A TAXONOMIC REVISION OF NW EUROPEAN OLIGOCENE AND MIOCENE FASCIOLARIIDAE TRADITIONALLY INCLUDED IN THE GENUS *STREPTOCHETUS* (MOLLUSCA, GASTROPODA)

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Cadée, M.C. & A.W. Janssen. A taxonomic revision of NW European Oligocene and Miocene Fasciolariidae traditionally included in the genus *Streptochetus* (Mollusca, Gastropoda). — Contr. Tert. Quatern. Geol., 31(2-4): 31-107, 37 figs, 6 pls. Leiden, December 1994.

A taxonomic revision is presented of Oligocene and Miocene species of the gastropod family Fasciolariidae from the North Sea, Paris and Mainz basins, previously assigned to the genus *Streptochetus*. No representatives of this group younger than Miocene (Syltian) have been encountered during this study. Four genera (*Fredenia* gen. nov., *Streptocarina*, *Streptodictyon* and *Streptolathyrus*) are distinguished. Five new species are described: *Streptodictyon impiger* (Late Rupelian), *S. schnetleri* (Chattian B), *S. twistringensis* (Reinbekian), *Streptolathyrus masculinus* (Chattian A), and *S. regularis* (Hemmoorian). In addition, the following species are accepted: *Fredenia ritzkowskii* (R. Janssen, 1979) (Chattian A/B); *Streptocarina klockenhoffi* (Hinsch, 1977) (Syltian); *Streptodictyon abruptus* (Beyrich, 1856) (Reinbekian), *S. cheruscus* (Philippi, 1843) (Chattian-Hemmoorian), *S. gottschei* (Gripp, 1914) (Chattian B-Vierlandian), *S. retrorsicosta* (Sandberger, 1860) (Rupelian-Chattian A), *S. sexcostatus* (Beyrich, 1856) (Hemmoorian-Reinbekian), *S. soellingensis* (Tembrock, 1965) (Chattian A), *S. sowerbyi* (Nyst, 1836) emend. (Early Rupelian-Chattian A), *S. subelongatus* (d'Orbigny, 1852) (Early Rupelian), *S. undatus* (Meunier, 1880) (Rupelian); *Streptolathyrus rothi* (Beyrich, 1856) (Chattian B-Langenfeldian). Two taxa from the Rupelian had to be recorded in open nomenclature: *Streptolathyrus* sp. and Fasciolariidae sp. Type material was studied for several taxa; lectotypes are designated for seven taxa of the species group.
Fusus dhondtae nom. nov. is introduced for *Fusus Sowerbyi* d'Orbigny, 1850, *non Fusus sowerbyi* Nyst, 1836 emend. Sexual dimorphism, suggested for this group of gastropods in the literature, could not be acknowledged. Some evolutionary trends are presented, but a cladogram was not constructed because of the impossibility to evaluate the relative value of morphological criteria.

Key words — Mollusca, Gastropoda, Fasciolariidae, North Sea Basin, Paris Basin, Mainz Basin, Oligocene, Miocene, systematics, new taxa.

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INTRODUCTION

In this paper a generally quite common group of NW European Cainozoic gastropod species is discussed in detail. Most species have been included in the literature in the genus *Streptochetus*. They are characterised by a fusiform shell, with a moderately long siphonal canal, usually a coarse collabral and a much finer spiral sculpture. All species have a multispiral, conical protoconch of at least three and a half whorls, which are either smooth or partially ornate. Usually the representatives of this group have been placed in the Fasciolariidae (*e.g.* Wenz, 1943, p. 1264; Glibert, 1963, p. 146; Anderson, 1964, p. 262; R. Janssen, 1979b, p. 297). Beets (1950) also used the family name Fasciolariidae and, apparently unintentionally, introduced (p. 23) the subfamily Streptochetinae, not previously described. The name *Streptodictyon* Tembrock, 1961 was erected as a subgenus, but not assigned to a family. Bouchet & Warén (1986, p. 495), however, considered it to belong in the Buccinidae.

Recent literature on modern neogastropods proves that relying on conchological characteristics can be extremely confusing in many cases with respect to the systematic position of genera and/or species. For instance, representatives of the genus *Manaria* Smith, 1906 (see Bouchet & Warén, 1986, p. 475, pls 13, 14) have shells closely resembling many of the species discussed in the present paper. The species of *Manaria*, however, have a radula formula typical of Buccinidae. At least one of the *Manaria* species mentioned by Bouchet & Warén has a paucispiral protoconch, but for most species the protoconch is still unknown.

Similar is *Pisanianura spiralis* (Marshall, 1918) from the Miocene of New Zealand. Its multispiral embryonic shell with reticulate surface sculpture, the transition to the teleoconch and the ornament of the teleoconch whorls at first glance resemble many of the species discussed in the present paper. In *P. spiralis*, however, the rather heavy protoconch sculpture starts abruptly just after the nucleus (Warén & Bouchet, 1990, fig. 142), whereas in the species discussed here the first 2-3 whorls have no sculpture. A further difference is the very short siphonal canal of the New Zealand species. Other species of *Pisanianura*, *e.g.* the type species *P. inflata* (Brocchi, 1814) are known from the European Cainozoic, but they deviate more strongly from the group treated here. Warén & Bouchet (1990, p. 63) introduced a subfamily Pisanianurinae within the Ranellidae (Tonnoidea), mainly founded by anatomical features.

Admittedly, the reticulate protoconch of many species might be considered a reason to include such taxa in the Ranellidae, but in our opinion the general shell form, the lack of varices, and the long siphonal canal differ too strongly from all representatives of that family, except *P. spiralis*. Up to now these and related species were usually considered to belong in the Buccinidae. We consider the protoconch reticulation as a convergence.

Lack of data on soft part morphology and considering the general shell form of the '*Streptochetus*'-group, it seems inevitable to consider them as either Buccinidae or Fasciolariidae. A direct comparison, however, with the type genera of these families demonstrates conspicuous differences, *e.g.* in general shell form, but especially in the protoconch, which is paucispiral in both cases. The outline of the '*Streptochetus*' species resembles more closely the representatives of the Fasciolariidae, subfamily Fusininae and probably for that reason most authors considered '*Streptochetus*' to belong to that group. We reluctantly maintain a classification in the Fasciolariidae, subfamily Fusininae.

ABBREVIATIONS

In this paper we use the following abbreviations:

def.	defective
juv.	juvenile
H	shell height
W	shell width

Collections/collectors:

AJB	A.C. Janse, Brielle, The Netherlands;
AJL	A.W. Janssen, NNHM (former RGM), Leiden, The Netherlands;
DLV	D. Ledon, Versailles, France;
DMM	the late D. van der Mark, Middelburg, The Netherlands (now in RGM);
FJR	the late F.J. Janssen, Rotterdam, The Netherlands (now in RGM);
FHK	F. von der Hocht, Kerpen-Balkhausen, Germany;
FWG	F. Weinbrecht, Glücksburg, Germany;
GLK	Geologisches Landesamt Nordrhein-Westfalen, Krefeld, Germany;
HBH	H.C.J. Bosch, Hilversum, The Netherlands;
JRP	J. Le Renard, Plaisir, France;
JVV	J. van der Voort, Venne, Germany;
IRScNB	Koninklijk Belgisch Instituut voor Natuurwetenschappen - Institut royal des Sciences naturelles de Belgique, Brussels, Belgium;
KGM	K. Gürs, Mainz, Germany;
KSL	K.I. Schnetler, Langå, Denmark;
MBL	M. van den Bosch, NNHM (former RGM), Leiden, The Netherlands;
MCL	M.C. Cadée, Leiden, The Netherlands;

MNHNP Musée national d'Histoire naturelle, Paris, France;
MNO M.S. Nielsen, Odense, Denmark;
NMV National Museum of Victoria, Melbourne, Australia;
PGL P.A.M. Gaemers, Leiden, The Netherlands;
PHB Paläontologisches Institut der Humboldt Universität, Berlin, Germany;
RGD Rijks Geologische Dienst, Haarlem, The Netherlands;
RGM National Museum of Natural History (formerly Rijksmuseum van Geologie en Mineralogie), Leiden, The Netherlands;
RHR R.E. Hamstra, Rotterdam, The Netherlands;
ROD former 'Dienst Rijksopsporing van Delfstoffen', The Netherlands;
SMF Senckenberg Museum, Frankfurt am Main, Germany.

STRATIGRAPHY

For the stratigraphical origin of the samples mentioned in this paper we apply the usual and well-known NW European stratigraphical terminology. There has been some discussion on the relative position of the Latdorfian, which sometimes was either considered to be Early Oligocene or Late Eocene. In agreement with the decisions of the International Geological Congress, Washington (1989) we consider the Rupelian as the first stage of the Oligocene. Therefore the Oligocene is subdivided into Early and Late Oligocene (Rupelian and Chattian, respectively).

HISTORY OF THE GENUS *STREPTOCHETUS* COSSMANN, 1889

Streptochetus Cossmann (1889, p. 170)

Type species — *Fusus intortus* Lamarck, 1803 (original designation).

Original diagnosis — 'Shell subumbilicate, with an obtuse apex, whorls with nodose ribs; canal intorted, not emarginate; columella excavated in the middle, flexuous, often smooth, for the rest with unequal and clearly oblique folds' (translated from Latin).

Remarks — The genus *Streptochetus*, subdivided into two 'sections' (*Pseudolatirus* and *Streptochetus* s. str.), was introduced by Cossmann, in his well-known 'Catalogue illustré'. The section *Streptochetus* s. str. in his concept comprised eight species from the Early and Middle Eocene of the Paris Basin, with *Fusus intortus* Lamarck as type species. Cossmann compared his new genus with *Latirus* de Montfort, 1810 (type species *Murex polygonus* Gmelin), from which it was assumed to differ in having a less complex ornament, its columella, the non-crenulated apertural margin, and its embryonic shell resembling that of *Clavella*. The name *Clavella* Swainson, 1835, being preoccupied by *Clavella* Oken, 1815 (Crustacea), was replaced by *Clavilithes* Swainson, 1840 (type species *Fusus longaevus* Deshayes *non* Solander = *Fusus parisiensis* Mayer-Eymar) (compare Grabau, 1904, p. 104).

The name *Streptochetus* has subsequently also been applied for a number of usually quite common species from Oligocene and Miocene deposits in the North Sea Basin and adjacent areas. Thus, for instance, Cossmann (1901, p. 31) considered the Oligocene species *Fusus elongatus* Nyst (= *Fusus subelongatus* d'Orbigny) and the Miocene *Fusus sexcostatus* Beyrich to be characteristic representatives of *Streptochetus* s. str. Later authors attributed several additional species, resembling either *F. subelongatus* or *F. sexcostatus*, to *Streptochetus*. All these species, however, differ basically from *Streptochetus* s. str. in the structure of their embryonic shell, which in each case is multispiral instead of paucispiral. In this respect we wish to quote Oppenheim (1922, p. 54, sub *Fusus pausramensis*):

'Unsere Form gehört so wenig zu *Streptochetus* wie der miocäne *F. sexcostatus* Beyr., den Cossmann [...] irrtümlich hierherstellt.'

A similar statement was made by Sorgenfrei (1958, p. 234), who suggested a closer relationship with *Aptyxis* Troschel, 1868 [type species: *A. syracusanus* (Linné)].

Evidently, Cossmann paid only scant attention to the morphology of the embryonic shell. It should be realised, of course, that the relevance of the protoconchs for gastropod systematics was hardly known at that time. Furthermore, it is quite probable, that in most of the specimens available to Cossmann protoconchs were missing or poorly preserved.

This may also explain why Cossmann considered his 'section' *Pseudolatirus* to belong to the genus *Streptochetus*. There is indeed a fair resemblance in the teleoconch characteristics. Cossmann described the protoconch of the monotype of *Pseudolatirus* (*S. Mellevillei*) as 'embryon obtus et lisse'.

The name *Pseudolatirus* Cossmann, 1898 was replaced by *Streptolathyrus* Cossmann, 1901, because of preoccupation by *Pseudolatirus* Bellardi, 1884 (type species *Fusus bilineatus* 'Partsch', subsequent designation Cossmann, 1901, p. 24). In that paper Cossmann gave a further description of the *Streptolathyrus* protoconch: 'protoconque paucispirée, à galbe conoïdal, à nucléus petit et obtus, ...'.

Tembrock (1965, pl. 34, figs 3, 4) was the first to illustrate the protoconch of *S. mellevillei*. Curiously enough, she figured a multispiral protoconch, thus differing from Cossmann's description. Like most other authors Tembrock maintained *Streptolathyrus* as a subgenus of *Streptochetus*.

Two further taxa have been introduced as subgenera of *Streptochetus*, *viz. Streptodictyon* Tembrock, 1961 [type species *Streptochetus elongatus* (Nyst) *sensu* Tembrock, original diagnosis], and *Streptocarina* Hinsch, 1977 (type species *S. klockenhoffi* Hinsch, 1977, by monotypy).

Streptodictyon sensu Tembrock, 1961 is characterised by a multispiral protoconch with a reticulate sculpture. Tembrock included five taxa in *Streptodictyon*, *viz. S. elongatus* (Nyst) (Rupelian), *S. söllingensis* Tembrock (Chattian), *S. retrorsicosta* (Sandberger) (Rupelian-Chattian), *S. abruptus* (Beyrich) ('Early' Miocene) and *S. sexcostatus* (Beyrich) (Miocene). The morphology of these complexes was carefully studied by Tembrock, which resulted in the conclusion that two morphotypes could be distinguished within each species complex, indicated as 'Form a' and 'Form b' (for characteristics see below in the description of *Streptodictyon*). These forms were interpreted to probably represent sexual dimorphs, 'Form a' representing the male and 'Form b' the female (Tembrock, 1961, p. 375).

Streptocarina Hinsch, 1977 was introduced as a subgenus of *Streptochetus*, for the Late Miocene North Sea Basin species *S. klockenhoffi* Hinsch, 1977. It is characterised by the presence of a carina-like spiral line on the two youngest whorls of the protoconch, which continues on the initial part of the first teleoconch whorl as a relatively strong spiral line.

Revised concept of the genus *Streptochetus* Cossmann, 1889

The genus *Streptochetus*, as defined by its type species, *S. intortus* (Lamarck, 1803) (see Pl. 1, figs 1-2), of which an abundant material from the Paris Basin was available to us from several collections, comprises fusiform gastropods with subangulate whorls (caused by the presence of a distinct subsutural depression) and a relatively long, somewhat contorted siphonal canal. The ornament consists of coarse collabral and much finer, fairly widely spaced spiral elements, developed in more than one generation. In fully-grown individuals, reaching a shell height of 55 mm, the base of the shell has a distinct pseudumbilicus. There is no columellar fold. A blunt parietal tooth is present in adult specimens, accentuating an adapical apertural channel. Spiral lirae on the inner apertural margin are lacking.

In his original description Cossmann gave no details of the embryonic shell (the only indication might be 'à sommet obtus'). Cossmann (1901, p. 29), however, described it as follows: 'protoconque paucispirée, à nucléus peu saillant et légèrement déviée'. A first attempt to illustrate the protoconch of *Streptochetus intortus* was made by Tembrock (1965, pl. 34, figs 1a-c, 2). These two specimens, however, originate from the famous Fresville locality in Normandy (Cotentin, France). Cossmann & Pissarro (1901, p. 102ff) mentioned five *Streptochetus* species from that locality: *S. brasili* Cossmann & Pissarro, *S. squamulosus* (Deshayes), *S. diplocophorus* Cossmann & Pissarro, *S. incertus* (Deshayes), and *S. surculaeformis* Cossmann & Pissarro. The specimen illustrated by Tembrock (1965, fig. 2, specimen with registration no. PHB Ga 66/67) is characterised by having two columellar folds. This agrees with the Cotentin species *S. brasili*, and certainly not with the Paris Basin species *S. intortus*. The specimen illustrated in her fig. 1a-c could very well be a juvenile of the same species *S. brasili*. Anyway, according to Cossmann & Pissarro, the species *S. intortus* does not occur at Fresville. So it seems that the embryonic shell of *S. intortus* has still not been illustrated.

In Text-fig. 1 and Pl. 1, fig. 2 the embryonic shell of *S. intortus* from its type locality Grignon (Paris Basin) is illustrated. The protoconch is dome-shaped and comprises about 1¾ smooth whorls. The nucleus is relatively small and flattened, the second half of the first whorl rapidly expanding and being even slightly wider than the first teleoconch whorl, which results in an oblique position of the protoconch on top of the teleoconch. At least the last half whorl of the protoconch has an extremely fine and dense spiral sculpture, whereas one of the later teleoconch spirals is already visible as an obtuse angularity in the upper part of the whorl. The transition to the first postembryonic whorl is gradual and accompanied by a number of narrow collabral riblets, about half a whorl later the much coarser spiral sculpture of the teleoconch develops rapidly.

In *S. incertus* (Deshayes), also from the Paris Basin Lutetian, we observed a very similar protoconch on specimens from Chaussy (JRP). This species undoubtedly belongs to *Streptochetus*. From Villiers-St. Frédéric (Paris Basin, Lutetian) we studied a sample (JRP) of *'Streptochetus' squamulosus* (Deshayes). In this species, which at first sight does not differ basically from *S. intortus*, the protoconch is admittedly paucispiral (slightly more than one whorl), but it is relatively higher and furthermore there is a very abrupt boundary between proto- and teleoconch, after which the spiral and radial sculpture develop immediately, without any transitional sculpture. We strongly doubt if this *'S.' squamulosus* does indeed belong to *Streptochetus*, but leave a decision in this matter to students of the true *Streptochetus*-group.

Fig. 1. *Streptochetus intortus* (Lamarck, 1803), protoconch and early teleoconch whorls. Grignon (France, Yvelines dép.), Eocene, Lutetian (Calcaire grossier). Coll. RGM 47.821, x 25.

Summarising we conclude that none of the species treated in the present paper matches the diagnosis of the genus *Streptochetus*, in spite of the fact that during the last decades they have invariably been referred to that genus. In our experience typical representatives of *Streptochetus* are restricted to Eocene deposits, mainly in the Paris Basin. The species discussed here represent several genera, as described in the systematic part below. Unequivocal representatives of the genera treated here from outside the North Sea, the Paris and the Mainz Basins are unknown to us. Some records of '*Streptochetus*' species in the literature, however, could not be checked on the original material and may represent such occurrences after all (Báldi, 1973; Hölzl, 1958, 1962).

SYSTEMATIC PART

In the lists of synonyms we apply Richter's (1948, p. 54) symbols:

1881	(year in italics) name cited without description or illustration;
1881	(year in roman) the cited reference contributes to the knowledge of the taxon;
*	first valid introduction of the taxon;
.	responsibility for the identification is accepted by the present authors; (no symbol) responsibility for the identification is not accepted by the present authors, but there is no reason for doubt;
?	in the opinion of the present authors there is reason to doubt the identification;
v	the original material of this reference was studied by the present authors;
(1881)	(date between brackets) the year of publication is uncertain (or the paper has not been published officially, *e.g.* thesis).

In synonyms we only include references of taxa with a recognisable description or illustration and omit names mentioned in faunal lists only.

Classis	Gastropoda
Ordo	Neogastropoda
Superfamilia	Muricoidea
Familia	Fasciolariidae
Subfamilia	Fusininae
Genus	*Fredenia* gen. nov.

Derivatio nominis — The genus is named after the type locality of *F. ritzkowskii*, Freden near Alfeld/Leine, Niedersachsen, Germany.

Diagnosis — Fasciolariid gastropod with elongate fusiform shell and flattened teleoconch whorls. Ornament of coarse, slightly prosocline collabral ribs on the upper three whorls (7 per whorl), overrun by five remarkably sharp spiral lirae that continue until the apertural margin. Secondary spirals developing in between the two upper spirals and below the periphery of the body whorl. Protoconch multispiral, slender, with about three whorls. Some radial riblets and weak spirals are present near the junction with the teleoconch.

Type species — *Streptochetus (Streptolathyrus) ritzkowskii* R. Janssen, 1979 (Late Oligocene, Germany).

Remarks — The embryonic whorls of this species bear some resemblance to those of *Streptolathyrus*, but the nucleus is much larger and its outline is distinctly more elongate.

There are, furthermore, considerable differences in form and sculpture of the teleoconch which lead us to the conclusion that '*S.*' *ritzkowskii* does not fit the genus *Streptolathyrus*. The characteristics of *Fredenia* deviate rather strongly from the other species discussed in this paper and resemble at first glance the general outline of *Dolicholatirus* Bellardi, 1883 s. str. (see Wenz, 1943, p. 1243), which differs amongst other traits by the presence of two columellar folds.

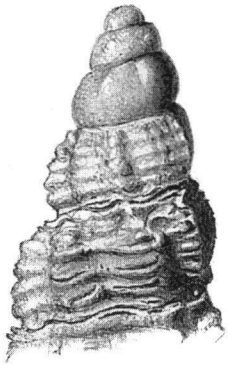


Fig. 2. *Fredenia ritzkowskii* (R. Janssen, 1979) (**holotype**), protoconch and early teleoconch whorls. Freden, near Alfeld/Leine (Germany, Niedersachsen), Oligocene, Eochattian ('Kalkmergel'). Coll. SMF 250712/1 (R. Janssen/Leunis, 1977), x 25.

Fredenia ritzkowskii (R. Janssen, 1979)
Pl. 1, fig. 3; Text-fig. 2

v* 1979b *Streptochetus (Streptolathyrus) ritzkowskii* n.sp., R. Janssen, p. 299, pl. 16, fig. 31 (*partim, non* fig. 32 = Fasciolariidae indet.) (exclusive of synonyms).

Type material — Holotype SMF 250712 (Leunis) (Pl. 1, fig. 3); paratypes (not studied by the present authors): 1 specimen from the type locality in SMF, 2 specimens from the type locality in the Römer-Pelizäus Museum, Hildesheim (Germany), 2 specimens from Niederkaufungen in the Geologisch-Paläontologisches Institut, Göttingen (Germany).

Locus typicus — Freden, near Alfeld/Leine, Germany (Niedersachsen), outcrop in a road-cut on the southern verge of the village.

Stratum typicum — 'Kalkmergel' (= calcareous marl) (Oligocene, Eochattian).

Original diagnosis or essential details of original description (translated from German) — This species admittedly resembles the other *Streptochetus*-species from the Oligocene and Miocene in outline, but can be distinguished by its extremely slender form, the very sharp spiral sculpture with secondary striation developing only very late, and the rapidly effacing ribs.

Revised diagnosis — See diagnosis of the genus.

Material studied — 1 specimen (holotype), as specified above.

Description (based on the holotype) — Shell height 6.5 mm, fusiform, slender, 2.9 times higher than wide, apical angle 28.5°.

The protoconch, fortunately, is well-preserved, multispiral (about three whorls) and rather slender (height = 1.05, width = 0.65 mm). The nucleus, compared to that of other species discussed in this paper, is voluminous (diameter 0.20 mm). The whorls are smooth, except for the last quarter of a whorl, which has a transitional sculpture consisting of weak spirals and two or three radial riblets on the boundary with the teleoconch.

The shell has four rather flat teleoconch whorls. The body whorl occupies 60% of the entire shell height. The periphery is rounded, with a rather abrupt transition into the base. The siphonal canal is straight and moderately elongate. The teleoconch has a very remarkable sculpture, consisting of seven coarse, slightly prosocline collabral ribs per whorl, continuous from one whorl to the next, that gradually flatten out on the third teleoconch whorl. The five primary spiral lirae of the teleoconch are strikingly sharp and high. The first and the second spiral are more widely spaced than the others. A secondary spiral develops in the interspace on the third teleoconch whorl. A further secondary spiral is present below the periphery of the body whorl.

Remarks — R. Janssen illustrated (see list of synonyms above), apart from the apparently juvenile holotype, also an adult paratype. This specimen has a stouter appearance (apical angle 34°), completely lacks the remarkable spiral sculpture (which may be due to abrasion) and the collabral sculpture is present to far beyond the point where it is already effaced in the holotype. In our opinion this specimen has to be indicated as Fasciolariidae indet.

Stratigraphical distribution — Oligocene, Chattian A or B.

Evolutionary developments — No additional species of the genus *Fredenia* are known to us.

Genus *Streptocarina* Hinsch, 1977

Original diagnosis (translated from German) — A *Streptochetus* with a carina on the two last whorls of the otherwise smooth protoconch.

Revised diagnosis — Fusiform shell with moderately convex teleoconch whorls. Ornament of coarse, almost straight collabral ribs (about 8 per whorl), overrun by six or seven thread-like spiral lirae that continue until the apertural margin. A secondary spiral develops rapidly in between the two upper spirals, later also between the others. Protoconch multispiral, conical, 3¾-4¼ whorls, the two last whorls carinated.

Monotype — Streptochetus (Streptocarina) klockenhoffi Hinsch, 1977 (Late Miocene, Syltian, Germany).

Streptocarina klockenhoffi (Hinsch, 1977)
Pl. 1, fig. 4; Text-fig. 3

? 1907 *Fusus crispus* Borson. — Ravn, p. 125 (329), pl. 6, fig. 10 (*non* Borson).
*v 1977 *Streptochetus (Streptocarina) klockenhoffi* nov. sp., Hinsch, p. 54, pl. 2, figs 9, 10a-b.
v. 1984 *Streptochetus (Streptocarina) klockenhoffi* Hinsch, p. 228, pl. 2, figs 27, 28.

Fig. 3. *Streptocarina klockenhoffi* (Hinsch, 1977) **(paratype)**, protoconch and early teleoconch whorls. Morsum Kliff, Isle of Sylt (Germany, Schleswig-Holstein), Miocene, Syltian (Pinneberg Formation, Level with *Aporrhais*). Coll. RGM 393.350 (AJL), x 25.

Type material — Holotype in the Klockenhoff Collection (Westerland, Sylt, Germany); paratypes from the type locality: 20 specimens in the Klockenhoff Collection, 13 specimens and 6 fragments in the RGM collections. An unknown number of paratypes was mentioned from the well Eidelstedt-Nordgetränke, depth 147-149.5 m, presumably in the collection of the Geologisches Landesamt Schleswig-Holstein, Kiel, Germany.
Locus typicus — Morsum Kliff, Isle of Sylt, Schleswig-Holstein, Germany.
Stratum typicum — Pinneberg Formation, Level with *Aporrhais*; Miocene, Syltian.
Description — Shell elongate fusiform, height to c. 15 mm; adult specimens were not available to us. The largest specimen has about five moderately convex teleoconch whorls.

The protoconch is conical, somewhat higher than wide, with 3¾-4¼ rather convex whorls. The nucleus has a diameter of 0.15 mm. The initial whorls are rounded. The last two whorls have a distinct carina, situated on the middle of the whorls, and a further, less accentuated, thread-like spiral just above the suture. The junction with the teleoconch is sharp, indicated by a difference in the lustre of the shell's surface, being glossy on the protoconch and dull on the teleoconch (exclusively visible on excellently preserved specimens, of which just one is available in the RGM sample). Just before the junction with the teleoconch a transitional sculpture is present, consisting of some four, orthocline to flexuous, rather widely spaced radial riblets, and the first indication of the teleoconch's spiral sculpture.

The teleoconch has about eight undulose, near-straight collabral ribs per whorl, not continuous from one whorl to the next. These ribs are overlain by a strong sculpture of thread-like spirals, the number of which varies from six to seven between the upper and lower suture. In between the two upper spirals a secondary spiral is present already on the first teleoconch whorl, soon reaching the strength of the primary ones. Also in the other interspaces do secondary spirals appear.

The continuation of the carina of the protoconch remains visible on the first half whorl of the teleoconch only. More anteriorly this spiral lies on or below the periphery of the whorls and can no longer be recognised as the primary one.

In the exclusively juvenile material available to us the columella has no folds. About eight spiral lirae are present on the inner apertural shell wall of the largest specimens.

The growth lines are distinctly visible in between the spiral sculpture and have a slightly lamellose appearance.
Material studied — The holo- and paratypes in the Klockenhoff Collection as specified above; 11 specimens, 6 fragm.; 1 juv. specimen, Text-fig. 3, 1 specimen, Pl. 1, fig. 4, RGM 220.071, 393.350-351, respectively (AJL) (all paratypes).
Stratigraphical distribution — Miocene, Syltian, exclusively known from the so-called *Aporrhais* level. Hinsch (1977) also mentioned material from the Late Langenfeldian of borehole Eidelstedt-Nordgetränke (depth 147-149.5 m below surface). As sediments of Syltian age are also penetrated in the same well the(se) specimen(s) might represent downhole contamination (compare Gaemers, 1987, p. 98).
Remarks — We noted a number of differences with the original description. The carina is not the only spiral on the embryonic whorls. In all specimens a second spiral is present just above the suture. This spiral has a thread-like appearance, but is not developed as a carina. It equally continues as a teleoconch spiral. Contrary to Hinsch's statement the carina of the protoconch does not continue as such on the initial teleoconch whorls, but merely on the first half one.

Ravn (1907) mentioned a specimen of '*Fusus crispus*' from the Late Miocene of 'Sild' (= Sylt). This shell was

considered to belong to *Latirus rothi* (Beyrich, 1856) by Kautsky (1925, p. 115), Sorgenfrei (1940, p. 45; 1958, p. 232), Rasmussen (1968, p. 144) and Anderson (1964, p. 262), but as that species does not occur in any of the large collections from Sylt and is, in fact, only known to range into the Langenfeldian, we assume that Ravn's specimen is an adult individual of *S. klockenhoffi*. Indeed the teleoconch sculpture of the two forms is very similar.
Evolutionary developments — We are not aware of any related species.

Genus *Streptodictyon* Tembrock, 1961

Original diagnosis (translated from German) — Shell usually moderately large to fairly large, fusiform. Embryonic shell conical, sometimes with a slightly deviated nucleus, initial whorls smooth, following whorls with reticulate sculpture; middle whorls with tuberculate radial ribs and spirals of various strength; form of aperture with columellar callus and variable, smooth or with columellar folds, tooth, spiral lirae on the internal apertural shell wall in every possible combination; siphonal thickening and umbilical slit rare; growth-lines curved in an elongate reverse S-shape. Separate forms a and b; possible sexual dimorphism.

Form a: usually with a constant number of ribs; ribs continuous from one whorl to the next, middle whorl without depression in its upper part; regular distribution of the various spirals.

Form b: partly with a reduction of the number of ribs, number of ribs higher than in form a, at least on the initial whorls; middle whorl with a depression in its upper part, 3 to 4 stronger spirals on the lower part of the whorl; tends to form a higher number of intermediate spirals; general outline: always wider than in form a (Tembrock, 1961, p. 373).
Revised diagnosis — Fasciolariid gastropod with elongate fusiform shell and moderately convex to almost flat teleoconch whorls. Ornament of relatively coarse collabral ribs, sometimes completely reduced on the later whorls, overrun by a variable number of considerably weaker, sometimes thread-like spiral lirae that continue until the apertural margin. Secondary spiral sculpture present. Fully-grown specimens occasionally with one or two columellar (pseudo-)folds and/or a parietal tooth. Occasionally spiral lirae on the internal apertural shell-wall. Pseudumbilicus inconspicuous.

Protoconch multispiral, conical to dome-shaped, with about 3 to 6¼ moderately to rather strongly convex whorls, initial whorls smooth, later whorls always with spiral sculpture. In many species also a radial sculpture is present, frequently resulting in a distinct reticulate sculpture. Sometimes this radial sculpture is merely represented as a transitional sculpture to the teleoconch on the last half protoconch whorl.
Type species — *Streptochetus (Streptodictyon) elongatus* Tembrock, 1961 (*non* Nyst) = *Streptodictyon sowerbyi* (Nyst, 1836) emend. (see discussion below) (Oligocene, North Sea Basin).
Discussion — As type species of *Streptochetus (Streptodictyon)* Tembrock designated the Rupelian species *S. elongatus* (Nyst). Neither her description nor her illustrations, however, represent this taxon, in this paper indicated as *S. subelongatus* (d'Orbigny). The name *elongatus* was introduced by Nyst (1843, p. 453) to replace an incorrect identification of de Koninck (1838, p. 17, as *Fusus porrectus* Nyst). Holotype (Glibert, 1957, p. 71, re-illustrated in this paper Pl. 4, fig. 13) is de Koninck's specimen from Baesele in Belgium (which therefore is the type locality, not Boom, as stated by Tembrock). It originates from the lower part of the Rupel Formation (Terhagen Member or lower part of Putte Member).

Tembrock (1961) gave two illustrations of *S. elongatus*, indicated as 'Form a' and 'Form b', interpreted as 'possible sexual dimorphism'. Her figure 3 (= 'Form a') is a specimen from the Rupelian of Bad Freienwalde, figure 4 is a specimen of the same age from Hermsdorf, both Germany. Judging from these illustrations there are obvious differences in protoconch features: 'Form a' has a much larger protoconch with an indistinct nucleus and only vaguely indicated reticulation on the later embryonic whorls; in 'Form b' the protoconch is relatively small, its nucleus distinctly protruding and the reticulate sculpture very obvious. A further clear difference is the fact that in 'Form a' the teleoconch collabral ribs are widely spaced, whereas they are much more closely spaced in 'Form b'.

Typical '*Fusus elongatus*' from the lower part of the Boom Clay is not rare, but we have not been able to trace specimens with well-preserved embryonic shells. On the remaining parts of the protoconch, however, we could ascertain the identity of very well-preserved specimens from the Nucula Clay (Kleine Spouwen Member) in Belgium, which is also of Early Rupelian age. The protoconch of typical *F. subelongatus* (see Text-fig. 21) differs both from Tembrock's 'Form a' and 'Form b'; it is slender, with a distinctly deviated nucleus and a granulate microsculpture. On the last whorl distinct spiral lirae and a radial sculpture transitional to that of the teleoconch are present, which do not form a distinct reticulate pattern.

'Form a' is a common constituent in a higher part of the Rupelian clays (Putte Clay Member in Belgium, Woold Clay Member in The Netherlands). In our opinion this form represents a new species, which we describe in this paper as *S. impiger* sp. nov.

Although the specimen illustrated by Tembrock as

'Form b' is only an apical fragment, which by its rather dense radial sculpture resembles *S. cheruscus* (which does not occur in the Rupelian clays), we can reach no other onclusion than that in reality it belongs to the fairly common Rupelian species *S. sowerbyi*, a taxon which has usually not been distinguished from '*S. elongatus*' (see below). This agrees with our observations on further available material and on own collecting activities (M.C. Cadée, 1993): from Bad Freienwalde we have only seen *S. sowerbyi* and *S. impiger*.

As typical characteristics of *Streptodictyon* Tembrock (1961, p. 373) mentioned: '.... Embryonic shell conical, with somewhat deviated nucleus, initial whorls smooth, following whorls with reticulate sculpture; ...' (see translated diagnosis above). These features apply to her 'Form b', *i.e.* to *S. sowerbyi*. Type species of *Streptodictyon* therefore in our opinion is *Streptochetus (Streptodictyon) elongatus* Tembrock, 1961 (*non* Nyst) = *Streptodictyon sowerbyi* (Nyst, 1836) emend.

Streptodictyon differs mainly from *Streptolathyrus* in having a distinct spiral sculpture on the likewise multispiral but considerably larger protoconch. In *Streptolathyrus* the protoconch sculpture exclusively consists of radial elements. We accord both taxa to have generic status.

In the Oligocene *S. soellingensis* and *S. undatus* the protoconch sculpture differs from the usual pattern in *Streptodictyon* by the fact that radial sculpture elements are virtually absent. Initially these rather striking differences lead us to the idea that a separate genus was present here. The fact, however, that in the Chattian B species *S. schnetleri* sp. nov., which we consider to be a younger evolutionary stage of *S. soellingensis*, a reticulate pattern is present again clearly indicates that such a reticulate pattern is not diagnostic at the generic level. Therefore we ultimately decided to expand the genus concept of *Streptodictyon* in such a way that it may include forms with either a reticulate or only a spiral sculpture pattern.

Streptodictyon abruptus (Beyrich, 1856)
Pl. 1, figs 5, 6; Text-fig. 4

v* 1856 *Fusus abruptus* Beyr., Beyrich, p. 286.
? 1861 *Fusus abruptus* Beyr. — Semper, p. 226.
. 1872 *Fusus abruptus* Beyr. — von Koenen, p. 172.
. 1886 *Fusus abruptus* Beyr. — Oehmcke, p. 16.
. 1914 *Fusus abruptus* Beyr. — Gripp, p. 23.
. 1933 *Fusus (Aquilofusus) abruptus* — Gripp, p. 92, pl. 6, fig. 3.
. 1962 *Streptochetus abruptus* (Beyrich) — Hinsch, p. 298, pl. 28, fig. 10.
. 1964 *Streptochetus (Streptodictyon) abruptus* (Beyrich 1856) — Anderson, p. 264, pl. 27, fig. 203.
. 1964 *Streptochetus abruptus* (Beyr.) — Gripp, pp. 121, 362, pl. 21, fig. 4.
. 1968 *Streptochetus abruptus* (Beyrich, 1856) —Rasmussen, p. 149, pl. 13, fig. 7; pl. 16, figs 1, 2, 5, 6.
? 1968 *Streptochetus 'quinquecostatus'* (nov. sp. ?) — Rasmussen, p. 148, pl. 15, figs 1, 4 (= intermediate form between *Streptodictyon sexcostatus* and *S. abruptus*).
v. 1983 *Streptochetus abruptus* (Beyrich, 1856) — Cadée & Janssen, p. 98, pl. 1, figs 8, 9.
v? 1983 *Streptochetus 'quinquecostatus'* Rasmussen, 1968, intermediate form between *Streptochetus (Streptodictyon) sexcostatus* (Beyrich, 1856) and *Streptochetus (Streptodictyon) abruptus* (Beyrich, 1856) — Cadée & Janssen, p. 99, pl. 1, figs 5-7.

Non:

1965 *Streptochetus (Streptodictyon) abruptus* (Beyrich 1856) — Tembrock, p. 434, fig. 4 [= *Streptodictyon gottschei* (Gripp, 1913)].

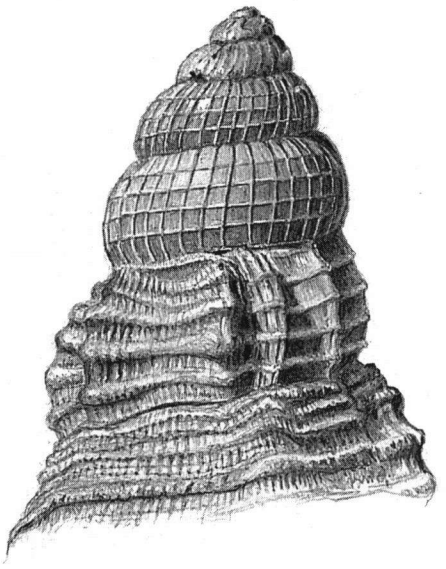


Fig. 4. *Streptodictyon abruptus* (Beyrich, 1856), protoconch and early teleoconch whorls. Nordlohne, Meistermann clay pit (Germany, Niedersachsen), Miocene, Reinbekian (Twistringer Schichten; from upper level). Coll. RGM 393.152 (PGL), x 25.

Type material — This species was based by Beyrich on some juvenile specimens from Reinbek (Germany) and external moulds in sandstones from Bokup (Germany), both samples in the Koch Collection. This collection was later sold to Australia, where it is still present in the Museum of Victoria, Melbourne. Thanks to the co-operation of Dr T.A. Darragh we were able to study the

specimens. As the syntypes of the taxon are still extant the neotype designation by Rasmussen (1968, p. 149, pl. 16, fig. 1) is invalid (ICZN art. 75-C-5; see Cadée & Janssen, 1983, p. 98).

The syntype material consists of a single fragmentary external mould (reg. no. P111994) and one (guttapercha) cast of another specimen (P111996), both from the Bokup sandstone. In the same sample is a specimen in shell preservation (P111995) that has obviously been mislaid, as it has the typical preservation of Reinbek specimens. Five additional syntypes are present from Reinbek (reg. nos P111997-P112001). Among these there is one moderately well-preserved specimen (no. P112001) still possessing the greater part of the embryonic whorls. This shell is herewith designated lectotype (Pl. 1, fig. 5), all other specimens being paralectotypes.

A specimen (guttapercha cast from a boulder found south of Schwerin lake, Germany), illustrated by Tembrock (1965, fig. 4) and erroneously assumed to be a syntype from the Koch Collection, does not belong to this species. The boulder yielded also specimens of *Haustator goettentrupensis* (Cossmann, 1899), indicating that the age is Chattian/Vierlandian; therefore it cannot be Bokuper Sandstein, which is Reinbekian. The specimen did not belong in the Koch Collection either, and cannot be a syntype of *S. abruptus*. It is listed in this paper as *S. gottschei*.

Locus typicus — Reinbek (Schleswig-Holstein, Germany). For detailed information on this locality see Anderson (1964, p. 41).

Stratum typicum — 'Reinbecker Gestein' (Miocene, Reinbekian, Reinbek Member; see Hinsch, 1958, p. 48; Hinsch, 1986, p. 34).

Essential details of original description — 'The shell starts with a high conical embryonic part of four whorls, of which the lower one (...) is covered with a fine hair-like longitudinal striation. Rather distant longitudinal ribs develop suddenly on the first middle whorl and disappear already on the next whorl. The lower middle whorls, which form the larger part of the spire, and the body whorl are exclusively covered with numerous close-set transverse ribbons' (translated from German by the present authors).

Revised diagnosis — *Streptodictyon* with a reticulate protoconch sculpture. Teleoconch with heavy collabral ribs restricted to the initial 1 to 3 whorls of the teleoconch, gradually, but rather rapidly effacing in apertural direction. Spiral sculpture of five or six primary spirals. Secondary spirals reaching the strength of the primary ones, resulting in a dense and regular striation with the spiral intervals about as wide as the spirals themselves. One or two columellar folds and a long parietal tooth usually present.

Description — Shell fusiform, height to c. 40 mm, about three times higher than wide when fully grown. Apical angle varying from about 40° in juvenile specimens to about 30° in adult shells.

Protoconch conical, consisting of 4¾ to 5¼ moderately convex whorls. Diameter of nucleus about 0.10 mm. The initial whorls are smooth, reticulation is present on the last 2 to 2½ whorls, anticipated by a few radial lines, which are distinctly opisthocline, changing to orthocline as soon as the radial elements develop. The reticulate sculpture is comparatively coarse, the number of spiral elements varying from 4 to 5 on the centre of the protoconch body whorl. The radial elements slowly increase in strength towards the boundary with the teleoconch, frequently clustering in groups of two. The boundary with the teleoconch is always sharp and particularly distinct by the sudden broadening of the spiral elements.

Teleoconch with up to about eight whorls, which are convex where collabral sculpture is present, and almost completely flat on the later whorls, where these are lacking. Suture distinct where the whorls are convex, but very superficial and slightly incised as soon as the whorls become flat. Height of the body whorl about half the entire shell height. Base and siphonal canal well defined. Pseudumbilicus absent.

