highly variable, any subdivision into more than one species appears artificial.

Distribution – Vijlen Member(?); Lanaye to Gronsveld members; Schiepersberg Member(?); Emael to Meerssen members. Common in the Meerssen Member.

Genus *Conorca* Regenhardt, 1961
***Conorca trochiformis* (von Hagenow, 1840)**
Pl. 4, figs. 10-13.

Description – Small to medium sized. The tube slowly increases in diameter; following an initial, non-spiral portion, the tube is coiled trochospirally to form an inverse cone, a cylinder, a truncated cone or a barrel. Sinistrally coiled spirals occur more commonly than dextrally coiled ones. An umbilicus is commonly present. The free tube portion is straight and may grow to rather great lengths. Some specimens possess a bulge at the transition from the spiral to the free portion. Four longitudinal edges occur; the two on the upper side may be more rounded than the others on the underside. The cross section of the tube is often quadrangular, but may also be triangular or pentagonal. Incremental lines usually strongly curve anteriorly in the middle of the upper side, and at the left and right margin of the base, causing either one spine to protrude over the aperture in the spiral portion or three spines around the aperture in the free portion. The surface usually is white, but dull.

Remarks – This species is the stratigraphically older one in a phylogenetic lineage leading from *C. trochiformis* to *C. conorca* Regenhardt, 1961. Although the morphology of both species is variable, several trends through time have been documented statistically (see Jäger, 1983). Average *C. trochiformis* spirals are wider and lower, show a wider umbilicus, less often have bulges and are more often dextrally coiled than average spirals of *C. conorca*. The taxonomic 'line of division' between the two species was drawn within the *fastigata* Zone (latest early Maastrichtian). That means that, irrespective of their individual morphology, all specimens found in the Beutenaken Member and in the lower and middle portion of the Vijlen Member should be referred to as *C. trochiformis*, whereas all material from the upper part of the Vijlen Member and from younger members are to be named *C. conorca*. '*Conorca* sp.' of Jäger (1988), and perhaps also '*Eoplacostegus* sp. or *Conorca* sp.' of Jäger (1987), belong to *C. conorca*.

Distribution – *Conorca trochiformis* is known from the Beutenaken Member and is common in the lower and middle part of the Vijlen Member. *Conorca conorca* ranges from the upper part of Vijlen Member into the Lixhe members, and perhaps into the Lanaye Member; rare. The total known range for *Conorca trochiformis* is late late Campanian to late early Maastrichtian (lower *fastigata* Zone); for *C. conorca* it is late early Maastrichtian (middle *fastigata* Zone) to late Maastrichtian (top of *danica/argentea* Zone).

Genus *Pyrgopolon* de Montfort, 1808
Subgenus *Pyrgopolon* (*Pyrgopolon*) de Montfort, 1808

Description – Medium to large in size, the fixed tube portion fragile and rapidly increasing in diameter, commonly not preserved. The base usually shows well-developed cells, leaving a characteristic pattern on the surface of the substrate (see Pl. 5, fig. 1) after most of the tube has broken off. However, tubes without cells occur as well. There is no '*Favosites* structure' in contrast to *P.* (*Septenaria*). Perforate tabulae are present only in extant species, which were formerly referred to *Sclerostyla*, a synonym.

The free tube portion in fossil species either has seven longitudinal edges or keels, or lacks these; transverse wrinkles may occur. Recent species may show a different ornament. In fossil species, the middle layer of the tube wall in the posterior tube portion presumably was aragonitic and, thus, is usually dissolved, so that the cylinder layer can be moved freely inside the outer parable layer. The cylinder layer is thick walled at the posterior end and thin walled at the anterior.

The operculum is completely calcified, presumably aragonitic, and distinctly separated into a cucullus and a calcar. The cucullus is funnel-shaped, bearing radial striation; the calcar is slender, circular to triangular in cross section.

Pyrgopolon (*Pyrgopolon*) *clava vittata* (Regenhardt, 1961)
Pl. 5, figs. 3, 4.

Description – Small to medium sized, the smallest subspecies of the subgenus. The fixed tube portion is unknown, but should have been small. The free tube normally is curved like a horn, more rarely straight. The tube diameter rapidly increases up to 4.5 mm, but the diameter is reduced at the aperture. Seven longitudinal edges may be present only at the beginning of the free tube portion or lack completely. The transverse ornament may consist of wrinkled incremental striation and, sometimes, shallow swellings. The tube wall is thick near the aperture. The operculum is unknown.

Remarks – This subspecies never attains the size of the similar *P.* (*P.*) *clava clava* (Lamarck, 1818), which is known from the Mons Basin (southern Belgium), but is absent from the type Maastrichtian. A few finds of the fixed tube portion of an undescribed *Pyrgopolon* (*Pyrgopolon*) sp. indet. from the Vijlen Member (Pl. 5, figs. 1, 2) are much too large to be accommodated in *P.* (*P.*) *clava vittata*. Moreover, they have distinct transverse ornament. Presumably, these represent ancestors of *P.* (*P.*) *regia regia* (Regenhardt, 1961) (see below).

Distribution – Lower part of the Vijlen Member.

Pyrgopolon (*Pyrgopolon*) *regia regia* (Regenhardt, 1961)
Pl. 5, figs. 5-8.

Description – Medium sized. A fixed tube portion is present, but is rarely found. In the free tube portion seven strong longitudinal edges occur, which remain strong and

distinct up to the aperture, in contrast to other species of *P.* (*Pyrgopolon*). The outer tube layer is massive or slightly porous, the tube wall being moderately thick. The operculum is unknown.

Distribution – Vijlen Member(?); Lixhe 1 to Gronsveld members. The total known range is early Maastrichtian(?); early late Maastrichtian.

***Pyrgopolon* (*Pyrgopolon*) *mosae mosae* de Montfort, 1808**
Pl. 5, figs. 11-16.

Description – Medium sized to large. The fixed tube portion usually is cellular at the base, while the free portion is either straight or slightly curved; strongly curved tubes are rare, in contrast to *P.* (*P.*) *clava*. Most specimens lack any ornament. However, some may have a single longitudinal edge, or a furrow instead, or irregular furrows or edges, and show incremental lines or transverse wrinkles. The tube wall is thin. The cucullus of the operculum occasionally is strongly funnel-shaped, showing many non-denticulate ribs on the basal plate.

Distribution – Vijlen Member(?); Lanaye to Meerssen members; mass occurrences are known from the Nekum and basal Meerssen members. In the Kunrade limestone facies, however, *P.* (*P.*) *m. ciplyana* is the predominant subspecies. The total known range is late Campanian(?) (southern Sweden; in need of revision); early Maastrichtian(?); early late Maastrichtian to Danian (Geulhem Member). Probably missing from the Mons Basin.

