

# DANIAN SERPULIDAE AND SPIRORBIDAE FROM NE BELGIUM AND SE NETHERLANDS: K/T BOUNDARY EXTINCTION, SURVIVAL, AND ORIGINATION PATTERNS

MANFRED JÄGER  
 Rohrbach Zement  
 Dotternhausen, Germany

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Twenty-two serpulid and spirorbid species and subspecies from the early Palaeocene (Danian) Geulhem Member (Houthem Formation) as exposed in the type area of the Maastrichtian Stage are illustrated, discussed in detail and assigned to the following genera: *Cycloserpula*, *Serpula*?, *Cementula*, *Rotularia*, *Ditrupea*, *Metavermilia*?, *Pyrgopolon*, *Placostegus*, *Neomicrorbis*, *Biphygmaeus*, *Pileolaria*? and *Neodexiospira*?. Three new subspecies are erected, viz. *Neomicrorbis parietalis jagti*, *Rotularia (R.) tobar gracilis* and *R. (R.) tobar vroenhovens*, while additional new species are of necessity described in open nomenclature as they are poorly known. Within the Geulhem Member there are but moderate changes in the serpulid/spirorbid faunas, which result mainly from differences between hard and soft substrates. Of twenty-two (sub)species seven have previously been recorded from the classic Danian of Denmark, which corroborates the correlation of the Geulhem Member with the type Danian, while two show slight differences at the subspecies level. Although data are at present insufficient to determine precisely the position of the Geulhem Member within the type Danian succession, faunal relationships suggest a middle and late Danian rather than an early Danian age for this member. A comparison of Danian serpulid/spirorbid faunas with Maastrichtian ones from the Maastricht area as well as from other parts of the world shows that the former in fact represent a slightly impoverished fauna of Maastrichtian type. Thirteen genera and subgenera became extinct at or near the K/T boundary: these were either shallow and warm water forms which for fixation needed a large substrate, or genera and subgenera comprising only few species. Most (sub)genera crossed the K/T boundary, the majority (seventeen to twenty-four) with different species below and above the boundary, some (eight) with identical species. Comparatively few (seven) genera and subgenera originated during the Danian/Palaeocene. Generally, the extinction, survival and origination patterns are similar to those described for other benthic suspension/detritus feeders, on which the K/T boundary event had only a limited influence.

Key words — Serpulidae, Spirorbidae, Maastrichtian, Danian, K/T boundary, NE Belgium, SE Netherlands, new taxa.

Dr M. Jäger, Rohrbach Zement, D(W)-7466 Dotternhausen, Germany.

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## INTRODUCTION

*Localities* — Meijer (1959) described four sections exposing early Palaeocene (Danian) strata in the type area of the Maastrichtian Stage, while Jagt &

Collins (1988, fig. 1) added a few others. The two most important localities in the environs of Maastricht are the former Curfs quarry at Geulhem (now Ankersmit Holding BV) and the temporary sections along the Albert Canal near Vroenhoven-Riemst between the Vroenhoven and Veldwezelt bridges. The section at the Ankersmit quarry was designated stratotype of the Geulhem Member (Houthem Formation) by Felder (1975); this will presumably remain well exposed through future quarrying. However, only eight metres of Danian strata are exposed there, this in contrast to c 12 metres in the Albert Canal sections. Van der Ham (1988) and van der Ham *et al.* (1987) discussed the implications of this difference in thickness with ref-

erence to the highly distinctive echinoid faunas recently collected from the uppermost part of the Geulhem Member along the Albert Canal. During 1985 and 1986 there were ample opportunities for extensive collecting, but, unfortunately, the various small outcrops could not be combined to a standard section. Most, if not all, outcrops are no longer accessible.

Most samples studied herein come from the Albert Canal sections, *e.g.* those of Meijer (1959), now incorporated into the collections of the Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, in addition to samples and specimens collected by E. Voigt, J.W.M. Jagt and M. Jäger. Only few of the samples studied were collected from the Geulhem section by M. Meijer and E. Voigt.

*Stratigraphy* — Meijer (1959) subdivided the sections exposed at Geulhem and along the Albert Canal into two units, a lower unit comprising more coarsely-grained, glauconitic biocalcarene with spines of the echinoid *Tylocidaris hardouini* (Desor, 1855) and few specimens of the inarticulate brachiopod *Danocrania geulhemensis* (Krøytzer & Meijer, 1958), and an upper unit consisting of less coarse-grained sediment with many specimens of the craniid brachiopod and few spines of the echinoid *T. bruennichi* Ravn, 1928. The reader is referred to Jagt & Collins (1988) and Jagt & Janssen (1988) for a more detailed discussion.

*Correlation with the type Danian* — *Tylocidaris bruennichi* is an important key index fossil for the middle Danian in Denmark; as mentioned above this species occurs in the upper unit of the Geulhem Member. A precise correlation of this member with the type Danian succession is currently impossible (see discussion in Jagt & Collins, 1988).

*Synonymies* — The taxa, *Cycloserpula lombricus*, *Pyrgopolon (Pyrgopolon) mosae mosae*, *P. (P.) m. ciphlyana* and *Bipygmaeus pygmaeus* also occur and are commoner in the underlying late Cretaceous strata. These species and subspecies will be described in detail (Jäger, in prep.) in the *Illustrated Catalogue of late Cretaceous fossils from Limburg (The Netherlands) and adjacent areas* (J.W.M. Jagt, editor). To avoid repetition, synonymies are here kept to a minimum, and reference is made to contributions now in press and in preparation.

*Frequency* — Below is tabulated the frequency of the various species in the two sections studied. Differences between the Geulhem and Albert Canal sections

result from the fact that more samples from the latter locality were studied.

Number of specimens	Albert Canal	Geulhem
> 200	extremely frequent	extremely frequent
101-200	very frequent	extremely frequent
51-100	frequent	very frequent
21-50	common	frequent
11-20	not rare	common
6-10	rare	not rare
3-5	very rare	rare
2	extremely rare	very rare
1	extremely rare	extremely rare

#### SYSTEMATIC DESCRIPTIONS

- Family Serpulidae Rafinesque, 1815  
 Subfamily Filograninae Rioja, 1923  
 Genus *Cycloserpula* Parsch, 1956 (= *Glomerula* Regenhardt, 1961 *sensu* Brünnich Nielsen, 1931; *Omasaria* Regenhardt, 1961)

*Type species* — *Serpula flaccida* Goldfuss, 1831.

*Remarks* — A more detailed study (in comparison with Jäger, 1983) of Jurassic and early Cretaceous serpulids, has shown beyond doubt that the late Bajocian (Dogger) species, *flaccida* Goldfuss, 1831 is congeneric, and very probably even conspecific with, *gordialis* von Schlotheim, 1820. Parsch (1956) designated *flaccida* type species of *Serpula (Cycloserpula)*, while *gordialis* was designated type species of *Glomerula* by Regenhardt (1961). Brünnich Nielsen (1931) had previously suggested the name *Glomerula* but had failed to designate a type species, which is why Regenhardt's designation is valid. Consequently, *Glomerula* is a junior synonym of *Cycloserpula*. In spite of the fact that *Glomerula* was well defined by Brünnich Nielsen, and that the combination with the specific name renders a clear picture of the characteristic shape of the tube, *Cycloserpula* was used as an artificial omnium gatherum for all kinds of circular tubes lacking distinct longitudinal sculpture.

*Diagnosis* — Tube solitary, or a number of intertwined tubes forming clusters. In clusters, tubes normally not parallel to each other; only occasionally may bundles be more or less parallel.

Tube very long, very slowly increasing in diameter, curved strongly, with anterior tube parts mostly

growing thigmotaxically along posterior parts, forming two-dimensional meanders, two- or three-dimensional irregular spirals or, highly characteristically, three-dimensional chaotic knots. Very often the substrate is a foreign body only in the posterior tube part, whereas in the anterior part the older tube parts are used as substrate. At the start of tube growth and between the strongly curved tube parts there may be straight or only slightly curved segments, which may or may not become erect above the substrate.

Breakage of tube during life frequently occurs: a new tube part then grows from the cavity of the irregularly broken tube end, the new tube at first having a slightly (rarely strongly) lesser diameter and often being more strongly curved than the old tube.

There is no regular ornament on the tube exterior, except for lines of former breakage, weak growth lines in some specimens, and, in a few Maastrichtian and Danian specimens, peculiar, occasionally perforate, rucksack-like protuberances. Tube wall consisting of cylinder layer only, parable layer absent. The base of attached tube parts is thus not broadened by a border, this weak attachment being somewhat strengthened by basal deformation of the circular cross-section, so that the tube clings closely to the substrate, but is not cemented to it. Even in diagenetically relatively strongly altered sediments, tube parts may often be easily loosened from the substrate without damaging the tube wall.

In contrast to the virtual absence of external ornament and generally simple tube structure, the cross-section and the tube interior display an enormous array of special features, the most important perhaps being the 'trilobate narrowing of the tube's lumen'. Most of these features are unknown in any other serpulid species. It should be stressed, however, that they are found only in a limited number of specimens in any sample and even do not occur at all in some populations or strata.

*Comparison* — In clusters of *Filograna* Oken, 1815 the tubes are often more or less parallel, and most of the special features of *Cycloserpula*, the 'trilobate narrowing of the tube's lumen' in particular, are absent. *Stratigraphic range* — Sinemurian ?, mid-Late Toarcian-Eocene (middle Lutetian), Oligocene ?, post-Oligocene ?.

*Remarks* — Sinemurian specimens from Sicily (Lentini, 1974, pl. 12, fig. 2; pl. 16, fig. 10) and a single early Sinemurian specimen from Wellendingen (SW Germany) before me may belong to *Cycloserpula*. If

not, the genus does not appear in central Europe before the mid-Late Toarcian. It is probably absent from the bifrons Zone of Somerset (England), and with certainty from the mid-Late Toarcian jurensis limestone nodule layer (*sensu stricto*) in SW Germany. At another late Toarcian nodule level, only one foot above the jurensis level, *Cycloserpula* suddenly becomes fairly common and it remains one of the commonest serpulids until Danian time, with a slight decline during the Bathonian.

The dominance of straight, *i.e.* non-coiled, tube parts in '*flaccida*' probably results from the common occurrence and comparatively large size of molluscan shells in the late Bajocian of SW Germany, so that the tubes could grow across a wide substrate area: '*flaccida*' is herein considered but a variety of *gordialis*.

Jurassic specimens, which often resemble a disorderly rolled up rope, have a slightly more constant curvature than do Cretaceous and Danian individuals, in which consecutive straight and narrowly curved parts often occur. However, the range of variation within a single sample exceeds this difference; the curvature is probably dependent in part on the environment.

The array of special features increases through the stratigraphic column and reaches an acme during the Maastrichtian and Danian. The peculiar 'trilobate narrowing of the tube's lumen' mentioned by Jäger (1983, p. 25) for material from the early Cenomanian onwards, has lately been observed also in specimens of middle Aptian age (Lower Greensand) from the Isle of Wight (material presented by Prof. Dr Herwig Wulf). It thus appears appropriate to subdivide the long-ranged material of *Cycloserpula* into a primitive and a more advanced species. It is not quite clear, however, where to fix the boundary between these, for there is only relatively few material of early Early Cretaceous age. At least, all Jurassic (up to and including the Tithonian) material represents the primitive species, *gordialis* (von Schlothheim, 1820) *sensu stricto*, and specimens occurring from at least the middle Aptian onwards represent the more advanced species, for which the name *lombricus* Defrance, 1827b is here provisionally used.

The social form, *plexus* (J. de C. Sowerby, 1829) is now considered to be but a subspecies of *lombricus*, while in *gordialis* there is no discrimination between solitary and social forms.

Very probably, *Serpulites contorquatus* von Schlothheim, 1820 belongs to *Cycloserpula* as well, but from

the original description (without illustrations and no types designated) it cannot be determined whether it represents the solitary or the social form. In the collections of the Museum für Naturkunde of the Humboldt-Universität Berlin, I was unable to trace any of the ten specimens from Aachen and from the English Chalk mentioned by von Schlotheim nor any other specimen labelled *contorquatus*. I did find a single specimen of the solitary subspecies from the English Chalk, without a species name on the accompanying label. Whether or not von Schlotheim used this specimen for the original description is unknown. Since there seems to be no material of the type lot left, it cannot be determined whether *contorquatus* is a senior synonym of *lombricus* or *plexus*.

It cannot be ruled out totally, that, contrary to Jäger's view (1983), '*Sarcinella* *sarcinella* Regenhardt, 1961 is not referable to *Filograna*, but in fact represents an atypical *Filograna*-like variety of *Cycloserpula lombricus plexus*. This problem can only be solved through an examination of special features of tube structure in additional material from the type locality of this species.

In the Maastricht-Aachen-Liège area, specimens from the Geulhem Member display nearly exactly the same array of special features as seen in material from the underlying Meerssen Member of the Maastricht Formation (late Maastrichtian). Thus, the Danian and Maastrichtian specimens, at least from this area, undoubtedly belong not only to the same species, but also to the same (unnamed) variety. *Cycloserpula* crosses the K/T boundary morphologically unchanged.

According to Rovereto (1904a, p. 12) the only difference between *eximPLICATA* (Rovereto, 1904a) (nom. nov. pro *gordialis sensu* Leymerie, 1846a, p. 369, pl. 13, fig. 16) and *Cycloserpula* specimens from the Maastrichtian of Rügen (NE Germany) is the smaller size of the former. Doncieux (1926, p. 19, pl. 2, figs 26-29), who provided relatively good photographs of *eximPLICATA*, recorded this species from the Ypresian to the middle Lutetian. However, material before me from around the Palaeocene/Eocene boundary of the Tremp Basin (NE Spain) presented by Drs R.H.B. Fraaye, cannot be distinguished from *lombricus*. Thus, *eximPLICATA* is herein considered to be synonymous with *lombricus*.

During the Eocene and post-Eocene other *Cycloserpula*-shaped tubes apparently do not grow to the size of Jurassic and Cretaceous species. The Eocene '*Serpula* *maeandrica* Schmidt, 1955b closely resembles very small meanders of *Cycloserpula*. Fleming

(1972, fig. 2g) illustrated a medium-sized specimen of '*Glomerula*' sp. from the New Zealand Oligocene, and recorded (p. 750) similar tubes from the late Eocene, early Miocene and even Holocene. As long as the tube structure of Schmidt's and Fleming's material remains unknown, interpretation of those species is difficult.

***Cycloserpula lombricus* (Defrance, 1827b)**  
Pl. 1, Figs 1-20

?1820 *Serpulites contorquatus* von Schlotheim, p. 96.  
1827b *Serpula* ? *lombricus* Defrance, p. 571.

*Type* — Defrance (1827b, p. 571) did not provide an illustration, nor did he designate a type specimen, and the description is very brief ('Ses tuyaux, qui n'ont qu'une demi-ligne de diamètre, sont lisses et entortillés sur eux-mêmes...'). Localities mentioned are the 'craie à Beauvais et à Meudon'. The Craie de Meudon is of late Campanian age. Hébert (1855) stated that *lombricus* and *gordialis* are conspecific, which means that *lombricus* is very probably a genuine species of *Cycloserpula*.

*Description* — For a full discussion of varieties and special features the reader is referred to Jäger (1983, pp. 24, 25, 29-31) and Jäger (in prep.).

In the Geulhem Member of the Maastricht-Aachen-Liège area the tube diameter is on average 0.7-1.3 mm, with a maximum of 1.8 mm. A continuous range of tube sizes is observed, this in contrast to the white chalk facies of and few other localities in northern Germany (Jäger, 1983, p. 25) and also to the chalky facies of the Gulpen Formation of the Maastricht-Aachen-Liège area, where two size groups may be distinguished.

Most specimens from the Geulhem Member are attached to a substrate (calcareous algal crusts, bryozoans etc., rarely small algal filaments). Often a substrate negative is preserved as an impression on the underside of the tube. Typically in high-energy biotopes, the tube first forms meanders (Pl. 1, Fig. 1) then three-dimensional chaotic knots (= 'Röhrenverlauf a' of Jäger, 1983, p. 29) (Pl. 1, Figs 2a, 20a-c), but these forms could be studied in a few specimens only, since most tubes were fragmentary.

Straight or slightly curved tube parts, which, because of the absence of substrate impressions on the tube's circumference, grew erect above the substrate, are much less common, but do occur (Pl. 1, Figs 3-5), with a maximum length of 16 mm. In the white chalk and chalky facies of northern Germany these erect tube parts are often broken at the top

and, following a sharp curve, successive tube parts enwrap the erect part more or less regularly ('Röhrenverlauf b' of Jäger, 1983, p. 29). This variation is rare in the material from the Geulhem Member. In a single specimen this envelopment does occur, but is rather irregularly developed (Pl. 1, Fig. 6). In another fragmentary specimen, the younger tube is only slightly curved and is directed in the same way as the broken part (Pl. 1, Fig. 5). In a third specimen, tube breakage occurred in a knot: the new tube part grew in a direction different from the broken old tube (Pl. 1, Fig. 2a, b).

The tube circumference is sometimes more or less regularly circular, but at times more or less deformed. Especially at the convex side of curved tube parts, rucksack-shaped protuberances of the tube's exterior occasionally occur (not mentioned by Jäger, 1983), which are either still closed (Pl. 1, Figs 7, 8) or broken open (Pl. 1, Figs 9, 10).

The thickness of the tube wall is extremely variable. Sometimes it is rather thin (Pl. 1, Figs 4, 11), but specimens in which the lumen is minimised by an extremely thick tube wall are not very rare. In thick-walled specimens the cylinder layer of the tube may consist of up to six (and perhaps even more) layers (Pl. 1, Fig. 12a) which are developed concentrically or, more frequently, eccentrically, leaving circular or crescentic interstices, as seen in cross-section (Pl. 1, Figs 12a, 13, 16, 19).

The cross-section of the innermost tube layers is mostly circular or deformed circular, but cross-sections with 'trilobate narrowing of the tube's lumen' (Pl. 1, Figs 14-16) are not at all rare. An 8-shaped knot fragment shows trilobate narrowing at both ends (Pl. 1, Fig. 14), but not in between, as seen in areas where the tube wall is broken. Trilobate narrowing is brought about by three gradually increasing and decreasing longitudinal swellings of up to about 3 mm in length (several cm long in an extraordinary early Cenomanian specimen before me), whereas a kidney-shaped lumen (not mentioned by Jäger, 1983) is the result of a single longitudinal swelling (Pl. 1, Figs 12b, 17-19).

Occasionally, the small inner tube layer may grow trochospirally within the lumen of the outer tube layer. Distinct corkscrews occur in a number of specimens from the Geulhem Member (Pl. 1, Fig. 20a-c), but the most instructive corkscrews have been collected from the Meerssen Member (see Jäger, in prep.). The same type of corkscrew structure also occurs in a unique, but worn and indeterminate tube (not assignable to *Cycloserpula*) from the

Oxfordian of Dotternhausen (SW Germany) before me.

Series of oblique step-shaped swellings at the tube's interior (Jäger, 1983, p. 30) do occur in the Geulhem Member (Pl. 1, Fig. 1, lower part of photograph), but are less common than in chalk facies.

*Discussion* — The following is a provisional interpretation of the special features seen in the tube structure of the present species: In Serpulinae with a well-developed parable layer, thickening of the tube wall results mainly from an addition of material onto the tube's exterior. In *Cycloserpula*, however, in which there is no parable layer, tube wall thickening can only result from adding material to the tube's interior. Thus, the unknown soft parts of *Cycloserpula* should have been extended anteriorly to give the prolonged tube parts a wider diameter, and had a gradual taper posteriorly to leave enough room for a thickening of the tube wall. In the modern species, *Filograna implexa* Berkeley, 1828, however, tube material is also added on the inner surface, but the soft parts taper only slightly (see Faulkner, 1930, fig. 3a).

Moreover, in order to produce an occasionally very thick tube wall in a species with rapid longitudinal growth, the area of aggregation of tube material should have been fairly long. If one accepts the hypothesis of a gradual taper of the soft parts, the common occurrence of several tube wall layers sheathed into one another concentrically or eccentrically with crescentic lumina between (as seen in cross-section) are easily explained by a rapid move forward of the soft parts during prolongation of the tube's anterior end. At a certain position of the tube's length, the soft parts became suddenly narrower, and thus the diameter of the new inner tube wall layer also diminished abruptly, leaving a cavity between the tube wall layers.

Sometimes the innermost tube wall layer leaves only very little room for the soft parts. The abdomen should therefore have tapered into a very thin 'tail', there where the aggregation of the innermost tube wall layer took place. Such a thin tail, however, does not occur in *F. implexa*. The corkscrew shape of the inner tube wall layer in some specimens requires a corkscrew-shaped tail, but this does not occur in *F. implexa* either.

To explain the 'trilobate narrowing of the tube's lumen' the soft body's posterior end ought to have been trilobate shaped, but not in all individuals and only during some (repeated) growth stages. Such a repeated short-time change of abdominal morphol-

ogy is usually related to phases of sexual activity. However, generally swelling of sexual organs occurs, whereas the 'trilobate narrowing of the tube's lumen' requires a periodic contraction of the abdomen. In *F. implexa*, 'posteriorly the body terminates in two lobes - the anal papillae' (Faulkner, 1930, p. 113). Perhaps the 'trilobate narrowing of the tube's lumen' as well as the corkscrew shape of the inner tube wall had a special function in the high-energy biotopes inhabited by *Cycloserpula* to ensure a more effective anchorage for the soft parts.

In *F. implexa*, 'in some cases the tube is notched dorsally, and when this is so the faeces are even more effectively removed' (Faulkner, 1930, p. 118). Such a notch is unknown in *Cycloserpula*.

The rucksack-shaped protuberances resemble the brood chambers of Recent *Chitinopoma arndti* Zibrowius, 1983 and *C. serrula* (Stimpson, 1854). In *Cycloserpula lombricus*, however, these structures often are too irregularly developed for them to be true brood chambers (ten Hove, *in litt.*, February 1990). *Comparison* — *Cycloserpula gordialis* shows a more regular curvature and fewer of the above-mentioned special features, in particular, there is no 'trilobate narrowing of the tube's lumen.'

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: extremely frequent, upper part, extremely frequent. Geulhem section, lower part of the Geulhem Member: extremely frequent, upper part, very frequent. There are no striking differences in the tube's shape or size or in the frequency of occurrence of special features within the Geulhem Member of these localities.

*Occurrence elsewhere* — Middle Aptian-Eocene (middle Lutetian), of Belgium, France, Spain, Great Britain, Austria, Germany, Denmark, Sweden, USA, Poland, Czechoslovakia, CIS and India.

Subfamily Serpulinae MacLeay, 1840  
Genus *Serpula* Linné, 1758

*Type species* — *Serpula vermicularis* Linné, 1767.

*Discussion* — It is impossible to give a diagnosis of the tube, because the genus is defined by characteristics of the soft parts (Hartmann-Schröder, 1971, p. 527), and because the tubes of various Recent species of the genus are very different from each other.

In addition, in palaeontology the name '*Serpula*' has been used as an omnium gatherum for all kinds of serpulid tubes: *Serpula* has often been used almost as a synonym of the family Serpulidae.

Two of the three species described below are assigned to *Serpula*, albeit with a query, in view of the fact that they show some similarities to certain (but not all) Recent species of this or of closely related genera. The generic assignment of the third species is very uncertain.

As the tubes are of so little value in identification, palaeontology cannot contribute anything to a reconstruction of the phylogeny of the genus *Serpula*. Ten Hove (1984) and ten Hove & Jansen-Jacobs (1984) pointed out the relationships between Recent species of *Serpula* and other Recent serpulid genera by referring to features of the soft parts and of the opercula.

***Serpula* ? *insiticia*** (Regenhardt, 1961)  
Pl. 2, Figs 1-13

- v 1961 *Proliserpula* (*Proliserpula*) *insiticia* Regenhardt, p. 54, pl. 6, fig. 3.  
? 1965 *Spirorbis ascendens* — Rasmussen, p. 35, pl. 8, fig. 9.

*Type* — Regenhardt described a long tube fragment in detail, but did not illustrate the specimen; it is here illustrated in Pl. 2, Fig. 8a, b. On microfossil cell no. 739, which contains three specimens, he wrote 'Holotypus/großes Stück/Nr. 739'. In the legend of the plates, however, he designated the left-hand specimen of his plate 6, fig. 3 (the shortest of the three) holotype. This designation is the valid one. The holotype (illustrated here in Pl. 2, Fig. 9a-c) is a slightly curved fragment of an erect tube, 2.5 mm long, with two peristomes 1.3 mm apart. Tube diameter is 0.9 mm between the peristomes, 1.3 mm at the peristomes. The lower lobes of peristomes are only weakly developed. Geulhem Member, collected from burrow infill at the K/T boundary, former Curfs quarry at Geulhem, Voigt & Meijer leg., GPI Hamburg Collections, type catalogue, no. 739.

*Description* — The tube has an initial non-spiral part (Pl. 2, Figs 1b, 2a, 3), followed mostly by a spiral (Pl. 2, Figs 1a-b, 2a, 4, 7) with normally 1-3, rarely 4 turns. Diameter and height of spiral are generally 3-5 mm. In most specimens, the spiral is attached by a broad base to a more or less planar substrate, the spiral then resembling a truncated cone, and being less frequently cylindrical. Occasionally the substrate is small, the spiral then being inversely conical or forming irregular loops. Spiral coiling is predominantly sinistral, but dextral specimens are not rare. An umbilicus is always present. Turns of the spiral appear cemented together, the sutures between

them being indistinct. Clusters of up to three specimens are known (Pl. 2, Fig. 1a, b).

The anterior tube part (Pl. 2, Figs 2, 5-10) is often obliquely, less commonly horizontally or steeply, erect, and is straight or slightly curved. Length up to 4.0 mm. The tube diameter gradually increases to a maximum of 1.2 mm between the peristomes and 1.8 mm at the peristomes.

Normally there is no longitudinal ornament, but two specimens before me have a keel of irregular height. A furrow is present at the beginning of the erect tube part. Peristomes are very rare on the spiral part, but are very common on the erect part (Pl. 2, Figs 1, 2, 6-12). Up to 4 peristomes are closely spaced: they are sharp, short and broad, the upper half being broader than the lower half. The circumference of the peristomes is near-circular, with a big lobe in the upper half and two small lobes in the lower half. In weakly developed peristomes these lobes may be indistinct. In the middle of the upper surface and occasionally also at the two lobes on the underside the peristomes slightly protrude. On the spiral part the top and base of the tube may also protrude (Pl. 2, Fig. 4). No growth lines are visible on the tube's exterior. The cross-section of the attached tube parts is inversely U-shaped, in the erect part circular. The lumen is circular. The tube wall is moderately thick, and consists of a thicker, yellowish, smooth outer parable layer and a thinner white inner layer, which probably represents the inner parable layer plus cylinder layer (Pl. 2, Fig. 3). In abraded specimens fine transverse wrinkles may sometimes be seen in the white layer as well as on the inner surface of the yellowish layer. No 'internal tube structures' such as those seen in *Spiraserpula* (see *Cementula* below) occur. At the sides of the base of attached tube parts, sometimes longitudinal cavities and rarely a construction of short cells [resembling those of *Neovermilia ampullacea* (J. de C. Sowerby, 1829), but less distinct] are visible.

A single specimen (Pl. 2, Fig. 13a-b) has two tabulae following the first spiral turn, plus remains of a third tabula just anterior of the initial part of the spiral. The tabulae are oblique, as they are fixed to the tube wall at the spiral's inner side more posteriorly and at the spiral's outer side more anteriorly. The tabulae are lightly vaulted (concave side anterior) and have two horizontal rows of minute perforations, one on the upper and one on the lower side. A somewhat larger perforation occurs at the border of the tabula at the inner side of the spiral.

The characteristic structures of the hydroid sym-

biont *Protulophila gestroi* Rovereto, 1901 are commonly found in tubes of the present species (Pl. 2, Figs 1, 2, 4), but do not occur in other serpulid and spirorbid species from the Geulhem Member, with the exception of a single specimen of *Placostegus erectus* (see below). A paper on Recent examples of *P. gestroi* is in preparation (Zibrowius & Jäger, in prep.). *Discussion* — Regenhardt described and figured only the erect anterior tube part. A spiral probably belonging to the present species was illustrated by Rasmussen (1965). *Serpula* ? *insiticia* is here assigned to the genus *Serpula*, as it resembles in some respects the Recent *Crucigera zygophora* (Johnson, 1901) and the genus *Cementula*, which both are representatives of the group comprising the genera *Serpula*, *Hydroides*, *Crucigera*, *Cementula* and *Spiraserpula*, the first-named taxon being the 'main genus' of this group for historical reasons.

*Comparison* — The shape of the spiral and the erect tube of *Conorca* Regenhardt, 1961 is very similar, but here the tube's cross-section is triangular, quadrangular or pentangular, the growth lines protrude more clearly in the centre of the tube's upper surface, and the peristomes are much longer than in the present species. *Rotularia hisingeri* (see below) is attached to the substrate generally by its non-spiral initial tube part only, and not by the first turn of the spiral itself. The spiral is lower, and peristomes are absent. The Recent *Crucigera zygophora* (Johnson, 1901) grows more than three times larger (maximum diameter at peristomes 6 mm according to ten Hove & Jansen-Jacobs, 1984, p. 167), and peristomes and erect tube parts are less common. *Cementula* has a similar tube structure (smooth outer surface, 'melting together' of the spiral's turns, absence of 'internal tube structures'). The general shape of the peristomes is also similar, but those of the *Cementula*/*Spiraserpula* group protrude much more clearly in the centre of the upper tube surface and at the lobes on the underside. In addition, the spirals of the *Cementula*/*Spiraserpula* group are in general flatter, so that several turns are in contact with the substrate, this in contrast to the present species in which only the first turn is.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: not rare, upper part, extremely rare. Geulhem section: lower part of the Geulhem Member: very frequent, upper part, extremely rare.

*Occurrence elsewhere* — Regenhardt (1961, p. 54) recorded one or two similar specimens from the Danian of Fakse (Denmark). The few fragments

from Fakse in my collection do not allow a decision as to their being conspecific or not.

***Serpula* ? aff. *trilineata* Roemer, 1841**

Pl. 2, Figs 14-19

aff. 1841 *Serpula trilineata* Roemer, p. 102.

aff. 1983 *Janita trilineata* (Roemer, 1841) — Jäger, p. 72, pl. 9, fig. 2 (with additional synonymy).

aff. 1987 *Janita* ? sp. — Jäger, p. 42, fig. 1; pl. 1, figs 27-30.

aff. 1988 *Janita* ? sp. — Jäger, p. 74, fig. 2.

*Type* — Jäger (1983, p. 72) failed to retrace Roemer's type material in the Roemer-Pelizaeus-Museum at Hildesheim, the present whereabouts of which is unknown.

*Description* — The tube is attached to large substrates (mainly oyster shells and calcareous algal crusts, but also planar bryozoan colonies) over its entire length with a broad border. Possibly erect anterior tube parts were occasionally present, but these have not been preserved.

The tube forms U's (Pl. 2, Figs 15-18) and irregular loops of up to 1½ turns (Pl. 2, Fig. 14), sometimes there are several successive loops in a single specimen. The length of the tube reaches 25-30 mm; with tube diameter gradually increasing to a maximum of 2.0 mm (exclusive of broad basal border) or 3.0 mm (inclusive of this border). There is no longitudinal ornament in juveniles (see juvenile part in Pl. 2, Fig. 14b), but in medium-sized and adult tubes there are always three straight (*i.e.* non-undulate), smooth and rounded keels (Pl. 2, Figs 14-19). The two peripheral keels are slightly wider than the median keel (Pl. 2, Fig. 18a).

Transverse ornament is already present in juveniles (Pl. 2, Fig. 14b) and in most of the medium-sized and adult tubes (distinct in Pl. 2, Figs 14b, 15; less distinct in Pl. 2, Figs 16-18, absent from Pl. 2, Fig. 19). It apparently becomes weaker and finally disappears in adults, but the material at hand does not allow to substantiate this. It consists of wrinkles or pustules which slightly protrude in the centre of the upper surface and at the base. Especially in concave parts of U's and loops the pustules are large (Pl. 2, Figs 14b, 15). Weakly to moderately developed annular peristomes are rather rare (Pl. 2, Figs 15, 16a), and they slightly protrude in the same way as do the wrinkles.

The cross-section is trapezoid, with the peripheral keels forming the upper edges of the trapezium, the upper side of the trapezium being lightly convex, so that the median keel is situated on a slightly

higher level than the others (Pl. 2, Fig. 19b), to rounded trapezoid (Pl. 2, Figs 14c, 17b) or sub-squarish (Pl. 2, Figs 16b, 18b). The lumen is circular.

The tube wall (Pl. 2, Fig. 19a, b) is white and moderately thick, and consists of a thicker outer parable layer, a thin, slightly brighter inner parable layer, over which the wall easily splits, and a moderately thin cylinder layer. In the upper half of the tube the ratio of thickness of the three layers is roughly 2-5 : 1 : 1-2, but the inner parable layer becomes thicker towards the base and may form rows of very short cells comparable to those seen in *Neovermilia ampullacea*, but less distinct, so that in most sections the base appears to be massive. When the cylinder layer is worn, the inner surface of the parable layer shows a fine transverse striation.

*Discussion* — *Serpula* ? aff. *trilineata* resembles some Recent species of the genera *Serpula* and *Hydroides*, *e.g.* *S.* cf. *kaempferi* (Kinberg, 1867) (see Imajima, 1978, fig. 2s-u), *H. exaltata* (Marenzeller, 1884) (see Imajima, 1976, fig. 4j), *H. externispina* Straughan, 1967 (see Imajima, 1976, fig. 3k). However, there is also a certain resemblance to the Recent genus *Metavermilia* (see below). For the time being, the species is here referred to the genus *Serpula* with a query.

*Comparison* — *Serpula* ? *trilineata* sensu stricto is very similar, but its cross-section is commonly more rounded than that of aff. *trilineata*, the keels may occasionally be weak or undulate, and peristomes do not occur at all, and the base may show longitudinal cavities.

Jäger (1983, 1987, 1988) erroneously assigned *trilineata* from NW Germany and conspecific or similar material from the Maastricht Formation of the Maastricht-Aachen-Liège area to the Recent genus *Janita*: in this genus the keels are much stronger and undulate.

The Eocene '*Serpula*' *trilineata* J. de C. Sowerby, 1844 is a much smaller and, most probably, different species. *Neovermilia ampullacea* generally has only a single keel or no keel at all, and its peristomes are much better developed.

Comparisons with similar Recent species as described and illustrated by Imajima (1976, 1978) are as follows: *Serpula* cf. *kaempferi* has three or five keels in the fixed tube part and a cylindrical erect anterior part with less pronounced keels or no keels at all, but with small flaring peristomes. *Hydroides exaltata* has, according to the description, many growth rings, (however, these are not distinct in the



illustration), and grows to larger sizes, the diameter at the aperture being 3 mm. *Hydroides externispina* closely resembles aff. *trilineata*, but weak peristomes or other transverse ornament apparently occur more commonly.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: not rare, upper part, rare. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, extremely rare. *Serpula trilineata* sensu stricto (or a closely related species) occurs in the late Maastrichtian Gronsvelt, ? Schiepersberg, Emael and ? Meerssen Members of the Maastricht Formation.

*Occurrence elsewhere* — Late Santonian (NW Germany): *Serpula trilineata* sensu stricto.

***Serpula* ? sp.**

Pl. 3, Figs 13-15; Pl. 7, Fig. 1

*Description* — The tube diameter increases gradually to rapidly to a maximum of less than 3 mm. The tube is attached to the substrate for its longest part, the anterior part, however, may dislodge itself from the substrate (Pl. 3, Fig. 14). Most specimens are curved, a few even form loops and trochospirals of up to 2½ turns (Pl. 3, Fig. 13), but these are only fragmentarily preserved. Often a median keel or crest occurs (Pl. 3, Fig. 14; Pl. 7, Fig. 1), but some specimens lack longitudinal ornament. Transverse ornament is only weakly developed, and there are no distinct peristomes.

A single well-preserved tube fragment (Pl. 3, Fig. 14) shows a posterior attachment to a narrow, unpreserved substrate; anteriorly it dislodges itself from the substrate for the last 1 mm of its length, but without marked erection. The apertural diameter is 1.3 mm. An undulate strong longitudinal crest protrudes over the aperture, and the growth lines also protrude distinctly towards the crest.

Another well-preserved fragment (Pl. 7, Fig. 1), originally attached to a large planar bryozoan colony, is relatively large (diameter almost 3 mm), has a strong longitudinal crest and transverse growth lines protruding towards the crest and towards the base.

The cross-section is inversely U-shaped in some specimens, near-triangular with convex sides in others. Generally there is a longitudinal cavity on each side of the tube's base (Pl. 3, Fig. 14c), but occasionally a cellular construction of the base occurs (Pl. 3, Fig. 15b) as in *Neovermilia ampullacea*. There is a fine transverse striation on the tube's

inner surface except in areas where small fragments of the non-striate cylinder layer are preserved.

*Discussion* — The present species resembles *Neovermilia ampullacea* (J. de C. Sowerby, 1829), a long-ranging and widely distributed species in the Late Cretaceous, showing an enormous range of variation (see Jäger, 1983), and ranging into the Danian of Denmark. Slightly more triangular, but probably conspecific, forms occur around the Palaeocene/Eocene boundary of the Tremp Basin (NE Spain; leg. Drs R.H.B. Fraaye). Regenhardt (1961) assigned *ampullacea* to the genus *Proliserpula* Regenhardt, 1961, but a comparison of *ampullacea* with the descriptions and figures of the Pliocene-Recent *Neovermilia falcigera* (Roule, 1898) in Zibrowius & ten Hove (1987) has shown that the tubes of these two species are closely similar in many respects. In some other features, however, there are differences, but similarities of *ampullacea* to another species of *Neovermilia* Day, 1961, *N. globula* (Dew, 1959), make an assignment of *ampullacea* to this genus more than probable.

*Comparison* — Characteristic, though facultative, features of *N. ampullacea* are absent from the present species, e.g. large size, fine transverse ornament, and annular peristomes. In view of the wide range of variation of *ampullacea*, single specimens often cannot be distinguished beyond doubt, but the material from the Geulhem Member of the Maastricht-Aachen-Liège area as a whole is clearly different. A few fragments from this member cannot be distinguished from *Serpula* ? aff. *trilineata* (see above) beyond doubt; however, typical examples of this species possess three longitudinal keels.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: very rare, upper part, common. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, absent.