Teleoconch sculpture starting on the first whorl with five or six thread-like spirals, which slightly weaken towards the adapical suture. The middle spirals are continuations of the protoconch spirals. Secondary sculpture developing in two generations, the first of these sometimes already on the first teleoconch whorl, especially so in the upper part of the whorls, but later also further down. They rather quickly reach the strength of the primary spirals and the younger teleoconch whorls are covered with a dense and regular spiral striation, separated by intervals that have about the same width as the spirals themselves. If the second generation of secondary spirals has not (yet) reached the strength of the first one, the spirals are alternately stronger and weaker. Heavy collabral ribs, six to eight on the first whorl, narrower than their interspaces, are restricted to the initial 1 to 3 whorls of the teleoconch. They fade gradually, but rather quickly in apertural direction.

Growth lines are well visible, frequently lamellose in the spiral intervals. Their shape is orthocline, slightly flexuous.

Aperture ovoid, suddenly narrowed where the siphonal canal begins. Columella with distinct traces of dissolution of calcareous material, removing the sculpture of the base completely and with a sharp boundary. Just above the transition into the canal lies a well-defined columellar fold, occasionally accompanied at its abapical side by a columellar tooth. Close to the point where the apertural margin touches the preceding whorl a sometimes very long parietal tooth is present. On the inner shell wall

occasionally spiral lirae are seen.

Material studied — Juvenile specimens are only listed here when coming from levels in which all adult specimens belong to *S. abruptus*. Juvenile specimens from levels in which both species occur cannot be confidently identified. These are listed under *S. sexcostatus*.

Miocene, Reinbekian (Breda Formation); The Netherlands (Limburg province) — **Broekhuizenvorst**, borehole 52E/114, depth 153-154 m, 1 def. specimen (illustrated in Cadée & Janssen, 1983, pl. 1, fig. 9), 1 def. specimen (RGD).

Miocene, Reinbekian (Twistringer Schichten; from upper level, or level not specified); Germany (Niedersachsen) — **Nordlohne**, Meistermann clay pit: 91 specimens, 1 specimen, Pl. 1, fig. 6, RGM 393.150, 393.359 (AJL); 52 specimens, 64 juv. specimens, RGM 393.151 (AJL); 49 specimens: 1 juv. specimen, Text-fig. 4, RGM 393.152, 393.379 (PGL); (31 specimens, MCL); **Nordlohne**, Meistermann clay pit, borehole VII, depth 9-10 m below surface: 1 specimen, RGM 393.153 (JVV); depth 11-12 m below surface: 1 specimen, 8 juv. specimens, RGM 393.154 (JVV); depth 12-13 m below surface: 3 specimens, RGM 393.155 (JVV); depth 13-14 m below surface: 3 specimens, RGM 393.156 (JVV); **Twistringen**, O. Sunder clay pit: 10 specimens, RGM 115.925 (MBL); 1 specimen, RGM 226.231 (MCL), illustrated in Cadée & Janssen (1983, pl. 1, fig. 8); 4 specimens, RGM 116.063 (H. Krock); 2 specimens, RGM 115.856 (AJL); 15 specimens, RGM 116.825 (AJL); 108 specimens, 21 juv. specimens, RGM 393.157-158 (AJL, 1975); 4 specimens, RGM 116.956 (FJR); 23 specimens, RGM 116.847 (DMM); 34 specimens, MCL.

Miocene, Reinbekian (Bokup Sand Member): Germany (Mecklenburg-Vorpommern) — **Bokup** (at Bokup there is no outcropping Reinbekian sediment, so this material presumably originates from boreholes or from reworked concretions in Pleistocene deposits): 1 specimen, external mould, 1 specimen, guttapercha cast of another specimen, 1 specimen in shell preservation, paralectotypes; NMV P111994, P111996, P111995 (Koch); **Malliß**, boreholes on the Wanzer Berg: 16 juv./def. specimens, Schwerin, RGM 393.159 (leg. O. Gehl, 1966, don. Geologisches Landesamt Mecklenburg-Vorpommern).

Miocene, Reinbekian (Reinbek Member): Germany (Niedersachsen) — **Reinbek**, 4 specimens, lectotype and paralectotypes, NMV P111997-P112001 (Koch).

Discussion — Cadée & Janssen (1983) demonstrated that *S. abruptus* and *S. sexcostatus* are members of the same evolutionary lineage, *S. abruptus* representing the younger species. Recent, still unpublished, studies of a temporary excavation and of boreholes at Nordlohne and Twistringen (both Germany, Niedersachsen) have validated their conclusions. It was established that the vertical zone of transition is restricted to one metre at the most. Both at Nordlohne and Twistringen this transitional zone was found to occur about two metres below a strikingly dark level in the otherwise greyish clay (at about 15 m below surface at Nordlohne). These observations contradict the statement in Cadée & Janssen (1983), who indicated the highest occurrence of *S. sexcostatus* at Twistringen at the level 16.90 m below surface in the section measured by Cadée & Janssen (1968, p. 83ff). In fact the dark horizon is situated at 10.40 to 10.65 m below surface, and the transitional zone between the two species should therefore be situated at about 12.50 m below surface in that clay-pit. These results agree with observations by Mr J. van der Voort (Venne, Germany).

In the transitional zone specimens of an intermediate form are fairly common. This form was indicated as *Streptochetus 'quinquecostatus'* by Rasmussen (1968). It is characterised by a distinct reduction in strength of the radial sculpture (Pl. 4, fig. 1), in such a way that the shell has a pentagonal outline when seen in apical view (Cadée & Janssen, 1983, pl. 1, figs 5a, 6a and 7a). It is, however, impossible to say to which species this *S. 'quinquecostatus'* should be assigned, as it is indeed intermediate.

Menzel *et al.* (1984, p. 147) analysed a series of samples from the Twistringen clay-pit. These authors apparently identified some juvenile *S. sexcostatus* specimens as *S. abruptus* (their samples from 12.15 to 14.75 m below surface). Indeed, in juvenile specimens with only one or two teleoconch whorls distinguishing these two species is impossible.

Gripp (1933, pl. 6, fig. 3; 1964, pl. 21, fig. 4) illustrated a strikingly thick-set form of this species from the Reinbekian of Langenfelde (Germany). The illustrated specimen has an apical angle of some 40°. During our study we never encountered such specimens.

Several authors (Gripp, 1914; Beets, 1950; Tembrock, 1961, 1965) considered the Late Oligocene/Early Miocene species *S. gottschei* (Gripp, 1914) to be a variety or subspecies of the Middle Miocene *S. abruptus*. In the present paper, however, *S. gottschei* is considered to be a distinct species (see below).

Stratigraphical distribution — This species is exclusively known from the Reinbekian: 'Reinbecker Gestein' and upper part of 'Twistringer Schichten' in Germany, from the 'Bokuper Sandstein' in Germany, the Hodde Formation in southern Jylland (Denmark) and from the Breda Formation (Broekhuizenvorst borehole) in The Netherlands. In older Reinbekian sediments (*e.g.* Bislicher and Dingdener Schichten, Stemerdink Bed of the Aalten Member) an ancestral form is found, *viz. Streptodictyon sexcostatus*.

The species is not recorded from outside the North Sea Basin.

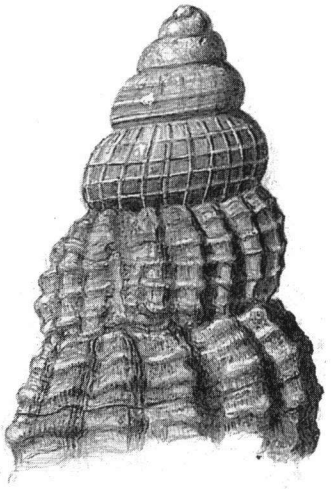


Fig. 5. *Streptodictyon cheruscus* (Philippi, 1843), protoconch and early teleoconch whorls. Rumeln, dump of mine shaft Diergardt VI (Germany, Nordrhein-Westfalen), Oligocene, Chattian A (Grafenberger Sande, presumably 'Schicht II' Görges, 1941). Coll. RGM 393.170 (AJL, 1976), x 25.

Streptodictyon cheruscus (Philippi, 1843)
Pl. 1, figs 7-14; Text-figs 5-7

? 1835 *Fusus intortus* Lamarck — von Münster, p. 450 (*non* Lamarck).
v.* 1843 *Fusus cheruscus* n. sp., Philippi, p. 59, pl. 4, fig. 21.
v. 1843 *Fusus Schwarzenbergii* n. sp., Philippi, p. 59, pl. 4, fig. 15, 15a.
. 1856 *Fusus elongatus* Nyst — Beyrich, p. 283, pl. 24, figs 3a, b, 4a-c (*non* Nyst) [*partim*, *non* fig. 5, 5a = *Streptodictyon sowerbyi*; *non* fig. 6 = *S. subelongatus* (d'Orbigny); not the specimens from 'Crefeld' = *S. soellingensis*].
. 1863 *Fusus elongatus* Nyst — Speyer, p. 193, pl. 34, figs 7, 7a, 8a-c (*non* Nyst).
? 1864 *Fusus elongatus* Nyst — Speyer, p. 265 (*non* Nyst) (? *partim*, includes *Streptodictyon sowerbyi* and, most probably, also *S. soellingensis*).
? 1866 *Fusus elongatus* Nyst — Speyer, p. 18 (*non* Nyst).
? 1867 *Fusus elongatus* Nyst — von Koenen, p. 79 (*partim*, *non* Nyst, ? only the Late Oligocene specimens).
? 1871 *Fusus elongatus* Nyst — Wiechmann, p. 52 (*non* Nyst).
? 1872 *Fusus elongatus* Nyst — Koch & Wiechmann, p. 24 (*non* Nyst) (*partim*, ? only the specimens from the 'Sternberger Gestein').
? 1891 *Fusus elongatus*, Nyst — Lienenklaus, p. 69 (*non* Nyst).
? 1907 *Fusus elongatus* Nyst — Ravn, p. 324, pl. 6, fig. 2 (*partim*, *non* Nyst, ? only the Late Oligocene specimens; *non* pl. 6, fig. 1 = ? *S. impiger*).
. 1913 *Fusus elongatus* Nyst — Harder, p. 80, pl. 6, figs 20, 21 (*partim*, *non* Nyst, *non* fig. 19a, b = ? *S. schnetleri*).
? 1913 *Fusus* sp. — Harder, p. 81, pl. 6, fig. 28.
. 1925 *Streptochetus sexcostatus* Beyr. — Kautsky, p. 116, pl. 8, fig. 21 (*partim*, *non* Beyrich, *non* fig. 20 = *Streptodictyon sexcostatus*).
. 1941 *Fusus elongatus* Nyst — Görges, p. 127 (*partim*, *non* Nyst, includes also *S. soellingensis*, according to R. Janssen, 1979b, p. 298).
v. 1950 *Streptochetus (Streptochetus) elongatus* (Nyst) — Beets, p. 21, pl. 1, fig. 46 [*partim*, *non* Nyst, *non* pl. 1, fig. 37 = ? (not seen), pl. 2, figs 21-23 = *Streptodictyon sexcostatus*, pl. 2, fig. 24 = ? (not seen)].
v. 1950 *Streptochetus (Streptochetus)* spec. nov. ? — Beets, p. 23, pl. 3, figs 1, 2.
v. 1950 *Streptochetus (Streptochetus)* spec. — Beets, p. 23, pl. 3, figs 3, 4.
1952 *Streptochetus elongatus* (Nyst, 1843) — Görges, p. 91 (*non* Nyst).
v. 1952 *Streptochetus sexcostatus* Beyrich, sp. 1856 — Glibert, p. 110, pl. 8, fig. 4a, b (*partim*, *non* Beyrich; Antwerp Sands only; see also below under *S. cheruscus* forma *fasciolaroides*).
. 1958 *Fusus* cf. *sexcostatus* Beyrich — Sorgenfrei, p. 233, pl. 50, fig. 158 (? *partim*, *non* Beyrich; it seems at least possible that *Streptodictyon sexcostatus* is also present in Sorgenfrei's material).
. 1961 *Streptochetus retrorsicosta* (Sandberger) — Tembrock, p. 370, pl. 1, fig. 6 (*non* Sandberger).
. 1961 *Streptochetus sexcostatus* (Beyrich) Form b — Tembrock, p. 372, pl. 1, fig. 8 (*partim*, *non* Beyrich, *non* pl. 2, fig. 6, 6a = *S. cheruscus* f. *fasciolaroides*).
? 1963 *Streptochetus* (s.s.) *elongatus* Nyst, sp. 1843. — Glibert, p. 147 (*partim*, only the Chattian specimens).
. 1965 *Streptochetus (Streptodictyon) cheruscus cheruscus* (Philippi 1843) Form a — Tembrock, p. 432, pl. 34, fig. 7.
? 1965 *Streptochetus (Streptodictyon) cheruscus cheruscus* (Philippi 1843) Form b — Tembrock, p. 432, pl. 34, fig. 8a, b (the illustrated specimen is, in fact, too immature for a sound identification).
. 1978 *Streptochetus (Streptodictyon) cheruscus cheruscus* (Philippi 1843) — R. Janssen, p. 111.
. 1979b *Streptochetus (Streptodictyon) cheruscus cheruscus* (Philippi 1843) — R. Janssen, p. 297, pl. 16, fig. 25.
? 1985 *Streptochetus (Streptodictyon) cheruscus cheruscus* (Philippi 1843) — Piehl, p. 260, fig. 6 (left hand figure).

Non:

1863 *Fusus Schwarzenbergi* Sp., Speyer, p. 195, pl. 34, fig. 6a-c (*non F. Schwarzenbergii* Philippi). It is not clear to which taxon Speyer's species should be

assigned. It is remarkably absent in subsequent literature.

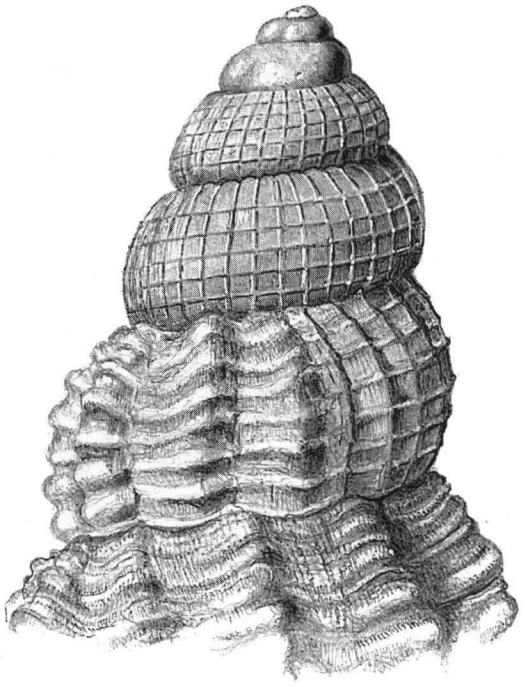


Fig. 6. *Streptodictyon cheruscus* (Philippi, 1843), protoconch and early teleoconch whorls. Brejning (Denmark, Jylland), Oligocene, Chattian B (Vejle Fjord Formation, Brejning Clay Member). Coll. RGM 393.175 (MNO), x 25.

Fig. 7. *Streptodictyon cheruscus* (Philippi, 1843), protoconch and early teleoconch whorls. Beringen, borehole 15 (58B8), depth 154-159 m (The Netherlands, Limburg province), Miocene, Hemmoorian (Breda Formation). Coll. RGM 393.181 (ROD, 1911), x 25.

Type material — Two specimens were available to Philippi, one collected by Leunis and one by Römer. Only the former survives, which fortunately is the one described and illustrated in Philippi's paper. Tembrock (1965, p. 432) considered this specimen to be the holotype ('kraft Monotypie' *sic* !). We designate this specimen lectotype, which in our opinion is the correct procedure. It is kept in PHB MB II. 157.21 Ga 123.

Locus typicus — Freden, near Alfeld/Leine, Germany (Niedersachsen).

Stratum typicum — Kasseler Meeressand (Late Oligocene, Chattian A or B; see R. Janssen, 1979a, p. 9). The morphology of the type specimen suggests a Chattian B age (see discussion below).

Original diagnosis — 'Shell elongated fusiform, with (c. 22) raised, close-set, alternately stronger and weaker transverse striae, and with fine raised growth lines; the whorls moderately convex with about 10 undulose ribs; the columella concave, the tail curved' (translated from German by the present authors). Note: with 'the tail' (German: der Schwanz) Philippi obviously meant the siphonal canal.

Revised diagnosis — *Streptodictyon* with a reticulate protoconch sculpture. Teleoconch with moderately heavy collabral ribs, either covering the entire shell up to the apertural margin or gradually fading during growth. On the first teleoconch whorl the radial elements are close-set, with the interspaces somewhat narrower than the ribs themselves; on later whorls the interspaces gradually become wider. Spiral sculpture of six or seven (frequently one lying in the lower suture) primary spirals. Secondary spirals in two generations, not reaching the strength of the primary ones, at first between the uppermost spirals.

Description — Shell fusiform, height to c. 40 mm; rather slender, 2.4-2.5 times higher than wide, juvenile specimens are relatively less slender (2.0-2.3 times higher than wide), apical angle of adult shells about 35°, slightly wider (about 40°) in juveniles.

The protoconch is multispiral, conical with a cyrtoconoid profile, comprising 4¾-5¼ convex whorls and about 1.45 (1.35-1.51) times higher than wide, its height varying from 1.8 to 2.2 mm. The nucleus has a diameter of 0.10 mm. The initial whorls are smooth, from the third whorl onwards a reticulate sculpture develops. This sculpture consists of numerous radial elements, starting strongly opisthocline but soon becoming more opisthocyrt, which are intersected by four to six spiral lines of about equal strength, the lowest one of which is the strongest. Together these elements form rectangles which on average are as wide as high. Close to the transition into the teleoconch the radial elements increase in strength, reaching ultimately the strength of the first teleoconch radial elements. The boundary with the teleoconch is

usually gradual, but occasionally sharp. When gradual it may be recognised by the radial elements suddenly becoming wider, but sometimes the transition is completely gradual indeed. In such cases it is impossible to give exact measurements for the protoconch.

The shell has moderately convex teleoconch whorls, the younger ones with a slight subsutural depression, which frequently is slightly angular abapically. The body whorl occupies two thirds of the entire shell height. The periphery is rounded, with a gradual transition into the base. The siphonal canal is slightly curved to the left (apertural view).

The sculpture of the teleoconch is composed of usually orthocline, sometimes slightly prosocline (lectotype !), fairly heavy collabral ribs, covering the entire shell until the apertural margin, or gradually effacing towards the aperture. On the first teleoconch whorl the number of radial elements is about 10-12, with the interspaces slightly narrower than the ribs; on later whorls the interspaces gradually become wider, but the number of radial ribs per whorl remains more or less the same.

Spiral sculpture of six or seven primary spirals (frequently one lying in the lower suture). The two upper spirals are distinctly weaker than the lower ones. Secondary spirals develop in two generations, at first between the uppermost spirals and there soon reaching equal strength, on lower parts of the whorls they remain weaker than the primary spirals. The secondary sculpture usually starts on the second whorl, but frequently already on the first one, and in exceptional cases even immediately behind the boundary with the protoconch. The presence of the many secondary spirals makes the sculpture relatively finer on the later whorls.

The growth lines are well developed, close set, and granulate the spiral sculpture. Frequently their appearance is quite lamellose in between the sculpture elements. They run, roughly parallel to the collabral sculpture, slightly opisthocyrt.

The inner shell wall bears spiral lirae at certain growth intervals. These lirae are especially developed in juvenile specimens. In fully-grown specimens a parietal tooth may be seen and the columella bears two very oblique, but weak spiral folds.

Stratigraphical distribution — Chattian to Hemmoorian (Oxlundian).

Material studied — ?? Oligocene, Rupelian (Rupel Formation, Putte Member): Belgium (Antwerpen province) — **Ramsel**: 2 specimens, IRScNB (Raeymakers), but not mentioned in Glibert, 1957; this sample contains also 52 specimens of *S. impiger* and 1 specimen of *Fusinus elatior* (Beyrich, 1856)]. The locality of these two specimens is here considered to be incorrect (glauconitic sandy sediment is present in both shells).

Oligocene, Chattian (Söllingen Sand Formation, Asterigerina Horizon): Germany (Niedersachsen) — **Söllingen**, railroad cut between Söllingen and Jerxheim: 1 specimen, 14 more or less juv. and/or def. specimens, RGM 393.160-161 (AJL, May 1982); 5 juv. specimens, MCL (PGL, May 1982); 3 specimens, 2 juv. specimens, 1 fragment, AJB.

Oligocene, Chattian A (Kasseler Meeressand): Germany (Hessen) — **Ahnetal** near Kassel, Brandkopf outcrop, 'Schill 2/3': 69 juv. specimens, RGM 393.162 (MBL, June 1973); 'Schill 3': 6 juv. specimens, RGM 393.163 (MBL, June 1973); **Glimmerode**, former lignite pit Höllkopf, 'Schill 1': 108 juv. specimens, RGM 393.164 (MBL, June 1973); 13 juv. specimens, MCL, June 1973; 'Schill 1, Schicht 4': 130 juv. specimens, 1 juv. specimen illustrated in R. Janssen, 1979, pl. 16, fig. 25, SMF 250778/130, 250706/1 (R. Janssen, 1972/1973); 'Schill 2': 122 juv. specimens, RGM 393.165 (MBL, June 1973); 4 juv. specimens, MCL, June 1973; 60 juv. specimens, SMF 250779/60 (R. Janssen, 1972/1973); exact level unknown: 1 specimen, Pl. 1, fig. 7, 7 specimens, 151 juv. specimens, KGM.

Oligocene, Chattian A (Doberg Formation, c. level 7 Hubach, 1957); Germany (Nordrhein-Westfalen) — **Bünde**, Doberg, outcrop along motorway: 27 juv. specimens, RGM 393.166 (MBL, October 1975); **Bünde**, Doberg, temporary excavation R. Janssen, 1975: ? 1 juv./def. specimen, RGM 393.167 (AJL, October 1975).

Oligocene, Chattian A (Grafenberger Sande): Germany (Nordrhein-Westfalen) — **Erkrath** near Düsseldorf: 1 external mould in iron sandstone with 3 casts, IRScNB (Piedboeuf), not mentioned in Glibert, 1963; 1 external mould in iron sandstone with 1 artificial cast, IRScNB (Piedboeuf), not mentioned in Glibert, 1963; **Krefeld**: 1 specimen, DLV; **Neukirchen**: 7 juv. specimens, MCL (FHK); **Rumeln**, dump of mine shaft Diergardt VI, presumably 'Schicht I' Görges, 1941: 103 mainly juv. specimens, RGM 393.168 (AJL, 1976); 103 specimens, MCL; presumably 'Schicht II' Görges, 1941: 1 specimen, Pl. 1, fig. 8, 59 specimens, 1 juv. specimen, Text-fig. 5, 319 juv. specimens, RGM 393.169-172 (AJL, 1976); 39 mainly juv. specimens, HBH.

Oligocene, Chattian A/B (Kasseler Meeressand): Germany (Hessen) — **Cassel**: 2 def. specimens, 1 juv. specimen, IRScNB (de Malgrinen), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; **Freden**: 1 specimen (lectotype, Pl. 1, fig. 9), PHB Ga 123 (Leunis); illustrated in Philippi (1843, pl. 4, fig. 21); 6 specimens (lectotype, Pl. 1, fig. 10, and paralectotypes of *Fusus schwarzenbergii* Philippi, 1843), PHB Ga 124 (Leunis); 3 specimens, IRScNB (Nyst), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; 2 specimens, IRScNB (Bosquet), mentioned in

Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*.

Oligocene, Chattian A/B (reworked boulders of 'Sternberger Gestein': Germany (Mecklenburg-Vorpommern) — **Pinnow**: (67 specimens, RGM 393.173 (R. Braasch); **Sternberg**: 2 specimens, IRScNB (Bosquet), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *Pisanella* sp.; 1 and 3 juv. specimens, IRScNB (Wiechmann/Nyst), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*.

Oligocene, Chattian A, later part (Grafenberg Member): Germany (Nordrhein-Westfalen) — **Krefeld**: 3 specimens, 26 juv. specimens, IRScNB (Nauck/Bosquet), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; **Krefeld**, Kempener Feld, borehole, depth c. 36 m below surface: 42 juv. specimens, RGM 393.174 (FHK, 1973); 13 juv. specimens, MCL (FHK, 1973).

Oligocene, Chattian B (Vejle Fjord Formation, Brejning Clay Member), Denmark (Jylland) — **Brejning**: 1 juv. specimen, Text-fig. 6, RGM 393.175 (MNO); 1 specimen, Pl. 1, fig. 11, RGM 393.176 (MNO); 2 specimens, 605 juv. specimens, MNO; 1 specimen, KSL, reg. 1986.199 (MNO); 2 specimens, 16 juv. specimens, KSL, reg. 1983.385 and 1985.279, respectively (MNO); 4 juv. specimens, MCL (MNO); 27 juv. specimens, KSL, reg. 1983.241; **Fakkegrav**: 4 specimens, 159 juv. specimens, MNO; 5 juv. specimens, 1 fragment, KSL, reg. 1985.727 (MNO/KSL); 4 juv. specimens, MCL (MNO); 3 juv. specimens, RGM 393.177 (AJL); 1 specimen, AJB; **Mogenstrup**: 28, 30, 24 and 3 juv. specimens, KSL, reg. 1987.561, 1987.325, 1989.141 and 1988.305, respectively). These samples were mentioned in Schnetler & Beyer (1990); **Nørre Vissing**: 5 specimens, 12 juv. specimens, KSL, reg. 1984.636; 1 juv. specimen, KSL, reg. 1979.180; 25 juv. specimens, MNO; 5 juv. specimens, 1 juv. specimen, KSL, unnumbered and reg. 1979.180, respectively (leg. S.B. Anderson); 1 def. specimen, AJB (all these samples were mentioned in Schnetler & Beyer, 1987); 1 specimen, MCL; **Skanderborg**: 93 juv. specimens, KSL, reg. 1979.85a (leg. S.B. Anderson, 1976).

Oligocene, Chattian B (Grafenberg Member): Germany (Nordrhein-Westfalen) — **Erkelenz**, K3 borehole for mine shaft Sophia Jacoba 8, depth 292-293 m below surface: 4 juv. specimens, RGM 393.178 (GLK); depth 288-289 m below surface, 98 juv. specimens, RGM 393.179 (GLK); **Krefeld-Gellep**, construction pit near harbour: 43 juv. specimens, RGM 393.180 (FHK, 1973); **Rheinberg**, shaft digging, 62 specimens, MCL, May 1989.

Oligocene, Chattian s. lat. (Veldhoven Formation, Voort Sand Member): The Netherlands (Limburg province) — **Beesel**, borehole 12 (58E61), depth 230-250 m below surface: 3 specimens, RGD (ROD, 1910), illustrated in Beets, 1950, pl. 1, fig. 46, pl. 2, figs 21 and 22-23 *sub nomine Streptochetus elongatus* (Nyst); **Eygelshoven** (shaft II of Laura colliery), depth 115-125 m: 1 specimen, Pl. 1, fig. 12, IRScNB TCCI 6044; 1 and 16 juv. specimens, IRScNB, mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 5 specimens of *Streptodictyon soellingensis* and 3 specimens of *Streptodictyon* sp.; **Kessel**, borehole 10 (58E49), depth 228-306 m below surface: 2 juv. specimens, RGD (ROD, 1909); depth 220-228 m below surface: 2 juv. specimens, RGD (ROD, 1909); depth 190-200 m below surface: 1 def. specimen, RGD (ROD, 1909); depth 180-190 m: 1 def. specimen RGD (ROD, 1909); depth 170-180 m: 2 juv. specimens, RGD (ROD, 1909); **Maasbree**, borehole 13 (58B4), depth 195-225 m: 1 specimen, RGD (ROD, 1910), illustrated in Beets, 1950, pl. 3, figs 1, 2 *sub nomine Streptochetus (Streptochetus)* spec. nov.?; depth 194 m (1 specimen, RGD (ROD, 1910), illustrated in Beets, 1950, pl. 3, figs 3, 4 *sub nomine Streptochetus* spec.

Miocene, Hemmoorian (Bolderberg Formation, Houthaelen Sand Member): Belgium (Limburg province) — **Houthalen**, shaft of colliery II, depth 80.50-81.52 m: 1 specimen, IRScNB (leg. unknown), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 1 specimen of *Chicoreus aquitanicus* (de Grateloup, 1833), which in Belgium was previously known only from Bolderberg; **Meeuwen**, borehole Meeuwen 2, depth 127.70-131.15 m: 2 specimens, IRScNB (Gulinck); this sample contains also 1 def. specimen of *Murex inornatus* Beyrich, 1854.

Miocene, Hemmoorian (Breda Formation): The Netherlands (Limburg province) — **America**, borehole 11 (52D18), depth 230-235 m below surface: 1 juv. specimen, probably downhole contamination in Voort Sand Member; depth 210-220 m below surface: 1 juv. specimen, probably downhole contamination in Voort Sand Member; depth 150-200 m below surface: 2 juv. specimens, all RGD (ROD, 1909); **Baarlo**, borehole 9 (58E/15), depth not specified: 5 specimens, RGD (ROD, 1908); **Beringen**, borehole 15 (58B8), depth ? 159-170 m: 10 specimens, RGD (ROD, 1911); depth 154-159 m: 1 specimen RGD (ROD, 1911); 1 juv. specimen, Text-fig. 7, 2 specimens, 57 specimens, RGM 393.181-183 (ROD, 1911); 4 specimens, SMF 253800/4 (Görges/Tesch); depth 144-154 m: 79 specimens, RGM 393.184 (ROD, 1911); depth 134-144 m: 4 specimens, RGM 228.901; 1 specimen, Pl. 1, fig. 13, RGM 393.185 (ROD, 1911); 4 specimens, RGD (ROD, 1911); without depth indication: 4 specimens, SMF 253801/4 (Görges/Neuenhaus); **Griendtsveen**, borehole 7 (52D/11) (= Helenaveen III), depth unknown: 1 specimen, RGD (ROD, 1906-1908); **Maasbree**, borehole 13 (58B4),

depth presumably 102-160 m below surface: 58 specimens, RGD (ROD, 1910).

Miocene, Hemmoorian (probably from reworked sediments in Quaternary deposits): Germany (Niedersachsen) — **Hemmoor**: 1 specimen, Pl. 1, fig. 14, IRScNB TCCI 6045 (Geol. Staatsinst. Hamburg/Chavan), mentioned in Glibert, 1963, p. 148 *sub nomine Streptochetus* (s.s.) *sexcostatus*; 1 specimen, RGD.

Miocene, ? Hemmoorian (reworked in fluvioglacial deposit): Germany (Niedersachsen) — **Werder**, municipality of Thedinghausen, Krinke gravel pit: 5 def. specimens, JVV, 1992.

Miocene, Hemmoorian (reworked in fluvio-glacial deposits, from Arnum Formation): Denmark (Jylland) — **Gram**, gravel pit at Enderupskov: 56 specimens, 10 juv. specimens, RGM 393.186 (leg. N. Vedsted-Hansen); 2 specimens, 9 juv. specimens, RGM 393.187 (AJL); 1 juv. specimen, MCL; 9 juv. specimens, FWG.

Discussion — The above description is based on specimens of Chattian B age (Erkelenz, Lower Rhine area). The lectotype fits this description completely, which is why we assume it to be of Chattian B age as well.

This species ranges from Chattian to Hemmoorian. Several populations differ markedly from the typical form described above, although the differences in our opinion are not constant enough to be interpreted as specific. We treat these forms here as unnamed varieties, briefly describing them below.

Two specimens (IRScNB collection) are labelled to originate from the Rupelian Boom Clay (Ramsel clay pit, Belgium). They strongly resemble the form described from the Edegem Sands. Both specimens contain remnants of a glauconitic sandy sediment, and therefore we consider the indicated locality as incorrect.

Populations of Chattian A age (*e.g.* those from Söllingen, or from Rumeln and various other Lower Rhine area localities) differ from the typical form in several respects. The most important of these are the smaller dimensions of the protoconch (4-4½ whorls, height = 1.50, width = 1.15 mm) and the higher number (15) of radial sculpture elements on the first teleoconch whorl, reducing to about 10 on later whorls. On the first teleoconch whorl therefore the ribs are characteristically more close-set. In Denmark this form is exclusively known from Nørre Vissing, all other localities yielded specimens of the Chattian B type (very fine and fully-grown specimens).

From the early Chattian of Söllingen (Germany) we have predominantly juvenile specimens before us. In this material *S. cheruscus* is easily recognised by its dense radial sculpture on the initial teleoconch whorls. In other specimens, however, the radial ribs are spaced, and there also is a small difference in the protoconch sculpture (transversely elongated rectangles, instead of more squarish ones). We identify these latter specimens as *S. sowerbyi*. Together with specimens from the Voort Formation in Belgium they represent the youngest known occurrences of this taxon.

In a sample from the so-called Sternberger Gestein (reworked from Chattian deposits) typical Chattian A types are abundant, but also many specimens occur in which the initial teleoconch whorls demonstrate a spaced radial sculpture, agreeing with the Chattian B populations.

The populations from the Danish Vierlandian (Klintinghoved) and the Belgian Edegem Sands (Hemmoorian, Behrendorfian) are described below as *S. cheruscus* forma *fasciolaroides*.

The specimens from the Middle Miocene (Behrendorfian/Oxlundian) of the Dutch Peel area differ completely from the Edegem shells, not only in having very convex protoconch whorls, but especially so by the development of the radial sculpture on the later whorls. The ribs are clearly less oblique and usually tend to efface towards the aperture. These specimens are the youngest ones that we consider to belong to this species.

Fusus schwarzenbergii Philippi is generally considered to be synonymous with *F. cheruscus* (*e.g.* Beyrich, 1856; Tembrock, 1965; R. Janssen, 1979b). More than 20 specimens of this species were available to Philippi, who illustrated a shell with a height of about 8.5 mm. Six syntypes are housed in the Berlin collection, amongst which not a single matches the height indicated. One of the shells is glued to a black cardboard (Pl. 1, fig. 10). This specimen is herewith designated lectotype of *F. schwarzenbergii*. It is kept, together with 5 paralectotypes, in PHB Ga 124. *F. schwarzenbergii* in our opinion is a synonym of *Streptodictyon cheruscus*, and therefore we accept *S. cheruscus*, introduced prior to '*F. Schwarzenbergii*' by Philippi (1843, p. 59) as the valid name (ICZN art. 69B-11).

Streptodictyon cheruscus (Philippi, 1843)
forma **fasciolaroides** (Nyst, 1861)
Pl. 2, figs 1-7; Text-fig. 8

v. 1861a *Fusus fasciolaroïdes*, Nob., Nyst, pp. [8], [16] (name only).

v* 1861b *Fusus fasciolaroïdes*, Nyst, p. [8] (frequently cited by later authors as '*fasciolaroides*', but the name is given as '*fasciolaroïdes*' in Nyst's text, the heading of the species on p. [8] is printed in small capitals, which is the reason that the vowel-mutation is missing there).

v. 1861b *Fusus scalaroïdes* — Nyst, p. [9] (*lapsus calami*!).

. 1901 *F. sexcostatus* Beyr. — Cossmann, p. 31 (*partim*, specimens from Edegem).

. 1940 *Streptochetus sexcostatus* Beyrich — Sorgenfrei, pp. 46, 108 (*non* Beyrich).

v. 1952 *Streptochetus sexcostatus* Beyrich, sp. 1856 — Glibert, p. 110, pl. 8, fig. 4a, b (*partim, non* Beyrich; Edegem Sands only).

. 1961 *Streptochetus (Streptodictyon) sexcostatus* (Beyrich), Form b — Tembrock, p. 372, pl. 2, figs 6, 6a (*partim, non* Beyrich, *non* pl. 1, fig. 8 = *S. cheruscus* s. str.).

1961 *Streptochetus fasciolarius* (Nyst) (1861) (*sic*!). — Tembrock, p. 373.

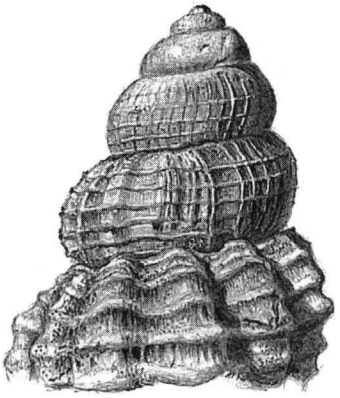


Fig. 8. *Streptodictyon cheruscus* (Philippi, 1843) forma *fasciolaroides* (Nyst, 1861), protoconch and early teleoconch whorls. Antwerpen, construction pit for E3 Kennedy-tunnel (Belgium, Antwerpen province), Miocene, Hemmoorian, Behrendorfian (Berchem Formation, Edegem Sand Member). Coll. RGM 393.189 (AJL), x 25.

Type material — Fusus 'fasciolaroïdes' Nyst, 1861 was based on specimens from the Edegem Sands in Belgium (Hemmoorian). A specimen from the material studied by Nyst was illustrated by Glibert (1952, pl. 8, fig. 4a, b) as *Streptochetus sexcostatus*. We here designate this specimen (IRScNB, Cat. Types Invert. no. 2437) lectotype of *Fusus 'fasciolaroïdes'* Nyst.

Diagnosis — A form of *S. cheruscus* characterised by a slightly more thick-set shell form and by a prosocline position of the radial sculpture elements on the teleoconch of adult specimens, usually forming distinct knobs on the middle of the whorl and causing a marked subsutural depression.

Material studied — Oligocene, Chattian B (Vejle Fjord Formation, Brejning Clay Member): Denmark (Jylland) — **Fakkegrav**: 1 specimen, MNO; **Nørre Vissing**: 1 specimen, KSL, reg. 1979.180.

Miocene, Vierlandian (Klintinghoved Formation): Denmark (Als) — **Klintinghoved**, near Sønderborg, outcrop on foreshore: 1 specimen, 4 juv. specimens, RGM 393.188 (AJL, May 1977); 2 specimens, Pl. 2, figs 1, 2, RGM 393.364-365 (FWG); 1 specimen, 4 juv./def. specimens, RGM 393.383 (AJL); 1 specimen, 3 juv. specimens FWG).

Miocene, Hemmoorian, Behrendorfian (Berchem Formation, Edegem Sand Member): Belgium (Antwerpen province) — **Antwerpen**: 3 specimens, IRScNB (Malaise) (the sediment contents of shells distinctly point to Edegem Sands), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 1 specimen of *Streptolathyrus rothi*; **Antwerpen**, 'Tête de Flandre', Scheldt tunnel for pedestrians : 2 specimens and 3 def. specimens, (sediment contents of shells distinctly point to Edegem Sands), IRScNB (leg. unknown), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 4 specimens of *Streptolathyrus rothi*; **Antwerpen**, 'enceinte' = moat of defence: 5 specimens, two of which with strikingly solid and oblique radial ribs (sediment contents of shells distinctly point to Edegem Sands, in spite of indication 'Sables à *P. pilosus*', which is usually interpreted as Antwerpen Sands), IRScNB (van den Broeck), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; **Antwerpen**, construction pit for E 3 Kennedy-tunnel: 34 specimens, IRScNB (leg. unknown, probably M. Glibert, ± 1965); this sample contains also 5 specimens of *Streptolathyrus rothi*; 1 def. specimen, Text-fig. 8, 1 specimen, 6 def. specimens, 11 specimens, 15 juv. specimens, RGM 393.189, 117 270, 182 984 and 117 271, respectively (AJL); 9 specimens, RGM 183.142 (FJR); 12 specimens, RGM 116.619 (A. Haandrikman); 5 specimens, RGM 183.246 (MBL); 36 specimens, 81 juv. specimens, RGM 182.610-611, respectively (DMM); 8 specimens, 35 juv. specimens (among which one specimen with a strikingly large protoconch), MCL; **Antwerpen**, borehole at construction pit for Slijkhoektunnel, depth 22 m below surface: 5 def. specimens, 6 juv. specimens, RGM 393.190 (AJL); **Boom**: 1 specimen, IRScNB (Malaise), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this specimen was included in a sample from the Boom Clay Formation, but according to its sediment contents it may originate from the Edegem Sands, therefore its locality is probably incorrect; this sample contains also 1 specimen of *Streptodictyon subelongatus*; **Burcht**, 138 specimens, IRScNB (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 1 specimen of *Streptolathyrus rothi*; **Deurne**, near Antwerpen: 1 specimen, IRScNB (Nyst), (sediment contents point distinctly to Edegem Sands, so obviously the locality is erroneous: as far as we know Edegem Sands have never been exposed at Deurne), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this

sample contains also 1 specimen of *Streptodictyon sexcostatus* (with sediment contents pointing to Antwerpen Sands) and 1 specimen of *Streptolathyrus rothi*; **Edegem**: 1 specimen and 1 specimen, Pl. 2, fig. 3, Cat. Types Invert. no. 2347, IRScNB (Nyst), mentioned and illustrated, respectively, in Glibert, 1952, p. 110, pl. 8, fig. 4 *sub nomine Streptochetus sexcostatus*; 2 specimens, IRScNB (purchased 1861 from Mrs Bernays De Gottal), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*]; 5 specimens, IRScNB (de Cort), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*]; 3 specimens, IRScNB (Rutot), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; 6 specimens, IRScNB (Th. Lefèvre), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 1 specimen of *Streptolathyrus rothi*; 207 specimens, IRScNB (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 2 specimens of *Streptolathyrus rothi*; 238 specimens, IRScNB (le Hon), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 1 specimen of *Streptolathyrus rothi*, 1 specimen of *Pterynotus nysti* (von Koenen, 1867) and 1 specimen of *Borsonia uniplicata* von Koenen, 1872; 403 specimens, IRScNB (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 3 specimens of *Streptolathyrus rothi* and 2 specimens of *Aquilofusus waeli auct. non* Nyst; 4 specimens, Pl. 2, figs 4-7, 559 specimens, IRScNB TCCI 6046-9 (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also 4 specimens of *Streptolathyrus rothi*; 2 specimens, RGM 393.191 (Technische Hoogeschool, Delft); **Kiel**: 2 specimens, IRScNB (leg. unknown), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; **without locality data**: 11 specimens, IRScNB (Nyst).

Miocene, Hemmoorian (Breda Formation): The Netherlands (Limburg province) — **Baarlo**, borehole 9, 58E15, depth 180-186 m below surface, 1 specimen, RGD (ROD, 1908).

Miocene, Hemmoorian, Oxlundian (Berchem Formation, Antwerpen Sand Member): Belgium (Antwerpen province) — **Berchem-Borgerhout**, temporary excavations for E3 'Kleine Ring' motorway, 1968: 1 juv. specimen, RGM 393.192 (AJL).

Miocene; lacking data: Belgium (Antwerpen province) — **Antwerpen**, '3me section': 1 specimen, IRScNB (Capt. Dural), mentioned in Glibert, 1952, p. 110; this sample also contains 2 specimens of *Streptodictyon sexcostatus*.

Discussion — For the population in the Belgian Edegem Sands (Hemmoorian, Berendorfian) Nyst (1861) introduced the name *F. fasciolaroïdes*. Kautsky (1925, pp. 116, 117), however, stated in his text on *Streptochetus sexcostatus*: 'Der *Fusus fasciolaroides* Nyst von Edeghem ist mit dieser Spezies identisch'. Kautsky's opinion was accepted by later authors, *e.g.* Beets (1950), Glibert (1952, p. 110), Tembrock (1961, p. 373) and, implicitly, Nordsieck (1972, p. 84).

Tembrock, incidentally, stated (p. 373, no reference given) that Nyst himself already concluded *S. fasciolaroides* to be identical with *S. sexcostatus*. This, however, does not seem to be the case. We have not been able to find any paper of Nyst in which this statement could be traced.