***Pyrgopolon* (*Pyrgopolon*) *mosae ciplyana* (de Ryckholt, 1852)**
Pl. 5, figs. 9, 10.

Description – Medium sized to large. The fixed tube portion usually is cellular at the base, the free tube portion commonly being straight or slightly curved, rarely strongly curved. Seven strong keels are present in the posterior part of the free tube portion. Near the aperture, several transverse wrinkles or small ribs stand close to each other. The tube wall is thin. The cucullus of the operculum is low funnel-shaped, showing relatively few denticulate ribs on the basal plate.

Remarks – This subspecies has often been confused with *P.* (*P.*) *m. mosae.* Specimens named '*Sclerostyla* sp.' by Jäger (1987, pl. 2, figs. 14-17 and, perhaps, fig. 13) belong to *P.* (*P.*) *m. ciplyana*. The operculum was named '*Serpula instabilis*' by Wrigley (1952).

Distribution – Kunrade limestone facies at Kunrade and Benzenrade (equivalents of Lanaye to Emael members); these data were inadvertently omitted in Jäger (1998, p. 120). Moreover, this subspecies is known from the Meerssen Member of the main Maastricht 'tuffaceous chalk facies'. The total known range is early Maastrichtian (*obtusa* Zone; Mons Basin) to Danian (Geulhem Member).

Subgenus *Pyrgopolon* (*Hamulus*) Morton, 1834

Description – Medium sized to large. The tube diameter commonly rapidly increases. The fixed tube portion is fragile in many species and, therefore, often not preserved, usually shorter than the free portion. To date, tabulae are known in a single species only. The free tube portion usually is curved like a horn. Usually six, in some species eight, keels or combs occur, in contrast to the usually odd number of longitudinal elements in other subgenera. Therefore, the cross section is hexagonal or octagonal, respectively. The combs enlarge the effective base of the tube which mainly resides in softground habitats.

In some species the tube wall is massive. However, in certain others the whole parable layer is dissolved; in yet other taxa, only the inner parable layer is dissolved. Thus, the cylinder layer can be isolated like in *P.* (*Pyrgopolon*). The operculum is entirely calcified, presumably aragonitic, and distinctly separated into a cucullus and a calcar. The cucullus is funnel-shaped, showing radial and/or concentric ribs on the outer and inner surface, while the calcar is more markedly triangular in cross section than in other subgenera.

Pyrgopolon (*Hamulus*) *sexcarinatus* (Goldfuss, 1841)

Pl. 5, figs. 17, 18.

Description – The fixed tube portion is short and strongly curved, while the free portion is curved like a horn, with six sharp keels or combs. Usually the outer lateral comb is the highest and tends to be frayed out. Of the six sides between the keels, the one on the upper side and the one on the underside are even, whereas the four other sides are concave. There is no transverse ornament. Probably, the whole parable layer was aragonitic originally, because it is either preserved as a hollow cast or silicified. However, the calcitic cylinder layer is preserved. The cucullus of the operculum is placed eccentrically upon the calcar. The cucullus is funnel-shaped to flat, has 30-35 strong radial ribs and seems to consist of one to four discs lying upon each other. The calcar is T-shaped in cross section, and bilobate in ventral and dorsal view.

Distribution – In the Kunrade limestone facies (equivalent of either Schiepersberg or Emael Member). In the main Maastricht 'tuffaceous chalk facies', it occurs in the basal Nekum Member (not too rare at levels of mass occurrence of *P.* (*P.*) *m. mosae*) and in the Meerssen Member.

Subgenus *Pyrgopolon* (*Septenaria*) Regenhardt, 1961

Description – Medium sized to very large. The fixed portion of the tube rapidly increases in diameter, is curved and usually well preserved. In the fixed portion, most species possess a single longitudinal ridge, keel or comb. Some species have more than one ridge or keel, few have none. Perforate tabulae are not too rare. The base is not cellular, but instead the lower half of the fixed tube portion shows '*Favosites* structure', which means that the interior of the tube wall consists of many small, oblique, hollow cylinders subdivided by many minute floors.

The free tube portion usually has seven (in some species five, nine or up to 24) longitudinal edges or keels. The surface of some specimens shows 'honeycomb ornament', that is, the outer tube layer consists of small, hollow, polygonal 'honeycombs', which are directed slightly obliquely towards the aperture. In contrast to *P.* (*Pyrgopolon*), the middle tube layer is not dissolved, so that the cylinder layer cannot be moved freely inside the outer parable layer.

No operculum of *P.* (*Septenaria*) is known from the type Maastrichtian. In other regions, it cannot be determined without doubt whether opercula found there belong to *P.* (*Septenaria*) or not.

Pyrgopolon (*Septenaria*) *macropus* (J. de C. Sowerby, 1829)

Pl. 6, figs. 1, 2.

Description – Medium sized to large. The fixed tube portion is markedly triangular in cross section, with straight side walls and with only a single sharp keel or comb. The free portion of the tube usually has seven longitudinal edges or blunt keels; more rarely pentagonal or nearly circular.

Remarks – In the Vijlen Member, 'old-fashioned' specimens with pentagonal or near-circular cross sections resembling the Santonian *P.* (*S.*) *septenaria* Regenhardt, 1961, are common. However, these are larger than ordinary specimens of that species and are here referred to *P.* (*S.*) *macropus*.

Distribution – Beutenaken to Gronsveld members; Schiepersberg to Nekum members(?); Meerssen Member. Common in the Kunrade limestone facies. The total known range is early Campanian to latest Maastrichtian (probably also Danian; see '*Pyrgopolon* (*Septenaria*) sp.' from the former Ankerpoort-Curfs quarry at Geulhem in Jäger (1993, pl. 97, fig. 4) and '*Pyrgopolon* (*Septenaria*) sp.?' from subunit IVf-7 at the Geulhemmerberg subterranean galleries in Jagt (1996, p. 160)).

Pyrgopolon (*Septenaria*) *voigti* Jäger, 2005

Pl. 6, figs. 3, 4.

Description – Commonly medium sized, occasionally large, up to 6.5 mm in diameter. The fixed tube portion only moderately increases in diameter and is straight to strongly curved, rarely forming a loop. The cross section is either rounded triangular with convex sides, tunnel-shaped or near circular. Mostly three, uncommonly one or five, more rarely seven, or an even number of longitudinal edges or keels. Often the median keel is the strongest; it may even form a tall comb. Rarely it protrudes anteriorly. The lateral longitudinal edges are introduced subsequently, so that the final number of longitudinal elements may be reached only near the end of the fixed tube portion. Most specimens lack transverse ornament, some possess a fine ornament composed of granules which usually are arranged in rows, thereby forming transverse or somewhat oblique wrinkles which may ramify or insert. The free portion of the tube has usually seven, rarely nine, longitudinal edges or keels, which commonly are narrow and low, yet distinct. Rarely, the median keel is a tall comb. 'Honeycomb ornament' is present in some specimens.