*Occurrence elsewhere* — Unknown.

Genus            *Cementula* Regenhardt, 1961 emend. Pillai (in press)

*Type species* — *Cementula sphaerica* Brünnich Nielsen, 1931.

*Remarks* — The name *Cementula* was first used by Brünnich Nielsen (1931), who failed to designate a type species. Thus it was Regenhardt (1961), who validly introduced the generic name. He distinguished two genera, *Cementula* and *Spiraserpula* Regenhardt, 1961, mainly on the shape of the spiral, which may either be higher or flatter. As the

shape of the spiral varies, Jäger (1983, p. 47; 1991) united these genera under *Cementula*. Very similar tubes also occur in Recent serpulid species usually assigned to *Serpula* sensu stricto (see Lommerzheim, 1979, p. 142; Jäger, 1983, pp. 47-49).

On the basis of Pillai's studies (in press) of Recent and fossil *Cementula*-like serpulids, two species groups may now be distinguished: one with 'internal tube structures' (henceforth: ITS), i.e. longitudinal protrusions of the tube wall into the lumen, and one

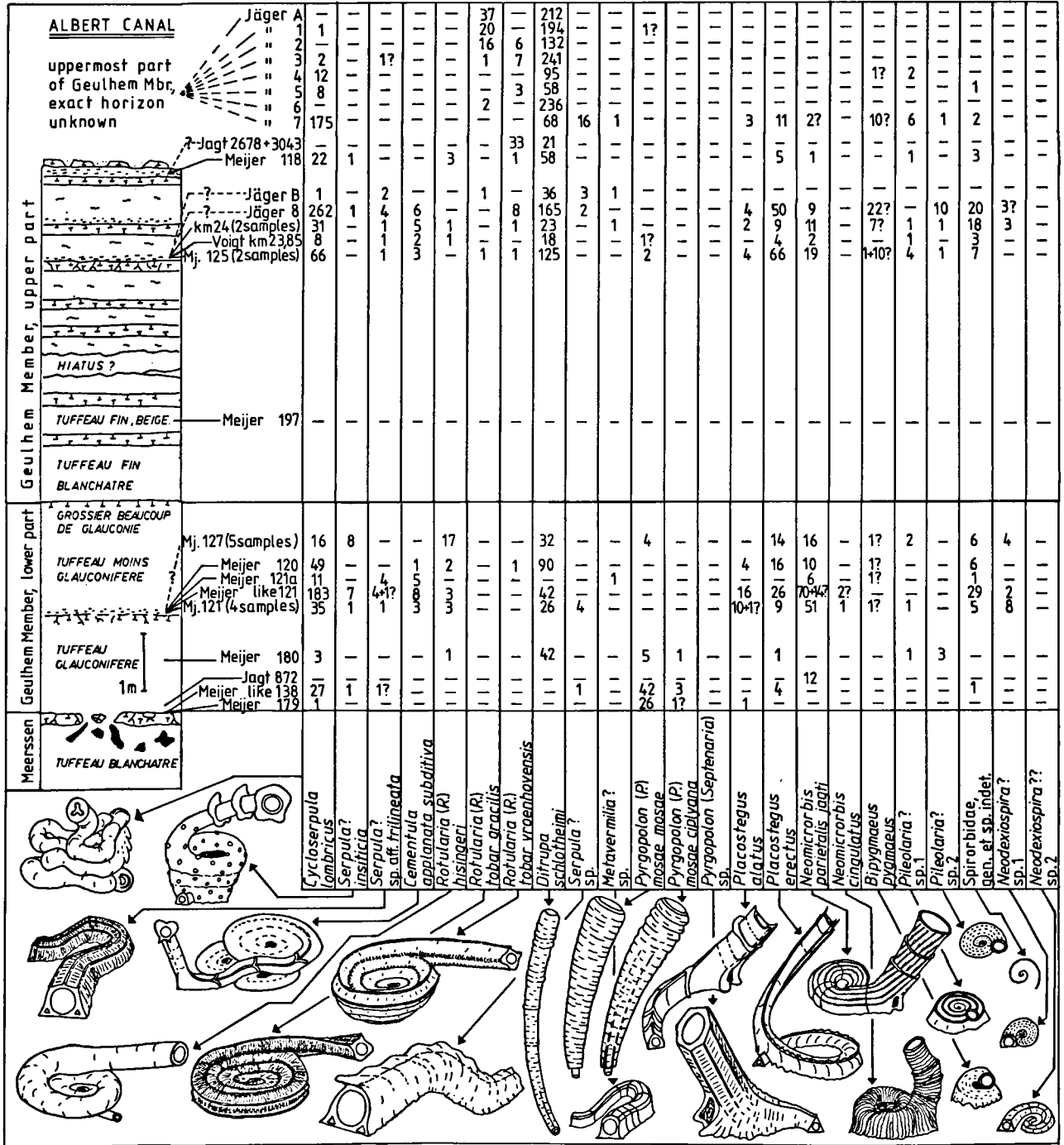


Table 1. Number of specimens of serpulid and spirorbid taxa collected from the Geulhem Member as exposed in the Albert Canal sections (Vroenhoven-Riemst, Belgium). Lithologic log based on Meijer (1959). Specimens from the J.W.M. Jagt Collection are now included in the Natuurhistorisch Museum Maastricht Collections (prefix NHMM, see plates). Meijer's and Voigt's samples are housed in the collections of the Geologisch-Paläontologisches Institut der Universität Hamburg (prefix GPI Hamburg).

without ITS. In Recent species this difference is correlated with distinct differences in the soft parts, which made Pillai decide to separate them at the generic level. From the absence or presence of ITS alone in otherwise very similar fossil tubes, one should rather expect a separation at the subgeneric or specific levels only. Pillai found ITS in the type species of *Spiraserpula* and noted their absence in the type species of *Cementula*, and thus the two genera are now distinguished on the basis of an utterly different main distinctive character than originally intended (Regenhardt, 1961).

*Diagnosis* — The increase in diameter of the tube is slow; it is attached to a substrate or to posterior tube parts over most of its length. Following upon an initial non-spiral part are one or several regular or irregular, mostly planar but occasionally taller spirals, often with short or long non-spiral parts in between. On the upper surface the tube parts appear cemented together, which is why often no suture is seen. Transverse ornament consists of birdwing-like 'alae', which are widely spaced and often do not occur at all. In contrast to the closely similar *Spiraserpula* there are no protruding ITS on the inner tube surface. The anterior tube part may become raised above the substrate and possess sharp quadripartite peristomes consisting of rounded 'alae' on the upper surface and two pointed processes on the underside. Often there is a longitudinal furrow on the underside.

*Comparison* — *Spiraserpula* has a very similar, often more planar tube, shows ITS (the main distinctive feature), and there are differences in the soft parts. The differentiation of *Cementula* from *Laqueoserpula* Lommerzheim, 1979 — both genera lacking ITS — is not quite clear. *Laqueoserpula* has a thick-walled, wide tube with only few spiral turns visible from the outside. The peristomes are more bulbous and only occasionally are birdwing-shaped. The anterior tube part often steeply erects.

*Stratigraphic range* — Middle Triassic-Sinemurian ?, Pliensbachian-Campanian ?, Maastrichtian-Recent.

*Remarks* — Up to now, only Campanian, Maastrichtian, Danian and Recent species were assigned to *Cementula* and *Spiraserpula* as currently defined. Other Cretaceous species still need to be assigned to either of these genera, while for most Jurassic specimens assignment is hampered by poor preservation of the tube's interior or scarcity of material which forbids sectioning. Thus *Cementula* and *Spiraserpula* are here treated together. In the two strati-

graphically oldest species, '*Serpulites*' *lithuus* von Schlothheim, 1820 from the Middle Triassic Muschelkalk of Germany, *Spiraserpula mikesia* Ziegler & Michalik, 1980 from the late Triassic of the western Carpathians and an unnamed unique specimen from the early Sinemurian of Wellendingen (mentioned above), it is uncertain whether they belong to the *Cementula/Spiraserpula* group at all.

Unequivocal members of the *Cementula/Spiraserpula* group are known from the early Pliensbachian onwards (the oldest specimens before me are from the ibex Zone of Caen, France, and the lower davoei Zone of Schömberg and Bisingen, SW Germany). To the end of the middle Jurassic these species remain rather uniform, and it is therefore possible that at least some of the available specific names, viz *complanata* (Goldfuss, 1831), *circinnalis* (Münster in Goldfuss, 1831), *filaria* (Goldfuss, 1831) and *ramentum* (Dumortier, 1874) are synonymous. Specimens from the Toarcian bifrons Zone of Somerset probably lack ITS and are therefore assignable to *Cementula*.

The Oxfordian and Kimmeridgian *spiroline*s (Münster in Goldfuss, 1831) with its sharp longitudinal keel and sharp alae is utterly distinct, whereas silicified specimens from the Tithonian of Nattheim (SW Germany) again resemble the early and middle Jurassic species.

There is practically no record so far of the *Cementula/Spiraserpula* group in the early Cretaceous. In the late Cretaceous and Palaeocene this group, and *Spiraserpula* in particular, shows a wider range of variation and a more rapid evolution. Following the discovery of the subdivision of the group into species with or without ITS, Jäger's (1983, p. 48) hypothesis of a polyphyletic derivation of large species (mainly *Spiraserpula*) from small species (mainly *Cementula*) can no longer be supported.

According to Pillai's and my own studies of the tube's interior, *Cementula sphaerica* Brünnich Nielsen, 1931 (Maastrichtian), *Spiraserpula spiraserpula* Regenhardt, 1961 (Campanian), *S. versipellis* Regenhardt, 1961 (Maastrichtian) and *S. scrupea* Regenhardt, 1961 (Maastrichtian) must be left in their original genus, whereas *S. subditiva* Regenhardt, 1961 is now assigned to *Cementula*. Material of *C. applanata* Brünnich Nielsen, 1931 from the Danian of Fakse (Denmark) lacks ITS. In material of an unnamed *Spiraserpula* species from the Palaeocene of Kazakhstan ITS are present (Pillai, in press). *Spiraserpula adunca* Regenhardt, 1961 (Maastrichtian) is a species of *Placostegus*.

Many more Cenomanian-Palaeocene species have been recorded and discussed by Lommerzheim (1979), Jäger (1983, pp. 47-49, who omitted *Cementula* ? *cauteshabitans* Lommerzheim, 1979 and *C.* ? *applanata* Brünnich Nielsen, 1931) and Jäger (1991). These species, as well as in Santonian material of *S. spiraserpula* and *C. sphaerica* recorded by Jäger (1983) and *S. parceproma* Regenhardt, 1961 from the Campanian, should still be thoroughly examined for presence or absence of ITS.

It appears that the small Maastrichtian species, *C. sphaerica*, produced two lineages of larger species in the Danian: one distinctly umbilicate, more planar lineage (*C. applanata subditiva*) and a higher lineage with its main species, *C. contorta* Brünnich Nielsen, 1931 (of which *C.* ? *ventosa* Regenhardt, 1961 may be a synonym).

Of post-Palaeocene fossil species it is uncertain whether they belong to the *Cementula/Spiraserpula* group at all. For Recent species the reader is referred to Pillai & ten Hove (in prep.).

#### ***Cementula applanata* Brünnich Nielsen, 1931**

1926 *Serpula (Hydroides) applanata* [sic] Br. N. — Ødum, p. 165.

1931 *Cementula applanata* Brünnich Nielsen, p. 97, pl. 2, fig. 7.

*Type* — Brünnich Nielsen (1931) illustrated but a single specimen, which he did not designate type. It is from the Danian Bryozoan Limestone of Rejstrup (Denmark), and is preserved in the collections of the Mineralogical and Geological Museum of Copenhagen University.

*Description* — The following description is based on material from the Bryozoan Limestone of Fakse: Tubes and spirals are medium-sized to moderately large, the maximum tube diameter being 3 mm, that of the spiral 8 mm. The spirals are planar or, more often, curved following the curvature of cylindrical substrates. Generally several spirals of the same specimen cover each other to a considerable degree due to the relatively small size of the substrate, forming an irregular three-dimensional cluster. Umbilicate and non-umbilicate spirals occur in about equal numbers. A longitudinal keel occurs only in the anterior part of very few specimens, much more often there is an indistinct rounded edge instead. Alae are common, especially in the outer whorls of large spirals, but also, though less distinctly developed, in posterior tube parts. Erect anterior tube parts are present, showing peristomes

of a shape typical of the *Cementula/Spiraserpula* group. Generally, the tube's exterior is smooth, but a few large spirals are granulate. Many specimens are broken and show the tube's interior from which ITS are absent.

*Discussion* — *Cementula applanata* from Fakse (topotypical material from Rejstrup was not available for study) and *C. subditiva* from the Maastricht-Aachen-Liège area are closely comparable, but not identical: although it is often impossible to assign single specimens to either species, 'populations' as a whole display several differences (see below). The two taxa may in fact represent geographic subspecies, which are best separated at the subspecific level.

#### ***Cementula applanata subditiva* (Regenhardt, 1961)**

Pl. 3, Figs 1-12

v 1961 *Spiraserpula subditiva* Regenhardt, p. 42, pl. 1, fig. 9.

*Type* — The specimen illustrated by Regenhardt is the holotype by original designation; it is here reillustrated in Pl. 3, Fig. 2a-c; it represents 3 (or 4 ?) spirals overlying to a considerable degree. The large anterior spiral (diameter of spiral 7 mm, maximum diameter of tube 1.4 mm) has c 4 turns, a narrow, deep umbilicus, 4 very prominent (plus 2-3 less distinct) alae on its anterior 1½ turns and a keel on its anterior 2/3 turn. The aperture is slightly bulbous with a tooth-like process. As far as can be seen in a broken posterior spiral and in damaged parts of the anterior spiral, ITS are absent. Geulhem Member, Albert Canal sections at km mark 23,850, sample no. 125 in the Meijer Collection (1959), GPI Hamburg Collections, type catalogue no. 725.

*Description* — A single exceptional specimen (Pl. 3, Fig. 1) attached to a slender cylindrical bryozoan colony has a very slightly curved initial tube part of 0.5-0.6 mm in diameter and a preserved length of 4 mm. The tube then enwraps the bryozoan as seen in *Pegmaticula wegneri* (Jäger, 1983) forming a spiral of 1½ turns, and finally is raised above the substrate. In all other specimens the spiral does not enwrap a foreign body.

Nearly all specimens have become detached from their (more or less planar and large) substrate and lack the non-spiral initial tube part. Most specimens show 2, some 3 or 4 and perhaps even more spirals, most spirals being more or less planar (Pl. 3, Figs

2-5), but occasionally very irregular and high (Pl. 3, Figs 6, 7). Spirals generally cover each other for more than half of their surface. Sometimes short remains of non-spiral, more or less straight tube parts are visible between the spirals (Pl. 3, Fig. 8). The diameter of the largest (anterior) spiral, with  $c$  4 turns, is 10.2 mm in an exceptionally large specimen (Pl. 3, Fig. 3): a diameter of 5-7 mm is normal. In a number of specimens the last half turn takes 'a short cut' by growing irregularly across the upper side of the spiral (Pl. 3, Figs 5, 7). Nearly always there is a distinct, narrow deep umbilicus in the centre of the spiral (see Pl. 3, Figs 2a, b, 3, 4, 6). The tube diameter increases slowly, and reaches a maximum of mostly 1.0-1.5 mm, rarely 2 mm.

Spirals rarely bear longitudinal and transverse ornament (only in the holotype [Pl. 3, Fig. 2] and in an additional specimen [Pl. 3, Fig. 5]): a keel may be present on the anterior  $2/3$  turn of the spiral, and some alae may occur on the anterior  $1\ 2/3$  turns. There is no granulation.

The anterior tube part may erect above the substrate, but only short fragments of less than 3 mm in length have been preserved (Pl. 3, Figs 5a, 9, 10). Nearly all fragments of the erect tube part possess a quadripartite peristome (Pl. 3, Figs 9, 10) similar to those of other specimens of the *Cementula/Spiraserpula* group. On the underside there often occurs a furrow (Pl. 3, Figs 9b, 10c), and occasionally a keel instead. The cross-section of the erect tube part (Pl. 3, Fig. 9c) is very slightly depressed-circular.

The tube wall (Pl. 3, Figs 3b, 7c, 11, 12a, b) is moderately thin, and consists of a lightly yellowish outer parable layer, as thick as or thicker than the two other layers together and cementing the turns, a white inner parable layer with transverse striation on its interior, and a white innermost cylinder layer, smooth on its interior and often broken or dissolved (in part preserved in Pl. 3, Figs 3b, 11). There are no ITS (Pl. 3, Figs 7c, 12a, b).

*Discussion* — Regenhardt (1961) thought that the shape of the aperture (bulbous and with alae) in the holotype was a feature characteristic of the species. However, most specimens of the species lack this attribute, and, moreover, it also occurs occasionally in other species of the *Cementula/Spiraserpula* group.

*Comparison* — *Cementula applanata applanata* grows to slightly larger sizes, while non-umbilicate spirals are more commonly found. Alae are not restricted to the outer parts of large spirals, but may also occur in juvenile tube parts. Large spirals may show granulation. *C. a. sphaerica* Brünnich Nielsen, 1931 often

comprises but a single spiral, and only rarely does an umbilicus occur. In *C. contorta* Brünnich Nielsen, 1931 the turns become fairly high. *C. ? boryszewiensis* Pugaczewska, 1967 from the Dano-Montian of Poland is often granulate. *Spiraserpula spiraserpula* Regenhardt, 1961 from the Campanian is indistinctly ornamented as is the present species, but the spirals envelop each other to a lesser degree at least when the substrate was large, and ITS are present. In *S. scruplea* from the Meerssen Member ITS occur, and the spirals are more depressed. An unnamed *Spiraserpula* species from the Palaeocene of Kazakhstan is larger and has ITS, and the spirals often become very high.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: not rare, upper part, not rare. Geulhem section, lower part of the Geulhem Member: very rare, upper part, absent.

*Occurrence elsewhere* — Unknown.

Genus *Rotularia* DeFrance, 1827a (= *Spirulaea* Bronn, 1827, *Tubulostium* Stoliczka, 1868, ? *Rotulispira* Chip-lonkar & Tapaswi, 1973)

*Type species* — *Serpula spirulaea* Lamarck, 1818.

*Remarks* — Contrary to Regenhardt (1961), Lommerzheim (1979, and *in litt.*, 1984) and Knight-Jones (1981), I still think that *Rotularia* and similar genera such as *Conorca* Regenhardt, 1961, and *Orthoconorca* Jäger, 1983 should be referred to the Serpulidae sensu stricto, instead of to the Spirorbidae.

In *Rotularia* as well as in Spirorbidae, the tube has a small non-spiral part (not clearly expressed by Jäger, 1983). In the Spirorbidae this tube part is very small and delicate and usually not preserved in adult tubes. However, in *Rotularia*, *Conorca* and related genera it is more distinct and longer — not only in absolute size, but also in relation to the size of the spiral of the adult tube — and is very often preserved. *Rotularia* is also much larger than spirorbids, with only few of the 'normal' spirorbid species reaching the size of *Conorca* and none reaching the size of at times very large *Rotularia*. Moreover, if *Rotularia* were to have had a calcareous operculum like 'normal' spirorbids, this should now have been found at least in some of the large and common species of this genus. Therefore, its operculum was probably not calcareous. The spiral coiling of adult tubes is an insufficient criterion for placing *Rotularia*

with the Spirorbidae, as other non-spirorbid Serpulidae are also more or less spirally coiled, e.g. *Cementula* and *Spiraserpula* (Pillai & ten Hove, in prep.). It is my opinion that the tribus Rotulariae Regenhardt, 1961 is but an artificial taxon, because the genera *Rotularia*, *Conorca* and *Gynaecoonitis* Regenhardt, 1961 are probably not closely related. *Diagnosis* — Tube with a small initial non-spiral part attached to a substrate, followed by a more or less regularly, tightly coiled planar or inversely conical spiral with coils cemented to each other, but normally not cemented to the substrate. The spiral usually has an umbilicus. The diameter of the spiral generally exceeds its height. Coiling of the spiral is predominantly sinistral but occasionally dextral. The tube wall consists of two layers, a thick outer one which may appear to comprise two layers and a thin inner one. The tube wall may be thickened by callous material. The free anterior non-spiral tube part is sometimes very long, straight or curved.

*Comparison* — In most other spirally coiled genera of Serpulidae the spiral is attached to the substrate by at least the entire first turn. *Orthoconorca conica* (von Hagenow, 1840) is an exception, but in this and other species of *Orthoconorca* and *Conorca* the very slender shape of the spiral differentiates them from *Rotularia*. Many species recorded by Rovereto (1904b) are coiled Serpulidae, not *Rotularia*. In some Jurassic species known exclusively from literature data it is difficult to distinguish *Rotularia* from *Nogrobs* de Montfort, 1808 (see Jäger, in press b). The cross-section of the latter genus normally is square or at least quadrangular, but it is modified in the spiral part of some species. Generally, a square cross-section occurs in the free, non-coiled anterior part of the tube, but even there it may be circular in some specimens. In general, however, the presence or absence of a square cross-section in the anterior part facilitates distinguishing *Nogrobs* from *Rotularia*. *Stratigraphic range* — Pliensbachian/Toarcian-Oxfordian?, early Kimmeridgian-late Eocene.

*Remarks* — Schmidt (1955a) presented a detailed revision of the present genus. Although most of his data and conclusions are followed here, I disagree with his assignment to *Rotularia* of a number of species, viz. *ampullacea* (J. de C. Sowerby, 1829) is a species of *Neovermilia*, *lithuus* (von Schlotheim, 1820) is a poorly preserved species of middle Triassic age, *trochiformis* (von Hagenow, 1840) is a species of *Conorca*, *heliciformis* (Goldfuss, 1831) is probably not referable to *Rotularia*, *subcarinata* (Goldfuss, 1833) is an internal mould only, and may either be a species

of *Rotularia* or a gastropod, *tumida* (J. de C. Sowerby, 1829) is a species of *Nogrobs*, but may be part of a phylogenetic lineage leading to *Rotularia*.

Some of the species Schmidt preferred to exclude from *Rotularia* are in fact true species of this genus, viz. *sowerbyi* (Mantell, 1822), *callosa* (Stoliczka, 1868), *polygonalis* (J. de C. Sowerby, 1829), and *quinquecarinata* (Roemer, 1841). Additional material of *ovata* (J. Sowerby, 1813) and *umbonata* (J. Sowerby, 1813) is needed to substantiate their assignment to the present genus.

'Definite but poorly preserved *Rotularia* first appear in the Ururoan stage' (Stevens, 1967, p. 354, = Pliensbachian-Toarcian). As Stevens did not provide figures of these specimens it cannot be decided whether they actually belong to *Rotularia* or *Nogrobs*. The same holds for a number of non-figured specimens from other strata recorded by Stevens (1967, pp. 354, 356, 357). Especially the specimens from the early Tithonian may turn out be species of *Nogrobs*, and the identification of the early-middle Callovian material is uncertain. Ball (1960, p. 21) referred *compressa* Young & Bird (1828, p. 250 = *concinus* J. de C. Sowerby, 1829, p. 195) from the late Toarcian of Yorkshire and *tumidus* J. de C. Sowerby, 1829 (p. 195) from the 'Corallian' to *Rotularia*, whereas Jäger (in press b) prefers assignment to *Nogrobs*.

*Rotularia* may have descended from *Nogrobs* during Callovian-Oxfordian time, as at that time some species of *Nogrobs* lost the characteristic square cross-section and had a callus filling the umbilicus as seen in some species of *Rotularia*, and in the Valanginian large planar *Nogrobs* spirals reached the size of *Rotularia*. However, this assumption is based on very few specimens and literature data only and needs to be substantiated.

The genus *Rotularia* is usually divided into four subgenera. This subdivision (Lommerzheim, 1979; Macellari, 1984) is followed here, although it is uncertain whether these subgenera really have a monophyletic origin. Some species described by early authors, amongst whom is Rovereto (1904b), cannot be fully discussed without additional data and are therefore omitted here.

The *Rotularia* sp. with a bicarinate periphery illustrated and described by Fleming (1972, p. 751) from the early Tithonian of New Zealand appears to be a true *Rotularia*, but the subgenus is uncertain (? *Austrorotularia*). The species *lituola* (Leymerie, 1846b) from the Neocomian cannot be appreciated through a lack of literature data.

— *R. (Austrorotularia)* Macellari, 1984 has a 'tricarinate keel present in juvenile, adult or in both stages. Tube commonly thickened by an external callosity' (Macellari, 1984, p. 1104). It is almost restricted to the southern hemisphere, but occurs also in India (Stoliczka, 1868) and Japan (Yabe & Nagao, 1928). It was originally recorded from the Aptian-Maastrichtian, but it appears that *Rotularia* sp. indet. described and figured by Stevens (1967, p. 353) from the ? early Kimmeridgian of Antarctica and recorded also from the early and middle Kimmeridgian of New Zealand should also be referred to this subgenus, which would make *Austrorotularia* and not *Praerotularia* is the stratigraphically oldest of the subgenera.

Cretaceous species of *Austrorotularia* include: *andina* (Camacho, 1949), *callosa* (Stoliczka, 1868), *ornata* (Wilckens, 1922), *fallax* (Wilckens, 1910), *tenuilaevis* Macellari, 1984, *zinsmeisteri* Macellari, 1984 and sp. Macellari (1984).

— *R. (Praerotularia)* Lommerzheim, 1979 appears to be the 'main line' of Cretaceous *Rotularia* with the most species and perhaps also the most specimens. It comprises fairly large tubes with transversely wrinkled surfaces and with or without simple longitudinal ornament. Range: Hauterivian-Eocene (Eocene according to Lommerzheim, 1979, p. 174; personally I know of no Cainozoic occurrence of this subgenus).

*Rotulispira* Chiplonkar & Tapaswi, 1973 (p. 209) probably is a synonym of *R. (Praerotularia)*; it appears doubtful whether the features mentioned by Chiplonkar & Tapaswi (p. 209), '... having detachment of the apertural portion without thickening by calcareous deposition and without constriction of the tube; also the detached portion of the tube is very much longer than what is found in *Rotularia*' are distinctive features important enough for separation at the generic level. The only specimen of *Rotulispira* known to date is the holotype of *R. stoliczkai* Chiplonkar & Tapaswi, 1973.

Species of the present subgenus include: *ovata* (J. Sowerby, 1813) ?, *phillipsii* (Roemer, 1841), *umbonata* (J. Sowerby, 1813) ?, *sowerbyi* (Mantell, 1822), *pupoides* (Stanton, 1901) ?, *australis* Cox, 1953, *kitchini* (Bonarelli & Nágera, 1921) ?, cf. *kitchini* ?, *concava* (J. Sowerby, 1813), *chathamensis* Boreham, 1959, *damesii* (Noetling, 1884), *saxonica* Müller, 1966, *spirulaeoides* Glaessner, 1958, *gregaria* (Etheridge, 1907) *sensu* Regenhardt, 1961, *dorsolaevis* Ball, 1960 ?, *shackletoni* (Wilckens, 1910), *libyca* Maccagno, 1946, *libyca* var. *ornata* Maccagno, 1946, *solarioides* (Wanner, 1902),

*stoliczkai* (Chiplonkar & Tapaswi, 1973), *inflata* Pasternak, 1973 and *varians* Pasternak, 1973 ?.

In the northern hemisphere, *R. (Praerotularia)* and *Rotularia* as a whole became rare, and in central Europe they appear to be absent from the Turonian (or Coniacian) to Maastrichtian, whereas in the southern hemisphere a number of species are fairly common. Obviously, the Cenomanian-Turonian boundary event affected the genus only in the northern hemisphere.

— *R. (Tectorotularia)* Regenhardt, 1961 has a planar spiral and a quadrangular to hexangular cross-section. Range: Hauterivian-Maastrichtian. Species included are: *quinquecarinata* (Roemer, 1841), *couloni* Defrance, 1827a ?, *gregaria* (Etheridge, 1907), *landereri* (Mallada, 1887), *polygonalis* (J. de C. Sowerby, 1829), *discoidea* (Stoliczka, 1868), *rotuloidea* Chiplonkar & Tapaswi, 1973, *westfalica* Lommerzheim, 1979, *rotula* (Goldfuss, 1831), cf. *discoidea* (Stoliczka, 1868) *sensu* Wilckens, 1924, *rotula* (Morton, 1834) ? (non *rotula* Goldfuss, 1831).

— *R. (Rotularia)*: see below.

Obviously, *Rotularia* became extinct at the Eocene-Oligocene boundary.

*Mode of life* — It is clear that *Rotularia* most commonly occurred on soft substrates (clay, marl, silt and/or sand), often associated with other soft-bottom dwelling serpulids such as *Pentaditrupe* or *Ditrupe*. In contrast to the size of the adult tube, *Rotularia* needed only a very small substrate for settlement. Probably the adult spiral tubes often broke off from the juvenile non-spiral parts and acted as an anchor lying on or partly sunken into the seafloor with the aperture pointing obliquely upwards.

Macellari (1984, p. 1103) found that in *T. (Austrorotularia)* specimens bored by carnivorous gastropods probably these predation traces were close to the aperture, and he concluded that perhaps *Rotularia* burrowed into the soft substrate with the aperture pointing almost vertically upwards. However, the anterior position of the gastropod predation traces could also be explained by the position of the worm's soft parts in the anterior tube. Moreover, it is not necessary for *Rotularia* to have burrowed actively into the sediment, but the spiral part of adult tubes might have been covered with sediment passively without being disadvantageous to the animal. I agree with Wrigley (1951, p. 182, on *R. (R.) bognoriensis*) that, 'The various modes of coiling, from almost discoid to conic, may have depended on the rate of accumulation of London Clay sediment. Where this was rapid, the creature

had to rise its tube in a conical form to keep its aperture in water, clear of silt. With slower accumulation, discoid forms might prevail.'

The total absence of *Rotularia* from the late Cretaceous chalk facies of central Europe may possibly be explained by the competition of similar spiral soft-bottom dwelling species such as *Conorca* and *Orthoconorca conica*.

Subgenus *Rotularia* DeFrance, 1827a

*Type species* — *Serpula spirulaea* Lamarck, 1818.

*Diagnosis* — The medium-sized spiral generally is planar to low trochospiral, with longitudinal ornament either present or absent, and when present there is no sharp quadrangular to hexangular cross-section of the tube. Transverse ornament is but weak, there are no laminated growth lines, and no peristomes.

*Comparison* — Discrimination from *Austrorotularia* is not always easy. Three keels may be also present in *Rotularia*, but in these cases the tube is not thickened by an external callosity. The tubes of *Tectorotularia* have a sharp quadrangular to hexangular cross-section. *Praerotularia* grows larger and has a transversely wrinkled surface. Longitudinal ornament is either absent or weakly developed.

*Stratigraphic range* — Danian-late Eocene.

*Remarks* — The derivation of the present subgenus, either from *Austrorotularia* or from *Tectorotularia*, is not yet clear. Derivation from the former taxon is favoured because of the fact that in the stratigraphically youngest species of *Austrorotularia* the tricarinate keel becomes indistinct, but then again this should not be overestimated. Already in the Palaeocene there is a wide range of variation as far as morphology is concerned.

Palaeocene species include: *hisingeri* (Lundgren, 1891). Probably, at the beginning of the Palaeogene, there had been a radiation; an unknown 'survivor' species had produced a considerable number of different but similar species, all of small size. The following 'species' are therefore considered to represent but subspecies of *tobar* (Gardner, 1935), viz. *mcglameryae* (Gardner, 1935), sp. (Gardner, 1935), *tobar* (Gardner, 1935), *gracilis* n. subsp. and *vroenhovensensis* n. subsp.

Eocene species include: *bognoriensis* (Mantell, 1822), *cortezi* (Gardner, 1939), *horatiana* (Gardner, 1939), *leymeriei* Rovereto, 1898 = nom. nov. pro *quadricarinata* Münster *sensu* Leymerie, 1846a (= *angulosa* Chenu, 1842, according to Schmidt, 1955a,

pp. 170, 177), *pseudospirulaea* (Oppenheim, 1901), *leptostoma* (Gabb, 1860), *nysti* (Galeotti, 1837), *spirulaea* (Lamarck, 1818), *nummularia* (von Schlotheim, 1820) = junior synonym of *spirulaea*, *mayeri* (Rovereto, 1898), *complanata* DeFrance, 1827a = junior synonym of *spirulaea*, *clymenioides* (Guppy, 1866), *angulosa* (Chenu, 1842), *angulosa* var. *crassa* (Doncieux, 1926), *corbarica* (Munier-Chalmas in Hébert, 1882) (fide Rovereto, 1904b), *dickhauti* (White, 1881) (illustrated in White, 1882), *subcarinata* (Goldfuss, 1833) ?, *cristata* DeFrance, 1827a ?, *lithuus* DeFrance, 1827a (non *lithuus* von Schlotheim, 1820)].

Records from the early Oligocene [*nummula* (von Koenen, 1891) and *koeneni* Rovereto, 1898 [= *tumida* (von Koenen, 1891) non Sowerby] have not been confirmed and are probably erroneous, see discussion in Schmidt (1955a, p. 178). The record of *Rotularia* cf. *pseudospirulaea* by Jakubowski & Musiał (1977) from the Polish Tortonian is very doubtful.

### ***Rotularia (Rotularia) hisingeri* (Lundgren, 1891)**

Pl. 4, Figs 14-19

- non 1820 *Serpulites lithuus* von Schlotheim, p. 98.  
1831 *Serpula lithuus* ? Hisinger, p. 134, pl. 3, fig. 6 (non vidi, fide Schmidt, 1969).  
1837 *Serpula Lituus* [sic] Schloth. — Hisinger, p. 20, pl. 4, fig. 8.  
1891 *Serpula Hisingeri* Lundgren, p. 119.  
1920 *Serpula Hisingeri* Lundgren — Rosenkrantz, p. 24.  
1926 *Serpula (Spirorbis) Hisingeri* Lundgr. — Ødum, p. 165.  
1931 *Spirorbula Hisingeri* Lundgr. sp. — Brünnich Nielsen, p. 103, pl. 3, figs 1-4.  
1955a *Rotularia hisingeri* (Lundgren) [sic] — Schmidt, p. 176.  
1960 *Spirorbula hisingeri* (Lundgr.) — Kühn, p. 164.  
1969 *Spirorbis (Dexiospira) hisingeri* (Lundgren), 1891 — Schmidt, p. 36.

*Type* — Hisinger's (1831, pl. 3, fig. 6) original specimen is probably lost (see Schmidt, 1969, p. 37). Hisinger's figure shows a spiral with five turns and a protruding straight anterior tube part, its length exceeding the diameter of the spiral.

Hisinger's specimen is stated to have come from the Silurian of Klinteberg (Gotland, Sweden), but Regnéll (*in* Schmidt, 1969) remarked that this must be a mistake. Most probably it originated from the Danian of Skåne (southern Sweden).

*Description* — The tube has a more or less straight non-spiral initial part (Pl. 4, Figs 14c, 15b, 16b, 17, 18c, 19c), of which only a short fragment of up to 4 mm is preserved. The attachment to a substrate is



preserved only in a single atypical specimen (Pl. 4, Fig. 19c, see below). The diameter of this tube part is up to 1.0 mm.

The diameter of the spiral is rather small, 4.0-5.2 mm, the spiral being inversely conical, but very low (Pl. 4, Figs 14b, 16b, 18b, 19b), with up to 3<sup>1</sup>/<sub>4</sub> turns in specimens from the Maastricht-Aachen-Liège area, and up to 5 turns in Danish and Swedish specimens according to Hisinger (1831, 1837) and Brünnich Nielsen (1931). The umbilicus is invariably wide. Of eighteen sufficiently well-preserved spirals from the Maastricht-Aachen-Liège area fifteen are sinistral (Pl. 4, Figs 14, 17, 19) and three are dextral (Pl. 4, Figs 15, 16, 18). The turns of the spirals are cemented together.

The tube diameter gradually increases up to the transition from the spiral to the protruding anterior part, where the tube may be slightly swollen and reach 1.5 mm, rarely up to 2.0 mm in diameter. In the horizontally protruding straight anterior part (Pl. 4, Figs 15, 16), which may be up to 4.2 mm in length, the tube diameter decreases slightly.

The tube normally bears no ornament. Rarely there may be a very shallow but wide, indistinct longitudinal furrow on the upper side of the spiral and a very weak longitudinal edge at the periphery of the spiral. In rare instances, there may be low swellings at the end of the spiral and at the beginning of the straight anterior tube part. A single specimen shows an incision in its spiral which was possibly brought about by an injury.

The cross-section of the tube is circular (Pl. 4, Figs 14b, 16b, 18b, d, 19b), the tube wall being moderately thick to thick. The lumen is circular, sometimes slightly eccentric (Pl. 4, Fig. 18d). The tube wall comprises a thicker outer layer and a thinner inner layer. The tube's exterior is smooth. Only when the inner layer is destroyed by weathering does the inner surface appear to bear a transverse striation.

A single specimen (Pl. 4, Fig. 19) differs from the others in the character of its attachment: not only was the non-spiral initial tube part attached to an unpreserved planar large substrate, but exceptionally also the spiral. The base with which the tube was attached to the substrate in part shows a cellular construction with very short closely spaced cells (Pl. 4, Fig. 19c). Confusion with *Serpula* ? *insiticia* would have been possible in this case, were it not for the fact that in all other features this specimen agrees wholly with normal *R. hisingeri*.

*Discussion* — It cannot be wholly ruled out that

*hisingeri* is not a true *Rotularia*, the shape of the spiral then being just a matter of convergence.

*Comparison* — *Rotularia hisingeri* differs from other species of the genus by the general absence of ornament and by its small size.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: common, upper part, very rare. Geulhem section, lower part of the Geulhem Member: absent, upper part, absent.

*Occurrence elsewhere* — Danian of Denmark, Sweden and Austria.

### ***Rotularia (Rotularia) tobar* (Gardner, 1935)**

1935 *Tubulostium tobar* Gardner, p. 281, pl. 26, figs 1-5.

1939 *Tubulostium tobar* Gardner — Gardner, p. 19.

1955a *Rotularia tobar* (Gardner) — Schmidt, p. 177.