The availability of quite a number of juvenile specimens in the RGM collection, however, made us change the current concept. The close-set configuration of the radial ornament on the initial teleoconch whorls is typical for *Streptodictyon cheruscus*. The fully-grown specimens from Edegem agree with some shells from Klintinghoved in Denmark. In this form the oblique position of the ribs in most specimens reminds of *S. retrorsicosta*, which makes the Edegem/Klintinghoved material one of the most curious forms of *S. cheruscus*, which should be indicated as forma *fasciolaroides* Nyst. Additionally, two typical specimens of this form are known from the Chattian B of Denmark (Nørre Vissing and Fakkegrav), where it co-occurs with *S. cheruscus* s. str. Furthermore, just one juvenile specimen from the Antwerpen Sands at Berchem-Borgerhout (Belgium) had to be identified as f. *fasciolaroides*. This latter specimen is the only representative of *S. cheruscus* from this part of the Belgian Miocene.

Quite surprising is the observation, that apparently the species *S. sexcostatus* has not yet been demonstrated in the Edegem fauna! This latter species obviously appears somewhat later, as it is found for the first time in the 'Middle Miocene' (Hemmoorian, ? Behrendorfian/Oxlundian) of the Peel area, where it co-occurs with *S. cheruscus*, indicating that both species have different evolutionary roots.

The forma *fasciolaroides* indeed closely resembles *S. sexcostatus*, but differs by its wider apical angle, its less convex initial whorls with close-set collabral ribs and a somewhat finer sculpture.

Stratigraphical distribution — This forma is known from deposits of Chattian B, Vierlandian and Hemmoorian (Behrendorfian) age.

Streptodictyon gottschei (Gripp, 1914)

Pl. 2, figs 8-12; Text-fig. 9

* 1914 *Fusus abruptus* var. **Gottschei** n. var., Gripp, p. 21,

pl. 2, figs 17-19 (excl. synon.).

v. 1950 *Streptochetus (Streptochetus) abruptus gottschei* (Gripp). — Beets, p. 19, pl. 2, figs 9-20.

1964 *Streptochetus abruptus* var. *Gottschei* Gripp — Gripp, p. 362 (note 41).

. 1965 *Streptochetus (Streptodictyon) gottschei* (Gripp 1913)— Tembrock, p. 435, fig. 3a, b.

v. 1965 *Streptochetus (Streptodictyon) abruptus* (Beyrich 1856) — Tembrock, pp. 433, 434, fig. 4 (*non* Beyrich).

1990 *Streptochetus (Streptodictyon)* sp. — Moths, p. 24, pl. 13, fig. 16.

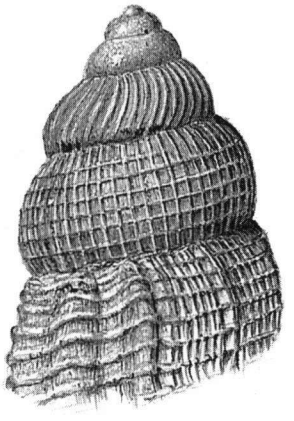


Fig. 9. *Streptodictyon gottschei* (Gripp, 1914), protoconch. Itzehoe, Ochsenkamp, clay pit of 'Alsensche Zementfabrik' (Germany, Schleswig-Holstein), Miocene, Vierlandian (Elmshorn Formation). Coll. RGM 393.207 (leg. Schlüter, 1890, K. Gripp Collection, don. Geologisch-Paläontologisches Institut, Hamburg), x 25.

Type material — A syntype each from Itzehoe is still housed in the Hamburg and Kiel collections. The latter specimen, with damaged apical and apertural parts, was illustrated by Gripp (1914, pl. 2, fig. 19); we here designate this specimen lectotype. The Hamburg specimen (paralectotype) has a better preserved apex, on which at least some details of the protoconch are still visible. No additional syntypes exist, but from partly sorted sieving residues donated to the RGM by the Hamburg institute many very immature specimens of *S. gottschei* could be isolated. These, however, although topotypes, cannot be considered syntypes.

Locus typicus — Itzehoe (Germany, Schleswig-Holstein), Ochsenkamp, clay-pit of 'Alsensche Zementfabrik'.

Stratum typicum — Miocene, Vierlandian, Elmshorn Formation. Gripp recorded specimens from both the 'Glimmerton' (= mica clay) and 'Glaukonitsand' (= glauconitic sand). The label of the lectotype bears no indication of its stratigraphic provenance, but its sediment contents clearly demonstrate that it comes from the glauconitic sand.

Original diagnosis (translated from German) — 'The most closely related older congener of the species under discussion is the Oligocene *Fusus elongatus* Nyst. The embryonic shells are closely similar, but the Miocene species from Itzehoe demonstrates much more numerous radial riblets on the [protoconch !] whorls bearing an intermediate sculpture, like those illustrated by Beyrich, pl. 24, fig. 2 for *F. sexcostatus*. Furthermore, *F. abruptus* var. *Gottschei* differs considerably from the older species in having a smaller apical angle, flatter whorls and almost completely disappearing ribs'.

Revised diagnosis — *Streptodictyon* with a reticulate protoconch sculpture. Teleoconch with narrow apical angle and relatively high whorls. Collabral ribs restricted to the initial three teleoconch whorls in the typical form, but sometimes persisting or re-appearing. Spiral sculpture dense, coarser on the lower part of the whorls, on larger shells often developed as flat ribbons separated by incised lines.

Description — Shell fusiform, height to c. 50 mm, about three times higher than wide. Apical angle increasing from about 25° in juveniles to about 30° in adults, the apical part thus having a slightly concave outline.

Protoconch conical, consisting of 4¾ to 5 moderately convex whorls. Diameter of nucleus about 0.10 mm. The initial whorls are smooth, sculpture is present on the last 2 to 2½ whorls, starting with radial lines, which are distinctly opisthocline, changing to orthocline after one whorl. Together with the radial elements spirals develop, at first just above the middle part of the whorl, followed by further spirals above and below the primary one. Near the boundary with the teleoconch six or seven spirals may be present. Spiral and radial elements are thread-like, of about the same strength. In some specimens the radial sculpture initially is close-set, decreasing in density towards the younger part of the shell.

On the last quarter of a whorl radial sculpture of the protoconch increases in strength, giving rise to a rather strong undulation of the shell-wall. The boundary with the teleoconch is sigmoid, following the course of the radial sculpture on the protoconch. The protoconch surface is distinctly glossier than that of the teleoconch.

Teleoconch with up to about eight whorls, which are remarkably high in comparison to its congeners. The initial three or four, on which collabral sculpture is present, are convex, while adjoining whorls are flat to slightly concave below the suture. In exceptional specimens the shell shows a thickening below the suture, with a distinctly concave

shell wall below it, resulting in a '*Terebra*'-like shell form (Pl. 2, fig. 9). Suture deep where the whorls are convex, but very shallow and only slightly incised as soon as the whorls become flat. Height of the body whorl about three fifths of the entire shell height. Base and siphonal canal well defined. Pseudumbilicus absent.

Teleoconch sculpture starting immediately after the boundary with the protoconch with seven spirals, which are continuations of the protoconch spirals; they are only slightly narrower than their interspaces, the lower four or five are stronger, which feature is even more obvious on later whorls. Secondary sculpture developing already on the boundary with the protoconch, not reaching the strength of the primary spirals. Two generations of secondary spirals are present. On the later whorls they become distinctly flattened and ribbon-like; they are separated by very narrow, barely incised interspaces. On the body whorl occasionally the spirals are almost flattened out.

Collabral sculpture only occurs on the apical whorls. The elements are very different from the spiral sculpture, in fact undulations of the shell's surface, vaguely delimited. Their form is somewhat more strongly sigmoid than the radial lines of the protoconch, which additionally facilitates distinguishing of the protoconch/teleoconch boundary. There are about 12 radial elements on the first teleoconch whorl, this number remaining more or less constant. The strength of the radial sculpture decreases gradually and from the fourth whorl downwards radials are absent. The orthocline growth lines are well visible.

Aperture elliptical, suddenly constricted where the siphonal canal begins. In some adult specimens the columella shows (traces of) one or two folds. Also a parietal tooth is only occasionally discernable. The presence of spiral lirae on the internal shell wall could not be demonstrated, despite the fact that such were mentioned by Gripp in the original description of the species.

Material studied — Oligocene, Chattian B (Grafenberg Sand Member): Germany, (Nordrhein-Westfalen) — **Erkelenz**, borehole K3 for mine shaft Sophia Jacoba 8, depth 238-267 m below surface: 9 juv. specimens, RGM 393.204 (GLK); **Meerbusch-Osterath**, borehole, depth 39-41 m below surface: 2 juv. specimens, RGM 393.205 (FHK).

Oligocene, Chattian (Veldhoven Formation, Voort Sand Member): The Netherlands (Limburg province) — **Beesel**, borehole 12, (58E/61), depth not indicated: 2 specimens, Pl. 2, figs 8, 9, illustrated in Beets (1950, pl. 2, figs 15, 16 and figs 19, 20 = aberrant specimen), *sub nomine Streptochetus abruptus gottschei* (Gripp), 5 specimens, referred to and/or illustrated in Beets (1950, p. 21) with the same identification, RGD (ROD, 1910); **Belfeld**, borehole 14 (58E/45), depth 250-350 m below surface: 1 specimen RGD (ROD 1911), illustrated in Beets (1950, pl. 2, figs 17, 18) *sub nomine Streptochetus abruptus gottschei* (Gripp); **Sevenum**, borehole 19, (52D/19), depth 285-290 m below surface: 1 specimen, RGD (ROD, 1914), referred to in Beets (1950, p. 21) *sub nomine Streptochetus abruptus gottschei* (Gripp).

Miocene, Vierlandian (Elmshorn Formation): Germany (Schleswig-Holstein) — **Itzehoe**, Ochsenkamp, clay-pit of 'Alsensche Zementfabrik': 1 specimen, lectotype, Pl. 2, fig. 10, K. Gripp Collection, Geologisch-Paläontologisches Institut und Museum der Universität, Kiel, Typ. Kat. Nr. 191a, illustrated in Gripp (1914, pl. 2, fig. 19); 1 juv. specimen, paralectotype, Pl. 2, fig. 11, K. Gripp Collection, Geologisch-Paläontologisches Institut, Hamburg; 135 juv. specimens, 1 juv. specimen, Text-fig. 9, RGM 393.206-207 (leg. Schlüter, 1890, K. Gripp Collection, don. Geologisch-Paläontologisches Institut, Hamburg); 30 juv. specimens, SMF 310377 (leg. Schlüter, 1890, K. Gripp Collection, don. Geologisch-Paläontologisches Institut, Hamburg/RGM); 155 juv. specimens, MCL (leg. Schlüter, 1890, K. Gripp Collection, don. Geologisch-Paläontologisches Institut, Hamburg/RGM).

Age unknown (reworked boulder in fluvioglacial deposits): Germany (Mecklenburg-Vorpommern) — **South of Schwerin lake**: 1 specimen (guttapercha cast), Pl. 2, fig. 12, PHB Ga 126 (II.155.14), referred to and illustrated in Tembrock (1965, pp. 433, 434, fig. 4), *sub nomine Streptochetus abruptus* (Beryrich 1856), erroneously assumed to have come from the Bokuper Sandstein specimen in the Koch Collection and therefore not a syntype of *S. abruptus*); the cast also contains 3 specimens of *Haustator goettentrupensis* (Cossmann, 1899), indicating the age of this material to be Chattian/ Vierlandian.

Stratigraphical distribution — Apart from some reworked specimens in boulders, a single specimen is known from a Danish locality of Chattian B age (Brejning); a number of specimens is in the RGD collections from the so-called 'Late Oligocene' of the Peel area (boreholes Belfeld, Sevenum and Beesel). Unfortunately the depth indications of these samples are very insufficient, and frequently lacking. Some juvenile specimens are known from the Lower Rhine District (dated Chattian B, or Neochattian). The species is common at its type locality Itzehoe (Schleswig-Holstein), which is of Vierlandian age.

Discussion — The typical form of this species is easily recognised by its relatively high whorls and effacing radial sculpture. This latter feature makes the species at first glance resemble *S. abruptus*. There are, however, obvious differences: in *S. abruptus* the whorls are relatively lower, the spiral sculpture is almost of the same strength in the upper and lower part of the whorls, and the initial teleoconch whorls are more convex. Juvenile specimens of *S.*

abruptus cannot be distinguished from *S. sexcostatus*, whereas juveniles of *S. gottschei* are utterly distinct.

From the Late Oligocene part of range we distinguish a forma *beetsi* n.f. (see below), as first described by Beets (1950, p. 21, pl. 2, figs 25-28) under the name of *Streptochetus (Streptochetus) pergracilis* (*non* von Koenen).

Evolutionary development — The most closely related precursor (which also ranges higher than does *S. gottschei*) is *S. cheruscus*. There are no clear indications, however, that *S. gottschei* should indeed be considered an offshoot of the *S. cheruscus* lineage. After the Vierlandian *S. gottschei* seems to disappear from the North Sea Basin.

Streptodictyon gottschei (Gripp, 1914)
forma **beetsi** n.f.
Pl. 3, figs 1-3

v. 1950 *Streptochetus (Streptochetus) pergracilis* (Von Koenen) — Beets, p. 21, pl. 2, figs 25-28 (*non* von Koenen).

Description — This form differs from typical *S. gottschei* in having a clearly persistent radial sculpture, which affects the outlines of the whorls to such an extent, that they usually have a distinct subsutural depression and a slightly convex lower part. The radial sculpture to a certain degree resembles that of *e.g. S. sexcostatus*, but in that species the radials are still markedly stronger and the whorls are also relatively lower and more convex; there are distinct differences in the spiral sculpture as well.

Material — Oligocene, Chattian B (Vejle Fjord Formation, Brejning Clay Member): Denmark, (Jylland) — **Brejning**: 1 juv. specimen, MNO; 1 juv. specimen, KSL, ex sample 1983.207; **Mogenstrup**: ? 1 def./juv. specimen, KSL, ex sample 1989.141.

Oligocene, Chattian (Veldhoven Formation, Voort Sand Member): The Netherlands (Limburg province) — **Baarlo**, borehole 9 (58E/15), depth 216-222 m below surface: 1 specimen RGD (ROD, 1908), referred to in Beets (1950, p. 22) *sub nomine Streptochetus pergracilis* (von Koenen); **Beesel**, borehole 12 (58E/61), depth not indicated: 9 specimens and 2 specimens, RGD (ROD, 1910), illustrated in Beets (1950, pl. 2, figs 26 and 28) *sub nomine Streptochetus pergracilis* (von Koenen); depth 230-250 m below surface: 1 specimen, Pl. 3, fig. 2, 2 specimens, RGD (ROD, 1910), referred to and one illustrated in Beets (1950, p. 22, pl. 2, fig. 25) *sub nomine Streptochetus pergracilis* (von Koenen), 1 specimen (Pl. 3, fig. 1); **Belfeld**, borehole 14 (58E/45), depth 260-270 m below surface: 1 specimen, Pl. 3, fig. 3, 1 specimen, RGD (ROD, 1914), both referred to and illustrated in Beets [1950, p. 22, pl. 2, fig. 27 *sub nomine Streptochetus pergracilis* (von Koenen)]; depth 250-350 m below surface: 5 specimens, RGD (ROD, 1914), referred to in Beets (1950, p. 22) *sub nomine Streptochetus pergracilis* (von Koenen).

Discussion — Well-developed specimens of this new form are quite unlike typical *S. gottschei* and we initially intended to erect a new species for these. A similar case occurs in the Middle Miocene *S. sexcostatus/S. abruptus* complex, for which we have demonstrated that a species with radial ribs developed into a species without such sculpture (Cadée & Janssen, 1983). In the present case, however, the data on the stratigraphical distribution are insufficient for a comparable interpretation. The only observation that can be made is that the smooth form (*S. gottschei* s. str.) outlived the ribbed one. They may have co-occurred, however, during the Chattian. In these circumstances we refrain from introducing a new species and prefer to distinguish such specimens at the infraspecific level. Some specimens are intermediate between *S. gottschei* s. str. and the forma *beetsi*.

This material cannot be assigned to *S. pergracilis* von Koenen, an exclusively Latdorfian species. The forma *beetsi* is known with certainty only from Chattian faunas. It apparently does not occur at Itzehoe. We dedicate this form to Dr C. Beets, of Wassenaar, who was the first to distinguish it.

Streptodictyon impiger sp. nov.
Pl. 3, figs 4, 5; Text-figs 10, 11

? 1867 *Fusus elongatus* Nyst. — von Koenen, p. 79 (*partim*, ? *non* Nyst, the species may be present among material from *e.g.* Hermsdorf, Freienwalde).

? 1889 *Fusus elongatus*, Nyst. — Haas, p. 23, pl. 2, fig. 26 (*partim*, *non* Nyst, *non* pl. 3, fig. 1 = *S. cheruscus*).

? 1896 *Fusus elongatus*, Nyst u. var. — Reinhard, p. 78 (*non* Nyst).

? 1907 *Fusus elongatus* Nyst — Ravn, p. 324 (120), pl. 6, fig. 1 (*partim*, *non* Nyst, only the Rupelian specimens, *non* pl. 6, fig. 2 = ? *S. cheruscus*).

1954 *Streptochetus elongatus* (Nyst) — Boekschoten, p 175, fig. 11 (*non* Nyst).

v. 1957 *Streptochetus* (s.s.) *elongatus* Nyst, sp. 1843 — Glibert, p. 71 (*partim*, *non* Nyst, only specimens from Ramsel, *non* pl. 5, fig. 19 = *S. cheruscus*).

v. 1961 *Fusus (Streptochetus) elongatus* Nyst — Cadée, p 16, figs 18, 18a (*non* Nyst).

v. 1975 *Streptochetus (Streptodictyon) cheruscus elongatus* (Nyst, 1845) — van den Bosch *et al.*, p. 66, pl. 4, fig.

1a, b (*partim, non* Nyst, *non* pl. 5, fig. 2 = *S. elongatus*).

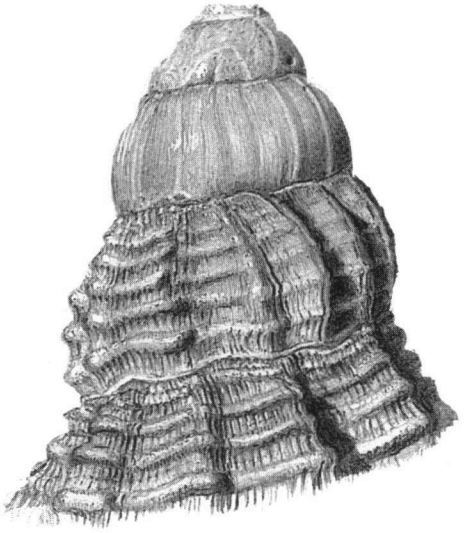


Fig. 10. *Streptodictyon impiger* sp. nov. (**paratype**), protoconch and early teleoconch whorls. Winterswijk, De Vlijt clay pit (The Netherlands, Gelderland province), Oligocene, Rupelian (Brinkheurne Formation, upper part of Woold Member). Coll. RGM 393.213 (MCL), x 25.

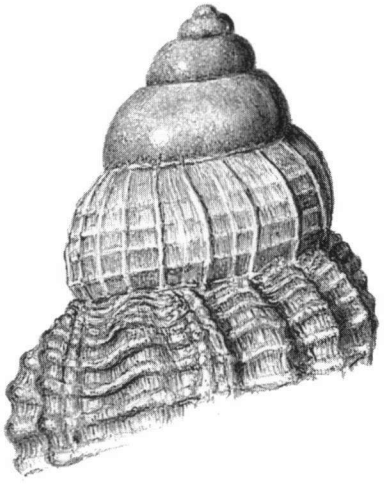


Fig. 11. *Streptodictyon impiger* sp. nov. (**paratype**), protoconch and early teleoconch whorls. Winterswijk, De Vlijt clay pit (The Netherlands, Gelderland province), Oligocene, Rupelian (Rupel Formation, Winterswijk Member). Coll. RGM 393.214 (S. van Schooten), x 25.

Holotype — Pl. 3, fig. 4, RGM 127.048, leg./don. M. Freudenthal, illustrated in van den Bosch *et al.*, 1975, pl. 4, fig. 1 *sub nomine Streptochetus (Streptodictyon) cheruscus elongatus*.

Locus typicus — Winterswijk, clay-pit complex 'De Vlijt' (The Netherlands, Gelderland province).

Stratum typicum — Brinkheurne Formation, upper part of Woold Member, Rupelian, Oligocene.

Derivatio nominis — named after the type locality: *impiger* (L., adj.) = diligent (diligence in Dutch = vlijt).

Diagnosis — *Streptodictyon* with a relatively large, rather dome-shaped protoconch. Initial whorls lack ornament; the last half protoconch whorl obvious spirals and somewhat irregularly spaced collabral ribs arise, together forming an irregular reticulation. Teleoconch with rugose sculpture, persistent to the apertural margin. Columella without folds; no parietal tooth.

Description — Shell fusiform, height to c. 23 mm, slender, 2.6-2.8 times higher than wide, juvenile specimens are less slender (2.0-2.3 times higher than wide), apical angle of adult shells about 30°; in juvenile shells the apical angle cannot be measured, on account of its dome-shaped outline.

The protoconch is multispiral, conical with cyrtoconoid tangents, comprising 4¼-5½ slightly convex whorls, and about 1.35 (1.30-1.40) times higher than wide, its height varying from 1.9 to 2.4 mm. The nucleus has a diameter of 0.10 mm. The initial whorls are smooth. The reticulate sculpture is poorly developed in this species and restricted to the ultimate protoconch whorl. On the last whorl six to seven rather solid spirals develop, gradually increasing in strength towards the boundary with the teleoconch. Close to this boundary irregular collabral riblets appear, which together with the spirals form an irregular reticulation, usually restricted to the last quarter whorl of the protoconch. The boundary with the teleoconch is sometimes sharp, but occasionally the transition is gradual, or even difficult to determine. The most useful criteria in the latter case are the appearance of obvious growth lines and the broadening of the spiral elements.

The shell has moderately convex teleoconch whorls with a slight subsutural depression. The body whorl occupies two thirds of the entire shell height. The periphery is rounded, with a gradual transition into the base. The siphonal canal is slightly curved to the left (apertural view).

The sculpture of the teleoconch is composed of orthocline, heavy collabral ribs, covering the entire shell to the apertural margin. On the first teleoconch whorl the number of radial elements is about 10-11, with interspaces as wide as the ribs; this number decreases to 8 or 9 towards the aperture.

Spiral sculpture of seven (sometimes six) well-defined, relatively high primary spirals (frequently one situated in the lower suture), forming obvious knobs on the radial ribs. The upper spirals are somewhat weaker than the lower ones. Secondary spirals develop from the end of the second teleoconch whorl onwards, at first on the lower part of the whorl. A further generation of secondary spirals is present only on the largest specimens. The secondary spirals never reach the strength of the primary ones.

The growth lines are well developed, especially between the spiral elements, rather close-set, and slightly lamellose. They run parallel to the collabral sculpture.

The inner shell wall bears obvious spiral lirae at frequent growth intervals. In the largest specimens available no parietal tooth, but merely a remnant of the spiral sculpture is present. There are no spiral folds on the columella.

Paratypes — Oligocene, Rupelian (Rupel Formation, Putte Member): Belgium (Antwerpen province) — **Antwerpen**, construction pit for E3-Scheldt tunnel (= Kennedytunnel): 8 specimens, RGM 393.208 (MBL); 18 specimens, RGM 393.376 (AJL); 1 specimen, Pl. 3, fig. 5, 19 specimens, RGM 393.209-210 (DMM): 8 specimens, MCL, 1965); **Kruibeke**, clay pit: 1 juv. specimen, HBH; **Ramsel**, municipality of Herselt, clay pit: 6 and 56 juv. specimens, RGM 220.919-920 (AJL, 1975): 10 and 66 juv. specimens, resp. RGM 221.171-172 (AJL, 1976); 13 specimens, RGM 393.211 (AJL): 52 specimens, IRScNB (Raeymakers), this sample contains also 2 specimens of *S. cheruscus* and 1 juv. specimen of *Fusinus elatior* (Beyrich, 1848); 1 specimen, IRScNB (F. Boisschot), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample contains also an apparently Miocene and therefore mislabelled specimen of *S. cheruscus*.

Oligocene, Rupelian (Rupel Formation, Putte Member): Belgium (Oost Vlaanderen province) — **Beveren**, construction pit for tunnel below 1st canal dock: 14 more or less def. specimens, RGM 220.871 (AJL, 1974-1975); **Beveren, Kallo**, construction pit of 4th harbour dock, from upper 2 m of Putte Clay: 10 more or less def. specimens, RGM 227.701 (AJL, 15 September 1984).

Oligocene, Rupelian (Rupel Formation, Terhagen Member, or, more probably, Putte Member): Belgium (Oost Vlaanderen province) — **Basele**, ? 2 juv. specimens, IRScNB (Nyst), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 juv. specimen of *S.* ? *subelongatus* and 1 specimen of *S. sowerbyi*.

Oligocene, Rupelian (Brinkheurne Formation, upper part of Woold Member: The Netherlands (Gelderland province) — **Winterswijk**, De Vlijt clay pit: 2 specimens, RGM 184.813 (M. Freudenthal): 1 specimen, 3 juv. specimens, RGM 393.212 (J.H. Drenth and H. Odé): 2 specimens, resp. RGM 76.005 and RGM 76.011 (G. Kortenbout van der Sluijs); 1 specimen, RGM 87.372 (H. Krul); 16 specimens, RGM 85.490 (P.L.F. de Groot, September 1956); 5 specimens, SMF 310374/5 (ex RGM 85.490); 7 specimens, 40 juv. specimens, HBH, 1956-1957); 31 specimens, 34 juv. specimens, MCL; 1 juv. specimen, Text-fig. 10, RGM 393.213 (MCL).

Oligocene, Rupelian (Rupel Formation, Winterswijk Member): The Netherlands (Gelderland province) — **Winterswijk**, De Vlijt clay pit: 14 specimens, MCL; 1 specimen, 2 juv. specimens, leg./coll. S. van Schooten; 1 juv. specimen, Text-fig. 11, RGM 393.214 (S. van Schooten).

Oligocene, Rupelian (Rupel Formation, Rupel Clay Member): Germany (Brandenburg) — **Bad Freienwalde**, Ziegel-Dränrohr clay pit: 5 specimens, MCL, 1993.

Discussion — Until now this species was never distinguished from *S. subelongatus* (see list of synonyms). Indeed, the general appearance of both species is very similar. The differences, however, cannot be overlooked, especially so in the morphology of the protoconch, but also in teleoconch sculpture. In addition, *S. subelongatus* grows to a considerably larger size than does *S. impiger*.

Streptodictyon impiger is distinguished from equal-sized (and therefore juvenile) specimens of *S. sowerbyi* by the shape and size of its protoconch and by the different development of the secondary sculpture, as described above. Additionally, equal-sized *S. sowerbyi* have a slightly wider apical angle, and their growth lines are generally less well developed than in *S. impiger*. Specimens not preserving the protoconch are difficult to assign to one of these two taxa.

Two specimens from the Winterswijk Member at Winterswijk differ from the other specimens in showing a distinct reticulate sculpture (Text-fig. 11) which covers the entire last embryonic whorl or even slightly more. Moreover, the secondary spiral sculpture of the teleoconch starts already near the end of the first teleoconch whorl. These specimens are reluctantly assigned to the present taxon. They might represent a younger evolutionary development of the species.

Fully-grown specimens from the Rupelian clays are for the greater part poorly preserved on account of pyrite oxidation, as is typical of these sediments.

Stratigraphical distribution — Rupelian, upper part of Woold Clay Member (Brinkheurne Formation) and lowermost part of the Winterswijk Member in The Netherlands; upper part of Putte Clay Member (Rupel Formation) in Belgium; Rupel Clay Formation in Germany.

Evolutionary developments — *S. impiger* is obviously related to *S. subelongatus*, as is indicated by the restricted

development of the reticulate protoconch sculpture.

Streptodictyon retrorsicosta (Sandberger, 1860)
Pl. 3, figs 6-11; Text-figs 12a, b, 13

v.* 1860 *Fusus retrorsicosta* Sandb., Sandberger, pl. 17, fig 6, 6a.
v. 1861 *Fusus retrorsicosta* Sandb. — Sandberger, p. 221.
. 1884 *Fusus retrorsicosta*, Sandberger — Cossmann & Lambert, p. 158, pl. 6, fig. 7a-c.
1893 *Latirus retrorsicosta*, (Sandberger) — Cossmann, p. 343.
1901 *Fusus retrorsicosta* Sandb. — Cossmann, p. 43.
1961 *Streptochetus (Streptodictyon) retrorsicosta* (Sandberger). Form b. — Tembrock, p. 373, pl. 2, fig. 4.
1964 *Streptochetus (Streptodictyon) retrorsicostus* (Sandberger, 1863) — Tembrock, p. 322.
1964 *Streptochetus (Streptodictyon) retrorsicosta* (Sandberger, 1863) — Tembrock, pl. 6, fig. 11.
? 1965 *Streptochetus (Streptodictyon) retrorsicostus* — Tembrock, p. 435 (? *partim*).
? 1973 *Streptochetus (Streptodictyon) retrorsicostus* (Sandberger, 1860). — Kuster-Wendenburg, p. 118 (? *partim*).
1978 *Streptochetus (Streptodictyon) retrorsicosta* (Sandberger 1860). — R. Janssen, p. 112.
1979b *Streptochetus (Streptodictyon) retrorsicosta* (Sandberger 1860). — R. Janssen, p. 298 (*partim*, *non* pl. 16, fig. 26 = *Streptodictyon sowerbyi*; not the specimens from Söllingen, ? not the specimens from the Sternberger Gestein).

Type material — Kuster-Wendenburg (1973) was unable to trace the type specimens in the Sandberger Collection at Wiesbaden.

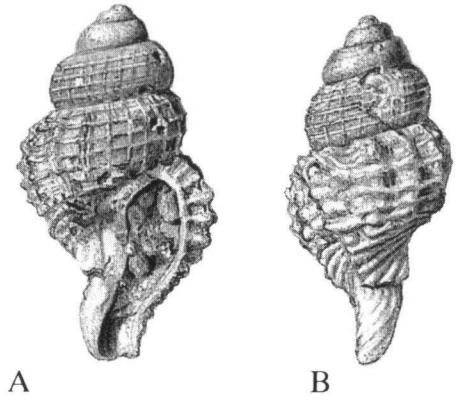


Fig. 12a, b. *Streptodictyon retrorsicosta* (Sandberger, 1860), protoconch and early teleoconch whorls. Weinheim, Zeilstück (Germany, Rheinland-Pfalz), Oligocene, Rupelian (Unterer Meeressand). Coll. KGM, x 25.

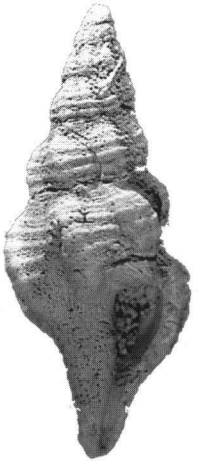


Fig. 13. *Streptodictyon retrorsicosta* (Sandberger, 1860) (**lectotype**), Weinheim near Alzey (Germany, Rheinland-Pfalz), Oligocene, Rupelian (Meeressand). Coll. Museum Wiesbaden IS 103, x 2.

She found only a fragment which has the characters of *S. retrorsicosta*, in a sample of *S. subelongatus*. Thanks to the kind co-operation of Mr K. Gürs (Kiel) and Mr E. Zenker (Museum Wiesbaden) we were able to study a sample of 6 specimens labelled '*Fusus elongatus* Nijst', and numbered IS 99-103. This lot included beyond any doubt the material of both *F. elongatus* and *F. retrorsicosta*, identified by Sandberger. These specimens had all been glued to a piece of cardboard, but K. Gürs recently removed five specimens, as the apertural characters were invisible. Two large fragments (IS 99), belonging to *Streptodictyon subelongatus* (illustrated by Sandberger, pl. 17, figs 5, 5a, 5c) had erroneously been glued together, but are again separated. A juvenile specimen of the same species (illustrated by Sandberger, pl, 17, fig. 5d) is numbered IS 101. The three remaining specimens (IS 100, 102 and 103) all belong to *S. retrorsicosta*. The shell numbered IS 103 clearly is the specimen illustrated by Sandberger (pl. 17, fig. 6, 6a), and we herewith designate this specimen lectotype (Text-fig. 13). The 'fragment' mentioned by Kuster-Wendenburg (1973, p. 118) as probably being the holotype of *S. retrorsicosta* (IS 102) and the third specimens (IS 100) are paralectotypes.

Locus typicus — Weinheim near Alzey, Mainz Basin, Germany.

Stratum typicum — 'Meeressande' (Oligocene, Rupelian).

Essential details of original description — The upper

whorls are weakly reticulate, the middle ones are characterised by 6-7 thick, more or less oblique radial ribs curving backwards, which appear crenulated by 4-5 well-defined primary spiral ribs. In between the primary spirals 3-5 finer secondary spirals are inserted. A thick spiral fold is present on the upper wall of the pear-shaped aperture, two smaller and very oblique ones are situated on the callous columella.

Revised diagnosis — A medium-sized species of *Streptodictyon* with radial and spiral sculpture persisting to the aperture. Protoconch conical, with about four convex whorls; on the last two whorls a distinct reticulate sculpture of fine collabral riblets, cut by five spirals. Teleoconch with coarse radial sculpture of circa seven distinctly prosocline ribs. Spiral sculpture of four to six well-defined primary elements. Secondary spiral sculpture in two generations which remain distinctly weaker than the primary spirals. Aperture in (sub)adult specimens with a solid parietal tooth and one or two oblique columellar folds. Siphonal canal relatively short.

Description — Shell fusiform, height to c. 30 mm, rather thick-set for the genus, about 2.3 times higher than wide, juvenile specimens are relatively less slender. Apical angle of adult shells about 35°, slightly wider (about 40°) in juveniles.

The protoconch is multispiral, conical with very slightly cyrtoconoid tangents, comprising 3¾-4¼ convex whorls and is about 1.3 times higher than wide; height 1.5 mm (measured in a single specimen from Weinheim-Zeilstück). The nucleus has a diameter of 0.10 mm. The initial whorls are smooth; on the last two whorls a reticulate sculpture develops, consisting of four to six thread-like spiral lines, which increase in strength from the adapical suture downwards, intersected on the last whorl by distant radial lines. Together these elements form rectangles which are distinctly wider than high. In between these sculpture elements an extremely fine spiral sculpture is visible in very well-preserved specimens. Close to the transition into the teleoconch two or three somewhat stronger radial riblets are present. The boundary with the teleoconch is rather abrupt.

The shell has convex teleoconch whorls, on the younger ones a slight subsutural depression is indicated, especially in between the radial ribs. The body whorl occupies six tenths of the entire shell height. The periphery is rounded, with a rather distinctly separated siphonal canal, which is straight and exceptionally short for a species of this genus.

The sculpture of the teleoconch consists of distinctly prosocline, heavy collabral ribs, covering the entire shell up to the apertural margin. On the initial teleoconch whorls the number of radial elements is about nine, with interspaces narrower than the ribs; on later whorls the interspaces gradually become wider, and the number of ribs decreases to six or seven.

Spiral sculpture of six or seven primary spirals (frequently one situated in the lower suture), increasing in strength from the upper to the lower suture. The spiral ribs are more accentuated on the apical whorls than on the lower ones, where they become obscured by the secondary sculpture. Secondary spirals develop, almost simultaneously, in two, rarely three, generations from the second teleoconch whorl onwards. The two generations reach almost the same strength, but remain recognisable as such up to the apertural margin. They never reach the strength of the primary spiral sculpture, which results usually in a sculpture consisting of rather coarse spirals with three or five finer ones in between. The growth lines are not pronounced, run parallel to the collabral sculpture, and are distinctly prosocline.

Weak spiral lirae were observed on the inner shell wall of some juvenile specimens. In (sub)adult specimens a strong parietal tooth is present and the columella bears a very oblique spiral fold, in larger specimens accompanied by a secondary one below it.

Material studied — Oligocene, Rupelian (Unterer Meeressand): Germany (Rheinland-Pfalz) — **Weinheim**: 3 specimens (lectotype and paralectotypes as designated above), IS 103 (Text-fig. 13), IS 100 and IS 102, respectively, Museum Wiesbaden, Wiesbaden; **Weinheim**, Zeilstück: 1 fragment, 2 specimens, 1 specimen, Pl. 3, fig. 6, 2 juv. specimens, 1 juv. specimen, Text-fig. 12a, b, KGM.

Oligocene, Rupelian (Sables de Fontainebleau, Falun de Pierrefitte): France (dép. Essonne) — **Pierrefitte**: 3 specimens, 2 specimens, Pl. 3, figs 7, 8, DLV; 2 specimens, 1 specimen, Pl. 3, fig. 9, MNHNP (Lozouet/-Maestrati).

Oligocene, Chattian A (Kasseler Meeressand): Germany (Hessen) — **Glimmerode**, former lignite pit Höllkopf, 'Verarmungshorizont': 1 specimen, Pl. 3, fig. 10, SMF 250780/1 (R. Janssen, 1972/1973).

Oligocene, Chattian B (Grafenberger Sande): Germany (Nordrhein-Westfalen) — **Erkelenz**, K-3 well for mine shaft Sophia Jacoba 8, depth 298-299 m below surface: 1 specimen, Pl. 3, fig. 11, RGM 393.215 (GLK).

Remarks — Well-preserved juvenile specimens of this species from the Mainz Basin demonstrate that at least the last protoconch whorl has a reticulate sculpture. Therefore we concur with Tembrock (1961), who referred it to *Streptodictyon*.

R. Janssen (1979b, p. 298) recorded two specimens from the Late Oligocene of Glimmerode, Germany, one of which was illustrated (pl. 16, fig. 26). Both specimens were available to us for study. The illustrated shell does not belong to *S. retrorsicosta*, since it has straight collabral ribs

and shows a peculiar development of the secondary spiral sculpture. We would rather refer it to the common Oligocene species *S. sowerbyi*. The second specimen (Pl. 3, fig. 10) has distinctly oblique collabral ribs, a well-developed columellar fold and the typical secondary sculpture of *S. retrorsicosta*. It is the only specimen of this species from Glimmerode.

From Söllingen R. Janssen (1979b, p. 298) recorded a sample of 27 specimens of *S. retrorsicosta*. We have not seen this material, but presume on the basis of material from the same locality in coll. RGM, that it belongs to *S. sowerbyi* (see below). Two specimens recorded by him from the Sternberger Gestein cannot be interpreted without studying the actual specimens.

In spite of the fact that we studied a substantial amount of material from the Rupelian clays we have not been able to recognise *S. retrorsicosta* from that deposit. Many specimens approach *S. retrorsicosta* in spiral sculpture, but additional characters all point to *S. sowerbyi*. This leaves us with a hiatus in the stratigraphic distribution for *S. retrorsicosta* from early Rupelian ('Unterer Meeressand', 'Sables de Fontainebleau') to Chattian.

Stratigraphical distribution — *S. retrorsicosta* is known from the 'Unterer Meeressand' in the Mainz Basin. We have seen specimens from Weinheim-Zeilstück, Kuster-Wendenburg also mentioned the localities Weinheim (? Trift and ? Würzmühle) and Waldböckelheim (Welschberg). In the Paris Basin the species occurs in the Falun de Pierrefitte. All these occurrences are of Rupelian age. The species is also known from the Chattian A and B (? Söllingen, Glimmerode, Erkelenz). Finally, Tembrock (1964) illustrated a large specimen from the Rupelian 'Magdeburger Sand' of Neustadt-Magdeburg.

Related forms — This species closely resembles *S. sowerbyi*, which has a similarly developed secondary sculpture. It can be distinguished from that species in having distinctly prosocline collabral sculpture, better developed columellar folds and parietal tooth, and short siphonal canal. Furthermore, *S. sowerbyi* grows to a larger size.

Both *S. retrorsicosta* and *S. sowerbyi* are known from the 'Unterer Meeressand' at Weinheim, Mainz Basin (although not co-occurring in any of the localities), which indicates that the two taxa should not be interpreted as subspecies.

Evolutionary developments — Precursor species of *S. retrorsicosta* are unknown to us. *S. twistringensis* may be a Miocene successor.

Streptodictyon schnetleri sp. nov.
Pl. 3, fig. 12; Text-fig. 14

? 1913 *Fusus elongatus* Nyst — Harder, p. 80, pl. 6, fig. 19a, b (*partim, non* Nyst, *non* figs 20, 21 = *Streptodictyon cheruscus*).

v. 1987 *Streptochetus (Streptolathyrus)* ? *soellingensis* Tembrock, 1965 — Schnetler & Beyer, p. 205.

v. 1990 *Streptochetus (Streptolathyrus) soellingensis* Tembrock, 1965 — Schnetler & Beyer, p. 49.

Fig. 14. *Streptodictyon schnetleri* sp. nov. (**paratype**), protoconch and early teleoconch whorls. Brejning (Denmark, Jylland), Oligocene, Chattian B (Vejle Fjord Formation, Brejning Clay Member). Coll. RGM 393.217 (MNO), x 25.

Type material — Holotype: Pl. 3, fig. 12, RGM 393.216 (leg./don. MNO).

Locus typicus — Brejning (Denmark, Jylland), coastal cliff outcrop.

Stratum typicum — Brejning Clay Member, Vejle Fjord Formation (Oligocene, Chattian B).

Derivatio nominis — named after Mr Kai Ingeman Schnetler of Langå, Denmark.

Diagnosis — *Streptodictyon* with a reticulate sculpture on the last two protoconch whorls. Teleoconch sculpture consisting of about ten collabral ribs on the initial whorls, decreasing to about seven on the younger ones. Spiral sculpture of eight primary spirals. Secondary spirals in two generations, not reaching the strength of the primaries. Columellar fold weakly indicated.

Description — Shell fusiform. Except for the single near-adult specimen known, which has almost 5¼ teleoconch whorls and a height of c. 18 mm, all specimens are immature individuals.

The protoconch is conical, with a height of 2.0-2.2 mm and a width of 1.2-1.4 mm, with c. 5-5¼ convex whorls. The nucleus is spherical and has a diameter of c. 0.12 mm. The boundary with the teleoconch is sharp. The terminal 2½ whorls of the protoconch have a reticulate sculpture, the radial elements of which initially are slightly opisthocline and gradually become more opisthocyrt. The number of spirals varies from 6 to 7, they are slightly stronger than the likewise thread-like radial elements. The reticulate pattern consists of rectangles which are slightly to distinctly wider than high.

The boundary with the teleoconch is indicated by a sudden thickening of sculpture elements. The teleoconch whorls are regularly convex, changing to slightly flattened below the suture on the later whorls. The sculpture consists of about ten, slightly prosocline collabral ribs on the first whorl, decreasing to seven ribs on the body whorl of the largest specimen. The radial ribs are not continuous from one whorl to the next. The interspaces between the collabral ribs are slightly wider than the ribs. The spiral sculpture comprises eight primary spirals, overriding the radial sculpture. They are of almost equal strength, but for the subsutural three spirals which are slightly weaker. Initially the interspaces between the primary spirals are slightly narrower than the spirals, but on later whorls the spirals are distinctly narrower than the interspaces. In some specimens the spiral sculpture is slightly coarser.