Distribution – Meerssen Member. The total known range is latest Maastrichtian. Perhaps it occurs also in the Danian(?) (from boundary layers, probably in unit IVf-7, at the Geulhemmerberg subterranean galleries).

Pyrgopolon (*Septenaria*) *erecta* (Goldfuss, 1831)

Pl. 6, figs. 5-7.

Description – Tube very large, up to 14 mm in diameter. The cross section of the fixed tube portion usually is low triangular, rounded at the top; few specimens have a comb instead. '*Favosites* structure' is present. The cross section of the free portion is circular to rounded subtetragonal. Three or four main longitudinal furrows occur, namely a distinct one at the underside, a medium one each at the left and right side, and, in some specimens, a weak one on the upper side. A few specimens possess a strong comb on the upper side instead, protruding over the aperture. There may be up to 20 additional, but weaker, longitudinal furrows, with many rounded longitudinal edges in between. Sometimes these edges are cut into rows of granules by transverse and oblique furrows. The tube wall is very thick. 'Honeycomb ornament' is either weak or absent.

Distribution – Emael to Nekum members(?); Meerssen Member. Most specimens are from the basal Meerssen Member.

Subfamily Spirorbinae Chamberlin, 1919

Description – Small to very small, with the tube forming a spiral. In the great majority of species the direction of coiling is the same in (nearly) all specimens. The operculum is calcitic.

Genus *Neomicrorbis* Rovereto, 1903

Description – Small, but larger than most other Spirorbinae; the diameter of the spiral may reach more than 5 mm. In contrast to most other spirorbines, sinistral and dextral specimens occur in about equal numbers. The tube is either smooth or ornamented by longitudinal rows of spines or granules, keels, transverse wrinkles or funnel-shaped peristomes. A corkscrew-shaped free portion may be present, but is usually short.

The operculum is calcitic, bilaterally symmetrical, consisting of a more or less massive, concave or convex cucullus and a large, more or less keeled calcar.

Neomicrorbis crenatostriatus crenatostriatus (Münster *in* Goldfuss, 1831)

Pl. 6, fig. 8.

Description – One to over 20 longitudinal rows of spines or granules are present, which are more distinct than the transverse wrinkles, which are either weak or absent altogether. However, one or a few peristomes may occur.

Remarks – Formerly, *crenatostriatus*, *hagenowii* and *subrugosus* were considered to be distinct species. However, specimens showing intermediate ornament are not rare.

Therefore, the three taxa have now been relegated to the status of subspecies of *crenatostriatus*. In many juvenile specimens, subspecific attribution cannot be made because the characteristic ornament is often formed only during later growth stages.

Distribution – Vijlen Member. Juveniles and fragments belonging to *N. crenatostriatus* (but subspecies indeterminate) are found in the Vijlen Member, Lixhe Member(?) and Lanaye Member. The total known range is early Cenomanian to Paleocene.

***Neomicrorbis crenatostriatus hagenowii* Jäger, 1983**

Description – One to 15 longitudinal rows of spines or granules present, but transverse wrinkles are as distinct or even more so.

Distribution – Vijlen Member. This is the rarest subspecies of the three. The total known range is middle Turonian to late Maastrichtian (*argentea/junior* Zone).

***Neomicrorbis crenatostriatus subrugosus* (Münster *in* Goldfuss, 1831)**
Pl. 6, fig. 9.

Description – No longitudinal rows of spines or granules. The only longitudinal elements of ornament that may be present are a lateral furrow and a weak, rounded edge. Transverse wrinkles or peristomes may be present.

Distribution – Beutenaken to Vijlen members. In the type Maastrichtian, *subrugosus* is the commonest subspecies of *N. crenatostriatus*. The total known range is early Cenomanian to latest Maastrichtian.

Genus *Bipygmaeus* Regenhardt, 1961
***Bipygmaeus pygmaeus* (von Hagenow, 1840)**
Pl. 6, figs. 10, 11.

Description – Very small, usually the diameter of the spiral is only 1-2 mm. The coiling is sinistral; in spirorbines this means that the spiral is coiled clockwise when viewed from above. The tube first forms a more or less low spiral, upon which a compact, conical spiral with steep, plain sides is constructed. Finally, a free, occasionally long, 'corkscrew' elevates vertically or obliquely, its length being controlled by ecological factors. The operculum was discovered by Lommerzheim (1979, p. 172), but has not yet been described in detail.

Distribution – Vijlen Member(?); Lanaye to Gronsveld members; Schiepersberg Member(?); Emael to Meerssen members. Also known from the Zeven Wegen Member (late Campanian) and Geulhem Member (early-middle Danian). The stratigraphic data given in Jäger (1998, p. 118) for this species are erroneous, due to an oversight in printing. The total known range is earliest Cenomanian to middle Danian.

Genus *Pileolaria* Claparède, 1868
***Pileolaria*? aff. *kronsmoorensis* (Jäger, 1983)**
Pl. 6, fig. 12.

Description – Very small, diameter of spiral *c*. 1.5 mm, sinistral. Three longitudinal rows of granules occur, which are fused to form three keels. The operculum has not been found as of yet, but should have a brood chamber as in other species of *Pileolaria*.

Distribution – Kunrade limestone facies (equivalent of Valkenburg Member) and Meerssen Member; rare. The total known range is of *Pileolaria*? *kronsmoorensis sensu stricto* is middle Santonian and early Maastrichtian (*obtusa* Zone) and of *P.*? aff. *kronsmoorensis*, late Maastrichtian.

Genus *Janua* de Saint-Joseph, 1894
Subgenus *Janua* (*Dexiospira*) Caullery & Mesnil, 1897
***Janua* (*Dexiospira*) *palaeoforaminosa* (Jäger, 2005)**
Pl. 6, figs. 13, 14.

Description – Very small, diameter of spiral up to 2.2 mm; dextral, which means that the spiral is coiled anti-clockwise when viewed from above. Three keels occur; these may be smooth, undulate or denticulate. Rarely, rows of granules are present instead of keels. Many specimens larger than 1.5 mm have three longitudinal rows of small pores; two rows between the keels, and one between the outer keel and the base. These outer pores are in contact with the cells at the base which are present only in specimens which have pores. Peristomes may be present. The operculum has a brood chamber.

Remarks – This species was named 'Spirorbidae, coiled dextral' and '*Neodexiospira* n. sp.' by Jäger (1988), and is perhaps identical with 'Spirorbidae indet.' of Jäger (1987).

Distribution – Kunrade limestone facies (equivalents of Lanaye to Gronsveld members) and Emael to Meerssen members in the main Maastricht 'tuffaceous chalk facies'. Relatively common in the Meerssen Member. The total known range is early Maastrichtian (*obtusa* Zone)(?); late Maastrichtian.