*Type* — Gardner (1939) designated holotype the specimen illustrated in figs 1-3. It is an almost planar spiral of 6 mm in diameter with a tube diameter (at aperture) of 1.0 mm, from the Wills Point Formation, Upper Midway Group (late Palaeocene), United States Geological Survey Station 11754, 6 miles south of McFarland sheep pens and 27 miles southeast of Eagle Pass, on the Windmill (Jacal) ranch road, Maverick County, Texas. United States National Museum Collections, no. 370940.

*Description* — 'Shell a small angular tube coiled almost in a single plane, with one surface flattened, and the other slightly depressed centrally. The tube, increasing very slowly in diameter, rudely quadrate in cross section, the outer angles lined by ill-defined spirals; outer margin between the spirals flattened. The upper and lower surfaces very feebly concave. Outer margin of the aperture subquadrate, the inner circular, firmly coherent to the preceding coil. Evidence of former growth lines probably discernible in certain rugosities which parallel the aperture and minutely wrinkle the shell. [...] ... characterized by the discoid outline and the quadrate outer margin of the aperture.' (Gardner, 1935, p. 281).

*Discussion* — The species shows an 'astonishing amount of variation' (Gardner, 1935, p. 281). Gardner listed specimens from different localities from the Wills Point (Upper Midway) and Kincaid (Lower Midway) Formations. Some of the specimens from certain localities 'develop a third spiral midway upon the keel, almost equal in prominence to those at the margins of the keel'. Also, 'the apex is as a rule more depressed upon the Maverick County forms' (= Wills Point Formation) 'than upon those

of the Colorado River drainage' (= Kincaid Formation).

Gardner (1939, p. 19) already stated when comparing *mcglameryae* with *tobar* that the 'range of variation in these forms is not very well known, and possibly these two Midway species may be only varietally distinct.' These two American species and the two taxa from the Maastricht-Aachen-Liège area described below are very similar in shape and are probably closely related to such an extent that they should not be distinguished at the species level. They possibly represent but ecological varieties, but are here considered subspecies of *tobar*, perhaps genuine geographic subspecies. In the Maastricht-Aachen-Liège area, neither a phylogenetic progression nor a geographic separation of the two subspecies can be found.

*Comparison* — *Rotularia hisingeri* is smaller and easily distinguished by the near-absence of any ornament, whereas *R. dickhauti* (White, 1881) is larger, but similar otherwise. Whether the latter is to be considered to represent yet another subspecies of *tobar* remains to be determined. In *R. leptostoma* (Gabb, 1860) the spiral is more distinctly trochospiral at least in juveniles, and the two sharp keels at the spiral's periphery are more closely spaced. *Rotularia horatianum* (Gardner, 1939) grows larger and has a very distinct transverse ornament. The three keels of many specimens of several subspecies of *tobar* (*gracilis* in particular) resemble those of *R. (Austrotularia)*, but this subgenus grows two to three times as large, and its umbilicus is narrower.

### ***Rotularia (Rotularia) tobar gracilis* n. subsp.**

Pl. 5, Figs 1-6

*Derivatio nominis* — *gracilis* (L.) meaning graceful, in comparison with *tobar vroenhovens* the tube being slightly smaller and having a somewhat thinner wall.

*Type* — The specimen figured in Pl. 5, Fig. 1 is here designated holotype; it is a sinistral spiral (6.5 mm in diameter) with  $4\frac{1}{2}$  turns, followed by a short, obliquely broken and somewhat distorted straight anterior tube part. Ornament is well developed. The third longitudinal keel is relatively weak, but present. Albert Canal sections, upper part of the Geulhem Member, Natuurhistorisch Museum Maastricht Collections, no. NHMM 1992201-1 (leg. M. Jäger).

*Diagnosis* — The diameter of the tube and spiral are

relatively small, the spiral being generally very low, almost totally planar. The cross-section of the tube is sharply square to trapezoid with the upper side of the trapezium mostly positioned at the periphery of the spiral, more rarely oblique between the upper side and the periphery. The two upper edges of the trapezium bear small, sharp granulate keels. In most specimens a third, small sharp keel in the centre of the trapezium's upper side. The transverse ornament consists of minute, somewhat undulate ridges. The tube wall is moderately thin to just moderately thick.

*Description* — The tube has a non-spiral initial part, of which only short fragments of up to 2.5 mm in length and up to 1.0 mm in diameter are preserved. The attachment area of this initial tube part to the substrate is not preserved. The diameter of the spiral is generally 4.5-7 mm; 7 mm also being the maximum diameter. The spiral is even lower than in that of *tobar vroenhovens*, with hardly any trace of becoming trochospiral. There are up to 5 turns, the umbilicus is always present and nearly always wide. Of sixty-eight sufficiently well-preserved spirals thirty-two are sinistral (Pl. 5, Figs 1, 3, 4) and thirty-six dextral (Pl. 5, Fig. 2).

In rare instances, the spiral is irregular. In a single specimen the impression of the substrate is seen, which means that several turns of the juvenile spiral must have been directly attached to this substrate.

In another specimen (Pl. 5, Fig. 4) the spiral had already reached at least 5 mm in diameter, when the tube broke at the periphery at  $\frac{3}{4}$  whorl distance from the aperture. At the point of breakage the animal then formed a new 9 mm long tube growing out of the old one. The new tube at first followed the periphery of the old one for  $\frac{1}{4}$  whorl, then formed a short straight anterior part. In a third specimen the tube had also broken. Here the new part at first grew away from the spiral for a short distance, then turned back to grow along the periphery of the spiral, leaving a cavity of 0.9 mm in length and 0.4 mm in width between the turns of the spiral. In a fourth specimen (Pl. 5, Fig. 3) the last  $\frac{1}{2}$  turn did not follow the periphery of the spiral, but grew across its underside.

The tube diameter gradually increases up to the transition from the spiral to the protruding anterior part, where the tube often is slightly ( $\approx 45^\circ$ ) distorted around its longitudinal axis (Pl. 5, Figs 1a, c, 4a, 4f), but scarcely swollen, and may reach a maximum diameter of 1.5 mm. In the horizontally protruding

straight anterior part (Pl. 5, Fig. 5), which may be up to 8.7 mm long, the diameter remains fairly constant. Generally, the tube has three (Pl. 5, Figs 2d, 3b, 4c), more rarely two small sharp keels. The tube's base is somewhat enlarged and forms rounded granulate edges on the left and right sides (*i.e.* at the upper and lower side of the spiral). The transverse ornament is marked especially at the keels and edges, where some small granules or pustules may appear, but occurs also in between.

The lumen is circular. In the tube wall (Pl. 5, Figs 1e, 4b, 5c, 6) two layers can be distinguished, the outer layer being slightly thicker than the inner one. Between them there very often is a delicate interstice formed by disintegration of tube material. Here the tube wall breaks easily, in which case a rather indistinct transverse striation becomes visible.

*Discussion* — The planar spiral would suggest a soft bottom habitat with a low sedimentation rate. In samples yielding *tobar gracilis*, the soft bottom dweller *Ditrupea schlotheimi*, which occurs in great numbers, is practically the only other serpulid associated.

*Comparison* — In the closely similar *tobar* s. str. only a few of the specimens have three longitudinal keels, and those from the type locality possess only two keels. In *tobar gracilis*, however, the three-keeled version is commoner than the two-keeled version.

*Rotularia tobar vroenhovens* is slightly more trochospiral, has a distinctly larger tube diameter, a far less distinct longitudinal and transverse ornament and a thicker tube wall. Most specimens of the two subspecies from the Maastricht-Aachen-Liège area are easily referred to either of these on account of their morphology; transitional specimens are rare.

Specimens of *Rotularia spiritorta* (Rovereto, 1904b) from around the Palaeocene/Eocene boundary of the Tremp Basin (NE Spain, leg. Drs R.H.B. Fraaye) possess a very similar ornament, but are easily distinguished by their high trochospirals. In *tobar mcglameryae* the transverse ornament and, in most specimens, the third longitudinal keel are absent.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: absent, upper part, frequent. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, very rare.

*Occurrence elsewhere* — Unknown.

**Rotularia (Rotularia) tobar vroenhovens**  
n. subsp.

Pl. 6, Figs 1-6

*Derivatio nominis* — After the village of Vroenhoven/Riemst, NE Belgium, near the Albert Canal sections.

*Type* — The specimen illustrated in Pl. 6, Fig. 1 is here designated holotype. The sinistral spiral (diameter 7 mm, height 3 mm) has three turns. At the transition from the spiral to the anterior tube part the tube diameter is 2.3 mm. At the broken anterior end the tube diameter is 1.8 mm, and the tube wall is apparently very thick there, but this is caused by another serpulid tube (very probably *Ditrupea schlotheimi*) filling the lumen (cone-in-cone structure). Geulhem Member (top) with *Tylocidaris bruennichi* Ravn, 1928 and *D. schlotheimi*, Albert Canal sections at Vroenhoven-Riemst, Natuurhistorisch Museum Maastricht Collections, no. NHMM 1992202-1 (leg. J.W.M. Jagt).

*Diagnosis* — The diameter of the tube and spiral are moderately small, the spiral being inversely conical, but relatively low to very low. The cross-section of the tube is rounded trapezoid with the upper side of the trapezium positioned obliquely between upper side and the spiral periphery. The upper side of the trapezium resembles a flat band protruding laterally and forming a rounded edge on the left and right margins. Transverse ornament is normally absent. The tube wall is relatively thick.

*Description* — The tube has a non-spiral initial part, of which only short fragments of up to 1.5 mm in length and up to 1.0 mm in diameter are preserved. Its attachment to a substrate is not preserved. The diameter of the spiral generally is 5.5-7 mm, more rarely does it reach a maximum of 8 mm. Most spirals are fairly regular, only few are slightly irregular (Pl. 6, Fig. 4). Although the spiral is relatively low, a trochospiral trend is recognisable (less distinct in Pl. 6, Figs 1c, 1e, 2b, more so in Pl. 6, Figs 4b, 5b, 6). The height of the spiral is more variable than it is in *R. hisingeri* or in *tobar gracilis*. Rarely does the height of the spiral reach 80 % of its diameter, and at the top of the spiral the diameter decreases again, so that the spiral becomes barrel-shaped (Pl. 6, Fig. 6). Up to 4½ turns, the umbilicus is always present and nearly always wide. Of forty-eight sufficiently well-preserved spirals twenty-seven are sinistral (Pl. 6, Figs 1, 3, 4, 6) and twenty-one dextral (Pl. 6, Figs 2, 5).

The tube diameter gradually increases up to the transition from the spiral to the protruding anterior tube part, where the tube often is slightly distorted and swollen (Pl. 6, Fig. 1a) and where it may reach a maximum diameter of 2.3 mm. In the horizontally protruding straight anterior tube part, which may be up to 6 mm long (Pl. 6, Fig. 3), the diameter decreases slightly.

The tube has two longitudinal edges. In most specimens these edges are prominent only laterally, whereas the upper side of the band is smooth (Pl. 6, Figs 1b, c, e, 3, 5b). However, in a few specimens these edges are prominent also on the upper side of the band (Pl. 6, Figs 2b, d, 4b). Rarely does a third weak longitudinal edge occur in the centre of the band. This band with the edges is present not only on the spiral, but also on the protruding tube part (Pl. 6, Figs 2d, 3).

Transverse ornament is generally absent. Only rarely do fine wrinkles or irregular swellings brought about by regeneration of injuries occur. The tube section is rather variable in detail. The tube wall reaches its maximum thickness at the transition from the spiral to the anterior protruding part (Pl. 6, Figs 1d, 2c), the lumen being circular. The tube wall consists of two layers, the outer being 1½ to 4 times as thick as the inner. Only when the inner layer has been destroyed by weathering, does the inner surface show a transverse striation. Often water movement washed tubes of *D. schlotheimi* or other cylindrical or conical objects (cone-in-cone structure) into the lumen. Moreover, recrystallisation, which has filled the interstices between these objects and the tube wall, is relatively strong in the interval from which most of the specimens were collected. Both post-mortem phenomena provide an explanation for the fact why the lumen appears to amount to only 20 % of the tube diameter in a number of specimens.

*Discussion* — *Rotularia tobar vroenhovensis* is found in relatively coarse-grained sediments and is thought to have been better adapted to slightly higher energy conditions than *tobar gracilis* on account of its thicker wall and slightly more distinct trochospiral shape.

*Comparison* — *R. tobar gracilis* has an even lower spiral, a distinctly smaller tube diameter, a much more marked longitudinal and transverse ornament and a thinner tube wall. *R. tobar mcglameryae* resembles *t. vroenhovensis*, but has a still lower spiral with only scarcely rounded longitudinal edges. *R. dickhauti* (White, 1881) is closely similar, but less

trochospiral, generally has (its range of variation is at present unknown) three longitudinal edges and 'shows under the lens a peculiar granular or rather an etched appearance' (White, 1881, p. 161).

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: extremely rare, upper part, frequent. Geulhem section, lower part of the Geulhem Member: absent, upper part, absent.

*Occurrence elsewhere* — Unknown.

Genus *Ditrupe* Berkeley, 1835

*Type species* — *Dentalium subulatum* Deshayes, 1825 = *Dentalium arietinum* O.F. Müller, 1776 (see ten Hove & Smith, 1990).

*Diagnosis* (see ten Hove & Smith, 1990, p. 102; data in brackets added by the present author) — Tube free, not attached to substratum, elongated curved fusiform (mostly shaped like an elephant's tusk with the curvature slightly decreasing towards the anterior end), circular in cross-section. Tube open at both ends, broadening anteriorly though exterior tapers just before the tube mouth. (In general, no longitudinal edges). Tube wall consisting of variably (thick) hyaline outer and opaque (thin, often bearing a transverse striation) inner layer.

*Range* — Danian-Recent.

*Remarks* — Derivation of *Ditrupe* from the pentangular genus *Pentaditrupe* Regenhardt, 1961 (early Sinemurian-Danian) via 'mixed populations' of *Pentaditrupe subtorquata* (Münster in Goldfuss, 1831) (middle Turonian-Danian) comprising specimens with either pentangular, subpentangular or circular cross-section, (as suggested by Jäger, 1983, p. 56), has now been substantiated by ten Hove's examination of the tube structure (see Jäger, in press a).

Except for the variety of *P. subtorquata* with circular cross-section, all of the hitherto examined (some being in need of further studies) so-called '*Ditrupe*' from the early Jurassic to the late Cretaceous have turned out to differ from true *Ditrupe*. The five '*Ditrupe*' species recorded by Tate (in Tate & Blake, 1876) all differ from true *Ditrupe*. '*Ditrupe*' *varicosa* Ball, 1960 has nodular swellings or more rarely annular constrictions and a different tube structure. *Ditrupe antarctica* Wilckens, 1907 has an irregular curvature, while *D. dentalina* (Leymerie, 1851) appears to be closely related to *Pyrgopolon* (see below). Lommerzheim (in litt., February 1984) now considers all his Cenomanian '*Ditrupe*' species to be related to *P. mosae* de Montfort, 1808. The two

species of '*Ditrupa*' of Chiplonkar & Tapaswi (1973) are dubious.

The stratigraphically youngest pentangular tubes with longitudinal edges have been described from the Danian of Denmark and Israel [see '*Ditrupa interjuncta*' Jessen & Ødum, 1923 and '*Hamulus subtorquatus*' of Avnimelech (1941), both being typical representatives of *P. subtorquata*]. Ten Hove (*in litt.*, September 1989) wrote, 'I have never seen a Recent *Ditrupa* (and I have seen literally thousands of specimens) starting off with an angular tube'. Thus it appears that longitudinal edges disappear altogether — even in early ontogenetic stages — during the Cainozoic.

The oldest unequivocal *Ditrupa* is *D. schlotheimi* from the Danian (see below). During the Cainozoic the tube shape changed only slightly, and discrimination of the various species described is rather difficult.

### ***Ditrupa schlotheimi* Rosenkrantz, 1920**

Pl. 4, Figs 1-13

- pars 1820 *Dentalites laevis* von Schlotheim, p. 93 (specimens from Copenhagen only, those from the Muschelkalk excluded).
- non 1822 *Dentalites laevis* von Schlotheim, p. 107, pl. 32, fig. 2.
- 1847 *Serpula liberaeformis* M. u. H. — Anonymous, p. 118.
- 1863 *Ditrypa liberaeformis* Mus. Univ. Hafn. Terkelskov. — Mørch, p. 467.
- 1920 *Ditrupa Schlotheimi* Rosenkrantz, p. 25, pl. 2, figs 8, 9.
- 1926 *Ditrupa Schlotheimi* Rosenkr. — Ødum, p. 167.
- 1931 *Ditrupula Schlotheimi* Rkz. sp. — Brünnich Nielsen, p. 95.
- 1961 *Ditrupa (Ditrupa) schlotheimi* Rosenkrantz — Regenhardt, p. 72.
- 1965 *Ditrupa schlotheimi* — Rasmussen, p. 35, pl. 8, fig. 26.
- 1967 *Ditrupa (Ditrupa) schlotheimi* Rosenkrantz, 1961 [*sic*] — Pugaczewska, p. 184, pl. 1, figs 1-4; pl. 2, figs 1-3.
- 1967 *Ditrupa schlotheimi* Rosenkrantz 1920 — Hucke & Voigt, p. 98, pl. 42, fig. 8.
- non 1973 *Ditrupa (Ditrupa) cf. schlotheimi* Rosenkrantz, 1920 — Pasternak, p. 33, pl. 5, figs 9-11.
- non 1984 *Ditrupa schlotheimi* Rosenkrantz, 1920 — Ziegler, p. 237, pl. 6, fig. 5.
- 1988 *Ditrupa schlotheimi* — Jagt & Janssen, table 1.
- 1988 *Ditrupa schlotheimi* Rosenkrantz, 1920 — Jagt & Collins, p. 190.

*Type* — The specimen illustrated by Rosenkrantz (1920, pl. 2, figs 8, 9) was designated 'holotype' by Ziegler (1984, p. 238), but in fact these are two specimens. Rosenkrantz's figure 8 is here designated lectotype; it is an anterior tube fragment with aperture, diameter *c* 1.5 mm, length *c* 11 mm (measurements taken from the illustration). Late Danian, lower *Crania* Limestone, Copenhagen, southern

port, Mineralogical and Geological Museum of Copenhagen University Collections.

*Description* — The tube is tusk-shaped, curved rather weakly (Pl. 4, Figs 1-9), being sometimes almost straight (Pl. 4, Fig. 10), with curvature decreasing towards the anterior end. The tube diameter gradually increases to an average of 0.8-1.5 mm, and a maximum of 1.6 mm. Towards the aperture the outer tube diameter slightly and gradually diminishes again, and the apertural region usually cannot be clearly discriminated from posterior tube parts. Only rarely is the aperture swollen club-shaped (Pl. 4, Figs 6a, 7a). Exceptionally, the apertural region is bottleneck-shaped (Pl. 4, Fig. 8). The maximum tube length is *c* 40 mm according to Rosenkrantz (1920).

Occasionally, there is an irregular narrow, sharp longitudinal furrow (Pl. 4, Figs 10, 11), but often this does not extend but for a few millimetres in which case it either disappears altogether or reappears after an interruption, brought about by torsion of the animal in its tube. Adjacent to the furrow two slightly elevated, rounded longitudinal edges may occur, and on the other sides of these two edges, there may be very weak furrows.

The tube surface is usually smooth. In some specimens growth lines (especially visible in abraded tubes), wrinkles, transverse constrictions and bulges (particularly in the anterior part) are seen (Pl. 4, Figs 2, 4, 5a, 7a, 8, 10). The tube and lumen are circular (Pl. 4, Figs 5b, 6b, 7b), the tube wall being moderately thick.

The outer parable layer is thick, and equals 65-80 % of the entire wall thickness. In longitudinal sections (Pl. 4, Figs 12, 13) the parable laminae are occasionally visible, and between the laminae and the tube's longitudinal axis is an angle of *c* 25-30°. At the junction of the outer and inner layers the wall separates easily, making a white layer bearing a strong transverse striation visible (Pl. 4, Fig. 13).

Often fragments of small specimens have been washed into the lumen of a larger tube. This cone-in-cone structure should not be confused with a more complex tube structure. Some tubes show predation traces of carnivorous gastropods.

*Discussion* — Within the Geulhem Member, the present species obviously preferred the fine-grained lithofacies, although it is not rare in the coarse-grained facies either. Thus, in contrast to *P. subtorquata*, it was not confined to muddy substrates in low energy settings.

*Comparison* — A variety of Campanian and

Maastrichtian representatives of *Pentaditrupe subtorquata* with but moderately curved tubes and circular cross-sections lacking longitudinal edges may closely resemble the present species, but generally grows larger, has a slightly darker colour, and the decrease in the outer tube diameter near the aperture is more distinct.

'*Ditrupe*' cf. *schlotheimi sensu* Pasternak, 1973 from the Campanian-Maastrichtian of European Russia is curved more strongly and cannot be referred to the present species; it may belong to *Pentaditrupe*. *Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: extremely frequent, upper part extremely frequent. Geulhem section, lower part of the Geulhem Member: extremely frequent, upper part extremely frequent.

*Occurrence elsewhere* — Danian of Poland, Denmark, in northern Germany in erratic boulders only.

Genus *Metavermia* Bush, 1904 emend.  
Zibrowius, 1971

*Type species* — *Vermilia multicristata* Philippi, 1844. *Diagnosis* — Most species are small, some medium-sized to large. In most species the tube is attached to the substrate over its entire length, but some also have erect tube parts, and of *M. (Vepreculina) fimbriata* (Regenhardt, 1961) only the non-attached tube parts are known. In some species loops and irregular spirals are common. The tube diameter increases slowly to moderately rapidly.

A distinct longitudinal ornament is usually present (except in *M. taenia* Zibrowius, 1971), consisting of up to 9 keels, which may be straight or undulate, smooth or denticulate or with spines or lobate protuberances, or the keels are replaced by longitudinal rows of granules or spines. Transverse ornament is generally less well developed, and occasionally consists of annular swellings, while some species possess flaring peristomes. The cross-section is circular to rounded triangular to quadrangular.

*Stratigraphic range* — Early Toarcian-Recent.

*Remarks* — In many Jurassic and Cretaceous sequences small to medium-sized attached tubes with a simple sculpture usually consisting of three longitudinal keels and weakly to moderately pronounced annular peristomes are common (e.g. '*Serpula*' *tricristata* Goldfuss, 1831). Obviously, they belong to the group of Recent genera such as *Vermiliopsis*, *Pseudovermia*, *Metavermia*, *Neovermia*, *Janita*, *Filograna* and others. However, within these genera tube morphology shows a wide range of

variation, and assignment of fossil species to a certain genus is problematical. The most practicable solution to this problem appears to be the placement of these small three-keeled species with annular peristomes in *Metavermia*, and species with flaring peristomes and rapidly increasing tube diameter in *Vermiliopsis* (e.g. *fluctuata* J. de C. Sowerby, 1829; *dorsolineata* Brünnich Nielsen, 1931). Formerly, such a classification was substantiated by the fact that *Metavermia* apparently lacks flaring (= funnel-shaped) peristomes (ten Hove, 1975, p. 57), but Imajima has subsequently described such peristomes for *Metavermia spicata* Imajima, 1977, *M. gravitesta* Imajima, 1978, *M. truncata* Imajima, 1978 and *M. ovata* Imajima, 1978, which record has made the classification of fossil tubes more difficult.

Another problem is that similar three-keeled species also occur in the genera *Serpula* and *Hydroides*.

Lommerzheim (1979, p. 158) described a species under the name *Metavermia* n. sp. with four weak keels from the early to middle Cenomanian. '*Serpula*' *cincta* Goldfuss, 1831 is either a primitive representative of *Filograna* or a specialised species of *Metavermia*. The genus *Vepreculina* Regenhardt, 1961 is now considered to be a subgenus of *Metavermia*. For '*Serpula*' *trilineata* Roemer, 1841, which was erroneously referred to *Janita* or *Janita* ? by Jäger (1983, 1987, 1988), see above.

### ***Metavermia* ? sp.**

Pl. 7, Figs 2, 3

*Description* — The five minute tubes before me are preserved as impressions on the underside of a bryozoan colony (Pl. 7, Fig. 2), tubes of *Placostegus alatus* (Pl. 7, Fig. 3), *P. erectus*, *Serpula* ? *insiticia* and *S.* ? sp. Probably the tubes of the present species were aragonitic and diagenetically dissolved.

Although only up to 4 mm of tube length are preserved, all specimens are more or less distinctly curved, some of them are hook-shaped or S-shaped. The tube diameter increases gradually to rapidly to a maximum of mostly 0.3-0.6 mm, in one specimen 0.8 mm. In all five specimens there are five narrow but sharp and fairly straight (non-undulate) keels on the upper and lateral sides of the tube. They are slightly more closely spaced at the periphery than on the upper side. In two specimens about three small but sharp peristomes occur, which are not flaring and not protruding. In one of them (Pl. 7, Fig. 2) these peristomes are situated close to the aperture. A third specimen (Pl. 7, Fig. 3) has one well-preserved, and an additional highly fragmen-

tary, peristome, which slightly protrudes at the median keel. The other two specimens do not show peristomes. The cross-section of all five specimens is inversely U-shaped (Pl. 7, Fig. 3b).

*Comparison* — Amongst late Cretaceous and Danian species, the tubes bear some resemblance to those of *Vermiliopsis dorsolineata* (Brünnich Nielsen, 1931), and of *V. fluctuata* (J. de C. Sowerby, 1829), which both have five keels as well, but grow to larger sizes, and generally have well-preserved tubes.

In *V. dorsolineata* the keels are more closely spaced on the upper side, leaving most of the lateral sides free. The peristomes are somewhat flaring and protrude at the median keel, at the two peripheral keels and at the base. In *V. fluctuata* the keels are often undulate, and the peristomes are somewhat flaring and distinctly protruding at the lateral sides towards the upper side.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: extremely rare, upper part, very rare. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, absent.

*Occurrence elsewhere* — Unknown.

Genus *Pyrgopolon* de Montfort, 1808 (= *Sclerostyla* Mørch, 1863, *Hepteria* Regenhardt, 1961)

*Type species* — *Pyrgopolon mosae* de Montfort, 1808.  
*Remarks* — A closer comparison of fossil species of *Pyrgopolon*, '*Sclerostyla*' and *Hamulus* with Recent '*Sclerostyla*' kindly received on loan from Dr H.A. ten Hove (Instituut voor Taxonomische Zoölogie, Universiteit van Amsterdam), and from Mr Alex Muir and Dr G.T. Pillai (Natural History Museum London), has shown that Jäger's (1983, pp. 79-82) classification of '*Sclerostyla*' is in part wrong: the differentiation between two groups of species is correct, but the Recent (and some of the Palaeogene) species of '*Sclerostyla*' are much more closely related and thus probably consubgeneric with his second group ('Zweite Gruppe') rather than with his first ('Erste Gruppe').

Consequently, the type species of '*Sclerostyla*', *S. ctenactis* Mørch, 1863, and the type species of *Pyrgopolon*, *P. mosae* de Montfort, 1808, belong both to Group 2 now, which makes *Sclerostyla* a junior synonym of *Pyrgopolon*.

For the first group, the name *Septenaria* Regenhardt, 1961 is available.

The genera *Hamulus* Morton, 1834 and *Turbinia* Michelin, 1845 (and possibly also *Ornatopora* Gardner, 1916, *Triditrupe* Regenhardt, 1961 and the 'Octogonae' of Regenhardt, 1961; no material was examined) closely resemble Jäger's second group in tube structure as well as in having a calcareous operculum, so that they too are here regarded to be subgenera of *Pyrgopolon*, rather than separate genera.

*Diagnosis* — Tube generally medium-sized to very large, with rapidly increasing diameter at least in the attached part of most species. Many species have a long erect anterior tube part. Longitudinal keels or crests, often six or seven in number, are common, whereas some species lack ornament. A few species possess peristomes. A relatively complex tube structure is often well developed. Perforate tabulae occur in some species, and in contrast to the great majority of other Serpulidae, the operculum is entirely calcareous (probably aragonitic), with a clearly marked differentiation into cucullus and calcar.

*Stratigraphic range* — Early Hauterivian ?, early Cenomanian-Recent.

Subgenus *Pyrgopolon* de Montfort, 1808

*Diagnosis* — Tube medium- to large-sized, with tube diameter rapidly increasing in the attached part, which is fragile and often poorly preserved in fossils. The base of the attached part generally shows a well-developed cellular construction (absent from a few specimens), invariably lacking '*Favosites*'-structure. Tabulae occur in modern species. In fossils, in the attached tube part and in the posterior region of the erect part, the tube wall easily splits into an outer (= outer parable) and an inner (= cylinder) layer over a weak median layer, which probably has a different mineralogical composition. Thus, the more or less intact inner layer may often be removed easily from the outer layer.

The erect tube part of fossil species either bears seven longitudinal edges or keels or has no longitudinal ornament at all, occasionally there are transverse wrinkles. In Recent species the ornament may differ. There is no 'honeycomb' ornament. The operculum has a funnel-shaped, radially striate cucullus and a slender calcar, circular to triangular in cross-section.

*Stratigraphic range* — Middle Cenomanian-Recent.

**Pyrgopolon (Pyrgopolon) mosae mosae** de  
Montfort, 1808  
Pl. 8, Figs 1-4, ? 5, ? 6

1808 *Pyrgopolon Mosae* de Montfort, p. 395, text-fig. on p. 394.

*Type* — Obviously no type specimen has so far been designated. De Montfort (1808, p. 394) illustrated a straight, unattached anterior tube part lacking longitudinal ornament, but with transverse growth lines, from 'dans l'intérieur de la montagne de Maastricht'. The subterranean galleries of Maastricht have mostly been excavated in the Nekum Member of the Maastricht Formation (late Maastrichtian). *Description* — Only tube fragments have been collected from the Geulhem Member. Opercula or external moulds of such are only known from the Maastrichtian (Cupedo, 1980). The great majority of the fragments represent the erect tube part. Remains of the attached tube part are also comparatively rare in the Maastrichtian, in comparison with the mass occurrence of the erect parts. The inner parable layer has normally been dissolved, and in washing residues (from the Geulhem Member as well as from the Maastricht Formation) the outer parable layer is found separated from the cylinder layer.

The generally rather thin to moderately thick outer parable layer (Pl. 8, Figs 1-4) is almost invariably fragmentary. Only in two specimens is the whole circumference preserved: one specimen (Pl. 8, Fig. 1), the only one from the Geulhem Member to show remains of the attached tube part, has a complete erect tube part of only 1.8 mm in length and 4.0 mm in diameter at the aperture, which equals the average diameter of specimens from the Geulhem Member as well as from the Maastricht Formation. The second specimen (Pl. 8, Fig. 2) is a fragment of the erect part, length 5.7 mm, and diameter a mere 2.3 mm.

The outer surface is generally smooth, but in a few specimens there are weak to moderate transverse wrinkles (Pl. 8, Fig. 1a, b) near the aperture or weak or irregular longitudinal furrows or edges, especially at the base of the erect tube part, as known from the Maastrichtian. Six specimens with a more distinct longitudinal ornament are assigned to the subspecies *P. mosae cipllyana* (see below). The inner surface of outer parable layer shows a fine transverse striation (Pl. 8, Figs 3b, 4).

The cylinder layer (Pl. 8, Figs 5, 6) is slender conical, and consists of several laminated concentric

layers. The length of the fragments is up to 5.5 mm, the diameter up to 1.7 mm. Much longer and somewhat thicker specimens are known from the Maastricht Formation. The cylinder layer is fairly thick posteriorly, and thin anteriorly. The cross-section (Pl. 8, Fig. 5b, c) generally is circular, but may occasionally be subtriangular posteriorly.

*Discussion* — Hitherto, *P. m. mosae* was not known to occur in the Palaeogene. Specimens found in the Geulhem Member could be considered to have been reworked from the underlying Maastricht Formation, and perhaps some of them really have. Three arguments can be put forward to rule out the possibility of all of them being reworked:

- although the material from the Geulhem Member is fragmentary, a few specimens are relatively complete and unabraded,

- although many of the Geulhem Member specimens were collected from the basal metre in the two sections studied, there are also several specimens (Albert Canal sections) and many specimens (Geulhem section) from strata some 8 m (first locality) or several metres (second locality) above the K/T boundary.

- in the late Maastrichtian Meerssen Member, *P. m. cipllyana* is the dominant subspecies, whereas in the Geulhem Member many *P. m. mosae* and only few *P. m. cipllyana* are found.

*Comparison* — *Pyrgopolon (P.) m. cipllyana* (de Ryckholt, 1852) has seven longitudinal edges on the erect tube part. Close to the aperture these edges disappear and a number of distinct transverse wrinkles or ribs appear. Dissociated parts of the cylinder layer cannot be distinguished from *P. m. mosae*. The opercula are different.

*Pyrgopolon (P.) m. clava* (Lamarck, 1818), a subspecies unknown from the Maastricht-Aachen-Liège area, but common at Ciplly, St Symphorien and Mons (southern Belgium) and at Köpings (southern Sweden, Campanian), is strongly curved in its erect part, with the tube wall becoming very thick towards the aperture.

Fragments of the outer parable layer may be confused with bivalve shells, while bits of the cylinder layer may be confused with chelae of decapod crustaceans, which, however, are often oval in cross-section.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: frequent, upper part, very rare. Geulhem section, lower part of the Geulhem Member: extremely frequent, upper part, extremely rare. This subspecies



also occurs in the Lanaye Member (Gulpen Formation), Valkenburg, Schiepersberg, Gronsveld, Emael, Nekum and Meerssen Members (Maastricht Formation) in the Maastricht-Aachen-Liège area, and is extremely common in some strata.

*Occurrence elsewhere* — Campanian ?, late Maastrichtian of northern Germany (Hemmoor, a few atypical fragments overlooked by Jäger, 1983), Belgium, Sweden ? and CIS.

**Pyrgopolon (Pyrgopolon) mosae cipliana**  
(de Ryckholt, 1852)

Pl. 8, Figs 7-9, ? 5, ? 6

1852 *Ditrupe cipliana* de Ryckholt, 1850 — de Ryckholt, p. 124, pl. 6, fig. 26.

*Type* — De Ryckholt's original specimen is from Ciplu (southern Belgium); its present whereabouts is unknown.

*Description* — The best-preserved specimen was found after the plates had been prepared and is therefore not illustrated. It is a fragment from the base of the Geulhem Member at the Geulhem section comprising the outer layer of the erect tube part, 8 mm long and 3 mm wide, with seven rounded longitudinal edges and transverse ribs in between. The other five are thin-walled fragments, all smaller than 4 mm in length and width, of the outer parable layer. Up to three, more often two longitudinal edges or keels are preserved (Pl. 8, Figs 7a, 8, 9). In some specimens there is a furrow on the inner surface underneath the edge or keel of the outer surface (Pl. 8, Fig. 7b). Transverse ribs are only visible in one of the five fragments (Pl. 8, Fig. 7a): no fragments from the aperture are available, where this ornament becomes stronger. At the inner surface of most, but not all specimens a fine transverse striation is seen (Pl. 8, Fig. 7b).

*Discussion* — The samples collected from burrow infill at the K/T boundary occasionally contain specimens which, judging from their preservational style, obviously stem from the underlying Meerssen Member (burrow walls). These specimens have been omitted from Tables 1-3. However, some specimens very probably are indigenous and occur in the Geulhem Member up to 1 m above the K/T boundary.

*Comparison* — In *P. (P.) m. mosae* longitudinal as well as transverse ornament is absent or at least weaker and more irregular. Dissociated parts of the cylinder layer cannot be distinguished. There are, however, differences in opercula. Fragments may be confused with bivalve shells, cirripedes and decapod crustaceans.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: very rare, upper part, absent. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, absent. This subspecies also occurs in the Lanaye to Emael Members exclusively in Kunrade facies, and in the Meerssen Member of the Maastricht Formation.

*Occurrence elsewhere* — Late Maastrichtian, Belgium.

Subgenus *Septenaria* Regenhardt, 1961

*Type species* — *Sclerostyla (Septenaria) septenaria* Regenhardt, 1961.

*Diagnosis* — Tube medium- to very large-sized, with rapidly to moderately rapidly increasing diameter in the attached part, which is often well preserved. The attached part in most species has one or several longitudinal edges or keels. The base lacks cellular construction, but shows 'Favosites' structure, *i.e.* the interior of the lower half of the tube wall consists of many minute oblique-polygonal 'tubes' with many transverse bottoms, closely resembling the Palaeozoic coral genus *Favosites*, but of much smaller size). At least in some species, tabulae occur occasionally.

The tube wall does not comprise a weak layer, so that it is impossible to extract the inner part of the tube wall from the outer part.

In the erect part tube often seven (or five, nine or more) longitudinal edges or keels occur. The erect part often has, the attached part less often has 'honeycomb' ornament (*i.e.* the outer layer of the tube wall consists of minute polygonal hollow 'honeycombs', which are somewhat oblique, and protrude in an apertural direction).

The operculum is unknown in all but one species; Lommerzheim (1979, pp. 160, 161, fig. 8) described opercula belonging to *P. (S.) cf. dilatata* (d'Archiac, 1847), but from the description it cannot be determined whether or not these were found *in situ*.

*Stratigraphic range* — Early Hauterivian ?, early Cenomanian-late Maastrichtian, Danian (see discussion), early Eocene-early Oligocene ?.

**Pyrgopolon (Septenaria) sp.**

Pl. 7, Fig. 4

*Description* — The sole specimen available from the Geulhem Member is broken both posteriorly and anteriorly, is 12 mm long and has a diameter of 3.5-4.5 mm. It consists of a very short fragment of the attached part with the socle and a long, slightly

curved and distinctly distorted fragment of the erect tube part (Pl. 7, Fig. 4a, b). The attached part has a single strong median crest and two rounded longitudinal edges, in the erect part the crest becomes lower (changing into a keel), and there are six rounded edges. Fine transverse wrinkles occur (Pl. 7, Fig. 4a, b). The cross-section is drop-shaped at the transition from the attached to the erect part (Pl. 7, Fig. 4c), and near-circular (subheptangular) in the erect part (Pl. 7, Fig. 4d). 'Favosites' structure does occur not only in the socle of the lower half of the tube, but also in the median crest on top of the attached part (Pl. 7, Fig. 4b, c). There is no 'honeycomb' ornament.