Secondary spiral sculpture starts on the second teleoconch whorl. The first secondary spirals appear on the periphery of the shell. In specimens with only one teleoconch whorl it can be seen that occasionally on the base of the shell the secondary sculpture starts immediately behind the boundary with the teleoconch. In the holotype, the largest specimen available, a second generation of secondary spirals starts on the base of the body whorl and below the suture starting from the fourth whorl. The secondary spirals remain distinctly weaker than the primaries.

The columella is sigmoid and has an incipient fold. A parietal tooth is absent in the only larger specimen available to us. The growth lines are distinct and lamellose.

Paratypes — Oligocene, Chattian B (Vejle Fjord Formation, Brejning Clay Member): Denmark (Jylland) — **Brejning**: 3 juv. specimens, MNO; 1 juv. specimen, Text-fig. 14, RGM 393.217 (MNO); 1 juv. specimen and 1 specimen juv./def. KSL, no. 1983.207 and 1983.241, respectively); **Mogenstrup**: 1 juv. specimen, KSL, ex sample 1987.561; 1 juv./def. specimen, KSL, ex sample no. 1987.325; 1 juv. specimen, KSL, no. 1987.562; **Nørre Vissing**: 1 juv. specimen, KSL; 1 juv. specimen, MNO; **Skanderborg**: 1 juv. specimen, KSL, no. 1979.86 (S.B. Andersen, 1976); 3 juv. specimens, KSL, ex sample 1979.85a (S.B. Andersen, 1976).

Oligocene, Chattian B (Grafenberg Member): Germany (Nordrhein-Westfalen) — **Erkelenz**, K3 borehole for mine shaft Sophia Jacoba 8, depth 320-321 m below surface: 3 juv. specimens, RGM 393.218 (GLK); depth 304-305 m: 1 juv. specimen, RGM 393.219 (GLK); depth 292-293 m: 5 juv. specimens, RGM 393.220 (GLK); depth 288-289: 4 juv. specimens, SMF 310375/4 (GLK/RGM); depth 284-285 m: 1 juv. specimen, RGM 393.221 (GLK); depth 282-283 m: 5 juv. specimens, RGM 393.222 (GLK); depth 268-281 m: 3 juv. specimens, RGM 393.223 (GLK); **Rheinberg**, mine shaft excavation: ? 1 poorly preserved juv. specimen, MCL, May 1989.

Discussion — This species demonstrates a striking resemblance to *S. soellingensis*, but differs especially in showing a reticulate protoconch sculpture, which ornament in *S. soellingensis* is completely absent. Remarkable is the occurrence of two juvenile, quite similar specimens from the Rupelian Winterswijk Member, which are distinctly older than the present specimens. If *S. schnetleri* is accepted as a younger evolutionary stage of the *S. soellingensis* lineage, these specimens cannot be identified as such. We discussed these specimens also in the description of *S. soellingensis*.

Stratigraphic range — This species is known in small numbers with certainty from deposits of Chattian B age.

Evolutionary developments — In view of the fact that all available material is consistently younger than material of *S. soellingensis* we assume *S. schnetleri* to be a subsequent and apparently final evolutionary stage of the same lineage.

Streptodictyon sexcostatus (Beyrich, 1856)

Pl. 3, figs 13-15; Text-figs 15, 16

* 1856 *Fusus sexcostatus* Beyr., Beyrich, p. 287, pl. 24, fig. 2a-c.

. 1872 *Fusus sexcostatus* Beyr. — von Koenen, p. 174 (*partim*, at least the specimens from Edegem do not belong to this species, but to *S. cheruscus* f. *fasciolaroides*).

1878 *Fusus sexcostatus* Beyr. — Gottsche, p. 183 (? *partim*, *Streptolathyrus rothi* may be included).

? 1886 *Fusus* cf. *sexcostatus* Beyr. — Oehmcke, p. 16.

. 1901 *F. sexcostatus* Beyr. — Cossmann, p. 31 (*partim*, specimens from Edegem excluded = *S. cheruscus* f. *fasciolaroides*).

1907 *Fusus sexcostatus* Beyrich — Ravn, p. 331 (127) (*partim*, exclusively the Middle Miocene specimens from Varde).

? 1916 *Fusus sexcostatus* Beyr. — Nørregaard, p. 27.

? 1917 *Streptochetus sexcostatus* (Beyrich) — Newton, p. 14, pl. 2, figs 2, 3.

. 1925 *Streptochetus sexcostatus* Beyr. — Kautsky, p. 116,

pl. 8, fig. 20 (*partim, non* pl. 8, fig. 21 = *S. cheruscus*).

. 1952 *Streptochetus sexcostatus* Beyrich, sp. 1856 — Glibert, p. 110 (*partim, non* pl. 8, fig. 4a, b, the entire material from the Edegem Sands belongs to *S. cheruscus* f. *fasciolaroides*).

? 1958 *Fusus* cf. *sexcostatus* Beyrich — Sorgenfrei, p. 233 (*partim, non* pl. 50, fig. 158 = *S. cheruscus*. It may be that *S. sexcostatus* is also represented in Sorgenfrei's material).

. 1961 *Streptochetus (Streptodictyon) sexcostatus* (Beyrich) — Tembrock, p. 373, pl. 1, fig. 7 (*partim, non* pl. 1, fig. 8 = *S. cheruscus*).

? 1961 *Streptochetus (Streptodictyon) sexcostatus* (Beyrich) Form a — Tembrock, p. 372, pl. 2, fig. 5.

. 1964 *Streptochetus (Streptodictyon) sexcostatus* (Beyrich 1856) — Anderson, p. 263, pl. 27, fig. 202.

. 1968 *Streptochetus sexcostatus* (Beyrich 1856) — Rasmussen, p. 147, pl. 12, figs 5, 6.

? 1968 *Streptochetus 'quinquecostatus'* (nov. sp. ?) — Rasmussen, p. 148, pl. 15, figs 1, 4 (= intermediate form between *Streptodictyon sexcostatus* and *S. abruptus*).

1972 *Streptochetus (Streptodictyon) sexcostatus* (Beyrich, 1854) (sic !) — Nordsieck, p. 84, pl. 20, fig. 121 (excl. distribution).

1981 *Streptochetus (Streptodictyon) sexcostatus* (Beyrich, 1856) — van der Hoek, p. 18, fig. 43 (mala).

v. 1983 *Streptochetus sexcostatus* (Beyrich, 1856) — Cadée & Janssen, p. 97, pl. 1, figs 1-4.

? 1983 *Streptochetus 'quinquecostatus'* Rasmussen, 1968, intermediate form between *Streptochetus (Streptodictyon) sexcostatus* (Beyrich, 1856) and *Streptochetus (Streptodictyon) abruptus* (Beyrich, 1856) — Cadée & Janssen, p. 99, pl. 1, figs 5-7.

v. 1984 *Streptochetus (Streptodictyon) sexcostatus* (Beyrich, 1856) — A.W. Janssen, p. 245, pl. 10, figs 3, 4; pl. 64, fig. 5.

Non:

1861b *Fusus fasciolaroides*, 1861, Nyst, Nyst, p. [8] (*fasciolaroïdes* in the text) (= *S. cheruscus* f. *fasciolaroides*).

1940 *Streptochetus sexcostatus* Beyrich — Sorgenfrei, p. 46, 108 (= *S. cheruscus* f. *fasciolaroides*).

1961 *Streptochetus (Streptodictyon) sexcostatus* (Beyrich) Form b — Tembrock, p. 372, pl. 2, figs 6, 6a (= *S. cheruscus* f. *fasciolaroides*).

1961 *Streptochetus fasciolarius* (Nyst) (1861) (sic !). — Tembrock, p. 373 (= *S. cheruscus* f. *fasciolaroides*).

Type material — Beyrich recorded specimens from Bersenbrück and Dingden (both Germany). We here designate the illustrated specimen (Beyrich, 1856, pl. 24, fig. 2a-c) lectotype.

Locus typicus — Dingden, Nordrhein-Westfalen, Germany.

Stratum typicum — Dingdener Schichten, or, less probably, Bislicher Schichten (Miocene, Reinbekian).

Original diagnosis or essential details of original description (translated by the present authors) — [...] 'The large conical embryonic part consists of five whorls, the three upper ones of which are smooth, the next two are covered with fine, thread-like longitudinal and transverse lines. [...] The number of middle whorls is up to six. Usually they have six strongly elevated longitudinal ribs, which are separated by wider [...] interspaces. [...] The transverse lines are narrow and sharp, five on the initial middle whorls; on the lower whorls they increase in number by the insertion of one intermediate line each. [...] In well-preserved specimens the growth lines are hairlike, close-set and cover the complete shell. [...] The spindle has usually a weak fold at the beginning of the canal. [...] Sometimes this fold is accompanied by a lower weak tooth and another in the upper angle of the aperture'.

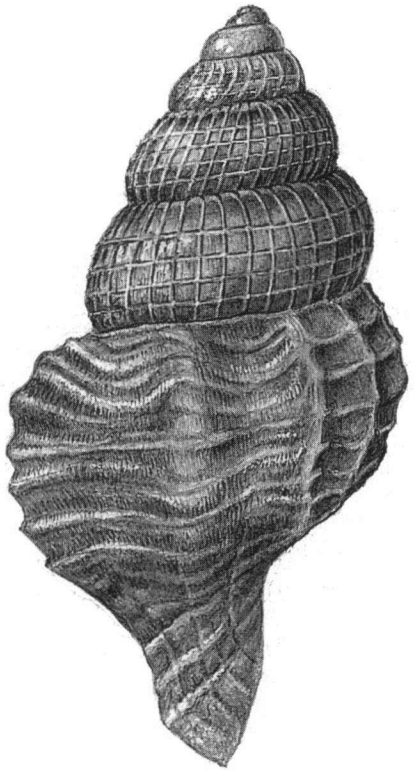


Fig. 15. *Streptodictyon sexcostatus* (Beyrich, 1856), protoconch and early teleoconch whorls. Nederweert, borehole I, depth unknown (The Netherlands, Limburg province), Miocene, Hemmoorian (Breda Formation). Coll. IRScNB TCCI 6043 (M. Masson), x 25.

Revised diagnosis — *Streptodictyon* with a reticulate protoconch sculpture. Teleoconch with six to eight heavy collabral ribs per whorl, persistent to the apertural margin. Spiral sculpture of six primary spirals. Secondary spirals in two generations, the first one of which reaches the strength of the primaries. Columellar fold and parietal tooth usually present.

Description — Shell relatively large, height up to about 55 mm, fusiform, about two and a half to three times higher than wide when fully grown. Apical angle varying from about 45° in juvenile specimens to about 35° in adult shells.

Protoconch conical, consisting of 4 to 5 moderately convex whorls. Diameter of nucleus about 0.10 mm. The initial whorls are smooth, reticulation is present on the last 2 to 2½ whorls, anticipated by a few radial lines, which are distinctly opisthocline, changing to orthocline as soon as the radial elements develop. The reticulate sculpture is comparatively coarse, the number of spiral elements is usually 4, sometimes a fifth spiral develops below the suture and occasionally a further spiral becomes visible in the lower suture. The radial elements slowly increase in strength towards the boundary with the teleoconch, especially so on the terminal protoconch whorl. The boundary with the teleoconch is usually sharp and particularly distinct by the sudden broadening of the spiral elements.

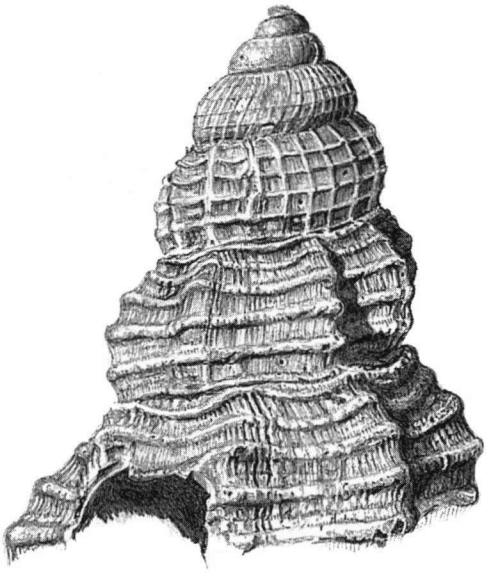


Fig. 16. *Streptodictyon sexcostatus* (Beyrich, 1856), protoconch and early teleoconch whorls. Dingden, temporary outcrop in bottom of Königsbach near Königsmühle (Germany, Nordrhein-Westfalen), Miocene, Reinbekian (Bislicher Schichten). Coll. RGM 393.245 (AJL, 1970), x 25.

Teleoconch with up to about eight convex whorls. A subsutural depression is absent, or only very faintly indicated on the youngest whorls of large specimens. Suture distinct. Height of the body whorl about two thirds of total shell height. Base and siphonal canal well separated. Pseudumbilicus absent.

Teleoconch sculpture starting on the first whorl with five or six thread-like spirals, which slightly weaken towards the adapical suture. The middle spirals are continuations of the protoconch spirals. Secondary sculpture developing in three generations, the first of these on the second teleoconch whorl. As soon as they reach the strength of the primary spirals a next generation of secondary spirals develops, a third generation is usually present on the youngest whorls.

Radial sculpture consists of about 8 (in spite of the name *sexcostatus* !) heavy, ortho- or slightly prosocline ribs, distinctly narrower than their interspaces. Their number remains constant on the later whorls. Growth lines well visible, especially so in between the spiral sculpture, but in well-preserved specimens also overriding the spirals. They are very regular, frequently lamellose in the sculpture intervals, orthocline to slightly opisthocyrt, sometimes slightly flexuous.

Aperture ovoid, abruptly constricted where the siphonal canal begins. Columella with distinct traces of dissolution of calcareous material, removing the sculpture of the base completely and with a sharp boundary. Just above the transition into the canal a well-defined columellar fold is present, which in rare cases may be either absent or doubled. Close to the point where the apertural margin touches the preceding whorl a parietal tooth may be present. On the inner shell wall occasionally short spiral lirae are seen, usually in places where a radial rib is present on the exterior. These lirae are usually commoner in juvenile specimens.

Material studied — Juveniles from levels at which also *S. abruptus* occurs cannot be recognised as either *S. abruptus* or *S. sexcostatus*. They are listed here, as are the transitional forms between these two taxa.

Miocene, Hemmoorian (Berchem Formation, Kiel Sand Member): Belgium (Antwerpen province) — **Antwerpen**, construction pit for E3 'Kleine Ring' motorway near Grote Steenweg, depth c. 9 m below surface: 6 fragmentary moulds, RGM 183.400, 183.413, 183.418-419, 183.427, 183.430 (AJL).

Miocene, Hemmoorian (Breda Formation): The Netherlands (Limburg province) — **America**: borehole 11 (52D18), depth 210-220 m below surface: 19 juv. specimens, RGD (ROD, 1909), probably downhole contamination in Voort Sand Member; depth 150-200 m: 58 juv. specimens, RGD (ROD, 1909); **Baarlo**, borehole 9 (58E/15), depth not specified: 109 specimens, RGD

(ROD, 1908); depth 100-160 m: 8 specimens, RGM 393.224 (ROD, 1908); **Beringen**, municipality of Helden, borehole 15 (58B/8), depth 154-159 m below surface: 263 specimens, RGD (ROD, 1911); 324 and 8 specimens, RGM 393.225-226 (ROD, 1911); 9 juv. specimens, MCL (ROD, 1911); depth 144-154 m: 146 juv. or def. specimens, RGM 393.227 (ROD, 1911) (contaminated sample); depth 134-144 m: 17 juv. specimens, RGM 228.902; 5 specimens, RGM 393.228 (ROD, 1911); 46 specimens, 5 juv. specimens, RGD (ROD, 1911); depth 124-134 m: 1 specimen, RGD (ROD, 1911); depth 119-124 m: 31 juv. or def. specimens, RGM 228.675 (ROD, 1911; 12 specimens, RGD (ROD, 1911); **Broekhuizenvorst**, borehole 52E/114, depth 157-158 m: 1 specimen (illustrated in Cadée & Janssen, 1983, pl. 1, fig. 4), 5 juv. specimens; 1 specimen (transitional form to *S. abruptus*; illustrated in Cadée & Janssen, 1983, pl. 1, fig. 6); depth 156-157 m: 1 specimen (transitional form to *S. abruptus*; illustrated in Cadée & Janssen, 1983, pl. 1, fig. 7); all RGD; **Griendtsveen**, borehole 7 (52D/11) (= Helenaveen III), depth 340-375 m below surface: 4 juv. specimens, RGD (ROD, 1906-1908); depth 250-260 m: 2 juv. specimens, RGD (ROD, 1906-1908) (both samples probably downhole contamination in Voort Sand Member); depth 150-210 m: 44 specimens, RGM 393.229 (ROD, 1906-1908); **Maasbree**, borehole 13 (58B/4), depth not specified: 26 specimens, RGD (ROD, 1910); depth 102-160 m: 27 juv. specimens, RGM 393.230 (ROD, 1910); **Meyel** borehole 8 (58B/6), depth 280-290 m below surface: 1 def. specimen, RGD, (ROD, 1908) (probably downhole contamination in Voort Sand Member); depth 175-200 m: 1 juv. specimen (RGD (ROD, 1908); **Nederweert**, borehole I, depth unknown: 43 juv. specimens, one of which with an exceptionally slender protoconch, 1 juv. specimen, Text-fig. 15, IRScNB TCCI 6043 (M. Masson).

Miocene, Hemmoorian (Breda Formation): The Netherlands (Noord Brabant province) — **Reek**, borehole 41 (571/24), depth 140-157 m: 7 specimens; depth unknown: 11 specimens, RGD (ROD, 1909).

Miocene, Hemmoorian (reworked in fluvio-glacial deposits, from Arnum Formation): Denmark (Jylland) — **Gram**, gravel pit at Enderupskov: 2 specimens, 3 juv. specimens, RGM 393.231 (N. Vedsted-Hansen); 5 juv. specimens, RGM 393.232 (AJL); 1 def. and 3 juv. specimens, MCL.

Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed, Hiatella arctica Acme Zone and/or Astarte radiata Acme Zone): The Netherlands (Gelderland province) — **Winterswijk**, Miste, temporary excavation, depth 2.00-3.75 m below surface: (887, 704 and 1.078 specimens, 1 specimen, Pl. 3, fig. 13, and 2 juv. specimens, illustrated in Janssen (1984, pl. 10, figs 3, 4 and pl. 64, fig. 5, respectively), RGM 225.518-519, 226.026, 393.352-354 (AJL 1971); 4 specimens, 10 juv. specimens, RGM 393.233 (FJR); 12 specimens, RGM 393.234 (MBL); 139 specimens, MCL.

Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed, presumably Astarte radiata Acme Zone): The Netherlands (Gelderland province) — **Eibergen**, temporary outcrop 34G.1-1 near Ticheloven: 53 specimens, RGM 393.235 (MBL, 1964).

Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed, presumably Astarte radiata Acme Zone): The Netherlands (Gelderland province) — **Eibergen**, (without further indication): 10 def. specimens, RGM 29.614 (Staring Collection no. 13.752), mentioned in von Koenen, 1882, p. 174 (this sample also contains 2 def. specimens of *Murex inornatus*); **Eibergen (Rekken)**: 1 specimen, 1 def. specimen, IRScNB (Nyst), mentioned in Glibert, 1963, p. 148; **Winterswijk, de Giffel**: 1 specimen, RGM 29.600, Staring Collection no. 4711; 8 specimens, IRScNB (Bosquet), mentioned in Glibert, 1963, p. 148; this sample contains also 1 def. specimen of *Streptolathyrus rothi*, 1 specimen of *Charonia tarbelliana* (Grateloup, 1840) and 1 specimen of *Crassispira borealis* (Kautsky, 1925).

Miocene, Hemmoorian, Oxlundian (Berchem Formation, Antwerpen Sand Member): Belgium (Antwerpen province) — **Antwerpen**, Ploegstraat, temporary excavation for underground parking, 1965-1966: 4 specimens, 10 juv. specimens, RGM 393.236 (DMM); 5 juv. specimens, 2 fragments, MCL; **Berchem**, 1 specimen, IRScNB (purchased Mme Bernays De Gottal, 1905), mentioned in Glibert, 1952, p. 110; **Berchem-Borgerhout**, temporary excavations for E3 'Kleine Ring' motorway, 1968: 29 specimens, RGM 393.237 (FJR); 1 def. specimen, RGM 393.238 (RHR); 33 specimens, RGM 393.239 (DMM); 18 specimens, RGM 393.240 (AJL); 2 specimens, MCL; **Deurne** near Antwerpen (sediment contents point distinctly to Antwerpen Sands): 1 specimen, IRScNB (Nyst), mentioned in Glibert, 1952, p. 110; this sample contains also 1 specimen of *Streptodictyon cheruscus* (with sediment contents pointing to Edegem Sands, so obviously mislaid) and 1 specimen of *Streptolathyrus rothi*.

Miocene, Hemmoorian, Oxlundian (Berchem Formation, Zonderschot Sand Member): Belgium (Antwerpen province) — **Booischot**, I (borehole ?): 24 specimens, IRScNB (leg. unknown), this sample contains also 12 specimens of *Streptolathyrus rothi*; **Heist-op-den-Berg**, borehole, depth 1.35-1.90 m below surface: 22 juv. specimens, RGM 226.922; depth 1,90-2,70 m: 5 juv. specimens, 2 fragments, RGM 227.045; **Heist-op-den-Berg**, temporary exposure, September 1989: 1 specimen, Pl. 3, fig. 14, 267 specimens, RGM 393.241-242 (AJL); **Zonderschot**: 10 specimens, IRScNB (leg. unknown), this

sample contains also 2 specimens of *Streptolathyrus rothi*.

Miocene, Hemmoorian/Reinbekian (Breda Formation, Aalten Member, Miste Bed and/or Stemerdink Bed): The Netherlands (Gelderland) — **Eibergse Veld**, borehole, depth 3.5-10.5 m, 1 specimen (RGD); **de Giffel**, borehole 53 (475/19), depth 4-12.5 m, 13 specimens (RGD); borehole 54 (475/20), depth 2.5-13 m, 6 specimens (RGD); no further indication, 1 specimen (RGD); **Rekken**, De Horst, borehole 72a (456/20), depth unknown, 1 fragm. (RGD); **Winterswijk**, Groenloseweg, borehole 48 (475/14), depth 10-11 m, 6 juv. specimens; no depth indication, 10 specimens (RGD).

Miocene, Reinbekian (Breda Formation, Aalten Member, Stemerdink Bed): The Netherlands (Gelderland) — **Winterswijk, Brinkheurne**, outcrop in Slinge brook near former Stemerdinkbrug: 38 specimens, RGM 226.471 (J.H. Drenth, B. Hubert, H. Odé); 11 specimens, RGM 61.927 (H. Krul, 1940); 3 specimens, RGM 85.426 (P.L.F. de Groot); 46 mainly juv. specimens, RGM 226.550 (C. Beets, 10.7.1969); 34 mainly juv. specimens, RGM 226.347 (MBL); 19 specimens, RGM 226.664 (AJL, 1967); 3 specimens, 1 fragment (RGD); all samples mentioned in Janse & Janssen (1983); **Winterswijk, Brinkheurne**, outcrop in Slinge Brook near Nieuw Wassink: 2 specimens, RGM 226.263 (AJL).

Miocene, Reinbekian (Bislicher Schichten): Germany (Nordrhein-Westfalen) — **Dingden**, temporary outcrop in bottom of Königsbach near Königsmühle: 89 specimens, 559 juv. specimens, RGM 393.243 (MBL); 265 specimens, RGM 393.244 (FJR); 1 specimen, Pl. 3, fig. 15, 1 juv. specimen, Text-fig. 16, 1602 specimens, 1170 juv. specimens, RGM 393.245-248 (AJL, 1970); 27 juv. specimens, MCL; 117 specimens, 147 juv. specimens, RGM 393.249 (RHR).

Miocene, Reinbekian (Dingdener Schichten and/or Bislicher Schichten not specified): Germany (Nordrhein-Westfalen) — **Dingden:** 1 specimen and 1 def. specimen, IRScNB (Nyst), mentioned in Glibert, 1963, p. 148; 2 specimens, IRScNB (Bosquet), mentioned in Glibert, 1963, p. 148.

Miocene, Reinbekian (Dingdener Schichten): Germany (Nordrhein-Westfalen) — **Dingden**, outcrop in bank and/or bottom of Königsbach near Königsmühle: 93 and 114 specimens, RGM 127.161-162 (M. Freudenthal); 121 specimens, RGM 393.250 (MBL); 14 specimens, RGM 393.374 (W. Backhuys, 6 August 1960); 39 juv. specimens, MCL; **Dingden**, Stapelbach exposure: 1 specimen, RGM 393.251 (AJL).

Miocene, Reinbekian (Twistringer Schichten, lower part of section exposed): Germany (Niedersachsen) — **Twistringen**, clay pit of O. Sunder brickworks: 13 specimens, 14 juv. specimens, 3 specimens (transitional form to *S. abruptus)* MCL; 27 specimens, 8 juv. specimens, RGM 393.252-253 (AJL, 1977); 1 specimen, RGM 226.227 (AJL, 1977) (illustrated in Cadée & Janssen, 1983, pl. 1, fig. 1); 6 juv. specimens (from concentration of *Limopsis aurita*), RGM 393.254 (G. Garding).

Miocene, Reinbekian (Twistringer Schichten, level not specified): Germany (Niedersachsen) — **Nordlohne**, Meistermann clay pit (58 specimens, 3 of which transitional to *S. abruptus*); **Nordlohne**, Meistermann clay pit, about 15 m below surface: 322 specimens, RGM 393.255 (AJL); **Nordlohne**, Meistermann clay pit, borehole VII, depth 14-15 m below surface: 15 juv. specimens, RGM 393.256 (JVV); depth 15-16 m: 2 juv. specimens, RGM 393.257 (JVV); depth 16-17 m: 1 juv. specimen, RGM 393.258 (JVV); depth 17-18 m: 2 juv. specimens, RGM 393.259 (JVV); depth 18-19 m: 1 specimen, 2 juv. specimens, RGM 393.260 (JVV); **Twistringen**, clay pit of O. Sunder brickworks (*Streptodictyon* sp. indet.): 7 juv. specimens, RGM 115.857 (AJL); (transitional form to *S. abruptus):* 1 specimen, Pl. 4, fig. 1, RGM 226.230 (MCL) (illustrated in Cadée & Janssen, 1983, pl. 1, fig. 5); 1 specimen, RGM 393.377 (AJL); 23 specimens, RGM 116.010 (R. Janssen); 2 specimens, RGM 115.855 (AJL); 12 specimens, RGM 116.866 (DMM); 1 specimen, RGM 393.261 (AJL); 2 specimens, RGM 226.228-229 (MCL), illustrated in Cadée & Janssen, 1983, pl. 1, figs 2, 3); **Woltrup**, abandoned Giesting clay pit: 7 specimens, RGM 393.262 (AJL, 1986).

Miocene, Reinbekian (Bokup Sand Member): Germany (Mecklenburg-Vorpommern) — **Malliß**, boreholes on the Wanzer Berg: 1 fragment, RGM 393.263 (leg. O. Gehl, 1966, don. Geologisches Landesamt Mecklenburg-Vorpommern).

Miocene, without further data: Belgium (Antwerpen province) — **Antwerpen**, '3me section': 2 specimens, IRScNB (Capt. Dural), mentioned in Glibert, 1952, p. 110; this sample also contains 1 specimen of *Streptodictyon cheruscus* f. *fasciolaroides*.

Discussion — Specimens from the Hemmoorian of the Dutch Peel area differ from the typical form (Dingden, Germany), especially in the development of the spiral sculpture on the early whorls. In the Peel specimens the upper three primary spirals are distinctly weaker than the lower three. In the Dingden shells this difference is less accentuated. The populations from the Antwerp Sands and Winterswijk-Miste are intermediate in this respect.

Juvenile specimens of *S. abruptus* (with only one or two teleoconch whorls) cannot be distinguished from equal-sized *S. sexcostatus* (see above, and Cadée & Janssen, 1983).

The Burdigalian specimen mentioned by Hölzl (1958, p. 248) from Nonnenwald-Schacht (Penzberg, Bayern, Germany) as *Streptochetus* aff. *'sextostatus'* is the only

record of this species from outside the area investigated in this paper. However, the description of the fragmentary external mould could not convince us of its identity.

Stratigraphical distribution — Contrary to Glibert's (1952) opinion, quite surprisingly *S. sexcostatus* is absent from the Edegem Sand fauna. All *Streptodictyon* material in the Edegem Sands belongs to *S. cheruscus* forma *fasciolaroides* Obviously *S. sexcostatus* appears somewhat later, as it is found for the first time in the Kiel Sand Member of the Berchem Formation in the Antwerpen area and in the Miocene Breda Formation (Hemmoorian, ? Behrendorfian-Oxlundian) of the Peel area.

In that area it co-occurs with *S. cheruscus*, thus indicating that these two species have different evolutionary roots. In the slightly younger Miocene of Winterswijk-Miste (Oxlundian) exclusively *S. sexcostatus* occurs, continuing upwards into the Reinbekian (Anderson, 1964, p. 264). At a certain level in the Reinbekian Twistringer Schichten *S. sexcostatus* rapidly evolves into *S. abruptus* (see Cadée & Janssen, 1983, and above).

Evolutionary developments — Although there is a certain similarity in form and sculpture between *S. cheruscus* and *S. sexcostatus* the co-occurrence of these two taxa clearly indicate that there is no evolutionary connection between them. We think it possible but not very likely that *S. sexcostatus* descended from *S. sowerbyi*, which is known from Rupelian and Chattian deposits. Neither of these species, however, is yet known from the Vierlandian and the early Hemmoorian. During the Hemmoorian *S. sexcostatus* suddenly appears from unknown origin.

Streptodictyon soellingensis (Tembrock, 1965)
Pl. 4, figs 2-4; Text-figs 17, 18

? 1864 *Fusus elongatus* Nyst — Speyer, p. 265 (*non* Nyst) (? *partim*, includes *Streptodictyon sowerbyi* and, most probably, also *Streptodictyon cheruscus*).

v. 1856 *Fusus elongatus* Nyst. — Beyrich, p. 283 [*partim*, *non* Nyst, the specimens from 'Crefeld' (leg. Nauck) are in PHB Ga 433; the species may also be represented in the other Late Oligocene samples; see also *Streptodictyon cheruscus*, *S. subelongatus* and *S. sowerbyi*].

? 1867 *Fusus elongatus* Nyst — von Koenen, p. 79 (? *partim*, the species may also be represented in the samples from Söllingen).

. 1941 *Fusus elongatus* Nyst — Görges, p. 127 (*partim*, *non* Nyst, includes also *Streptodictyon cheruscus*).

v. 1961 *Streptochetus (Streptodictyon) elongatus* (Nyst), var. *söllingensis* nov. var. — Tembrock, p. 370, pl. 1, fig. 5 (*partim*, not 'Form b' = ? *Streptodictyon sowerbyi*).

*v. 1965 *Streptochetus (Streptolathyrus) soellingensis* Tembrock, p. 430, fig. 1.

v. 1978 *Streptochetus (Streptolathyrus) soellingensis* n. sp., Tembrock 1965. — R. Janssen, p. 113 (*partim*, includes also *Streptolathyrus masculinus*).

v. 1979b *Streptochetus (Streptolathyrus) soellingensis* Tembrock 1965, ♀ ?. — R. Janssen, p. 298, pl. 16, figs 29, 30 (*partim*, *non* pl. 16, figs 27, 28 = *Streptolathyrus masculinus*).

Fig. 17. *Streptodictyon soellingensis* (Tembrock, 1965), protoconch and early whorls. Söllingen, railroad cut between Söllingen and Jerxheim (Germany, Niedersachsen), Oligocene, Chattian A (Söllingen Sand Formation, Asterigerina Horizon). Coll. RGM 393.265 (PGL, May 1982), x 25.

Fig. 18. *Streptodictyon soellingensis* (Tembrock, 1965), protoconch and early whorls. Rumeln, dump of mine shaft Diergardt-VI (Germany, Nordrhein-Westfalen), Oligocene, Chattian A (Grafenberg Member). Coll. RGM 393.274 (AJL), x 25.

Type material — Holotype: Tembrock (1965, fig. 1), PHB Ga 125 (here illustrated in Pl. 4, fig. 2).
Locus typicus — Söllingen (Germany, Niedersachsen), railroad cut between Söllingen and Jerxheim.
Stratum typicum — Söllingen Sand Formation (Oligocene, Chattian A, *Asterigerina* Horizon).
Original diagnosis — Embryonic shell conical, acuminate, with a somewhat deviating nucleus, followed by three to four smooth whorls and a half to two ones with 6-9 thin spirals which sometimes (individually), anteriorly of the middle whorls, are crossed by irregularly spaced axial threads; middle whorls with 6-9 wide, ribbon-like, close-set spirals, the lower ones somewhat wider than the upper ones, in between the lower ones spirals that remain narrow are intercalated, furthermore 9-12, usually 10-11 strong radial ribs that run from suture to suture; body whorl covered with wide and close-set spirals until the end of the canal, aperture pear-shaped. Columella smooth, canal moderately long, the lower part somewhat curved outwards; concave growth lines, slightly curved in posterior direction to almost straight.
Revised diagnosis — *Streptodictyon* with rather small to large protoconch of which the ultimate two to three whorls are covered only with spiral lirae, except for the last half whorl or so, where some rather spaced radial elements are usually present. Siphonal canal comparatively long.
Description — Shell fusiform. The largest specimens have a height of about 16 mm and about 4½ rather convex teleoconch whorls. Apical angle about 32° in adult specimens, distinctly wider in very immature specimens. The height of the body whorl is about 0.7 times the entire shell height. The base of the shell gradually tapers into the siphonal canal. The columella is sigmoid, without a trace of folds or spirals. A parietal tooth is absent in all available specimens. The inner shell wall bears dense spiral lirae in juvenile specimens.

The upper whorls of the holotype protoconch are conical, the two final whorls show a reduced width development, and therefore the protoconch as a whole is cyrtoconoid. The height of the protoconch in the holotype is 2.2 mm; its width is 1.4 mm, the height thus equalling about 1.6 times the width. The number of its moderately convex embryonic whorls is almost five, the diameter of the nucleus is 0.1 mm.

The range of variation of protoconch features in this species is considerable. In most specimens the shape is regularly conical; a cyrtoconoid outline, as in the holotype, is rather exceptional. Measurements on specimens from various populations demonstrate a height range from 2.1 to 3.2 mm and a height/width ratio ranging from 1.5 to 1.8 mm. The number of protoconch whorls in these specimens ranges from 4¾ to 6¼, with a general tendency for the highest number of whorls to occur in the largest specimens. The smallest protoconchs are found on specimens from Söllingen, shells from Glimmerode generally have a larger protoconch, but the largest larval shells are present in the population from Rumeln. The nucleus has a diameter of 0.10 mm. The boundary with the teleoconch is sharp and indicated by a rather sudden widening of the spiral sculpture and a distinct broadening of the radial elements. The upper protoconch whorls are smooth. On the ultimate two whorls a spiral sculpture of 8-10 thread-like, widely and regularly spaced spirals occurs. On the last half whorl a radial sculpture develops, initially consisting of thin and widely spaced elements, which gradually increase in strength and width towards the boundary with the teleoconch.

Teleoconch sculpture comprises 9 to 11 straight to slightly prosocline radial ribs on the initial whorls, which are somewhat narrower than their interspaces. Their number remains constant, or increases with one or two depending on the size of the specimens. Even when their number remains constant they are as a rule not continuous from one whorl to the next. The radial sculpture is overlain by 10-12 much finer spirals, the interspaces being of about equal width as the spirals. A single generation of secondary spiral sculpture develops rather late, near the middle (one specimen) or rather near the end of the third teleoconch whorl, at first on the lower part of the whorl, but fairly soon also higher up. In all available specimens the secondary spirals do not reach the strength of the primary ones.

The growth lines are regularly spaced and distinctly visible between the spiral elements and have a somewhat lamellose appearance.
Material studied — Oligocene, Chattian (Veldhoven Formation, Voort Sand Member): The Netherlands (Limburg province) — **Eygelshoven** (shaft II of Laura colliery), depth 115-125 m: 5 specimens, IRScNB (leg. unknown), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 18 specimens of *S. cheruscus* and 3 specimens of *S.* sp.

Oligocene, Chattian A (Söllingen Sand Formation, Asterigerina Horizon): Germany (Niedersachsen) — **Söllingen**: 1 specimen (holotype), PHB (Bamberg coll.) Ga 125, Inv. Nr. II.155.13, illustrated in Tembrock, 1965, fig. 1; this paper Pl. 4, fig. 2; 1 juv. specimen (paratype), PHB Ga 5 Inv. Nr. II.151.06, leg. unknown, ex coll. Beyrich, illustrated *sub nomine Streptochetus elongatus* var. *söllingensis* nov. var. in Tembrock, 1961, pl. 1, fig. 5; **Söllingen**, railroad cut between Söllingen and Jerxheim: 13 juv./def. specimens, RGM 393.264 (AJL, May 1982); 1 juv. specimen, MCL (PGL); 1 juv. specimen, Text-fig. 17, RGM 393.265 (PGL, May 1982).

Oligocene, Chattian A (Kasseler Meeressand); Germany (Hessen) — **Ahnetal** near Kassel, Brandkopf

outcrop, 'Schill 3': 1 juv. specimen, RGM 393.266 (MBL, June 1973); 'Schill 2/3': 4 def./juv. specimens, RGM 393.267 (MBL, June 1973); **Glimmerode**, former lignite pit Höllkopf 'Schill 1': 6 adult, 56 juv. specimens, RGM 393.268 (MBL, June 1973); 'Schicht 4': 67 juv. specimens, SMF 250781/67 (R. Janssen, 1972-1973), 1 juv. specimen, SMF 250711/1 (R. Janssen, 1972-1973), illustrated in R. Janssen, 1979b, pl. 16, fig. 30; 6 juv. specimens, MCL, June 1973); 'Schill 2': 4 juv. specimens, RGM 393.269 (MBL, June 1973); 'Schill 3': 1 def. juv. specimens, RGM 393.270 (MBL, June 1973); level unknown: 1 specimen, Pl. 4, fig. 3, SMF 250710/1 (H. Humberg, 1977), illustrated in R. Janssen, 1979b, pl. 16, fig. 29; 4 juv. specimens, KGM).

Oligocene, Chattian A (Grafenberg Member): Germany (Nordrhein-Westfalen) — **Erkelenz**, K3 borehole for mine shaft Sophia Jacoba 8, depth 396-397 m below surface: 1 juv. specimen, RGM 393.271 (GLK); **Krefeld**: 2 specimens (paratypes), PHB Ga 433, Inv. Nr. II.157.23, leg. unknown, ex coll. Beyrich; **Rumeln**, dump of mine shaft Diergardt-VI: 32 specimens, RGM 393.272; 81 juv. specimens, RGM 393.273; 1 juv. specimen, Text-fig. 18, RGM 393.274 (AJL); 24 specimens, SMF 250345/24 (Görges); 9 specimens, MCL; 1 specimen, Pl. 4, fig. 4, RGM 393.275 (AJB); 11 juv. specimens, AJB; 5 juv. specimens, HBH.

Oligocene, Chattian A, later part (Grafenberg Member): Germany (Nordrhein-Westfalen) — **Krefeld**, Kempener Feld, borehole, depth c. 36 m below surface: 2 juv. specimens, RGM 393.276 (FHK, 1973).

Remarks — Tembrock (1961, p. 370) distinguished in her var. *söllingensis* a 'Form a' and a 'Form b', which she (p. 375) thought represented male and female, respectively. The illustrated 'Form a' (which we received on loan) is a typical specimen of *S. soellingensis*, as described above. We were unable to study the specimen indicated as 'Form b', but Tembrock's description (reticulate protoconch sculpture, and up to five secondary spirals between the teleoconch spiral sculpture) leads us to the supposition that this specimen should be assigned to *S. sowerbyi*. R. Janssen (1979b, p. 299) accepted Tembrock's assumption of sexual dimorphism, but curiously enough he interpreted Tembrock's male as being the female, apparently because of a different interpretation of Tembrock's 'Form b', which, in his opinion, belongs to *Streptochetus retrorsicosta*. In fact, R. Janssen, as match-maker, associated Tembrock's *S. söllingensis* 'Form a' (female !), with a small form from Glimmerode which he supposed to be the male. Previously (R. Janssen, 1978, p. 113), he had erroneously identified this small form with Tembrock's (1965, p. 429) *S.* cf. *undatus*. However, Tembrock's 'Form a' (= *S. soellingensis* herein) occurs in several associations (*e.g.* in the Lower Rhine area), in the absence of 'males'. Thus, we reject the concept of sexual dimorphism in this group of gastropods, and consider the small form from Glimmerode to be a separate species of the genus *Streptolathyrus*, to be introduced below as a new species, *S. masculinus*.

S. soellingensis is confined to the early Late Oligocene, and is widely distributed in both the Kassel area and the Lower Rhine District. There is a wide range of variation, especially in the dimensions of the larval shells. Specimens from the type locality have small-sized protoconchs, while at Glimmerode and especially in the Lower Rhine the larval shells are much larger, as mentioned above.

From younger Chattian deposits in Denmark and the Lower Rhine District we have specimens that closely resemble *S. soellingensis* in shape and sculpture, but which have a distinctly reticulated protoconch sculpture. Such specimens eventually prevented us from placing *S. undatus* and *S. soellingensis* in a separate genus. The differences from typical *S. soellingensis*, however, are marked enough to allow the introduction of a new species, *S. schnetleri* (see above).

Two enigmatic juvenile specimens from the Rupelian Winterswijk Member (MCL) differ from the present species in having a distinctly reticulated protoconch sculpture, whereas the teleoconch sculpture is quite typical. This is puzzling, as the *S. soellingensis* lineage develops a reticulate sculpture in populations of Chattian B age only (*S. schnetleri*). For the time being these specimens are not assigned to species, also because completely adult specimens are not available.

Stratigraphical distribution — *Streptodictyon soellingensis* is known from the Late Oligocene (Chattian A) of the Kassel area, the Lower Rhine District and from one locality (Eygelshoven) in the former coal-mining district in the southern part of the province of Limburg, The Netherlands.

Evolutionary developments — We consider the Rupelian *S. undatus*, occurring in the North Sea, Mainz and Paris Basins, to be the precursor of *S. soellingensis*. The main differences are the relatively shorter siphonal canal of *S. undatus*, and the better developed protoconch spiral sculpture in *S. soellingensis*. The lineage apparently continues and ends with *S. schnetleri*.

Streptodictyon sowerbyi (Nyst, 1836) emend.
Pl. 4, figs 5-12; Text-figs 19, 20

*v. 1836 *Fusus Sowerbei*, Nob., Nyst, p. 34, pl. 4, fig. 89.
v. 1845 *Fusus elongatus* Nyst, p. 493, pl. 38, fig. 25a, b (*partim*, includes also *S. subelongatus*).
? 1856 *Fusus elongatus* Nyst — Beyrich, p. 283, pl. 24, fig.

5, 5a (*non* pl. 24, fig. 6 = *S. subelongatus*, pl. 24, figs 3a, b, 4a, b = *S. cheruscus*).