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Plate 1

Figs. 1, 3. *Glomerula serpentina* (Goldfuss, 1831).
Fig. 1. GPI HH (Voigt) 2618, tubes fixed to a hardground, probably Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 4.1.
Fig. 3. GPI HH (Voigt) 4402, cross section showing trilobate narrowing of the lumen, Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 15.1.

Fig. 2. *Glomerula lombricus* (Defrance, 1827), NHMM JJ 3195, knot, Vijlen Member, interval 6, CPL SA-Haccourt quarry. × 5.0.

Fig. 4. *Filograna filosa* (Dujardin, 1837), NHMM 2001 097, bundle, Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht, in (a) cross section and (b) cross- and longitudinal section. × 8.7.

Figs. 5, 6. *Nogrobs* (*Tetraditrupa*) *canteriata* (von Hagenow, 1840), lower Vijlen Member, Nieuwe Weg Zeven Wegen (Vijlenerbosch).
Fig. 5. NHMM 2001 098; tube fragment, (a) upper side showing chevron-shaped pattern at the edges, × 6.6; (b) aperture, × 8.7.
Fig. 6. NHMM GK 901-902; tube fragment, lower side. × 5.2.

Fig. 7. *Nogrobs* (*Tetraditrupa*) *superiora* (Jäger, 1983), NHMM GK 851, tube fragment, lateral view, lower Vijlen Member, Nieuwe Weg Zeven Wegen (Vijlenerbosch). × 4.2.

Figs. 8-10. *Vermiliopsis fluctuata* (J. de C. Sowerby, 1829).
Fig. 8. NHMM JJ 2934; curved tube fragment, lateral view showing aperture, Meerssen Member, former Blom quarry, Berg en Terblijt. × 7.5.
Fig. 9. GPI HH (Voigt) 2619; upper side of tube, Meerssen Member, Albert Canal near Vroenhoven (Riemst, Belgium). × 7.5.
Fig. 10. GPI HH (Voigt) 4408; aperture, Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 15.1.

Fig. 11. *Metavermilia* (*Vepreculina*) *tuberculifera* (Brünnich Nielsen, 1931), NHMM GK 1191, tube fragment, upper side, probably Vijlen Member, Kosberg sample 771. × 8.7.

Fig. 12. *Metavermilia* (*Vepreculina*) *schulzi* Jäger, 2005, NHMM 2001 100, tube fragment, upper side, Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 8.7.

Figs. 13, 14. *Filogranula cincta* (Goldfuss, 1831).
Fig. 13. NHMM JJ 698; two fixed tubes with annular peristomes and with non-undulose keels, upper side, Lanaye Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 5.0.
Fig. 14. NHMM GK 901-902; fragment of free tube portion with undulate keels, upper side, lower Vijlen Member, Nieuwe Weg Zeven Wegen (Vijlenerbosch). × 8.7.

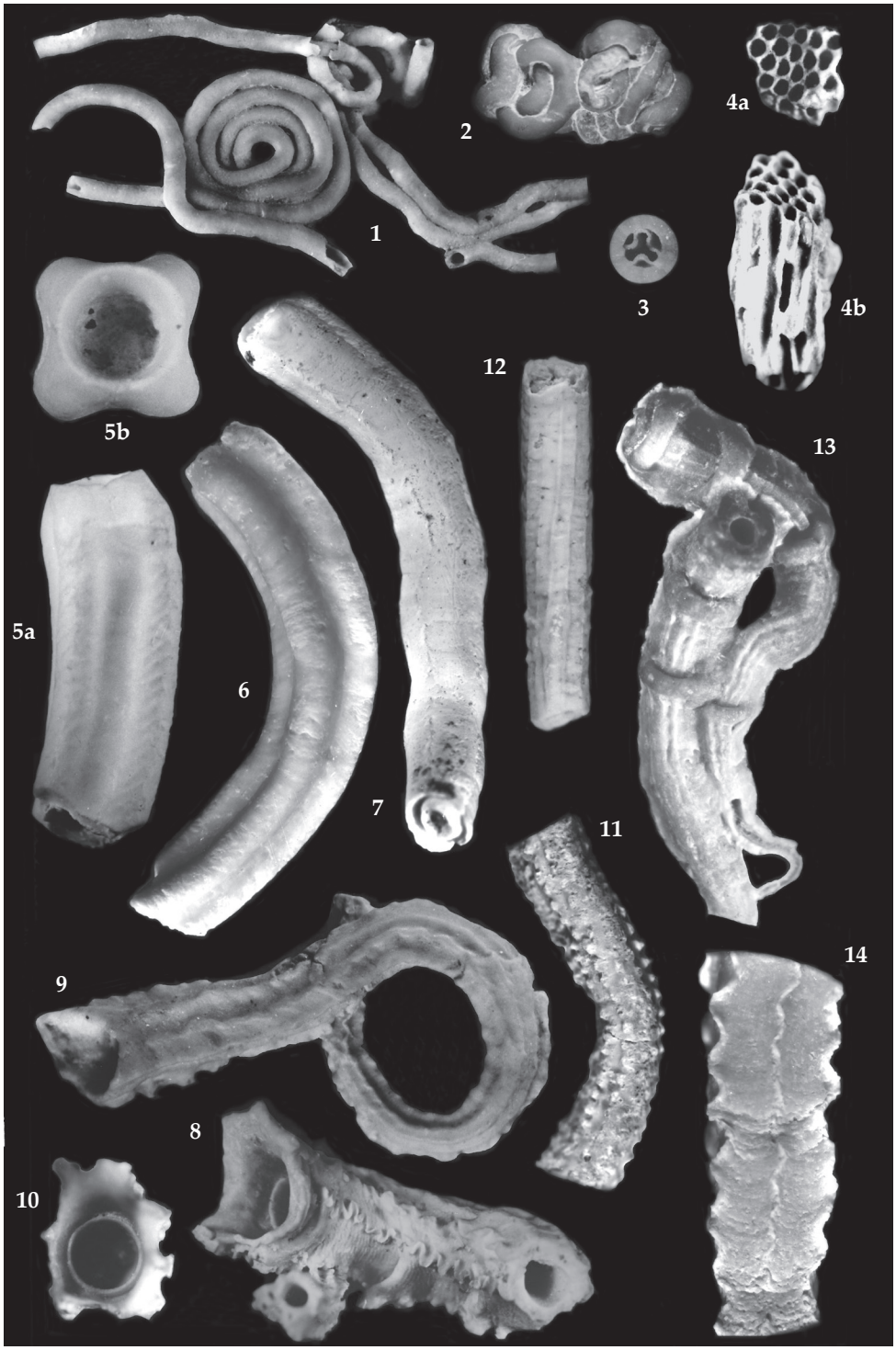
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Plate 2

Figs. 1-3. *Neovermilia ampullacea* (J. de C. Sowerby, 1829).
Fig. 1. GPI HH (Voigt) 741; spiral tube with peristomes, upper side, infested by the symbiont *Protulophila gestroi* Rovereto, 1901; late Maastrichtian (unknown level within the Maastricht Formation), Biebosch near Valkenburg aan de Geul. × 2.3.
Fig. 2. NHMM JJ 3622; fragments of two fixed tubes, upper sides, on the right, where broken, showing the cellular base, Lixhe 1 Member, CPL SA quarry, Haccourt. × 1.3.
Fig. 3. NHMM JJ 3047; fragments of two fixed tubes, the upper one with an undulate comb, lateral view, Emael Member, CBR-Romontbos quarry, Eben Emael (Liège). × 4.1.