*Discussion* — Three species of the subgenus are known from the late Maastrichtian Meerssen Member in the Maastricht-Aachen-Liège area, the present specimen possibly being the only representative in the Geulhem Member. The accompanying label states that the sample which yielded the specimen was collected from burrow infill directly at the K/T boundary at Geulhem and notes the possibility of it being reworked from the underlying late Maastrichtian. However, the same sample also contains specimens of the exclusively Danian species *Serpula* ? *insiticia* and *Neomicrorbis cingulatus* in exactly the same state of preservation (unworn, same colour and fine structure). In addition, *Pyrgopolon (Septenaria)* becomes rarer towards the top of the Meerssen Member. Thus, I assume this specimen to be autochthonous.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: absent, upper part, absent. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, absent.

*Occurrence elsewhere* — Unknown.

Genus *Placostegus* Philippi, 1844 (= *Eoplacostegus* Regenhardt, 1961)

*Type species* — *Serpula tridentata* Fabricius, 1780.

*Diagnosis* — In many, but not all, species the attached tube part often forms loops. The tube cross-section is generally triangular with a keel on the upper side. The growth lines are curved forwards towards the keel. The anterior tube part becomes more or less steeply erect, the cross-section being triangular in most species, and circular in others. In most, but not all, species there are three protruding teeth at the aperture. The tube diameter increases slowly to gradually. Tubes of modern species are usually translucent.

*Stratigraphic range* — Oxfordian-Recent.

*Remarks* — Triangular tubes without protruding teeth from the Pliensbachian are attached apically only, being free for their longest part. They occur commonly in soft bottom settings (claystones) and probably their mode of life was similar to that of *Pentaditrupe* or *Ditrupe*. Presumably, they do not belong to *Placostegus*, and their triangular cross-section is a matter of convergence.

The late Jurassic '*Serpula*' *prolifera* Goldfuss, 1831 with unusually strong peristomes might well be the stratigraphically oldest species of *Placostegus*.

During the late Cretaceous and especially in Palaeocene time many species occur, some of which were assigned by Regenhardt (1961) to *Eoplacostegus*. An examination of fossil and Recent material has shown that the differences between *Eoplacostegus* and *Placostegus* (Jäger, 1983, pp. 96, 98) are too small to warrant generic separation. Lommerzheim (1979, p. 163; *in litt.*, February 1984) shares this view.

In the late Maastrichtian of the Maastricht-Aachen-Liège area, *P. aduncus* (Regenhardt, 1961), erroneously referred to *Spiraserpula* originally, is a common species.

*Paliurus* Gabb, 1876, which closely resembles *Placostegus*, has comparatively sharp edges, a club-like swollen apertural region, and perhaps a calcareous operculum (Lommerzheim, 1979, p. 164). It is not clear whether these differences warrant a generic separation.

*Conorca* Regenhardt, 1961 *sensu stricto* probably descended from *Placostegus* during the late Cretaceous (Jäger, 1983, p. 98).

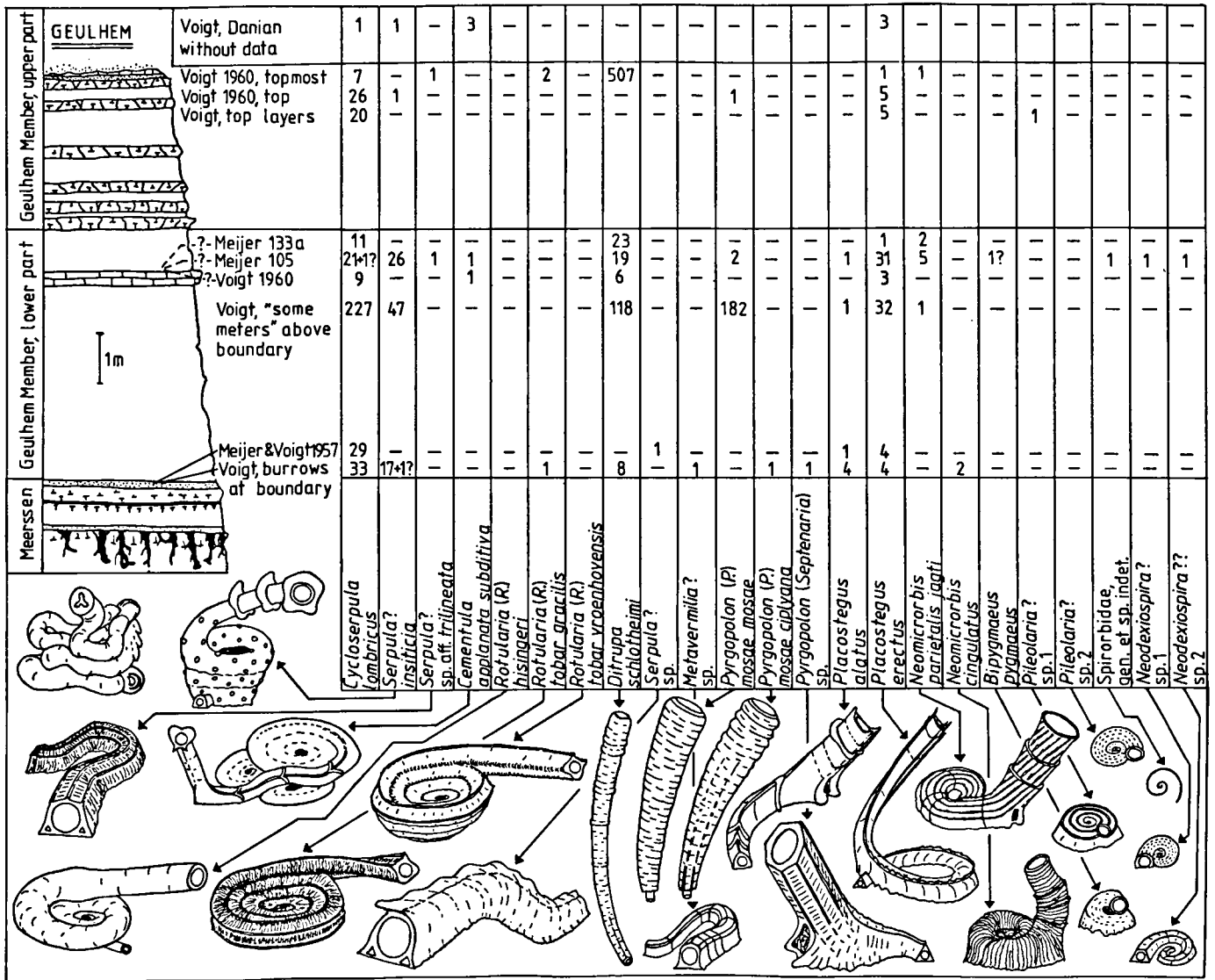
### ***Placostegus alatus* (Brünnich Nielsen, 1931)**

Pl. 8, Figs 10-18

1931 *Serpentula alata* Brünnich Nielsen, p. 109, pl. 3, figs 18, 19.

*Type* — Brünnich Nielsen's (1931, pl. 3, fig. 18) original is designated lectotype herein. It is a curved fragment of the attached tube part, with a keel and a single birdwing-like peristome (ala). Middle Danian, Coral Limestone, Fakse (Denmark), Mineralogical and Geological Museum of Copenhagen University Collections.

*Description* — The attached posterior part (Pl. 8, Figs 10-13) is curved or twisted, the free anterior tube part (Pl. 8, Figs 11-18) usually steeply erect (Pl. 8, Figs 12b, 13a), straight, curved or rarely twisted and often distorted. In the attached part the tube diameter (as far as can be seen in the short fragments available) gradually increases up to generally *c.* 1.5 mm, with a maximum of 2 mm.



11) is strongly rounded subtriangular to inversely U-shaped with convex sides, that of the erect part (Pl. 8, Figs 13c, 14b, 15d, 16) being drop-shaped on account of the unequal distances between the three edges. The tube wall is moderately thick to thick, especially at the transition from the attached to the erect part. The lumen is circular.

The tube wall is crystalline yellowish. In most specimens the wall appears to be homogeneous, and only occasionally may a thicker outer parable layer and a somewhat thinner inner parable layer be distinguished. Occasionally remains of a very thin cylinder layer occur. Only rarely does the inner surface show a distinct transverse striation. The tube wall lacks cells and longitudinal cavities.

*Comparison* — *Placostegus erectus* (Brünnich Nielsen, 1931) is smaller, has no 'alae', a different tube structure and a different cross-section of the erect part.

The alae of *Cementula* and *Spiraserpula*, which closely resemble those of *P. alatus* on the upper side of the tube, are of a more complex construction at the underside of the erect part. In these genera the tubes form spirals, whereas *P. alatus* does not.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: common, upper part, not rare. Geulhem section, lower part of the Geulhem Member: not rare, upper part, absent.

*Occurrence elsewhere* — Coral Limestone (Middle Danian), Fakse (Denmark).

### **Placostegus erectus** (Brünnich Nielsen, 1931)

Pl. 7, Figs 5-14

- v non 1831 *Serpula erecta* Goldfuss, p. 238, pl. 70, fig. 15.  
1926 *Serpula (Pomatocerus) [sic] erecta* Br. N. — Ødum, p. 167.  
1931 *Serpentula erecta* Brünnich Nielsen, p. 99, pl. 2, figs 12, 13.  
1961 *Eoplacostegus (Eoplacostegus) erectus* (Nielsen) — Regenhardt, p. 61.  
1961 *Eoplacostegus (Concamerarius) inexpectatus* Regenhardt, p. 62, pl. 9, fig. 10.

*Type* — Brünnich Nielsen's (1931, pl. 2, fig. 13) original is designated lectotype herein. It is a fragment showing the transition from the attached to the erect part, which is not very steep. Bryozoan Limestone (Middle Danian), Fakse (Denmark). Mineralogical and Geological Museum of Copenhagen University Collections.

*Description* — A rather small species, with the attached tube part curved irregularly (Pl. 7, Fig. 6), twisted (Pl. 7, Fig. 8) or forming a generally wide

loop of up to 2½ turns anteriorly, sinistral (Pl. 7, Figs 5, 7b, d, e) and dextral (Pl. 7, Fig. 10) loops both occur. At the base there is a generally moderately broad, rarely very broad border (Pl. 7, Fig. 6). Rarely does the border form a narrow, but high, caterpillar-like socle (Pl. 7, Fig. 7a-c) as seen in many representatives of the late Maastrichtian *P. aduncus* (Regenhardt, 1961).

The anterior tube part becomes erect under an angle of  $c$  45-60° (Pl. 7, Fig. 9), but this angle may also be greater (Pl. 7, Fig. 10), or smaller (Pl. 7, Fig. 7d, e). Erect tube parts are often slightly curved and distorted (Pl. 7, Fig. 10).

In the attached part, the tube diameter gradually increases, in the erect part it remains constant (Pl. 7, Fig. 11). In general, the tube diameter is  $c$  1.0 mm, with a maximum of 1.4 mm. Fragments of the attached part reach up to 14 mm in length, of the erect part up to 6 mm.

In the attached part a keel, often slightly undulate, is generally very distinct (Pl. 7, Figs 5-8), but in some specimens there is only an indistinct edge (Pl. 7, Fig. 10). The keel is usually non-denticulate, less commonly denticulate (Pl. 7, Figs 6, 7b, d, e) consisting of low, forward-directed little teeth, which may either occur on top of the keel or replace it. In two specimens it is seen that the denticulation ends exactly at the transition from the attached to the erect part. At the lower half of the two lateral walls there often is a weak seam-like furrow on either side (Pl. 7, Fig. 7b, d).

In the erect part there are three fairly sharp edges or keels (Pl. 7, Fig. 11), non-denticulate over most of their length, but forming three sharp protruding teeth at the aperture (Pl. 7, Figs 9, 12-14). The upper keel and tooth often bear a narrow median furrow (Pl. 7, Fig. 11a). At the lower part of the two lateral walls there is a weak seam-like furrow on each side (Pl. 7, Fig. 11a, b) as seen in the attached part. At the underside of the erect part there often is an obtuse median edge (Pl. 7, Figs 11c, 12b, 13), less commonly a seam-like furrow.

Transverse ornament is often absent or very weakly developed. Some erect parts may show weak peristomes, especially in their anterior regions, where the protruding teeth of former apertures may be seen (Pl. 7, Fig. 14a, b).

The cross-section of the attached part is strongly rounded-triangular to inversely U-shaped or subcircular, with obtuse edges and convex sides, that of the erect part being triangular (Pl. 7, Figs 12b, 13, 14c) with usually sharp edges and near-straight (nei-

ther convex nor concave) lateral walls. The tube wall of the attached part is fairly thick, that of the erect part moderately thin; the lumen is circular.

The tube wall is chalky white, and consists of parable and cylinder layer. The inner part of the parable layer is well developed, 0.5 to 3 times (at the keels), generally 1 to 1.5 times as thick as the cylinder layer. Between these two layers there is a laminated very thin bright white layer (Pl. 7, Fig. 11c, top), over which the wall easily loosens. The inner surface does not show a transverse striation. The base lacks cells and longitudinal cavities.

A single specimen (from Geulhem, GPI Hamburg Collections) shows the characteristic structures caused by the hydroid symbiont *Protulophila gestroi* Rovereto, 1901.

*Discussion* — A single specimen (Pl. 7, Fig. 14a-c) is here illustrated, on account of a circular operculum-like object with fine, concentric and radial ornament that occupies the lumen near the the aperture (Pl. 7, Fig. 14c). The operculum of Recent species of *Placostegus* is not calcareous. The tube was subsequently intentionally broken, and the alleged operculum turned out to be a fragment of an echinoid spine.

*Comparison* — *Placostegus alatus* is larger and has alae, its tube structure being different as well. *Placostegus tridentiger* (Regenhardt, 1961) has a sharp triangular cross-section, and occasionally the keels are somewhat undulate and irregular. *P. aduncus* (Regenhardt, 1961) is larger, and transverse ribs are common; its range of variation being wider. *P. indistinctus* (Brünnich Nielsen, 1931) has more distinct growth lines, while *P. dentatus* (Brünnich Nielsen, 1931) has strongly denticulate edges, and *P. unduliferus* (Brünnich Nielsen, 1931) has more strongly ornamented edges.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: frequent, upper part, very frequent. Geulhem section, lower part of the Geulhem Member: very frequent, upper part, common.

*Occurrence elsewhere* — Danian of Denmark and northern Germany (in erratic boulders).

#### Family Spirorbidae Pillai, 1970

*Diagnosis [of tube and operculum]* — Tube with a very small, fragile and generally unpreserved non-spiral initial part, followed by a spiral of few millimetres diameter only. Generally the tubes do not intertwine to form clusters, but often many specimens

grow in close proximity. Within a single species the direction of coiling (sinistral or dextral) is fairly constant with the exception of the genus *Neomicrorbis* and a few species of other genera. The tube ornament is well developed. The operculum, when known, is invariably calcareous.

*Comparison* — *Rotularia*, *Conorca* and other genera always or occasionally also form spirals, but their initial parts are larger and often well-preserved. As mentioned above, placement in the family Serpulidae is preferred for these genera.

*Stratigraphic range* — Cambrian ?, Ordovician-Recent.

*Remarks* — The genus *Neomicrorbis* Rovereto, 1904a is here included in spite of the fact that there are differences between the soft parts of this genus and of 'normal' Spirorbidae (see Zibrowius, 1972).

Spirorbidae have perhaps existed since the Cambrian (Lommerzheim, 1979, p. 166) and with certainty since the Ordovician (Ruedemann, 1934). They are common in many marine strata up to the late Triassic and also in fresh and brackish water settings from the early Devonian (Schweitzer, 1983) to the late Triassic (Kelber, 1986). Many authors have focused their attention at these non-marine spirorbids, for post-Triassic and Recent representatives are exclusively marine. In the Palaeozoic most species are sinistral, but there are also dextral species from the Palaeozoic onwards.

Many of the Palaeozoic and Triassic spirorbids are poorly known in detail; some of them could even be gastropods rather than worms (Burchette & Riding, 1977). Opercula have been described from the Cretaceous onwards. In view of this, I agree with Lommerzheim (1979, p. 167) in using the old genus name *Microconchus* Murchison, 1839 for Palaeozoic spirorbids again, instead of uniting them with the Recent genus *Spirorbis* Daudin, 1800. Triassic spirorbids should be treated in the same way.

There is a distinct break in spirorbid phylogeny from the early Jurassic to the early Cretaceous, when Spirorbidae have not entirely disappeared, but have become much rarer and not so widely distributed [with the exception of the common species *planorbiformis* (Münster in Goldfuss, 1831)] in comparison with Serpulidae, which during the Jurassic become distinctly commoner and more diverse. Perhaps Serpulidae ousted the spirorbids from their marine habitats. What caused the disappearance of freshwater spirorbids is still a matter of conjecture.

From the early Cenomanian onwards, Spiror-

bidæ have become diverse and common again. Lommerzheim (1979, p. 167) compared Cenomanian spirorbid species with the Recent taxa *Spirorbis* sensu stricto, *Pileolaria*, *Metalaeospira*, *Eulaeospira* and *Janua*, and stated that in reality his Cenomanian species probably did not belong to any of these. In addition, *Bipygmaeus* and *Neomicrobis* are already present in the Cenomanian.

Unfortunately, the succession of the first fossil occurrence (as known to date) of Recent genera (or similar fossil genera) is not in accord with the phylogenetic scheme elaborated by Pillai (1970) and complemented by Zibrowius (1972), based on research into Recent material (for details see below).

Genus *Neomicrobis* Rovereto, 1904a (= *Spirorbula* Howell, 1962)

*Type species* — *Serpula crenatostriatum* Münster in Goldfuss, 1831.

*Diagnosis [of tube and operculum]* — Spiral relatively large (diameter about 5 mm), within a single species or subspecies sinistral and dextral specimens occur in about equal numbers. Tubes are either smooth or ornamented with longitudinal rows of spines or granules, longitudinal keels, transverse wrinkles, funnel-shaped peristomes.

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

*Comparison* — Nearly all other Spirorbidae are much smaller. In the great majority of species the direction of coiling is constant within a species.

*Stratigraphic range* — Early Tithonian-Recent.

*Remarks* — *Neomicrobis*, which has serpulid-like soft parts with relatively many thoracical segments and a spirorbid-like tube and operculum (Zibrowius, 1972) could be considered to represent an intermediate, close to the common ancestor of the families Serpulidae and Spirorbidae: 'It is certainly a link between the two families ...' (Knight-Jones, 1981, p. 197). Although Jäger (1983, p. 120) stated that *Neomicrobis* should therefore occur already in pre-Cretaceous strata, it has still not proved possible to demonstrate their occurrence in units predating the early Tithonian. Thus from the fossil record it appears that this genus is a relatively young offshoot of the Serpulidae. The scenario could then be as follows: spirorbids could either have descended from Jurassic or Cretaceous species of *Neomicrobis* or from Palaeozoic or Triassic species of *Microconchus*.

The stratigraphically oldest known species of *Neomicrobis* is an as yet undescribed species from the early Tithonian coral limestone of Nattheim (SW Germany), which resembles the late Cretaceous *N. crenatostriatum crenatostriatum* in size, ornament and equal numbers of sinistral and dextral individuals, but its operculum is yet unknown.

Nothing definite can be stated on a single specimen from the Hauterivian of Heligoland (Stühmer *et al.*, 1982, pl. 21, fig. 10).

During the late Cretaceous *Neomicrobis* is fairly common. Its tube ornament is very variable, and there are many transitions between the extremes. Jäger (1983, p. 121) already remarked that it was quite possible that the three late Cretaceous 'species' *crenatostriatum* (Münster in Goldfuss, 1831), *hagenowii* Jäger, 1983 and *subrugosum* (Münster in Goldfuss, 1831), which usually are easily distinguished by their ornament, are not really good species. I now regard them as ecological varieties or subspecies of a single variable species, *crenatostriatum*. Some observations on Recent Spirorbidae support this view: Knight-Jones (1978, p. 234) remarked that, 'Tubes that usually bear longitudinal ridges commonly lack them in the younger stages of growth (Crisp, Bailey & Knight-Jones, 1967; Knight-Jones, Knight-Jones & Llewellyn, 1974) and may lack them throughout life in areas of reduced water movement (Gee, 1964).' This observation conflicts with observations on late Cretaceous *Neomicrobis*, of which *N. crenatostriatum subrugosum* appears to have preferred a higher energy setting than the longitudinally ornamented *N. c. crenatostriatum*.

In some *Neomicrobis* specimens the anterior tube part becomes erect like a corkscrew. Recent Spirorbidae show a similar intraspecific variation (Knight-Jones, 1978, pp. 234, 235): 'The terminal coils of tubes may ascend or become evolute, when in dense aggregations ... or covered by algal filaments or encrustations (Gee & Knight-Jones, 1962). In deep silty areas most of the tube can become erect (Knight-Jones, Knight-Jones & Bregazzi, 1973; Bailey-Brock & Knight-Jones, 1977).'

The taxonomic position of *N. fawarensis* Avnimelech, 1941 from the Campanian of Israel is uncertain as the range of variation of the direction of coiling is unknown; it may perhaps be *N. c. subrugosum*.

With regard to longitudinally ornamented specimens: in the Palaeocene of New Zealand there are individuals that are indistinguishable from *N. c. crenatostriatum* (see Fleming, 1972, fig. 4d). In the Dan-

ian of Denmark and northern Germany (erratic boulders) some specimens are also very similar to *N. c. crenatostriatus*, but in others changes in the number and strength of elements of longitudinal ornament [e.g. in *N. serratus* (Brünnich Nielsen, 1931)] or in the shape of the spiral (see below) take place, so that a taxonomic separation is called for.

Within the group of prevalently transversely ornamented specimens, there is a change from the late Cretaceous *N. c. subrugosus* to the Danian *N. cingulatus* (see below).

Jäger (1983, p. 122) stated that an operculum from the Danian of Kagstrup (Denmark) showed no significant differences to opercula from the late Cretaceous from a number of northern German localities. However, the cucullus of the operculum of the new subspecies described below is concave as in the Recent species, *N. azoricus*, this in contrast to the convex cucullus of *N. crenatostriatus*. But, because of the specialised shape of spiral in the new species, this is probably not the direct ancestor of the Recent species, but rather an offshoot.

As to Eocene and Recent species (see Jäger, 1983, p. 122) no new data are available.

*Neomicrorbis* shows an even wider range of variation in the Palaeogene than in the late Cretaceous. If the Eocene species described by Rovereto (1904a) from the locality Kressenberg (Bavaria, Germany) are true *Neomicrorbis*, then this genus, like *Rotularia*, would have lost its significance at about the Eocene/Oligocene boundary, but unlike *Rotularia*, *Neomicrorbis* is still extant.

***Neomicrorbis parietalis*** (Brünnich Nielsen, 1931)

1931 *Spirorbula parietalis* Brünnich Nielsen, p. 105, pl. 2, figs 30, 31.

*Type* — Brünnich Nielsen (1931) illustrated but a single specimen, and this was not designated type. It is from the middle Danian Bryozoan Limestone of Fakse (Denmark), and is part of the collections of the Mineralogical and Geological Museum of Copenhagen University.

*Description* — The following description is based on toptotypical material. The tube forms an initial planar spiral of up to 2 mm in diameter. Sinistral and dextral spirals occur in about equal numbers. The umbilicus is rather narrow and usually closed by a callosity. Following the spiral, the tube remains attached to the substrate, but the contact with the previous whorl is lost. After this short intermediate

part the tube erects rather abruptly; this near-vertical tube part is distorted and slightly curved and only up to 3.5 mm long. The aperture is generally flaring as are the peristomes, reaching a maximum tube diameter of 1.4 mm.

At the end of the spiral there are 5-7 longitudinal keels, and up to 13 at the aperture, which are thin and low, but fairly distinct and show a tendency to become divided up into rows of minute forward-directed teeth.

The operculum is unknown as yet.

*Discussion* — *N. parietalis* s. str. from Fakse and *p. jagti* (see below) from the Maastricht-Aachen-Liège area are very similar, but not identical. For some specimens an assignment to either subspecies may be difficult, but the 'populations' as a whole show several differences. The two taxa may be geographic subspecies, and are differentiated at that level.

***Neomicrorbis parietalis jagti*** n.subsp.

Pl. 9, Figs 1-7

*Derivatio nominis* — In honour of John W.M. Jagt, in recognition of his publications on the late Cretaceous and Palaeogene of the Maastricht area.

*Type* — The complete tube illustrated in Pl. 9, Fig. 1, is designated holotype. The small dextral initial spiral of 2.8 mm in diameter has seven longitudinal keels, followed by a barely 2 mm long attached intermediate tube part and a vertical anterior part erecting 4 mm above the base, reaching 1.8 mm in diameter at its end and with a flaring aperture surrounded by sixteen slightly protruding longitudinal keels. Geulhem Member, 0-0.4 m above the K/T boundary, Albert Canal sections north of Vroenhoven bridge, Natuurhistorisch Museum Maastricht Collections, NHMM 1992204-1 (including eleven paratypes, leg. J.W.M. Jagt).

*Diagnosis* — The tube has a small initial spiral, which is followed by a short, attached intermediate part, growing laterally away from the spiral, and finally by a long steeply erected anterior tube part. The umbilicus is usually closed by a callosity. There are six to seventeen narrow, sharp, weakly denticulate longitudinal keels, and weak flaring peristomes and a flaring aperture. The tube wall apparently consists of an inner parable layer only (a cylinder layer is not preserved). The operculum has a concave cucullus.

*Description* — The tube has a planar base, and is attached by a moderately broad border on a large, planar substrate, which in most specimens is pre-

served as an impression only. In rare instances did an oyster shell serve as a substrate. In contrast to many late Cretaceous specimens of the present genus an attachment on thin cylindrical algal (?) filaments has not been observed.

The tube has an initial planar spiral (Pl. 9, Figs 1, 2, 4-6) of generally 3 (maximum 4) turns and with a rather narrow umbilicus, which is usually closed by a callosity (Pl. 9, Figs 4b, 5b). The final diameter of the spiral is 2.5-3.7 mm. Of 130 sufficiently well-preserved specimens fifty are sinistral (Pl. 9, Fig. 6) and eighty dextral (Pl. 9, Figs 1-5).

Following the spiral the tube remains attached to the substrate, but the curvature diminishes distinctly, so that the contact with the previous whorl of the spiral is lost (Pl. 9, Figs 1a, 2, 4a, 5a, 6a). The length of this intermediate tube part usually does not exceed the spiral diameter.

The transition to the erect part is rather abrupt, at the end of the attached part occurs a socle (Pl. 9, Figs 2, 4c). The lateral parts of the base protrude to form two edges between the base and the underside of the erect part, constructing a small cavity below the erect part (similar to the one seen in *Pyrgopolon*).

The anterior tube part (Pl. 9, Figs 1a, b, d, 2, 3, 5a, b, 6a, b) at first becomes erect under an angle usually in excess of 45°, then generally curves into a vertical position and grows to 5 mm above the base. It is distorted and curved slightly in the same direction of coiling as the older spiral (Pl. 9, Figs 1a, 3). The aperture is often flaring (Pl. 9, Figs 1b, c, e, 3) as are the peristomes (of the proles oscitans type, see Regenhardt, 1961). At the aperture the increase in the tube's inner diameter exceeds that of its outer diameter.

The tube diameter increases moderately rapidly in the attached part, and rapidly in the erect part, where it may reach up to 1.8 mm.

The longitudinal keels are similarly shaped (Pl. 9, Figs 1-6), but they are situated mainly on the upper tube part, whereas the sides, especially their lower halves, bear fewer or no keels: six to nine may be counted at the end of the spiral, twelve to seventeen at the aperture. During ontogeny their number increases by insertion of new keels between previous ones, and, at the base of the erect part, by addition of several new keels on the lower half of the tube. There is a narrow suture-like longitudinal furrow on the underside of the erect part, with the neighbouring keels being more widely separated than the other keels. Rarely do the keels slightly protrude at the aperture (Pl. 9, Fig. 1).

Weak flaring peristomes, which often are not stronger than growth lines are common (Pl. 9, Figs 4-6).

The cross-section is inversely U-shaped in the attached part, circular in the erect part and at the aperture (Pl. 9, Figs 1e, 2, 4c, 5b, 6b). The tube wall is moderately thick, and the lumen circular.

The tube structure: in view of the fact that the cylinder layer is not preserved, the tube appears to consist of an inner parable layer only. The inner surface is frequently somewhat constricted by sharp, backward-directed rings, in irregular distances, which continue as flaring peristomes from the outside into the tube's interior (not illustrated for the present species, but see Pl. 9, Fig. 9, *N. cingulatus*).

The sole operculum available of the present species (Pl. 9, Fig. 7) was found *in situ* in a typical, dextral tube. The total length of the operculum is 0.8 mm, its cucullus (diameter a mere 0.5 mm) being circular in outline (Pl. 9, Fig. 7d) and slightly concave, in a near-perpendicular position to the axis of the calcar. This (Pl. 9, Fig. 7a-c) is slender with near-parallel sides and slight curvature. The two lateral alae and the carina interna are well developed, whereas the carina externa appears to be absent.

*Discussion* — In many samples, remains of the spiral tube part are remarkably rare, most specimens being fragments of the erect part. They appear to have been transported by water movement away from the original habitat.

*Neomicrorbis parietalis jagti* was obviously better adapted to current action than was *N. c. crenatostriatum*, which preferred lower energy settings and which is absent from the tuffaceous chalk facies of the Maastrichtian type area (however, it does occur in the Gulpen Formation). The return of the genus *Neomicrorbis* just above the K/T boundary in this area is striking.

*Comparison* — *N. p. parietalis* resembles a miniature version of the present subspecies. The general shape of the tube of these two taxa is near-equal, but length and diameter of tube of the former remain much smaller. *N. parietalis* s. str. does not represent juvenile individuals of *N. p. jagti*, as, even when complete tubes with erect anterior parts are compared, the diameter of the spiral part and the length of the intermediate part are considerably smaller in the former. In contrast to the present subspecies, the number of dextral spirals is only slightly higher than the number of sinistral ones or not at all. Moreover, the longitudinal keels in *parietalis* s. str. are not only



fewer in number, but also distinctly thinner and lower, and denticulate. However, the absence of denticulation in *p. jagti* may be the result of abrasion during transport in a high-energy environment.

In *N. c. crenatostriatus*, there is no intermediate attached non-spiral tube part between the spiral and the erect part, and the cucullus of the operculum is convex and much more massive. In *N. serratus* (Brünnich Nielsen, 1931) stronger and weaker lines of longitudinal ornament co-occur within a single tube. '*Spirorbula*' *multilineata* Brünnich Nielsen, 1931 has a wide umbilicus, while '*Spirorbula*' *ampla* Brünnich Nielsen, 1931 has a thinner tube wall. In the operculum of the Recent species, *N. azoricus* Zibrowius, 1972, the cucullus is also concave, but in an oblique position to the longitudinal axis of the calcar, the latter being wider, and having a triangular outline.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: very frequent, upper part, common. Geulhem section, lower part of the Geulhem Member: not rare, upper part, extremely rare. At the Albert Canal sections there is a frequency maximum approximately 1.50 m above the K/T boundary, in fossiliferous lenses with the spines of the echinoid *Tylocidaris hardouini* (Desor, 1855).

*Occurrence elsewhere* — This is a geographic subspecies of *N. parietalis parietalis* (Brünnich Nielsen, 1931) from the Danish and southern Swedish Danian.

**Neomicrorbis cingulatus** (Brünnich Nielsen, 1931)  
Pl. 9, Figs 8, 9

non 1831 *Serpula cingulata* Münster — Goldfuss, p. 233, pl. 69, fig. 4a-c.

1926 *Serpula (Spirorbis) cingulata* Br. N. — Ødum, p. 166.

1931 *Spirorbula cingulata* Brünnich Nielsen, p. 111, pl. 3, figs 23, 24.

non 1981 *Circeis* ? sp. (*cingulata* [Nielsen] - Wuchsform). — Lommerzheim, p. 42, fig. 3.

1983 *Neomicrorbis cingulatus* (Nielsen 1931) — Jäger, p. 122.

*Type* — The specimen illustrated by Brünnich Nielsen (1931, pl. 3, fig. 24) is here designated lectotype. It has a relatively small dextral spiral and a long corkscrew-shaped erect anterior part with many narrow but sharp peristomes. Middle Danian, Coral Limestone, Fakse (Denmark). Mineralogical and Geological Museum of Copenhagen University Collections.

*Description* — The tube starts with a planar to low inversely conical spiral (Pl. 9, Fig. 8), attached with an occasionally broad border to relatively large substrates (here: planar bryozoan colonies and other individual of the same species [Pl. 9, Fig. 8b, small specimen lower right-hand side]) or to small substrates (a thin bryozoan branch in the sinistral Fakse specimen). Sinistral and dextral spirals occur. The spiral has 3½-4 turns and a narrow, deep umbilicus, which probably is not filled by a callosity. The diameter of the spiral reaches at most 5 mm in Denmark; and up to 4.5 mm in the Maastricht-Aachen-Liège area. The tube diameter increases gradually to rapidly to a maximum of 2 mm.

At the end of the spiral the tube often forms a small socle and becomes erect very steeply, almost vertically (Pl. 9, Figs 8, 9a). This erect part is corkscrew-shaped and continues the direction of coiling of the spiral. In the Maastricht-Aachen-Liège area, this corkscrew may be up to 2.5 mm long and raise the aperture up to 4.3 mm above the substrate (Pl. 9, Fig. 8). In Denmark the erect part may even be considerably longer.

Longitudinal ornament does not occur. Transverse ornament consists of several to many small, narrow but sharp flaring peristomes (Pl. 9, Fig. 8c, d). In some specimens there are fine transverse wrinkles as well (Pl. 9, Fig. 8). The cross-section is inversely U-shaped in the spiral, and circular in the erect part (Pl. 9, Fig. 8b), the lumen being circular. The tube wall is moderately thick, the tube structure (Pl. 9, Fig. 9) resembling that of *N. parietalis jagti* (see above).

*Discussion* — In both specimens figured by Brünnich Nielsen (1931) the spiral is dextral. In view of the fact that sinistral tubes of the present species have so far not been described, Lommerzheim (1981, p. 42, fig. 3) referred to fifty-eight small dextral tubes of similar shape from the Palaeocene of the Emperor Seamounts as '*Circeis* ? sp. (*cingulata* [Nielsen] - Wuchsform)'. Recent species of *Circeis* are dextral and possess an operculum of characteristic shape, as yet unknown from *N. cingulatus*.

However, in a sample from the type locality Fakse supplied by Mr and Mrs Krause (Wennigsen), there is a fine and characteristic but sinistral specimen of *N. cingulatus*. Amongst the five specimens from the Maastricht-Aachen-Liège area, two (although fragmentary and dubious) specimens are also sinistral. Thus, sinistral and dextral specimens appear to co-occur in about equal numbers in Denmark as well as in the Maastricht-Aachen-Liège area, and, more-

over, the tubes of *cingulatus* are comparatively large for 'normal' spirorbids, and distinctly larger than Lommerzheim's Emperor Seamount specimens. Therefore, the present species is assigned to *Neomicrorbis* for the time being; Lommerzheim's specimens belong to another genus, possibly to *Circeis*. As long as opercula are unknown, a definite assignment cannot be made.

Lommerzheim (1981, p. 42) correctly stated that the corkscrew-shape of the erect tube part might be present in several Recent spirorbids, as a reaction to environmental conditions (muddy bottom or incrustation by algae), which makes the corkscrew-shape into a feature of low diagnostic value. The few specimens of the present species from Denmark and from the Maastricht-Aachen-Liège area show a wide range of variation: the erect part may be long or short or even absent. The same holds for late Cretaceous species of the genus (Jäger, 1983, pl. 15, compare fig. 4 with the other figures). However, keeping in mind that the corkscrew-shape of the erect tube part is a facultative feature, it may aid — in combination with size, ornament and direction of coiling — in distinguishing the present species from other spirorbids and serpulids.

*Comparison* — *Neomicrorbis crenatostriatus subrugosus* is similar, but this has generally fewer and weaker peristomes. *Circeis* ? sp. (*cingulatus* [Nielsen] - Wuchsform) *sensu* Lommerzheim, 1981 is smaller and exclusively dextral. In Recent species of *Circeis* the transverse ornament is weaker or absent.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: very rare, upper part, absent. Geulhem section, lower part of the Geulhem Member: very rare, upper part, absent.

*Occurrence elsewhere* — Danian of Denmark and southern Sweden.

#### Genus *Bipygmaeus* Regenhardt, 1961

*Type species* — *Serpula pygmaeus* von Hagenow, 1840.

*Diagnosis* — Small, sinistral. Tube starts with a planar spiral, upon which rests a conical spiral with an upward decreasing diameter, followed by a corkscrew-shaped, nearly vertically erected anterior part.

*Comparison* — *Bipygmaeus* is similar to Recent *Proto-laespira*, *Paralaespira* and *Helicosiphon*, which are shown to be relatively primitive in Pillai's (1970) scheme.

*Range* — Early Cenomanian-Danian.

*Remarks* — All known European specimens of *B. pygmaeus* are sinistral. Thus it is doubtful whether dextral '*Bipygmaeus*' sp. from the middle Palaeocene of the Emperor Seamounts described by Lommerzheim (1981, p. 52) really belong here.

#### ***Bipygmaeus pygmaeus*** (von Hagenow, 1840)

Pl. 6, Figs 9, ?7, ?8.

1840 *Serpula pygmaea* von Hagenow, p. 667.

v 1983 *Bipygmaeus pygmaeus* (Hagenow, 1840) — Jäger, p. 132, pl. 16, figs 13-15.

*Type* — A lectotype has not yet been designated.

*Description* — All specimens from the Geulhem Member are attached by a broad border to a planar or curved substrate (mostly a calcareous crust or a bryozoan colony, but also on other secondary hardgrounds), but not to thin cylindrical algal filaments. Occasionally, specimens are attached to the same substrate in close proximity.

Almost all specimens are more or less planar sinistral spirals (Pl. 6, Figs 7, 8) with approximately 3 turns and with a moderate to fairly wide umbilicus. The diameter of the spiral is generally 1.0-1.4 mm, the tube diameter at the aperture being 0.4-0.5 mm. A distinct ornament is entirely missing. Many specimens start raising their apertures, but do not lose contact with the previous whorl of the planar spiral. This appears to be the beginning of the conical spiral, which is very characteristically developed in late Cretaceous specimens.