1860 *Fusus elongatus* Nyst — Speyer, p. 482 (*non* Nyst).

1864 *Fusus elongatus* Nyst — Speyer, p. 265 (*partim, non* Nyst; includes, most probably, also *Streptodictyon cheruscus* and *S. soellingensis*).

? 1867 *Fusus elongatus* Nyst. — von Koenen, p. 79 (? *partim, non* Nyst, in the Rupelian material *S. sowerbyi* may be included).

? 1889 *Fusus elongatus* Nyst — von Koenen, p. 185 (? *partim, non* Nyst, in the Rupelian material *S. sowerbyi* may be included).

1889 *Fusus elongatus*, Nyst. — Haas, p. 23, pl. 3, fig. 1 (*partim, non* Nyst, *non* pl. 2, fig. 26 = *S. impiger*).

v. 1954 *Aquilofusus elongatus* Nyst, sp. 1843 — Glibert & de Heinzelin de Braucourt, p. 392 (*partim, non* Nyst, includes also *S. subelongatus* and Fasciolariidae sp.).

v. 1957 *Streptochetus* (s.s.) *elongatus* Nyst, sp. 1843 — Glibert, p. 71, pl. 5, fig. 19 (*partim, non* Nyst, specimens from the Voort Sand Member and part of the Rupelian specimens, includes also *S. subelongatus*).

? 1961 *Streptochetus elongatus* (Nyst) Form b — Tembrock, p. 367, pl. 1, fig. 4 (*non* Nyst).

1961 *Streptochetus (Streptodictyon) elongatus* (Nyst), var. *söllingensis* nov. var., Form b. — Tembrock, p. 370.

? 1965 *Streptochetus (Streptodictyon) retrorsicostus*. — Tembrock, p. 435 (? *partim, non* Sandberger).

v. 1969 *Streptochetus cheruscus elongatus* — Cadée, p. 43, fig. 5 [as *Scalaspira* (sic !) *cheruscus elongatus*].

? 1973 *Streptochetus (Streptodictyon) retrorsicostus* (Sandberger, 1860). — Kuster-Wendenburg, p. 118 (? *partim, non* Sandberger).

v. 1975 *Streptochetus (Streptodictyon) cheruscus elongatus* (Nyst, 1845). — van den Bosch *et al.*, p. 66, pl. 5, fig. 2 (*partim, non* pl. 4, fig. 1a, b = *Streptodictyon impiger*; includes also *Streptodictyon subelongatus*).

v. 1979b *Streptochetus (Streptodictyon) retrorsicosta* (Sandberger 1860). — R. Janssen, p. 298, pl. 16, fig. 26 (*partim, non* Sandberger, not the second specimen from Glimmerode = *S. retrorsicosta*, ? nor the specimens from the Sternberger Gestein).

v. 1983 *Streptochetus (Streptodictyon) elongatus* (Nyst, 1843). — Müller, p. 49 (*partim, non* Nyst, *non* pl. 4, fig. 15; pl. 31, figs 8, 10 = *Streptodictyon subelongatus*, *non* pl. 31, fig. 7 = *Streptodictyon* sp. juv. specimens indet.; see also *S. subelongatus*).

Type material — The specimen described and illustrated by Nyst (1836) as *Fusus Sowerbei* was traced in a sample of the Nyst Collection (IRScNB IG 2738) containing 2 specimens. The preservation of the other specimen differs slightly from material as present in the Berg Sand Member. It is discussed below as Fasciolariidae sp. Originally, only a single specimen was available to Nyst, as implicitly stated in his 1836 paper (p. 34: '....; nous tenons cette coquille ....'), we assume the second specimen to have been added to this sample at a later stage.

Fig. 19. *Streptodictyon sowerbyi* (Nyst, 1836) emend., protoconch and early whorls. Weinheim, Kanalbau (Germany, Rheinland-Pfalz), Oligocene, Rupelian (Unterer Meeressand). Coll. KGM, x 25.

Fig. 20. *Streptodictyon sowerbyi* (Nyst, 1836) emend., protoconch and early whorls. Vliermaal, Mommen sand pit (Belgium, Limburg province), Oligocene, Rupelian (Rupel Formation, Kleine Spouwen Member = Nucula Clay). Coll. RGM 393.281 (AJL), x 25.

The specimen illustrated by Nyst we take to be the

holotype (IRScNB Cat. Types Invert. 6042). It is here illustrated in Pl. 4, fig.5.

Locus typicus — Kleine Spouwen, municipality of Bilzen, province of Limburg, Belgium.

Stratum typicum — Not indicated in the original publication. The state of preservation of the holotype indicates beyond doubt that it originates from the well-known Berg Sands Member, Rupel Formation (Rupelian).

Original description (translated by the present authors) — 'Shell with an acute spire, comprising 6 whorls, provided with 10 longitudinal, undulating ribs, cutting fine transverse striae, a fine and a coarser one alternate; right lip straight, thick; canal rather long'.

Diagnosis — A large species of *Streptodictyon* with radial and spiral sculpture persisting to the aperture. Protoconch slightly cyrtoconoid, with about 4 convex whorls, on the last 2 whorls a distinct reticulate sculpture of fine collabral riblets, cut by 5 spirals.

Teleoconch with coarse radial sculpture of some 12 straight ribs, reduced to 8 in large specimens. Spiral sculpture of 5-7 well-defined primary elements. Secondary spiral sculpture in two generations which soon become equally strong but remain distinctly weaker than the primaries. Aperture in (sub)adult specimens with a parietal tooth and one or two oblique columellar folds. Siphonal canal straight and moderately long.

Description — Shell fusiform, height to over 50 mm, about 2.4-2.8 times higher than wide, juvenile specimens are relatively less slender, apical angle of adult shells about 35°, slightly wider (about 40°) in juveniles.

The protoconch is multispiral, conical with slightly cyrtoconoid tangents, comprising 4¼ - 4½ convex whorls and about 1.5 times higher than wide, height 1.65 mm. The nucleus has a diameter of about 0.12 mm. The initial whorls are smooth, on the last two whorls a reticulate sculpture develops, consisting of four or five thread-like spiral lines, intersected by distant radial lines. Together these elements form rectangles which are distinctly wider than high. In between these sculpture elements an extremely fine spiral sculpture is visible in very well-preserved specimens. On the last protoconch whorl the radial sculpture gradually increases in strength. The boundary with the teleoconch is abrupt, and obvious because of a further, sudden increase in strength of the radial sculpture.

The shell has regularly convex teleoconch whorls; however, a subsutural depression is occasionally present. The body whorl occupies slightly more than six tenths of the entire shell height. The periphery is rounded, with a straight, rather distinctly separated siphonal canal.

The sculpture of the teleoconch is composed of orthocline collabral ribs, covering the entire shell to the apertural margin. On the first teleoconch whorls the number of radial elements is about 9 or 10, with the interspaces slightly narrower than the ribs. In the holotype the number of ribs quite exceptionally increases to 12, but in all other specimens available the number of ribs remains almost constant.

Spiral sculpture of five or six primary spirals, the upper two being distinctly weaker. Secondary spirals develop, in two generations from the second teleoconch whorl onwards. The secondary spirals reach almost the same strength, but remain recognisable to the apertural margin. They never reach the strength of the primary spiral sculpture, which results in a sculpture consisting of rather coarse spirals with 3 finer ones in between. The growth lines are not much accentuated and run parallel to the collabral sculpture.

In adult specimens a parietal tooth is present and the columella bears one or two very oblique spiral folds.

Material studied — Oligocene, Rupelian (Böhlener Schichten, Basissand): Germany (Sachsen) — **Zwenkau**, 1 specimen, Pl. 4, fig. 6, Mauritianum Naturkundliches Museum, Altenburg (A. Müller), mentioned in Müller, 1983, p. 49; this sample also contains 1 specimen of *S. subelongatus*.

Oligocene, Rupelian (Unterer Meeressand): Germany (Rheinland-Pfalz) — **Weinheim**, Kanalbau: 1 juv. specimen, Text-fig. 19, 24 juv. specimens, 1 specimen, Pl. 4, fig. 7, KGM; **Weinheim**, Zeilstück: 1 juv. specimen, KGM.

Oligocene, Rupelian (Rupel Formation, Berg Sand Member): Belgium (Limburg province) — **Berg**, near Kleine Spouwen, IRScNB (Bosquet Coll.), 1 specimen, mentioned in Glibert & de Heinzelin, 1954, p. 392 as *Aquilofusus elongatus*; furthermore this sample contains 1 specimen of *S. subelongatus* and 3 specimens of Fasciolariidae sp. (see below); Keistraat, temporary exposure: 3 specimens, 14 juv. specimens, RGM 393.277 (MBL & AJL, 1971); 1 specimen, 4 juv. specimens, MCL; **Borgloon**, road cut: 3 juv. specimens, RGM 393.278 (AJL); 5 juv. specimens, MCL; **Kleine Spouwen**, Level with *Astarte trigonella*: 1 specimen, Pl. 4, fig. 5, holotype, IRScNB Cat. Types Invert. no. 6042; illustrated in Nyst, 1836, pl. 4, fig. 89 *sub nomine Fusus Sowerbei* Nyst (no syntype !); mentioned in Nyst, 1845, p. 493 as *Fusus elongatus* (junior ?); mentioned in Glibert & de Heinzelin, 1954, p. 392 as *Aquilofusus elongatus*; furthermore this sample contains 1 specimen of Fasciolariidae sp. (see above in the paragraph 'type material').

Oligocene, Rupelian (Rupel Formation, Kleine Spouwen Member = Nucula Clay): Belgium (Limburg province) — **Kleine Spouwen**, Bosselaarstraat outcrop: 1 juv. specimen, 2 fragments, RGM 393.279 (ex RGM 222.323) (AJL, 1972-1973); **Vliermaal**, Mommen sand pit: 2 juv. specimens, 1 juv. specimen, Text-fig. 20, RGM

393.280-281 (AJL); 2 juv. specimens, MCL.

Oligocene, Rupelian (Rupel Formation, Terhagen Member and/or Putte Member): Belgium (Antwerpen province) — **Boom**: 1 specimen, RGM 393.375 (MBL); 3 specimens, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains 3 specimens of *Streptodictyon subelongatus*; 1 specimen and ? 1 specimen (poorly preserved), IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 1 specimen of *Streptodictyon subelongatus*; 1 specimen, IRScNB (G. Hasse), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 2 specimens of *Streptodictyon subelongatus*; **Burcht**: 1 specimen, IRScNB (van der Bruggen), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 1 def. specimen of *Streptodictyon subelongatus*; **Edegem**: 1 specimen, IRScNB (leg. Stevens), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 1 specimen of *Streptodictyon subelongatus*; 3 specimens, IRScNB (Nyst), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 1 specimen of *Streptodictyon subelongatus* and 1 specimen of *Bathytoma leunisii* (Philippi, 1843); **Hemiksem**: 1 specimen poorly preserved, with two columellar folds, IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; **Niel**: 5 specimens, RGM 393.282 (M. Vervoenen); 1 specimen, RGM 393.283 (FJR); 1 specimen, RGM 393.284 (AJL, September 1963); 4 specimens, RGM 393.285 (MBL); 1 specimen, RGM 184.688 (MBL), illustrated in van den Bosch *et al.*, 1975, pl. 5, fig. 2 *sub nomine Streptochetus (Streptodictyon) cheruscus elongatus*; 1 specimen, Pl. 4, fig. 8, RGM 393.286 (HBH); 2 specimens, KBIN (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 8 specimens of *Streptodictyon subelongatus*; 3 specimens, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 5 specimens, IRScNB (van den Broeck), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 1 specimen of *Streptodictyon subelongatus* and 1 specimen of *Aquilofusus waeli auct. non* Nyst; 5 specimens, IRScNB (Daimeries/Dautzenberg); this sample also contains 8 specimens of *Streptodictyon subelongatus* and 2 specimens of *Aquilofusus waeli auct. non* Nyst; 32 specimens, IRScNB (purchased Piret), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 47 specimens of *Streptodictyon subelongatus*, 2 specimens of *Aquilofusus waeli auct. (non* Beyrich) and 2 specimens of *Fusiturris selysii* (de Koninck, 1838); **Niel and/or Boom**: 1 specimen, Pl. 4, fig. 9, IRScNB TCCI 6050 (Delheid), 1 specimen, IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 3 specimens of *Streptodictyon subelongatus*; 7 specimens, MCL; **Noeveren**: 2 specimens, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 1 juv. specimen of *Streptodictyon subelongatus*; 1 def. specimen, IRScNB (leg. unknown), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; **Rumst** (labelled 'Rumpst'): 1 specimen, IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*, this sample also contains 2 specimens of *Streptodictyon subelongatus*; 2 juv. specimens, IRScNB (Dujardin), mentioned in Glibert, 1957 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 2 adult specimens of *Streptodictyon subelongatus*.

Oligocene, Rupelian (Rupel Formation, Terhagen Member and/or Putte Member): Belgium (Oost Vlaanderen province) — **Ba(e)sele** (nowadays Bazel): 1 specimen, Pl. 4, fig. 10, IRScNB TCCI 6051 (Nyst), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 1 juv. specimen of *Streptodictyon* ? *subelongatus* and 2 juv. specimens of *S. impiger*; 1 specimen, IRScNB (le Hon), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 3 specimens, IRScNB (le Hon), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 2 specimens of *Streptodictyon subelongatus*; 2 specimens, IRScNB (G. & E. Vincent), mentioned in Glibert, 1957 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 5 specimens of *Streptodictyon subelongatus* and 1 specimen gen. et sp. indet.; 4 specimens, IRScNB (Daimeries/Dautzenberg); **Rupelmonde**: 3 specimens, IRScNB (Th. Lefèvre), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 5 specimens of *Streptodictyon subelongatus*; **Steendorp**: 2 specimens, IRScNB (Delveaux), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 2 specimens of *Streptodictyon subelongatus*; 1 specimen, IRScNB (Germaine De Gottal, 4-4-1900), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 4 specimens of *Streptodictyon subelongatus*; **locality unknown**: 1 specimen, IRScNB (Daimeries/Dautzenberg).

Oligocene, Rupelian (Brinkheurne Formation, Woold Member): The Netherlands (Gelderland province) — **Winterswijk**, de Vlijt clay pit: 1 juv. specimen, MCL.

Oligocene, Rupelian (Rupel Formation, Putte Clay Member): Belgium (Antwerpen province) — **Antwerpen**, construction pit for E3 (= Kennedy) tunnel: 1 specimen,

RGM 393.287 (MBL); 7 specimens, RGM 393.288 (AJL); 1 specimen, RGM 393.289 (AJL), illustrated in Cadée (1969, p. 43, fig. 5), *sub nomine Scalaspira* (sic !) *cheruscus elongatus*; 9 specimens, RGM 393.290 (DMM); 1 specimen, MCL; **Kruibeke**; 4 specimens, RGM 221.031 (AJL, 1972-1975); 6 specimens, MCL, 1972-1975; ? 2 juv. specimens, HBH; 1 specimen, IRScNB (E. van den Broeck), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*.

Oligocene, Rupelian (Rupel Formation, Rupel Clay Member): Germany (Brandenburg) — **Bad Freienwalde**: 2 specimens, IRScNB (Schenck); mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; Ziegel-Dränrohr clay pit: 1 specimen, MCL, 1993; **Hermsdorf**: 1 specimen, IRScNB (Dejaer), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; 4 specimens, IRScNB (G. & E. Vincent), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*.

Oligocene, Rupelian (Rupel Formation, Rupel Clay Member): Germany (Mecklenburg-Vorpommern) — **Malliß**, 1 specimen, MCL.

Oligocene, Chattian A (Söllingen Sand Formation, Asterigerina Horizon): Germany (Niedersachsen) — **Söllingen**, railroad cut between Söllingen and Jerxheim: 73 juv. specimens, RGM 393.291 (AJL, May 1982); 3 def. specimens, 18 juv. specimens, MCL (PGL, May 1982); 17 juv. specimens, AJB, May 1982.

Oligocene, Chattian A (Kasseler Meeressand, 'Schill 1'), Germany (Hessen) — **Glimmerode**, former lignite pit Höllkopf: 1 juv. specimen, RGM 393.292 (MBL, June 1973); exact level unknown: 1 specimen, leg. H. Humberg, 1977, SMF 250707/1, illustrated in R. Janssen, 1979b, pl. 16, fig. 26 *sub nomine Streptochetus (Streptodictyon) retrorsicosta*).

Oligocene, Chattian A (Grafenberger Sande): Germany (Nordrhein-Westfalen) — **Rumeln**, dump of mine shaft Diergardt VI: 1 juv. specimen, HBH.

Oligocene, Chattian ? A (Voort Formation, Veldhoven Member): Belgium (Limburg province) — **Houthalen**, shaft of coal mine I, depth 98-100.50 m below surface: 1 def. specimen, IRScNB (leg. IRScNB), mentioned in Glibert, 1957, p. 71 sub nomine *Streptochetus* (s.s.) *elongatus*; depth 84-98 m: 1 specimen, IRScNB (leg. unknown), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; **Houthalen**, shaft of coal mine II, depth 94-102.50 m below surface: 1 specimen and 6 specimens, IRScNB (leg. IRScNB), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; the first sample also contains an unidentifiable fragment; the second sample also contains 2 specimens of *Charonia flandrica* (de Koninck, 1838) and 1 specimen of *Aquilofusus* sp. indet.; depth 88-94 m: 1 specimen, Pl. 4, fig. 11, IRScNB TCCI 6052 (leg. IRScNB), 7 specimens, IRScNB (leg. IRScNB), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; Voort, municipality Zolder, shaft of coal mine I, depth 86-90 m below surface: 2 specimens, IRScNB (leg. IRScNB), mentioned in Glibert, 1957, p. 71 sub nomine *Streptochetus* (s.s.) *elongatus*; depth 83-90 m: 6 specimens and 1 specimen, Pl. 4, fig. 12, IRScNB (leg. IRScNB) Cat. Types Invert. no. 4744, mentioned and illustrated, respectively, in Glibert, 1957, pl. 5, fig. 19 *sub nomine Streptochetus* (s.s.) *elongatus*; depth 80-83 m: 1 specimen, IRScNB (leg. IRScNB), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; **Voort**, municipality Zolder, shaft of coal mine II, depth 83 - 91.50 m below surface: 4 specimens, 10 def. specimens/ fragments, IRScNB (leg. IRScNB), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*.

Oligocene, Chattian A/B (reworked boulders of 'Sternberger Gestein': Germany (Mecklenburg-Vorpommern) — **Sternberg**: 1 specimen, IRScNB (Rutot), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*.

Remarks — The above description is based on the holotype, and on predominantly juvenile specimens from sandy deposits in the North Sea and Mainz Basins. Most of the available specimens, however, originate from Rupelian clays in the North Sea Basin. These specimens, generally adults, with usually eroded apical whorls, differ from the typical form from sandy deposits by the presence, from the fourth or fifth whorl onwards, of a well-developed subsutural depression. On the boundary between the concave and the convex parts of the whorl the radial ribs form knobs, above which the ribs efface towards the upper suture. In a few specimens the ribs are slightly prosocline, rather than orthocline. Forms like these more closely resemble *S. retrorsicosta*, but may be distinguished by their relatively long siphonal canal and the less pronounced columellar and parietal teeth. Furthermore, they grow to considerably larger sizes.

This species has usually not been distinguished from the accompanying *S. subelongatus*. Even Nyst himself, after having introduced the species on the basis of Berg Sands material, from 1845 onwards no longer considered it a separate taxon, which explains the subsequent confusion in the literature (compare *e.g.* d'Orbigny, 1852, p. 68 and especially Deshayes, 1865, p. 254).

Nyst's text of *'Fusus Sowerbei'* is full of conflicting details. He synonymised *Murex rugosus* Sowerby and changed the genus to *Fusus*. Therefore the taxon, in his view, became a homonym of *Fusus rugosus* Lamarck, and thus a trivial name had to be proposed: *'F. Sowerbei'*. However, the plate in Sowerby (1821, pl. 274, figs 8, 9)

Nyst referred to makes it clear that this situation may be interpreted in a different manner. Here, instead of *Murex rugosus*, curiously enough, *Fusus rugosus* is found, and amongst the synonyms given by Sowerby '*Fusus rugosus* La Marck' occurs, an Eocene species utterly distinct from the specimen described and illustrated by Nyst. In 1836, Nyst, however, considered the two conspecific. The name *Murex rugosus* as used by Nyst, probably is not just an error, but most certainly the incorrect plate number was given by Nyst. What Nyst apparently wished to refer to is the text of *Murex rugosus*, in Sowerby (1813, p. 75), referring to plate 34 'upper figures' which illustrate a species from the 'Crag of Suffolk' (Nyst also mentioned 'le Crag de Suffolk' !), now known as *Searlesia costifera* (S.V. Wood, 1848). Incidentally, Sowerby's name '*Murex rugosus*' is erroneously cited, again as '*Fusus rugosus*', in Wood's (1848, p. 48) description of *Trophon costiferum*. As a way out of this taxonomic confusion we have to accept the name *F. Sowerbei* as a sp. nov.

There is, moreover, the problem of the incorrect spelling of the epitethon specificum. From Nyst's text we may safely assume that the species was named after [J.] Sowerby; thus the correct spelling should have been '*Fusus sowerbyi*'. In this context it is interesting to note, that Nyst in his 1845 paper on p. 493 used the spelling *Fusus Sowerbei*, the index (p. 666) gives *Fusus Sowerbyi*.

This clearly is a case of 'incorrect original spelling' as outlined in art. 32(c) of ICZN, which has to be corrected [art. 32(d)], and thus we emend the name to *Fusus sowerbyi* Nyst, 1836 emend. In so doing, *Fusus Sowerbyi* d'Orbigny, 1850, introduced as a nom. nov. for *Fusus bulbiformis* Sowerby, *non* Lamarck, becomes a junior homonym, for which we have not been able to find an available junior synonym. Therefore we substitute:

Fusus dhondtae nom. nov.
pro *Fusus Sowerbyi* d'Orbigny, 1850
non *Fusus sowerbyi* Nyst, 1836 emend.

in recognition of Dr Annie Dhondt of IRScNB, whose assistance during our study is much appreciated.

The *stratum typicum* of *S. sowerbyi*, the Early Rupelian Berg Sand Member in Belgium, has yielded, in addition to the holotype, only specimens that differ from the typical form in several respects. In these shells the radial sculpture is markedly finer, with more (up to c. 15) and weaker radial ribs, which is why such specimens resemble *S. cheruscus*. Thus they can easily be separated taxonomically, *e.g.* as a forma, or even at species level. The fact, however, that the few available protoconchs (from the Berg Sands and from the Kleine Spouwen Member; a single similar specimen was found in the Rupelian clays of Malliß, FRG) are identical, and that the secondary spiral sculpture is the same as in the holotype (and in the Boom Clay specimens), made us decide not to distinguish these specimens from the nominal form. In so doing we accept a fairly wide range of variation for the present species.

Only very few juvenile, very well-preserved specimens are available from the Rupelian Kleine Spouwen Member (= the well-known 'Nucula Clay'). A comparison of these specimens with juvenile shells from other localities indicated a closer resemblance to *S. sowerbyi* than to *e.g. S. cheruscus* (density of radial ribs on the initial teleoconch whorls, elongate quadrangles in protoconch sculpture, etc.).

Stratigraphical and geographical distribution — *S. sowerbyi* is known from the 'Unterer Meeressand' in the Mainz Basin, from the 'Böhlener Schichten' (Rupelian) of the Leipzig area and from the Berg Sands Member and the Boom Clay in the North Sea Basin (Oligocene, Rupelian). Furthermore, a number of juvenile specimens of Chattian A age from Söllingen (Germany) are considered to belong to this species (see remark in the description of *S. retrorsicosta*), as are some samples from the Belgian Voort Formation (Voort and Houthalen shafts).

Evolutionary developments — In some respects *Streptodictyon sowerbyi* resembles *S. retrorsicosta*, *e.g.* in the development of the secondary sculpture and in apertural characteristics. The embryonic shells are very similar. Both species, however, co-occur in the sandy Rupelian deposits in the Mainz Basin, although not together at a single locality. The available data, however, are insufficient for determining which of the two taxa should be looked upon as the ancestral species.

S. cheruscus might be a descendant of *S. sowerbyi*. However, these species co-occur in the Early Chattian of Söllingen. We assigned all specimens from the Voort Formation in Belgium to *S. sowerbyi*, although their state of preservation is occasionally rather poor.

Streptodictyon subelongatus (d'Orbigny, 1852)
Pl. 4, figs 13, 14; Pl. 5, figs 1-5; Text-figs 21, 22

(A separate list of synonyms is given for the forma *speyeri*)

v. 1835 *Fusus rugosus* ? — Nyst, p. 30 (*partim*, only the specimens from Boom).
? 1836 *Fusus porrectus*, Nob., Nyst, p. 33 (*non Murex porrectus* Solander *in* Brander, 1766).
v. 1838 *Fusus porrectus*. — de Koninck, p. 17 (*partim*, only the specimens from Belgium).
v 1843 *Fusus elongatus* Nyst, p. 453.
v. 1845 *Fusus elongatus* Nyst, p. 493, pl. 38, fig. 25a, b (*partim*, includes also *S. sowerbyi*).

? 1848 *Fusus Deshayesii* De Kon. — Beyrich, p. 13 (? *non* de Koninck; may be only part of the specimens from Hermsdorf).

1848 *Fusus elongatus* Nyst — Bronn, p. 512.

* 1852 *Fusus subelongatus*, d'Orb., 1847, d'Orbigny, p. 13 (26e étage, no. 204) (partim) [substitute name for *F. elongatus* Nyst, 1843 *non* Bronn, 1847; localities partly incorrect, at least not mentioned in Nyst, 1845].

1856 *Fusus elongatus* Nyst — Beyrich, p. 283, pl. 24, fig. 6 (*partim*, *non* pl. 24, figs 3a, b, 4a-c = *Streptodictyon cheruscus*; *non* pl. 24, fig. 5, 5a = ? *Streptodictyon retrorsicosta*).

? 1867 *Fusus elongatus* Nyst. — von Koenen, p. 79 (*partim*, not the Late Oligocene specimens; among the Rupelian material *S. subelongatus* may have been present).

? 1878 *Fusus elongatus* Nyst. — Credner, p. 647.

? 1886 *Fusus elongatus* Nyst — von Koenen, p. 886.

? 1889 *Fusus elongatus* Nyst — von Koenen, p. 185 (*partim*, ? pl. 15, figs 1, 2, not the Chattian specimens).

1901 *Fusus elongatus* Nyst — Cossmann, p. 31 (*partim*, not the specimens from Kassel, nor those from France).

? 1907 *Fusus elongatus* Nyst. — Ravn, p. 120, pl. 6, fig. 1 (*partim*, *non* Nyst, only the Rupelian specimens, *non* pl. 6, fig. 2 = *S. cheruscus*).

? 1926 *Fusus elongatus* Nyst. — Warneck, p. 32 (? partim).

v. 1954 *Aquilofusus elongatus* Nyst, sp. 1843 — Glibert & de Heinzelin de Braucourt, pp. 392, 393 (*partim*, includes also *S. sowerbyi* and Fasciolariidae sp.).

v. 1957 *Streptochetus* (s.s.) *elongatus* Nyst, sp. 1843 — Glibert, p. 71 (*partim*, only part of the Rupelian specimens, *non* pl. 5, fig. 19 = *S. cheruscus*).

? 1963 *Streptochetus* (s.s.) *elongatus* Nyst, sp. 1843. — Glibert, p. 147 (*partim*, only the Rupelian specimens from the North Sea Basin).

1967 *Streptochetus* (s.s.) *elongatus* (Nyst, 1843) — Bosch, p. 6, pl. 1, fig. 7 (mala) (excl. syn.).

v. 1975 *Streptochetus (Streptodictyon) cheruscus elongatus* (Nyst, 1845). — van den Bosch *et al.*, p. 66 (*partim*, *non* pl. 4, fig. 1a, b = *Streptodictyon impiger*; *non* pl. 5, fig. 2 = *Streptodictyon sowerbyi*).

v. 1983 *Streptochetus cheruscus elongatus* (Nyst, 1843). — Geys & Marquet, p. 174, pl. 75, fig. 6 (holotype !).

v. 1983 *Streptochetus (Streptodictyon) elongatus* (Nyst, 1843). — Müller, p. 49, pl. 4, fig. 15; pl. 31, figs 8, 10 (*partim*, *non* pl. 31, fig. 7 = *Streptodictyon* sp. juv. indet.; see also *S. sowerbyi*).

Non:

1835 *Fusus elongatus* (beck), Beck, p. 218 (*nomen nudum*).

1840 *Fusus elongatus* Kiener, p. 53, pl. 28 (*non* pl. 27).

1936 *Fusus elongatus* Nyst — Gillet & Theobald, p. 62, pl. 3, fig. 18 = *Typhis cuniculosus* (Nyst, 1836).

Fig. 21. *Streptodictyon subelongatus* (d'Orbigny, 1852), protoconch and early teleoconch whorls. Berg, Kleine Spouwen, Dorpsstraat outcrop (Belgium, Limburg province), Oligocene, Rupelian (Rupel Formation, Kleine Spouwen Member). Coll. RGM 222.405 (MBL, 1964), x 25.

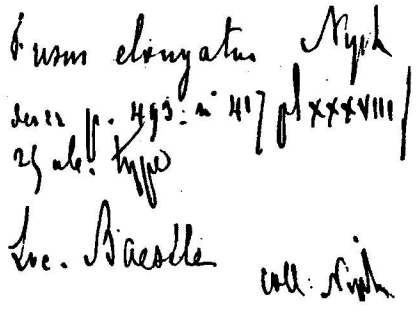


Fig. 22. *Streptodictyon subelongatus* (d'Orbigny, 1852) (**holotype**). Original label in H. Nyst's hand, stating: '*Fusus elongatus* Nyst / descr p. 493 n. 417 pl xxxviii f / 25ab. type / Loc. Baesele coll. Nyst', KBIN 6060.

Type material — Holotype: Pl. 4, fig. 13, IRScNB (de Koninck/Nyst), Cat. Types Invert. no. 3870, illustrated in Nyst (1845, p. 493, pl. 38, fig. 25a, b). One of the accompanying labels (Text-fig. 22), in H. Nyst's hand, bears the indication 'type' (compare also Glibert & de Heinzelin, 1954, p. 369).

Locus typicus — The holotype originates from a former clay-pit at Baesele (nowadays Bazel), province of Oost-

Vlaanderen, Belgium.
Stratum typicum — Rupel Formation, Terhagen Member or lower part of Putte Member.
Original diagnosis — Not given.
Diagnosis — A large species of *Streptodictyon* with radial and spiral sculpture persistent towards the aperture. Protoconch conical to slightly cyrtoconoid, nucleus swollen, initial 4½ whorls without macrosculpture, the last one occasionally slightly carinated in its lower part. On the following whorl a sculpture develops of c. 6 spirals and irregularly spaced collabral ribs, transitional to the teleoconch radial sculpture and hardly producing a reticulate pattern as in the type species, or not at all. Teleoconch with coarse radial and much finer spiral sculpture persisting to the apertural margin.
Description (typical form) — Shell large (height in excess of 75 mm), fusiform, slender, up to 3.3 times higher than wide, juvenile specimens are relatively less slender (2.8 times higher than wide at a shell height of some 20 mm), apical angle of adult shells about 25°, slightly wider (about 35°) in juveniles.

The protoconch is multispiral, conical with straight tangents. The transition to the teleoconch is gradual in all available specimens, so the exact number of protoconch whorls cannot be determined. The slightly swollen, semispherical nucleus has a diameter of 0.10 mm. The initial 4½ whorls are rather convex, with a slightly carinated lower part. Their surface is smooth, but at higher magnification (50 x) a microsculpture is visible, consisting of numerous spiral rows of granules, elongated in the same direction (only occasionally seen in excellently preserved specimens!). This microsculpture remains present until at least the second teleoconch whorl. On the second half of the fifth whorl a transitional sculpture develops, consisting of some seven spiral lirae and widely spaced collabral elements. Both spiral and radial elements increase gradually in strength and imperceptibly turn into the teleoconch sculpture. A reticulate pattern as seen in *e.g. S. cheruscus* or *S. sexcostatus* is absent.

The shell has moderately convex teleoconch whorls. From teleoconch whorl 4 or 5 onwards a distinct subsutural depression is present. The body whorl occupies slightly less than two thirds of the entire shell height in fully-grown specimens. The periphery is slightly carinated on the boundary of the subsutural depression. The transition into the base is gradual. The siphonal canal is slightly curved to the left (apertural view). In large specimens a pseud-umbilicus is indicated, but the base remains imperforate. It is accentuated by a produced siphonal fasciole.

The sculpture of the teleoconch is composed of orthocline, rather heavy collabral ribs, covering the entire shell to the apertural margin. On the somewhat shouldered lower margin of the subsutural depression the radial ribs form distinct knobs. On the initial teleoconch whorls the number of radial elements is about 10-12, with the interspaces as wide as the ribs; only on very large specimens do the interspaces become somewhat wider, but the number of radial ribs usually remains more or less constant.

Spiral sculpture of seven to ten primary spirals (frequently one is situated in the lower suture). The spirals are thread-like, especially so on the first whorls. Secondary spirals develop in two generations, at first near the upper and lower suture, later also on the middle part of the whorls. They do not attain the strength of the primaries; all generations remain recognisable as such. The secondary sculpture usually starts on the fourth radially sculptured whorl. In adult specimens the sculpture may be slightly reduced and irregular.

The growth lines are distinct, but not very close-set or lamellose. They run, parallel to the collabral sculpture, slightly opisthocyrt.

The inner shell wall of medium-sized specimens bears spiral lirae at certain growth intervals. In adult specimens such lirae are absent, but here the inner apertural margin has short grooves, corresponding with the spiral sculpture. Even in fully grown specimens a parietal tooth is absent, although unabsorbed remnants of the spiral sculpture do occur. A columellar fold is usually absent, but sometimes one, or even two, weakly developed folds may be seen.

Material studied — Oligocene, Rupelian (Böhlener Schichten, Basissand): Germany (Sachsen) — **Zwenkau**, 1 specimen, Pl. 5, fig. 3, Mauritianum Naturkundliches Museum, Altenburg (leg. A. Müller), illustrated in Müller, 1983, pl. 4, fig. 15; this sample also contains 1 specimen of *S. sowerbyi.*

Oligocene, Rupelian (Rupel Formation, Berg Sand Member): Belgium (Limburg province) — **Berg**, Kleine Spouwen, lower part = level with *Callista kickxi* Nyst, 1836: 2 specimens, IRScNB (Bosquet), mentioned in Glibert & de Heinzelin, 1954, p. 392 *sub nomine Aquilofusus elongatus*; Level with *Astarte trigonella*: 2 specimens, IRScNB (Bosquet), mentioned in Glibert & de Heinzelin, 1954, p. 392 *sub nomine Aquilofusus elongatus*; this sample furthermore contains 1 specimen of *S. sowerbyi* and 3 specimens of Fasciolariidae sp.; **Berg**, Kleine Spouwen, Keistraat temporary exposure: 2 specimens, Pl. 4, fig. 14; Pl. 5, fig. 1, RGM 393.193-194 (MBL & AJL, 1971); 49 specimens, 34 juv. specimens, RGM 393.195 (MBL & AJL, 1971); 5 specimens, 8 juv. specimens, MCL; **Borgloon**, roadcut, 6 specimens, 5 juv. specimens, RGM 393.196 (AJL); 10 specimens, 7 juv. specimens, MCL.

Oligocene, Rupelian (Rupel Formation, Kleine Spouwen Member): Belgium (Limburg province) — **Kleine**

Spouwen, Berg: 1 specimen, IRScNB (Bosquet), mentioned in Glibert & de Heinzelin, 1954, p. 393 *sub nomine Aquilofusus elongatus*; Dorpsstraat outcrop: 1 juvenile specimen, Text-fig. 21, RGM 222.405 (MBL, 1964); Bosselaarstraat outcrop: 2 juv. specimens, RGM 222.323 (AJL, 1972-1973); 1 juv. specimen, MCL; **Vliermaal**, Mommen sandpit: 1 specimen, RGM 222.191 (J. Mommen); 2 juv. specimens, RGM 222.119 (AJL); 1 specimen, 1 juv. specimen, MCL.

Oligocene, Rupelian (Boom Clay Formation, Terhagen and/or Putte Member): Belgium (Oost Vlaanderen province) — **Basele**: 1 specimen, Pl. 4, fig. 13, IRScNB (de Koninck/Nyst), Cat. Types Invert. no. 3870, holotype, illustrated in Nyst, 1845, pl. 38, fig. 25a, b *sub nomine Fusus elongatus*, mentioned as *Aquilofusus elongatus* in Glibert & de Heinzelin (1954, p. 368) and as *Streptochetus* (s.s.) *elongatus* by Glibert, 1957, p. 71; ? 1 juv. specimen, Pl. 5, fig. 2, IRScNB TCCI 6053 (Nyst), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 3 specimens and 2 juv. specimens, IRScNB (G. & E. Vincent), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 2 specimens of *S. sowerbyi* and 1 specimen gen. et sp. indet.; 2 specimens, IRScNB (leg. unknown), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 2 specimens, IRScNB (le Hon), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 3 specimens of *S. sowerbyi*; **Rupelmonde**: 6 specimens, IRScNB (Storms), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 5 specimens, IRScNB (Th. Lefèvre), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus* this sample contains also 3 specimens of *S. sowerbyi*; **Rupelmonde** and/or **Steendorp**: 8 specimens, IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; **Steendorp**: 2 specimens, IRScNB (purchased Vve v.d. Wouwe), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*]; 1 specimen, Pl. 5, fig. 4, 1 specimen (strongly knobbed and shouldered), Pl. 5, fig. 5, 2 specimens, IRScNB TCCI 6054-5 (leg. Germaine De Gottal, 4.4.1900), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. sowerbyi*; 1 specimen, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 2 specimens, IRScNB (Delveaux), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. sowerbyi*; 1 specimen, IRScNB (Société Royale de Zoologie d'Anvers), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*.

Oligocene, Rupelian (Rupel Formation, Terhagen Member and/or Putte Member): Belgium (Antwerpen province) — **Boom**: 1 specimen, RGM 393.197 (MBL); 3 specimens, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 6 specimens of *S. sowerbyi*; 1 specimen, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 2 specimens of *S. sowerbyi*; 2 specimens, IRScNB (Stevens), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 2 specimens, IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 1 specimen, IRScNB (Malaise), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. cheruscus* f. *fasciolaroides*, judging from its sediment contents this specimen may originate from the Edegem Sands, and therefore most probably the locality is incorrect; 2 specimens, IRScNB (G. Hasse), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. sowerbyi*; **Burcht**: 1 def. specimen, IRScNB (van der Bruggen), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. sowerbyi*; **Edegem**: 1 specimen, IRScNB (leg. Stevens), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. sowerbyi*; 1 specimen, IRScNB (Nyst), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. sowerbyi* and 1 specimen of *Bathytoma leunisii* (Philippi, 1843); **Hemiksem**: 1 specimen, IRScNB (Storm), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 2 specimens, IRScNB (leg. unknown), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; **Niel**: 6 specimens, RGM 393.198 (M. Vervoenen); 1 specimen, RGM 393.199 (FJR); 10 specimens, RGM 393.200 (MBL); 1 specimen, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *Glibertturricula vervoeneni* Cadée & Janssen, 1985 and 1 specimen of *Acamptogenotia morreni* (de Koninck, 1838); 9 specimens, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 8 specimens, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 2 specimens of *S. sowerbyi*; 1 specimen, IRScNB (van den Broeck), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 5 specimens of *S. sowerbyi* and 1 specimen of *Aquilofusus waeli auct. non* Nyst; 8 specimens, IRScNB (Daimeries/Dautzenberg), this sample contains also 5 specimens of *S. sowerbyi* and 2 specimens of *Aquilofusus waeli auct. non* Nyst; 47

specimens (locality uncertain), IRScNB (purchased Piret), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 32 specimens of *S. sowerbyi*, 2 specimens of *Aquilofusus waeli auct. (non* Beyrich), and 2 specimens of *Fusiturris selysii* (de Koninck, 1838); **Niel** and/or **Boom**: 3 specimens (one of these: height = 80 mm !), coll. IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 2 specimens of *S. sowerbyi*; 18 specimens, MCL; **Noeveren**: 1 juv. specimen, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. sowerbyi*; ? 1 def. specimen, IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; **Rumst**: (labelled 'Rumpst') 2 specimens, IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*, this sample also contains 1 specimen of *Streptodictyon sowerbyi*; 2 specimens, IRScNB (Dujardin), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 2 juv. specimens of *S. sowerbyi*; **Schelle**: 2 specimens, IRScNB (Daimeries/Dautzenberg); **Terhagen**: 2 specimens, IRScNB (Delheid), mentioned in Glibert, 1957, p. 71 *sub nomine Streptochetus* (s.s.) *elongatus*; 2 specimens, IRScNB (Dautzenberg, Mus. Brux. 9.4.1989); **locality unknown**: 1 specimen, IRScNB (Daimeries/Dautzenberg).

Discussion — The first description of the present taxon was given by Nyst (1835), who recorded a specimen from Boom (Belgium) as *'Fusus rugosus ?'*. A year later a fragmentary shell from 'Kleyn-Spauwen' was described by Nyst (1836, p. 33) as *Fusus porrectus*.

There has been some confusion over the first valid introduction of the name *Fusus elongatus* Nyst. It is usually cited with the year 1843, referring to Nyst's well-known publication 'Les coquilles et polypiers fossiles ... etc.'. Anderson (1964, p. 121, note 8) was the first to draw attention to the fact that the two different editions of this book were not published until 1845. However, the first valid introduction of the taxon is not found in that paper, but in an earlier one. The first recognisable description of this species was given by de Koninck (1838), as *Fusus porrectus*, a name taken from an earlier species list provided by Nyst (1836). Nyst (1843), after having realised that this identification was erroneous, introduced the name *Fusus elongatus*, referring to de Koninck's description. Therefore de Koninck's specimen may be considered holotype. Thus, after all, the indication 'Nyst, 1843' is correct, although with reference to another paper.

Unfortunately, however, Nyst's name is preoccupied by *Fusus elongatus* Kiener, 1840, a Recent species from the Indo-Pacific (Kiener, 1840, p. 53, pl. 27).

The next available synonym is a name introduced by d'Orbigny (1852, p. 13), who substituted Nyst's name *Fusus elongatus* by the name *Fusus subelongatus*, because of supposed preoccupation by Bronn, 1847. Bronn (1848, p. 512, which presumably is the paper meant by d'Orbigny), however, did not introduce a name *Fusus elongatus*, but merely referred to *Fusus elongatus* Beck, 1835, which he considered to be a *nomen nudum*. Indeed, Beck (1835-1836, p. 218) just mentioned this name in a short list of Palaeocene fossils, without giving any description or illustration. Thus, d'Orbigny apparently misunderstood the situation, but anyway, the substitution of the name remains valid, and therefore we accept the name *Fusus subelongatus* d'Orbigny, 1852. Of course, the holotype of Nyst's *Fusus elongatus* is also the holotype of *F. subelongatus*.