Fig. 4. *Serpula*? *trilineata* Roemer, 1841, NHMM 2011 054, tube fragment, Emael Member, borehole Thermae 2000 near Valkenburg aan de Geul. (a) upper side; (b) lateral view; (c) cross section. × 13.1.

Figs. 5, 6. *Neovermilia*? *hemmoorensis* (Jäger, 1983), Lanaye Member, ENCI-Heidelberg Cement Group quarry, Maastricht. Both × 10.4.
Fig. 5. NHMM JJ 3046b; tube fragment, (a) upper side; (b) lateral view.
Fig. 6. NHMM JJ 3045; tube fragment with peristome. (a) upper side; (b) cross section.

Figs. 7, 8. *Serpula* (*Cementula*) *sphaerica* Brünnich Nielsen, 1931.
Fig. 7. NHMM JJ 2442a; spiral, upper side, Meerssen Member, Albert Canal near Vroenhoven (Riemst, Belgium). × 8.1.
Fig. 8. GPI HH (Voigt & Weitschat) 2620; underside of a tube which originally was fixed to a flat substrate, Meerssen Member, former Ankerpoort-Curfs quarry, Geulhem. × 5.6.

Figs. 9-11. *Spiraserpula scrupea* Regenhardt, 1961.
Fig. 9. GPI HH 724; tube upon which a small tube of *Josephella subanulata* Regenhardt, 1961, is fixed. Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht. (a) upper side, × 5.2; (b) cross section showing internal tube structures, × 15.1.
Fig. 10. GPI HH (Voigt) 4410; tube showing alae and adnate cheilostome bryozoans, probably Meerssen Member, former Ankerpoort-Curfs Quarry, Geulhem. × 5.2.
Fig. 11. GPI HH (Voigt) 4411; a long, straight, intermediate tube portion, upper side, probably Meerssen Member, former Ankerpoort-Curfs Quarry, Geulhem. × 6.4.

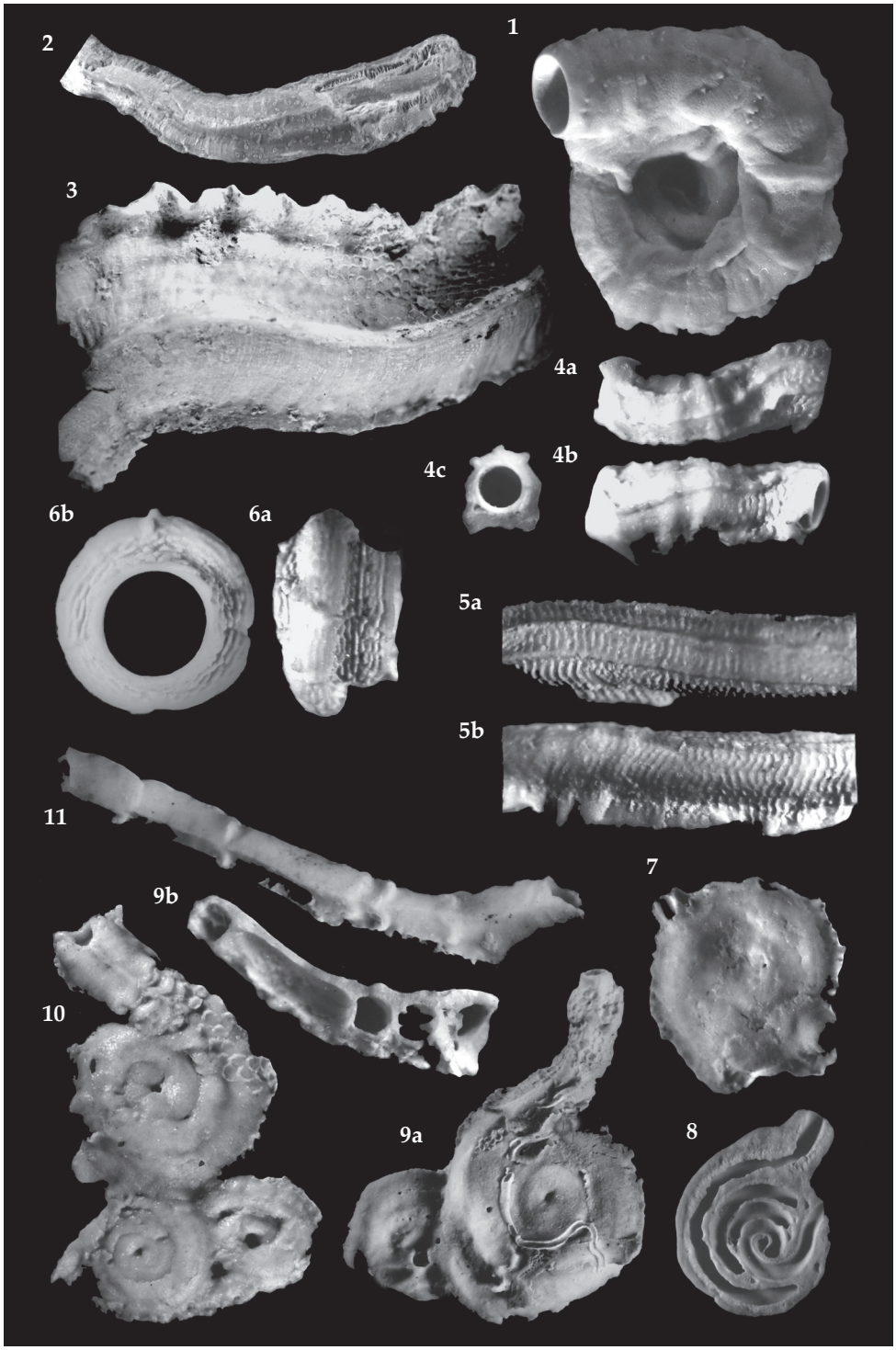
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Plate 3

Fig. 1. *Protectoconorca senonensis* Jäger, 1983, GPI HH (Wiesemann & Voigt) 4414, spiral tube, Kunrade limestone facies (equivalent of Gronsveld, Schiepersberg or Emael Member), Kunrade. (a) upper side; (b) lateral view showing aperture. Both × 6.4.