In the Geulhem Member, however, only in a single specimen (Pl. 6, Fig. 9a-c) is the planar spiral (diameter 1.3 mm) followed by a well-developed conical spiral of only 3/4 turn. This spiral grows upwards by diminishing the diameter of the spiral and by closing the umbilicus. The height of the conus is at least 0.8 mm (aperture damaged). The sides of the conus are near-straight, neither concave nor convex, and the suture between the turns is a narrow indistinct line. This is the only specimen from the Geulhem Member that may be identified beyond doubt.

*Discussion* — In the late Cretaceous, many adult specimens of the present species possess a well-developed, near-vertical corkscrew, but in the Geulhem Member none of the specimens available does, and only one has a characteristic conical median tube part. The great majority of the Geulhem Member specimens has a simple planar spiral lacking distinct ornament. These may be juvenile individ-

uals, but, in the absence of any characteristic features, it cannot be ruled out that some of them actually belong to different taxa. There is a close resemblance to *Pileolaria* ? sp. 1, the lack of ornament being the only, but striking, distinctive feature. Thus the question arises whether the planar spirals are more closely related to *B. pygmaeus* or to *Pileolaria* ? sp. 1, or whether a third taxon may be involved. An argument against interpreting them as juveniles of *B. pygmaeus* is that in some specimens with raised aperture, there is a very distinct furrow between the whorls, which is never developed in typical specimens.

*Comparison* — Late Cretaceous representatives of *B. pygmaeus* from northern Germany attached not only to hard substrates, but also to algal filaments. The planar spirals may grow to a somewhat larger size (diameter slightly over 2 mm and of up to 4 turns; see Müller, 1966, p. 1055) and may possess a rounded longitudinal edge in some individuals. The conical spiral is much more common and consists of up to 2½ turns (Müller, 1966, p. 1055) instead of only 3/4.

*Pileolaria* ? sp. 1 is closely comparable as far as size, broad border, direction of coiling (exclusively sinistral, usually planar spirals with only slight erection of the aperture, very rarely conical spiral following planar spiral) are concerned, but has three distinct longitudinal keels.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: very rare, upper part, frequent. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, absent.

*Occurrence elsewhere* — Middle Santonian, early Maastrichtian-Danian of northern Germany and Denmark.

Genus *Pileolaria* Claparède, 1868

*Type species* — *Pileolaria militaris* Claparède, 1868.

*Diagnosis* — Tube sinistral, with or without longitudinal and/or transverse ornament. The anterior tube part may ascend. The operculum has a brood chamber, for details see Knight-Jones (1984, p. 111).

*Comparison* — Most species of the Recent genus *Romanchella* Caullery & Mesnil, 1897 are also sinistral, but several species are dextral. As in *Pileolaria*, longitudinal keels are developed in some species but not in others. On average, keels are stronger in the former than in the latter genus, and keels more

often form teeth at the aperture. The operculum of *Romanchella* lacks a brood chamber.

*Stratigraphic range* — Early Cenomanian ?, middle Santonian-Neogene ?, Recent.

*Remarks* — *Pileolaria* belongs to the most progressive Recent genera in Pillai's scheme (1970, p. 148). Thus caution is called for in referring Cretaceous species to this genus as long as their opercula remain unknown. The status of the two early Cenomanian '*Spirorbis* (aff. *Pileolaria*)' species recorded by Lommerzheim (1979) is uncertain: *vastus* is very large and its ornament rather weak, *articulatus* is dextral and has strong, flaring peristomes.

'*Spirorbis*' *kronsmoorensis* Jäger, 1983 from the middle Santonian and early Maastrichtian (a single specimen from the Maastricht-Aachen-Liège area, Meerssen Member, may be conspecific) resembles the specimens from the Geulhem Member. All are sinistral and possess three longitudinal keels. A *Pileolaria*-like species also occurs commonly in the Maastrichtian of northern Kazakhstan (material presented by Prof. Dr D. Naidin). It is uncertain whether '*Spirorbis* (*Neomicroorbis*)' *macrotuberculatus* Müller, 1966 from the early Maastrichtian belongs to the present genus, because its spines are unusually strong.

The following Cainozoic species may belong to the present genus, but are in need of detailed studies: '*Spirorbula*' *expansa* Brünnich Nielsen, 1931 (middle Danian of Fakse, Denmark), '*Spirorbis*' *conoideus* Lamarck, 1818 (Eocene), '*S.*' *conoideus* Lamarck var. *gouetensis* Rovereto, 1904a (Lutetian), '*S.*' *dollfusi* Rovereto, 1904a (Helvetian), '*S.*' *spirintortus* Rovereto, 1898 (Helvetian), '*S.*' *declivis* Reuss, 1860 (Tortonian) and '*S.*' *catagraphus* Rovereto, 1904a (Pliocene).

***Pileolaria* ? sp. 1**

Pl. 6, Figs 11, 12, 14

*Description* — All specimens are or were attached by a broad border to a planar or slightly curved substrate (mostly to a calcareous crust, a bryozoan colony or an oyster shell, etc.), but not to thin cylindrical algal filaments.

Nearly all specimens are more or less planar sinistral spirals (Pl. 6, Figs 11, 12) with approximately 3 turns and with a moderately wide umbilicus. The diameter of the spiral is 1.1-1.6 mm, that of the tube at the aperture 0.4-0.5 mm. Three very distinct, smooth, generally non-granulate and non-denticulate, and equally strong longitudinal keels in equal

distances from each other. Keels do not form teeth at the aperture.

Many specimens raise their apertures, but do not lose contact with the previous whorl of the planar spiral. In a single specimen (Pl. 6, Fig. 14) the planar spiral (of 1.2 mm diameter) is followed by a conical spiral of only  $\frac{1}{2}$  turn. This spiral grows upwards by diminishing its diameter and closing the umbilicus. The height of the cone is at least 0.6 mm (aperture damaged). The sides of the cone are near-straight, neither concave nor convex, the suture between the turns being a narrow indistinct line.

*Discussion* — For a comparison with very similar, but unornamented, *Bipygmaeus pygmaeus*, see above.

*Comparison* — In *Pileolaria* ? sp. 2 (see below) the keels are weaker and often indistinct, whereas transverse wrinkles do occur. The tube is slightly smaller, but becomes somewhat higher. The tube wall is apparently thinner.

In '*Spirorbis*' *kronsmoorensis* Jäger, 1983 the keels often bear granules, whereas they are smooth in the present species.

Amongst Recent species, *P. quasimilitaris* (Bailey, 1970) (keels may be indistinct or absent) and *Nidificaria pocillator* (Vine, 1977) (previously referred to *Pileolaria*, and closely related, keels forming teeth at the aperture, coil diameter 2.0 mm) are similar. The Recent *Metalaeospira armiger* Vine, 1977 is even larger (3.0 mm), and its median keel is stronger than the peripheral ones.

Several Recent species of *Romanchella* (*perrieri* Caullery & Mesnil, 1897; *quadricostalis* Knight-Jones, 1973; *solea* Vine, 1977) have three well-developed keels as well, or even four or five, but the keels form teeth at the aperture. *Romanchella bicava* Knight-Jones, 1978 is similar, but dextral.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: very rare, upper part, not rare. Geulhem section, lower part of the Geulhem Member: absent, upper part, extremely rare.

*Occurrence elsewhere* — Unknown.

#### ***Pileolaria* ? sp. 2**

Pl. 6, Fig. 13

*Description* — The tubes are either attached by a small border to planar calcareous crusts or have become detached of their substrates (bryozoans ?, algae ?). All specimens are sinistral spirals with approximately 3 turns and with a moderately wide umbilicus, coil diameter being 1.0-1.4 mm, and tube diameter at the aperture 0.4-0.5 mm. Spirals

are more or less planar at first, but in most specimens the aperture tends to ascend, without forming a cone. Only in one specimen does the apertural region lose contact with the previous whorls and erects 0.7 mm above the substrate.

Two to three weak, smooth to faintly granulate longitudinal keels occur. The tube's surface is somewhat curved, thus the median keel lies on a slightly higher level than the other two. The inner keel may be absent. Fine transverse wrinkles may be present, the wrinkles slightly protrude at the median keel and may form a small lip over the aperture. The tube wall is thin.

*Discussion* — In some specimens, discrimination between *Pileolaria* ? sp. 1 and sp. 2 is difficult.

*Comparison* — Amongst Recent species, *Nidificaria nidica* (Knight-Jones, 1978) and *Simplaria ovata* (Vine, 1977), both previously assigned to the present genus, are similar, although the latter is larger (coil diameter 2.0 mm).

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: very rare, upper part, not rare. Geulhem section, lower part of the Geulhem Member: absent, upper part, absent.

*Occurrence elsewhere* — Unknown.

#### Spirorbidae gen. et sp. indet.

Pl. 6, Fig. 10

*Discussion* — Often the tube surface of small spirorbids is damaged to such an extent that only the base of the planar spiral is preserved. Sinistral spirals probably belong either to *Bipygmaeus pygmaeus* ? or to *Pileolaria* ? sp. 1 or sp. 2.

Damaged dextral spirals, however, are here referred to *Neodexiospira* ? sp., because amongst well-preserved small dextral spirorbids this genus is the only one to occur in the Geulhem Member.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: common, upper part, frequent. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, absent.

*Occurrence elsewhere* — Unknown.

Genus *Neodexiospira* Pillai, 1970 (= *Dexiospira* Caullery & Mesnil, 1897 non Ehrenberg, 1859)

*Type species* — *Neodexiospira formosa* (Bush, 1904).

*Remarks* — *Dexiospira* Caullery & Mesnil, 1897 was

recognised as a junior homonym of *Dexiospira* Ehrenberg, 1859, probably a protozoan (see Knight-Jones, 1984, p. 110). Pillai (1970, p. 143) designated *formosa* as type species; Knight-Jones (1984, p. 110) erroneously mentioned *pseudocorrugata* (Bush, 1904) as type species, this being the type of *Dexiospira* Caullery & Mesnil, 1897.

*Diagnosis* — Tube dextral in most species. Generally longitudinal keels, often three in number, occur. Between them transverse ornament is often seen. The tube wall has longitudinal rows of small perforations in some species. The operculum has a brood chamber, 'distal part of brood chamber with calcified walls' (Knight-Jones *et al.*, 1975, p. 93).

*Comparison* — The tube of *Janua* de Saint-Joseph, 1894 *sensu stricto* is very similar, but obviously lacks perforations.

*Stratigraphic range* — Early Maastrichtian ?, late Maastrichtian-Recent.

*Remarks* — *Neodexiospira* is one of the most progressive Recent genera in Pillai's scheme (1970, p. 148). Its occurrence in the late Maastrichtian may therefore be surprising at first, but definite proof has been furnished by opercula found *in situ*.

Already in Cenomanian time there are finds resembling Recent *Metalaespira* and *Eulaespira* (see Lommerzheim, 1979). Palaeocene *Metalaespira* and *Circeis* have been recognised on the basis of opercula by Lommerzheim (1981). *Metalaespira*, *Eulaespira* and *Circeis* are also fairly progressive in Pillai's scheme.

Other Cenomanian spirorbids resemble the Recent genus *Spirorbis* *sensu stricto*. Knight-Jones (1981, p. 197) compared the Eocene species *S. elegans* Defrance, 1827c with the genus *Protolaespira*.

It appears that the different constructions of Recent Spirorbidae, *e.g.* their different equipment for brood protection, might have been evolved in a rapid radiation during the middle Cretaceous, whereas the evolution of other Recent spirorbid genera not mentioned here could have been slower during the Cainozoic.

I doubt that the Cenomanian species (*gamigensis* Geinitz, 1872 and *bipartita* Reuss, 1845) compared by Lommerzheim (1979) with the Recent genus *Janua* are at all spirorbids.

The generic status of '*Spirorbis*' *labiatus* Jäger, 1983 (late Santonian-late Maastrichtian) is uncertain, whereas '*S.*' *junior* Jäger, 1983 (late Maastrichtian) and '*S.*' *carinatus* Müller, 1964 (junior homonym of *carinatus* Daudin, 1800, *carinatus* Montagu, 1803 and *carinata* Defrance, 1827c) (early

Maastrichtian) may belong to the present genus.

The stratigraphically oldest genuine species of *Neodexiospira* known to date is a yet undescribed (Jäger, in prep.) species from the Emael to Meerssen Members of the Maastricht-Aachen-Liège area, which is reminiscent of the Recent *N. foraminosa* (Moore & Bush, 1904), in having perforations in its tube, and an operculum with brood chambers found *in situ*.

Lommerzheim (1981) described '*Janua* (*Dexiospira*)' cf. *pseudocorrugata* (Bush, 1904), '*J. (D.)*' *quasiacuta* Lommerzheim, 1981 and '*J. (D.)*' *bilineata* (Schmidt, 1951) from the Palaeocene. In cf. *pseudocorrugata* and *quasiacuta* also the operculum is known.

Miocene species include '*Spirorbis*' *lovisatoi* Rovereto, 1904a (Tortonian), '*S.*' *heliciformis* (von Eichwald, 1830) and '*S.*' *bilineatus* (Schmidt, 1951) (both Sarmatian). Belokryz (1984) described quite a number of species of '*Spirorbis* (*Dexiospira*)', which probably are conspecific in part.

'*Spirorbis*' *nevianii* Rovereto, 1904a is a Pleistocene species.

### **Neodexiospira ? sp. 1**

Pl. 6, Figs 15, 16

*Description* — Spiral attached without a border to a planar substrate (mostly calcareous crusts, oyster shells, walls of cavities bored by bivalves into coarse-grained limestones), not to algal filaments. Sometimes several specimens are attached to the same substrate in close proximity.

All specimens available are small planar dextral spirals with approximately 2½ turns and with a moderately wide umbilicus. The aperture is still in contact with the substrate and shows no tendency to erect above it. The diameter of the spiral is 0.6-1.0 mm, that of the tube at the aperture approximately 0.2-0.3 mm.

Longitudinal ornament consists of 3, 4 or 5 (mostly 3) small but rather sharp keels, the middle one(s) at a somewhat higher level than the peripheral ones. Only rarely are weak annular peristomes seen. The tube wall is thin and fragile, and no perforations are visible.

*Comparison* — '*Spirorbis*' *carinatus* Müller, 1964 was attached to small algal filaments or seagrass roots, and the tube cross-section is more angular. '*Spirorbis*' *junior* Jäger, 1983 is similar, has 4 or 5 keels, a less rounded, but more trapezoid to square cross-section, and the aperture may ascend somewhat above the substrate. Amongst Recent spirorbids,

several species of *Neodexiospira* as well as *Janua pagenstecheri* (de Quatrefages, 1865) are similar.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: not rare, upper part, rare. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, absent.

*Occurrence elsewhere* — Unknown.

### ***Neodexiospira* ? sp. 2**

Pl. 6, Fig. 17

*Description* — On the inner surface of an oyster shell a single dextral planar spiral with 11/4 regular turns is preserved, its coil diameter being 0.6 mm, the diameter of the tube at the aperture < 0.2 mm, the aperture not ascending above the substrate. This spiral differs from all other spirorbids from the Geulhem Member by leaving a distinct space between the turns, so that the spiral resembles a heteromorphic ammonite.

The cross-section of the tube is squarish, with two sharp edges on the upper left and upper right. The upper side is slightly concave between these edges, lateral sides slightly convex, but do not form a border at the base.

*Discussion* — The relationship of this enigmatic specimen with Recent genera is puzzling. The only reason for comparing it with the genus *Neodexiospira* is its mode of coiling, but it should be borne in mind that other Recent spirorbid genera are dextral as well. In spite of its very regular coil it cannot be ruled out that this specimen is in fact a juvenile serpulid.

*Geographic and stratigraphic distribution* — Albert Canal sections, lower part of the Geulhem Member: absent, upper part, absent. Geulhem section, lower part of the Geulhem Member: extremely rare, upper part, absent.

*Occurrence elsewhere* — Unknown.

### DISCUSSION

Tables 1 to 3 show a comparison of the geographic and stratigraphic distribution of serpulids and spirorbids in the Geulhem Member as exposed in the Maastricht-Aachen-Liège area.

The serpulid and spirorbid faunas from the two localities studied are almost identical. The sole striking difference is the rareness of representatives of the genus *Rotularia* at the Geulhem section. In addition, some extremely rare species are absent from one or the other locality. However, some of these

discrepancies are explained by the fact that fewer samples (and fewer specimens) were available from the Geulhem section.

At both localities, the lower unit of the Geulhem Member is somewhat richer in serpulid/spirorbid taxa. Some uncommon taxa are absent from the upper unit [*Pyrgopolon* (*Septenaria*) sp., *P. (P.) m. cipllyana*, *Neomicrorbis cingulatus*, and *Neodexiospira* ? sp. 2]. However, three taxa are distinctly commoner in the upper than in the lower unit, viz. *Rotularia (R.) tobar vroenhovens*, *R. (R.) tobar gracilis* and *Ditrupe schlottheimi*, the latter being extremely common in the lower unit, but reaching an acme (mass occurrence) in the upper part. These three species are all soft-bottom dwellers lacking attached tube parts (*Ditrupe*), or with only very small attachment areas (*Rotularia*), whereas taxa preferring the lower unit all possess an attached tube part of variable length. Thus the differences between the faunas of the two units appear to roughly correspond to changes in main lithofacies types: preponderate hard bottom settings below, preponderate soft bottom ones above. It should be stressed, however, that both lithofacies types may co-occur throughout the sections studied, and that the fauna of the few hard-bottom samples of the upper unit is fairly closely comparable to that of the lower unit.

### COMPARISONS

#### 1. Denmark

The most important area for comparison is the type area of the Danian Stage. Seven of twenty-two taxa found in the Geulhem Member of the Maastricht-Aachen-Liège area have also been recorded from Denmark, viz. *Cycloserpula lombricus*, *Rotularia (R.) hisingeri*, *Ditrupe schlottheimi*, *Placostegus alatus*, *P. erectus*, *Neomicrorbis cingulatus* and *Bipygmaeus pygmaeus*. Two additional taxa are very similar to Danish specimens and there are only small differences at the subspecies level, viz. *Cementula applanata subditiva* and *Neomicrorbis parietalis jagti*. Ødum (1926) and Brünnich Nielsen (1931), who studied the serpulid/spirorbid faunas from the Danish Danian, divided this stage into two units: older and younger Danian, with the latter including the Middle Danian of Fakse. Four of the seven plus two species and subspecies mentioned above have been recorded from the older as well as from the younger Danian, while the other five (*R. (R.) hisingeri*, *D. schlottheimi*, *P. alatus*, *N. parietalis* and *B. pygmaeus*) are only known from the younger. *Bipygmaeus pygmaeus* should not be consid-

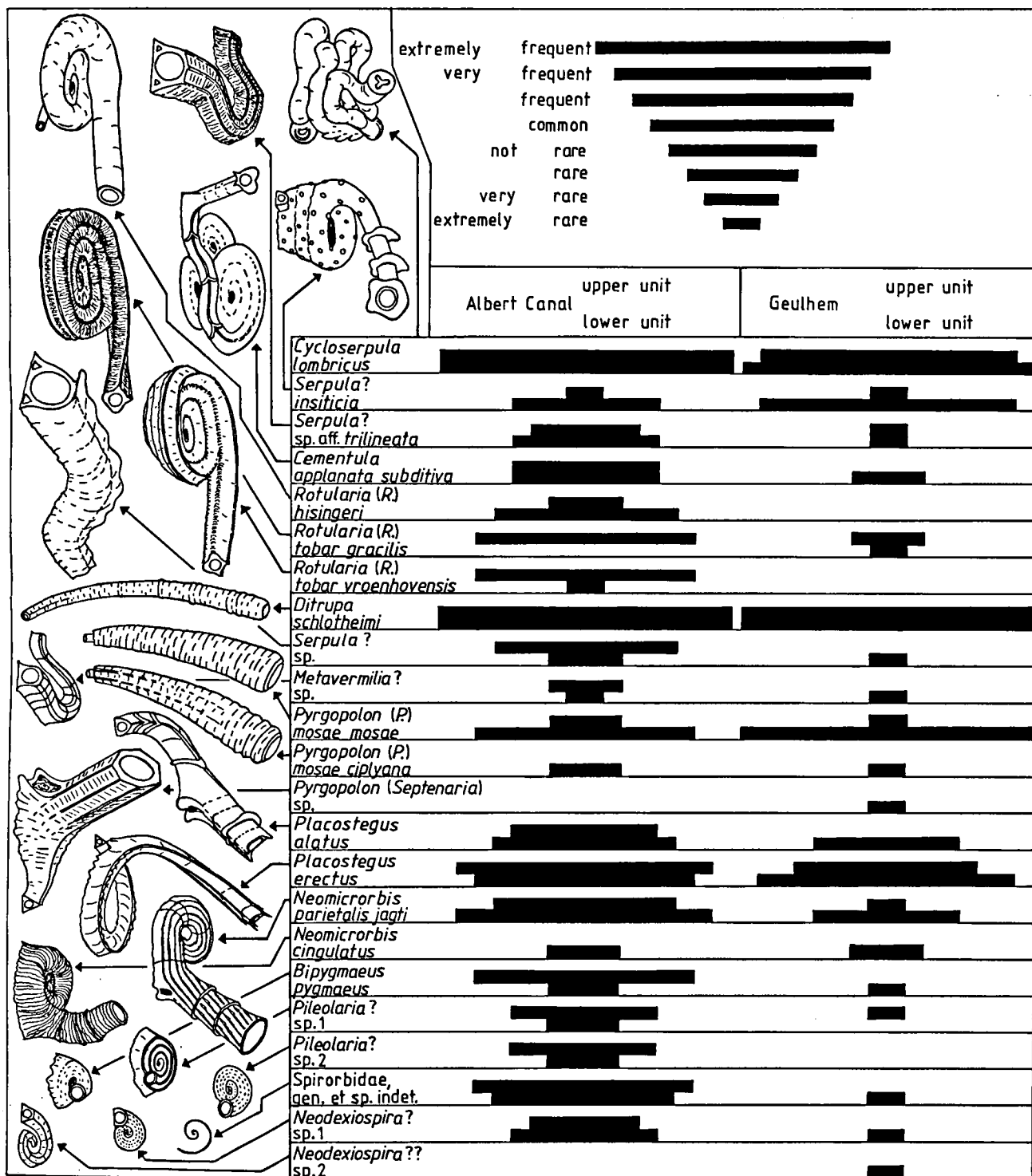


Table 3. Frequency of all serpulid and spirorbid recorded from the Geulhem Member as exposed along the Albert Canal and at Geulhem. For details see text.

ered in this respect, as it appeared already in the late Cretaceous. *Placostegus alatus* is restricted to the Middle Danian of Fakse (Coral Limestone), whereas *D. schlotheimi*, *N. parietalis* and *R. hisingeri* have been recorded from several localities in Denmark, and from other countries (see below).

## 2. Northern Germany

Some of the taxa found in Denmark are also known from northern Germany, exclusively from erratic boulders, which is why they are omitted here.

## 3. Southern Sweden

*Rotularia* (*R.*) *hisingeri*, *N. parietalis*, *N. cingulatus* and other species are known from Danian strata in Skåne (Brünnich Nielsen, 1931).

## 4. Belgium (Mons Basin)

Rasmussen (1965) described and illustrated *C. lombricus*, *D. schlotheimi* and a third species from the Danian of Ciply (Mons Basin).

## 5. Poland

Pugaczewska (1967) recorded *C. lombricus*, *D. schlotheimi* and a third species from the Dano-Montian of the Boryszew borehole.

## 6. Austria

From the Danian of Bruderndorf, Kühn (1960) recorded *R. hisingeri* and two additional species.

## 7. Kazakhstan

Amongst a diverse fauna of Palaeocene species from various localities in Kazakhstan furnished by Prof. Dr D. Naidin (Moscow), are *C. lombricus* and a species of *Rotularia*, similar to *R. (R.) tobar gracilis*, but much larger and more trochospiral, both from the Danian of Kaurtakapy, western Kazakhstan.

## 8. Crimea

In the E. Voigt Collection at Hamburg University there is a single specimen of *Placostegus*, resembling *P. erectus*, but at least twice as large.

## 9. United States

Gardner (1935, 1939) described and illustrated similar *Rotularia* species, which are herein regarded as subspecies of *R. tobar*, viz *tobar tobar* and *tobar mcglameryae*, from the Palaeocene Midway Group of Texas, Alabama and possibly Mississippi. Gardner (1916) and Regenhardt (1961) discussed several species resembling our species of *Placostegus* from the

Rancocas Formation of Maryland and from the Danian or late Palaeocene of New Jersey.

## 10. New Zealand

Fleming (1972) recorded comparable species from the Palaeocene: a dubious *Cementula* from the latest Teurian-Waipawan, a species of *Ditrupea* from the Teurian (= Danian and early late Palaeocene) and a species of *Neomicrorbis* from the Waipawan (= latest Palaeocene to early Eocene).

## 11. Emperor Seamounts, NW Pacific

Lommerzhim (1981) recorded several species from the Palaeocene, some of which were compared with *N. cingulatus* and *B. pygmaeus*. However, there are differences in size and direction of coiling, so that this fauna does not appear to have any close relationship with the Geulhem Member assemblages.

## K/T BOUNDARY EXTINCTION, SURVIVAL AND ORIGINATION EVENTS

Of the twenty-two species and subspecies known to date from the Geulhem Member, four have also been recorded from the underlying late Cretaceous, viz. *C. lombricus*, *Pyrgopolon (P.) mosae mosae*, *P. (P.) m. ciphlyana* and *B. pygmaeus*. In the Maastricht-Aachen-Liège area these four species are known from most of the members from the Lanaye Member to the Nekum Member, and all occur in the Meerssen Member. *C. lombricus* and *B. pygmaeus* occur in pre-Lanaye strata as well. In the Geulhem Member the extremely variable *C. lombricus* display the same array of special features as it does in the Meerssen Member, and the two subspecies of *Pyrgopolon (P.) mosae* also agree well with representatives from the Meerssen Member, whereas *B. pygmaeus* shows (intraspecific ?) differences.

The status of *Serpula* aff. *trilineata* is not quite certain. It may be conspecific with late Cretaceous *trilineata* or not.

The remaining seventeen species and subspecies from the Geulhem Member have not been recorded from Cretaceous strata, neither in the Maastricht-Aachen-Liège area nor anywhere else. A few of them are known from the Danian or the Palaeocene of other countries (see above). However, almost all of these species (including *S.* aff. *trilineata*) are closely related to other congeneric species, or, in the case of *Ditrupea/Pentaditrupea* to species of a closely related genus, so that there are no real newcomers in the serpulid/spirorbid faunas in the area with the onset of deposition of the Geulhem Member.



Not only on a global scale, but also within the Maastricht-Aachen-Liège area are the relationships between late Cretaceous and Danian serpulid/spirorbid faunas close: in the Geulhem Member only the three (sub)species of *Rotularia* and the unique specimen of *Neodexiospira* ? sp. 2 have no counterparts in the Maastrichtian of the area. *Serpula* ? *insiticia* and *S.* sp. differ considerably from Cretaceous species referred to the genus. The remaining sixteen species and subspecies are closely related to Maastrichtian taxa occurring in the area.

Thus, the serpulid/spirorbid faunas of the Geulhem Member comprise mainly in character Maastrichtian faunal elements that experienced a slightly higher rate of evolution at the K/T boundary. The similarities between the faunas of the Maastricht Formation and those of the Geulhem Member are not surprising in view of the more or less comparable environmental and lithofacies conditions that prevailed during the deposition of these units. However, a slight impoverishment of the serpulid/spirorbid faunas around the K/T boundary should be noted: twenty-four species and subspecies are known from the Meerssen Member, while twenty-two are herein recorded from the Geulhem Member.

In principle, Danish sections show a comparable picture, although environmental conditions and lithofacies types differed considerably from those of the Maastricht-Aachen-Liège area. Here too, Danian lithofacies types closely resemble Maastrichtian ones. 'The reconstituted, typical Danian communities in many respects can be considered less diverse duplicates of Maastrichtian communities (Håkansson and Thomsen, 1979). It is noteworthy, however, that some specialized ecological types, which are important in the Maastrichtian chalk communities, are virtually lacking in the Danian' (Birkelund & Håkansson, 1982, p. 381).

For a more detailed discussion of serpulid/spirorbid faunal changes at the K/T boundary see below. The lists below comprise not only genera and subgenera occurring in the Maastricht-Aachen-Liège area, but all genera and subgenera previously recorded from the Maastrichtian and/or Palaeocene over the world. These lists are of a preliminary nature, and in part include revised (yet unpublished) data, data in need of confirmation, and, in a few cases, data from the literature simply repeated here without comment. In comparison with the works of Brünnich Nielsen (1931), Regenhardt (1961) and Howell (1962), this is a

much more advanced attempt at providing an overview of serpulid/spirorbid evolution and extinction around the K/T boundary.

With the exception of material from northern Germany, the Maastricht-Aachen-Liège area and the Emperor Seamounts, the literature comprises but limited stratigraphically well-documented serpulid/spirorbid faunas. In addition, modern papers describing biozonations rarely, if ever, make mention of serpulid/spirorbid faunas. This is why the stratigraphic scheme used below is of necessity rather crude, too crude really for a proper description of an extinction event of short duration.

It could be quite revealing to follow Danian species into the late Palaeocene, and Eocene and to see what happens at the Eocene/Oligocene boundary; data available to date are too scanty for a detailed description of extinction/survival and origination patterns in these stratigraphic intervals.

1. Genera and subgenera present in the Maastrichtian, but absent from the Cainozoic, becoming extinct either during the course of the Maastrichtian or at the K/T boundary:

- *Protula* (*Longitubus*) Howell, 1943. In the United States, this subgenus ranges from the early Campanian Merchantville Formation to the early Maastrichtian Navesink Formation; it probably became extinct long before the K/T boundary.

- *Jereminella* Lugeon, 1919. Poorly known genus, a single species having been recorded from the Maastrichtian of a restricted area (see Regenhardt, 1961, p. 34).

- *Serpula* (n. subgen.).

- *Pegmaticula* Regenhardt, 1961. Originally introduced as a subgenus of *Gynaconitis* Regenhardt, 1961, but diagnosis entirely altered (Jäger, in prep.), to contain spiral and non-spiral tubes with a generally 'smooth' surface and an occasional 'secondary tube' (= Nebenröhre of Jäger, 1983, pp. 11, 38): *turpificiata* Regenhardt, 1961 (type species), '*Parsimonia*' *wegneri* Jäger, 1983, an undescribed subspecies of *wegneri*, an undescribed species from the Maastrichtian of Kazakhstan, and *delphinula* (Goldfuss, 1831) of Oxfordian-Tithonian age.

- *Parsimonia* Regenhardt, 1961 ?. It is not clear whether this genus ranges into the Maastrichtian, as doubts exist on the status of *frustulenta* (Regenhardt, 1961).

- *Mucroserpula* Regenhardt, 1961.

- *Laqueoserpula* Lommerzheim, 1979. Discrimination between this genus and *Cementula* is not entirely clear.

- *Nogrobs* (*Tetraditrupe*) Regenhardt, 1961. See Jäger (in press b) for details.
- *Ornatoporta* Gardner, 1916. This is either a subgenus of *Pyrgopolon* or a closely related, but poorly known taxon. Maastrichtian (Monmouth Formation), United States.
- *Conorca* Regenhardt, 1961. See Jäger (1983).
- *Protectoconorca* Jäger, 1983.
- *Rotularia* (*Tectorotularia*).
- *Rotularia* (*Austrorotularia*).

2a. Genera and subgenera present in Maastrichtian (or Mesozoic) as well as in Cainozoic, but with different species on either side of the K/T boundary.

- *Protula* (*Protula*) Risso, 1826. Unpublished material of Hauterivian age from France.
- *Josephella* Caullery & Mesnil, 1896.
- *Serpula* Linné, 1758.
- *Spiraserpula* Regenhardt, 1961 emend. Pillai (in press).
- *Cementula* Regenhardt, 1961 emend. Pillai (in press).
- *Rotularia* (*Praerotularia*) Lommerzheim, 1979 ?. According to Lommerzheim (1979, p. 174) this subgenus ranges into the Eocene, but I know of no Cainozoic species. However, one of the three subgenera of *Rotularia* must have crossed the K/T boundary to give rise to the Palaeogene subgenus *R.* (*Rotularia*).
- *Nogrobs* (*Nogrobs*) de Montfort, 1808. See Jäger (in press b).
- *Galeolaria* Lamarck, 1818 ?. See Lommerzheim (1979, p. 153).
- *Pomatoceros* Philippi, 1844. Discrimination from *Dorsoserpula* Parsch, 1956 not clear.
- *Metavermilia* (*Metavermilia*) Bush, 1904. See Lommerzheim (1979, p. 158).
- *Metavermilia* (*Vepreculina*) Regenhardt, 1961.
- *Filogranula* Langerhans, 1884.
- *Pseudovermilia* Bush, 1907 ?. See Lommerzheim (1979, p. 159).
- *Janita* de Saint-Joseph, 1894. See Lommerzheim (1979, p. 157).
- *Pyrgopolon* (*Septenaria*) Regenhardt, 1961. Upon a closer inspection of Cainozoic and Recent material the only representatives of this subgenus are the sole specimen from the Geulhem Member described herein and possibly *gallica* (Wrigley, 1951) of early Eocene-early Oligocene age.
- *Pyrgopolon* (*Hamulus*) Morton, 1834. Three Cainozoic species may belong here, viz. *hexagonum*

(Marinoni, 1878) [unspecified Cainozoic], *kaufmanni* (Mayer-Eymar, 1887) [Eocene] and *ouyensis* (Chapman, 1913) [early Miocene]; detailed studies are needed.

- *Placostegus* Philippi, 1844 (= *Eoplacostegus* Regenhardt, 1961).
- *Paliurus* Gabb, 1876. See Lommerzheim (1979, p. 163).
- *Orthoconorca* Jäger, 1983. Jäger's (1983) interpretation of this genus was too wide; a group of species reminiscent of the type species is known to range from the late Cretaceous into the Danian.
- *Pileolaria* Claparède, 1868. See Jäger (in prep.).
- *Neodexiospira* Pillai, 1970. See Jäger (in prep.).
- *Spirorbis* Daudin, 1800 ?, *Metalaeospira* Pillai, 1970 ? and *Eolaeospira* Pillai, 1970 ?. Lommerzheim (1979, pp. 167, 169, 170) did no more than compare Cenomanian material with and not refer to these Recent genera. *Spirorbis* in palaeontological literature has often been used for all Spirorbidae gen. indet.

2b. Genera and subgenera of which at least one (sub)species crosses the K/T boundary morphologically unchanged (given in [] brackets)

- *Filograna* Oken, 1815. [*F. socialis* (Goldfuss, 1831)]. The occurrence in the Danian of Denmark is in need of confirmation. Otherwise, this genus should be in category 2a.
- *Cycloserpula* Parsch, 1956 (= *Glomerula* Regenhardt, 1961 *sensu* Brünnich Nielsen, 1931). [*C. implicata* (von Hagenow, 1840)].
- *Pentaditrupe* Regenhardt, 1961. [*P. subtorquata* (Münster in Goldfuss, 1831)].
- *Vermiliopsis* de Saint-Joseph, 1894. [*V. dorsolineata* (Brünnich Nielsen, 1931) and *V. fluctuata* (J. de C. Sowerby, 1829)].
- *Neovermilia* Day, 1961 (= *Proliserpula* Regenhardt, 1961). [*N. ampullacea* (J. de C. Sowerby, 1829)].
- *Pyrgopolon* (*Pyrgopolon*) de Montfort, 1808. [*P.(P.) mosae mosae* de Montfort, 1808 and *P.(P.) m. cipllyana* (de Ryckholt, 1852)].
- *Neomicrorbis* Rovereto, 1904a. [*N. c. crenatostriatus* (Münster in Goldfuss, 1831)].
- *Bipygmaeus* Regenhardt, 1961. [*B. pygmaeus* (von Hagenow, 1840)].

*Protulophila gestroi* Rovereto, 1901, a hydroid symbiont in serpulid tubes also crosses the K/T boundary and ranges from Pliensbachian to Recent (see Zibrowius & Jäger, in prep.).

### 3. Genera and subgenera first occurring in the Palaeocene

- *Hydroides* Gunnerus, 1768. Recorded with a query from the middle Palaeocene by Lommerzheim (1981, p. 36); also recorded by Howell (1948, p. 5) from the late Palaeocene Vincentown Formation of New Jersey.
- *Rotularia* (*Rotularia*) DeFrance, 1827a. The phylogenetic relationships between the four subgenera recognised is unclear and the separation at the K/T boundary is slightly arbitrary.
- *Ditruha* Berkeley, 1835.
- *Pyrgopolon* (*Turbinia*) Michelin, 1845. Recorded by Wrigley (1950) from the Thanetian (late Palaeocene) onwards.
- *Circeis* de Saint-Joseph, 1894. See Lommerzheim (1981). The only known Palaeocene species is *C. paleocaenicum* Lommerzheim, 1981; *cingulatus* Brünich Nielsen, 1931 is here referred to the genus *Neomicrorbis*.
- *Paralaeospira* Caullery & Mesnil, 1897. See Lommerzheim (1981).
- *Cubiculovinea* Lommerzheim, 1981.

The K/T boundary witnessed the mass extinction of dinosaurs, ammonites, belemnites, inoceramid bivalves, planktonic foraminifera, phytoplankton and other groups. As far as level bottom communities are concerned, however, the K/T boundary is listed only as a fourth-class extinction event by Boucot (1990, p. 22, fig. 1).

At the K/T boundary the families that disappeared were first of all consumers, and secondly phytosymbionts, whereas suspension feeders were less affected (Roy *et al.*, 1990, fig. 6). Sheehan & Hansen (1986) stated that, after a breakdown of photosynthesis for several months, detritus feeders were less affected than were herbivores and carnivores. As a result, serpulids/spirorbids as benthic animals which in fact do not depend on living phytoplankton for nourishment are naturally less affected than are animals with a different feeding strategy.

However, Birkelund & Håkansson (1982) stated that, due to changes in temperature, sedimentation of carbonate decreased and thus hardgrounds became rarer at the K/T boundary. The pioneer fauna of the earliest Danian from Denmark is a soft bottom community of low diversity.

Thus, amongst the serpulid and spirorbid taxa which survived the K/T boundary, there should predominantly be forms which need only a small

attachment area, *e.g.* spiral tubes. Several forms which needed a large attachment area, *e.g.* many specialised shallow-water dwellers, became extinct. These shallow water forms are often also warm water forms (reef inhabitants). The decrease in temperature at the K/T boundary generally affected warm water forms more than it did cold water forms.