Streptodictyon subelongatus, in line with several other species in this fasciolariid group, apparently was not very fastidious in the choice of its habitat. Populations are known from heavy clays, as well as from high-energetic environments with sandy or even gravelly deposits. In large specimens it can be observed that the radial sculpture decreases in strength towards the aperture.

There is some variation in the height/width ratio of *S. subelongatus*. In general this variation is stronger in populations from clayey environments.

Stratigraphical distribution — Streptodictyon 'elongatus' has been recorded by several authors, from sediments of Latdorfian age. Although material of that age is not included in the present study, we should point out that von Koenen's illustrations (1889, pl. 15, figs 1, 2) do appear to represent this species. That author also mentioned specimens from the Belgian localities of Vliermael, Lethen, Hoesselt and Grimmertingen. We have substantial material from the two last-mentioned localities, but *S. subelongatus* is absent. We have seen a single, unequivocal specimen in IRScNB (Bosquet), in a sample of five specimens from Lethen (Grimmertingen Sand Member), labelled *'Fusus crassisculptus* ?? Beyrich'. This specimen, however, does not show the normal Grimmertingen preservation and we assume it came from the Kleine Spouwen Member.

To our knowledge *S. subelongatus* is present in the lower part of the Rupelian (s. str.) deposits of the North Sea Basin (Bilzen Formation, Berg Sand and Kleine Spouwen Members; Boom Clay Formation, Terhagen Member; Brinkheurne Formation, Kotten Member; and several equivalents of these units in Germany).

Evolutionary developments — The evolutionary roots of this species are unknown. It occurs in the Rupelian and might be the predecessor of *S. impiger*, which is known from the higher parts of the Rupelian deposits (Putte Clay Member, Woold Clay Member).

Fig. 23. *Streptodictyon subelongatus* (d'Orbigny, 1852) forma *speyeri* (Deshayes, 1865), protoconch and early whorls. Waldböckelheim (Germany, Rheinland-Pfalz), Oligocene, Rupelian (? Oberer Meeressand). Coll. KGM, x 25.

Streptodictyon subelongatus (d'Orbigny, 1852)
forma **speyeri** (Deshayes, 1865)
Pl. 5, figs 6-8; Text-fig. 23

* 1865 *Fusus Speyeri*, Desh., Deshayes, p. 270, pl. 85, fig.7.

v. 1860 *Fusus elongatus* Nyst — Sandberger, pl. 17, fig. 5, 5a-d.

1860 *Fusus Waelii* Nyst var. — Sandberger, pl. 19, fig. 1, 1a-b (*non* Nyst; the identification of the illustrated specimen is indicated as a 'lapsu calami' in the text, see reference below).

v. 1861 *Fusus elongatus*. Nyst — Sandberger, p. 219.

? 1880 *Fusus elongatus* (Nyst.) — Meunier *in* Meunier & Lambert, p. 250, pl. 14, figs 15, 16.

? 1884 *Fusus elongatus*, Nyst. — Cossmann & Lambert, p. 156, pl. 5, fig. 16 (poorly preserved specimen ?).

1884 *Fusus Speyeri* Deshayes. — Cossmann & Lambert, p. 157, pl. 5, fig. 15.

1893 *Siphonalia Speyeri* (Deshayes). — Cossmann, p. 342.

1893 *Streptochetus elongatus* (Nyst). — Cossmann, p. 344.

1901 *Fusus elongatus* Nyst — Cossmann, p. 31 (*partim*, only the specimens from Pierrefitte).

?v. 1928 *Streptochetus (Streptochetus) elongatus* (Nyst) — Zinndorf, p. 24, pl. 2, figs 1, 1a.

?v. 1928 *Streptochetus hahni* Kocks, Zinndorf, p. 26, pl. 2, fig. 2, 2a.

? 1949 *Fusinus elongatus* Nyst — Gillet, p. 65, pl. 4, fig. 17, 17a.

? 1963 *Streptochetus* (s.s.) *elongatus* Nyst, sp. 1843. — Glibert, p. 147 (*partim*, only the specimens from Weinheim).

1973 *Streptochetus (Streptodictyon) cheruscus elongatus* (Nyst, 1843). — Kuster-Wendenburg, p. 116 (? *partim*, *Streptodictyon undatus* might be included).

Type material — Holotype is Deshayes's (1865, pl. 85, fig. 7), the whereabouts of which is unknown to us.

Locus typicus — 'Jeures' (= Jeurre) (France, Essonne department).

Stratum typicum — Sables de Fontainebleau, Falun de Jeurre (Oligocene, Rupelian).

Essential details of original description — *Fusus* with a slender, elongate shell, apex acuminate, eleven convex whorls slowly increasing in diameter, suture simple, undulating, flattened. Initial two whorls smooth, the others with slightly oblique longitudinal ribs, broadening from the upper to the lower suture. Spiral sculpture of eight similar, equidistant, simple spirals. Body whorl short, ovate, gradually narrowing anteriorly, siphonal canal missing. The spirals on the base are coarser and more widely spaced, with a finer intermediate spiral. Aperture ovate, weakly angular posteriorly.

Description — This form of *S. subelongatus* reaches the same height, but differs from the typical form by having oblique radial ribs, especially on the initial whorls. The spirals on the early whorls are more close-set than in *S. subelongatus* s. str. Furthermore, on the youngest whorls the transition between the excavated subsutural part of the shell into the more convex lower part is developed as a weak to rather distinct carina. Also, the shape of the protoconch differs somewhat, with slightly cyrtoconoid instead of straight sidelines. The protoconch sculpture is identical.

Material studied — Oligocene, Rupelian (Unterer Meeressand): Germany (Rheinland-Pfalz) — **Weinheim**: 1 juvenile specimen, 2 fragments (illustrated in Sandberger, 1860, pl. 17, fig. 5d, 5/5a, 5c), IS 101 and IS 99, respectively, Museum Wiesbaden, Wiesbaden; ? 1 specimen, IRScNB (Nyst), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample contains also 1 specimen of *S. undatus*; **Weinheim**, Würzmühle ('Kanalbau'): 3 specimens, 1 specimen, Pl. 5, fig. 7, KGM; **Weinheim**, Zeilstück sandpit: 1 specimen, RGM 393.201 (AJL), 5 specimens, 3 juv. specimens (cf.), KGM; 1 specimen, MCL.

Oligocene, Rupelian (? Oberer Meeressand): Germany (Rheinland-Pfalz) — **Waldböckelheim**: 14 specimens, 1 juv. specimen, 1 juv. specimen, Text-fig. 23, KGM.

Oligocene, Rupelian (Sables de Fontainebleau, Falun de Jeurre): France (Essonne department) — **Auvers-St.**

Georges: 1 specimen, DLV.

Oligocene, Rupelian (Sables de Fontainebleau, Falun de Morigny): France (Essonne department) — **Morigny-Champigny**: 7 juv. specimens, RGM 393.202 (AJL, 1974); 5 juv. specimens, MCL; 13 specimens, 1 specimen, Pl. 5, fig. 8, MNHNP (Lozouet/Maestrati); 2 specimens, 3 juv. specimens, DLV; **Ormoy-la-Rivière**, borehole: 15 specimens, MNHNP (Lozouet/Maestrati).

Oligocene, Rupelian (Sables de Fontainebleau, Falun de Pierrefitte): France (Essonne department) — **Pierrefitte**: 6 specimens, 1 specimen, DLV; **St. Hilaire**, abandoned railroad cut: 2 specimens, MCL.

Oligocene, Rupelian (Kleine Spouwen Member): Belgium (Limburg province) — **Vliermaal**, Mommen sandpit: 2 juv. specimens, RGM 393.203 (AJL).

Oligocene, Rupelian (Rupelton): Germany (Rheinland-Pfalz) — **Offenbach**: 1 specimen, SMF (J. Zinndorf, 1901), illustrated *sub nomine Streptochetus (Streptochetus) elongatus* in Zinndorf, 1928, pl. 2, fig. 1, 1a; 1 def. specimen, SMF (J. Zinndorf, 1901; F. Kinkelin); **Offenbach**, Armenhaus: ? 1 specimen, Pl. 5, fig. 6, SMF 122905a/1 (J. Zinndorf, 1901; O. Boettger), holotype of *Streptochetus hahni* Zinndorf, 1928.

Remarks — Deshayes (1865) erected this taxon for a single specimen from Jeurre, its basal part not preserved, comparing it with '*S. elongatus*', which he found to be very similar in general form, but to differ in all other characteristics. These differences were elaborated by Cossmann & Lambert (1884, p. 157). In their opinion *S. speyeri* is smaller, with a more acuminate apical part, more numerous and more convex whorls, with less accentuated, more numerous and more oblique radial ribs, the main differences being the absence of the subsutural depression and the smooth columella without folds.

In Paris Basin material available to us fully adult specimens are rare and have their apical parts damaged or worn. So, we think that such larger shells were considered to represent '*S. elongatus*', whereas the younger individuals, on which the oblique axial sculpture is evident, were assigned to *S. speyeri*. This follows also from the illustrations in Cossmann & Lambert (1884, pl. 5). Their fig. 15 represents *S. speyeri* in a magnification of 1.5. '*S. elongatus*' is illustrated at natural size in fig. 16; this figure is just as large as that of *S. speyeri*, and therefore shows fewer details. It represents a distinctly worn specimen, with almost completely obsolete spiral sculpture.

Cossmann (1893, p. 342) described the protoconch of a very immature specimen as 'l'embryon a le dernier tour papilleux comme celui des *Siphonalia* ...' and therefore placed the species in the genus *Siphonalia*, family Buccinidae. His statement that the present species cannot be confused with '*S. elongatus*', because that species belongs in a completely different genus and even family, apparently is based on his observations of the protoconch. However, also the very few excellently preserved protoconchs of that species have their nucleus 'papilleux' (somewhat swollen). Additional differences with '*S. elongatus*' were not given by Cossmann, who compared *S. speyeri* more extensively with *S. undatus*.

We have not been able to recognise two taxa in the material from the Paris Basin Oligocene identified as '*S. elongatus*' and/or *S. speyeri*. Adult specimens closely resemble *S. subelongatus*, although they frequently have a well-marked subsutural depression, with a somewhat sharper carina and more accentuated knobs, than do typical *S. subelongatus* from the North Sea Basin. The combination of these characteristics makes such specimens approach the shape of *Acamptogenotia*. Juvenile shells, however, differ distinctly in their spiral and radial sculpture, details of which are always invisible in adult specimens. One might therefore interpret *S. speyeri* as a geographical subspecies of *S. subelongatus*.

Well-preserved juvenile specimens from the Belgian Kleine Spouwen Member, however, demonstrate that both types of protoconch (*S. subelongatus* and *S. speyeri*) co-occur there. Considering *S. subelongatus* and *S. speyeri* as subspecifically distinct would lead to the conclusions that both subspecies are present in the Kleine Spouwen Member, which is not acceptable. So, there are two possibilities, either:

- *S. subelongatus* and *S. speyeri* are two separate, partly sympatric species, or
- *S. speyeri* is a forma of *S. subelongatus*.

We finally opted for the second interpretation, mainly from a practical point of view, since the option of two separate species would mean that a large number of specimens could not be identified to species level with any certainty. In fact, even the holotype of *S. subelongatus* would thus become unidentifiable!

From the Mainz Basin we saw fairly well-preserved specimens from the 'Unterer Meeressand'. These have in general the same characteristics as Paris Basin *S. speyeri*, although slight differences occur in details of the sculpture and general shell form. In some specimens the axial sculpture on the early teleoconch whorls is less oblique than in material from the Paris Basin. We here assign such specimens to *S. subelongatus* forma *speyeri* as well.

We saw a rather limited number of specimens from the Mainz Basin Rupelian clays. We think that the specimen from Offenbach (Germany), illustrated in Zinndorf (1928, p. 26, pl. 2, fig. 2, 2a) as *Streptochetus hahni* 'Kocks' (SMF 122905a) cannot be separated from *S. subelongatus* f. *speyeri*. Preservation is poor, as is apparent from

Zinndorf's photographs. In fact, the second specimen illustrated by Zinndorf (1928, pl. 2, figs 1, 1a) as *S. elongatus*, by its thick-set form differs more strongly from typical *S. subelongatus* than does *S. hahni*. We consider both specimens to fall within the range of variation of *S. subelongatus* f. *speyeri*.

Stratigraphical distribution — The forma *speyeri* is known from the Rupelian s. str. of the Mainz ('Unterer Meeressand', ? 'Oberer Meeressand', 'Septarienton') and Paris Basins (Sables de Fontainebleau, lower part), and from the Rupelian Kleine Spouwen Member in the North Sea Basin.

Fig. 24. *Streptodictyon twistringensis* sp. nov. (**paratype**), protoconch and early teleoconch whorls. Twistringen, O. Sunder clay pit (Germany, Niedersachsen), Miocene, Reinbekian (Twistringen Clay Member, lower part of section exposed, in concentrations of teredinid material). Coll. RGM 393.294 (JVV), x 25.

Streptodictyon twistringensis sp. nov.
Pl. 5, figs 9, 10; Text-fig. 24

Type material — Holotype: Pl. 5, fig. 9, RGM 393.293 (JVV).

Locus typicus — Twistringen (Germany, Niedersachsen), O. Sunder clay pit.

Stratum typicum — Twistringen Clay Member (Miocene, Reinbekian), lower part of section exposed, in concentrations of teredinid material.

Derivatio nominis — Named after the type locality.

Diagnosis — A small species of *Streptodictyon* with radial and spiral sculpture persisting to the aperture. Protoconch conical, with 4¾ convex whorls, on the last 2½ whorls a distinct reticulate sculpture of fine collabral riblets, cut by 5 thin spirals. A sixth spiral is occasionally visible in the abapical suture. Teleoconch with coarse radial sculpture of 7 distinctly prosocline ribs. Spiral sculpture of 6-9 strikingly well-defined primary elements. Secondary spiral sculpture in a single generation, confined to the adapical part of the whorl and remaining distinctly weaker than the primary spirals. Aperture in (sub)adult specimens with a prominent parietal tooth and a columellar fold. Siphonal canal relatively short.

Description — Shell fusiform, rather small (up to 11 mm height) and thick-set for the genus, about 2.3 times higher than wide, juvenile specimens are relatively less slender (about 2 times higher than wide), apical angle of the largest specimen about 40°, slightly wider (about 45°) in juveniles.

The protoconch is multispiral, conical with slightly cyrtoconoid tangents comprising 4¾ convex whorls (but a single complete specimen available) and about 1.3 times higher than wide, height 1.6 mm. The nucleus has a diameter of 0.15 mm. The initial whorls are smooth, on the last 2½ whorls a reticulate sculpture develops, consisting of 5 to 6 equally strong, thread-like spiral lines, intersected by similar radial lines. Together these elements form rectangles which are about as high as wide, but on the last ½-¼ whorl of the protoconch the rectangles become relatively wider, as the radial sculpture elements are more widely spaced. In between these sculpture elements an extremely fine spiral sculpture is visible in very well-preserved specimens. On the terminal part of the protoconch the last six radial riblets gradually increase in strength. The boundary with the teleoconch is abrupt and distinct, as the first radial rib of the teleoconch is considerably stronger than the last one of the protoconch.

The shell has gradually curved, convex teleoconch whorls, lacking any subsutural depression. The body whorl occupies six tenths of the entire shell height. The periphery is rounded. Base with a well-separated siphonal canal, which is straight and remarkably short.

The sculpture of the teleoconch consists of distinctly prosocline, heavy collabral ribs, covering the entire shell up to the apertural margin. The number of radial elements is 7, with interspaces as wide as the ribs. The number of ribs remains constant. In apical view this results in a very regular spiral alignment of the radial sculpture.

Spiral sculpture of six to nine very well-defined primary spirals, the uppermost two or three slightly weaker than the lower ones. A single generation of secondary spirals develops from the second whorl onwards, at first on and immediately above the periphery, later also on the base of the shell. These spirals remain considerably weaker than the primaries. The growth lines are clearly visible and distinctly prosocline, as is the collabral sculpture.

Spiral lirae are present on the inner shell wall of a few specimens. In nearly all available specimens a distinct

parietal tooth is present and the columella bears a single, oblique spiral fold.

Paratypes — One paratype, Text-fig. 24, Pl. 5, fig. 10, RGM 393.294 (JVV); two paratypes in JVV. All specimens from the type locality.

Discussion — This species is close to *S. retrorsicosta*, and it is likely that taxa are members of the same lineage, an interpretation which is in agreement with their respective stratigraphical distributions.

S. twistringensis is easily distinguished from *S. retrorsicosta* by its having regularly convex whorls, sharply delimited spiral sculpture, and by just one generation of secondary sculpture. It displays a remarkable similarity to *Urosalpinx sismondai* (Michelotti, 1847) (see A.W. Janssen, 1972, p. 32, pl. 7, figs 3, 4; 1984, p. 225, pl. 9, fig. 11; pl. 61, fig. 1). Adult specimens of that species clearly differ in having a well-developed pseudumbilicus, but juvenile shells are very similar. They have, however, a slightly angular periphery, a more widely spaced spiral sculpture and a different protoconch.

Stratigraphical distribution — This species is exclusively known from the lower part of the Twistringer Schichten (Miocene, Reinbekian).

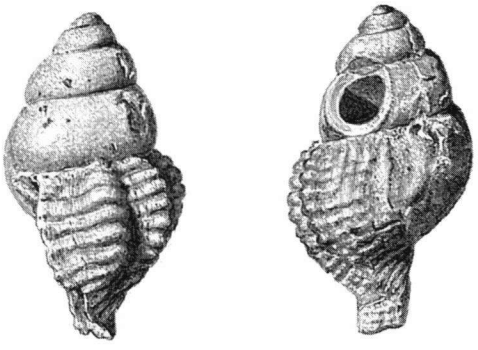


Fig. 25. *Streptodictyon undatus* (Meunier, 1880), protoconch and early teleoconch whorls. St. Hilaire, abandoned railroad cut (France, Essonne department), Oligocene, Rupelian (Sables de Fontainebleau, Falun de Pierrefitte, base). RGM 393.300 (AJL, April 1981), x 25.

Streptodictyon undatus (Meunier, 1880)
Pl. 5, figs 11-13; Text-figs 25-28

1880* *Fusus undatus* (San. Meun.) (*sic!*), Meunier, *in* Meunier& Lambert, p. 251, pl. 14, figs 19, 20.

1884 *Fusus undatus*, Stan. Meunier. — Cossmann & Lambert, p. 158, pl. 6, fig. 5.

1893 *Suessionia undata* (St. Meunier). — Cossmann, p. 341.

1901 *Suessionia undata* (Stan. Meun.). — Cossmann, p. 176.

? 1961 *Streptochetus septenarius* (Beyrich). — Tembrock, p. 368 (*partim*, *non* Beyrich, 1856, only the specimens from the Mainz Basin).

1965 *Streptochetus (Streptolathyrus)* cf. *undatus* (St. Meunier 1880). — Tembrock, p. 429, pl. 34, figs 5, 6.

Non:

1978 *Streptochetus (Streptolathyrus)* cf. *undatus* (Meunier 1880) cf. Tembrock 1965. — R. Janssen, p. 113 (= *Streptolathyrus masculinus*).

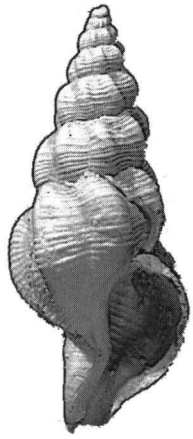
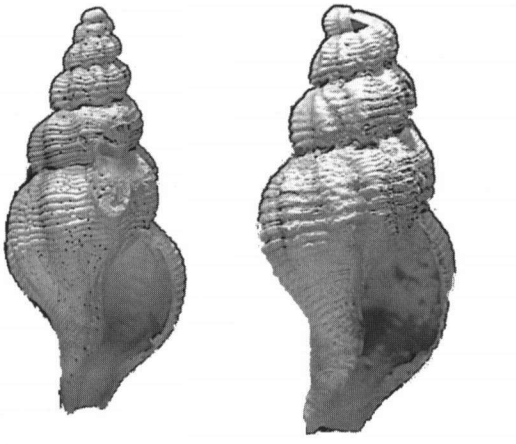


Fig. 26. *Streptodictyon undatus* (Meunier, 1880) (**lectotype**). Pierrefitte (France, Essonne), Oligocene, Rupelian, Sables de Fontainebleau, Falun de Pierrefitte. Coll. Lab. de Géol. MNHNP, x 3.

Type material — Three specimens in the collection of the Laboratoire de Géologie du Muséum national d'Histoire naturelle de Paris are supposed to be S. Meunier's originals. These specimens were made available to us by Drs F. Frohlich and P. Maestrati. The label accompanying this sample, supposedly not in S. Meunier's hand, states '*Fusus elongatus* Nyst — Pierrefitte — M. St. Meunier'.

The largest specimen agrees reasonably well with the illustration given by Meunier (*in* Meunier & Lambert, 1880, pl. 14, figs 19, 20). It is herewith designated lectotype (Text-fig. 26). The two smaller specimens are paralectotypes (Text-figs 27, 28).



Figs 27, 28. *Streptodictyon undatus* (Meunier, 1880) (**paralectotypes**). Pierrefitte (France, Essonne), Oligocene, Rupelian, Sables de Fontainebleau, Falun de Pierrefitte. Coll. Lab. de Géol. MNHNP, x 4 (fig. 27), x 5 (fig. 28).

Locus typicus — Pierrefitte (France, dép. Essonne, municipality of St. Hilaire).

Stratum typicum — Sables de Fontainebleau, Falun de Pierrefitte (Oligocene, Rupelian).

Original diagnosis — '*Fusus* with an elongate-oval shell, spire elongate conical; whorls narrow, slowly increasing in size, with longitudinal ribs, ornamented with numerous striae; aperture ovate, anteriorly attenuate; canal short, narrow, contorted, right margin simple' (translated from Latin).

Revised diagnosis — *Streptodictyon* with a protoconch having predominantly smooth whorls. On the last quarter of the protoconch body whorl a spiral sculpture occurs. Teleoconch with a very short canal, rather strongly curved to the left in apertural view. Spiral sculpture strikingly dense, with interspaces distinctly narrower than spirals.

Description — Shell fusiform. The largest specimens are about 16 mm high and have some six fairly convex teleoconch whorls. Apical angle varying from 28 to 36°, distinctly wider in very immature specimens. The height of the body whorl is about three fifths of the entire shell height. The base of the shell is rather abruptly contracted to a short canal, shorter than in any other species of the group under study. The columella is sigmoid, lacking any trace of folds or spirals. A parietal tooth is usually present in well-developed specimens. The inner shell wall bears dense spiral lirae, which are distributed in interrupted sets, situated at those places where a radial rib is present exteriorly.

The protoconch is conical, sometimes cyrtoconoid, about 1.6 times higher than wide, but with considerable variation, with 3¾ to 4¾ rather convex whorls. Its height varies from 1.0 to 1.8 mm. The nucleus has a diameter of 0.10 mm. The boundary with the teleoconch is usually sharp (only visible on excellently preserved specimens), but in a few specimens it is gradual. On the ultimate ¼ to ½ protoconch whorl a transitional sculpture occurs, consisting of about 7 faint spirals. Close to the actual boundary one or two collabral riblets are present. In extremely well-preserved specimens a very fine secondary spiral sculpture is seen on the protoconch's surface (magnification 50 x).

The teleoconch has seven or eight slightly prosocline, slightly flexuous or virtually straight collabral ribs per whorl, frequently continuous from one whorl to the next, at least on part of the shell. These ribs are overlain by a strikingly regular, dense sculpture of slightly flattened, close-set spirals separated by narrow furrows. Their number varies from seven to eight between the upper and lower suture. A secondary sculpture develops from the second whorl onwards, at first on the lower half of the whorl, but soon also higher. These spirals reach the strength of the primary ones and can no longer be distinguished, with the appearance of an additional generation of spirals.

The growth lines are regularly spaced and clearly visible between the spiral elements and have a slightly lamellose appearance.

Material studied — Oligocene, Rupelian (Berg Sand Member): Belgium (Limburg province) — **Berg**, near Kleine Spouwen, Keistraat temporary exposures, level with *Astarte trigonella*; 2 specimens, Pl. 5, figs 11, 12, 2 specimens, 4 juv. specimens, RGM 393.295-297, respectively (MBL & AJL, 1971); 2 juv. specimens, MCL; **Borgloon**, roadcut: 1 specimen, 2 juv. specimens, RGM 393.298 (AJL); 2 juv. specimens, MCL.

Oligocene, Rupelian (Unterer Meeressand): Germany (Rheinland-Pfalz) — **Bretzenheim**, Kreuzberg: 8 juv. specimens, RGM 393.299 (D.J. Mol, 1973); **Waldböckelheim**: 2 juv. specimens, PHB (Bamberg Coll.) Ga 70/71, illustrated in Tembrock, 1965, pl. 34, figs 5, 6; **Weinheim**: 1 specimen, IRScNB (Nyst), mentioned in Glibert, 1963, p. 147 *sub nomine Streptochetus* (s.s.) *elongatus*; this sample also contains 1 specimen of *Streptodictyon ? retrorsicosta*; **Weinheim**, Zeilstück sandpit: 45 juv. specimens, KGM.

Oligocene, Rupelian (Sables de Fontainebleau, Falun de Pierrefitte, base), France (Essonne) — **St. Hilaire**, abandoned railroad cut: 1 specimen, 1 juv. specimen, Text-fig. 25a, b, RGM 228.523 and RGM 393.300, respectively (AJL, April 1981); **St. Hilaire, Pierrefitte**: lectotype and paralectotypes as specified above (Figs 26-28); 1 specimen, Pl. 5, fig. 13, 22 specimens, RGM 393.301 and RGM 228.396, respectively (DLV); 2 specimens, 3 specimens, 1 specimen, DLV; 20 specimens,

MNHNP. (Lozouet/Maestrati).

Oligocene, Rupelian (Rupel Formation, Terhagen Member and/or Putte Member): Belgium (Antwerpen province) — **Niel**: 1 specimen, HBH; **Niel** and/or **Boom**: 2 specimens, MCL.

Oligocene, Rupelian (Rupel Formation, Putte Member): Belgium (Antwerpen province) — **Kruibeke**, clay pit: 1 specimen, RGM 221.032, 3 specimens, RGM 393.355 (AJL, 1972-1975): 2 juv. specimens, HBH.

Oligocene, Rupelian (Rupel Formation, Woold Member): The Netherlands (Gelderland province) — **Winterswijk**, De Vlijt clay pit complex: 1 specimen, RGM 393.302 (P.L.F. de Groot, September 1956).

Remarks — In comparison with typical *Streptodictyon* species, *S. undatus* differs distinctly by its short siphonal canal, and by a small protoconch the sculpture of which is restricted to spirals on the ultimate ½ protoconch whorl or less. Radial elements are present only on the transition to the teleoconch. The quite aberrant protoconch features of this species could easily be considered to be generic features. Still, seeing that this species is the precursor of *S. soellingensis*, which in its turn leads to forms having a reticulate protoconch sculpture, we decided to include all such forms in *Streptodictyon*, which therefore is characterised mainly by the presence of spirals in its protoconch sculpture.

Cossmann (1901, p. 176) assigned the present species to *Suessionia* Cossmann [1889, p. 161; monotype *S. exigua* (Deshayes)]. On account of protoconch morphology, Cossmann (1889) had considerable doubts on the systematic position of the taxon and provisionally placed it between the Buccinidae and the Turbinellidae. Wenz (1941, p. 1200, fig. 3416, as '*Suessonia*' (*sic* !) placed it with the Buccinidae.

S. undatus differs strongly from the type species of *Suessionia*, *e.g.* by its longer siphonal canal, absence of varices, completely different sculptural development, and in having a protoconch which is is less broadly conical and demonstrates spiral sculpture, absent from *Suessionia*.

Fusus undatus Meunier, 1880 is not a primary homonym of *Fusus undatus* (Gmelin, 1791) (*Murex*), a Recent species ('*habitat rarus in India*', Gmelin, 1791, p. 3556, no. 115).

In a sample from Weinheim (Zeilstück, KGM) we identified numerous juvenile specimens as *S. undatus*. Larger specimens from the same sample do not agree with that species, because of a less close-set spiral sculpture. Among the juveniles, two specimens have a protoconch that is distinctly wider than that of *S. undatus*. The larger specimens and the two juveniles had to be referred to *S. subelongatus* f. *speyeri*, despite the fact that they do not show the oblique axial sculpture on the early teleoconch whorls.

Specimens from the Rupelian Septaria Clay in the North Sea Basin differ consistantly from the population from sandier deposits in having relatively higher teleoconch whorls, a later onset of the secondary sculpture and a slightly longer siphonal canal. Still, these differences, presumably brought about by environmental conditions, appear insufficient for a taxonomic separation.

Stratigraphical distribution — *S. undatus* is known from deposits of Rupelian age (Sables de Fontainebleau, Falun de Pierrefitte, Paris Basin; 'U. Meeressand', Mainz Basin; Berg Sand and 'Rupel clay' deposits, North Sea Basin). Up to now this species was only recorded from the Paris and the Mainz Basins.

Evolutionary developments — *S. undatus* might be the precursor of *S. soellingensis* (Tembrock, 1961), a species from Late Oligocene (Chattian A) sediments of the North Sea Basin.

Genus *Streptolathyrus* Cossmann, 1901

1889 *Streptochetus (Pseudolatirus)* nov. sect. (*non* Bellardi, 1883) — Cossmann, p. 174.

1901 *Streptochetus (Streptolathyrus)* nom. mut., Cossmann, p. 31.

Type species — *Streptochetus Mellevillei* Cossmann, 1889 (monotype).

Original diagnosis — 'Size below average; form fusoid and elongate; size of spire slightly more than that of aperture, protoconch paucispiral, with a conical shell, with a small and obtuse nucleus; whorls with spiral threads and very obsolete ribs that in general disappear on the last ones. Aperture pear-shaped, not very wide, with a groove of variable depth in the lower angle, ending anteriorly in a moderately long canal, strongly curved to the right; lip hardly sinuous, slightly thickened, internally marked with some lirae; columella posteriorly very excavated, with a sudden curvature without a trace of folds, at the beginning of the canal; columellar margin thin, not free opposite the rolled swelling on the neck, not covering any umbilical slit (Note: to correctly interpret this diagnosis, if at all possible, the shell has to be held the 'French way': apex down !).

Revised diagnosis — Fasciolariid gastropod with elongate fusiform shell and convex teleoconch whorls. Ornament of coarse, predominantly straight, to slightly prosocline collabral ribs (about 7 per whorl), tending to disappear on the later whorls, overridden by three generations of spiral lirae that continue to the apertural margin. Protoconch multispiral, conical, of variable dimensions, with about 4 smooth whorls, sometimes with a spiral line along the lower suture. Close to the boundary with the teleoconch some radial riblets appear. Columella with one or more

denticles, sometimes elongated to short spirals. Parietal tooth usually present.

Remarks — The name *Streptolathyrus* was introduced by Cossmann (1901, p. 31) to replace *Pseudolatirus* Cossmann 1889, *non* Bellardi, 1884. Therefore the monotype of *Pseudolatirus* Cossmann also is the type species of *Streptolathyrus*. Some pages earlier Cossmann (1901, p. 24) emended *Pseudolatirus* Bellardi to *Pseudolathyrus*. The North Sea Basin species *'Fusus' rothi* was by some authors considered to belong in the taxon *Pseudolatirus* Bellardi (type species *Fusus bilineatus* Hoernes, 1856; subsequent designation Cossmann, 1901; emended to *Pseudolathyrus* by Cossmann, 1901), by others, however, in the taxon *Streptolathyrus* Cossmann, 1901 (type species *Streptochetus Mellevillei* Cossmann, 1889) = *Pseudolatirus* Cossmann, 1889, or in *Dolicholatirus* Bellardi, 1884 (type species *Turbinella bronni* Michelotti, 1847; emended to *Dolicholathyrus* by Cossmann, 1901 = ? *Latirofusus* Cossmann, 1889, type species *Fusus funiculosus* Lamarck, 1804). Cossmann (1901, p. 43), however, considered *rothi* to belong in *'Lathyrus'* (= *Latirus* de Montfort, 1810; *'Lathyrus'* emend. Latreille, 1825).

The smooth whorls of the protoconch distinguish this taxon readily from all other genera treated in this paper. The fact that Tembrock (1965, pl. 34, figs 3, 4) illustrated a multispiral protoconch for *S. mellevillei* was rather puzzling, as Cossmann originally described it as paucispiral (see diagnosis above). Therefore, we tried to obtain material of *S. mellevillei*. This appeared to be quite difficult, as genuine specimens were not easily available. We received Tembrock's sample (PHB Ga 68/69) on loan, but were unable to isolate the species in the French collections accessible to us. Ultimately this led to a rediscovery of the type-locality of *S. mellevillei*, which is the railway cut at St. Gobain, near Laon, in the Paris Basin (dép. Aisne). Here an abundant material of *S. mellevillei* was collected (shell height up to 13 mm, but some fragments indicate larger shells), including many specimens with excellently preserved protoconchs.
This sample convincingly confirmed Tembrock's observations concerning the presence of a multispiral protoconch (see Text-fig. 29).

Another species that we consider to be a *Streptolathyrus* is a Late Oligocene species from the North Sea Basin, referred to as *Streptochetus septenarius* var. ? by Tembrock (1961, p. 368, pl. 1, fig. 2) and as *S. (Streptolathyrus) soellingensis*, ? male, by R. Janssen (1979b, p. 298, pl. 16, fig. 28), whose protoconch differs only slightly from that of *S. mellevillei*. For this Late Oligocene (Chattian) North Sea Basin species we introduce the name *Streptolathyrus masculinus* sp. nov.

Fig. 29. *Streptolathyrus mellevillei* (Cossmann, 1889), protoconch and early teleoconch whorls. St. Gobain, railway cut (France, Aisne), Eocene, Cuisian (Sables de Pierrefond). Coll. RGM 393.361 (AJL, 1985), x 25.

In this species the transition from protoconch to teleoconch is rather similar as in *S. mellevillei*, but in the Chattian species the spiral sculpture starts already c. ¼ whorl before the transition. This makes the protoconch resemble that of some *Streptodictyon* species in which a distinct reticulation is absent (see above), but in those species the spiral sculpture starts earlier, and the spirals are consistently narrower than those of the teleoconch, with a rather sharp boundary.

The Miocene North Sea Basin species traditionally referred to as *Latirus rothi* (Beyrich, 1856) differs markedly from the genus *Latirus* and, in spite of its relatively large protoconch, fits quite well in *Streptolathyrus*.

Finally, from Winterswijk-Miste a new species is introduced here, *S. regularis*, which was recorded by A.W. Janssen (1984, p. 243, pl. 10, fig. 2; pl. 64, fig. 7) as *Peristernia patruelis* (Bellardi, 1884).

Incidentally, it cannot be ruled out that among the many taxa from the Paratethys and Mediterranean Basin placed in genera such as *Fusus* or *Latirus* several may be found to fit *Streptolathyrus* as defined here.

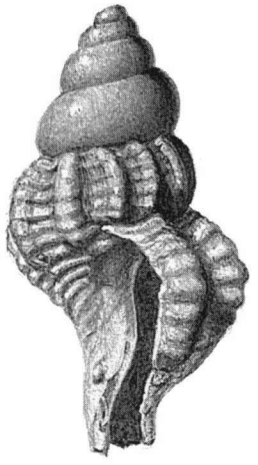


Fig. 30. *Streptolathyrus masculinus* sp. nov. **(paratype)**, protoconch and early teleoconch whorls. Glimmerode, former lignite pit Höllkopf (Germany, Hessen), Oligocene, Chattian A (Kasseler Meeresssand, 'Schillage 1'). Coll. RGM 393.306 (MBL, June 1973), x 25.

Fig. 31. *Streptolathyrus masculinus* sp. nov. **(paratype)**, protoconch and early teleoconch whorls. Erkelenz, borehole K3 for mine shaft Sophia Jacoba 8, depth 268-281 m (Germany, Nordrhein-Westfalen), Oligocene, Chattian B (Grafenberg Member). Coll. RGM 393.314 (GLK), x 25.

Streptolathyrus masculinus sp. nov.
Pl. 6, figs 1, 2; Text-figs 30, 31

1961 *Streptochetus septenarius* (Beyrich) var. ? — Tembrock, p. 368, pl. 1, fig. 2 (*non* Beyrich).

v. 1978 *Streptochetus (Streptolathyrus)* cf. *undatus* (Meunier 1880) cf. Tembrock 1965. — R. Janssen, p. 113 (*non* Meunier, 1880, nec Tembrock, 1965 = *S. undatus*).

v. 1978 *Streptochetus (Streptolathyrus) soellingensis* Tembrock 1965. — R. Janssen, p. 113 (*partim, non* Tembrock, includes also *Streptodictyon soellingensis*).

v. 1979b *Streptochetus (Streptolathyrus) soellingensis* Tembrock 1965, ♂ ? — R. Janssen, p. 298, pl. 16, figs 27, 28 (*partim, non* Tembrock, *non* pl. 16, figs 29, 30 = *Streptodictyon soellingensis*).

Type material — Holotype: Pl. 6, fig. 1, RGM 393.303.
Locus typicus — Germany (Hessen), Glimmerode, former lignite pit Höllkopf (see map in Anderson *et al.*, 1969, p. 60, fig. 11).
Stratum typicum — 'Kasseler Meeressand, Schillage 1', as indicated by R. Janssen (1978, p. 7) (Chattian A, Oligocene).
Derivatio nominis — L. *masculinus* (adj.) = male, unnatural (!); the name alludes to the supposed sexual dimorphism of *S. soellingensis*, as suggested by Tembrock (1961), according to which the present species was considered to possibly be the male (R. Janssen, 1979b, p. 298).
Diagnosis — Relatively small *Streptolathyrus* species with regularly convex teleoconch whorls. Teleoconch with a short canal. Columella smooth. Parietal tooth present in fully grown specimens (just a single shell available !). Ornament regular, consisting of predominantly straight collabral ribs (about 9 per whorl), continuous to the apertural margin, overridden by two generations of spiral lirae. Protoconch with about 4½ whorls, with a very weak spiral along the lower suture, transition into the teleoconch gradual: on the last ¾ of the protoconch body whorl a transitional sculpture occurs, consisting of radial riblets and, subsequently, a spiral sculpture.
Description — Shell fusiform. The single adult specimen known to date has almost 6 teleoconch whorls and a height of about 17 mm.

The protoconch is conical, with a glossy surface. Its dimensions are height 1.1-1.25 mm, and width 0.8-0.9 mm; it comprises about 4½ convex whorls, the earlier whorls somewhat flatter than the later ones. The nucleus has a diameter of almost 0.1 mm. The whorls are smooth; a thread-like spiral above the suture, as present in some other species of this genus, is very weak or absent. The boundary

with the teleoconch is gradual. On the terminal three quarters of the protoconch's body-whorl spaced, slightly opisthocyrt riblets appear, which regularly increase in strength. Somewhat later a spiral sculpture starts, which imperceptibly passes into the teleoconch's spirals.

The teleoconch whorls are regularly convex, or slightly flattened below the suture. The sculpture consists of about ten, slightly prosocline collabral ribs on the first whorl, decreasing to about eight ribs per whorl in larger specimens. Generally the radial ribs are not continuous from one whorl to the next. The interspaces between the collabral ribs are of about equal width as the ribs. The spiral sculpture comprises eight primary spirals, forming faint knobs on the points of intersection with the radial sculpture. They are of almost equal strength, or the peripheral spirals are somewhat stronger. The lowermost spiral may partly be covered by the suture. Initially the interspaces between the primary spirals are as wide as the spiral threads, but on later whorls the spirals are narrower than the interspaces.

Secondary spiral sculpture starts relatively late, usually at the end of the third, or the beginning of the fourth teleoconch whorl. The first secondary spirals may appear below the suture, on the periphery or on the base of the shell. Just one generation of secondary spirals is present (in the only adult specimen a beginning of a third series of spirals is visible). The secondary spirals eventually reach almost the same strength as the primaries, but in all available specimens they can be distinguished.

The siphonal canal is relatively short. The columella is smooth, devoid of teeth or folds. A distinct parietal tooth is present in the adult specimen. Discontinuous sets of spiral lirae are present on the inner apertural shell wall of larger specimens. The growth lines are distinctly visible in between the sculptural elements and rather lamellose on the later whorls.

Paratypes — Oligocene, Chattian A (Söllingen Sand Formation): Germany (Niedersachsen) — **Söllingen**, outcrop along railroad between Söllingen and Jerxheim at KM 17.9: 32 juv. specimens, RGM 393.304 (AJL, May 1982); 1 juv. specimen, AJB; 5 juv. specimens, MCL (PGL, May 1982).

Oligocene, Chattian A (Kasseler Meeressand): Germany (Hessen) — **Ahnetal** near Kassel, outcrop Brandkopf, 'Schill 3': 1 juv. specimen, RGM 393.305 (MBL, June 1973); **Glimmerode**, former lignite pit Höllkopf (type locality), exact level unknown: 1 specimen adult, Pl. 6, fig. 2, SMF 250708/1 (H. Humberg, 1977); 68 juv. specimens, KGM; 'Schillage 1' type locality and level): 1 juv. specimen, Text-fig. 30, 517 juv. specimens, RGM 393.306, 393.362 (MBL, June 1973); 74 juv. specimens, MCL, June 1973; 1 juv. specimen, illustrated in R. Janssen, 1979b, pl. 16, fig. 28, SMF 250709/1 (R. Janssen, 1972-1973); 523 juv. specimens, SMF 250783/540 (R. Janssen, 1972/1973), this sample also contains 17 unidentifiable fragments; 'Schillage 2': 85 juv. specimens, RGM 393.307 (MBL, June 1973); 'Schillage 3': 19 juv. specimens, RGM 393.308 (MBL, June 1973).

Oligocene, Chattian A (Grafenberg Member): Germany (Nordrhein-Westfalen) — **Rumeln**, dump of mine shaft Diergardt VI, presumably 'Schicht II' Görges, 1941: ? 1 def. specimen RGM 393.309 (AJL, 1976).

Oligocene, Chattian B (Grafenberg Member): Germany (Nordrhein-Westfalen) — **Erkelenz**, borehole K3 for mine shaft Sophia Jacoba 8, depth 320-321 m below surface: 1 juv. specimen, RGM 393.310 (GLK); depth 316-317 m: 1 juv. specimen, RGM 393.311 (GLK); depth 292-293 m: 1 juv. specimen, RGM 393.312 (GLK); depth 288-289 m: 1 specimen, RGM 393.313 (GLK); depth 268-281 m: 1 juv. specimen, Text-fig. 31, RGM 393.314 (GLK).

Discussion — In its type area near Kassel this species occurs in populations of numerous strikingly small specimens. Initially we considered these to be juveniles, but we saw only one distinctly larger shell (SMF 250708, see Pl. 6, fig. 2). As it is quite unlikely that this is the only adult specimen we suppose that the smaller specimens in fact were sexually mature, and consider the only larger specimen as gerontic. Therefore we decided not to choose this quite exceptional specimen as the holotype, but selected a well-preserved smaller specimen instead. Not only does this specimen have a well-preserved protoconch, but it is more closely comparable with the bulk of the available material and its precise stratigraphical provenance is also known. The large SMF specimen was picked from the surface of the exposure at Glimmerode.