Figs. 2, 3. *Laqueoserpula schmidwallisi* Jäger, 2005.
Fig. 2. GPI HH (Voigt) 4412; two tubes, one of them infested by the symbiont *Protulophila gestroi* Rovereto, 1901, lateral view, Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 4.9.
Fig. 3. GPI HH (Voigt & Lafrenz) 4413; twisted fragment of free tube portion, infested by the symbiont *Protulophila gestroi* Rovereto, 1901, lateral view showing aperture, probably Meerssen Member, Albert Canal, Neerkanne. × 7.1.

Fig. 4. *Serpula*? *klaumanni* Lommerzheim, 1979, GPI HH (Voigt) 4416, tube fragment, upper side, probably Meerssen Member, former Van der Zwaan quarry, St. Pietersberg, south of Maastricht. × 4.5.

Figs. 5, 6. *Dorsoserpula wegneri wegneri* (Jäger, 1983), M.J. van Birgelen Collection (Heerlen, unregistered), spiral tubes with side tube, lateral views, Benzenrade Member (Vaals Formation), De Dael near Benzenrade. Both × 6.4.

Fig. 7a-c. *Dorsoserpula* (*Pegmaticula*) *turpificata* (Regenhardt, 1961), NHMM MK 1183, gall-shaped lump, broken and corroded, basal Meerssen Member, Ankerpoort-'t Rooth quarry, Bemelen. × 1.5.

Figs 8-11. *Dorsoserpula wegneri maastrichtensis* Jäger, 2005.
Fig. 8. NHMM JJ 3046a; fixed and free tube portions, Lanaye Member, ENCI-Heidelberg Cement Group quarry, Maastricht. (a) upper side showing keel; (b) underside showing cellular base. Both × 7.7.
Fig. 9. NHMM 2011 055; free tube portion, cross section showing keel and side tube, Valkenburg, Gronsveld or Schiepersberg members, borehole Thermae 2000, Valkenburg aan de Geul. × 15.3.
Fig. 10. GPI HH (Voigt) 4418; tube fragment with keel, upper side, Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 15.1.
Fig. 11. GPI HH (Voigt) 4419; tube fragment showing cellular base, view oblique to underside, Valkenburg Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 15.1.

Figs. 12, 13. *Pentaditrupa subtorquata* (Münster *in* Goldfuss, 1831).
Fig. 12. NHMM JJ 2998; near-complete tube, strongly curved, circular in cross section, Vijlen Member, interval 6, CPL SA, Haccourt. (a) lateral view, × 4.1; (b) aperture, × 6.4.
Fig. 13. NHMM GK 901-902; near-straight tube, pentagonal in cross section, lower Vijlen Member, Nieuwe Weg Zeven Wegen (Vijlenerbosch). (a) lateral view, × 2.2; (b) aperture, × 6.4.


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Plate 4

Figs. 1-4. '*Mucroserpula*' *felderi* Jäger, 2005. All from Ankerpoort-'t Rooth quarry, Bemelen, except Fig. 2.
Fig. 1. NHMM 004668; two or three tubes fixed to each other, Meerssen Member. (a, b) lateral views. Both × 1.6.
Fig. 2. NHMM 005994/2; fixed tube portion, together with a tube of *Dorsoserpula* (*Pegmaticula*) *turpificata* Regenhardt, 1961, oblique view showing aperture, no data, probably from the type area of the Maastrichtian. × 1.3.
Fig. 3. NHMM MK 136; free tube portion, probably Meerssen Member. (a) upper side; (b) aperture. Both × 3.2.
Fig. 4. NHMM MK 2093; fixed and free tube portions lacking ornament, oblique lateral view, Meerssen Member. × 2.0.

Figs. 5-9. *Placostegus aduncus* (Regenhardt, 1961). Figs. 6-8 from ENCI-Heidelberg Cement Group quarry, Maastricht.
Fig. 5. NHMM JJ 2935; spiral-shaped fixed tube portion with short free tube portion, oblique lateral view, Meerssen Member, former Blom quarry, Berg en Terblijt. × 6.5.
Fig. 6. GPI HH (Voigt) 4425; loop-shaped fixed tube portion with straight free tube portion, aperture with three spines, probably Meerssen Member. (a) lateral view, × 4.5; (b) aperture, × 13.1.
Fig. 7. GPI HH (Voigt) 4424; aperture of a fixed tube with one spine, Meerssen Member. × 13.1.
Fig. 8. GPI HH (Voigt) 4420; tube only locally fixed to a cheilostome bryozoan by toe-like expansions, Meerssen Member. (a) upper side; (a) lateral view. Both × 10.1.
Fig. 9. GPI HH (Voigt) 4422; tube fixed to a cheilostome bryozoan, lateral view, Meerssen Member, Albert Canal, Kanne (Belgium). × 9.0.

Figs. 10-13. *Conorca trochiformis* (von Hagenow, 1840). Figs. 10, 11 and 13, Vijlen Member, Aachen.
Fig. 10. NHMM GK 1975; barrel-shaped spiral, morphologically close to *C. conorca* Regenhardt, 1961, oblique lateral view. × 7.5.
Fig. 11. NHMM GK 1975; spiral with short straight free tube portion, upper side. × 7.5.
Fig. 12. NHMM 2011 056; wide, characteristic spiral, oblique lateral view, lower Vijlen Member, Nieuwe Weg Zeven Wegen (Vijlenerbosch). × 7.5.
Fig. 13. GPI HH (Voigt) 4409; spiral, morphologically resembling *C. conorca* Regenhardt, 1961, lateral view. × 7.5.