Thus the Danian serpulid and spirorbid faunas represent, as do the Danian bryozoan faunas (Voigt, 1985), an impoverished Maastrichtian fauna with but very few new taxa.

As a result of sea level changes and sedimentary breaks in the great majority of K/T boundary sections, these show breaks in the palaeontological and evolutionary record (see Birkelund & Håkansson, 1982, fig. 11), which explains the great number of taxa in category 2a.

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#### REFERENCES

- Anonymous, 1847. Anlagen zu den öffentlichen Sitzungen. Verzeichniss der Naturaliensammlung. In: G.A. Michaelis, & H.F. Scherk (eds). Amtlicher Bericht über die 24. Versammlung deutscher Naturforscher und Aerzte in Kiel 1846. Kiel (Akademische Buchhandlung): 109-119.
- Archiac, A. d', 1847. Description des fossiles recueillis par M. Thorent dans les couches à Nummulines des environs de Bayonne. — Mém. Soc. géol. Fr., (2)2(1): 189-217, pls 5-9.
- Avnimelech, M., 1941. Upper Cretaceous serpulids and scaphopods from Palestine. — Bull. geol. Dept Hebrew Univ., 3(2): 1-16, 21 figs.
- Bailey, J.H., 1970. Spirorbinae (Polychaeta) from the West Indies. — Studies on the Fauna of Curaçao and other Caribbean Islands, 118: 58-81, figs 125-159.
- Bailey-Brock, J.H., & P. Knight-Jones, 1977. Spirorbidae (Polychaeta) collected by R.V. "Vitjas" from abyssal depths of the Pacific Ocean. — J. zool. Lond., 181: 315-321, 1 fig.

- Ball, H.W., 1960. Upper Cretaceous Decapoda and Serpulidae from James Ross Island, Graham Land. — Falkland Isl. Depend. Surv., Sci. Rept., 24: 30 pp., 4 figs, 7 pls.
- Belokryz, L.S., 1984. Spirorbiny pricernomorskogo miocena. — Paleont. Zhurnal, 1984/2: 26-39, 1 fig., 3 tabs.
- Berkeley, M.J., 1828. A short account of a new species of *Modiola* and of the animal inhabitants of two British Serpulae. — J. zool. Lond., 3: 229-231 (not seen).
- Berkeley, M.J., 1835. Observations upon the *Dentalium subulatum* of Deshayes. — J. zool. Lond., 5: 424-427 (not seen).
- Birkelund, T., & E. Håkansson, 1982. The terminal Cretaceous extinction in Boreal shelf seas - A multicausal event. In: L.T. Silver & P.H. Shultz (eds). Geological implications of impacts of large asteroids and comets on the earth. — Geol. Soc. Am., Spec. Pap., 190: 373-384, 11 figs.
- Bonarelli, G., & J.J. Nágera, 1921. Observaciones geológicas en las inmediaciones del Lago San Martín (Territorio de Santa Cruz). — Min. Agric. Dir. gen. Minas, Geol. e Hidrol., Bol., 27(B, Geol.): 39 pp., 6 figs, 6 pls.
- Boreham, A.U.E., 1959. Cretaceous fossils from the Chatham Islands. — Trans. r. Soc. N.Z., 86(1): 119-125, 2 figs, pl. 11.
- Boucot, A.J., 1990. Phanerozoic extinctions: How similar are they to each other? In: E.G. Kauffman & O.H. Walliser (eds). Extinction events in earth history. Lecture Notes in Earth Sciences, 30. Berlin (Springer Verlag): 5-30, 1 fig.
- Bronn, H.G., 1827. Verzeichnis der bei dem Heidelberger Mineralien-Komptoir verkäuflichen Konchylien-, Pflanzentier- und anderen Versteinerungen. — Z. Min., 2: 544 (not seen).
- Burchette, R.P., & R. Riding, 1977. Attached vermiform gastropods in Carboniferous marginal marine stromatolites and biostromes. — Lethaia, 10(1): 17-28, 8 figs.
- Bush, K.J., 1904. Tubicolous annelids of the tribes Sabellides and Serpulides from the Pacific Ocean. — Harriman Alaska Exped., 12: 169-355, pls 21-44 (not seen).
- Bush, K.J., 1907. Descriptions of the two genera of tubicolous annelids, *Paravermilia* and *Pseudovermilia*, with species from Bermuda referable to them. — Am. J. Sci., (4)23: 131-136 (not seen).
- Camacho, H.H., 1949. La fauna cretácica del Hito XIX (Tierra del Fuego). — Rev. Asoc. geol. Argentina, 4(4): 249-262, pl. 1 (not seen).
- Caullery, M., & F. Mesnil, 1896. Note sur deux serpulides nouveaux (*Oriopsis metchnikowi* n. g., n. sp. et *Josephella marenzellaria* n. g., n. sp.). — Zool. Anz., 10: 482-486 (not seen).
- Caullery, M., & F. Mesnil, 1897. Études sur la morphologie comparée et la phylogénie des espèces chez les spirorbies. — Bull. Soc. Sci. Fr. Belg., 30: 185-233, pls 7-10.
- Chapman, F., 1913. Description of new and rare fossils obtained by deep boring in the Mallee, 1. Plantae; and Rhizopoda to Brachiopoda. — Proc. r. Soc. Vict., n.s., 26(1): 165-191, pls 16-19.
- Chenu, J.C., 1842-1855. Illustrations conchyliologiques. Paris (not seen).
- Chiplonkar, G.W., & P.M. Tapaswi, 1973. Fossil polychaetes from the Upper Cretaceous rock formations of South India, part 1 + 2. — Proc. Indian Acad. Sci., (B)77(3): 116-130; (5): 202-213, pls 8, 11.
- Claparède, É., 1868-1870. Les annélides chétopodes du Golfe de Naples. — Mém. Soc. phys. hist. nat. Genève, 20(1): 1-225, pls 17-31; (2): 366-542, pls 1-14.
- Cox, L.R., 1953. Lower Cretaceous Gastropoda, Lamellibranchiata and Annelida from Alexander I Land. — Falkland Isl. Depend. Surv., Sci. Rept, 4: 14 pp., 1 fig., 2 pls.
- Crisp, D.J., J.H. Bailey & E.W. Knight-Jones, 1967. The tube-worm *Spirorbis vitreus* and its distribution in Britain. — J. mar. biol. Assoc. UK, 47: 511-521 (not seen).
- Cupedo, F., 1980. De opercula van *Sclerostyla mellevillei* (Nijst et le Hon), "*Serpula*" *instabilis* (Wrigley) en "*Ditrupa*" *mosae* (Bronn), en hun betekenis voor de systematiek van deze soorten. — Publ. Natuurhist. Genootsch. Limburg, 29(3)(1979): 1-19, 33 figs.
- Daudin, F.M., 1800. Recueil de mémoires et de notes sur des espèces inédites ou peu connues de mollusques, de vers et de zoophytes. Paris (Fuchs), xviii + 50 pls (not seen).
- Day, J.H., 1961. The polychaete fauna of South Africa, 6. Sedentary species dredged of Cape shores with a few new records from the shore. — J. linn. Soc. London, Zool., 44(299): 463-560, 18 figs.
- Defrance, M., 1827a. Rotulaire. In: F.G. Levrault (ed.). Dictionnaire des sciences naturelles, 46. Paris/Strasbourg: 321, 322.
- Defrance, M., 1827b. Serpule. In: F.G. Levrault (ed.). Dictionnaire des sciences naturelles, 48. Paris/Strasbourg: 549-572.
- Defrance, M., 1827c. Spirorbe. In: F.G. Levrault (ed.). Dictionnaire des sciences naturelles, 50. Paris/Strasbourg: 302-304.
- Deshayes, G.-P., 1825. Anatomie et monographie du genre *Dentalium*. — Mém. Soc. hist. nat. Paris, 2: 321-378, pls 15-18.
- Dew, B., 1959. Serpulidae (Polychaeta) from Australia. — Rec. Austr. Mus., 25(2): 19-56, 21 figs.
- Doncieux, L., 1926. Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault, 2(3). Corbières septentrionales. — Anns Univ. Lyon, n.s., Sci. Médic., 45: vii + 99 pp., 33 figs, 8 pls.
- Dumortier, E., 1874. Études paléontologiques sur les dépôts jurassiques du Bassin du Rhône, 4. Lias supérieur. Paris (F. Savy), 335 pp., 62 pls.
- Ehrenberg, C.G., 1859. Fortschreitende Erkenntnis massenhafter mikroskopischer Lebensformen in den untersten silurischen Thonschichten bei Petersburg. — Mber. preuß. Akad. Wiss. Berlin, physik.-math. Kl., 1859: 295-337.
- Eichwald, K.E. von, 1830. Naturhistorische Skizze von Lithauen, Volhynien und Podolien in geognostisch-mineralogischer, botanischer und zoologischer Hinsicht entworfen. Wilna, 256 pp., 3 pls (not seen).
- Etheridge, R. jr., 1907. Lower Cretaceous fossils from the sources of the Barcoo, Ward and Nive Rivers, South Central Queensland, 1. Annelida, Pelecypoda and Gasteropoda. — Rec. Austr. Mus., 6: 317-329, pls 57-62.
- Fabricius, O., 1780. Fauna Groenlandica. Hafniae, xvi + 452 pp. (not seen).
- Faulkner, G.H., 1930. The anatomy and the histology of bud-formation in the serpulid *Filograna implexa*, together with some cytological observations on the nuclei of the neoblasts. — J. linn. Soc. London, Zool., 37: 109-188, 33 figs, pls 7, 8.
- Felder, W.M., 1975. Lithostratigrafie van het Boven-Krijt en het Dano-Montien in Zuid-Limburg en het aangrenzende gebied. In: W.H. Zagwijn & C.J. van Staalduinen (eds). Toelichting bij geologische overzichtskaarten van Nederland. Haarlem (Rijks Geologische Dienst): 63-75.
- Fleming, C.A., 1972. A preliminary list of New Zealand fossil polychaetes. — N. Z. J. Geol. Geophys., 14(4): 742-756, 4 figs.
- Gabb, W.M., 1860. Descriptions of new species of American Tertiary and Cretaceous fossils. — J. Acad. nat. Sci. Philad., (2)4(4): 375-406, pls 47-49 (not seen).

- Gabb, W.M., 1876. Notes on American Cretaceous fossils, with descriptions of some new species. — Proc. Acad. nat. Sci. Philad., (3)28: 276-324, pl. 17.
- Galeotti, H., 1837. Mémoire sur la constitution géognostique de la province de Brabant. — Mém. r. Acad. Sci. Belg., 12 (not seen).
- Gardner, J., 1916. Systematic paleontology. Upper Cretaceous. Vermes. — Maryland geol. Surv., Upper Cret. vol.: 745-749, pl. 47.
- Gardner, J., 1935. The Midway Group of Texas. — Univ. Texas Bull., 3301: 403 pp., 4 figs, 28 pls.
- Gardner, J., 1939. Notes on fossils from the Eocene of the Gulf Province. — U.S. geol. Surv., Prof. Paper, 193-B: 17-37, 6 figs, pls 6-8.
- Gee, J.M., 1964. The British Spirorbinae with a description of *S. cuneatus* sp. n. and a review of the genus *Spirorbis*. — Proc. zool. Soc. London, 143: 405-441 (not seen).
- Gee, J.M., & E.W. Knight-Jones, 1962. The morphology and larval behaviour of a new species of *Spirorbis* (Serpulidae). — J. mar. biol. Assoc. UK, 42: 641-654 (not seen).
- Geinitz, H.B., 1871-1875. Das Elbthalgebirge in Sachsen. — Palaeontographica, 20: 319 + 245 pp., 67 + 46 pls.
- Glaessner, M.F., 1958. New Cretaceous fossils from New Guinea. — Rec. Austr. Mus., 13: 199-226, 5 figs, pls 24-26.
- Goldfuss, A., 1826-1844. Petrefacta Germaniae. Düsseldorf (Arnz & Co), vii + 252 + iii + 312 + iv + 128 pp., 200 pls.
- Gunnerus, J., 1768. Om nogle norske Coraller. — Skr. k. norske Vidensk. Selsk., 4: 38-73, pl. 2, figs 11-13 (not seen).
- Guppy, R.J.L., 1866. On the relations of the Tertiary formations of the West Indies. — Q. Jl geol. Soc. London, 22: 570-590, 2 tabs, pl. 26.
- Hagenow, F. von, 1840. Monographie der Rügen'schen Kreideversteinerungen, 2. Radiarien und Annulaten. — N. Jb. Mineral., Geol., Geogn., 1840: 631-672, pl. 9.
- Håkansson, E., & E. Thomsen, 1979. Distribution and types of bryozoan communities at the boundary in Denmark. In: T. Birkelund & R.G. Bromley (eds). Cretaceous-Tertiary boundary events symposium, 1. The Maastrichtian and Danian of Denmark. Copenhagen (University of Copenhagen): 78-91, 5 figs.
- Ham, R.W.J.M. van der, 1988. Echinoids from the Early Palaeocene (Danian) of the Maastricht area (NE Belgium, SE Netherlands): preliminary results. In: J.W.M. Jagt & A.W. Janssen (eds). Faunal and stratigraphical aspects of the Early Palaeocene (Danian) in the SE Netherlands and NE Belgium. — Meded. Werkgr. Tert. Kwart. Geol., 25(2-3): 127-161, 1 fig., 1 tab., 9 pls.
- Ham, R. van der, W. de Wit, G. Zuidema & M. van Birgelen, 1987. Zeeëgels uit het Krijt en Tertiair van Maastricht, Luik en Aken. — Publ. Natuurhist. Genootsch. Limburg, 36: 43 pp., 17 figs, 3 tabs, 24 pls.
- Hartmann-Schröder, G., 1971. Annelida, Borstenwürmer, Polychaeta. In: M. Dahl & F. Peus (eds). Die Tierwelt Deutschlands und der angrenzenden Meeresteile, 58. Jena (VEB Gustav Fischer Verlag), 594 pp., 191 figs.
- Hébert, E., 1855. Tableau des fossiles de la Craie de Meudon et description de quelques espèces nouvelles. — Mém. Soc. géol. Fr., (2)5(2): 345-374, pls 27-29.
- Hisinger, W., 1831. Anteckningar i Physik och Geognosie under resor uti Sverige och Norrige. Stockholm (not seen).
- Hisinger, W., 1837. Lethaea suecica, seu Petrificata Sveciae iconibus et characteribus illustrata. Holmiae (Nordstedt), 124 pp., 3 + 26 pls.
- Hove, H.A. ten, 1975. Serpulinae (Polychaeta) from the Caribbean. 3. The genus *Pseudovermilia*. — Studies on the Fauna of Curaçao and other Caribbean Islands, 47: 46-101, figs 114-186, 1 tab., 8 pls.
- Hove, H.A. ten, 1984. Towards a phylogeny in serpulids (Annelida; Polychaeta). In: P.A. Hutchings (ed.). Proceedings of the First International Polychaete Conference, Sydney. Sydney (Linnean Soc. NSW): 181-196, 7 figs.
- Hove, H.A. ten, & M.J. Jansen-Jacobs, 1984. A revision of the genus *Crucigera* (Polychaeta; Serpulidae); a proposed methodical approach to serpulids, with special reference to variation in *Serpula* and *Hydroides*. In: P.A. Hutchings (ed.). Proceedings of the First International Polychaete Conference, Sydney. Sydney (Linnean Soc. NSW): 143-180, 12 figs.
- Hove, H.A. ten, & Smith, R.S., 1990. A re-description of *Ditrupa gracillima* Grube, 1878 (Polychaeta, Serpulidae) from the Indo-Pacific, with a discussion of the genus. — Rec. Austr. Mus., 42(1): 101-118, 62 figs.
- Howell, B.F., 1943. *Hamulus*, "Falcula", and other Cretaceous Tubicola of New Jersey. — Proc. Acad. nat. Sci. Philad., 95: 139-166, pls 19, 20.
- Howell, B.F., 1948. New records and descriptions of Upper Cretaceous and Eocene serpulid worms from New Jersey. — Notula naturae Acad. nat. Sci. Philad., 202: 1-7, 14 figs.
- Howell, B.F., 1962. Worms. In: R.C. Moore & C. Teichert (eds). Treatise on Invertebrate Paleontology, part W. The Geological Society of America (Boulder)/The University of Kansas Press (Lawrence): W144-177, figs 85-108.
- Hucke, K., & E. Voigt, 1967. Einführung in die Geschiebeforschung (Sedimentärgeschiebe). Oldenzaal (Nederlandse Geologische Vereniging), 132 pp., 24 figs, 5 tabs, 50 pls, 2 maps.
- Imajima, M., 1976. Serpulid polychaetes from Tanega-shima, Southwest Japan. — Mem. nat. Sci. Mus. Tokyo, 9: 123-143, 11 figs.
- Imajima, M., 1977. Serpulidae (Annelida, Polychaeta) collected around Chichi-jima (Ogasawara Islands). — Mem. nat. Sci. Mus. Tokyo, 10: 89-111, 10 figs.
- Imajima, M., 1978. Serpulidae (Annelida, Polychaeta) collected around Nii-jima and O-shima, Izu Islands. — Mem. nat. Sci. Mus. Tokyo, 11: 49-72, 9 figs.
- Jäger, M., 1983. Serpulidae (Polychaeta sedentaria) aus der norddeutschen höheren Oberkreide - Systematik, Stratigraphie und Ökologie. — Geol. Jb., (A)68: 3-219, 7 figs, 15 tabs, 16 pls.
- Jäger, M., 1987. Campanian-Maastrichtian serpulids from Thermae 2000 borehole (Valkenburg a/d Geul, The Netherlands). In: M.J.M. Bless, J. Bouckaert, H.-R. Langguth & M. Streef (eds). Upper Cretaceous and Dinantian geology and hydrogeology of the Thermae boreholes of Valkenburg aan de Geul (South-Limburg, The Netherlands). — Annls Soc. géol. Belg., 110(1): 39-46, 1 fig., 2 pls.
- Jäger, M., 1988. Serpulids around the Gulpen/Maastricht Formation boundary (Upper Maastrichtian) in South Limburg (The Netherlands) and adjacent Belgian areas. In: M. Streef & M.J.M. Bless (eds). The Chalk District of the Euregio Meuse-Rhine. Selected papers on Upper Cretaceous deposits. Natuurhistorisch Museum Maastricht/Laboratoires de Paléontologie de l'Université d'Etat à Liège: 69-75, 2 figs, 2 tabs.
- Jäger, M., 1991. Serpulidae und Spirorbidae (Polychaeta sedentaria) aus dem Alb und der Oberkreide Helgolands (Norddeutschland). — Geol. Jb., (A)120: 139-175, 1 tab., 6 pls.

- Jäger, M., in press a. Genus *Pentaditrupe* Regenhardt, 1961. In: J.W.M. Jagt (ed.). An Illustrated Catalogue of Late Cretaceous fossils from Limburg (The Netherlands) and adjacent areas. — Meded. Rijks geol. Dienst.
- Jäger, M., in press b. Genus *Nogrobs* de Montfort, 1808. In: J.W.M. Jagt (ed.). An Illustrated Catalogue of Late Cretaceous fossils from Limburg (The Netherlands) and adjacent areas. — Meded. Rijks geol. Dienst.
- Jagt, J.W.M., & J.S.H. Collins, 1988. The biostratigraphy of the Geulhem Member (Early Palaeocene), with reference to the occurrence of *Pycnolepas bruennichi* Withers, 1914 (Crustacea, Cirripedia). In: J.W.M. Jagt & A.W. Janssen (eds). Faunal and stratigraphical aspects of the Early Palaeocene (Danian) in the SE Netherlands and NE Belgium. — Meded. Werkgr. Tert. Kwart. Geol., 25(2-3): 175-196, 2 figs, 1 pl.
- Jagt, J.W.M., & A.W. Janssen, 1988. The Danian in the Maastrichtian type area (SE Netherlands, NE Belgium): past, present and future research. In: J.W.M. Jagt & A.W. Janssen (eds). Faunal and stratigraphical aspects of the Early Palaeocene (Danian) in the SE Netherlands and NE Belgium. — Meded. Werkgr. Tert. Kwart. Geol., 25(2-3): 213-223, 1 tab.
- Jakubowski, G., & T. Musiał, 1977. Lithology and fauna from the Upper Tortonian sands of Monastyrz and Długi Goraj (Southern Roztocze - Poland). — Prace Muz. Ziemi, 26: 63-126, 5 figs, 16 tabs, 16 + 7 pls.
- Jessen, A., & H. Ødum, 1923. Senon og Danien ved Voxlev. — Danm. geol. Unders., (2)39: 1-73, 12 figs, 4 tabs, 2 pls.
- Johnson, H.P., 1901. The Polychaeta of the Puget Sound region. — Proc. Boston Soc. nat. Hist., 24(18): 381-437 (not seen).
- Kelber, K.-P., 1986. Taphonomische Konsequenzen aus der Besiedlung terrestrischer Pflanzen durch Spirorbidae (Annelida, Polychaeta). — Cour. Forsch.-Inst. Senckenberg, 86: 13-26, 7 figs, 1 pl.
- Kinberg, J.G.H., 1867. *Annulata nova*. — Öfvers. k. Vet.-Akad. Förh., 23: 337-357 (not seen).
- Knight-Jones, E.W., P. Knight-Jones & P.K. Bregazzi, 1973. *Helicosiphon biscoeensis* Gravier (Polychaeta: Serpulidae) and its relationship with other Spirorbinae. — Zool. J. linn. Soc. London, 52: 9-21, 5 figs.
- Knight-Jones, E.W., P. Knight-Jones & L.C. Llewellyn, 1974. Spirorbinae (Polychaeta: Serpulidae) from Southeastern Australia. Notes on their taxonomy, ecology, and distribution. — Rec. Austr. Mus., 29(3): 107-151, 14 figs.
- Knight-Jones, P., 1973. Spirorbinae (Serpulidae: Polychaeta) from southeastern Australia. A new genus and seven new species. — Bull. Br. Mus. nat. Hist. (Zool.), 24: 230-259 (not seen).
- Knight-Jones, P., 1978. New Spirorbidae (Polychaeta: Seditaria) from the East Pacific, Atlantic, Indian and Southern Oceans. — Zool. J. linn. Soc. London, 64: 201-240, 18 figs.
- Knight-Jones, P., 1981. Behaviour, setal inversion and phylogeny of Sabellida (Polychaeta). — Zool. Scripta, 10: 183-202, 75 figs.
- Knight-Jones, P., 1984. A new species of *Protoleodora* (Spirorbidae: Polychaeta) from eastern U.S.S.R., with a brief revision of related genera. — Zool. J. linn. Soc. London, 80: 109-120, 3 figs.
- Knight-Jones, P., E.W. Knight-Jones & T. Kawahara, 1975. A review of the genus *Janua*, including *Dexiospira* (Polychaeta: Spirorbinae). — Zool. J. linn. Soc. London, 56(2): 91-129, 6 figs.
- Koenen, A. von, 1891. Das norddeutsche Unter-Oligocän und seine Mollusken-Fauna, 3. — Abh. geol. Spec. Kt. Preußen, 10(3): 575-817, pls 35-52.
- Krutzler, E.M., & M. Meijer, 1958. On the occurrence [*sic*] of *Crania brattenburgica* (v. Schlotheim 1820) in the region of Maastricht (Netherlands) (Brachiopoda, Inarticulata). — Natuurhist. Maandbl., 47(11-12): 135-141, 8 figs.
- Kühn, O., 1960. Neue Untersuchungen über die dänische Stufe in Oesterreich. — In: A. Rosenkrantz & F. Brotzen (eds). Part V. Proceedings of Section 5. The Cretaceous-Tertiary Boundary. Reports of the International Geological Congress, 21st Session. Copenhagen (Det Berlingske Bogtrykkeri): 162-169.
- Lamarck, J.B. de, 1818. Histoire naturelle des animaux sans vertèbres, 5. Paris (Verdière), 612 pp.
- Langerhans, P., 1884. Die Wurmfauuna von Madeira, 4. — Z. wiss. Zool., 40(2): 247-285, pls 15-17.
- Lentini, F., 1974. I molluschi del Lias inferiore di Longi (Sicilia nord-orientale). — Boll. Soc. Paleont. Ital., 12(1): 23-75, 6 figs, pls 12-19.
- Leymerie, A., 1846a. Mémoire sur le terrain à Nummulites (Épicrétacé) des Corbières et de la Montagne Noire. — Mém. Soc. géol. Fr., (2)1(2): 337-373, pls 12-17.
- Leymerie, A., 1846b. Statistique minéralogique et géologique du Département de l'Aube. Paris, xvi + 676 pp., 10 pls (not seen).
- Leymerie, A., 1851. Mémoire sur un nouveau type pyrénéen parallèle à la Craie proprement dite. — Mém. Soc. géol. Fr., (2)4(1): 177-202, 1 tab., pls 9-11.
- Linné, C. von, 1758, 1767. Systema naturae. Holmiae (Laurentius Salvius), 10th ed., 1(6): iv + 824 pp.; 12th ed., 1(2): 533-1327 (not seen).
- Lommerzheim, A., 1979. Monographische Bearbeitung der Serpulidae (Polychaeta sedentaria) aus dem Cenoman (Oberkreide) am Südwestrand des Münsterländer Beckens. — Decheniana, 132: 110-195, 17 figs.
- Lommerzheim, A., 1981. Paläozäne Serpulidae und Spirorbidae (Polychaeta) von den Emperor Seamounts, NW-Pazifik. — Zitteliana, 7: 31-54, 11 figs.
- Lugeon, M., 1919. Sur l'inexistence de la nappe du Augsmatt-horn. — Bull. Soc. vaud. Sci. nat., 51: 55-57 (not seen).
- Lundgren, B., 1891. Studier öfver fossilförande lösa block. — Geol. Fören. Stockh. Förh., 13(2): 111-121, 2 figs.
- Maccagno, A.M., 1946. Su di una "Burtinella" del Maëstrichtiano della Tripolitania. — Boll. Uff. geol. Ital., 69(8): 152-157, 1 pl.
- Macellari, C.E., 1984. Revision of serpulids of the genus *Rotularia* (Annelida) at Seymour Island (Antarctic Peninsula) and their value in stratigraphy. — J. Paleont., 58(4): 1098-1116, 11 figs.
- MacLeay, W.S., 1840. Note on the Annelida. — Ann. Mag. nat. Hist., (1)4: 385-388.
- Mallada, L., 1887-1888. Sinopsis de las especies fósiles que se han encontrado en España, 3. Terreno Mesozoico (Cretáceo inferior). — Bol. Comis. Mapa geol. España, 14: xix + 171 pp., 20 pls; 15: 16 pls.
- Mantell, G.A., 1822. The fossils of the South Downs; or illustrations of the geology of Sussex. London (Lupton Relfe), xviii + 327 pp., 42 pls.
- Marenzeller, E. von, 1884. Südjapanische Anneliden. 2. Ampharetea, Terebellacea, Sabellacea, Serpulacea. — Denkschr. kaiserl. Akad. Wiss. Wien, math.-naturwiss. Kl., 49(2): 197-224, 4 pls.

- Marinoni, C., 1878. Contribuzioni alla geologica del Friuli. — *Atti. Soc. Ital. Sci.*, 21: 647-661 (not seen).
- Mayer-Eymar, K., 1887. Systematisches Verzeichniss der Kreide- und Tertiär-Versteinerungen der Umgegend von Thun nebst Beschreibung der neuen Arten. — *Beitr. geol. Kt Schweiz*, 24(2): xxviii + 128 pp., 6 pls.
- Meijer, M., 1959. Sur la limite supérieure de l'étage Maastrichtien dans la région-type. — *Bull. Acad. r. Belg., Cl. Sci.*, (5)45: 316-338, 7 figs.
- Michelin, J.L.H., 1840-1847. Iconographie zoophytologique; description par localités et terrains des polyptères fossiles de France et pays environnants. Paris, xii + 348 pp., 79 pls (not seen).
- Montagu, G., 1803. Testacea Britannica, or an account of all the shells hitherto discovered in Britain. London (Hollis), xl + 606 pp., 16 pls (not seen).
- Montfort, D. de, 1808. Conchyliologie systématique et classification méthodique des coquilles, 1. Coquilles univalves, cloisonnées. Paris (F. Schoell), lxxxvii + 409 pp., 100 figs.
- Moore, J.P., & K.J. Bush, 1904. Sabellidae and Serpulidae from Japan, with descriptions of new species of Spirorbis. — *Proc. Acad. nat. Sci. Philad.*, 56(1): 157-179, figs a-h, pls 11, 12.
- Mørch, O.A.L., 1863. Revisio critica Serpulidarum, et Bidrag til Røromenes Naturhistorie. — *Naturhist. Tidsskr.*, (3)1(3): 347-370, pl. 11.
- Morton, S.G., 1834. Synopsis of the organic remains of the Cretaceous groups of the United States. Philadelphia (Key & Biddle), viii + 88 pp., 1 fig., 19 pls.
- Müller, A.H., 1964. Ein weiterer Beitrag zur Serpuliden-Fauna der Oberkreide. — *Geologie*, 13(5): 617-627, 9 figs, 1 pl.
- Müller, A.H., 1966. Zur Kenntnis mesozoischer Serpuliden (Annelida, Polychaeta). — *Geologie*, 15(9): 1053-1075, 22 figs, 3 pls.
- Müller, O.F., 1776. Zoologicae Danicae Prodomus seu Animalium Danicae et Norvegiae indigenarum Characteres, Nomina, et Synonyma imprimis popularium. Havniae (Typis Hallageriis), xxxii + 282 pp. (not seen).
- Murchison, R.I., 1839. The Silurian System. London (John Murray), xxii + 768 pp., 14 + 112 figs, 37 pls, 5 + 1 maps.
- Nielsen, K. Brünnich, 1931. Serpulidae from the Senonian and Danian deposits of Denmark. — *Meddr dansk geol. Foren.*, 8: 71-113, 2 figs, pls 1-3.
- Noetling, F., 1885. Die Fauna der baltischen Cenoman-Geschiebe. — *Paläont. Abh.*, 2: 199-247, pls 16-23.
- Ødum, H., 1926. Studier over Daniet i Jylland og paa Fyn. — *Danm. geol. Unders.*, (2)45: 1-306, 7 pls.
- Oken, L., 1815. Lehrbuch der Naturgeschichte, 3. Zoologie, 1. Fleischlose Thiere. Leipzig, xxviii + 842 pp. (not seen).
- Oppenheim, P., 1901. Über einige alttertiäre Faunen der österreichisch-ungarischen Monarchie. — *Beitr. Paläont. Österreich-Ungarns Orients*, 13: 141-277, figs 11-18, pls 11-19.
- Parsch, K.O.A., 1956. Die Serpuliden-Fauna des südwestdeutschen Juras. — *Palaeontographica*, (A)107: 211-240, 1 fig., 3 tabs, pls 19-21.
- Pasternak, S.I., 1973. [Cretaceous serpulids of the European part of the USSR]. Kijev (Naukova Dumka), 82 pp., 7 figs, 9 pls. [in Russian].
- Philippi, A., 1844. Einige Bemerkungen über die Gattung Serpula, nebst Aufzählung der von mir im Mittelmeer mit dem Thier beobachteten Arten. — *Arch. Naturgesch.*, 10(1): 186-198, pl. 6.
- Pillai, T.G., 1970. Studies on a collection of spirorbids from Ceylon, together with a critical review and revision of spirorbid systematics, and an account of their phylogeny and zoogeography. — *Ceylon J. Sci., Biol. Sci.*, n.s., 8(2): 100-172, 14 figs, 3 tabs.
- Pillai, T.G., in press [MS]. A review of some Cretaceous and Tertiary serpulid polychaetes of the genera *Cementula* and *Spiraserpula* Regenhardt, 1961, *Laqueoserpula* Lommerzheim, 1979 and *Protectoconorca* Jäger, 1983: 27 pp., 9 figs [submitted to *Paläont. Z.*].
- Pugaczewska, H., 1967. Serpulidae from the Dano-Montian borehole at Boryszew, Poland. — *Acta palaeont. pol.*, 12(2): 179-194, 3 pls.
- Quatrefages, A. de, 1865-1866. Histoire naturelle des Annélés marines et d'eau douce. Annélides et Gephyriens. Paris (Librairie Encyclopédique de Roret), 588 + 794 pp., atlas (not seen).
- Rafinesque, C.S., 1815. L'analyse de la nature. Palermo, 224 pp. (not seen).
- Rasmussen, H. Wienberg, 1965. The Danian affinities of the Tuffeau de Cipluy in Belgium and the "Post-Maastrichtian" in the Netherlands. — *Meded. geol. Sticht.*, n.s., 17: 33-38, 2 tabs, pls 8, 9.
- Regenhardt, H., 1961. Serpulidae (Polychaeta sedentaria) aus der Kreide Mitteleuropas, ihre ökologische, taxionomische und stratigraphische Bewertung. — *Mitt. geol. Staatsinst. Hamburg*, 30: 5-115, 5 figs, 1 tab., pls 1-9.
- Reuss, A.E., 1845-1846. Die Versteinerungen der Böhmisches Kreideformation. Stuttgart (E. Schweizerbart), iv + 58 + iv + 148 pp., 51 pls.
- Reuss, A.E., 1860. Die marinen Tertiärschichten Böhmens und ihre Versteinerungen. — *Sitzber. kaiserl. Akad. Wiss., math.-naturwiss. Cl.*, 39: 207-285, 8 pls.
- Rioja, E., 1923. Estudio sistemático de las especies ibéricas del suborden Sabelliformia. — *Trab. Mus. nac. cienc. nat. Madrid, Zool.*, 48: 1-144 (not seen).
- Risso, A., 1826. Histoire naturelle de principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, 4. Paris, 7 + 439 pp. (not seen).
- Roemer, F.A., 1840-1841. Die Versteinerungen des norddeutschen Kreidegebirges. Hannover (Hahn'sche Hofbuchhandlung), iv + 145 pp., 2 tabs, 16 pls.
- Rosenkrantz, A., 1920. Craniakalken fra Kjöbenhavn's Sydhavn. — *Danm. geol. Unders.*, (2)36: 79 pp., 2 pls.
- Roule, L., 1898. Notice préliminaire sur les espèces d'Annélides recueillies dans les explorations sous-marines du "Travailleur" et du "Talisman". — *Bull. Mus. natn Hist. nat. Paris*, 4: 190-195 (not seen).
- Rovereto, G., 1898. Serpulidae del Terziario e del Quaternario in Italia. — *Palaeontographia Ital.*, 6: 47-91, pls 6, 7.
- Rovereto, G., 1901. Briozoi, anellidi e spugne perforanti del Neogene Ligure. — *Palaeontographia Ital.*, 7: 219-225, 5 figs, pl. 28.
- Rovereto, G., 1904a. Studi monografici sugli Anellidi fossili, 1. Terziario. — *Palaeontographia Ital.*, 10: 1-73, 2 figs, pls 1-4.
- Rovereto, G., 1904b. Contributo allo studio dei Vermeti fossili. — *Boll. Soc. geol. Ital.*, 23: 67-83, pl. 3.
- Roy, J.M., M.A.S. McMenamin & S.E. Alderman, 1990. Trophic differences, originations and extinctions during the Cenomanian and Maastrichtian Stages of the Cretaceous. In: E.G. Kauffman & O.H. Walliser (eds). Extinction events in earth history. *Lecture Notes in Earth Sciences*, 30. Berlin (Springer Verlag): 299-303, 6 figs.

- Ruedemann, R., 1934. Paleozoic plankton of North America. — Mem. geol. Soc. Am., 2: vii + 141 pp., 6 figs, 26 pls.
- Ryckholt, P. de, 1852. Mélanges paléontologiques. — Mém. cour. Mém. Sav. étr. Acad. r. Sci. Lett. B.-Arts Belg., 24: 176 pp., 10 pls.
- Saint-Joseph, A. de, 1894. Les annélides polychètes des côtes de Dinard, 3. — Anns Sci. nat., (7) Zool., 17: 395 pp., 13 pls.
- Schlotheim, E.F. von, 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte. Gotha (Becker), lxii + 437 pp., 29 pls.
- Schlotheim, E.F. von, 1822. Nachträge zur Petrefactenkunde, 1. Gotha (Becker), 100 pp., 31 pls. (not seen).
- Schmidt, W.J., 1951. Neue Serpulidae aus dem tertiären Wiener Becken. — Ann. naturhist. Mus. Wien, 58: 77-84, 9 figs.
- Schmidt, W.J., 1955a. Nomenklatur und Systematik der Serpuliden-Gattung *Rotularia* DeFrance (= *Tubulostium* Stoliczka). — Mitt. geol. Ges. Wien, 47(1954): 159-182, 1 pl.
- Schmidt, W.J., 1955b. Die tertiären Würmer Österreichs. — Denkschr. österr. Akad. Wiss., math.-naturwiss. Kl., 109(7): 1-121, 2 tabs, 8 pls.
- Schmidt, W.J., 1969. Vermes. — Catalogus fossilium Austriae, 5a. Wien (Springer Verlag), 56 pp.
- Schweitzer, H.-J., 1983. Die Unterdevonflora des Rheinlandes, 1. — Palaeontographica, (B)189(1-6): 1-138, 95 figs, 5 tabs, 24 pls.
- Sheehan, P.M., & T.A. Hansen, 1986. Detritus feeding as a buffer to extinction at the end of the Cretaceous. — Geology, 14: 868-870, 1 fig.
- Sowerby, J., 1813. The Mineral Conchology of Great Britain, 1(4). London (The author): 49-60, pls 16-21.
- Sowerby, J. de C., 1829, 1840-1846. The Mineral Conchology of Great Britain. London (The author), 6: 230 pp., pls 598-609 (1829); 7: 80 + 11 pp., pls 610-618 (1840); 7: pls 619-623 (1841); 7: pls 624-628 (1843); 7: pls 629-643 (1844); 7: pls 644-648 (1846).
- Stanton, T.W., 1901. The marine Cretaceous invertebrates. — Repts Princeton Univ. Exped. Patagonia 1896-1899, 4. Paleontology, 1(1): 1-44, pls 1-10.