In the remarks concerning the species *Streptodictyon soellingensis* (see above) we expose the situation with respect to the supposed sexual dimorphism. It may be clear that the choice of the new name for this species was induced by this discussion.

This species resembles *Streptodictyon soellingensis*, in which, however, the spiral sculpture is always denser and there invariably is a difference in the protoconch's morphology. The reader is referred to the description of that species. For the distinction of *S. soellingensis* and *S. undatus* see the relevant descriptions.

Streptolathyrus masculinus co-occurs with *Streptodictyon cheruscus*, which is easily distinguished by its reticulate protoconch sculpture and the dense radial sculpture on the initial teleoconch whorls.

A single defective specimen from the Rumeln mine shaft dump differs from this species by its strikingly slender shell. As far as visible the protoconch features resemble this species quite well. Therefore we assign it to the present species with a query.

Stratigraphical distribution—*Streptolathyrus masculinus* is known exclusively from some Late Oligocene (Chattian A and B) deposits in Germany, predominantly in the Kassel area.

Evolutionary developments — We do not know of any precursor or successor species.

Streptolathyrus regularis sp. nov.
Pl. 6, fig. 3; Text-fig. 32

v. 1984 *Peristernia (Peristernia) patruelis* (Bellardi, 1884). — A.W. Janssen, p. 243, pl. 10, fig. 2; pl. 64, fig. 7 (*non* Bellardi).

Type material — Holotype: Pl. 6, fig. 3, RGM 226.027, illustrated in A.W. Janssen (1984, pl. 64, fig. 7).

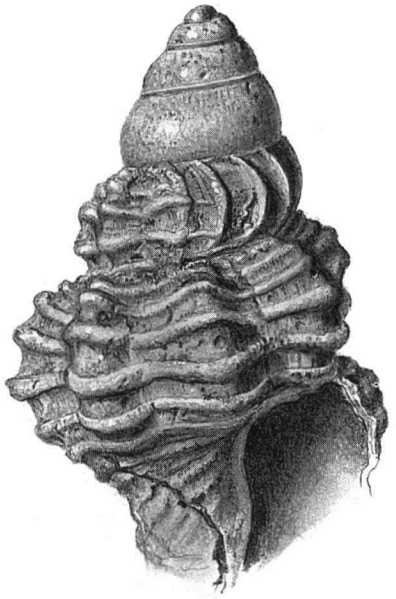


Fig. 32. *Streptolathyrus regularis* sp. nov. **(paratype)**, protoconch and early teleoconch whorls. Winterswijk-Miste, temporary excavation, depth 2-3.75 m below surface (The Netherlands, Gelderland province), Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed; Hiatella arctica Acme Zone or basal part of Astarte radiata Acme Zone). Coll. RGM 225.517 (AJL, 1971), x 25.

Locus typicus — Winterswijk-Miste, province of Gelderland, The Netherlands; temporary excavation, coordinates x = +88 200, y = -23 750, depth 2-4 m below surface.

Stratum typicum — Breda Formation, Aalten Member, Miste Bed; Hiatella arctica Acme Zone or basal part of Astarte radiata Acme Zone.

Derivatio nominis — The species is named after the strikingly regular surface sculpture.

Diagnosis—Relatively small *Streptolathyrus* species with regularly convex teleoconch whorls. Ornament strikingly regular, consisting of predominantly straight collabral ribs (about 8 per whorl), continuous to the apertural margin, overridden by two or three generations of spiral lirae. Protoconch comparatively small, with a spiral line along the lower suture. Columella without continuous spirals, but frequently with one or two oblique teeth. Parietal tooth sometimes present. Canal comparatively short.

Description—Shell fusiform. Adult specimens have up to 6 teleoconch whorls and reach a height of about 18 mm.

The protoconch is conical and has about 4½ slightly convex whorls, with a glossy surface. Its dimensions are rather variable: height 0.95-1.55 mm, width 0.85-1.10 mm. The nucleus has a diameter of 0.10 mm. The whorls are smooth, but for a thread-like spiral just above the suture of the last protoconch whorl. The boundary with the teleoconch is sharp, usually distinct because of the less glossy surface of the teleoconch. Near the end of the fourth whorl spaced riblets appear, which are almost orthocline in their upper part and more strongly curved forward towards the abapical suture. Just in front of the boundary with the teleoconch the spiral sculpture starts and the radial riblets become stronger.

The teleoconch whorls are regularly convex. The sculpture consists of about eight, slightly prosocline collabral ribs per whorl, generally not continuous from one whorl to the next. Initially the interspaces are about as wide as the ribs or even somewhat narrower, on the later whorls, however, the interspaces become gradually wider than the ribs. The spiral sculpture has five or six primary spirals, which are sharply delimited, with a rectangular transverse section, forming slight knobs on the points of intersection with the radial sculpture. They increase in strength from the upper suture downward. The lowermost spiral, partly covered by the suture, however, is considerably weaker than the one above it, which lies on the periphery of the whorl. The interspaces between the primary spirals are wider than the spiral threads.

Secondary spiral sculpture starts on the second teleoconch whorl, at first above the peripheral spiral, and near the upper suture. Two generations of secondary spirals are present, the first reaching almost the same strength as the primary spirals. In between the spirals a weak and irregularly distributed spiral striation is sometimes visible from the third whorl onwards.

The siphonal canal is relatively short. At the point of transition into the canal the columella bears one or (usually) two weak, obliquely elongate knobs, which are not continuous. A quite strong parietal tooth is present in fully grown specimens. Spiral lirae are present on the inner

apertural shell wall of many specimens. The growth lines are distinctly visible, rather rugose on the later whorls.

Paratypes — Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed, Hiatella arctica Acme Zone and/or Astarte radiata Acme Zone): The Netherlands (Gelderland province) — **Winterswijk, Miste**, temporary excavation: 1 juv. specimen, Text-fig. 32, RGM 225.517, illustrated in A.W. Janssen, 1984, pl. 10, fig. 2; 40 specimens, RGM 393.315; 2 specimens, MCL; 3 specimens, SMF 310376/3 (RGM).

Miocene, Hemmoorian (Breda Formation): The Netherlands (Limburg province) — **Beringen** (Helden municipality), borehole DB 15 (58B/8), depth 154-159 m below surface: 1 specimen, RGD (ROD, 1911); 2 specimens, RGM 393.316 (ROD, 1911); depth 144-154 m: 1 juv. specimen, RGM 393.317 (ROD, 1911), originating from a sample that has been contaminated, presumably with material from Dingden, but the species is not known to occur in the Reinbekian.

Discussion — The present species was recorded for the first time from the North Sea Basin by A.W. Janssen (1984), who identified it as *Latirus patruelis* Bellardi, 1884 and tentatively placed it in the genus *Peristernia* Mörch, 1852. The specimens were isolated from large numbers of *Streptodictyon sexcostatus* and *Streptolathyrus rothi*, which are quite similar at first glance. The Winterswijk-Miste material closely agrees with the original description and illustration of *Latirus patruelis* in Bellardi (1884, p. 44, pl. 2, fig. 21a, b) and also with the photograph of one of the syntypes in Ferrero Mortara *et al.* (1982, p. 144, pl. 39, fig. 6). A direct comparison with the syntype illustrated in Ferrero Mortara *et al.* (collection of the Museo Regionale di Scienze Naturali at Torino, registration no BS.017.-03.063) showed that there are several important differences between the Italian taxon and that from the North Sea Basin. In *L. patruelis* the whorls are less convex and therefore the suture is more superficial. The sculpture is considerably less well-marked and there are only three primary spirals and a fourth one in the lower suture. In between the primary and secondary spiral sculpture the shell is covered with a distinct spiral micro-sculpture. The apical parts of the studied syntype are worn, but probably the protoconch comprises only one whorl.

Stratigraphical distribution — This species is exclusively known from the Miocene, Hemmoorian of the North Sea Basin (The Netherlands).

Evolutionary developments — Any precursor or successor species is unknown to us.

Streptolathyrus rothi (Beyrich, 1856)
Pl. 6, figs 4-9; Text-figs 33, 34

1856* *Fusus Rothi* Beyr., Beyrich, p. 289, pl. 24, fig. 1a-c.
1872 *Fusus crispus* Borson. — von Koenen, p. 172 (*partim, non* Borson, only the North Sea Basin specimens).
1901 *Fusus Rothi* Beyr. — Cossmann, p. 43.
? 1925 *Dolicholathyrus (Pseudolathyrus) Rothi* Beyr. — Kautsky, p. 115, pl. 8, fig. 19.
1937 *Lathyrus (Dolicholathyrus) rothi* Beyr. — Sieber, p. 141 (*partim*, only the North Sea Basin material ?).
1940 *Dolicholathyrus (Pseudolathyrus) Rothi* Beyrich. — Sorgenfrei, p. 45 (108), pl. 6, fig. 7.
v. 1952 *Lathyrus (Dolicholathyrus) rothi* Beyrich, sp. 1856. — Glibert, p. 111, pl. 8, fig. 11.
1958 *Lathyrus (Dolicholathyrus) rothi* (Beyrich). — Sorgenfrei, p. 232, pl. 50, fig. 157.
1964 *Latirus (Dolicholatirus) rothi* (Beyrich 1856). — Anderson, p. 262, pl. 27, fig. 201.
1968 *Lathyrus rothi* (Beyrich 1856). — Rasmussen, p. 143, pl. 13, fig. 8; pl. 17, fig. 3.
1972 *Latirus (Pseudolatirus) rothi* (Beyrich, 1854). — Nordsieck, p. 83, pl. 20, fig. 120.
1981 *Latirus (Dolicholatirus) rothi* (Beyrich, 1856) — van der Hoek, p. 18, fig. 42 (mala).
1984 *Latirus (Pseudolatirus) rothi* (Beyrich, 1856). — A.W. Janssen, p. 242, pl. 10, fig. 1; pl. 64, fig. 4.
1985 *Latirus (Pseudolatirus) rothi* (Beyrich, 1856). — Lierl, p. 14, fig. 31.
1988 *Pseudolatirus rothi* (Beyrich 1856). — Moths & Piehl, p. 248, pl. 8, fig. 34a, b.
1989 *Pseudolatirus rothi* (Beyrich, 1856). — Moths, p. 111, pl. 15, fig. 73.
1990 *Latirus (Pseudolatirus)* sp. — Schnetler & Beyer, p. 64, pl. 3, fig. 2.

Type material — Not studied. Beyrich described this species from the Wellenkamp Collection, the whereabouts of which is unknown.

Locus typicus — 'Am Schildstein bei Lüneburg' (Germany, Niedersachsen).

Stratum typicum — Unknown, presumably Late Miocene (Langenfeldian).

Essential details of original description — [....] 'nine high longitudinal ribs, in the interspaces of which the shell wall is only slightly convex. The longitudinal ribs are weak near the undulated upper suture and reach their maximum strength at about the middle of the whorl. The transverse sculpture consists of rather spaced transverse riblets, each with three rather regularly intercalated finer transverse threads. The middle whorls have only two stronger transverse riblets in their lower half, in the upper half a third, less strongly developed one, hardly stronger than the intermediate threads. [....] The columella is smooth'. [....] (translated from German).

Revised diagnosis — Large *Streptolathyrus* species with

regularly convex teleoconch whorls in its typical form; sometimes the upper part of the whorls is flat or even concave, as a result of which the lower part of the whorls is more strongly convex.

Fig. 33. *Streptolathyrus rothi* (Beyrich, 1856), protoconch and early teleoconch whorls. Dingden, temporary outcrop in bottom of Königsbach near Königsmühle (Germany, Nordrhein-Westfalen), Miocene, Reinbekian (Bislicher Schichten). Coll. RGM 393.341 (AJL, 1970), x 25.

Fig. 34. *Streptolathyrus rothi* (Beyrich, 1856), protoconch and early teleoconch whorls. Groß Pampau, Olen sand pit (Germany, Schleswig-Holstein), Miocene, Langenfeldian (Eidelstedt Formation). Coll. RGM 393.346 (MCL), x 25.

Ornament of predominantly straight collabral ribs (about 8 per whorl), continuous to the apertural margin, overridden by three generations of spiral lirae (in very large specimens even a fourth generation may be discernable). Protoconch comparatively large, with a spiral line along the lower suture. Columella with one or two weak spirals. Parietal tooth present.

Description — (Typical form of Langenfeldian age) Shell fusiform. Adult specimens have up to 7 teleoconch whorls and reach a length of about 40 mm.

The protoconch is conical and has about 4 slightly convex whorls. Although difficult to measure because of the vague boundary with the teleoconch, its dimensions are approximately height 1.5 mm, width 1.1 mm. The nucleus has a diameter of 0.10 mm. The second protoconch whorl has a delicate surface sculpture of granules in an irregular spiral arrangement; the lower protoconch whorls are smooth, but for a thread-like spiral just above the suture, which, however, may be absent in some cases. The transition to the teleoconch is gradual. Near the end of the third whorl spaced opisthocyrt riblets appear, which are more strongly curved forward in their lower part. After half a whorl the teleoconch's spiral sculpture starts and the radial riblets become gradually stronger.

The teleoconch has about eight undulating, nearly straight, but sometimes slightly proso- or orthocline collabral ribs per whorl, generally not continuous from one whorl to the next. The interspaces are slightly wider than the ribs. These ribs are overlain by a strong sculpture of thread-like primary spirals, which are distinctly heavier on the radial ribs than in between. The number of primary spirals varies from three to six, separated by interspaces, varying from hardly wider to distinctly wider than the spirals. The two spirals on the middle part of the whorls are strongest. Secondary spiral sculpture starts on the second teleoconch whorl. In fully-grown specimens three generations of such spirals are present, reaching almost the same strength, but remaining considerably weaker than the primaries.

The columella has one or two weak spirals. A quite strong parietal tooth is usually present, also in near-adult specimens. Spiral lirae are present on the inner apertural shell wall of many specimens. The growth lines are distinctly visible.

Material studied — Oligocene, Chattian B/C (Grafenberg Sand Member): Germany (Nordrhein-Westfalen) — **Meerbusch-Ostenrath**, borehole, 39-41 m below surface: 1 specimen, Pl. 6, fig. 4, FHK.

Miocene, Vierlandian (Klintinghoved Formation): Denmark (Als) — **Klintinghoved**, near Sønderborg, outcrop on foreshore: from this locality we saw several specimens in the collection FWG.

Miocene, Hemmoorian, Behrendorfian (Berchem Formation, Edegem Sand Member): Belgium (Antwerpen province) — **Antwerpen** (sediment contents of shells distinctly point to Edegem Sands): 1 specimen, IRScNB (Malaise), mentioned in Glibert, 1952, p. 11 *sub nomine Streptochetus sexcostatus*; this sample also contains 3 specimens of *Streptodictyon cheruscus* forma *fasciolaroides*; **Antwerpen**, construction pit for E3 Kennedy-tunnel: 5 specimens, IRScNB (leg. unknown, probably M. Glibert, ± 1965); this sample also contains 34 specimens of *Streptodictyon cheruscus* forma *fasciolaroides*; 1 specimen, RGM 183.143 (FJR, ± 1965); 1 specimen, 1 def. specimen, RGM 182.985 (RHR, ± 1965): 2 juv. specimens and 1 def. specimen, RGM 117.272 (AJL, 1964-1966); 1 specimen, Pl. 6, fig. 5, 7 specimens, RGM 393.360 and 182.612, respectively (DMM, 1964-1966); **Antwerpen** ('Tête de Flandre', Scheldt tunnel for pedestrians) (sediment contents of shells distinctly point to Edegem Sands): 4 specimens, IRScNB (leg. unknown), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 5 specimens of *Streptodictyon cheruscus* forma *fasciolaroides*; **Antwerpen**, borehole at construction pit for Slijkhoektunnel, depth 22 m below surface: 1 def. specimen RGM 393.318 (AJL); **Burcht**: 16 specimens, IRScNB (Nyst), mentioned in Glibert, 1952, p. 111; 1 specimen, IRScNB (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 138 specimens of *Streptodictyon cheruscus* forma *fasciolaroides*; **Edegem**: 1 specimen, IRScNB (E. de Jaer), Cat. Types Invert. no. 3640, illustrated in Glibert, 1952, p. 111, pl. 8, fig. 11; 2 specimens, IRScNB (purchased Mme Bernas De Gottal), mentioned in Glibert, 1952, p. 111; 2 specimens, IRScNB (Th. Lefèvre), mentioned in Glibert, 1952, p. 111; 1 specimen, IRScNB (Colbeau), mentioned in Glibert, 1952, p. 111; 117 specimens, IRScNB (Nyst), mentioned in Glibert, 1952, p. 111; 2 specimens, IRScNB (de Cort), mentioned in Glibert, 1952, p. 111; 3 specimens, IRScNB (Colbeau), mentioned in Glibert, 1952, p. 111; 4 specimens, IRScNB (Daimeries/Dautzenberg); 3 specimens, IRScNB (van Ertborn/Dautzenberg); 1 specimen, IRScNB (Th. Lefèvre), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 6 specimens of *Streptodictyon cheruscus* forma *fasciolaroides*; 2 specimens, IRScNB (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 207 specimens of *Streptodictyon cheruscus* forma *fasciolaroides*; 4 specimens, IRScNB (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 565 specimens of *Streptodictyon cheruscus* forma *fasciolaroides*; 3 specimens, IRScNB (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 403 specimens of *Streptodictyon cheruscus* forma *fasciolaroides* and 2 specimens of *Aquilofusus waeli auct. non* Nyst; 1 specimen, IRScNB (le Hon), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 238 specimens of *Streptodictyon cheruscus* forma *fasciolaroides*, 1 specimen of *Pterynotus nysti* (von Koenen, 1867) and 1 specimen of *Borsonia uniplicata* von Koenen, 1872.

Miocene, Hemmoorian (Breda Formation): The Netherlands (Noord Brabant province) — **Reek**, borehole 41 (571/24), depth 140-157 m, 6 specimens; no depth indication, 2 specimens, RGD (ROD, 1909).

Miocene, Hemmoorian (Breda Formation): The Netherlands (Limburg province) — **Baarlo**, borehole 9 (58E/15), depth 100-160 m below surface: 10 specimens, RGM 393.319 (ROD, 1908); depth 100 m: 2 specimens, RGD (ROD, 1908); no depth indicated: 32 specimens, RGD (ROD, 1908); **Beringen**, municipality of Helden, borehole 15 (58B/8), depth unknown: 1 specimen, RGM 393.320 (van der Sleen, 1911); depth 159-170 m, 4 specimens, RGD (ROD, 1911); depth 154-159 m: 591 specimens, 1 specimen with teleoconch sculpture strongly resembling *Streptodictyon sexcostatus*, RGD (ROD, 1911); 1 specimen, Pl. 6, fig. 6, 20 specimens, 253 specimens, RGM 393.321-323 (ROD, 1911); depth 134-149 m: 10 specimens, RGM 393.324 (ROD, 1911); depth 144-154 m, 1 specimen, RGD (ROD, 1911); depth 134-144 m: 22 specimens, RGM 228.900 (ROD, 1911); 11 specimens, RGD (ROD, 1911); depth 124-134 m: 1 specimen, RGD (ROD, 1911); depth 119-124 m: 1 def. specimen, RGM 228.674 (ROD, 1911); 11 specimens, RGD (ROD, 1911); **Belfeld**, borehole 14 (58E/45), depth unknown, 2 specimens, RGD (ROD, 1911); **Griendtsveen**, borehole 7 (52D/11) = Helenaveen III, depth 150-210 m below surface: 3 specimens, RGM 393.325 (ROD, 1906-1908); **Maasbree**, borehole 13 (58B/4), depth not specified: 3 specimens, RGD (ROD, 1910).

Miocene, Hemmoorian (reworked in fluvio-glacial deposits, from Arnum Formation): Denmark (Jylland) — **Gram**, gravel pit at Enderupskov: 31 specimens, RGM 393.326 (N. Vedsted-Hansen); 2 specimens, 5 juv. specimens, RGM 393.327 (AJL); 1 def. specimen MCL.

Miocene, Hemmoorian, Oxlundian (Berchem Formation, Antwerpen Sand Member): Belgium (Antwerpen province) — **Antwerpen**, Ploegstraat, temporary excavation for underground parking, 1965-1966: 1 specimen, 2 juv. specimens, RGM 393.328 (DMM); **Berchem-Borgerhout**, temporary excavations for E3 'Kleine Ring' motorway: 5 juv. specimens, RGM 393.329 (FJR); 1 juv. specimen, RGM 393.330 (RHR); 3 specimens, RGM 393.331 (DMM); 1 juv. specimen, RGM 393.332 (AJL); **Deurne** near Antwerpen, 1 specimen,

IRScNB (Nyst), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 1 specimen of *Streptodictyon sexcostatus* (with sediment contents pointing to Antwerpen Sands) and 1 specimen of *Streptodictyon cheruscus* forma *fasciolaroides* (with sediment contents pointing to Edegem Sands, so obviously mislaid).

Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed, Hiatella arctica Acme Zone and/or Astarte radiata Acme Zone): The Netherlands (Gelderland province) — **Winterswijk, De Krim**, temporary excavation along Gorleseweg, depth 4.00-6.00 m below surface: 3 specimens, RGM 393.333 (AJL, October 1982); **Winterswijk, Miste**, temporary excavation, depth 2.00-3.75 m below surface: 1 juv. specimen, illustrated in Janssen (1984, pl. 10, fig. 1), 1.097, 929 and 801 specimens, 1 specimen, Pl. 6, fig. 7, also illustrated in Janssen (1984, pl. 64, fig. 4), RGM 225.516, 393.356-358, 226.025 (AJL, 1971) 18 specimens RGM 393.380 (FJR); 11 specimens, RGM 393.381 (MBL); 78 specimens and 66 juv. specimens, MCL.

Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed, presumably Astarte radiata Acme Zone): The Netherlands (Gelderland province) — **Eibergen**, temporary outcrop 34G.1-1 near Ticheloven, 1964: 5 specimens, RGM 393.334 (MBL); **Winterswijk**, de Giffel: 8 specimens, RGM 31.226, Staring collection nr. 4711; 1 def. specimen, IRScNB (Bosquet), mentioned in Glibert, 1952, p. 110 *sub nomine Streptochetus sexcostatus*; this sample also contains 8 specimens of *Streptodictyon sexcostatus*, 1 specimen of *Charonia tarbelliana* (de Grateloup, 1840) and 1 specimen of *Crassispira borealis* (Kautsky, 1925).

Miocene, Hemmoorian, Oxlundian (Berchem Formation, Zonderschot Sand Member): Belgium (Antwerpen province) — **Booischot** (borehole) I: 12 specimens, IRScNB (leg. unknown); this sample also contains 24 specimens of *Streptodictyon sexcostatus*; **Heist-op-den-Berg**, borehole, depth 1.35-1.90 m below surface: 1 specimen, 2 juv. specimens, RGM 226.921; depth 1.90-2.70 m: 3 def. specimens, RGM 227.044; **Heist-op-den-Berg**, temporary exposure, September 1989: 1 specimen, Pl. 6, fig. 8, 247 specimens, RGM 393.335-336, respectively (AJL, 1991); **Zonderschot**: 2 specimens, IRScNB (leg. unknown), identified as *Streptochetus sexcostatus* by M. Glibert, 1977; this sample also contains 10 specimens of *Streptodictyon sexcostatus*.

Miocene, Hemmoorian/Reinbekian (Breda Formation, Aalten Member, Miste and/or Stemerdink Bed): The Netherlands (Gelderland province) — **De Giffel**, no further indication, 7 specimens RGD; **Winterswijk**, Groenloseweg, borehole 48 (475/14), depth 10-11 m, 2 specimens; no depth indication, 4 specimens, RGD.

Miocene, Reinbekian (Bislicher Schichten): Germany (Nordrhein-Westfalen) — **Dingden**, temporary outcrop in bottom of Königsbach near Königsmühle: 9 specimens, RGM 393.337 (RHR); 14 specimens, RGM 393.338 (MBL); 187 specimens, 186 juv. specimens, 1 juv. specimen, Text-fig. 33, RGM 393.339-341 (AJL, 1970); 28 mainly juv. specimens, RGM 393.342 (FJR).

Miocene, Reinbekian (Dingdener Schichten): Germany (Nordrhein-Westfalen) — **Dingden**, outcrop in bank and/or bottom of Königsbach near Königsmühle: 3 specimens, RGM 393.343 (M. Freudenthal); 14 specimens, RGM 393.344 (Backhuys, 6.8.1960).

Miocene, ? Langenfeldian (Breda Formation): The Netherlands (Noord Brabant province) — **Reek**, borehole 41 (571/24), depth 14-31.80 m, 1 specimen, RGD (ROD, 1909).

Miocene, Langenfeldian (formation not indicated): Germany (Hamburg area) — **Langenfelde**: 1 specimen, Pl. 6, fig. 9, 1 specimen, respectively RGM 393.345 and RGM 56.503 (Krause).

Miocene, Langenfeldian (Eidelstedt Formation): Germany (Schleswig-Holstein) — **Groß Pampau**, Olen sand pit: 1 specimen, 2 juv./def. specimens, MCL; 1 juv. specimen, Text-fig. 34, RGM 393.346 (MCL); 'lower sample': 30 juv./def. specimens, RGM 393.347 (AJL, 1985): 'upper sample': 10 juv./def. specimens, RGM 393.348 (AJL, 1985).

Discussion — The description of the typical form given above is based on Langenfeldian specimens from Groß Pampau and Langenfelde in northern Germany. Beyrich based his taxon on a single specimen from the Lüneburg area, from which we conclude that it was also a specimen of Langenfeldian age. From The Netherlands we saw but a single specimen of this typical form, *viz.* from the Reek borehole (see list of material above).

Five immature specimens (1 from Mogenstrup and 4 from Kirstinebjerg Skov; Denmark, Jylland, Chattian B) were described by Schnetler & Beyer (1990, p. 64, pl. 3, fig. 2). These specimens have a last protoconch whorl with a restricted number of radial riblets, and a slightly smaller apical angle. Schnetler & Beyer suggested that these specimens might be taxonomically separated, but this can only be determined on additional material. At any rate the differences seem to be less substantial than those between *e.g.* Middle Miocene and Late Miocene forms. For that reason we include this material in *S. rothi* for the time being.

A single specimen (Pl. 6, fig. 4) of Chattian B/C ('Neochattian') age available to us and all older Miocene populations (no Vierlandian material was studied in detail) differ in several respects from the typical form. In specimens from *e.g.* the Edegem Sands in Belgium, the

Miste Bed in The Netherlands and the Bislicher Schichten in Germany the protoconch is larger (height 2.0 mm), comprising 4¾ whorls, which are considerably less convex (to almost flat !) than in the Langenfeldian form. The radial sculpture on the last protoconch whorl and at the transition from protoconch to teleoconch is opisthocyrt in the Late Miocene form, but entirely straight (orthocline) in specimens from older deposits.

A further important difference in these older populations occurs in the development of the spiral sculpture of the teleoconch. The two central spirals are very strong, whereas especially the higher primary spirals are reduced and of about the same strength as the secondary sculpture. As a result, the whorl profile is different: the lower part strongly convex and the upper part flat to excavated.

In the typical (Late Miocene) form the whorl profile is regularly convex and the differences in strength of the primary spirals are not so strongly marked. Still, some Middle Miocene specimens resemble the younger ones closely in sculpture development, and, on the other hand, in some specimens from Groß Pampau the development of the secondary spiral sculpture resembles that of the Middle Miocene populations. But, when specimens from various Early to Middle Miocene populations are compared, there also appear to be quite considerable differences, occasionally to such an extent that it is difficult to accept that they all belong to a single species. An attempt, however, to separate such forms would mean the introduction of quite a lot of new names. Therefore we refrained from introducing new (sub)species, although it should be pointed out that a certain evolutionary trend does occur.

The specimen illustrated by Kautsky (1925, pl. 8, fig. 19) cannot be recognised as a true *S. rothi*. It is listed in the synonymy with a query. Kautsky, and others after him publishing on North Sea Basin material, included a form from the Miocene of the Vienna Basin, usually referred to as *Fusus crispoides* Hoernes & Auinger, 1890. Also Miocene taxa described from the Mediterranean and Aquitaine Basins were held to be conspecific with *S. rothi*. We had no such material from outside the North Sea Basin available for comparison and therefore decided to let the matter rest for now. At any rate the name *Fusus rothi* Beyrich, 1856 predates all others.

Anderson (1964, p. 262) considered the material described by von Koenen (1882, p. 180) as *Fusus Sismondai* Michelotti, 1847 to be incorrectly identified and assignable to *Lathyrus rothi*. We do not agree as von Koenen explicitly mentioned the presence of an umbilicus. Von Koenen's form is now indicated as *Urosalpinx sismondai* (see *e.g.* A.W. Janssen, 1972, p. 32).

Stratigraphical distribution — *Streptolathyrus rothi* is known from the Chattian B/C of the Lower Rhine District, the Vierlandian of Klintinghoved (Denmark; Sorgenfrei, 1940), from many Hemmoorian and Reinbekian faunas in The Netherlands, Belgium, Denmark and Germany, and from the Langenfeldian of Langenfelde and Groß Pampau in Germany.

Evolutionary developments — Unknown.

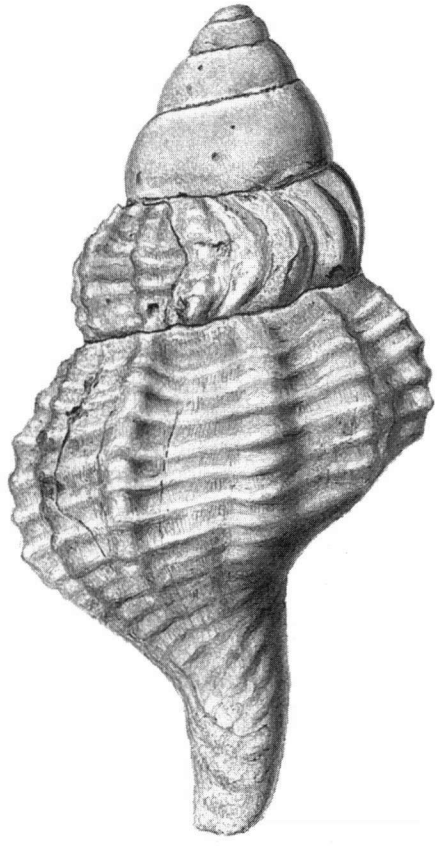


Fig. 35. *Streptolathyrus* sp., protoconch and early teleoconch whorls. Kruibeke, Gralex clay pit (Belgium, Antwerpen province), Oligocene, Rupelian (Rupel Formation, Putte Clay Member). Coll. RGM 393.349 (AJL), x 25.

Streptolathyrus sp.
Text-fig. 35

Description — The sole juvenile specimen available (height 4.4 mm) has a protoconch which closely resembles that of *S. rothi*, but it is considerably wider (height = 1.65 mm, width = 1.2 mm). Also the teleoconch is relatively

wider. There are six primary spirals on the first teleoconch whorl. The two spirals on the middle part of the whorl are only slightly stronger than the others. The specimen has almost two teleoconch whorls, on which no secondary spiral sculpture is developed, apart from a weak spiral just above the suture. Quite curiously the upper primary spiral disappears near the end of the second whorl, a feature not observed in any of the species discussed in the present paper.

The columella shows no sign of a columellar fold and there is no parietal tooth developed in this immature specimen.

Material studied — Oligocene, Rupelian (Rupel Formation, Putte Clay Member): Belgium (Antwerpen province) — **Kruibeke**, Gralex clay pit: 1 juv. specimen, Text-fig. 35, RGM 393.349 (AJL).
Remarks — The present specimen cannot be assigned to any of the other representatives of this genus known to us. It may represent an undescribed taxon.

Fasciolariidae sp.
Pl. 6, figs 10, 11

1954 *Aquilofusus elongatus*. — Glibert & de Heinzelin de Braucourt, p. 392 (*partim, non* Nyst, only some of the specimens from Berg)
1957 *Streptochetus* (s.s.) *elongatus* Nyst, sp. 1843. — Glibert, pp. 71, 87 (*partim, non* Nyst, only some of the specimens from Berg).

Description — Shell moderately large (height to about 30 mm), fusiform, very slender, about 3 times higher than wide. Apical angle about 23°, slightly wider in juvenile shells.

The protoconch is not preserved in the available specimens. The shell has moderately convex to rather flat teleoconch whorls, with a distinct and rather narrow subsutural depression. The body whorl occupies slightly less than two thirds of the entire shell height in fully-grown specimens. The transition into the base is gradual. The siphonal canal is slightly curved to the left (apertural view). Pseudumbilicus absent.

The sculpture of the teleoconch is composed of orthocline collabral ribs, covering the entire shell to the apertural margin. On the first teleoconch whorls the number of radial ribs is about 10-11, with the interspaces as wide as the ribs. The number of radial ribs remains more or less constant on the later whorls.

Spiral sculpture of seven to nine primary spirals (frequently one lying in the lower suture). The spirals are thread-like, especially so on the initial whorls. Secondary spirals develop in two generations. They do not reach the strength of the primaries; all generations remain recognisable.

The growth lines are distinct, parallel to the collabral sculpture, slightly opisthocyrt.

No spiral lirae were observed on the inner shell-wall. Even fully-grown specimens lack a parietal tooth. There is no columellar fold.

Material studied — Oligocene, Rupelian (Rupel Formation, Berg Sand Member): Belgium (Limburg province) — **Kleine Spouwen**: 1 specimen, Pl. 6, fig. 10, IRScNB TCCI 6056 (Nyst), mentioned in Glibert & de Heinzelin, 1954, p. 392 *sub nomine Aquilofusus elongatus*; furthermore this sample contains the holotype of *Streptodictyon sowerbyi*; **Kleine Spouwen, Berg**, level with *Astarte trigonella*: 1 specimen, Pl. 6, fig. 11, IRScNB TCCI 6057, 2 specimens, IRScNB (Bosquet), mentioned in Glibert & de Heinzelin, 1954, p. 392 *sub nomine Aquilofusus elongatus*. This sample furthermore contains 2 specimens of *Streptodictyon subelongatus* and 1 specimen of *S. sowerbyi*.
Remarks — The four specimens listed above are the only representatives of this form known to us. They are better preserved than other material (*e.g.* in coll. RGM) from this locality, more closely approaching the quality of Kleine Spouwen Member material. Several of these specimens, however, still contained a fine, well-sorted white quartz sand, which could indeed be Berg Sand, whereas the sediment of the Kleine Spouwen Member is sandy clay. Three of these specimens are from the J. Bosquet Collection. Bosquet was a well-known and usually reliable collector.

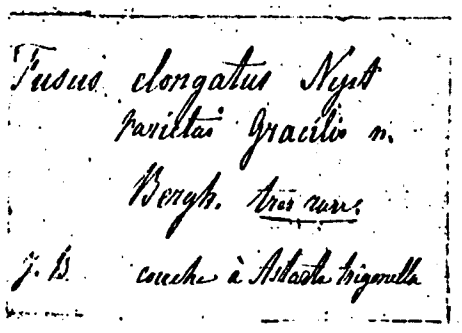


Fig. 36. Original label of Fasciolariidae sp. in J. Bosquet's hand, stating: '*Fusus elongatus* Nyst / varietas *gracilis* n. / Bergh, très rare / J.B. couche à *Astarte trigonella*', KBIN 6061.

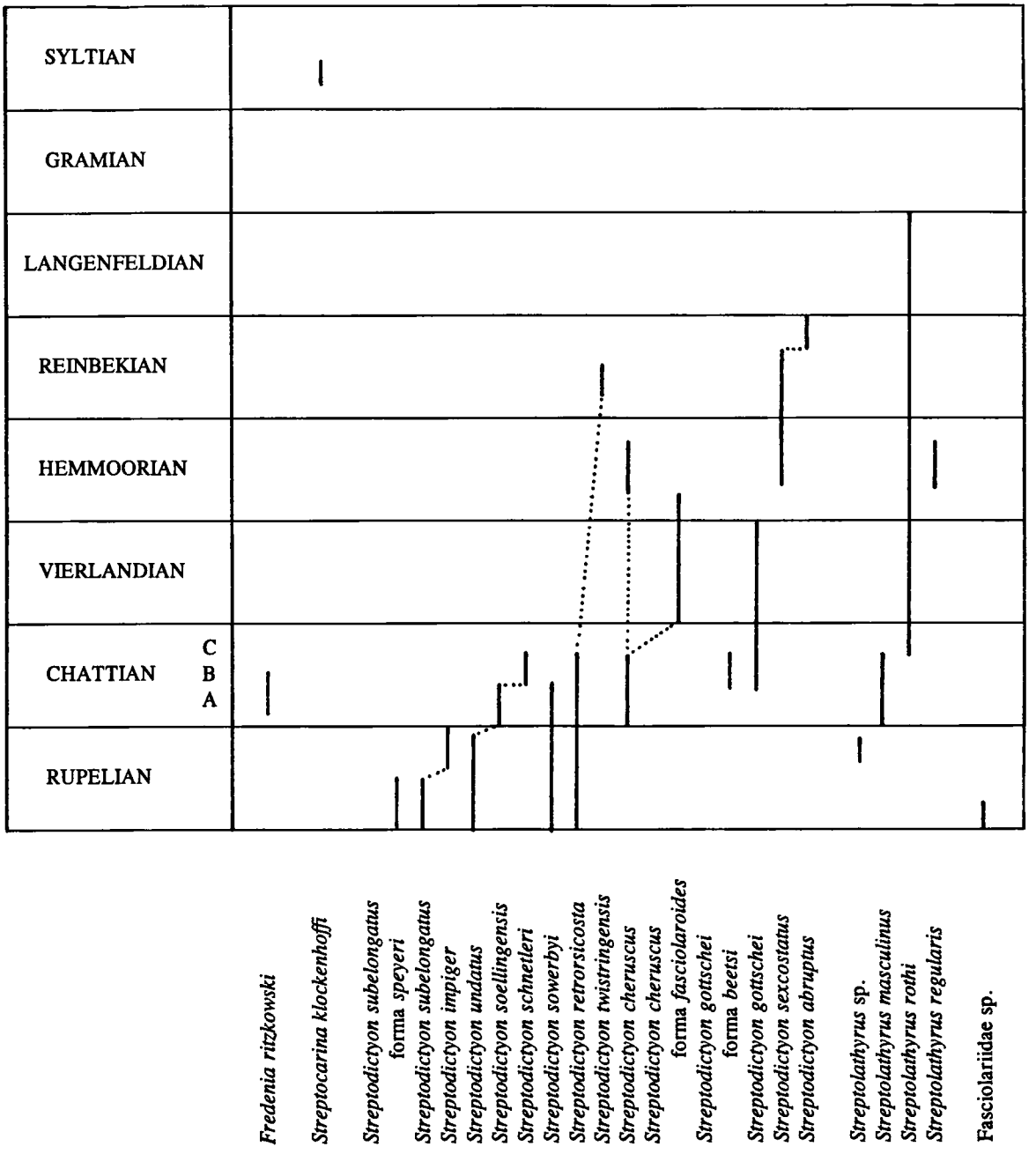


Fig. 37. Stratigraphical range of Fasciolariidae species discussed in this paper. Supposed evolutionary lineages are indicated by dotted lines.

The label in Bosquet's hand (Text-fig. 36) states explicitly 'Bergh, très rare' and a manuscript name '*Fusus elongatus* Nyst varietas *Gracilis* n., couche à *Astarte trigonella*' accompanies the specimens.

It is puzzling, however, that this form is absent from the rich fasciolariid material in the RGM collections from the same locality (Horizon with *Astarte trigonella*). In view of this we seriously doubt whether these specimens do come from the Berg Sand Member.

In our opinion this enigmatic form is not closely related to *S. subelongatus*, because of differences in general shell form and details of ornament. The state of preservation of the four available specimens, each of them without embryonic shell, prevents a more precise assignment.

EVOLUTIONARY LINEAGES

In Text-fig. 37 the known stratigraphic ranges of the various taxa distinguished in this paper are represented. Latdorfian material has not been included. We are not aware of any representatives of the group studied in this paper from deposits younger than Syltian.

There are striking differences in the numbers of species in the various stages: Rupelian 7, Chattian 9, Vierlandian 2, Hemmoorian 4, Reinbekian 4, Langenfeldian 1, Gramian 0 and Syltian 1. There is a general tendency of a decreasing number of species with time.

Some of the species are less facies dependent than others and occur in both fine-grained sediments from deeper water, as well as in sandier deposits from shallower water. Other species, however, seem to have no preference for a certain type of sediment. This was already recorded by Anderson (1964, p. 94) for *Streptodictyon abruptus*. Arranging the species according to sediment type gives the following result:

— Present in both sand and clay:

Streptodictyon abruptus
S. subelongatus
S. gottschei
S. schnetleri
S. sexcostatus
S. sowerbyi
S. undatus
Streptolathyrus rothi.

— occurring only in clayey sediments:

Streptocarina klockenhoffi
Streptodictyon impiger
S. twistringensis
Streptolathyrus sp.

— occurring only in sandy deposits:

Fredenia ritzkowskii
Streptodictyon cheruscus
S. retrorsicosta
Streptolathyrus masculinus
S. regularis
Fasciolariidae sp.

Evolutionary relationships in the studied group are, generally speaking, difficult to establish. Apparently, the morphology of the taxa depends rather strongly on facies and less distinctly on genotypic characteristics. Therefore it is almost impossible to find criteria for the construction of an evolutionary tree. In rare cases evolutionary developments are clear from stratigraphical observations, *e.g.* the gradual transition of *Streptodictyon sexcostatus* into *S. abruptus* in a restricted lithostratigraphic interval of the Twistringer Schichten, with intermediate forms (Cadée & Janssen, 1983). *Streptodictyon undatus* — *S. soellingensis* — *S. schnetleri* are members of a comparable lineage. This series is admittedly less distinct, as intermediate forms were not found. Still we consider this a good example of an evolutionary succession, because a number of morphological characteristics remain constant. More frequent, however, is the situation of taxa appearing without known roots, and disappearing leaving no successors. In such cases, migrations of taxa from or to areas beyond the geographic scope of this paper may provide an explanation. Other possibilities, as *e.g.* incompleteness of the fossil record, or inadequate collecting, in our opinion are irrelevant, considering the amount of fossil material available from the stratigraphic interval concerned.

The supposed migration remains entirely hypothetical, as very few observations from outside the area are recorded. Well-studied faunal provinces, such as the Aquitaine Basin and the Paratethys, have yielded not a single representative as far as we know (this is certainly true for *Streptodictyon*, a possible exception may occur in the genus *Streptolathyrus*, as we have not studied these from the Vienna Basin and the Mediterranean area).

Since it is unfeasible to evaluate the relative value (weight) of morphological criteria in evolutionary processes we refrained from a computerised statistic approach to obtain a cladogram, as this would result in numerous purely theoretical schemes. It would be impossible to select the most probable path, even with the inclusion of stratigraphical and environmental data.