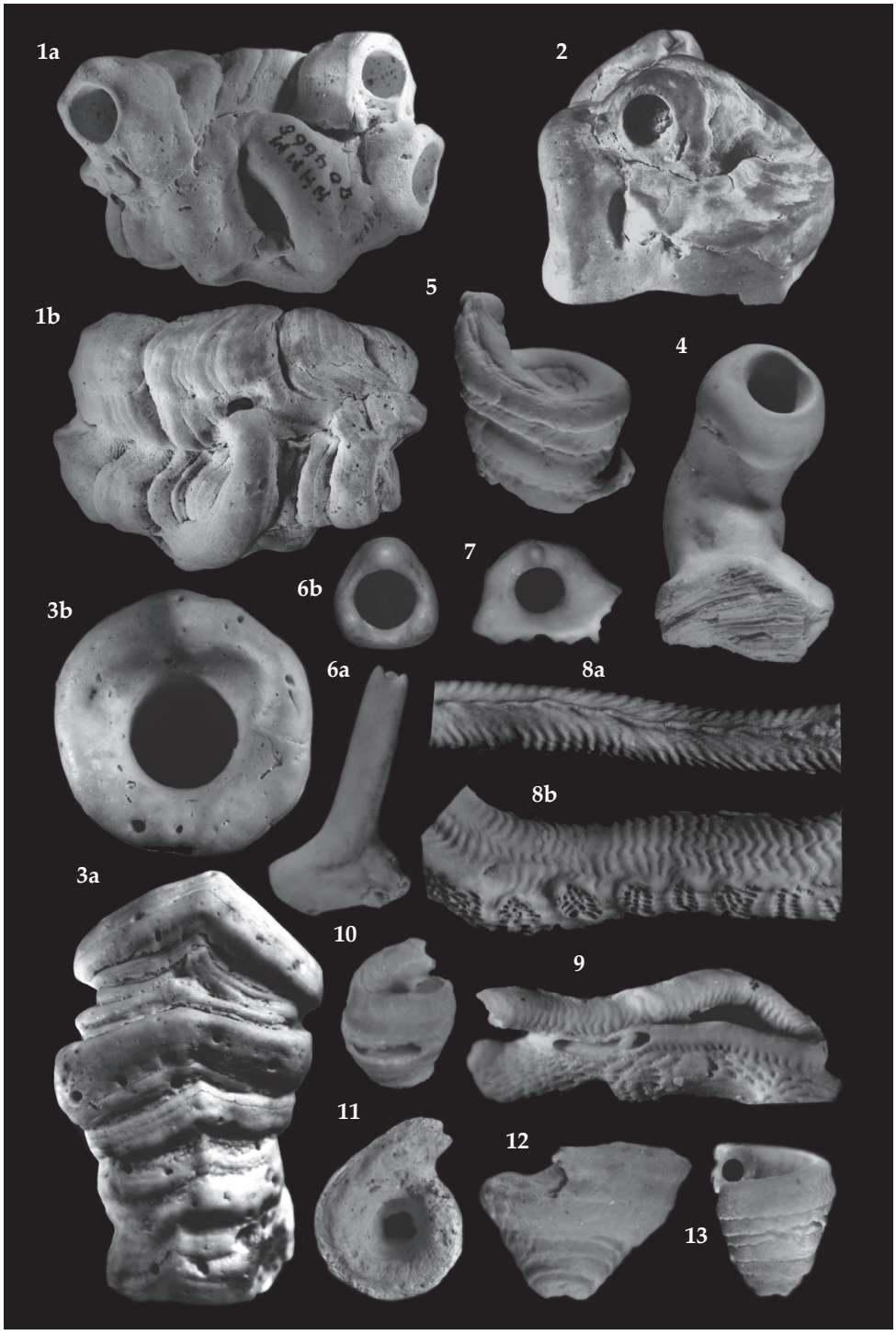
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Plate 5

Figs. 1, 2. *Pyrgopolon* (*Pyrgopolon*) sp. indet., Vijlen Member, interval 6, CPL SA quarry, Haccourt.
Fig. 1. NHMM JJ 2287; base of a broken fixed tube portion (formerly named '*basisculpta*') showing cells and, in the posterior portion, remains of the inner tube layer, top view. × 3.5.
Fig. 2. NHMM JJ 3092; fixed tube portion, posterior portion broken showing inner tube layer, view obliquely from above. × 2.4.

Figs. 3, 4. *Pyrgopolon* (*Pyrgopolon*) *clava vittata* (Regenhardt, 1961), lower Vijlen Member, Nieuwe Weg Zeven Wegen (Vijlenerbosch).
Fig. 3. NHMM GK 688; tube, broken at the posterior end showing inner tube layer. (a) lateral view, × 4.2; (b) aperture, × 5.0.
Fig. 4. NHMM 2001 102; tube showing heptagonal cross section at the posterior end, lateral view. × 5.0.

Figs. 5-8. *Pyrgopolon* (*Pyrgopolon*) *regia regia* (Regenhardt, 1961).
Fig. 5. NHMM JJ 882b; free tube portion, Lanaye Member, CBR-Lixhe quarry. (a) lateral view, bryozoans in the centre and on the left-hand side; (b) aperture. Both × 4.5.
Fig. 6. NHMM 2001 103; small tube fragment showing strong transverse ornament partially covered by a thin outermost layer, Lanaye Member, Lanaye-Vogelreservaat. (a) view from outside; (b) view from inside. Both × 9.0.
Fig. 7. GPI HH (Voigt) 4430; small tube fragment, transverse ornament present only between the keels, Valkenburg Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 4.5.
Fig. 8. GPI HH (Voigt) 4431; small tube fragment lacking transverse ornament, Valkenburg Member, ENCI-Heidelberg Cement Group quarry, Maastricht. × 4.5.

Figs. 9, 10. *Pyrgopolon* (*Pyrgopolon*) *mosae ciplyana* (de Ryckholt, 1852), M.J. van Birgelen Collection (Heerlen, unregistered), Rijksweg 76, Benzenrade, Kunrade limestone facies (equivalent of Gronsveld Member).
Fig. 9. Two silicified tube fragments. (a) upper side; (b) lateral view; (c) aperture of the upper tube. All × 4.5.
Fig. 10. Operculum. (a) lateral view; (b) frontal view. Both × 6.1.

Figs. 11-16. *Pyrgopolon* (*Pyrgopolon*) *mosae mosae* de Montfort, 1808, Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht.
Fig. 11. GPI HH (Voigt) 4426; fixed and free tube portions, underside. × 3.5.
Fig. 12. GPI HH (Voigt) 4427; free tube portion, partially broken to show the inner tube layer, lateral view. × 3.5.
Fig. 13. GPI HH (Voigt) 4428; isolated inner tube layer, lateral view. × 3.5.
Fig. 14. GPI HH (Voigt) 4429; aperture of free tube portion. × 3.5.
Fig. 15. NHMM 2011 057; negative cast of the cucullus of the operculum on the underside of a bryozoan which used the operculum as a substrate. × 10.1.
Fig. 16. NHMM 2011 058; negative cast of the cucullus of the operculum in marly limestone. × 10.1.

Figs. 17, 18. *Pyrgopolon* (*Hamulus*) *sexcarinatus* (Goldfuss, 1841), NHMM 003256 [Boetzkes Collection], probably from the type area of the Maastrichtian.
Fig. 17. Negative cast of free tube portion with preserved inner tube layer, lateral view. × 3.5.
Fig. 18. Negative cast of free tube portion, cross section. × 7.1.


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Plate 6

Figs. 1, 2. *Pyrgopolon* (*Septenaria*) *macropus* (J. de C. Sowerby, 1829).
Fig. 1. GPI HH (Voigt) 2621; anterior fixed tube portion and short free tube portion, Kunrade limestone facies (equivalent of Lanaye, Valkenburg or Gronsveld members), Rijksweg 76, Benzenrade. (a) lateral view; (b) cross section through the fixed tube portion; (c) aperture. All × 6.0.
Fig. 2. NHMM 2011 059; anterior portion of fixed tube portion and long free tube portion, lateral view, Meerssen Member, former Blom quarry, Berg en Terblijt. × 4.5.