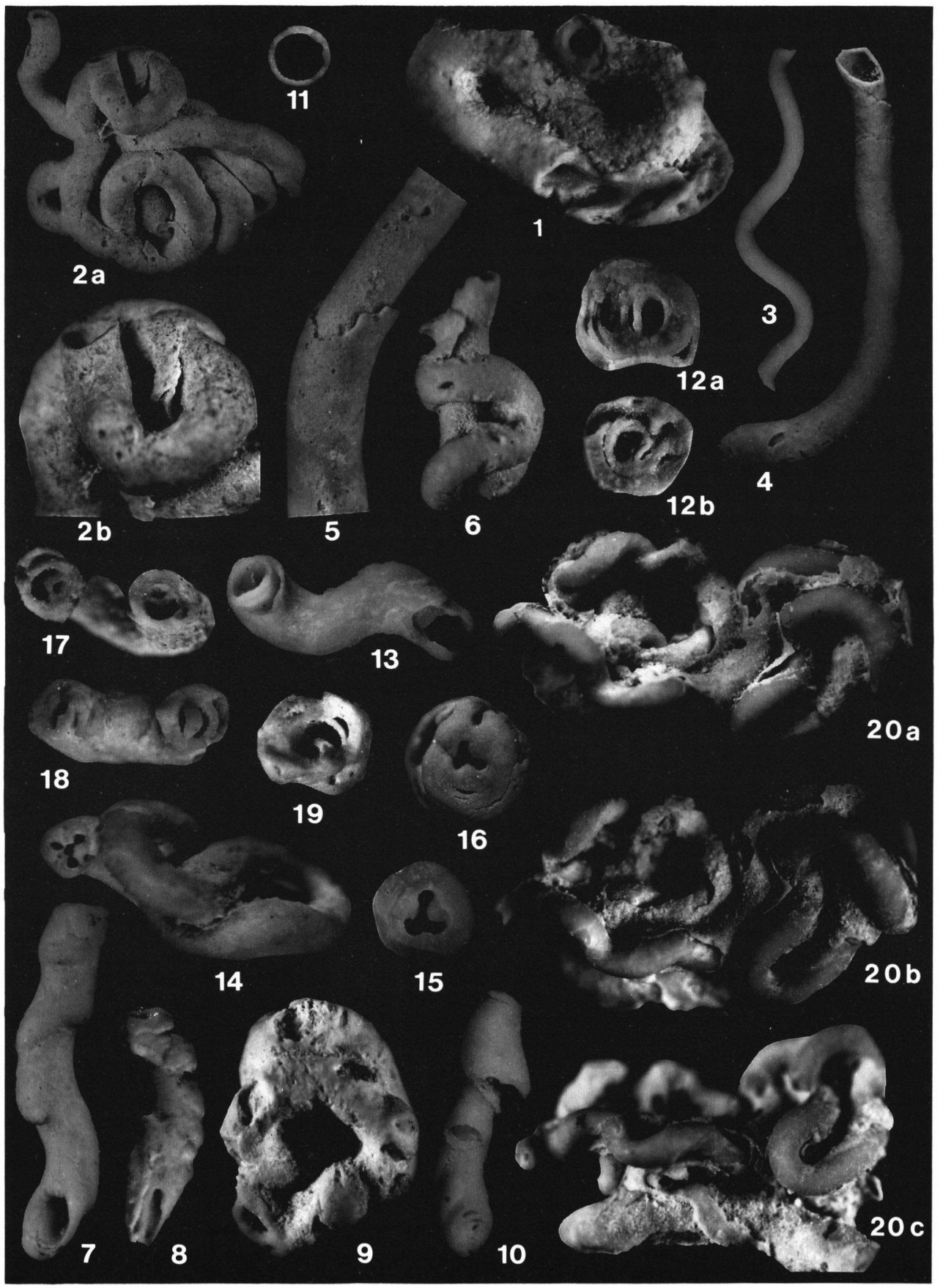
## PLATE 1

*Cycloserpula lombricus* (DeFrance, 1827b). Houthem Formation, Geulhem Member.

- Fig. 1. Meander-shaped attached tube part, lower part of figure showing oblique step-shaped swellings on the (broken) tube's interior. Albert Canal sections, north of km mark 24.000, x 11.5. Coll. GPI Hamburg, no. 3300.
- Fig. 2. Tube forming three-dimensional chaotic knot (normal shape of tube) with an injury: after breakage of tube the new part does not follow the direction of the previous part, a - overall view, b - detail showing breakage (upper right), U-shaped new part and remains of broken old part (upper right to lower centre). Geulhem section, burrow infill at the K/T boundary, x 5.8 (a) and x 11.5 (b). Coll. GPI Hamburg, no. 3301.
- Fig. 3. Undulate erect tube part. Geulhem section, burrow infill at the K/T boundary, x 7.7. Coll. GPI Hamburg, no. 3302.
- Fig. 4. Curved, fairly long erect part, same sample as Fig. 3, x 5.8. Coll. GPI Hamburg, no. 3303.
- Fig. 5. Erect tube part, showing breakage and straight new part (upper half figure), same sample as Fig. 3, x 11.5. Coll. GPI Hamburg, no. 3304.
- Fig. 6. After breakage of erect part, the new part 'enwraps' the old part rather irregularly. Albert Canal sections, as sample 121, x 11.5. Coll. GPI Hamburg, no. 3305.
- Fig. 7. Closed rucksack-shaped protuberances (left), Albert Canal sections, as sample 121, x 15.3. Coll. GPI Hamburg, no. 3306.
- Fig. 8. Closed rucksack-shaped protuberances (right) in rather irregular tube. Albert Canal sections, as sample 121, x 15.3. Coll. GPI Hamburg, no. 3307.
- Fig. 9. Broken open rucksack-shaped protuberances in knot-shaped tube. Albert Canal sections, north of km mark 24.000, x 11.5. Coll. GPI Hamburg, no. 3308.
- Fig. 10. Broken open rucksack-shaped protuberances (centre and right). Albert Canal sections, as sample 138, x 15.3. Coll. GPI Hamburg, no. 3309.
- Fig. 11. Cross-section of a thin-walled erect tube part. Albert Canal sections, as sample 121, x 15.3. Coll. GPI Hamburg, no. 3310.
- Fig. 12. Two cross-sections of tube of a thick-walled knot, a - very small eccentric lumen, six layers of tube wall visible with crescentic interstices in between, b - kidney-shaped lumen. Albert Canal sections, north of km mark 24.000, x 15.3. Coll. GPI Hamburg, no. 3311.
- Fig. 13. S-shaped tube with eccentric lumen and two layers of tube wall with crescentic interstices visible in both cross-sections. Albert Canal sections, as sample 138, x 19.2. Coll. GPI Hamburg, no. 3312.
- Fig. 14. 8-shaped fragment of knot with 'trilobate narrowing' at both ends (one visible, left), but without 'trilobate narrowing' in between. Albert Canal sections, north of km mark 24.000, x 19.2. Coll. GPI Hamburg, no. 3313.
- Fig. 15. Cross-section of rather thick-walled tube with 'trilobate narrowing'. Albert Canal sections, sample 127 III, x 19.2. Coll. GPI Hamburg, no. 3314.
- Fig. 16. Cross-section of very thick-walled tube with crescentic interstices between the layers (lower third) and with 'trilobate narrowing?'. Albert Canal sections, sample 118, x 15.3. Coll. GPI Hamburg, no. 3315.
- Fig. 17. S-shaped fragment with kidney-shaped lumen visible in both cross-sections. Albert Canal sections, sample 118, x 23. Coll. GPI Hamburg, no. 3316.
- Fig. 18. Curved fragment with kidney-shaped lumen visible in both cross-sections. Albert Canal sections, sample 118, x 19.2. Coll. GPI Hamburg, no. 3317.
- Fig. 19. Cross-section of rather thick-walled tube with crescentic interstices between the layers (upper right) and with kidney-shaped lumen. Albert Canal sections, as sample 121, x 15.3. Coll. GPI Hamburg, no. 3318.
- Fig. 20. Three-dimensional knot with outer layer of tube wall broken, showing corkscrew-shaped inner layer, a-c - different views of same specimen. Albert Canal sections, as sample 138, x 11.5. Coll. GPI Hamburg, no. 3319.



PLATE 1



- Stevens, G.R., 1967. Upper Jurassic fossils from Ellsworth Land, West Antarctica, and notes on Upper Jurassic biogeography of the South Pacific region. — *N.Z. J. Geol. Geophys.*, 10(2): 345-393, 45 figs.
- Stimpson, W., 1854. Synopsis of the marine Invertebrata of Grand Manan, or the region about the mouth of the Bay of Fundy, New Brunswick. — *Smiths. Contr. Knowl.*, 6: 1-67, pls 1-3 (not seen).
- Stoliczka, F., 1867-1868. The Gastropoda of the Cretaceous rocks of Southern India. — *Mem. geol. Surv. India, Palaeont. Indica*, 5: xiii + 497 pp., 28 pls.
- Straughan, D., 1967. Some Serpulidae (Annelida: Polychaeta) from Heron Island, Queensland. — *Univ. Qld Papers*, 1(2): 27-45, 5 figs.
- Stühmer, H.H., C. Spaeth & F. Schmid, 1982. Fossilien Helgolands, Teil 1, Trias und Unterkreide. Otterndorf (Niederelbe Verlag), 184 pp., 9 + 19 figs, 70 pls.
- Tate, R., & J.F. Blake, 1876. The Yorkshire Lias. London (J. van Voorst), viii + 475 + xii pp., 23 pls.
- Vine, P.J., 1977. The marine fauna of New Zealand: Spirorbinae (Polychaeta: Serpulidae). — *Mem. N.Z. Oceanogr. Inst.*, 68: 1-68, 35 figs, 6 tabs.
- Voigt, E., 1985. The Bryozoa of the Cretaceous-Tertiary boundary. *In*: G.P. Larwood & C. Nielsen (eds). *Bryozoa: Ordovician to Recent*. Fredensborg (Olsen & Olsen): 329-342, 2 tabs.
- Wanner, J., 1902. Die Fauna der obersten weissen Kreide der libyschen Wüste. — *Palaeontographica*, 30(2): 91-152, pls 13-19.
- White, C.A., 1881. Descriptions of new invertebrate fossils from the Mesozoic and Cenozoic rocks of Arkansas, Wyoming, Colorado, and Utah. — *Proc. U.S. natl Mus.*, 3: 157-165.
- White, C.A., 1882. On certain Cretaceous fossils from Arkansas and Colorado. — *Proc. U.S. natl Mus.*, 4: 136-139, 1 pl.

PLATE 2

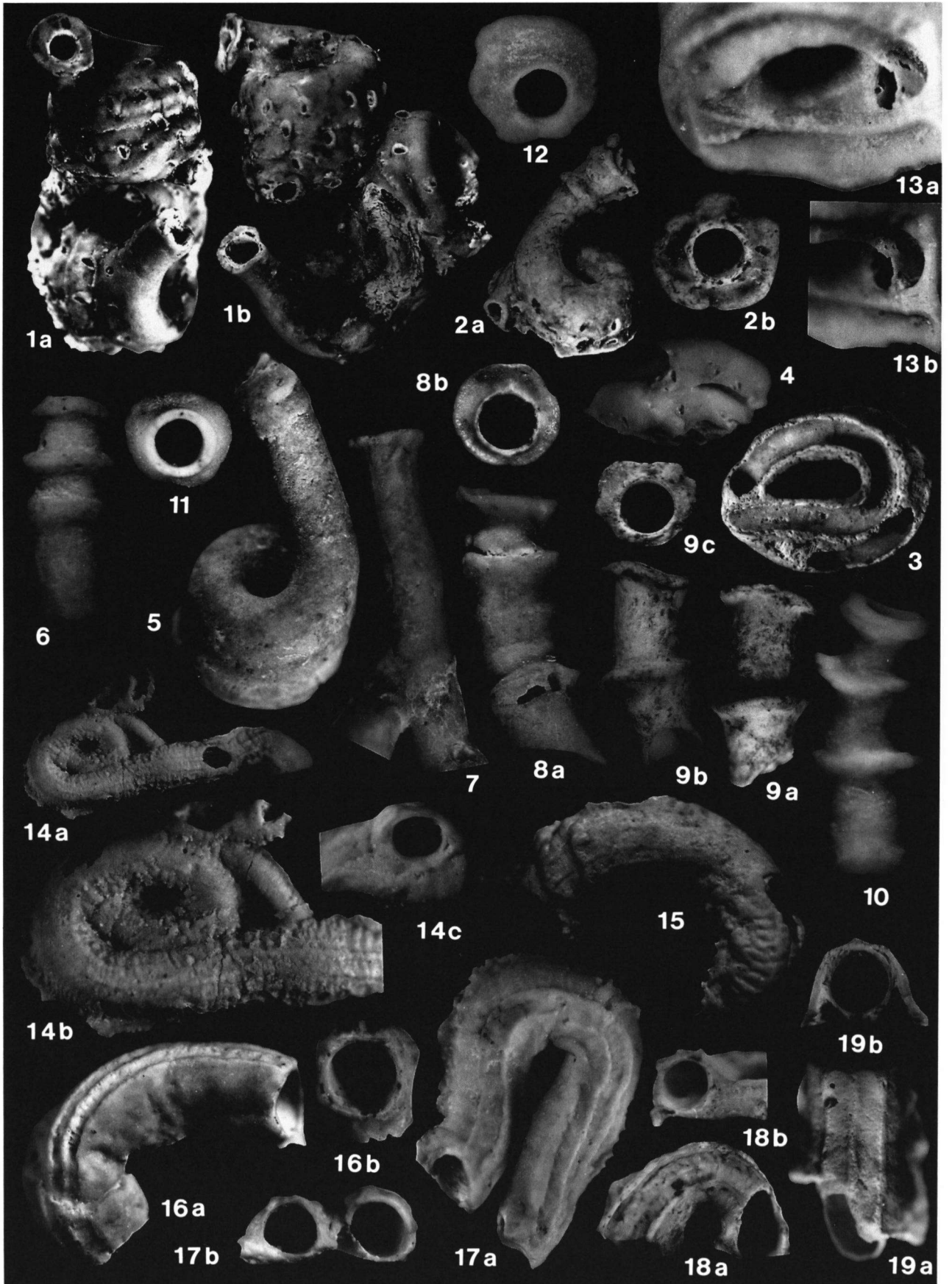
*Serpula ? insiticia* (Regenhardt, 1961). Houthem Formation, Geulhem Member.

- Fig. 1. Cluster of three specimens affected by the symbiont *Protulophila*, b - remains of non-spiral initial tube part (left centre). Geulhem section, burrow infill at K/T boundary, x 7. Coll. GPI Hamburg, no. 3320.
- Fig. 2. Low spiral with erect tube part, affected by *Protulophila*, a - overall view, showing remains of non-spiral initial tube part (left), b - aperture with peristome. Geulhem section, burrow infill at K/T boundary, x 7 (a), x 14 (b). Coll. GPI Hamburg, no. 3321.
- Fig. 3. Spiral detached from substrate, bottom view, showing straight initial tube part and structure of tube wall. Geulhem section, burrow infill at K/T boundary, x 10.5. Coll. GPI Hamburg, no. 3322.
- Fig. 4. Spiral of juvenile specimen, affected by *Protulophila*, lateral view, showing protruding top and base at aperture. Albert Canal sections, as sample 138, x 10.5. Coll. GPI Hamburg, no. 3323.
- Fig. 5. Spiral with long erect tube part. Geulhem section, burrow infill at K/T boundary, x 10.5. Coll. GPI Hamburg, no. 3324.
- Fig. 6. Erect tube part with three peristomes. Geulhem section, some metres above K/T boundary, x 14. Coll. GPI Hamburg, no. 3325.
- Fig. 7. End of broken spiral with long erect tube part with one peristome. Geulhem section, burrow infill at K/T boundary, x 10.5. Coll. GPI Hamburg, no. 3326.
- Fig. 8. Erect tube part described by Regenhardt (1961), with three peristomes, a - lateral view, b - frontal view of aperture. Geulhem section, burrow infill at K/T boundary, x 14. Coll. GPI Hamburg, no. 3327.
- Fig. 9. Holotype, erect tube part with two peristomes, a - top view, b - lateral view, c - frontal view of aperture. Geulhem section, burrow infill at K/T boundary, x 14. Coll. GPI Hamburg, no. 739.
- Fig. 10. Erect tube part with three peristomes. Albert Canal sections, as sample 121, x 14. Coll. GPI Hamburg, no. 3328.
- Fig. 11. Erect tube part, peristome seen from behind. Geulhem section, some metres above K/T boundary, x 10.5. Coll. GPI Hamburg, no. 3329.
- Fig. 12. Erect tube part, strongly developed peristome. Geulhem section, some metres above K/T boundary, x 10.5. Coll. GPI Hamburg, no. 3330.
- Fig. 13. Spiral detached from substrate, oblique bottom view, showing two perforated tabulae (right centre), a - remains of a third tabula (lower left). Geulhem section, sample 105, x 21. Coll. GPI Hamburg, no. 3331.

*Serpula ? aff. trilineata* (Roemer, 1841). Houthem Formation, Geulhem Member.

- Fig. 14. Near-complete tube, a - overall view, b - detail showing loops, well-developed ornament of adult tube and juvenile part (right centre) lacking longitudinal ornament, c - aperture. Albert Canal sections, as sample 121, x 5.3 (a), x 10.5 (b, c). Coll. GPI Hamburg, no. 3332.
- Fig. 15. U-shaped fragment with weak longitudinal ornament and in places strong transverse ornament including peristomes. Albert Canal sections, sample 121, x 8.7. Coll. GPI Hamburg, no. 3333.
- Fig. 16. U-shaped fragment with strong longitudinal ornament and weak transverse ornament including weak peristomes, a - top/lateral view, b - aperture. Albert Canal sections, sample 121a, x 8.7 (a), x 10.5 (b). Coll. GPI Hamburg, no. 3334.
- Fig. 17. U-shaped fragment with strong longitudinal ornament and weak transverse ornament, a - top view, b - cross-sections. Albert Canal sections, sample 121a, attached to same substrate as Fig. 16, x 10.5. Coll. GPI Hamburg, no. 3334.
- Fig. 18. U-shaped fragment, the two keels at the periphery being broader than the median keel, a - top view, b - cross-section. Albert Canal sections, sample 121a, x 10.5. Coll. GPI Hamburg, no. 3335.
- Fig. 19. Fragment of largest tube seen, with strong longitudinal ornament and lack of transverse ornament, showing some details of tube wall, a - top view, b - cross-section. Geulhem section, topmost strata, x 8.7. Coll. GPI Hamburg, no. 3336.

PLATE 2



- Wilckens, O., 1907. Die Lamellibranchiaten, Gastropoden etc. der oberen Kreide Südpatagoniens. — Ber. naturf. Ges. Freiberg i. Br., 15: 97-166, pls 2-9.
- Wilckens, O., 1910. Die Anneliden, Bivalven und Gastropoden der antarktischen Kreideformation. — Wiss. Ergebn. schwed. Südpolarexped., 3(12): 1-132, 4 pls (not seen).
- Wilckens, O., 1922. The Upper Cretaceous gastropods of New Zealand. — N.Z. Dept Mines, Geol. Surv., Paleont. Bull., 9: v + 42 pp., 2 figs, 1 map, 5 pls.
- Wilckens, O., 1924. Lahillia and some other fossils from the Upper Senonian of New Zealand. — Trans. N.Z. Inst., 55: 539-544.
- Wrigley, A., 1950. Les opercules de serpulidés de l'Eocène du Bassin de Paris. — Bull. Soc. géol. Fr., (5)19: 499-505, 5 figs.
- Wrigley, A., 1951. Some Eocene serpulids. — Proc. Geol. Assoc., 62(3): 177-202, 66 figs.
- Yabe, H., & T. Nagao, 1928. Cretaceous fossils from Hokkaidô: Annelida, Gastropoda and Lamellibranchiata. — Sci. Repts Tôhoku Imp. Univ., Sendai, 9: 77-96, pls 16, 17.
- Young, G., & J. Bird, 1828. A geological survey of the Yorkshire coast. Whitby [2nd ed.], 367 pp., 19 pls (not seen).
- Zibrowius, H., 1971. Revision of *Metavermilia* Bush (Polychaeta, Serpulidae), with descriptions of three new species from off Portugal, Gulf of Guinea, and Western Indian Ocean. — J. fish. Res. Board Canada, 28(10): 1373-1383, 4 figs.
- Zibrowius, H., 1972. Une espèce actuelle du genre *Neomicrorbis* Rovereto (Polychaeta Serpulidae) découverte dans l'étage bathyal aux Açores. — Bull. Mus. natn Hist. nat. Paris, (3)39(33, Zool.): 423-430, 1 fig.
- Zibrowius, H., 1983. *Chitinopoma arndti* n. sp., an incubating bathyal serpulid polychaete from Saint-Paul Island, southern Indian Ocean. — Tethys, 11(1): 21-24, 1 fig.
- Zibrowius, H., & H.A. ten Hove, 1987. *Neovermilia falcigera* (Roule, 1898), a deep- and cold-water serpulid polychaete common in the Mediterranean Plio-Pleistocene. — Bull. biol. Soc. Wash., 7: 259-271, 6 figs.
- Ziegler, V., 1984. Family Serpulidae (Polychaeta, Sedentaria) from the Bohemian Cretaceous basin. — Sborník Národního Muzea v Praze, 39B(4): 213-254, 8 pls.
- Ziegler, V., & J. Michalik, 1980. Late Triassic serpulids (Annelida, Polychaetia, Sedentaria) in the western Carpathians. — Geol. Zbornik, Geol. Carp., 31(4): 627-640, 13 figs.

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### PLATE 3

*Cementula applanata subditiva* (Regenhardt, 1961). Houthem Formation, Geulhem Member.

- Fig. 1. Atypical specimen; following a near-straight initial tube part (left), the tube enwraps the substrate, a bryozoan, and then ascends above this (right). Geulhem section, without stratigraphic data, x 8.7. Coll. GPI Hamburg, no. 3337.
- Fig. 2. Holotype, a - top view, b - top/lateral view, c - detail showing anterior tube part with alae, aperture and keel. Albert Canal sections, sample 125, x 5.3 (a, b), x 10.5 (c). Coll. GPI Hamburg, no. 725.
- Fig. 3. Exceptionally large spiral, a - top view, b - bottom view, detail, showing tube interior. Geulhem section, without stratigraphic data, x 5.3 (a), x 8.7 (b). Coll. GPI Hamburg, no. 3338.
- Fig. 4. Slightly oblique spiral, top view. Albert Canal sections, hardground at km mark 23.850, x 5.3. Coll. GPI Hamburg, no. 3339.
- Fig. 5. Spirals with alae and keel anteriorly, last half turn taking a 'short cut' by growing across spiral and finally becoming erect, a - lateral view, b - top view. Geulhem section, without stratigraphic data, x 7. Coll. GPI Hamburg, no. 3340.
- Fig. 6. Tall spirals, tube partially broken. Lateral view. Albert Canal sections, sample 125, x 5.3. Coll. GPI Hamburg, no. 3341.
- Fig. 7. Tall spirals, tube partially broken, last half turn taking a 'short cut' by growing across spiral, a - top view, b - lateral view, c - detail of other lateral view, showing tube interior, especially absence of 'internal tube structures' (ITS) such as seen in *Spiraserpula*. Albert Canal sections, sample 121a, x 5.3 (a, b), x 8.7 (c). Coll. GPI Hamburg, no. 3342.
- Fig. 8. Bottom view of spiral, showing tube interior and non-spiral intermediate part (left of centre). Albert Canal sections, sample 120, x 10.5. Coll. GPI Hamburg, no. 3343.
- Fig. 9. Fragment of erect anterior tube part with alae, a - top view, b - bottom view, c - cross-section. Albert Canal sections, as sample 121, x 14. Coll. GPI Hamburg, no. 3344.
- Fig. 10. Fragment of erect anterior tube part with alae, a - top view, b - lateral view, c - bottom. Albert Canal sections, as sample 121, x 14. Coll. GPI Hamburg, no. 3345.
- Fig. 11. Bottom view of spiral, showing tube interior. Albert Canal sections, sample 121, x 8.7. Coll. GPI Hamburg, no. 3346.
- Fig. 12. Cluster of spirals, broken, showing tube interior, especially absence of 'internal tube structures' (ITS) as seen in *Spiraserpula*, a, b - lateral views. Geulhem section, sample 105, x 10.5. Coll. GPI Hamburg, no. 3347.

*Serpula* ? sp. Houthem Formation, Geulhem Member.

- Fig. 13. Broken spiral, bottom view, showing tube interior. Albert Canal sections, sample 121, x 5.3. Coll. GPI Hamburg, no. 3348.
- Fig. 14. Tube with projecting crest, a - top view (aperture right), b - lateral view, c - cross-section of broken posterior end, showing sections of longitudinal cavities at base, d - aperture. Albert Canal sections, as sample 138, x 14. Coll. GPI Hamburg, no. 3349.
- Fig. 15. Tube fragment, a - lateral view, b - bottom view, showing cellular construction of tube base and interior. Albert Canal sections, sample 121, x 8.7. Coll. GPI Hamburg, no. 3350.

PLATE 3

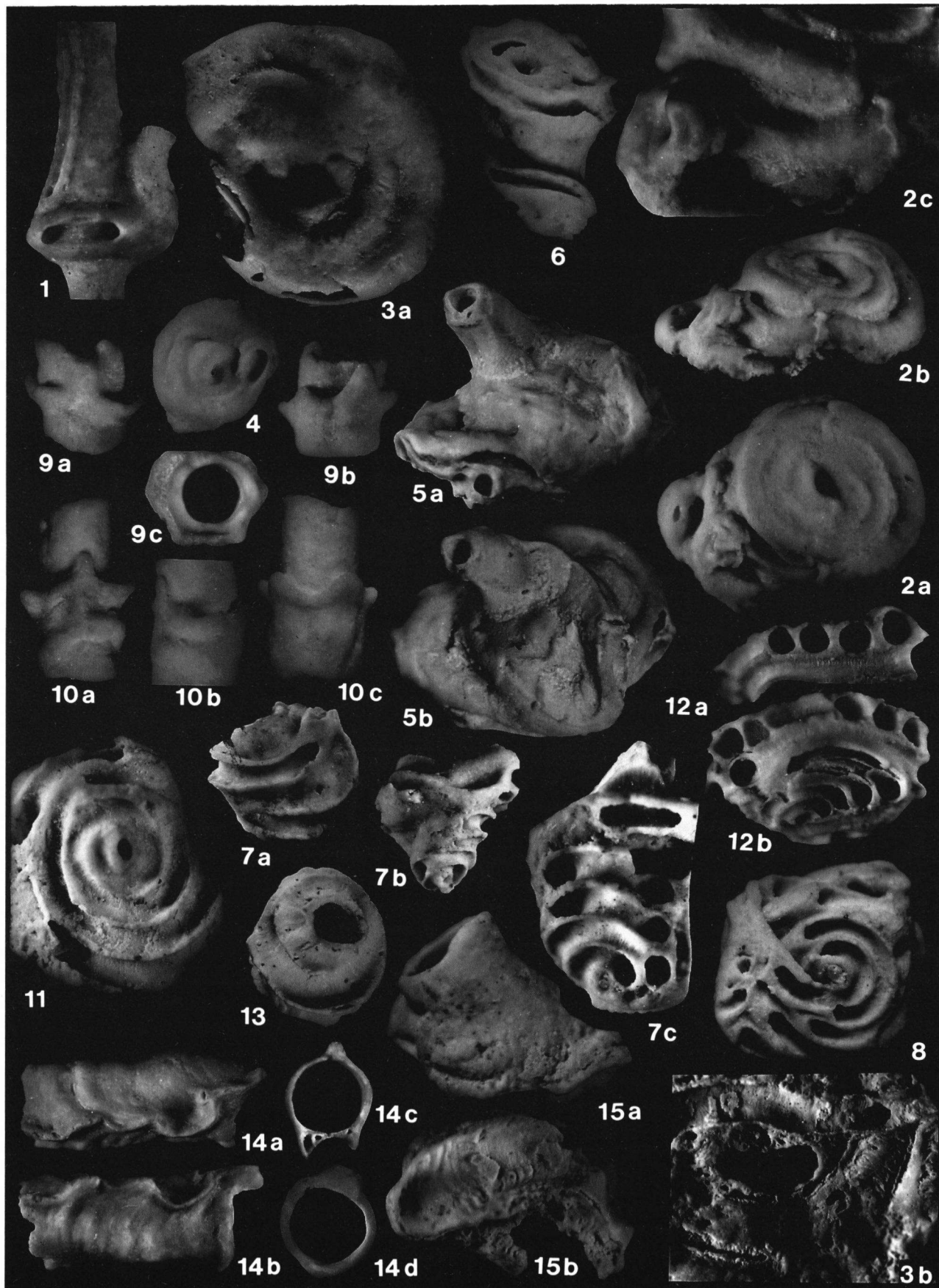


PLATE 4

*Ditrupe schlotheimi* (Rosenkrantz, 1920). Houthem Formation, Geulhem Member.

- Fig. 1. Fairly complete tube. Albert Canal sections, Geulhem Member, sample B, x 5.8. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-1.
- Fig. 2. Anterior tube fragment, with wrinkles. Albert Canal sections, Geulhem Member, sample B, x 5.8. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-2.
- Fig. 3. Fairly complete tube. Albert Canal sections, Geulhem Member, sample A, x 5.8. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-3.
- Fig. 4. Fairly complete tube, with bulges. Albert Canal sections, Geulhem Member, sample B, x 5.8. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-4.
- Fig. 5. Anterior tube fragment, with wrinkles, a - lateral view, b - cross-section, Albert Canal sections, Geulhem Member, sample B, x 9.6 (a), x 11.5 (b). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-5.
- Fig. 6. Anterior tube fragment, swollen club-shaped near aperture, a - lateral view, b - cross-section, Albert Canal sections, Vroenhoven, Geulhem Member, sample A, x 9.6 (a), x 15.3 (b). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-6.
- Fig. 7. Anterior tube fragment, with wrinkles, swollen club-shaped near aperture, a - lateral view, b - cross-section, Albert Canal sections, upper part of Geulhem Member, x 9.6 (a), x 11.5 (b). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-7 (leg. J.W.M. Jagt, no. 3043).
- Fig. 8. Anterior tube fragment, with wrinkles and bottle-neck shape of apertural region, Albert Canal sections, Geulhem Member, sample B, x 9.6. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-8.
- Fig. 9. Fragment with irregular curvature, Albert Canal sections, sample 180, x 9.6. Coll. GPI Hamburg, no. 3351.
- Fig. 10. Fragment of straight tube, with longitudinal furrow and transverse bulges, Albert Canal sections, sample 180, x 5.8. Coll. GPI Hamburg, no. 3352.
- Fig. 11. Tube fragment, with longitudinal furrow, view of convex side. Geulhem section, Geulhem Member above hardground, Voigt 1960, x 11.5. Coll. GPI Hamburg, no. 3353.
- Fig. 12. Oblique longitudinal section, showing tube structure. Albert Canal sections, Geulhem Member, sample A, x 15.3. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992200-9.
- Fig. 13. Longitudinal section, showing tube structure and strong transverse striation on interior. Geulhem section, topmost part of Geulhem Member, x 15.3. Coll. GPI Hamburg, no. 3354.

*Rotularia (Rotularia) hisingeri* (Lundgren, 1891)

- Fig. 14. Immature individual, spiral lacking straight anterior tube part, a - top view, b - lateral view, showing aperture, c - bottom view, showing broken straight initial tube part. Albert Canal sections, sample 127(2), x 7.7 (a-c). Coll. GPI Hamburg, no. 3355.
- Fig. 15. Spiral with long straight anterior tube part, a - top view, b - bottom view, showing short straight initial tube part. Albert Canal sections, sample 127(2), x 5.8. Coll. GPI Hamburg, no. 3356.
- Fig. 16. Spiral with long straight anterior tube part, a - top view, b - lateral view, showing short straight initial tube part (lower centre) and cross-section. Albert Canal sections, sample 127 III, x 7.7. Coll. GPI Hamburg, no. 3357.
- Fig. 17. Spiral with short straight anterior tube part and fairly long straight initial tube part (centre to lower right), bottom view, Albert Canal sections, sample 127(1), x 9.6. Coll. GPI Hamburg, no. 3358.
- Fig. 18. Spiral with short straight anterior tube part, a - top view, b - lateral view, showing cross-section of anterior tube part, c - bottom view, showing short straight initial tube part, d - cross-section of anterior tube part. Albert Canal sections, sample 127(1), x 9.6 (a, c), x 7.7 (b), x 15.3 (d). Coll. GPI Hamburg, no. 3359.
- Fig. 19. Extraordinary specimen attached to substrate by broad base, a - top view, b - lateral view, showing cross-section, c - bottom view, showing near-straight initial tube part and attachment area with cellular construction of base. Albert Canal sections, sample 127 III, x 7.7 (a), x 9.6 (b, c). Coll. GPI Hamburg, no. 3360.

PLATE 4

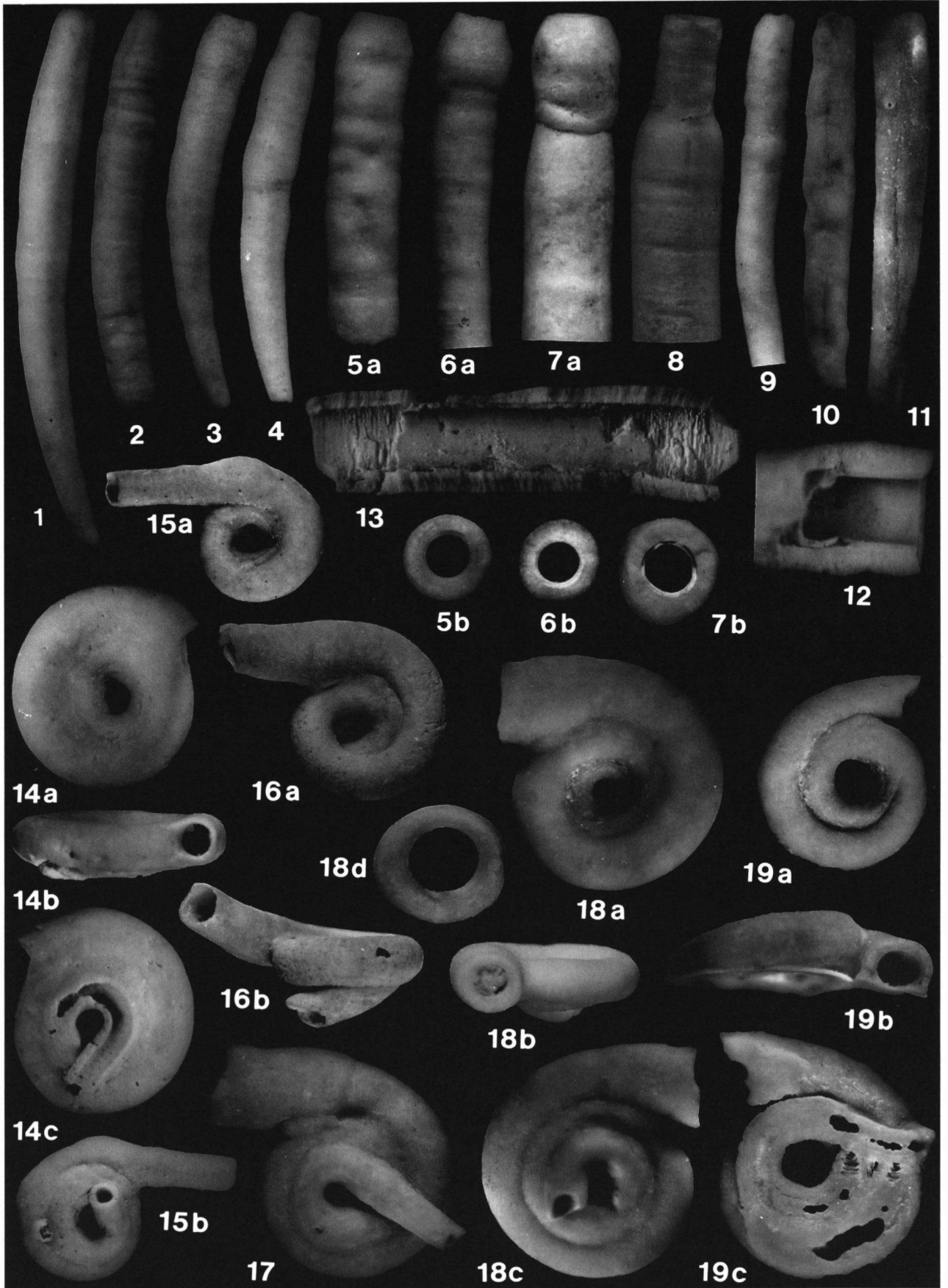


PLATE 5

*Rotularia (Rotularia) tobar gracilis* n. subsp. Houthem Formation, Geulhem Member.

- Fig. 1. Holotype, a - top view, b - detail showing ornament, c - detail showing distortion at the base of the (broken) straight anterior tube part, d - lateral view, detail showing ornament, e - lateral view including cross-section of straight anterior tube part, f - bottom view, detail showing ornament, g - bottom view, overall view. Albert Canal sections, Geulhem Member, sample A, x 7 (a, e, g), x 10.5 (b-d, f). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992201-1.
- Fig. 2. Spiral, a - top view, b - detail showing ornament, c - lateral view with slightly damaged aperture, d - detail of other lateral view showing ornament, e - bottom view. Albert Canal sections, Geulhem Member, sample A, x 7 (a, c, e), x 8.7 (b), x 10.5 (d). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992201-2.
- Fig. 3. Spiral, the last  $\frac{1}{2}$  turn (damaged) not following the spiral periphery, but growing across its underside, a - top view, b - detail of lateral view showing ornament, c - bottom view, showing irregular last  $\frac{1}{2}$  turn (damaged). Albert Canal sections, Geulhem Member, sample A, x 7 (a, c), x 10.5 (b). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992201-3.
- Fig. 4. Spiral, following an injury, the new tube growing from the broken old part, a - top view, injury left, distortion at base of straight anterior tube part, b - aperture of new tube at end of straight anterior tube part, c - lateral view, showing injury (left half) and somewhat damaged aperture of old tube part (right), d - oblique lateral/bottom view, e - detail showing injury (top centre) and new tube growing from old part (top left), f - bottom view (injury right, new tube top). Albert Canal sections, Geulhem Member, sample A, x 7 (a, c, d, f), x 14 (b, e). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992201-4.
- Fig. 5. Long fragment of straight anterior tube part, a - top view, b - bottom view, c - cross-section. Albert Canal sections, Geulhem Member, sample A, x 10.5 (a, b), x 14 (c). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992201-5.
- Fig. 6. Broken spiral, detail showing tube structure, Albert Canal sections, Geulhem Member, sample A, x 14. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992201-6.