ACKNOWLEDGEMENTS

The authors are extremely grateful to the following colleagues, who made available or donated material from their collections or from collections in their care, or supplied literature and/or information on localities and/or stratigraphy: Mr H.C.J. Bosch (Hilversum, The Netherlands); Mr R. Braasch (Schwerin, Germany); Dr T. Darragh (Museum of Victoria, Division of Natural History and Anthropology, Melbourne, Australia); Mrs Dr A.V. Dhondt (Institut royal des Sciences naturelles de Belgique, Brussels, Belgium); Dr F. Frohlich (Laboratoire de Géologie du Muséum national d'Histoire naturelle, Paris, France); Professor E. Gittenberger and Mr J. Goud (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands); Mr W. Groeneveld (Santpoort-Noord, The Netherlands); Dipl.-Geol. K. Gürs (Geologisches

Landesamt Schleswig-Holstein, Kiel, Germany); Dipl.-Geol. F. von der Hocht (Kerpen-Balkhausen, Germany); Dr N. Höser (Mauritianum, Naturkundliches Museum, Altenburg, Germany); Mr A.C. Janse (Brielle, The Netherlands); Dr R. Janssen (Senckenberg Museum, Frankfurt am Main, Germany); Mr D. Ledon (Versailles, France); Mr J. Le Renard (Plaisir, France); Drs P. Lozouet and P. Maestrati (Musée national d'Histoire naturelle, Laboratoire des Invertébrés marins et Malacologie, Paris, France); Mr T. Meijer (Rijks Geologische Dienst, Haarlem, The Netherlands); Dr A. Müller (Westfälische Wilhelms-Universität, Geologisch-Paläontologisches Institut und Museum, Münster, Germany); Mr M.S. Nielsen (Odense, Denmark); Professor G. Pavia (Università degli Studi di Torino, Dipartimento di Scienze della Terra, Torino, Italy); Mr S. van Schooten (Almelo, The Netherlands), Mr K.I. Schnetler (Langå, Denmark); the late Dr M.-L. Tembrock (Berlin, Germany); Mr J. van der Voort (Venne, Germany); Mr F. Weinbrecht (Glücksburg, Germany), Dr W. Weitschat (Institut für Paläontologie und Geologie, Universität Hamburg, Hamburg, Germany), and Mr E. Zenker, Museum Wiesbaden (Wiesbaden, Germany).

Dr G.C. Cadée, Den Burg (The Netherlands), Professor E. Gittenberger, Dr R. Janssen and Mr J.W.M. Jagt are thanked for critical reading of the manuscript; the last-named also improved the English.

Mrs I. Henneke and Mr A. 't Hooft (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands) took care of the photographic work. We are especially grateful to Mr G.A. Peeters (Schiedam, The Netherlands), who produced the magnificent drawings of protoconchs.

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Manuscript received 4 June 1994, revised version accepted 22 October 1994.

PLATE 1

Fig. 1. *Streptochetus intortus* (Lamarck, 1803). Grignon (France, Yvelines dép.), Eocene, Lutetian (Calcaire grossier). Coll. JRP *ex* no. 90 001; x 1.5.

Fig. 2. *Streptochetus intortus* (Lamarck, 1803), protoconch and early teleoconch whorls. Grignon (France, Yvelines dép.), Eocene, Lutetian (Calcaire grossier). Coll. JRP *ex* no. 90 001, x 5.

Fig. 3. *Fredenia ritzkowskii* (R. Janssen, 1979) (**holotype**). Freden, near Alfeld/Leine (Germany, Niedersachsen), Oligocene, Eochattian ('Kalkmergel'). Coll. SMF 250712/1 (R. Janssen/Leunis, 1977), x 10.

Fig. 4. *Streptocarina klockenhoffi* (Hinsch, 1977) (**paratype**). Morsum Kliff, Isle of Sylt (Germany, Schleswig-Holstein), Miocene, Syltian (Pinneberg Formation, Level with *Aporrhais*). Coll. RGM 393.351 (AJL), x 10.

Fig. 5. *Streptodictyon abruptus* (Beyrich, 1856) (**lectotype**). Reinbek (Germany, Schleswig-Holstein), Miocene, Reinbekian ('Reinbecker Gestein', Reinbek Member). Coll. MOV P112001 (F.E. Koch), x 4.

Fig. 6. *Streptodictyon abruptus* (Beyrich, 1856). Nordlohne, Meistermann clay pit (Germany, Niedersachsen), Miocene, Reinbekian (Twistringer Schichten). Coll. RGM 393.359 (AJL, 1987), x 2.

Fig. 7. *Streptodictyon cheruscus* (Philippi, 1843). Glimmerode, former lignite pit Höllkopf (Germany, Hessen), Oligocene, Chattian A (Kasseler Meeresssand). Coll. KGM, x 4.

Fig. 8. *Streptodictyon cheruscus* (Philippi, 1843). Rumeln, dump of mine shaft Diergardt VI (Germany, Nordrhein-Westfalen), Oligocene, Chattian A (Grafenberger Sande, presumably 'Schicht II' Görges, 1941). Coll. RGM 393.169 (AJL, 1976),- x2.

Fig. 9. *Streptodictyon cheruscus* (Philippi, 1843) (**lectotype**). Freden (Germany, Hessen), Oligocene, Chattian A/B (Kasseler Meeressand). Coll. PHB Ga 123 (Leunis), x 2.5.

Fig. 10. *Streptodictyon cheruscus* (Philippi, 1843) (lectotype of *Fusus schwarzenbergii* Philippi, 1843). Freden (Germany, Hessen), Oligocene, Chattian A/B (Kasseler Meeressand). Coll. PHB Ga 124 (Leunis), x 11.

Fig. 11. *Streptodictyon cheruscus* (Philippi, 1843). Brejning (Denmark, Jylland), Oligocene, Chattian B (Vejle Fjord Formation, Brejning Clay Member). Coll. RGM 393.176 (MNO), x 1.5.

Fig. 12. *Streptodictyon cheruscus* (Philippi, 1843). Eygelshoven, shaft II of Laura colliery, depth 115-125 m (The Netherlands, Limburg province), Oligocene, Chattian s. lat. (Veldhoven Formation, Voort Sand Member). Coll. IRScNB TCCI 6044, x 4.

Fig. 13. *Streptodictyon cheruscus* (Philippi, 1843). Beringen, borehole 15 (58B8), depth 134-144 m (The Netherlands, Limburg province), Miocene, Hemmoorian (Breda Formation). Coll. RGM 393.185 (ROD, 1911; Technische Hoogeschool, Delft), x 2.

Fig. 14. *Streptodictyon cheruscus* (Philippi, 1843). Hemmoor (Germany, Niedersachsen), Miocene, Hemmoorian (probably from reworked sediments in Quaternary deposits). Coll. IRScNB TCCI 6045 (Geol. Staatsinst. Hamburg/Chavan), x 3.

PLATE 1

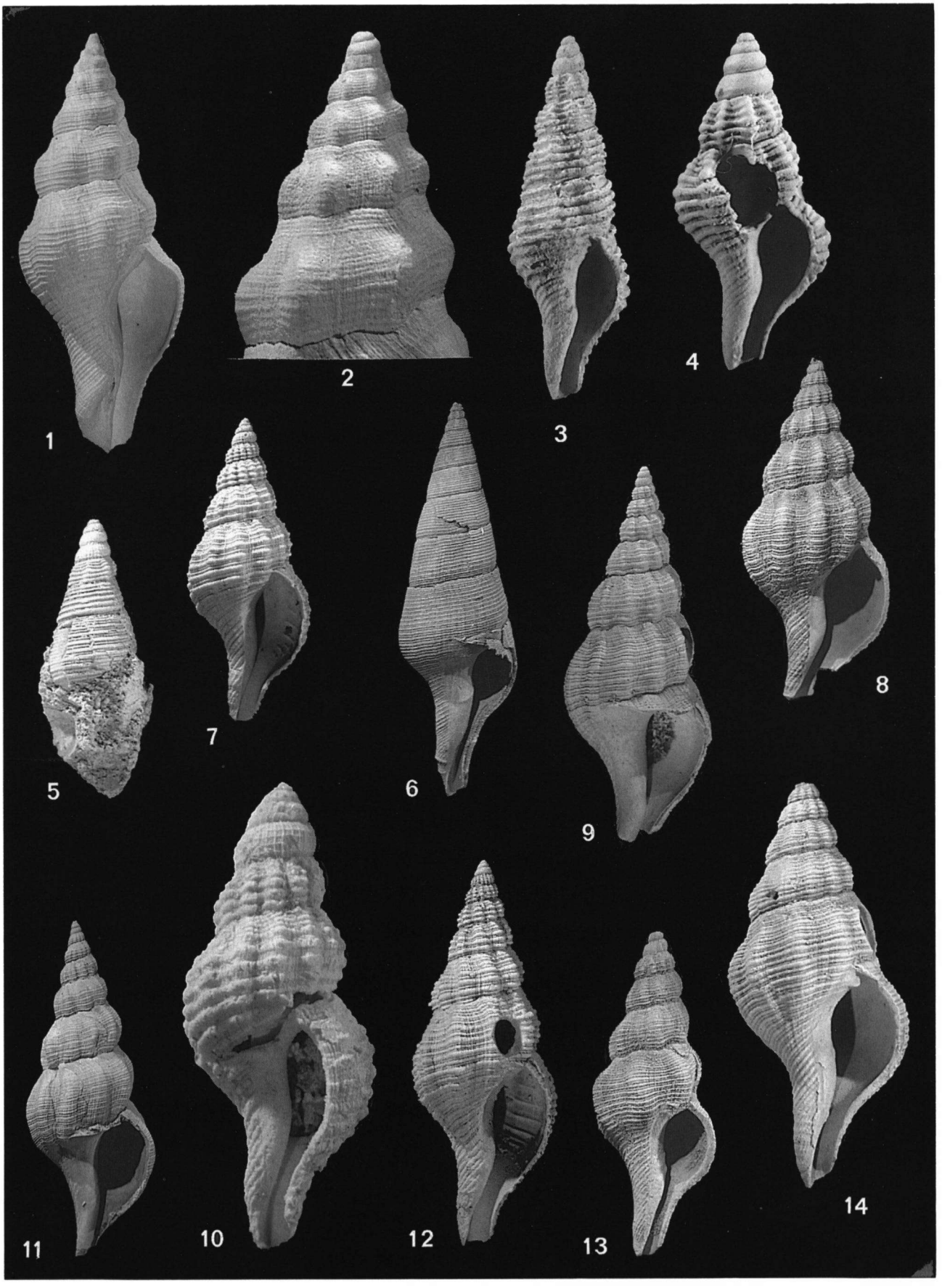

PLATE 2

Figs 1, 2. *Streptodictyon cheruscus* (Philippi, 1843) forma *fasciolaroides* (Nyst, 1861). Klintinghoved, near Sønderborg, outcrop on foreshore (Denmark, Als), Miocene, Vierlandian (Klintinghoved Formation). Coll. RGM 393.364-365 (FWG), x 2.5.

Fig. 3. *Streptodictyon cheruscus* (Philippi, 1843) forma *fasciolaroides* (Nyst, 1861). Edegem (Belgium, Antwerpen province), Miocene, Hemmoorian (Behrendorfian (Berchem Formation, Edegem Sand Member). Coll. IRScNB, Cat. Types Invert. no. 2347 (Nyst), x 2.5.

Figs 4-7. *Streptodictyon cheruscus* (Philippi, 1843) forma *fasciolaroides* (Nyst, 1861). Edegem (Belgium, Antwerpen province), Miocene, Hemmoorian (Behrendorfian (Berchem Formation, Edegem Sand Member). Coll. IRScNB TCCI 6046-9 (Nyst), x 2.5 (figs 4, 5), x 3 (figs 6, 7).

Figs 8, 9. *Streptodictyon gottschei* (Gripp, 1914). Beesel, borehole 12 (58E/61), depth not indicated (The Netherlands, Limburg province), Oligocene, Chattian (Veldhoven Formation, Voort Sand Member). Coll. RGD (ROD, 1910), x 1.5 (fig. 8), x 2.5 (fig. 9).

Fig. 10. *Streptodictyon gottschei* (Gripp, 1914) (**lectotype**). Itzehoe, Ochsenkamp, clay pit of 'Alsensche Zementfabrik' (Germany, Schleswig-Holstein), Miocene, Vierlandian (Elmshorn Formation). Coll. Geologisch-Paläontologisches Institut, Kiel (K. Gripp), x 3.

Fig. 11. *Streptodictyon gottschei* (Gripp, 1914) (**paralectotype**). Itzehoe, Ochsenkamp, clay pit of 'Alsensche Zementfabrik' (Germany, Schleswig-Holstein), Miocene, Vierlandian (Elmshorn Formation). Coll. Geologisch-Paläontologisches Institut, Hamburg (K. Gripp), x 3.

Fig. 12. *Streptodictyon gottschei* (Gripp, 1914), guttapercha cast. South of Schwerin lake (Germany, Mecklenburg-Vorpommern). Age unknown [reworked boulder in fluvioglacial deposits; the cast also contains 3 specimens of *Haustator goettentrupensis* (Cossmann, 1899), indicating the age of this material to be Chattian/Vierlandian]. Coll. PHB Ga 126 (II.155.14) (Beyrich), x 2.5.

PLATE 2

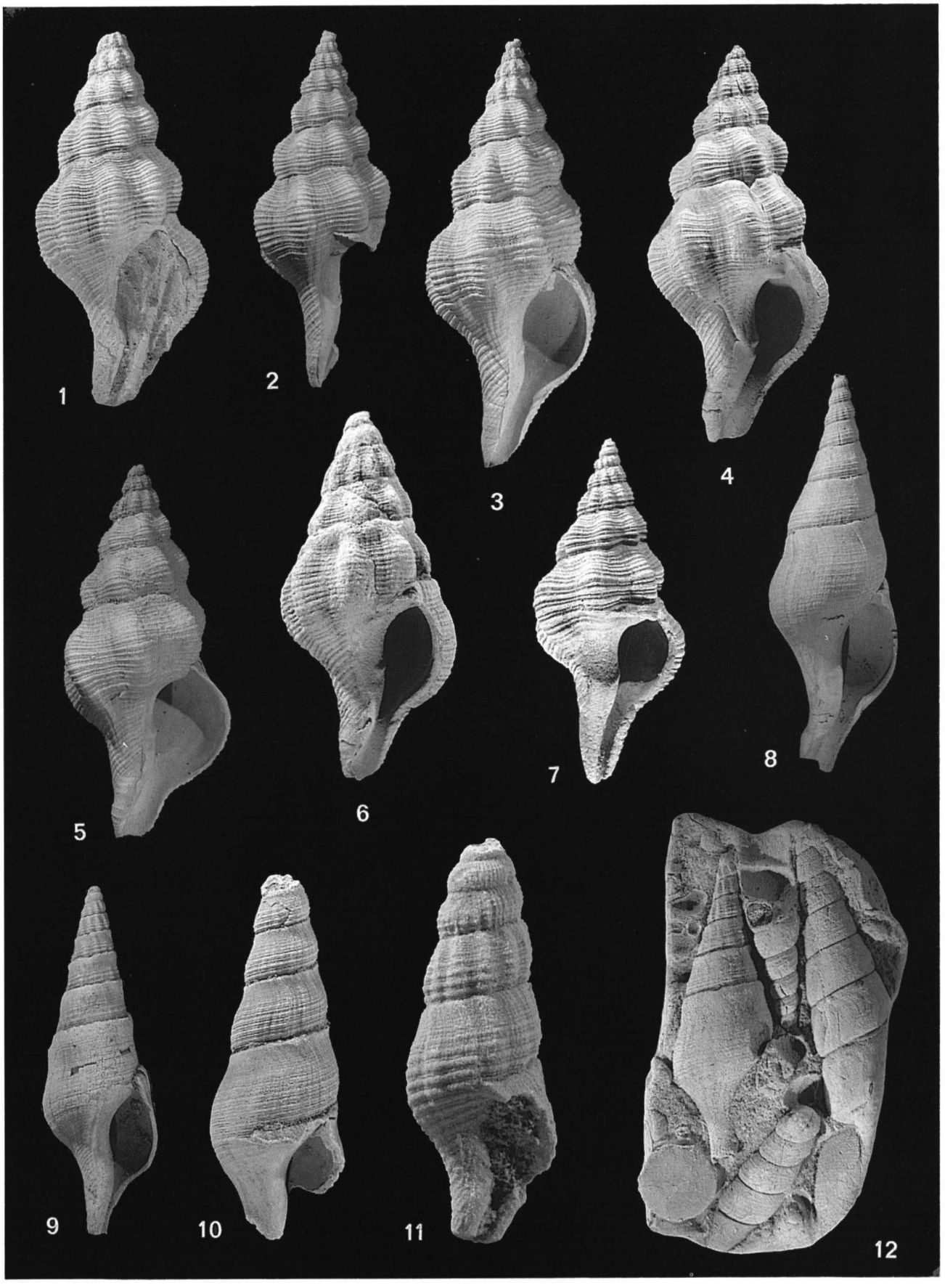

PLATE 3

Figs 1, 2. *Streptodictyon gottschei* (Gripp, 1914) forma *beetsi* n.f. Beesel, borehole 12 (58E/61), depth 230-250 m below surface (The Netherlands, Limburg province), Oligocene, Chattian (Veldhoven Formation, Voort Sand Member). Coll. RGD (ROD, 1910), x 2.5 (fig. 1), x 2 (fig. 2).

Fig. 3. *Streptodictyon gottschei* (Gripp, 1914) forma *beetsi* n.f. Belfeld, borehole 14 (58E/45), depth 260-270 m below surface (The Netherlands, Limburg province), Oligocene, Chattian (Veldhoven Formation, Voort Sand Member). Coll. RGD (ROD, 1914), x 2.

Fig. 4. *Streptodictyon impiger* sp. nov. (**holotype**). Winterswijk, clay pit complex 'De Vlijt' (The Netherlands, Gelderland province), Oligocene, Rupelian (Brinkheurne Formation, upper part of Woold Member). Coll. RGM 127.048 (M. Freudenthal), x 4.5.

Fig. 5. *Streptodictyon impiger* sp. nov. (**paratype**). Antwerpen, construction pit for E3-Scheldt tunnel (= Kennedy tunnel) (Belgium, Antwerpen province), Oligocene, Rupelian (Rupel Formation, Putte Member). Coll. RGM 393.209-210 (DMM), x 4.

Fig. 6. *Streptodictyon retrorsicosta* (Sandberger, 1860). Weinheim, Zeilstück (Germany, Rheinland-Pfalz), Oligocene, Rupelian (Unterer Meeressand). Coll. KGM, x 3.

Figs 7, 8. *Streptodictyon retrorsicosta* (Sandberger, 1860). Pierrefitte (France, Essonne dép.), Oligocene, Rupelian (Sables de Fontainebleau, Falun de Pierrefitte). Coll. DLV, x 4.

Fig. 9. *Streptodictyon retrorsicosta* (Sandberger, 1860). Pierrefitte (France, Essonne dép.), Oligocene, Rupelian (Sables de Fontainebleau, Falun de Pierrefitte). Coll. MNHNP (Lozouet/Maestrati), x 4.

Fig. 10. *Streptodictyon retrorsicosta* (Sandberger, 1860). Glimmerode, former lignite pit Höllkopf (Germany, Hessen), Oligocene, Chattian A (Kasseler Meeressand, 'Verarmungshorizont'). Coll. SMF 250780/1 (R. Janssen, 1972/1973), x 4.

Fig. 11. *Streptodictyon retrorsicosta* (Sandberger, 1860). Erkelenz, K-3 well for mine shaft Sophia Jacoba 8, depth 298-299 m below surface (Germany, Nordrhein-Westfalen), Oligocene, Chattian B (Grafenberger Sande). Coll. RGM 393.215 (GLK), x 11.

Fig. 12. *Streptodictyon schnetleri* sp. nov. (**holotype**), Brejning, coastal cliff outcrop (Denmark, Jylland), Oligocene, Chattian B (Brejning Clay Member, Vejle Fjord Formation). Coll. RGM 393.216 (MNO), x 3.

Fig. 13. *Streptodictyon sexcostatus* (Beyrich, 1856). Winterswijk, Miste, temporary excavation, depth 2.00-3.75 m below surface (The Netherlands, Gelderland province), Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed, Hiatella arctica Acme Zone and/or Astarte radiata Acme Zone). Coll. RGM 226.026 (AJL), x 1.5.

Fig. 14. *Streptodictyon sexcostatus* (Beyrich, 1856). Heist-op-den-Berg, temporary exposure (Belgium, Antwerpen province), Miocene, Hemmoorian, Oxlundian (Berchem Formation, Zonderschot Sand Member). Coll. RGM 393.241 (AJL, September 1989), x 2.

Fig. 15. *Streptodictyon sexcostatus* (Beyrich, 1856). Dingden, temporary outcrop in bottom of Königsbach near Königsmühle (Germany, Nordrhein-Westfalen), Miocene, Reinbekian (Bislicher Schichten). Coll. RGM 393.245 (AJL), x 2.

PLATE 3

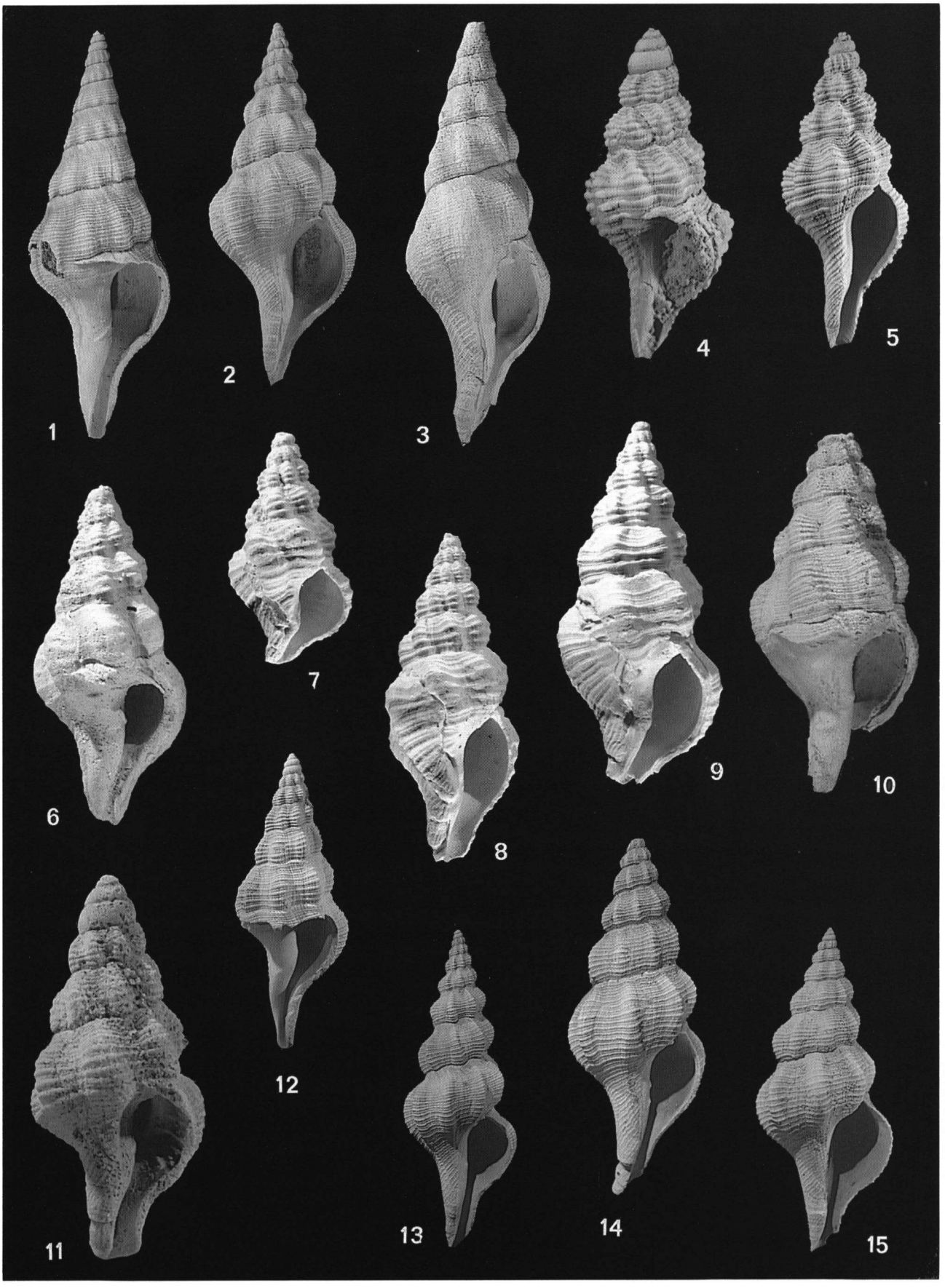

PLATE 4

Fig. 1. *Streptodictyon sexcostatus* (Beyrich, 1856), transitional form to *S. abruptus* (Beyrich, 1856). Twistringen, clay pit of O. Sunder brickworks (Germany, Niedersachsen), Miocene, Reinbekian (Twistringer Schichten, level not specified). Coll. RGM 226.230 (MCL), x 3.

Fig. 2. *Streptodictyon soellingensis* (Tembrock, 1965) (**holotype**). Söllingen, railroad cut between Söllingen and Jerxheim (Germany, Niedersachsen), Oligocene, Chattian A (Söllingen Sand Formation, *Asterigerina* Horizon). Coll. PHB Ga 125 (II.155.13) (Bamberg), x 15.

Fig. 3. *Streptodictyon soellingensis* (Tembrock, 1965). Glimmerode, former lignite pit Höllkopf, level unknown (Germany, Hessen), Oligocene, Chattian A (Kasseler Meeressand). Coll. SMF 250710/1 (H. Humberg, 1977), x 4.

Fig. 4. *Streptodictyon soellingensis* (Tembrock, 1965). Rumeln, dump of mine shaft Diergardt-VI, Germany (Nordrhein-Westfalen), Oligocene, Chattian A (Grafenberg Member). Coll. RGM 393.275 (AJB), x 3.5.

Fig. 5. *Streptodictyon sowerbyi* (Nyst, 1836) emend. (**holotype**). Kleine Spouwen, municipality of Bilzen (Belgium, Limburg province), Oligocene, Rupelian (level not indicated, state of preservation indicates Berg Sands Member). Coll. IRScNB Cat. Types Invert. no. 6042 (Nyst), x 2.5.

Fig. 6. *Streptodictyon sowerbyi* (Nyst, 1836) emend. Zwenkau (Germany, Sachsen), Oligocene, Rupelian (Böhlener Schichten, Basissand). Coll. Mauritianum Naturkundliches Museum, Altenburg (A. Müller), x 1.5.

Fig. 7. *Streptodictyon sowerbyi* (Nyst, 1836) emend. Weinheim, Kanalbau (Germany, Rheinland-Pfalz), Oligocene, Rupelian (Unterer Meeressand). Coll. KGM, x 4.

Fig. 8. *Streptodictyon sowerbyi* (Nyst, 1836) emend. Niel (Belgium, Antwerpen province), Oligocene, Rupelian (Rupel Formation, Terhagen Member and/or Putte Member). Coll. RGM 393.286 (HBH), x 2.

Fig. 9. *Streptodictyon sowerbyi* (Nyst, 1836) emend. Niel or Boom (Belgium, Antwerpen province), Oligocene, Rupelian (Rupel Formation, Terhagen Member and/or Putte Member). Coll. IRScNB TCCI 6050 (Delheid), x 2.

Fig. 10. *Streptodictyon sowerbyi* (Nyst, 1836) emend. Ba(e)sele (nowadays Bazel), Belgium (Oost Vlaanderen province), Oligocene, Rupelian (Rupel Formation, Terhagen Member and/or Putte Member). Coll. IRScNB TCCI 6051 (Nyst), x 3.

Fig. 11. *Streptodictyon sowerbyi* (Nyst, 1836) emend. Houthalen, shaft of coal mine II, depth 88-94 m (Belgium, Limburg province), Oligocene, Chattian ? A (Voort Formation, Veldhoven Member). Coll. IRScNB TCCI 6052 (leg. IRScNB), x 2.

Fig. 12. *Streptodictyon sowerbyi* (Nyst, 1836) emend. Voort, municipality Zolder, shaft of coal mine I, depth 86-90 m below surface (Belgium, Limburg province), Oligocene, Chattian ? A (Voort Formation, Veldhoven Member). Coll. IRScNB (leg. IRScNB, Cat. Types Invert. no. 4744), x 2.

Fig. 13. *Streptodictyon subelongatus* (d'Orbigny, 1852) (**holotype**). Baesele (nowadays Bazel) (Belgium, Oost Vlaanderen province), Oligocene, Rupelian (Rupel Formation, Terhagen Member or lower part of Putte Member). Coll. IRScNB Cat. Types Invert. no. 3870 (de Koninck/Nyst), x 1.

Fig. 14. *Streptodictyon subelongatus* (d'Orbigny, 1852). Berg, Kleine Spouwen, Keistraat, temporary exposure (Belgium, Limburg province), Oligocene, Rupelian (Rupel Formation, Berg Sand Member). Coll. RGM 393.193 (MBL & AJL, 1971), x 1.

PLATE 4

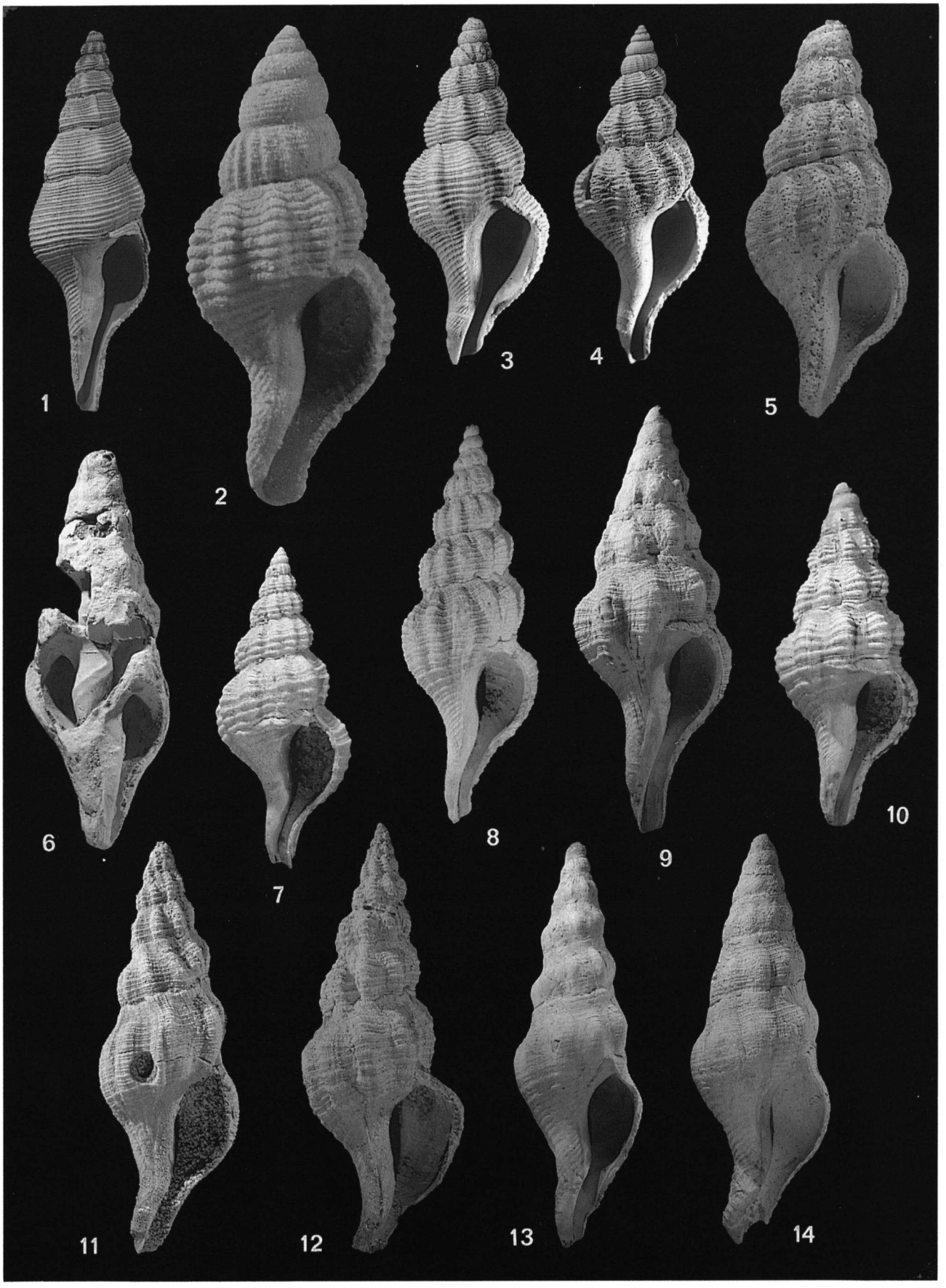

PLATE 5

Fig. 1. *Streptodictyon subelongatus* (d'Orbigny, 1852). Berg, Kleine Spouwen, Keistraat, temporary exposure (Belgium, Limburg province), Oligocene, Rupelian (Rupel Formation, Berg Sand Member). Coll. RGM 393.194 (MBL & AJL, 1971), x 1.

Fig. 2. *Streptodictyon subelongatus* (d'Orbigny, 1852) ?. Basele, Belgium (Oost Vlaanderen province), Oligocene, Rupelian (Boom Clay Formation, Terhagen and/or Putte Member). Coll. IRScNB TCCI 6053 (Nyst), x 4.

Fig. 3. *Streptodictyon subelongatus* (d'Orbigny, 1852). Zwenkau (Germany, Sachsen), Oligocene, Rupelian (Böhlener Schichten, Basissand). Coll. Mauritianum Naturkundliches Museum, Altenburg (A. Müller), x 1.5.

Figs 4, 5. *Streptodictyon subelongatus* (d'Orbigny, 1852). Steendorp (Belgium, Oost Vlaanderen province), Oligocene, Rupelian (Boom Clay Formation, Terhagen and/or Putte Member). Coll. IRScNB TCCI 6054-5 (Germaine De Gottal, 4.4.1900), x 2.

Fig. 6. *Streptodictyon subelongatus* (d'Orbigny, 1852) forma *speyeri* (Deshayes, 1865) ?. Offenbach, Armenhaus (Germany, Rheinland-Pfalz), Oligocene, Rupelian (Rupelton). Coll. SMF 122905a/1 (J. Zinndorf, 1901), x 1.5. (holotype of *Streptochetus hahni* Zinndorf, 1928).

Fig. 7. *Streptodictyon subelongatus* (d'Orbigny, 1852) forma *speyeri* (Deshayes, 1865). Weinheim, Würzmühle ('Kanalbau') (Germany, Rheinland-Pfalz), Oligocene, Rupelian (Unterer Meeressand). Coll. KGM, x 1.5.

Fig. 8. *Streptodictyon subelongatus* (d'Orbigny, 1852) forma *speyeri* (Deshayes, 1865). Morigny-Champigny (France, Essonne dép.), Oligocene, Rupelian (Sables de Fontainebleau, Falun de Morigny). Coll. MNHNP (Lozouet/Maestrati), x 1.5.

Fig. 9. *Streptodictyon twistringensis* sp. nov. (**holotype**). Twistringen, O. Sunder clay pit (Germany, Niedersachsen), Miocene, Reinbekian (Twistringen Clay Member, lower part of section exposed, in concentrations of teredinid material). Coll. RGM 393.293 (JVV), x 5.

Fig. 10. *Streptodictyon twistringensis* sp. nov. (**paratype**). Twistringen, O. Sunder clay pit (Germany, Niedersachsen), Miocene, Reinbekian (Twistringen Clay Member, lower part of section exposed, in concentrations of teredinid material). Coll. RGM 393.294 (JVV), x 10.

Figs 11, 12. *Streptodictyon undatus* (Meunier, 1880). Berg, near Kleine Spouwen, Keistraat, temporary exposure (Belgium, Limburg province), Oligocene, Rupelian (Berg Sand Member, level with *Astarte trigonella*). Coll. RGM 393.295-296 (MBL & AJL, 1971), x 5 (fig. 11), x 4 (fig. 12).

Fig. 13. *Streptodictyon undatus* (Meunier, 1880). St. Hilaire, Pierrefitte (France, Essonne dép.), Oligocene, Rupelian (Sables de Fontainebleau, Falun de Pierrefitte, base). Coll. RGM 393.301 (DLV), x 4.

PLATE 5

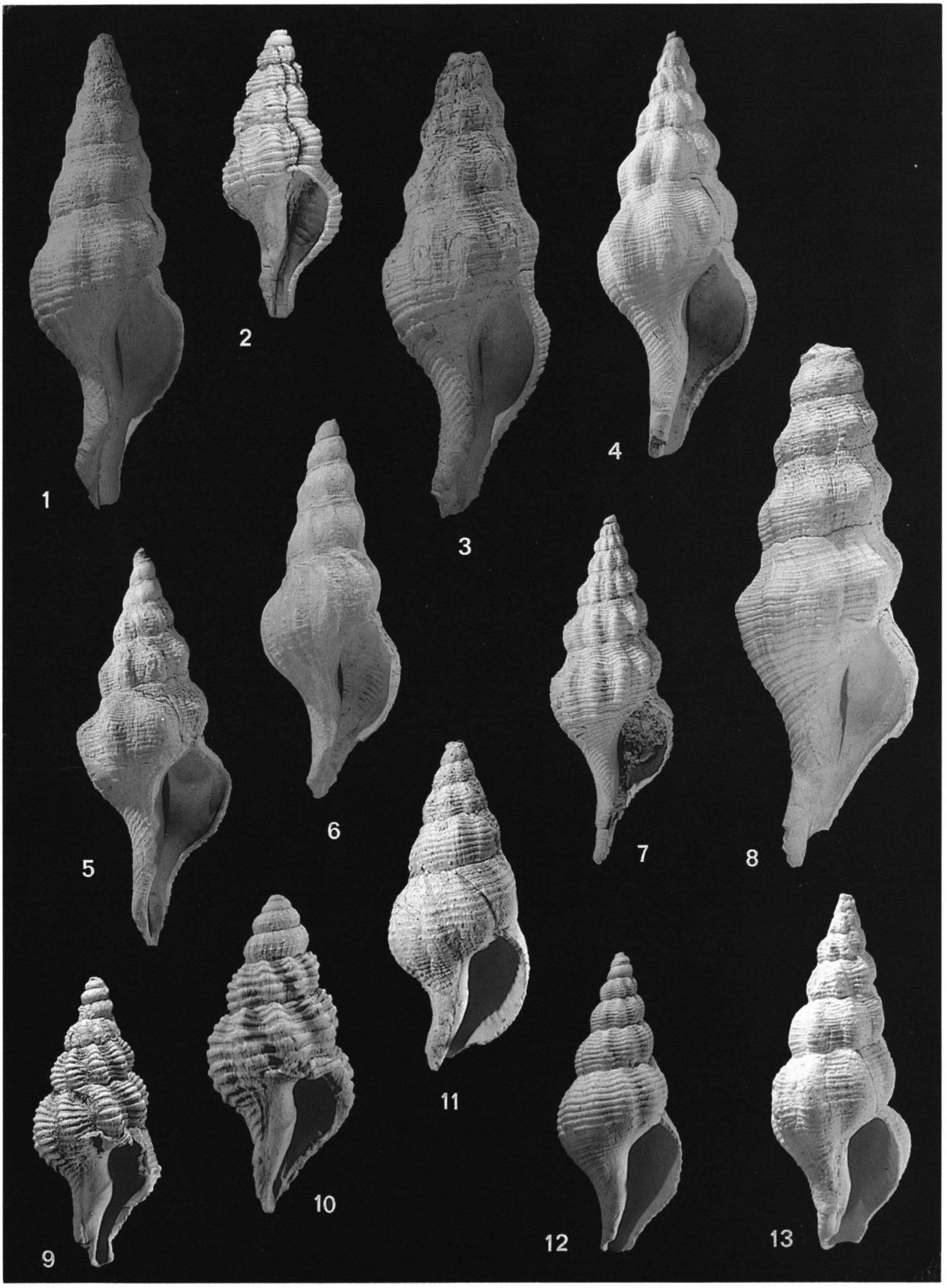

PLATE 6

Fig. 1. *Streptolathyrus masculinus* sp. nov. (**holotype**). Glimmerode, former lignite pit Höllkopf (Germany, Hessen), Oligocene, Chattian A ('Kasseler Meeressand, Schillage 1'). Coll. RGM 393.303 (MBL, June 1973), x 12.5.

Fig. 2. *Streptolathyrus masculinus* sp. nov. (**paratype**). Glimmerode, former lignite pit Höllkopf (Germany, Hessen), Oligocene, Chattian A ('Kasseler Meeressand, exact level unknown). Coll. SMF 250708/1 (H. Humberg, 1977), x 4.

Fig. 3. *Streptolathyrus regularis* sp. nov. (**holotype**). Winterswijk-Miste, temporary excavation, depth 2.00-3.75 m below surface (The Netherlands, Gelderland province), Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed; Hiatella arctica Acme Zone or basal part of Astarte radiata Acme Zone). Coll. RGM 226.027 (AJL, 1971), x 4.

Fig. 4. *Streptolathyrus rothi* (Beyrich, 1856). Meerbusch-Ostenrath, borehole, 39-41 m below surface (Germany, Nordrhein-Westfalen), Oligocene, Chattian C (Grafenberg Sand Member). Coll. FHK, x 4.5.

Fig. 5. *Streptolathyrus rothi* (Beyrich, 1856). Antwerpen, construction pit for E3 tunnel (= Kennedy-tunnel) (Belgium, Antwerpen province), Miocene, Hemmoorian, Behrendorfian (Berchem Formation, Edegem Sand Member). Coll. RGM 393.360 (DMM, 1964-1966), x 3.

Fig. 6. *Streptolathyrus rothi* (Beyrich, 1856). Beringen, municipality of Helden, borehole 15 (58B/8), depth unknown (The Netherlands, Limburg province), Miocene, Hemmoorian (Breda Formation). Coll. RGM 393.321 (ROD, 1911; Techn. Hoogeschool, Delft), x 2.

Fig. 7. *Streptolathyrus rothi* (Beyrich, 1856). Winterswijk, Miste, temporary excavation, depth 2.00-3.75 m below surface (The Netherlands, Gelderland province), Miocene, Hemmoorian, Oxlundian (Breda Formation, Aalten Member, Miste Bed, Hiatella arctica Acme Zone and/or Astarte radiata Acme Zone). Coll. RGM 226.025 (AJL, 1971), x 1.5.

Fig. 8. *Streptolathyrus rothi* (Beyrich, 1856). Heist-op-den-Berg, temporary exposure (Belgium, Antwerpen province), Miocene, Hemmoorian, Oxlundian (Berchem Formation, Zonderschot Sand Member). Coll. RGM 393.335 (AJL, September 1989), x 2.

Fig. 9. *Streptolathyrus rothi* (Beyrich, 1856). Langenfelde (Germany, Hamburg area), Miocene, Langenfeldian (formation not indicated). Coll. RGM 393.345 (Krause), x 2.

Fig. 10. Fasciolariidae sp. Kleine Spouwen (Belgium, Limburg province), Oligocene, Rupelian (Rupel Formation, Berg Sand Member). Coll. IRScNB TCCI 6056 (Nyst, from sample containing the holotype of *Streptodictyon sowerbyi*), x 2.5.

Fig. 11. Fasciolariidae sp. Kleine Spouwen, Berg (Belgium, Limburg province), Oligocene, Rupelian (Rupel Formation, Berg Sand Member, level with *Astarte trigonella*). Coll. IRScNB 6057 (Bosquet), x 2.

PLATE 6