Figs. 3, 4. *Pyrgopolon* (*Septenaria*) *voigti* Jäger, 2005.
Fig. 3. GPI HH (Voigt) 4440; anterior part of fixed tube portion and free tube portion, Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht. (a) lateral view, × 4.5; (b) aperture, × 6.6.
Fig. 4. GPI HH (Voigt) 4441; loop-shaped fixed tube portion, upper side, Meerssen Member, Albert Canal, Vroenhoven (Riemst, Belgium). × 6.5.

Figs. 5-7. *Pyrgopolon* (*Septenaria*) *erecta* (Goldfuss, 1831).
Fig. 5. NHMM JJ 3053; free tube portion with strong median keel and eight weaker longitudinal edges, Meerssen Member, Albert Canal, Kanne (Belgium). (a) upper side, × 3.7; (b) aperture, × 4.2.
Fig. 6. NHMM MK 791; free tube portion showing numerous longitudinal edges, Meerssen Member, former Ankerpoort-Curfs quarry, Geulhem. (a) lateral view; (b) aperture. Both × 2.0.
Fig. 7. NHMM MK 1147; anterior part of the fixed tube portion and long free tube portion, oblique lateral view, Meerssen Member, Ankerpoort-'t Rooth quarry, Bemelen. × 1.5.

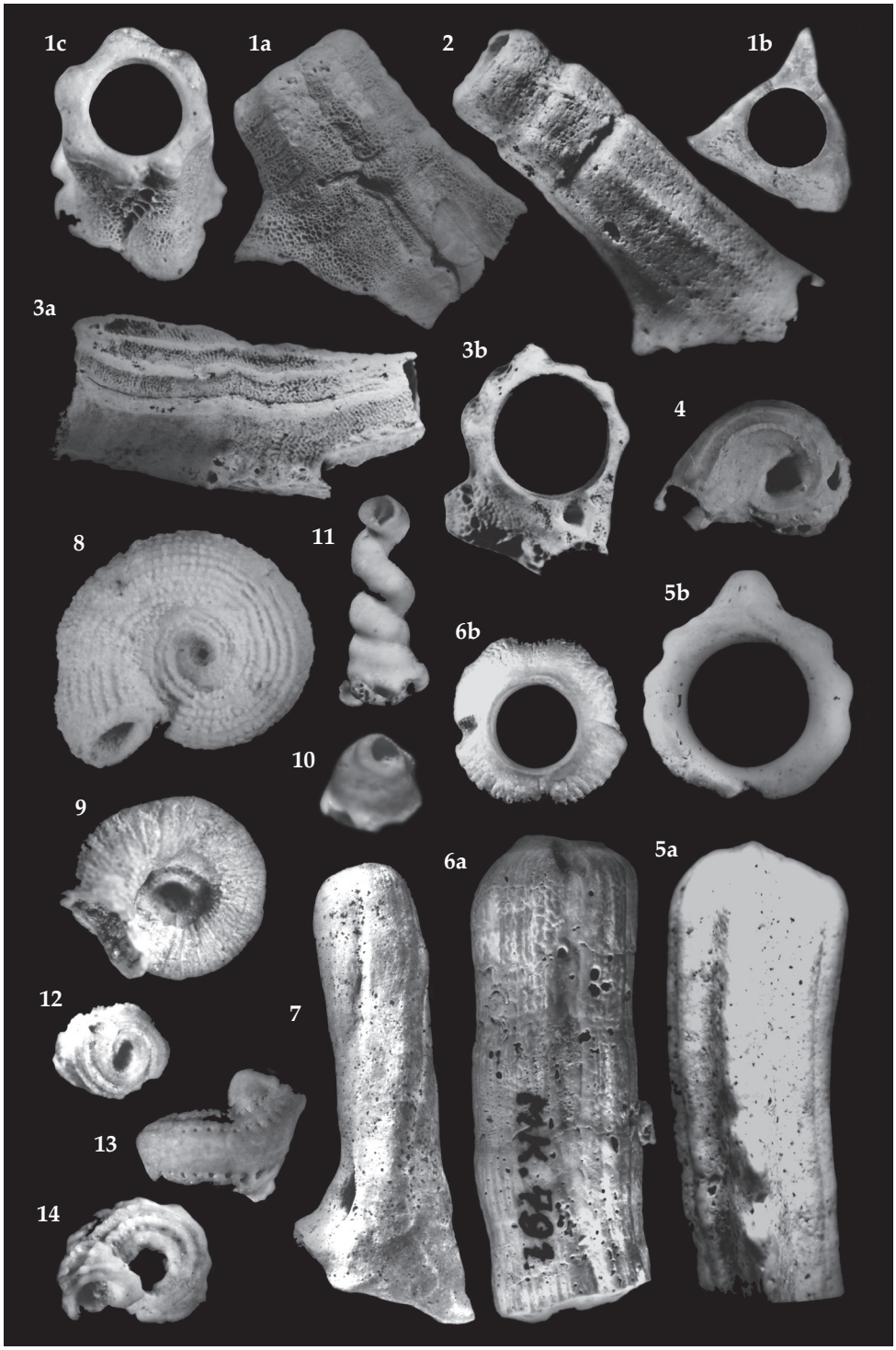
Fig. 8. *Neomicrorbis crenatostriatus crenatostriatus* (Münster *in* Goldfuss, 1831), NHMM 2011 060, spiral, upper side, lower Vijlen Member, Nieuwe Weg Zeven Wegen (Vijlenerbosch). × 7.5.

Fig. 9. *Neomicrorbis crenatostriatus subrugosus* (Münster *in* Goldfuss, 1831), NHMM GK 1975, spiral, upper side, middleVijlen Member, Aachen. × 7.5.

Figs. 10, 11. *Bipygmaeus pygmaeus* (von Hagenow, 1840), Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht.
Fig. 10. GPI HH (Voigt) 4432; cone-shaped spiral of juvenile specimen, oblique lateral view. × 13.1.
Fig. 11. GPI HH (Voigt) 4433; adult specimen with long corkscrew-shaped free tube portion, lateral view. × 13.1.

Fig. 12. *Pileolaria*? aff. *kronsmoorensis* (Jäger, 1983), NHMM 2001 105, spiral, upper side, Kunrade limestone facies (equivalent of Valkenburg Member), Rijksweg 76, Benzenrade. × 13.1.

Figs. 13, 14. *Janua* (*Dexiospira*) *palaeoforaminosa* (Jäger, 2005), Meerssen Member, ENCI-Heidelberg Cement Group quarry, Maastricht.
Fig. 13. GPI HH (Voigt) 4438; spiral showing ornament, rows of pores, and a short free tube portion, lateral view. × 13.1.
Fig. 14. GPI HH (Voigt) 4437; spiral showing ornament, rows of pores and peristomes, upper side. × 13.1.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