PLATE 5

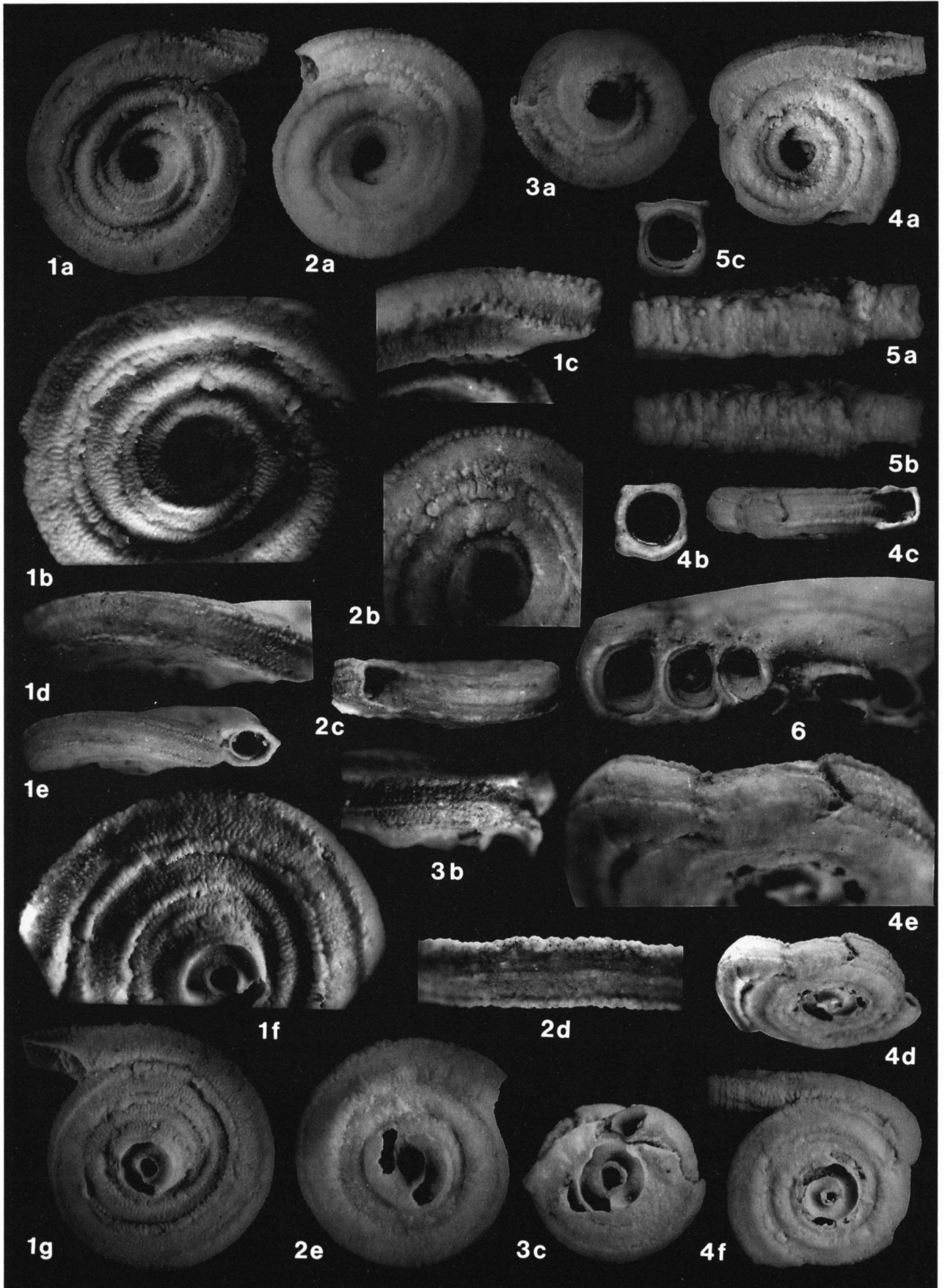


PLATE 6

*Rotularia (Rotularia) tobar vroenhovens* n. subsp. Houthem Formation, Geulhem Member.

- Fig. 1. Holotype, a - top view, showing swelling at the base of the (broken) straight anterior tube part, b - detail showing transition spiral/straight anterior tube part (right), c - lateral view, d - detail showing cross-section of straight anterior tube part, with tube of ? *Ditrupea schlotheimi* inside lumen, e - other lateral view, f - bottom view. Albert Canal sections, upper part of Geulhem Member, x 7 (a, c, e, f), x 10.5. (b), x 14 (d). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992202-1 (leg. J.W.M. Jagt, no. 2678).
- Fig. 2. Spiral with relatively strong longitudinal edges, a - top view, b - lateral view, c - detail showing cross-section of (broken) straight anterior part, with object inside, d - lateral view, showing transition spiral/straight anterior part (right), e - bottom view. Albert Canal sections, upper part of Geulhem Member, x 7 (a, b, e), x 14 (c), x 10.5 (d). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992202-2 (leg. J.W.M. Jagt, no. 2678).
- Fig. 3. Spiral with very long straight anterior tube part, top view. Albert Canal sections, upper part of Geulhem Member, x 5.3. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992202-3 (leg. J.W.M. Jagt, no. 2678).
- Fig. 4. Slightly irregular spiral with relatively strong longitudinal edges, a - top view, b - oblique lateral view. Albert Canal sections, upper part of Geulhem Member, x 7. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992202-4 (leg. J.W.M. Jagt, no. 2678).
- Fig. 5. Relatively high trochospiral, a - oblique lateral view, b - lateral view. Albert Canal sections, upper part of Geulhem Member, x 7. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992202-5 (leg. J.W.M. Jagt, no. 2678).
- Fig. 6. Barrel-shaped spiral with straight anterior tube part, lateral view. Albert Canal sections, upper part of Geulhem Member, x 7. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992202-6 (leg. J.W.M. Jagt, no. 2678).

*Bipygmaeus pygmaeus* (von Hagenow, 1840) ?

- Fig. 7. Planar spiral, aperture slightly erect. Albert Canal sections, sample 125, x 21. Coll. GPI Hamburg, no. 3361.
- Fig. 8. Planar spiral, aperture slightly erect. Albert Canal sections, north of km mark 24,000, x 21. Coll. GPI Hamburg, no. 3362.

*Bipygmaeus pygmaeus* (von Hagenow, 1840)

- Fig. 9. Planar spiral, followed by conical spiral, a - top view, b - oblique lateral view, c - lateral view. Albert Canal sections, sample 125, x 21. Coll. GPI Hamburg, no. 3363.

Spirorbidae gen. et sp. indet.

- Fig. 10. Base of broken spiral, top view. Albert Canal sections, north of km mark 24,000, x 21. Coll. GPI Hamburg, no. 3364.

*Pileolaria* ? sp. 1

- Fig. 11. Planar spiral, aperture slightly erect. Albert Canal sections, sample 127 II, x 21. Coll. GPI Hamburg, 3365.
- Fig. 12. Planar spiral, aperture slightly erect, a - top view, b - oblique lateral view, c - lateral view. Albert Canal sections, sample 127(1), x 21. Coll. GPI Hamburg, no. 3366.

*Pileolaria* ? sp. 2

- Fig. 13. Planar spiral, aperture slightly erect, a - top view, b - oblique lateral view. Albert Canal sections, sample 180, x 21. Coll. GPI Hamburg, no. 3367.

*Pileolaria* ? sp. 1

- Fig. 14. Planar spiral, followed by conical spiral, lateral view. Albert Canal sections, north of km mark 24,000, x 21. Coll. GPI Hamburg, no. 3368.

*Neodexiospira* ? sp. 1

- Fig. 15. Planar spiral, a - top view, b - oblique lateral view. Albert Canal sections, as sample 121 (attached to same substrate as Pl. 2, Fig. 14), x 28. Coll. GPI Hamburg, no. 3332.
- Fig. 16. Planar spiral. Albert Canal sections, sample 121, x 28. Coll. GPI Hamburg, no. 3369.

*Neodexiospira* ? sp. 2

- Fig. 17. Planar spiral with free space between the turns. Geulhem section, sample 105, x 28. Coll. GPI Hamburg, no. 3370.

PLATE 6

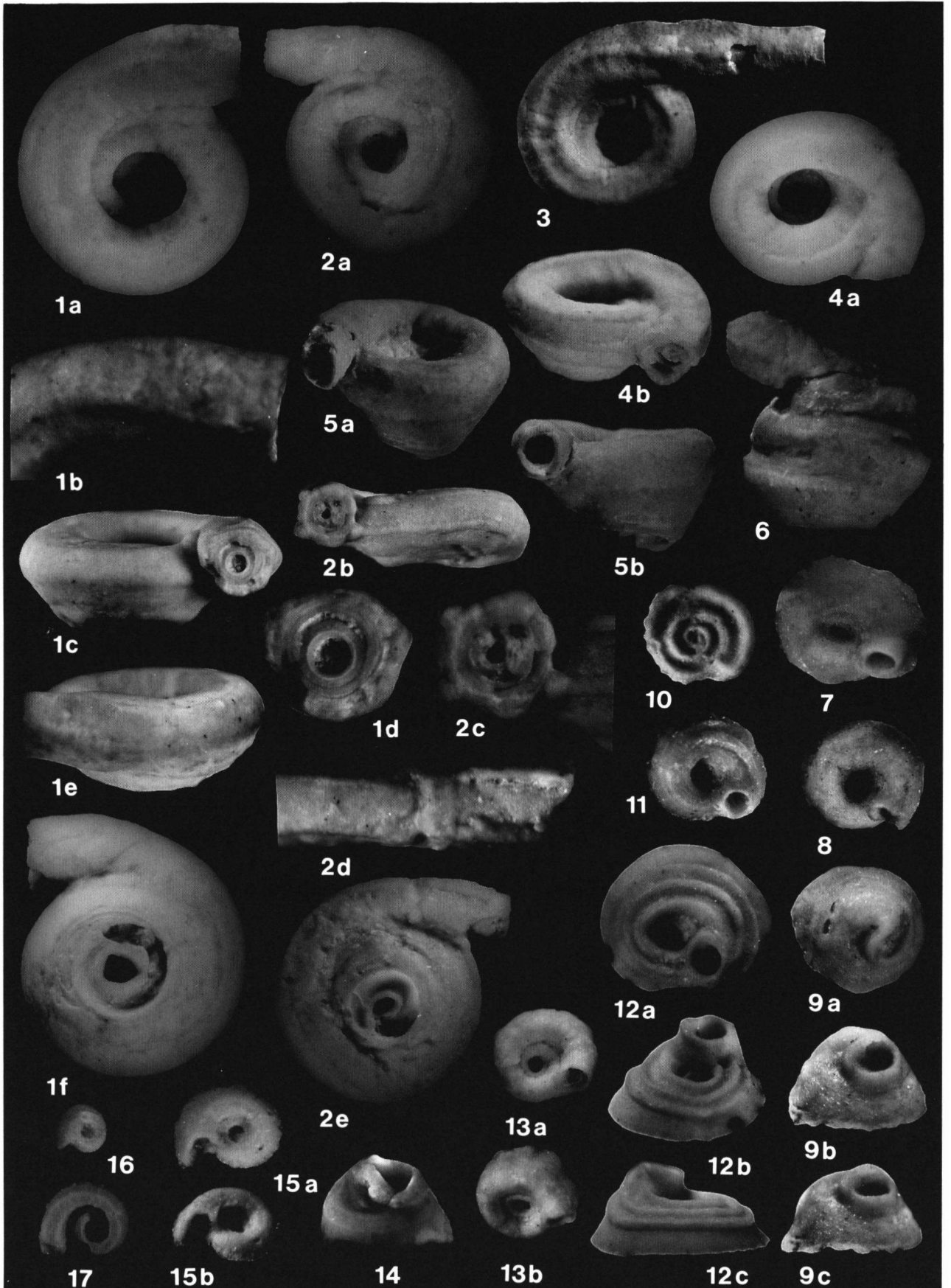


PLATE 7

*Serpula* ? sp.

Fig. 1. Large fragment of attached tube part with strong crest, a - top view, b - oblique lateral view. Albert Canal sections, Geulhem Member, sample B, x 6.3. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992203.

*Metavermilia* ? sp.

Fig. 2. Hook-shaped curved tube, bottom view of impression on substrate showing tube's exterior surface. Albert Canal sections, sample 121a, x 21. Coll. GPI Hamburg, no. 3371.

Fig. 3. S-shaped tube fragment, a - bottom view of impression on substrate showing tube's exterior surface, b - impression showing inversely U-shaped cross-section. Albert Canal section, north of km mark 24.000, x 21. Coll. GPI Hamburg, no. 3372.

*Pyrgopolon (Septenaria)* sp.

Fig. 4. Tube fragment, a - lateral view, b - opposite lateral view, c - cross-section at transition attached/erect tube parts, showing structure, d - cross-section of erect tube part. Geulhem, burrow infill directly at K/T boundary, x 6.3 (a, b), x 10.5 (c), x 8.4 (d). Coll. GPI Hamburg, no. 3373.

*Placostegus erectus* (Brünnich Nielsen, 1931)

Fig. 5. Attached tube part, forming loop, showing undulate keel and transition attached/erect tube part (lower right). Albert Canal sections, sample 125, x 12.6. Coll. GPI Hamburg, no. 3374.

Fig. 6. Attached tube part, curved, showing denticulate keel. Albert Canal sections, sample 125, x 12.6. Coll. GPI Hamburg, no. 3375.

Fig. 7. Two specimens: attached tube part, showing narrow, high, caterpillar-like socle lifting tube relatively highly above substrate (bryozoan), a - lateral view, c - cross-section. Albert Canal sections, sample 127(2), x 16.8 (a), x 21 (c). Coll. GPI Hamburg, no. 3376. b - lateral view, showing narrow, high, caterpillar-like socle lifting tube relatively highly above substrate, d - opposite lateral view, showing transition attached/erect part (right), e - top view, showing denticulate keel. Albert Canal sections, sample 125, x 12.6. Coll. GPI Hamburg, no. 3377.

Fig. 8. Attached tube part, including transition attached/erect tube part, twisted S-shaped, showing keel. Albert Canal sections, as sample 121, x 12.6. Coll. GPI Hamburg, no. 3378.

Fig. 9. Tube fragment, showing transition attached (right, damaged)/erect tube part (upper left), forming teeth at aperture, lateral view. Albert Canal sections, as sample 138, x 12.6. Coll. GPI Hamburg, no. 3379.

Fig. 10. Attached tube part, forming narrow loop with but weak longitudinal edge, and steep slightly distorted erect part (right, broken anteriorly). Albert Canal sections, sample 127 II, x 12.6. Coll. GPI Hamburg, no. 3380.

Fig. 11. Long fragment of erect tube part, showing strong longitudinal ornament, a - top view, b - oblique lateral/bottom view, c - bottom view, showing structure of damaged tube wall (top). Geulhem section, sample 105, x 12.6. Coll. GPI Hamburg, no. 3381.

Fig. 12. Fragment of erect tube part, with teeth at aperture (tips of some teeth broken off), a - oblique lateral view (left)/bottom view (right), showing longitudinal ornament, b - aperture. Albert Canal sections, hardground at km mark 23.850, x 16.8 (a), x 21 (b). Coll. GPI Hamburg, no. 3382.

Fig. 13. Aperture of erect tube part, with teeth (some broken off). Geulhem section, some metres above K/T boundary, x 16.8. Coll. GPI Hamburg, no. 3383.

Fig. 14. Fragment of erect tube part, with teeth at aperture and strong transverse ornament, a - top view, b - lateral view (upper side left), c - aperture, showing section of echinoid spine resembling operculum. Specimen intentionally broken after photography. Geulhem section, sample 105, x 16.8 (a, b), x 23.5 (c). Coll. GPI Hamburg, no. 3384.

PLATE 7

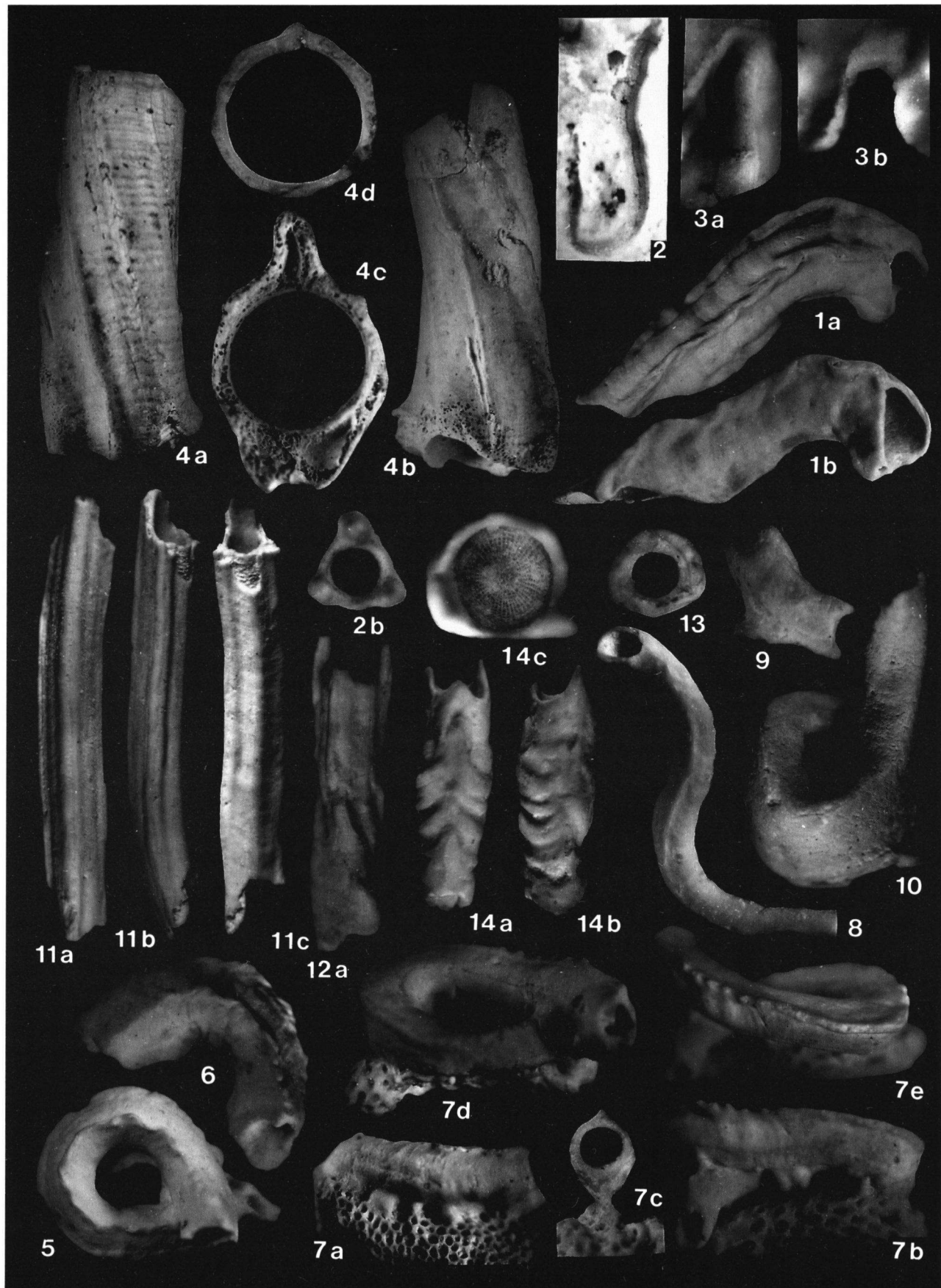


PLATE 8

*Pyrgopolon (Pyrgopolon) mosae mosae* de Montfort, 1808

- Fig. 1. Outer parable layer, complete but short erect tube part, a - top view, showing transverse wrinkles near aperture, b - lateral view, showing remnants of base of attached tube part (lower left), c - aperture. Albert Canal sections, as sample 138, x 8.4. Coll. GPI Hamburg, no. 3385.
- Fig. 2. Outer parable layer, large fragment of erect tube part. Albert Canal sections, as sample 138, x 10.5. Coll. GPI Hamburg, no. 3386.
- Fig. 3. Outer parable layer, small fragment of erect tube part, a - exterior, b - detail of interior, showing longitudinal section of tube wall with parable lamellae (top) and transverse striation. Albert Canal sections, sample 125, x 10.5 (a), x 16.8 (b). Coll. GPI Hamburg, no. 3387.
- Fig. 4. Outer parable layer, small fragment of erect tube part. Detail of interior, showing transverse striation. Geulhem section, some metres above K/T boundary, x 16.8. Coll. GPI Hamburg, no. 3388.

*Pyrgopolon (Pyrgopolon) mosae* subsp. indet.

- Fig. 5. Fragment of cylinder layer, a - lateral view, b - anterior cross-section, c - posterior cross-section. Geulhem section, sample 105, x 10.5 (a), x 16.8 (b). Coll. GPI Hamburg, no. 3389.
- Fig. 6. Fragment of cylinder layer, lateral view. Geulhem section, some metres above K/T boundary, x 12.6. Coll. GPI Hamburg, no. 3390.

*Pyrgopolon (Pyrgopolon) mosae cipllyana* (de Ryckholt, 1852)

- Fig. 7. Outer parable layer, small fragment, a - lateral view of exterior, showing keels and transverse ribs, b - interior, showing transverse striation and longitudinal furrow underneath keel, c - cross-section, showing keels. Albert Canal sections, as sample 138, x 12.6. Coll. GPI Hamburg, no. 3391.
- Fig. 8. Outer parable layer, small fragment, showing longitudinal edges. Albert Canal sections, as sample 138, x 12.6. Coll. GPI Hamburg, no. 3392.
- Fig. 9. Outer parable layer, small fragment, showing longitudinal keels. Albert Canal sections, sample 180, x 16.8. Coll. GPI Hamburg, no. 3393.

*Placostegus alatus* (Brünnich Nielsen, 1931)

- Fig. 10. Fragment of curved attached tube part, oblique lateral view (direction of growth from right to lower left), showing keel and peristomes. Albert Canal sections, north of km mark 24.000, x 10.5. Coll. GPI Hamburg, no. 3394.
- Fig. 11. Fragment of transition attached/erect tube parts, cross-section of attached part, showing keel and peristomes. Albert Canal sections, sample 120, x 16.8. Coll. GPI Hamburg, no. 3395.
- Fig. 12. Fragment of transition attached/erect tube part, a - top view, showing weak ornament, b - oblique lateral view, showing socle at anterior end of base and median furrow at underside of erect part. Albert Canal sections, as sample 121, x 10.5. Coll. GPI Hamburg, no. 3396.
- Fig. 13. Fragment of transition attached/erect tube parts, a - lateral view, showing socle, b - bottom view, showing socle and median furrow at underside of erect part (right), c - cross-section of erect tube part. Albert Canal sections, sample 125, x 12.6 (a, b), x 16.8 (c). Coll. GPI Hamburg, no. 3397.
- Fig. 14. Fragment of erect tube part, showing median furrow and bulges at underside and peristome, a - bottom view, b - cross-section. Albert Canal sections, sample 125, x 12.6 (a), x 16.8 (b). Coll. GPI Hamburg, no. 3398.
- Fig. 15. Fragment of erect tube part, showing peristome, a - top view, b - lateral view, c - bottom view, showing median furrow, d - cross-section. Albert Canal sections, sample 121, x 10.5 (a-c), x 16.8 (d). Coll. GPI Hamburg, no. 3399.
- Fig. 16. Fragment of erect tube part, cross-section. Albert Canal sections, sample 121, x 16.8. Coll. GPI Hamburg, no. 3400.
- Fig. 17. Fragment of curved erect tube part, top view, showing peristomes. Albert Canal sections, sample 121, x 10.5. Coll. GPI Hamburg, no. 3401.
- Fig. 18. Fragment of curved erect tube part, showing ornament and aperture with teeth, a - top view (aperture left), b - bottom view (aperture right). Albert Canal sections, sample 179, x 12.6. Coll. GPI Hamburg, no. 3402.

PLATE 8

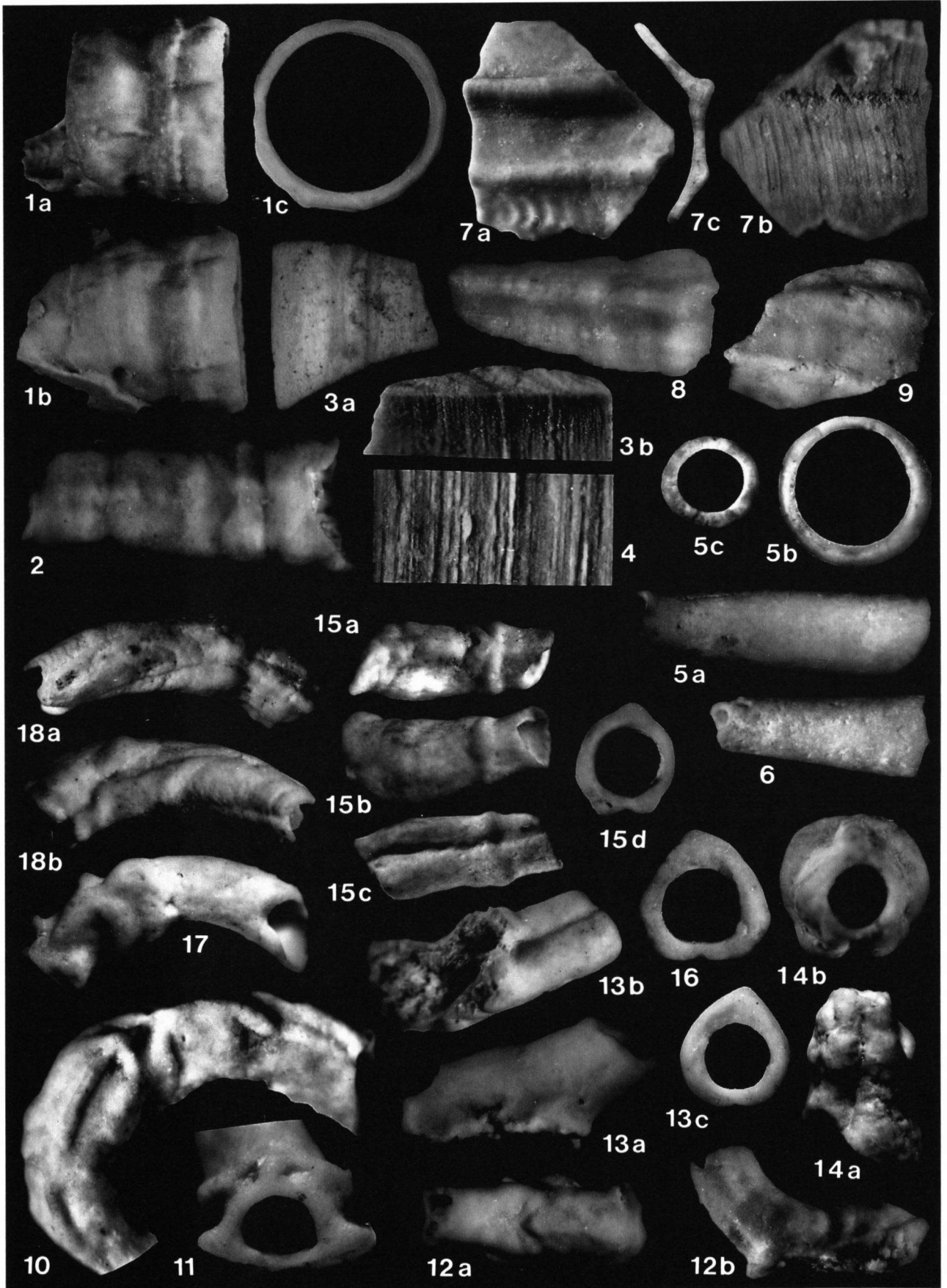


PLATE 9

*Neomicrorbis parietalis jagti* n. subsp.

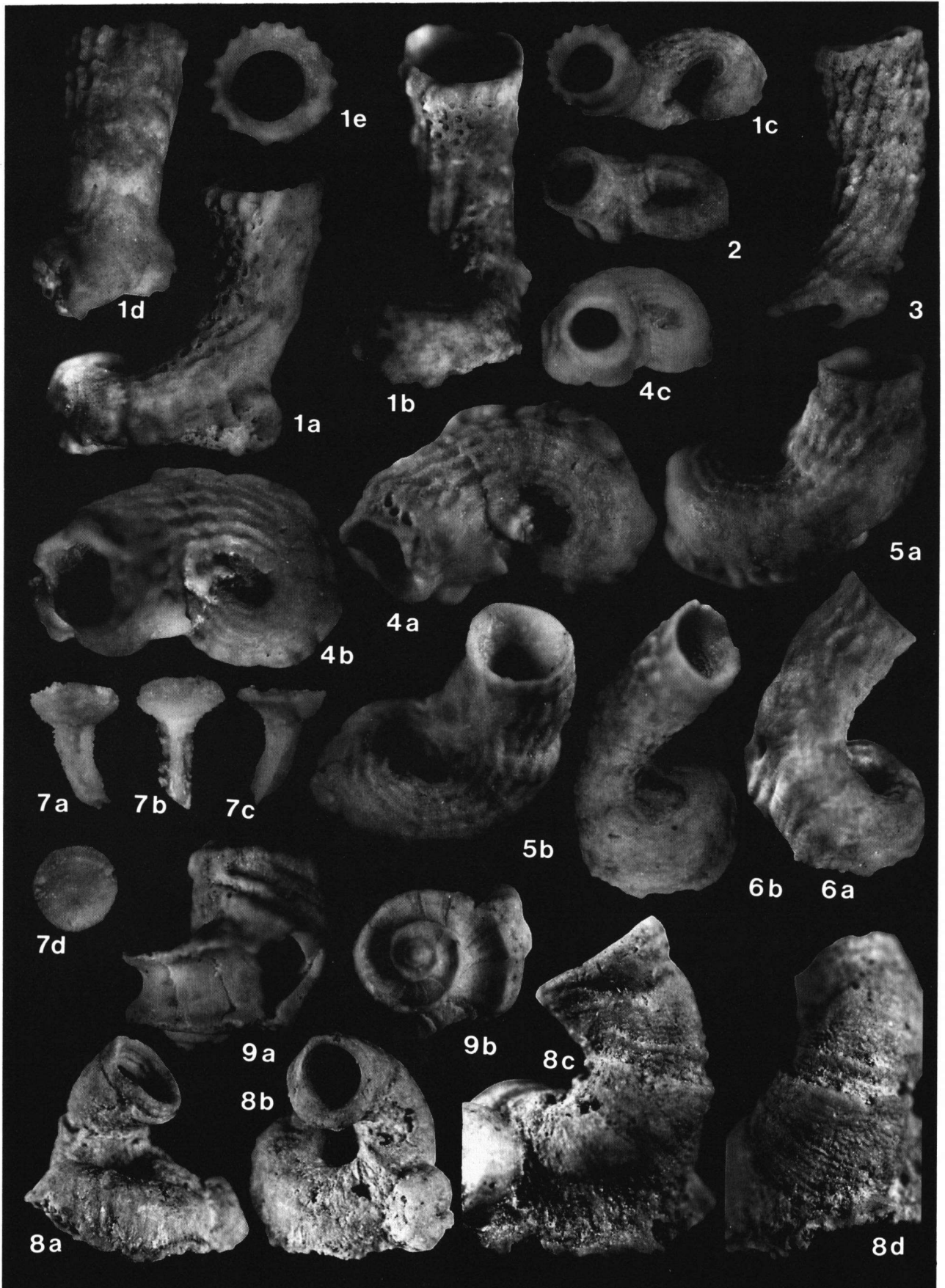
- Fig. 1. Holotype, a - lateral view, showing spiral (left), intermediate tube part (bottom centre), erect tube part (right) and torsion of this, b - another lateral view, showing spiral and erect part with aperture, c - oblique top view, d - other lateral view, showing erect part, e - aperture, surrounded by protruding keels. Albert Canal sections, 0-0.4 m above K/T boundary, x 12.6 (a, b, d, e), x 8.4 (c). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992204-1 (leg. J.W.M. Jagt, no. 872).
- Fig. 2. Very small spiral with intermediate and erect tube part, showing socle and aperture. Albert Canal section, sample 125, x 16.8. Coll. GPI Hamburg, no. 3403.
- Fig. 3. Erect tube part (broken), showing torsion. Albert Canal sections, sample 120, x 12.6. Coll. GPI Hamburg, no. 3404.
- Fig. 4. Paratype. Spiral, intermediate tube part and very short erect part, a - top view, showing keels and peristomes, b - oblique top view, showing callosity in umbilicus, c - lateral view showing socle and aperture. Albert Canal sections, 0-0.4 m above K/T boundary, x 12.6 (a, b), x 8.4 (c). Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992204-2 (leg. J.W.M. Jagt, no. 872).
- Fig. 5. Paratype. Spiral, intermediate tube part and erect part, a - oblique lateral view showing peristomes, b - top view, showing keels, aperture and callosity in umbilicus. Albert Canal sections, 0-0.4 m above K/T boundary, x 12.6. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992204-3 (leg. J.W.M. Jagt, no. 872).
- Fig. 6. Paratype. Spiral, intermediate tube part and erect part, a - oblique top view, showing peristomes and slightly irregular keels, b - lateral view, showing aperture. Albert Canal sections, 0-0.4 m above K/T boundary, x 10.5. Coll. Natuurhistorisch Museum Maastricht, no. NHMM 1992204-4 (leg. J.W.M. Jagt, no. 872).
- Fig. 7. Operculum, isolated from typical tube, a-c - lateral views, showing cucullus and calcar, d - top view of cucullus. Albert Canal sections, sample 125, x 33.6. Coll. GPI Hamburg, no. 3405.

*Neomicrorbis cingulatus* (Brünnich Nielsen, 1931)

- Fig. 8. Large tube with strong transverse ornament, a - oblique top view, showing corkscrew-shaped erect tube part, b - top view, showing aperture and small second specimen (lower right) of same species, c, d - lateral views of erect part, showing ornament. Geulhem section, burrow infill at K/T boundary, x 8.4 (a, b), x 12.6 (c, d). Coll. GPI Hamburg, no. 3406.
- Fig. 9. Broken tube, showing interior structure, a - lateral view (broken spiral bottom, erect part upper right), b - broken spiral bottom view. Albert Canal sections, sample 121, x 12.6. Coll. GPI Hamburg, no. 3407.



PLATE 9



Thus he attempted to reconstruct environmental conditions for fossil biota, using data on environmental requirements of modern species inhabiting the marine shelf as a starting point.

He collected comparative material himself, through diving sessions in the Baltic Sea, the Black Sea, the Adriatic and the Caribbean. He also organised Cuban—Czecho-Slovak expeditions in the Caribbean and was responsible for the intimate collaboration with the Institute for Marine Research in Rovinj during 1965-1975.

Apart from his scientific work for the Academy he attempted to pass on his knowledge to younger generations by lecturing at the Comenius University (Bratislava), and at the J.E. Purkyně, now Masaryk University (Brno), where he was appointed lector in 1967. In the same year he took his doctor's degree at Bratislava, on a paper on Neogene palaeogeography of the western Carpathians; in fact, data presented are valid for the whole of central Europe. At this time, he reintroduced and defined the term Paratethys for the, in part, isolated marine basins of western, central and eastern Europe.

Of his many papers published during these years, the one entitled 'Chronostratigraphie und Neostratotypen', which he edited and co-authored, was of special importance. The regional stages of the Miocene (Badenian, Sarmatian, Pannonian, Pontian) not only had a bearing on the central European stratigraphy, but were also important as far as correlations in the Neogene in all parts of the world and the establishment of global chronostratigraphic stages were concerned.

His organisational talent did not stop at publishing on subjects of chronostratigraphy. From 1967 onwards, he was a member of the National Stratigraphic Committee of the Czecho-Slovak Academy of Sciences, and in the same year he joined the managing committee of the Regional Committee on Mediterranean Neogene Stratigraphy (RCMNS), and was appointed president at the Lyon congress in 1971. The fact that he held this position for two terms, a rare phenomenon in the framework of the International Union of Geological Sciences (IUGS), is relevant in this respect. In 1979, he was elected president of the Subcommission on World Neogene Stratigraphy (SNS).

The above-mentioned talent, as well as his personality, came to the fore during the execution of the extensive correlation project, IGCP-UNESCO no. 25 during 1973-1983, which was based on the activ-

ities of a working group, established in 1967 principally to unravel Paratethys stratigraphy and palaeogeography, but soon extended to the whole of Europe, and parts of Asia and Africa. This project suggested correlations between the Neogene basins of western, central and southern Europe, North Africa and the Near East, as far east as the shores of the Indian Ocean. It unified the work of hundreds of geologists and palaeontologists, and the result of this effort is the synthesis entitled 'Neogene of the Mediterranean Tethys and Paratethys', in which the Neogene stratigraphic successions of the basins of this extensive area are described and illustrated. Many awards from institutions and universities in Czecho-Slovakia and abroad were conferred on Ján Seneš in recognition of his scientific contributions. The gold medal of Dionýz Štúr, the decoration of merit for the furtherance of the natural sciences and the medal of J.E. Purkyně were awarded to him. He was a member of the Czecho-Slovak National Committee for Geology, and an honorary member of the Hungarian and Austrian Geological Societies.

Ján Seneš published nine monographs and more than 180 papers in domestic and foreign journals, and co-authored editions of various geological maps.

He was a personality, not only in scientific circles, but also in everyday life: in spite of his scientific burdens, he never ceased to be human, and this character trait made him so popular and appreciated. He was always there for help or advice in word or deed. He knew how to appreciate the beauties of nature and art, and as an active mountaineer, he experienced the heights of this earth, as a diver he explored the depths of the sea, as an amateur pilot he ventured the skies, as a philatelist he had a proper sense of detail, and as an organiser a sense for synthesis. It is in this way that most of us remember him; we should follow his example, in order to pass on his message to younger generations and actively support the advancement of geology, which he lived for.

Dr Michal Kováč  
Geological Institute  
Slovakian Academy of Sciences  
Dubrávská Cesta 9  
84226 Bratislava, Czecho-Slovakia